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Changing Hemisphere Dominance by Changing Reward Probability in Split-Brain Monkeys

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The manifested dominance split-brain monkeys usually show for performing visual tasks through one hemisphere, when perceptual information is equally available to both, was analyzed. Three split-brain monkeys, each being trained similar yet different discriminations to each hemisphere, were allowed the opportunity to choose between the two problems when both were presented simultaneously. Initially all consistently preferred to respond with the right hemisphere. Subsequently, in separate training, the reward schedule for the dominant eye was advanced to FR-6 while the nondominant hemisphere was maintained on FR-1 or continual reward. Simultaneous exposure of the two problems now found the animals altering their original dominance and consistently performing through the nondominant hemisphere. The results are consistent with the view that attentional or preference processes, or both, are amenable to reward probability. Also, each half of the bisected brain can reliably keep different assigned reward values localized and specific to each hemisphere.

Introduction

After brain bisection in primates, it is commonly observed that one hemisphere will take the lead and tend to control behavior (1). If, for example, each hemisphere has free access to a visual discrimination, the leading hemisphere tends to learn the problem before or even instead of the other (2, 3). Moreover, when both hemispheres know a problem and each is free to respond, one side usually controls responses (3). While the dynamic forces leading to the original establishment of this kind of dominance and to its maintenance are not completely understood, it has been generally maintained that hand and eye use play critical and interrelated roles.

Conversely, the role that stimulus features and reward probability play in determining hemisphere dominance in the split-brain primate have never been thoroughly analyzed. In the present experiment preestablished hemi-

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sphere dominance was easily changed by varying the probability that each hemisphere would be rewarded for a correct response.

Method

Three monkeys *(Macaca mulatta)* were used, and all had undergone midline section of the corpus callosum, anterior and hippocampal commissures, and optic chiasm. They were restrained by specially designed collars which allowed them complete freedom of motion of the arms, legs, and body throughout the training and testing procedure. They were maintained on a 23-hr water-deprivation schedule. In previous training all three monkeys had performed at least two other discrimination tasks in this same apparatus. The brain of one animal (SNY) has been examined: The optic chiasm was completely sectioned as was the anterior commissure. There was approximately 1 mm of the corpus callosum intact in the genu.

Each animal, during an experimental session, 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 eye holes (Fig. 1). Head movement was limited so that each opening could be used by only one eye.

Centered on the panel were two 5 $\times$ 6.3-cm transparent plastic windows, one immediately above the other. Two IEE one-plane readout projectors were placed behind the windows and a trial was initiated by projecting a pair of stimuli on each window. 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 eye holes. 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 projected onto a black background. Throughout all phases of the experiment the right eye viewed an A vs B discrimination and the left eye viewed a C vs D discrimination, with B and D being rewarded. During some trials only one eye viewed the discriminative cues and an opaque occluder was placed over the eye hole of the other eye. The stimuli were within the center of the monkey's field of vision and could be easily reached by either hand. Responding to either window caused all stimuli to be turned off and initiated a 2.5-sec intertrial interval. A response to the window displaying the positive stimulus yielded several drops of water presented through a tube near the monkey's mouth. With an incorrect response the stimuli reappeared in the same position. 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. The presentation of trials, delivery of reinforcement, and the recording of responses were

