

Interhemispheric Cuing Systems Remaining after Section of Neocortical Commissures in Monkeys

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Split-brain monkeys permanently fitted with goggles equipped with a red filter over one eye and a blue filter over the other were placed in a specially-designed testing apparatus which could be illuminated by either red or blue light. They were trained and maintained in blue light, thereby allowing vision through only the eye covered with the blue filter. Under these conditions other visual stimuli were briefly presented to the opposite hemisphere in red light. Stimuli with emotional quality presented in this manner were distractive and could affect the normal performance of the ongoing activity of the opposite working hemisphere. Additionally, if a fear-producing stimulus was directly presented to a hemisphere while it was engaged in some visuomotor task, immediate testing of the opposite hemisphere showed it to be relatively undisturbed provided the exposure was brief. With protracted exposure, the animal's behavior was found to be equally disturbed in each hemisphere.

Introduction

Surgical section of the cerebral commissures and optic chiasm in mammals has repeatedly been shown to be effective in eliminating transfer to one half brain of tasks already learned by the other hemisphere (3, 4). Additional studies have also demonstrated that the psychological properties of each hemisphere are for the most part identical, as indicated by the ability of each to learn discriminations of all types in equal times and with remarkably similar learning curves. While evidence continues to accumulate on the extent to which brain bisection produces mental duplicity, it now seems relevant to consider the opposite side of the matter and question the degree to which each hemisphere might be affected by subcortical or peripheral influences, or both, created by the opposite half brain.

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Methods

Five monkeys (*Macaca nemestrina*) were used throughout all testing and training procedures. Four underwent midline section of the corpus callosum, anterior and hippocampal commissures and optic chiasm; only the chiasm was sectioned in the other animal. The animals were placed in the training apparatus shown in Fig. 2. After each had become familiar with the training situation and had learned a visual discrimination, additional surgery was carried out to attach the mask pictured in Fig. 1.

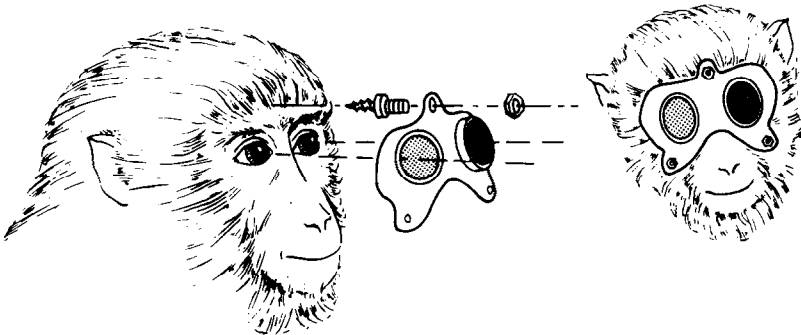


FIG. 1. Attachment of mask to skull. Specially-designed bone screws were made of inert vitallium.

Three specially-designed vitallium bone screws² were affixed to the skull and their placement was reinforced with anchor screws plus an overlying coating of dental cement. The mask, an adaptation of that used by Hamilton (2), was molded out of sheet aluminum $\frac{1}{16}$ in. thick. It was individually fitted to each animal and was bolted onto the machine screw protuberances of each bone screw. Barring excessive accidental jarring against the sides of the cage the mask could be worn comfortably for a month with no apparent adverse inflammation or other tissue reactions. After a month's use the mask and screws were removed.

The eye holes of the mask were fitted with slightly modified Kodak Series 4 filter holders which permitted interchange of the red and blue filters between the eyes. The filters were $\frac{1}{16}$ in. thick and $\frac{1}{2}$ in. in diameter and were made of Plexiglass (blue #2152; red #2444).

The training apparatus was kept in a light-proof but ventilated room which contained an observation window allowing full surveillance of the monkey's activity. The color of the room's lighting and of the stimulus pattern could be changed by remote control. In most instances the

² Manufactured by the Austenal Company according to our specifications.

animal was trained and maintained exclusively in blue light thus permitting the detection of the visual stimulus only by the eye covered with the blue filter.

The discrimination and testing apparatus was positioned at one end of the cage (Fig. 2). The monkey looked through a half-silvered mirror (fitted at an angle of 45°) at a vertically placed response panel situated immediately in front of the viewing box. The response panel was auto-

