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Interhemisphere Imitation in Split-Brain Monkeys

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Three experienced split-brain monkeys were taught a visual pattern discrimination in one eye hemisphere. After several hundred over-learning trials, the opposite untrained eye hemisphere was allowed to observe 40 perfect trials. Subsequently, ten test trials in which every response was reinforced were delivered exclusively to the untrained hemisphere. Two monkeys performed perfectly while another required 40 additional observation trials before a perfect score was realized. The results are consistent with the view that errors during acquisition training need not be a necessary condition for visual discrimination learning and suggest that learning through observation may be more efficient than trial and error learning in some situations.

Introduction

In studies of imitation learning, animals given the opportunity to observe other animals performing or learning a task can subsequently perform the same task with considerably fewer errors. Subjects in these experiments apparently learn the task simply by having the opportunity to observe another subject usually of the same species learn or perform the task. Studies with cats (3) and monkeys (7) demonstrated that an animal observing from an adjacent cage would then perform the same task with very few incorrect responses, But the effectiveness of the observing experience on learning cannot be accurately assessed in these experiments. The observing animal was simply placed in an adjacent cage and there was no way to judge how much time was actually spent observing, nor can it be known exactly what was being observed.

In the present experiment, error-free learning was demonstrated using a paradigm that allows the experimenter to control more exactly what the observer experiences. Split-brain monkeys were used in which one hemisphere served as a performing model and the other hemisphere was an observer. Innumerable studies (2) have shown that when the cortical commissures are severed, one hemisphere may learn a task while the other hemisphere remains naive when visual patterns are used as the discriminating cues. In this experiment one hemisphere was taught a discrimination

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task by trial and error. The opposite naive hemisphere learned the discrimination task by observing these errorless trials.

Methods

Three monkeys (*Macca mulatta*) were used. All had undergone midline section of the corpus callosum, anterior and hippocampal commissures, and optic chiasm. Throughout all the training and testing procedures they sat in restraining chairs. Head and arm movements were not restricted. During an experimental session the chair was placed in a soundproof box in which the animals faced a panel. Centered on the panel were two 5-x 6.3-cm transparent plastic discs, one immediately above the other. Two readout projectors were placed behind the discs and a trial was initiated by projecting a pair of stimuli onto the transparent discs. The stimuli used in this experiment were white arabic numbers *3* and *7* within a black background. The stimuli were matched for brightness and the pattern of the stimuli was the only reliable dimension by which they could be discriminated. A response was recorded by pressing one of the discs. The stimuli were in the center of the monkey's field of vision and could equally well be reached by either hand. Responding to either stimulus caused both to be turned off and introduced an 8-sec intertrial interval. Response to only one of the stimuli yielded several drops of water presented through a tube off to one side of the mouth. Each trial continued indefinitely until a response was made. Normally the animal was given 80–100 trials a day. After each daily session the monkeys were allowed free access to water for 5 min and then were deprived of water until the experimental session 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 with the camera being mounted above and behind the monkey allowing easy observation of hand use.

Before their operation the animals were taught a discrimination task with both eyes open. After reaching criterion performance they were given several hundred additional trials to allow them to become familiar with the testing situation. Following the operation and before this experiment, two monkeys (BT & BH) performed six discrimination tasks, and the third monkey (SC) had performed five tasks. The nature of the tasks varied, for they consisted of behavioral tests to determine whether the operations were successful and pilot studies for several experiments. On entering the present experiment both hemispheres of all three monkeys had had extensive and nearly equal experience learning and performing in the apparatus used. The animals were naive only in terms of the discrimination stimuli. It is unlikely that a general learning set improved appreciably during the course of the experiment. Two of the monkeys (BH & SC) entered the experiment immediately after finishing these other tasks, while the third monkey (BT) had been idle for 2 weeks. It is possible that this animal spent the initial trials of this experiment readjusting to the experimental situation.

The experiment was divided into three stages. In stage I an occluder was placed in one eye. Since the monkeys had undergone chiasm and midline commissure section, the stimuli were viewed by only one hemisphere. This half of the brain was taught a discrimination task while the opposite half remained naive. After criterion of 20/20 was achieved 200–300 additional trials were allowed. On the last day of stage I the occluder was momentarily switched to the opposite eye. This half of the brain, which presumably had remained naive, was given ten trials in which responding to either stimulus was reinforced. These trials indicated whether a bias existed to respond to one stimulus more than to the other.

Stage II began the day following the end of stage I. During stage II neither eye was occluded. The animal resumed the discrimination task learned in stage I. With both eyes open the monkeys were given 40 trials.

