Some Effects of Non-Reinforcement in Split-Brain Monkeys'

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JOHNSON, J. D. AND M. S. GAZZANIGA. Some effects of non-reinforcement in split-brain monkeys. PHYSIOL. BEHAV. 6 (6) 703-706, 1971.—Three experienced split-brain monkeys were taught a visual pattern discrimination in one eye hemisphere and shifted to an FR-2 schedule of reinforcement. The opposite hemisphere was then allowed to view the discrimination on thenon-reinforced trials. Under this condition the untrained hemisphere began disrupting the performance of the trained hemisphere. This was reflected in an increase in response latencies and number of errors. In a second experiment, both hemispheres independently learned the same discrimination on FR-2. Again, a disruption in responding occurred when one hemisphere viewed the discrimination only on the non-reinforced trials. The results suggest that reinforcement aids learning by eliminating the disruptive responses of non-reward. Also the data gives some indication of the brain processes involved in extinction and secondary reinforcement.

Split-brain Learning Extinction Secondary reinforcement Unity of consciousness Frustration

In an earlier report [8] it was found that an untrained hemisphere of a slit-brain monkey could learn a visual discrimination by observing the errorless performance of the task by the opposite hemisphere. These results indicated that a half brain need not experience errors or make overt responses in order to learn a discrimination.

Further consideration of the minimal conditions for learning drew attention to the role of reinforcement. In that experiment, liquid reinforcement was experienced by both hemispheres on every trial. In the present study, in an effort to determine the role of reinforcement, one hemisphere was trained on a visual discrimination task and placed on an FR-2 schedule of reinforcement. After steady, near perfect performance was acheived the opposite hemisphere was allowed to view the discrimination on the non-reinforced trials, while the other hemisphere was responding to a discrimination task in which every other trial was reinforced.

Contrary to our expectation there was no evidence of learning. Rather the half brain that observed the discrimination only on the non-reinforced trials began to disrupt the ongoing behavior of the opposite hemisphere.

METHOD

Three monkeys (Maccaca mulatta) were used in this study. All had undergone midline section of the corpus callosum, anterior and hippocampal commissures and optic chiasm [5]. The monkeys were maintained in specially designed restraining chairs throughout the training and testing procedures. During an experimental session, the chair was placed in a soundproof box facing a response panel. Vision was restricted on three sides by a Plexiglas shield, allowing the panel to be viewed only through two small eyeholes. Arm movements were not restricted, but head movement was limited

so that each opening could only be used by one eye.

Centered on the panel were two 5×6.3 cm transparent plastic discs, one immediately above the other. Two IEE one-plane readout projectors were placed behind the discs and a trial was initiated by projecting a pair of stimuli at the monkey through the transparent discs. Two polarizing filters were placed within each readout projector so that either horizontally or vertically polarized light could be emitted from each projector. Polarizing filters were also placed in front of the eyeholes. In this way different stimuli could be simultaneously presented to each eye from the same readout projector.

The discriminative stimuli used in this study were white letters (A, B) projected on a black background. The stimuli were matched for brightness with the pattern of the stimuli being the only reliable dimension by which discrimination could occur. During some trials only one eye viewed the discriminative cues, while the other eye simultaneously viewed at the same point in space, a white blank field. The stimuli were within the center of the monkey's field of vision and could be reached by either hand. A response was recorded by pressing one of the discs. Responding to either disc caused all stimuli to be turned off and initiated a 2.5 sec inter-trial interval. A response to the disc displaying the positive stimulus yielded several drops of water presented through a tube near the monkey's mouth.

The positive stimulus randomly appeared on either the top or bottom disc, but if an incorrect response was made it appeared in the same position on the following trial. Each trial continued indefinitely until a response was made. Normally the animal was given 100 trials per day. After each daily session the monkeys were allowed free access to water for 5 min, and were then deprived of water until the experimen-

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tal session on the following day. The presentation of trials, delivery of reinforcement and the recording of responses were performed automatically. All behavior was monitored by a closed circuit television system and microphone with the camera mounted above and behind the monkey.

Before entering this study, the monkeys had performed eight discrimination tasks over a period of a year. The nature of these tasks varied for they consisted of behavioral tests to determine whether the operations were successful, pilot studies for several experiments as well as an experiment reported elsewhere [8]. These earlier tasks were performed in an apparatus similar to the one used here. Though they had to adjust to looking through the eyeholes, it is presumed that the animals entered this study with a well developed learning set for this kind of task. They were naive only in terms of a discriminative cue specific to the task.