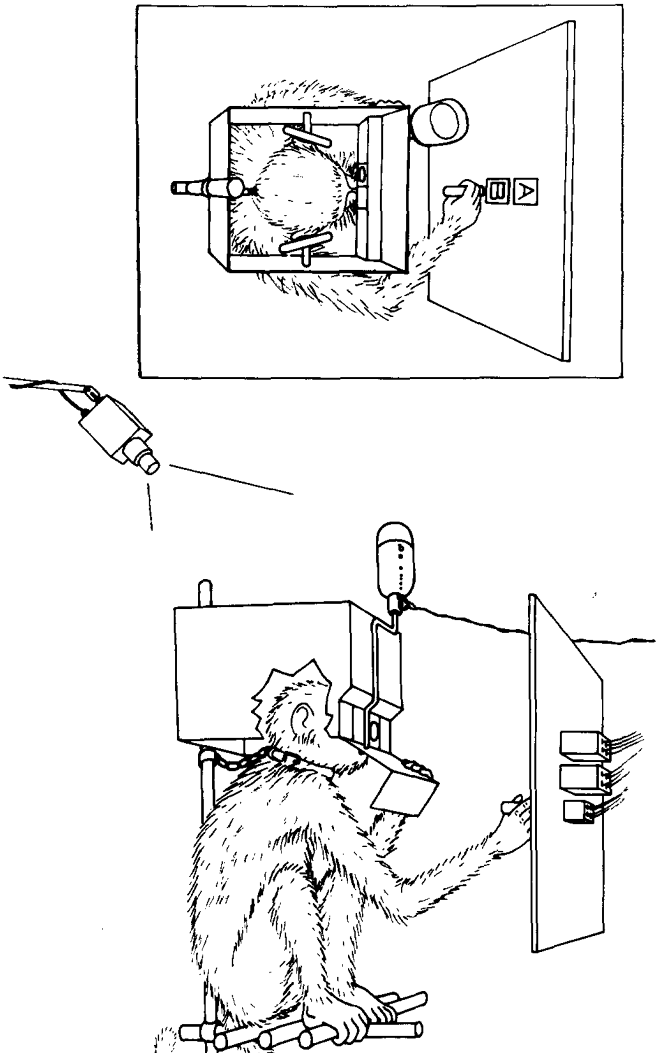

FIG. 1. The primate training apparatus which delivers a drop of water directly to mouth for correct response. Each trial is initiated by triggering a response and the trial is terminated by pushing one of the two display screens. Animals are maintained on special-design pole chairs which allow for maximum freedom in nontesting situations and also for extremely easy handling and transport.

performed automatically. All behavior was monitored by a closed circuit television system and microphone with the camera mounted above and behind the monkey. Hand use was recorded manually by the experimenter.

Each animal was first taught each discrimination—A vs B to the right eye and C vs D to the left. Subsequently, both eyes were exposed to both problems simultaneously. The demonstrably preferred eye was then advanced to an FR-6 schedule of reinforcement while the nonpreferred eye remained at FR-1.

During both the pretest and the final test where both eyes were open, trials were presented from a test sequence containing four conditions: (a) the two positive stimuli appeared on the upper window; (b) the two positive stimuli appeared on the lower window; (c) the positive stimulus, or B of A vs B projected to the right eye appeared on top and the positive stimulus, or D of C vs D, projected to the left eye appeared on the bottom; (d) the reverse of C.

The test for hemisphere preference consisted of opening both eye holes and presenting the two discrimination tasks according to the sequence outlined above. The "conflict" trials (conditions c and d) when both hemispheres had an opportunity to respond correctly were analyzed to determine hemisphere preference (e.g., the left to the top button, the right to the bottom button).

Results

Figures 2, 3, and 4 show the results of the pretest, training, and final test.

All animals were pretested after learning A vs B in the right eye and C vs D in the left eye. As seen from the top graph in each figure, all responses made during conflict trials, during the pretest found all monkeys held a preference initially for the right eye. All animals also freely responded with the left hand.

In the next graphs in each figure, the number of trials correct in 20 is scored for the right eye (A vs B discrimination) with an FR-6 schedule of reinforcement. All responses during this phase were made with the left (contralateral) hand.

Next, the number of trials correct in 20 using the left eye (C vs D discrimination) with an FR-1 schedule is shown. Animals LVE and FGS showed a preference to respond with the right (contralateral) hand. Animal SNY continued to respond with his left (ipsilateral) hand.

After consistently high-level responding was achieved with these schedules for each eye, the animals were advanced to the test phase and both eyes viewed their respective problems simultaneously. The last graph in each figure shows the results of the testing in terms of the percentage of eye use and hand use during the conflict trials for every 20 trials.

