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INTERHEMISPHERIC COMMUNICATION OF VISUAL LEARNING*

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Abstract—Variable partial midline surgery on monkeys has revealed several characteristics of interhemispheric communication of visually learned pattern discriminations. The results show both that interhemispheric communication of visual information in the commissure-intact animal need not be immediate, and that when communication does occur transmission involves specific forebrain commissural components.

1. INTRODUCTION

A SERIES of three experiments was undertaken in monkeys with section of the chiasm alone or of the chiasm and various interhemispheric commissures in an attempt to better understand the basis of interhemispheric visual communication. The first experiment demonstrated a heretofore unexpected failure of immediate interocular communication for two-dimensional pattern discriminations learned through one eye in the chiasm-sectioned monkey, although such communication was obtained for subsequent visual tasks. In the second experiment partial brain bisection was carried out on the chiasm-sectioned monkeys in an attempt to define the commissural components responsible for interocular communication. Lastly, preliminary observations were made on the effects produced by temporal lobe resections on interhemispheric communication in these partially brain-bisected animals.

2. METHODS

A total of five monkeys (Macaca nemestrina) were used, each undergoing various degrees of midline surgery. In all experiments the stimulus pattern consisted of a pair of white letters or numbers on a black background projected side by side onto a pair of 3.5×4.5 cm translucent response panels that were positioned above a reward trough where peanuts were automatically delivered for correct responses. The stimulus patterns were approximately 2 cm high and were displayed at a distance of 15–16 cm from the monkey's eye. The response panel unit was rigidly mounted on the training apparatus pictured in Fig. 1, which is part of the general testing equipment developed at Caltech for use in the testing and training of split-brain monkeys. Simple adjustments allow for and make possible the separate testing of all eye–hand combinations. Wedged plexiglass head restrainers on both sides and in back of the head chamber are easily adjusted for individual

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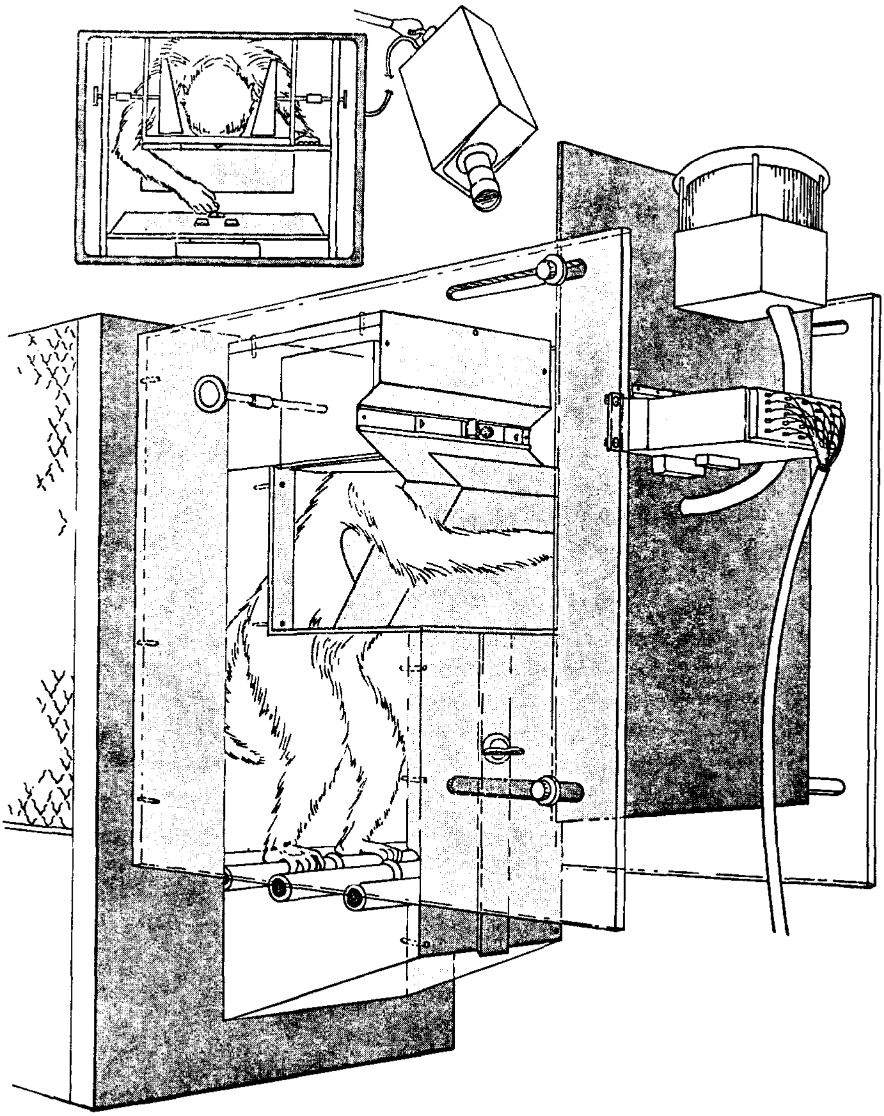