The monkeys were trained for the first of two experiments by being taught a visual discrimination task to one hemisphere and were advanced to a schedule in which only every other correct response was reinforced. The first experiment commenced when responding on the FR-2 schedule by one hemisphere was at a criterion level (less than 6 errors in 60 trials). The experiment was run in four days. The experimental condition was introduced during the second and fourth days. The control condition (which was a continuation of the training situation where the untrained hemisphere viewed only white blank fields) was recorded on Days 1 and 3. During the experimental condition (Days 2 and 4) the trained hemisphere continued to view the discrimination on each trial, but the untrained hemisphere was presented the discrimination only during the non-reinforced trials. The untrained hemisphere continued to see only blank fields on the display panel during the reinforced trials.

Ten all-reinforced probe trials were presented exclusively to the untrained hemisphere after the experimental session on Day 2 and before and after the experimental session on Day 4. In five trials the positive stimulus appeared on the upper disc and on five on the lower disc. These trials were intended to determine if the experience of the untrained hemisphere during the experimental sessions affected its bias to either stimulus. On each day the time necessary for making a hundred responses was recorded. The experimenter observed the temporal pattern of responding and noted on which trials errors occurred.

To prepare for the second experiment the untrained hemisphere was taught the discrimination. Thus both hemispheres entered the second experiment each having independently learned the same task. Again the experiment was run in four days, with Days 1 and 3 providing control data. The experimental condition on Days 2 and 4 consisted of presenting the discrimination on each trial to the hemisphere that had been second to learn the task. The hemisphere that was initially trained now viewed the discrimination only on the nonreinforced trials and saw blank fields on the reinforced trials. During the control condition (Days 1 and 3) the initially trained hemisphere viewed blank fields on each trial, while the other hemisphere viewed the discrimination on each trial and was reinforced for every other correct response. Again a record was made of the time necessary to make a hundred responses on each day. The experimenter recorded where the errors occurred and noted the temporal pattern of responding.

RESULTS

In the first experiment responses during the probe trials suggested no learning had occurred in the naive hemisphere. All

animals went into a position habit on these trials.

In both the first and second experiment, the rate of responding during the control condition (Days 1 and 3) was notably faster than during the experimental condition (Days 2 and 4) (see Table 1). Also in both experiments the number of errors during the experimental conditions was significantly greater

TABLE 1

	1	2	3	4
ВН	6.25	5.50	5.50	24.00
BT	6.25	14.50	7.25	16.50
SC	7.25	19.00	5.75	30.00
Mean	6.58	13.00	6.16	23.50
	I	Experimen	т И	
	1	2	3	4
DII	5.75	15.00	7.25	17.75
BH		0.75	6.25	6.75
BT BH	5.50	8.75	0.20	0.75
	5.50 6.75	8.75 6.25	6.50	22.25

The values represent the duration in min of each daily session in Experiments 1 and 2. Values were taken to the nearest quarter minute. One hundred trials were run each day with an intertrial time of 2.5 sec. On the fourth day of the first experiment, one animal (SC) was removed after making only 48 responses in 30 min.

than during the control conditions (see Figs. 1 and 2). In the first experiment there were 20 errors in the 600 control session trials and 146 errors in the 600 experimental session trials. In the second experiment there were 13 errors in 600 control session trials and 157 errors in the 600 experimental session trials.

In the first experiment the hemisphere observing the cues on only the non-reinforced trials had not been trained the discrimination. Approximately 4/5 of the errors were made on these non-reinforced trials when both the trained and untrained hemispheres viewed the discrimination. It was observed that the overall rate of responding decreased as the experimental session progressed. Responses typically occurred in couplets. Long pauses were observed during the non-reinforced trials, but once made, it introduced a trial where reinforcement could be obtained and here responses were quick. Most of the overall decrease in response rate can be attributed to pauses in the non-reinforced trials.

In the second experiment where both hemispheres had learned the same discrimination task but only one had viewed the discrimination on the reinforced trials, errors occurred mostly during the reinforced trials (129 out of 157). The low incidence of errors during the non-reinforced trials was particularly evident in monkeys BT and BH who had only 3 and 4 errors respectively. This contrasted markedly with the first experiment in which the majority of errors were made during

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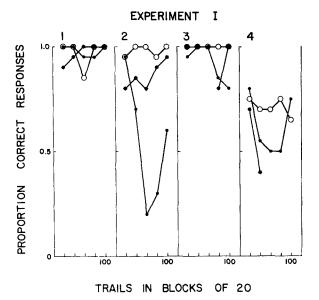


FIG. 1. The curves represent the levels of correct responding of the three animals during the four testing days of Experiment 1. The control condition was run on Days 1 and 3 and the experimental condition on Days 2 and 4. Open circles = BH; Solid dots = BT;

Asterisks = SC.