Animal LVE showed an initial preference to the right eye (FR-6). This preference was seen to change to exclusive use of only the left eye (FR-

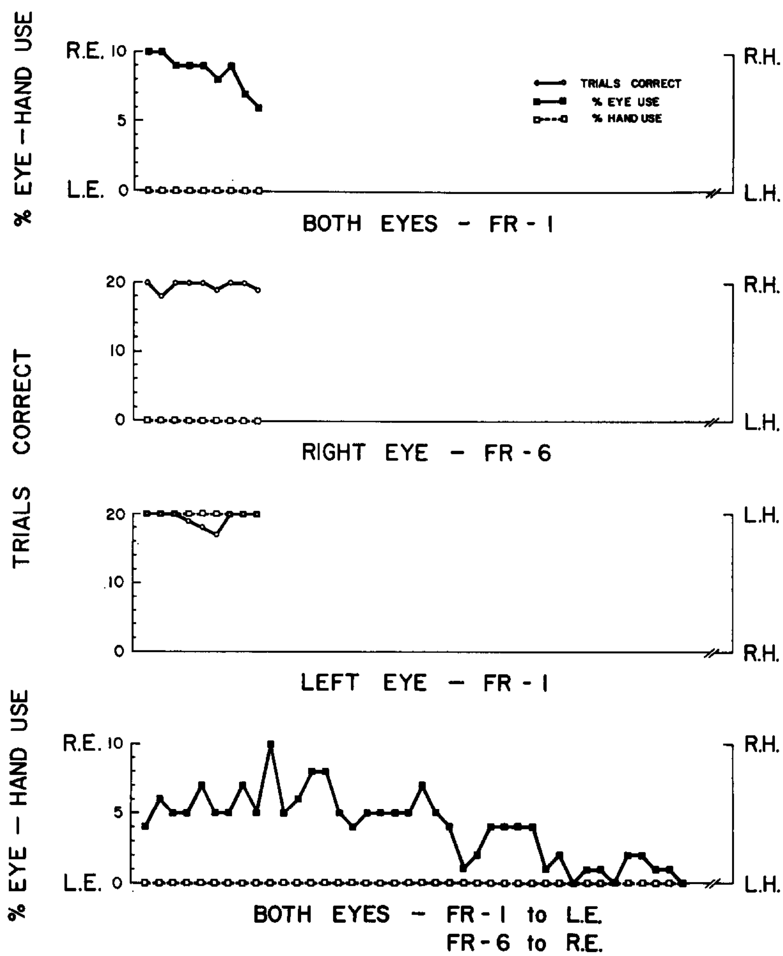

FIG. 2. Monkey SNY. Each graph first shows which eye and hand was initially preferred when each hemisphere had an equal opportunity to respond. Subsequently each eye was given the same number of trials with the preferred being advanced to FR-6. Lastly under both eye conditions, the eye originally preferred yielded control to the originally nonpreferred eye. Further explanation in text.

1). The pattern of responding was from one of predominantly right-hand use to one of exclusively the right hand.

Animal FGS initially showed a slight preference for the right eye (FR-6) which changed quickly to nearly exclusive use of only the left eye (FR-1). Initially she responded predominantly with her left hand. Here again the pattern of responding changed from one of predominantly left hand use to one of nearly exclusive use of the right hand.