Stage III followed immediately and was introduced by placing an occluder in the eye that had learned the task in stage I and allowing the opposite eye to perform ten test trials in which every response was reinforced. If all ten responses were made correctly, 60 additional discrimination trials were immediately presented to this hemisphere to assure the experimenter that the correct performance during the test trials represented an established habit to respond correctly. If the animal did not respond perfectly on the test trials, stage II was repeated, followed by stage III.

Results

With one eye occluded animals reached a criterion performance on the discrimination task within 200–400 trials (Fig. 1). Additional trials were given to insure a perfect level of performance would continue in stage II. A test of the naive hemisphere at the end of stage I indicated that none of the animals had acquired in this hemisphere a noticeable bias to respond to either stimulus. In all three monkeys, responses were divided equally between the two stimuli. During this test all animals responded to both the upper and lower discs on the first few trials but tended to revert to a position habit on the last responses.

Both hemispheres were allowed to view the stimuli in stage II. All three monkeys responded perfectly while both eyes were open. It may be drawn from this that initially, at least, the responding was controlled by the hemiphere that had learned the task in stage I. The perfect level of responding was controlled by the hemisphere that had learned the task in stage I. The perfect level of responding was attributed to the overlearning trials, for

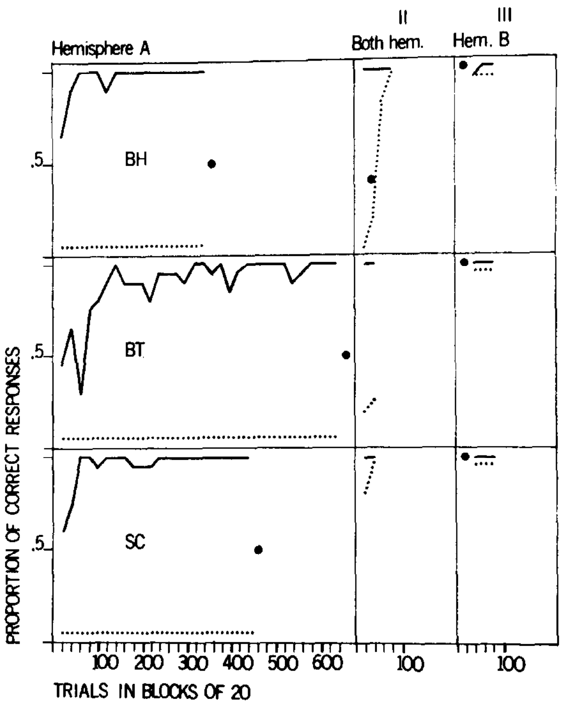

FIG. 1. The large dots at the end of stage I represent ten test trials presented to the naive hemispheres in which responses to either stimulus was reinforced. However, only responses to the normally positive stimulus were counted. Similarly, the large dots in stages II and III represent ten test trials presented to the same hemispheres after observing the performance of correct responses. The values for the use of hand in stages I and III are approximate. On the average 1 response in 20 was made by the hand ipsilateral to the open eye. Trials in blocks of 20 for monkeys BH, BT and SC on horizontal axis. Discrimination trials: solid lines. Use of hands contralateral to hemisphere B: dotted lines.

in an earlier pilot study it was found that the naive hemisphere tended to interfere with the performance of the experienced hemisphere when no overlearning trials were given. Without the trials of overlearning the performance with both eyes open was considerably below the criterion performance that had been achieved with one hemiphere, indicating that the opposite naive hemisphere was controlling some of the responses.

After 40 trials with both eyes open, an occluder was placed in the eye that had been open during stage I. On ten test trials two monkeys (BT & SC) made all responses to the stimulus that had been reinforced in stage I. The third monkey (BH) made only four responses to the positive stimulus. This animal was given 40 more trials with both eyes open and then presented again with 10 test trials to the naive eye. At this time all ten responses were made to the stimulus that had been reinforced in stage I.

The monkeys were then given 60 discrimination trials with the same negative and positive stimuli used in the first and second stages. Only the eye that was occluded in stage I was allowed to view the stimuli. Under these conditions two animals responded perfectly on 60 trials. One animal (BH) made one error in 60 trials.

The animals' behavior during the experimental sessions was observed with the closed-circuit TV system and record was made of which hand the monkey used on each trial. During stage I the responses for all animals were made almost entirely (19 out of 20) with the hand contralateral to the open eye. In stage II all animals made initial responses with the hand that had been used predominantly in stage I. However, as events progressed each animal began using the other hand more often than it had been used in stage I. At the end of stage II two monkeys were responding entirely with the hand contralateral to the open eye.