FIG. 1. Sketch of automated testing apparatus. Compartment is attached to back of monkey's home cage and various adjustments permit selective control of eye and hand use. Knobs on each side control wedged plexiglass head restrainers and are easily adjusted for each animal. TV camera allows continuous non-disruptive observation.

fit of each animal's head, thereby preventing visual exposure to the wrong eye. The right–left programming of stimuli and the recording of the monkey's responses were all carried out automatically. The entire unit was mounted on the back of the animal's home cage, thereby eliminating animal transport and handling problems. Behavior of the animal in critical test situations could be directly observed without interference by means of remote control television. Criterion was set at 90 per cent correct on 40 consecutive trials.

All animals were sacrificed and the extent of each surgical lesion was checked. The chiasm was sectioned completely in every case except BRN where some posterioventral extrafoveal fibers remained intact. These peripheral fibers, however, appeared to have been ineffectual in contributing to interocular communication of pattern discriminations. The callosum was cut to the degree shown in Fig. 2 for each animal. The temporal lobe transection in LDR was complete to the degree described and there was no histological evidence of geniculo-striate damage. In RST, the transection of the left temporal lobe left intact a few sparse connections on the medial side of the hippocampal gyrus.

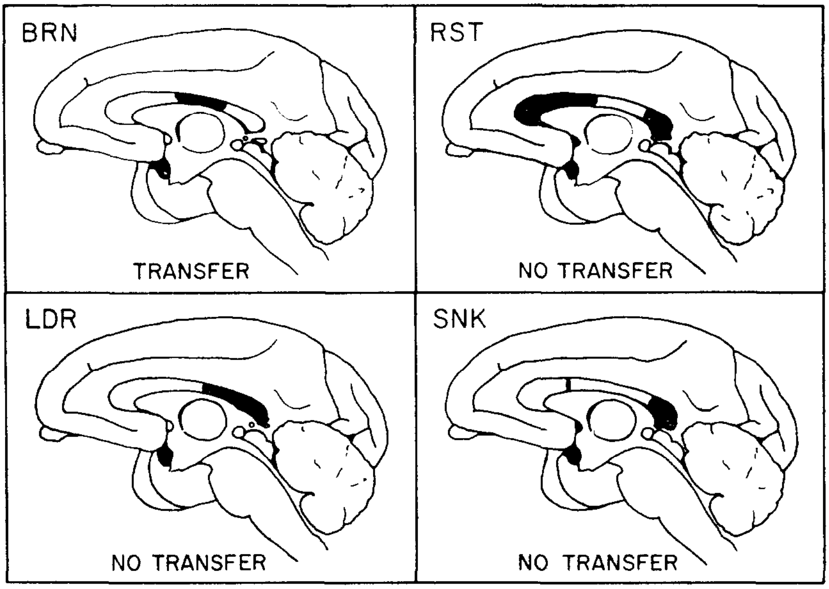

FIG. 2. Shows extent of brain bisection. See text for description of each animal.

