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Interhemispheric Comparison of Color in Split-brain Monkeys

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Monkeys with varying degrees of brain bisection were trained on a visual discrimination that required interhemispheric integration of sensory information for its solution. A matching-to-sample task was used in which the sample was projected to one hemisphere and the two choices for the match were projected to the other hemisphere. Monkeys with complete section of the optic chiasm and forebrain commissures could not solve this task. There was some evidence of interhemispheric integration via portions of the hippocampal commissure or corpus callosum anterior to the splenium. Various strategems unrelated to the visual stimuli were sometimes employed for above-chance performance.

Introduction

The major role played by the forebrain commissures in permitting interhemispheric transfer of visual discriminations learned via one hemisphere has been extensively demonstrated. In the absence of these commissures, "split-brain" animals are unable to perform such learned discriminations when tested through the untrained eye (11). The few qualifications to this generalization involve gross brightness discrimination in cats, which can be transferred via the midbrain roof (6, 7); pattern discriminations trained with shock-avoidance methods, which appear to transfer in cats through routes other than the corpus callosum or hippocampal commissure (9), possibly through the anterior commissure; and brightness and color discriminations which have been reported to transfer via subcortical pathways in primates, although the data are conflicting (4, 10, 14).

Even though it appears that the cerebral commissures are necessary for the interhemispheric transfer of most visual discriminations, it has yet to be established whether they are necessary for the simultaneous cross comparison or cross integration of visual information projected in part to each hemisphere. Split-brain cats with the midbrain roof intact can apparently

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cross-compare two brightnesses projected separately to the two eyes (8). It has been reported that matching-to-sample and several kinds of relational comparisons between patterns can be performed by split-brain monkeys when part of the input is projected to one hemisphere and the remainder to the other (15). In a later study, however, split-brain monkeys were found to be unable to fuse two halves of a circle into a whole circle when the halves were separately projected to each hemisphere (13). We report here some effects of cerebral commissure section in monkeys on the performance of a color match-to-sample problem in which the sample is projected to one hemisphere and the matching stimuli to the other.

Materials and Methods

Four adolescent monkeys *(M. nemestrina)* served as subjects. They underwent different degrees of split-brain surgery in the order indicated in Table 1. Under sodium amytal anaesthesia the skull was opened, dura mater reflected, and one hemisphere retracted slightly. Selected midline structures were sectioned under direct visual control using techniques described elsewhere (12). At the end of the experiment the subjects were killed, 40-μ sections taken, and their brains examined histologically to determine the completeness of brain bisection (Weil stain).

Training was carried out in an apparatus designed specifically for training and testing split-brain monkeys (Fig. 1). The training units were attached permanently to each monkey's home cage and the stimulus presentation was programmed automatically. The monkeys voluntarily peered through two eyeholes to see the visual stimuli, which were located before them on a vertical panel placed at arm's length. The visual display consisted of a plastic "sample" panel, 38 × 38 mm, which was centered directly above two similar "response" panels, placed side by side. On a given trial, the sample panel was transilluminated through either a red (Wratten No. 25) or green (Wratten No. 58) filter, and the response panels were similarly illuminated, one red and the other green. The subjects' task was to push the response panel that was the same color as the sample. The sample color and the left-right orientation of the colors on the response panels varied from trial to trial according to a 20-trial Gellerman sequence (3). The intensities of the panels, which were approximately matched for luminosity, were varied independently at intervals with filters of 0.5 or 1.0 neutral density to insure that discriminations were being made on the basis of hue rather than brightness. One monkey (MK) was originally trained with red and white and then switched to red and green stimuli. Correct responses on the match-to-sample task were rewarded by a food pellet delivered to a tray directly below the response panels. All the animals were permitted to use either hand to press the panels. The criterion for learning was chosen as 90% correct over 40 consecutive responses.

Polaroid filters were placed on the front of the panels and before each eyehole. Changing the relative orientations of the filters allowed the entire problem to be presented to both eyes, to one eye alone, or in divided form

TABLE 1

TRIALS TO CRITERION PRE- AND POSTOPERATIVELY

Subject	Preop. Train.[a]		Surgery[b]	Postop. Train.[a]	
MK	Both Eyes	740	1. oc, ac	Both Eyes	80
	LE/sample	0	ant cc	RE alone	360
			hbc, pc	LE alone	160
			csc, cic	LE/sample	40
			2. post cc	RE alone	40
			hpc	LE alone	120
				RE/sample	400
				LE/sample	440
RM	RE/sample	440	oc, ac	RE alone	1,520
			cc, hpc	LE alone	880
				RE/sample	> 12,700[c]
OP	None		oc, ac	Both Eyes	880
			cc, hpc	RE alone	160
			hbc, pc	LE alone	920
			csc, cic	RE/sample	> 3,520
				LE/sample	> 5,120
BG	None		1. oc	RE/sample	1,840
			2. post 1/3cc	RE/sample	640
			3. ac	RE/sample	> 7,020[d]
			4. ant 2/3cc	RE/sample	> 5,400[c]
			hpc	LE/sample	> 2,680[c]
				Both Eyes	1,160
				LE alone	0
				RE alone	160
				RE/sample	> 2,280[c]

[a] Both eyes: unseparated input, sample and match viewed by both eyes. RE or LE alone: similar unseparated input, but one eye closed. RE/sample or LE/sample: separated inputs with indicated eye viewing sample, other viewing match.