Discussion

For all three animals the hemisphere that was occluded during stage I showed no bias to either stimulus during the test trials at the end of stage I. However, when made to respond alone in stage III this hemisphere made almost all its responses to the positive stimulus. This suggests that the experience during stage II was a sufficient condition for learning the discrimination task. During stage II the naive unbiased hemisphere had the opportunity to observe the experienced hemisphere make responses to the positive stimulus. These responses were followed by reinforcement to both hemispheres. Learning took place in the naive hemisphere under this condition without the experience of errors.

With the opportunity to observe correct responses by the opposite hemisphere, the naive hemispheres of two monkeys learned the discrimination task within 40 trials and the third monkey (BH) responded perfectly on 10 test trials after 80 observation trials. Comparing these results with the trials necessary to reach criterion in stage I suggests that learning in this errorless manner was as efficient (possibly more so) as the trial and error method employed by the hemispheres that learned the task in stage I. Except for one monkey (SC) there was no indication from previous studies on these animals that the hemispheres which learned the task in stage II were more efficient learners *per se* than those which were taught the task in stage I. On several earlier tasks, the hemisphere of SC that learned by observation in stage II always reached criterion with fewer errors than did its opposite hemisphere. But with monkeys BT and BD there was no consistent difference in the rate of learning by the two hemispheres.

After 40 trials of observing correct responses, the naive hemisphere of one subject (BH) made only four responses to the positive stimulus during ten all-reinforced test trials. Apparently these 40 trials had little or no effect on this hemisphere. However after 40 more observation trials the hemisphere responded perfectly to the positive stimulus on ten trials. A further study with this subject using the same experimental design has indicated that the test trials serve an important function for this monkey. After 1000 observation trials *without any test trials* the naive hemisphere of this monkey showed no evidence of having learned the task (four out of ten responses were made to the positive stimulus). However, 60 observation trials *after* the test trials this hemisphere made eight of its ten responses to the positive stimulus. While the test trials carry no information about the positive stimulus (all responses are reinforced) they appear to have an alerting effect on the observing hemisphere. By forcing this hemisphere to respond on its own (the opposite experienced hemisphere is occluded during the test trials), it becomes alert and on subsequent observation trials it learns the task quickly. These results suggest the interesting possibility that in trial and error learning an important function of error may be to arouse the attention of the subject.

The animals' use of hands were observed and it was found that each hemisphere carried out most responses with the contralateral arm. This phenomenon has been previously observed by Trevarthen (6), Downer (1) and Gazzaniga (2). This simple correlation between hemisphere and hand use enables the experimenter to determine with some confidence which hemisphere is in control for any particular response. Assuming this to be the case, at the beginning of stage II, all animals were responding with the hemisphere that had learned the task in stage I. As the stage progressed all animals began making responses with the opposite hemisphere as indicated by a change of hand preference. At the end of this stage, two monkeys (BH & SC) were responding entirely with this hemisphere. The third monkey (BT) still responded mainly with the hemisphere that had initially learned the task. These results suggest that as the observing hemisphere learns the task it begins to take part in the perfromance of the behavior. At the same time, learning the task does not depend on making responses, for the observing hemisphere of monkey BT learned the task with very few responses being controlled by that hemisphere.

It may be that all the observational learning took place on the first few trials (those which were still directed by the experienced hemisphere). However, in this experiment it was not practical to introduce test trials after only several observation trials. Introducing test trials involves putting a contact lens occluder in the animal's eye. This disturbed the monkey somewhat and probably interacted with learning on the immediately preceding trials.

In errorless learning training it is assumed that a model serves to direct the attention of the subject to the relevant or reinforcing cues. Few or no errors are made because the subject that has observed the model enters the test situation with a bias to respond to the relevant or reinforcing stimuli. The errorless learning studies by Terrace suggest that the model need not by another animal. In his first errorless learning situation (4) the model may be the organism's own propensity to respond to a lighted disc. In Terrace's second errorless learning situation (5) a previously learned discrimination may serve as the model. By superimposing new stimuli upon these old cues, attention is directed to the new positive stimulus. In the present experiment one hemisphere serves as a model for the other hemisphere. The performance of the experienced hemisphere directs the attention of the observing hemisphere to the reinforcing stimulus and this hemisphere develops a bias to respond to this stimulus.

Since split-brain monkeys maintain conjugate eye movements, the observing and performing hemispheres experience almost exactly the same stimuli. Under this condition the observer monkey receives a maximum amount of information about the task. The results of this experiment therefore reflect more accurately the effectiveness of the observing experience on learning. The design also allow the experimenter to determine how associated experiences (such as reinforcement) affect observational learning. In the present study both hemispheres received the reinforcement experience following each observed response. A variation on this design is presently being developed which will allow the experimenter to chart the growth of the habits learned through observation by introducing a single test trial after every few observation trials.

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