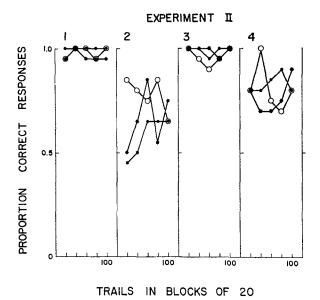


FIG. 2. The curves represent the levels of correct responding of the three animals during the four testing days of Experiment 2. The control condition was run on Days 1 and 3 and the experimental condition on Days 2 and 4. Open circles = BH; Solid dots = BT;

Asterisks = SC.

the non-reinforced trials. In the second experiment responses were observed to occur in bursts on the experimental days. Long delays between groups of responses were observed, but were not particularly associated with the reinforced or non-reinforced trials.

HISTOLOGY

All animals were killed and perfused with 10% formalin. The hippocampal and anterior commissures and the optic chiasm of monkeys BT and BH were completely severed. The entire callosum, save for some fibers at the anterior tip were also severed. The hippocampal and anterior commissures, and the optic chiasm of SC were completely severed. All of the anterior callosum was severed, but a small portion of the splenium (< 5 mm) remained intact. Also there was some damage to the left frontal lobe, apparently the result of an infection.

Comment. The brains of BT and BH were similar in that the cerebral commissures were completely severed except for a small portion of the anterior callosum. To date no particular function has been attributed to these anterior fibers [5] though they probably aid in some way to unify cerebral function. The observation that part of the splenium of SC was intact is puzzling, for some earlier results suggested that transfer could take place when this part of the callosum remained intact [5]. Yet, repeatedly during probe trials SC was unable to perform with one hemisphere the task taught to the other. This would indicate that habits do not necessarily become established in both hemispheres when the splenium is intact. This is in agreement with the observation that in some cases visual discriminations in the normal monkey are laid down unilaterally [2, 3]. Furthermore the results indicate that SC did not use the remaining part of the splenium to tab information about the habit in the opposite hemisphere.

DISCUSSION

Separate testing of the untrained hemisphere during the probe trials indicated that learning without reinforcement had not occurred. Because on these trials all animals adopted a position habit it can be concluded the untrained hemisphere chose not to attend to the discriminative cues on the earlier experimental trials. It may be that in response to the experience of viewing the discrimination only on non-reinforced trials, the untrained hemisphere refused to allow its behavior to become controlled by these cues. Rather than learning by observation on the experimental sessions, the untrained hemisphere began to disrupt the behavioral output of the opposite hemisphere. Comparing these results with those of an earlier report where learning did occur by observation in the presence of continuous reward [8] indicates that while reinforcement may not be necessary to the basic processes underlying learning it does serve to eliminate the disruptive behavior generated by lack of reward.

Because of the decrease in overall response rate in both experiments during the experimental sessions it can be inferred that extinction processes may have been active. These two experiments, however, are not extinction situations as they are ordinarily described. In neither experiment is there a decrease in the number of reinforcements available. Rather the effects are observed when one hemisphere is provided with additional information during the non-reinforced trials. This paradox can be explained in the following way: In the first experiment the observing hemisphere does not know the task that it views on the non-reinforced trials; yet, it enters the situation with a well developed learning set for solving this kind of discrimination problem. The information available during the nonreinforced trials is not in itself sufficient to solve the problem. Its responses to either visual pattern go unreinforced. Therefore, the attempts of this hemisphere to solve the problem may begin to be extinguished.

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In the second experiment the hemisphere viewing only the non-reinforced trials had previously performed successfully on an FR-2 schedule of reinforcement the discrimination that it is now observing. Although reinforcement continued to be available every other trial, it was now never experienced contiguous with the discrimination cues. Under this condition the discrimination cues were primarily associated in this hemisphere with a series of non-reinforced trials. Apparently the reinforcements do not ameliorate the effect of the non-reinforced trials as they had when this hemisphere was working alone on an FR-2 schedule. As a result this hemisphere interprets its experience as a continuous series of non-reinforcements and initiates extinction processes.