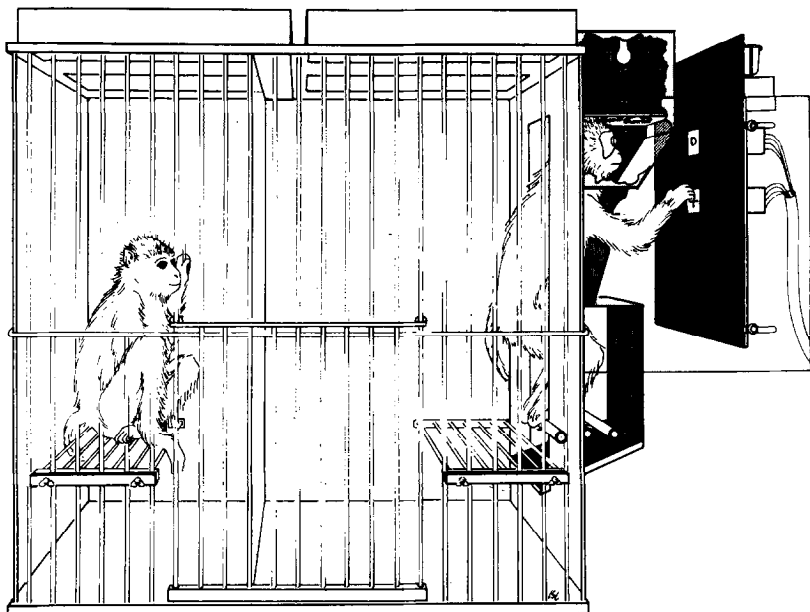


FIG. 2. Testing and training apparatus used throughout all experimentation. Color of room environment as well as stimulus patterns on response panel could be changed from red to blue by remote control. For complete description, see text.

matically controlled and programmed by electronic equipment placed outside the training room. The visual stimuli were displayed on two translucent Plexiglass screens placed one above the other and separated by a reward trough. The monkey learned to respond to the discrimination task by pressing the correct screen. Situated on top of the monkey's viewing box was a red light source which, when turned on, illuminated various objects placed in the viewing chamber that then appeared by reflection to be located directly in front of the response panels. The blue environmental and stimulus lights remained on during red light presentation. Perception of the distractive objects was exclusively limited to the eye covered with the red filter.

In order to avoid a climate of isolation, a normal monkey was usually

kept in the partitioned-off area of the apparatus. Both were fed once a day, late each afternoon. Testing of the experimental animal took place in the morning when the monkeys displayed a good appetite and a consistent eagerness to work.

All animals were eventually killed and their brains examined. The chiasm, corpus callosum, anterior and hippocampal commissures were found to be completely sectioned in all.

Results

First Experiment. Three monkeys with chiasm and commissures sectioned (CFL, BLL and MIN) and one with chiasm alone sectioned (FNK) were used; all were normally more calm than aggressive. Following surgery and prior to the mask fitting, they were acclimated to the testing apparatus with the blue light conditions. Each animal learned a plus-zero discrimination task to a criterion of 90% correct in 40 trials and each was over trained a minimum of 500 trials. The mask was then affixed to the skull and the animal was returned to the apparatus at least 2 days before testing was resumed. Criterion was then re-established on the discrimination task which was now visible only to the blue-filtered eye. The distractions were presented when the animal was looking straight into the half-silvered mirrored apparatus and about to respond in routine fashion to the plus-zero discrimination. At this point the red light was briefly flashed on, thereby making the viewing chamber and its contents visible to the red-filtered eye.

Following distractive stimulation of this type, the monkey with chiasm sectioned would stop and, depending on the nature of the stimulus, react in either of two fashions. If the distractive stimulus was a flash of light, the animal would briefly stop working and glance about, but then would continue quickly about the task. If the viewing chamber contained a toy snake, the animal reacted violently and would leap back from the working area to the back of the cage.

All three monkeys with bisected brains reacted similarly, and for descriptive purposes, will be considered together. As before, the distractive (red) stimulus was presented when the monkey was positioned and ready to respond to the discrimination. If only a flash of red light was presented at this point, they usually paid little or no attention to the disturbance and completed the task. If the toy snake was present in the viewing area, however, brief illumination of the snake by red light resulted in the monkey's jumping back and looking around. After a few moments they would reposition themselves for the next trial as though nothing had happened.

Individual variations occurred in the responses during the next forty

trials. Monkey CLF would characteristically leap back after each distractive stimulus presentation, look around, and then begin to work again. On several trials it appeared reluctant to get into the working position, but generally returned within a few moments. After this series of trials the animal became more hesitant to work. Instead of the usual slow and deliberate movement of the hand to the response panel while it was in working position, monkey CLF would now jab with its hand at the panel and hold the body as if in a position to make a fast getaway from the viewing area of the apparatus. At about the fiftieth trial, this hesitation appeared to wane and presentation of the snake began to exert less influence on its behavior; finally, it no longer appeared concerned.

Monkeys BLL and MIN, on the other hand, became habituated to presentation of the snake much sooner. At about the eighth trial, presentation of the snake produced no gross behavioral response. The initial responses were much like those described for monkey CLF in that following the first few presentations of the snake, both monkeys moved back from the working area and circled the cage for a short period before continuing the discrimination task.

To summarize, distractive stimulation of one hemisphere of a split-brain animal disrupted the on-going visuomotor activity of the opposite hemisphere if that distractive stimulus possessed sufficient emotional novelty to precipitate gross bodily reactions. Repeated stimulation, however, eventually produced habituation after which there was little or no interference with the activity of the opposite half brain.

