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Cross-Cuing Mechanisms and Ipsilateral Eye-Hand Control in Split-Brain Monkeys

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It was proposed that split-brain monkeys are able to perform ipsilateral eye-hand response because the seeing hemisphere can cross-cue the blind hemisphere, which is in major motor control of the arm, by orienting toward a point in space and, thereby, allow for the bilateral registration of head, neck, and eye position. In the present study, accuracy of ipsilateral eye-hand response was measured in normal and split-brain animals under conditions of free and restrained head movement. The results confirm the view that split-brain monkeys rely on cross-cuing information in order to maintain this kind of behavioral unity.

Introduction

The general problem of neural mechanisms underlying visual-motor coordination has been studied extensively in the split-brain monkey (2, 4, 5, 8, 10). In brief, a major hope was to delineate central pathways active in the communication and synthesis of information between the sensory receptive sphere and the motor expressive sphere by sectioning down the midline of the brain or across the length of the interhemisphere commissures until the critical disconnection was realized. In the initial studies, the degree and extent of ipsilateral impairment observed in the monkey with forebrain divided was disputed, but, in general, the over-all conclusion was that monkeys with cerebral commissurotomy were able to guide and control both the contralateral as well as the ipsilateral hand from one disconnected hemisphere.

Some of the possible mechanisms active in effecting this control were analyzed and eliminated in a previous paper (5). Severe ablations in one hemisphere, in the parietal and frontal lobes, failed to impede that hemisphere from directing accurate ipsilateral eye-hand responses. These data argued against the concept of ipsilateral, corticospinal control being the mechanism involved. It was also shown that deep-split surgery, which extended the midline section down to the medulla, failed to critically interrupt ipsilateral eye-hand control. This confounded the notion that

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subcallosal pathways were active. Instead, it was proposed that the mechanism used by the split-brain monkey was one that employed cross-cuing strategies whereby, the seeing hemisphere succeeded in communicating the target information of the object to be localized over to the hemisphere in major control of the hand. This was accomplished by the seeing hemisphere orienting toward the object with the result that the final eye, head, and neck position became available to the nonseeing hemisphere. This target information it was concluded, was sufficient for the nonseeing hemisphere to precipitate an accurate motor response.

In the present experiment, normal and split-brain monkeys were tested under a variety of eye-hand conditions with the head both held and free in an effort to determine the role of proprioceptive information from head movements in performing accurate ipsilateral eye-hand responses. The results support the notion of cross-cuing strategies being the key mechanism of control.

Materials and Methods

Both *Macaca nemestrina* and *Macaca mulata* were used in testing. The controls were a normal, BNE; a callosum section-chiasm intact, CLN; and a chiasm section-callosum intact, NTW. The latter animal had a small lesion in the body of the callosum. All with split brains (BDT, CLD, BRY, GRG) had the anterior and hippocampal commissures and the corpus callosum sectioned along with midline section of the optic chiasm. Animals GRG, CLD reported below were killed and their brains examined to check for completeness of surgery. Surgical section was complete. Monkeys BDT, BRY, CLN, and NTW are being used in further experiments.

The apparatus was especially designed for the experiment and consisted of ten response levers, 1 cm wide, spaced 3.8 cm apart on center (Fig. 1). The animal's head when fixed straight ahead was 17.5 cm from the panel. With the midline falling between levers five and six, lever one was 38 deg lateral to the left; lever two, 33 deg; lever three, 25 deg; level four, 16 deg; and lever five, 6 deg; with the same relation holding for levels six to ten off the right. Between each lever was placed a solid divider, which, in effect, required the animal to make an individual finger movement to hit in between the divider on each side of a lever.