[b] Abbreviations: oc = optic chiasm, ac = anterior commissure, cc = corpus callosum, hpc = hippocampal commissure, hbc = habenular commissure, pc = posterior commissure, csc = commissure of superior colliculus, cic = commissure of inferior colliculus.

[c] Maximum score about 30/40, maintained about 60% correct responses; performance unaffected by reversing problem.

[d] Maximum score = 35/40; maintained about 70% correct responses; fell below chance when problem reversed.

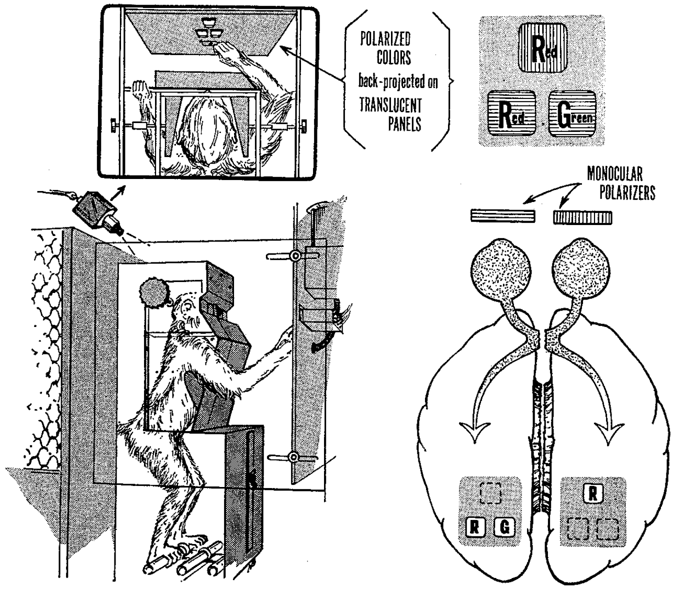

FIG. 1. Top and side views of the training apparatus are depicted on the left of the figure. The arrangement of the stimuli, with the direction of polarization indicated by lines, and the resultant cortical projection of the stimuli, are shown on the right.

such that one eye saw only the sample color while the other eye saw only the colors on the response panels. The latter arrangement (separated inputs) formed the critical tests that required interocular comparison of the inputs for consistent correct performance (Fig. 1). The design and presentation of this task is essentially the same as that used by Trevarthen (15).

The sequences of training and surgery were varied for different monkeys as indicated in Table 1, in case certain procedures in the initial training of the problem might bias the subject's subsequent approach to solving the task when the inputs were separated. For example, if a normal monkey first learned how to solve the problem with both eyes viewing the entire panel, this experience might interfere with subsequent learning of the separated-input problem, especially if first presented after split-brain surgery. Alternatively, if the problem had been trained only as a separated-input task to the monkeys which were already split, failure to perform might only signify that the subjects didn't attain the concept of matching-to-sample.

Finally, the visual input is clearly different for animals with section of the optic chiasm because of blindness of the temporal half field for each eye, which might affect the generalization of preoperatively learned problems to postoperative tests of retention. Therefore each monkey was taught the problem in a way that would minimize one or another of these potential difficulties.

Several control procedures were required because the split-brain monkeys managed to improve their performance level by various strategems other than comparison of the visual stimuli. When performance with the inputs separated remained somewhat above chance but did not reach criterion, some or all of the following controls were run to determine the cause of the improvement: (*a*) One eye at a time was occluded with the polaroid filters in place to see if the problem would continue to be solved monocularly (e.g., polaroid leak or reflections); (*b*) the specific Gellerman sequence was varied to test for memorization of segments of the repeating program; (*c*) the sequence was changed from an advance-every-correct-response, which was used to disrupt position preferences, to an advance-every-response in order to test for strategems such as "win-stay, lose-shift"; (*d*) the sample colors were reversed relative to the match so that the reinforcement was then contingent on matching-not-to-sample in order to ascertain whether, in fact, the subject was responding on the basis of the visual discriminanda.

If the animals failed to perform above chance after extensive training on the separated input problem, they were tested monocularly for retention of the unseparated problem, and retrained to criterion if necessary. If they had not yet received monocular training, they were trained to criterion with unseparated inputs. Then all subjects were returned to training with separated inputs.

Results

The principal results are presented in Table 1, with the data arranged in the order obtained. Representative samples of the performance curves are given in Fig. 2. In brief, three of the four monkeys did not solve the separated input problem after section of the optic chiasm and all the forebrain commissures, although all animals could perform the problem through either eye without separation of the inputs. The histological results confirmed that the surgical sections were complete with the exception of a few fibers in the posterior portion of the chiasm of monkey RM. The remaining subject (MK) successfully solved the separated input problem after brain bisection (Fig. 2). Histological investigation of its brain disclosed a band of unsectioned fibers in the corpus callosum and adjacent hippocampal commissure, about 3.5 mm long, the posterior edge of which was located about 5 mm from the posterior end of the splenium.