Second Experiment. The foregoing experiment indicates that activity of one hemisphere can influence that of the other in split-brain animals. It does not answer the question of whether or not continued emotional traumatizations of one half brain can affect psychological changes in the other hemisphere. Would the disconnected nontraumatized half brain become equally aroused and react in an emotional fashion to previously neutral environmental situations?

Three monkeys with split brains (MZQ, BLL and MIN) and one with chiasm sectioned (FNK) were used as subjects. During the performance of the discrimination task, the toy snake was either directly lowered in front of the monkey's gaze without the half-silvered mirror intervening, or was briefly introduced directly into the cage. In the latter procedure the snake was held by the experimenter. No matter which method was used, these procedures, because of the prolonged exposure of the snake stimulus along with its proximity to the animal, proved to be far more traumatic than that described in the first experiment.

The general test procedure involved presentation of the snake while

the animal was working in a blue-light environment thereby limiting all visual information to one eye. Subsequently, the lights in the room were switched from blue to red, thus bringing the opposite eye into use. The animal's behavior was then observed.

Following the first exposure of the snake, the monkey with chiasm sectioned leaped back, screamed, and began rapid circling movements around the cage. Upon taking the snake out the animal resumed the working position, although somewhat cautiously, and prepared for another trial. A second stimulus exposure yielded similar reactions including exaggerated vocalization and overt heavy breathing. Subsequent change of the existing blue environment to red which shifted vision to the opposite eye-hemisphere combination resulted in no discernible change in the monkey's behavior. It remained disturbed and continued circling, vocalizing, etc.

All split-brain animals reacted in much the same fashion. Monkeys BLL and MIN were trained and tested under similar conditions to those just described. Monkey MZQ was run only on this experiment and its behavior will be described in detail as representative of all three animals.

After monkey MZQ had learned a plus-zero discrimination in red light, and had become fully acquainted with the apparatus, a snake was momentarily lowered during a response sequence. The monkey jumped back and began to circle the cage nervously, showing new interest in the point of the snake's entrance. After two more snake presentations it refused to work and characteristically circled the cage. At this point the room environment was switched to blue, thereby allowing visibility of his surroundings only through the left eye and therefore the left hemisphere. There was a definite change in its emotional state as was evidenced by the cessation of circling activity and willingness to respond in the discrimination apparatus. After a few trials, switching back to the red environment once again promptly gave rise to concerned inspection of the area where the snake had entered and the taking up of a position in the back of the cage for much of the time.

At this stage, and again in the red environment, the snake was directly introduced onto the floor of the cage. Monkey MZQ reacted violently by displaying frantic vocalizations and rapid movements around the bars toward the top of the cage. The experimenter then picked the snake up, and holding it in his hand, reached for the monkey. Following this, the animal was totally aroused. The snake was then removed and the light was changed to blue, introducing the unexposed eye and hemisphere. This time, instead of the usual calm reaction at the entrance of the experimenter, the animal vocalized violently and continued its hyperactivity with no interruption.

Discussion

First, all monkeys having undergone neocortical commissurotomy combined with prolonged visual exposure to only one hemisphere were found to be equally as responsive to visual stimuli briefly presented to the visually deprived eye as was an animal with only midline section of the optic chiasm. However, stimuli that did not have a novel quality or novel stimuli presented several times tended not to elicit detectable responses in the split-brain animals.

Secondly, following surgical section of the neocortical commissures, emotionally traumatic stimulation of one half brain renders the opposite disconnected hemisphere equally disturbed and aroused. On the other hand, less vigorous presentation of such stimuli appears not to precipitate identical strong reactions in the unstimulated hemisphere.

The first experiment showed that the one hemisphere of split-brain animals can be distracted by stimulus presentation to the opposite hemisphere. Explanation of this crossed hemispheric effect in terms of interhemispheric transfer of the perceptual nature of the distracting stimuli seems unlikely. Related experiments carried out on human beings with brain bisection indicate that while emotional reactions triggered by one hemisphere are sensed by the opposite half brain, the unstimulated hemisphere remains totally incognizant of what produced the reaction (1).

The exact mechanism responsible for this interhemispheric interaction remains unknown. It would appear that the observed reaction was due either to the fact that the hemisphere directly perceiving the distracting stimulus dominated the motor control, or that this hemisphere introduced its own emotional tone into the opposite half brain either through brain stem neural mechanisms or more indirectly by endocrine reactions. The results of the second experiment would argue against the former alternative as necessary for interhemispheric interaction in animals with commissures sectioned. Thus, the monkeys when tested and observed were thoroughly emotionally affected in their nonexposed hemisphere several minutes after stimulation irrespective of their position in the cage.

Consideration of the results of the second experiment by itself would suggest that there exists a threshold of emotional stimulus strength, beyond which secondary emotional reaction can be induced into a hemisphere insulated from direct perceptual exposure to traumatic stimulation. When stimuli fall below this threshold no emotional reaction is induced, even though physical activity may be apparent.

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