Directly beneath the series of response levers and in the midline, was another lever which was used by the animal to initiate the trial. Triggering this lever resulted in illumination of one of the ten lights. Before each trial, a ten-position ring counter is circulated at a 50 kHz rate. A response on the ready lever stops a ring counter at a random position, illuminating one of the ten response switches, while at the same time starting a three digit, 1 msec based latency time. The subject presses one of the response switches, stopping the latency timer, and initiating a record cycle which

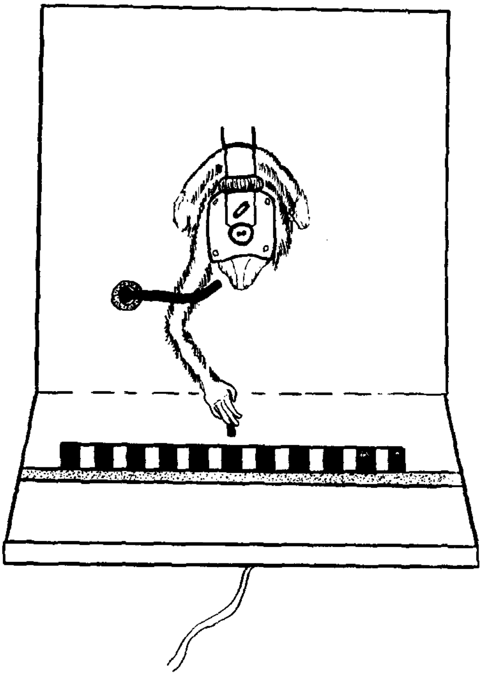

FIG. 1. Monkey in head restraining apparatus in front of response panel. The lever activating each trial is below the row of response levers. The liquid reward is delivered in a small tube to the right of the animal's mouth. All training was carried out automatically.

commits the latency measurement, the stimulus position, and response choice to an eight-channel paper-tape perforator. Data are encoded into five frames of ASC II format, and submitted to a DEC PDP-8/S computer for analysis. Coincidence of stimulus position and response choice commands a grape-juice dispenser to reinforce the subject. An ITI cycle disarms the ready lever and response panel for 10 sec, followed by the next trial.

Restraining head movements involved implanting four stainless steel machine screws (2 cm) two on each side of the midline of the skull (Fig. 2). The two screws were reinforced by including between them, a stainless steel separating bar (3). A light-weight but sturdy aluminum hat was fitted onto the four protruding bolts with a hole in the center taped to accept the screw connector of a universal Leitz ball and socket camera mount. With the ball and socket joint loose, free head movements were easily possible, but with the joint fixed, no head movements were possible, leaving the animal free to make only eye movements.

Liquid reinforcement was used and was delivered through a tube placed

FIG. 2. Head restraining helmet and camera mount ball and socket joint. Bolts protruding from the head are implanted and reinforced by the method described by Evarts (3).

at the side of the mouth (Fig. 1). This eliminated the animal having to retrieve food morsels which would confuse the visual-motor responses. After the animals had been shaped up on the problem, they were generally allowed to work from 1 to 2 hours a day. During this time, they consumed approximately 500 ml of their favorite beverage.

In addition to the behavioral data collected, during all phases of critical testing closed circuit TV monitoring allowed for the close observation of the animal's overt responses including examination of individual finger and eye movements. The videotape was subsequently replayed for careful study.

Because of the large number of eye-hand combinations possible for each animal, only one hand was tested. The animals were usually run through training in the following ways: Both eyes and one hand, head free condition was followed by the same but head held. The contralateral eye-hand pair was next with the head first free, and then held. Lastly, the ipsilateral eye-hand pair was run with the same sequence of head free and head held conditions. The scores were analyzed in blocks of 100 trials and percentage correct of usually ten trials was calculated.

The results of experiments using controls and split-brain monkeys were illustrated graphically but are not included in this paper. They will be made available to reads upon request.

Results

Three control animals, BNE—unoperated, CLN—callosal section-chiasm intact, and NTW—chiasm section-partial callosal section, performed with accuracy and good control in all eye-hand combinations and with the head either held or free. Performance of monkey NTW dropped off in the blind half field of each eye, but this reflects a sensory deficit more than a visual-motor inadequacy. In general, as long as sensory information was available to each hemisphere, either through the callosum, or the uncut chiasm, or both, no deficits were observed in the tests used. In the following, therefore, the deficits recorded were not a product or artifact of the procedure and apparatus itself.

With no restrictions on visual input or restraining of head movements, the four split-brain animals, using one hand, were able to reach accurately with little or no practice to all levers on the horizontal scale. With the head fixed, only minor difficulties were seen.