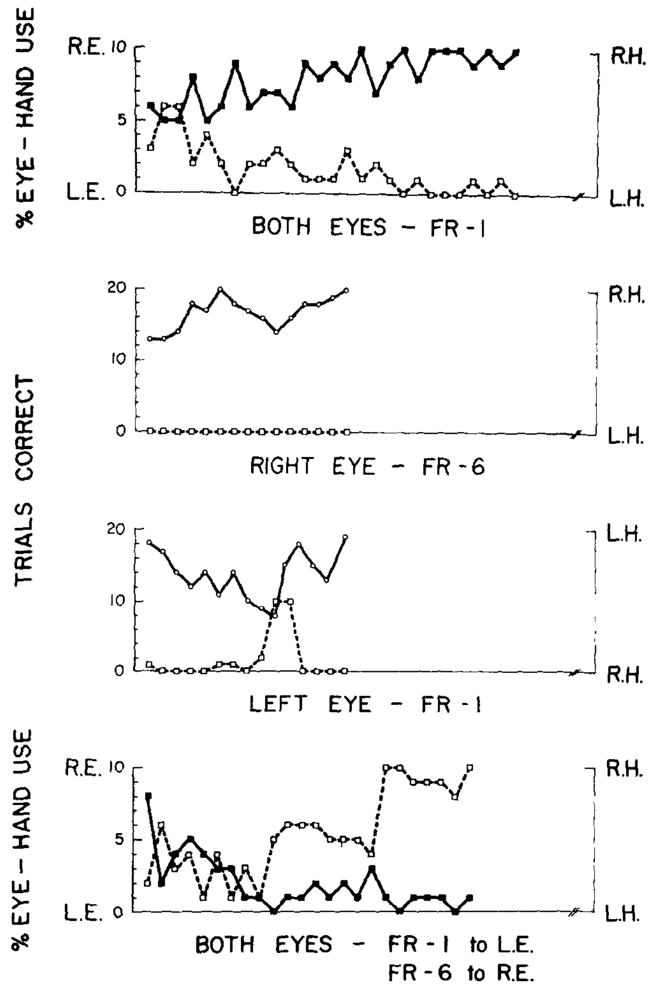

FIG. 3. Monkey FGC; see legend of FIG. 2.

Animal SNY initially during the test showed no preference. Gradually SNY changed to nearly exclusive use of the left eye (FR-1). This animal continued to respond with only the left hand.

Discussion

The foregoing results demonstrate that hemisphere dominance in the split brain monkey can be changed by manipulating reward probability. The influence of hand use and stimulus features on dominance can all be overruled by the better reward value of responding from one hemisphere over the other. The results suggest the underlying factors leading to the establishment of dominance are amenable to the laws of reward and learning.

The demonstration that hemispheric dominance can be controlled by factors other than handedness or natural preferences suggests that hemispheric-hand intrahemispheric interactions and the like are not necessary conditions for its establishment. It appears that eye or hemisphere preference can be manipulated, developed, and maintained independently of hand preference.

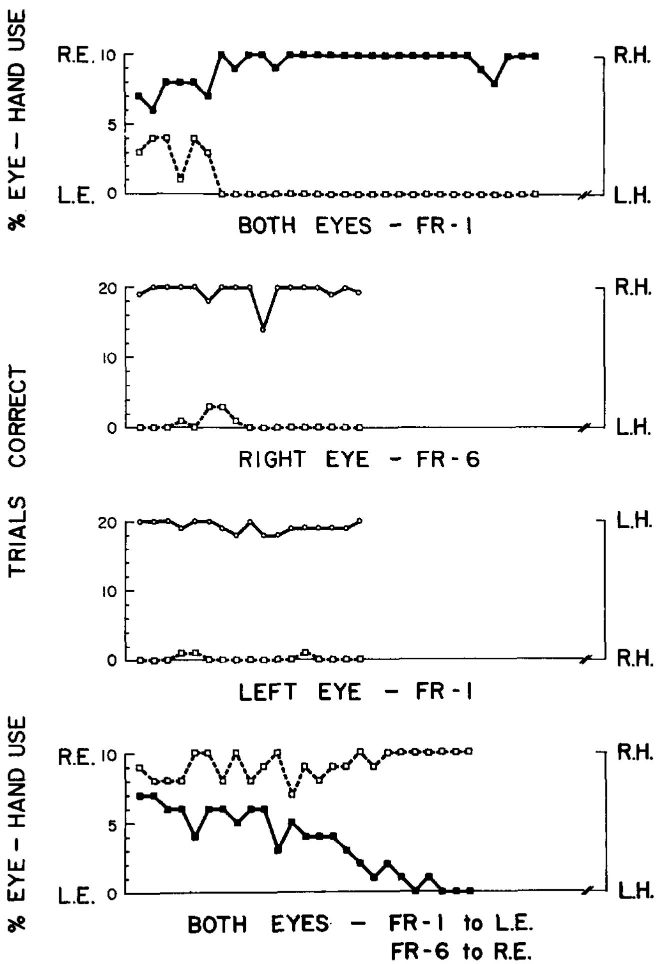

Fig. 4. Monkey LVE; see legend of Fig. 2.

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