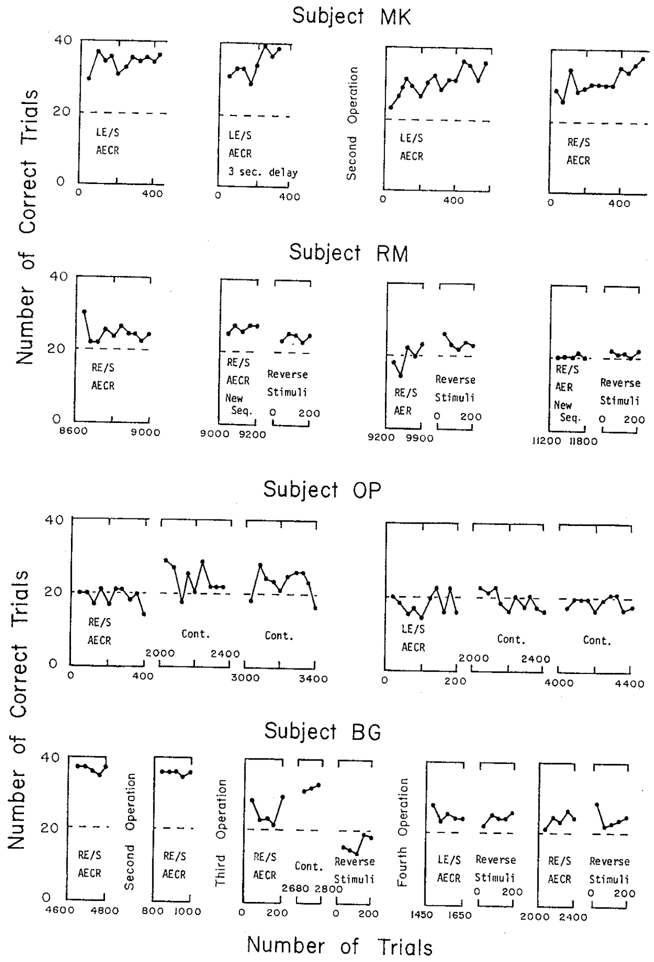

FIG. 2. Examples of postoperative performance with presentation of sample to one eye and match to the other. RE/S: right eye sees the sample, left eye sees the match. AECR; sequence advances every correct response. AER; advance every response. New Seq.: the Gellerman sequence was changed. The structures sectioned in each operation are listed in Table 1.

Monkeys RM and BG, which did not perform the split-input problem at criterion levels when completely sectioned, nevertheless often showed greater than chance performance (about 60–75% correct) over long intervals. This level, however, was unaffected by reversing the sample color (i.e., when the rewarded response was match-not-to-sample), which shows that this performance was independent of the relationship between the stimuli (Fig. 2). Other control procedures indicated the actual strategems employed. The performance of monkeys BG and RM was unaffected by altering the specific sequence of stimulus presentation but fell to chance when the program was changed from an advance-every-correct-response to an advance-every-response sequence, suggesting a "win-stay, lose-shift" strategem. This was confirmed by a detailed analysis of the errors made over many trials. Subsequently monkey RM improved again, but fell to chance when the specific sequence was changed, indicating that portions of the advance-every-response sequence had been memorized (Fig. 2).

Following the third operation, which left only the anterior two-thirds of the corpus callosum and adjacent hippocampal commissure unsectioned, monkey BG maintained a 70–75% level of correct performance with inputs separated but did not reach the 90% criterion. Reversing the sample color caused this performance to drop to 35–40%, showing that the stimuli relationships were still being used at this stage (Fig. 2). These two performance levels are symmetrically distributed around the mean response level of the fully split subjects. The exact amount of corpus callosum and hippocampal commissure remaining after the third operation is only an estimate since these commissures were entirely sectioned before histology. The fourth operation finally eliminated this remaining cross-comparison ability.

After the final operation, monkey BG was also unable to perform better than chance on a discrimination based on the relative sizes of two outline circles, one presented on a panel to one eye and one to the other. A graded series of six circles was used, which yielded a total of 15 pairings of different size circles from which BG was required to choose the larger of any pair in order to obtain a reward. Although monkey BG could perform this task with separated inputs preoperatively, and after the second operation, it never rose above the level of the control tests (during which only one of the comparison circles was presented) during 4,600 trials given after the fourth operation. Finally, after the third operation when monkey BG could still do interhemispheric comparisons of color, it showed little evidence of interocular transfer of pattern discriminations when tested on five simple problems (median savings = 10%). It did somewhat better before the third operation (median = 63%, five problems), in line with earlier

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comparing the discriminanda, such as used by monkeys in the present study, led to the results in the discrepant report. Alternatively, particular moods or states of attention might be able to induce the monkeys to utilize subcortical visual mechanisms, as recently suggested by Trevarthen (16).

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