If the increases in response latencies during the experimental sessions are interpreted as indications of extinction processes, these results have implications for theories of extinction. The extinction processes are not purely cortical as the Pavlovian model would suppose, for they are initiated in a cortically separated hemisphere, but are felt in both hemispheres. The experience in one hemisphere interferes with the normal responding of the opposite hemisphere. These results are more consistent with the hypothesis that extinction occurs when the non-reinforced trials produce frustration [1]. An emotional response can presumably be mediated subcallosally. Gazzaniga, for example [4] has shown that the ongoing behavior in one hemisphere of a split-brain monkey can be interrupted by an aversive experience presented exclusively to the opposite hemisphere. Consistent with the frustration hypothesis was the observation that during the experimental sessions the animals cried and shook the apparatus more than during the control sessions.

An analysis of the results of this study also allow for some inferences on the brain structures involved in secondary reinforcement. When the animals were placed on an FR-2 schedule, they learned to perform correctly on the non-reinforced discrimination trials. Numerous studies (e.g. [11])

have shown that when a stimulus situation is repeatedly paired with a primary reinforcer it acquires reinforcing properties. As a secondary reinforcer this stimulus can control responding on non-reinforced trials. If it is accepted that behavior on the non-reinforced trials in this study was under the control of secondary reinforcement the question arises whether the effects of secondary reinforcement are limited to the hemisphere that is experiencing the secondary reinforcing stimuli. While the cues themselves may be stored within one hemisphere, their secondary reinforcing effect may not be. The question is whether secondary reinforcement is a cortical phenomenon (or a closed cortical–subcortical system) or whether its effect is a general response at the subcortical level which is felt in both hemispheres.

The results seem to imply the first alternative, for during the non-reinforced trials a disruptive influence was able to develop in the observing hemisphere when it viewed the cues on the non-reinforced trials. This suggests that the effects of secondary reinforcement on these trials was limited to the performing hemisphere. This conclusion is supported by the results of an earlier report [7]. In that study a secondary or higher-order reinforcer presented to one hemisphere of a split-brain human patient did not reinforce behavior of the opposite hemisphere.

These findings indicate that the split hemispheres can experience reinforcing events independently. This might be seen as support for the hypothesis that two separate spheres of consciousness are produced when the hemispheres are cortically separated [5, 12]. MacKay [9] has maintained that this hypothesis depends on whether the two hemispheres form independent priority determining systems. Independent systems of this sort appear to exist in the above studies, for at the moment one hemisphere is experiencing a particular stimulus as an effective reinforcer the other hemisphere is either oblivious of this assigned value or free to respond negatively to its own experience.

REFERENCES

- 1. Amsel, A. The role of frustrative nonreward in noncontinuous reward situations. *Psychol. Bull.* 55: 102-119, 1958.
- 2. Doty, R. W. and N. Negrao. Forebrain commissures and vision. In: *Handbuch der Sinnesphysiologie*, edited by R. Jung. Berlin: Springer-Verlag, (in press), 1970.
- Gazzaniga, M. S. Effects of commissurotomy on a pre-operatively learned visual discrimination. Expl Neurol. 8: 14-19, 1963.
- Gazzaniga, M. S. Interhemispheric cueing systems remaining after section of neocortical commissures in monkeys. Expl Neurol. 16: 28-35, 1966.
- 5. Gazzaniga, M. S. *The Bisected Brain*. New York: Appleton-Century-Crofts, 1970.
- Grossman, S. P. A Textbook of Physiological Psychology. New York: John Wiley; 1967.
- Johnson, J. D. and M. S. Gazzaniga. Cortical-cortical pathways involved in reinforcement. *Nature* 223: 71, 1969.

- Johnson, J. D. and M. S. Gazzaniga. Interhemisphere imitation in split-brain monkeys. Expl Neurol. 27: 206-212, 1970.
- MacKay, D. M. Brain and conscious experience. In: Brain and Conscious Experience, edited by J. C. Eccles. Berlin: Springer-Verlag, 1966, pp. 422-445.
- Myers, R. E. Transmission of visual information within and between the hemispheres: A behavioral study. In: *Interhemispheric Relations and Cerebral Dominance*, edited by V. B. Mountcastle. Baltimore: Johns Hopkins Press, 1962, pp. 51-73.
- Saltzman, I. J. Maze learning in the absence of primary reinforcement: A study of secondary reinforcement. J. Comp. physiol. Psychol. 42: 161-173, 1949.
- Sperry, R. W. Mental unity following surgical disconnection of the cerebral hemispheres. In: *The Harvey Lecture Series*, 62. New York: Academic Press, 1968, pp. 293-323.