Contralateral eye-hand, pairing revealed only a slightly different picture. With the head free, good performance was seen for lights falling into the intact visual field and with little or no practice, responses became accurate in the blind field. In carrying out these latter responses, each animal would characteristically scan the response panel until catching sight of the illuminated lever and then, orienting towards it, would respond. With the head fixed, the responses in the intact visual field remained good, while the accuracy of responses in the blind half field dropped off. In the animals allowed additional blocks of trials, the score improved for the stimuli falling into the blind field. Close observation of the animal's behavior under these conditions revealed scanning movements with the eyes were frequent. Upon seeing the stimulus they would hold their eyes fixed until the response was made. All responses made with the contralateral eye-hand pair appeared crisp and directive with good control of hand movement especially evident.

The most severe deficits were observed with ipsilateral eye-hand combinations. With head free, ipsilateral responses were relatively good in the good visual half field, but generally decreasing in accuracy in the blind field. With practice, however, responses even in the blind field greatly improved. Again, direct observation of the animal's responses during these trials showed them to be scanning the board until the illuminated lever came into view and then, to fixate on it during the response. With the head held, large deficits were seen in both the intact and the blind visual field with the accuracy improving across the board with practice. Generally, using this eye-hand combinations proved disturbing for the animals. All took longer to respond and became agitated.

With the head either free or held, one of the striking features of the response was the complete awkwardness of hand movement. Instead of the hand striking a lever with precision and tone as seen with the contralateral eye-hand pair, the response (with respect to the hand, not the arm) would take on a blind, groping posture with the fingers widely separated. Only with effort and usually some practice could the animal control the hand sufficiently well to depress one of the levers in between the two side guards.

Discussion

Several trends are clearly apparent. First, the experimental monkeys always performed consistently better when their heads were free. The degree of impairment produced by holding the head progressed as more stringent visual restraints were imposed. These findings are consistent with the view that head position is contributing to over-all accuracy of visual-motor responses, especially when the sensory information is projected to one hemisphere and the motor control is featured mainly in the opposite hemisphere.

The critical test for the foregoing hypothesis is the difference between head held and head free under conditions of ipsilateral eye-hand control. In all cases, the animal performed poorly with the head held. This suggests that some of the information used by the animal on localizing points in space comes from the nonseeing hemisphere registering the position of the head. At the same time, since control was finally realized under these conditions, the hypothesis would predict the blind hemisphere was then being cued in some way by the only available, remaining information source —eye position. Elimination of eye movement in split-brain monkeys would be a difficult procedure. In recent experiments on brain-bisected adults, however, it has been clearly shown in an essentially identical test situation that eye position does contribute in a dramatic way to the over-all accuracy of ipsilateral eye-hand tasks. With the head held and no eye movements allowed, their responses are very poor (7).

An alternative explanation for the data is that the seeing hemisphere can realize enough ipsilateral control to direct the arm to the appropriate point in space so long as the integrity of the contralateral motor cortex is assured. This hypothesis, however, can not predict poorer performance with the head held than with the head free during ipsilateral eye-hand responses.

The cross-cuing mechanism proposed appears sufficient to explain all previous reports on ipsilateral eye-hand control in cat (9), monkey (2, 4, 5, 8), and man (6). Studies carried out to date in the chimpanzee (1) cannot be explained by this mechanism but close analysis of this study suggest visual-motor control was not in fact, being examined. The data clearly suggest that the chimpanzees were learning a tactile-motor discrimination which would automatically put the findings into another class of phenomena. In the other aforementioned studies, save one or two specific tests in man, the theory can account for the behavioral data. In the human cases, a specific test was designed which required individual responses of the fingers, a response sequence which cannot be cross-cued, due to the localized nature of the response occurring in the most distal part of the extremity. As a result, an enduring incapacity in ipsilateral control in the split-brain patients is the individual control of the fingers by the ipsilateral hemisphere.

The implications for these findings in the wider context of brain mechanisms underlying visual-motor coordination are of interest. It seems abundantly clear that a simple connectionist view of interaction between sensory and motor elements is not helpful in understanding the real circuitry and mechanisms involved. The present data supports the earlier view (5) that a general orientation toward a stimulus first takes place involving eye, head, and neck position and that this information feeds back, and further sets and resets, the lower motor apparatus. The view is that sensory-motor integration commences its long sequencing of events in the visual system itself, and that a highly integrated sensory-motor message is delivered to the more clearly efferent motor system controlling specific extremities.

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