3. RESULTS

3.1. *Experiment* 1*: Effects of chiasm-section*

Four chiasm-sectioned animals were monocularly trained on a series of visual pattern discriminations. A fifth chiasm-sectioned animal with prior visual discrimination experience of another kind and with additional surgery including the anterior commissure and anterior one-third of the callosum was also trained. On each test the animals learned the problem through one eye paired with the contralateral hand. Before shifting to the untrained eye, performance with the second hand was tested. Testing of the untrained eye was carried out with the hand contralateral to that eye. The results are shown in Table 1.

In all naive animals with chiasm-section there was failure of immediate interocular transfer on the first problem. Subsequent discriminations, however, were performed immediately with the untrained eye in SNK, while LDR, BRN and JFF showed some transfer in the form of savings. RST who had general laboratory experience on other visual discriminations that required interhemispheric integration of the two visual fields also showed good interhemispheric communication.

Different procedures were used in attempts to rule out possible interpretations of the trouble with transfer in terms of novel visual field defects imposed by surgery and to which animals must learn to adjust. For example, to insure simultaneous viewing of both

Table 1. Results of test on interocular performance capacity in chiasm-sectioned monkeys*

Animal	Stimulus	Problem	Eye 1		Eye 2	
			Hand 1	Hand 2	Hand 1	Hand 2
LDR	P/M	1	400	0	400	0
	S/2	2	280	0	960	0
	E/A	3	240	40	120†	0
BRN	2/S	1	640	120	80	0
	A/E	2	40	0	80	0
	P/M	3	80	0	0	0
JFF	L/S	1	1000	40	680	0
	M/A	2	600	40	80	0
	D/S	3	40	0	120‡	0
SNK¶	2/F	1	1440	—	600	—
	S/X	2	440	—	0	—
RST§	+/△	Gen. exp.	80	—	0	—

* Scores refer to number of trials to criterion. When testing for interocular transfer Hand 1 was always contralateral to the exposed eye. All animals performed first 40 trials at chance unless otherwise noted.

† Moments before this initial chance performance the animal scored at criterion on quick test of the preceding problem.

‡ First 40 trials were above 75 per cent level.

¶ Response panels for this animal were arranged in a vertical direction.

§ This animal also had the anterior commissure and genu of the corpus callosum sectioned in addition to the optic chiasm. Response was allowed with either hand.

discriminanda in one visual field, the response panels for SNK were placed in a vertical plane with the peanut rewards presented in a trough between the screens instead of using the horizontal screen arrangement described above. Also, LDR, before being tested with the untrained eye on the third discrimination, was allowed to work that eye at criterion on the previous discrimination. Neither of these procedures produced immediate communication.

3.2. *Experiment 2: Rôle of interhemispheric commissures*

In an attempt to directly determine the interhemispheric connections subserving interocular communication of visual discriminations, four of the animals having undergone variable section of the commissures as shown in Fig. 2 were trained and tested for interocular performance capacity on additional visual discriminations (Table 2). In RST, who showed

Table 2. Interocular communication following partial hemisphere disconnection*

Animal	Problem	Eye 1		Eye 2	
		Hand 1	Hand 2	Hand 1	Hand 2
LDR	G/M	160	240	240	80
(posterior half)					
BRN	P/M	80	0	0	0
(middle third)					
RST	G/M	160	—	200	—
(posterior fifth	S/E	120	—	160	—
anterior half and anterior commissure)	Y/R	160	—	160	—
SNK	R/L	80	—	200	—
(posterior fifth)	O/E	160	—	40	
	△/+	240		40	
SNK	G/M	120	—	120	—
(posterior fifth and	+/⌟	320	—	520	—
anterior commissure)	Ш/∩	200	—	200	—

* Scores refer to number of trials to criterion.

good interhemispheric communication with midline section of optic chiasm, anterior commissure and anterior one-half of the corpus callosum, additional section of the posterior one-fifth of the callosum completely eliminated subsequent communication on three problems. Following section of the posterior one-fifth of the callosum, SNK showed savings on the second and third interhemispheric tests, but not on the first. Subsequent section of the anterior commissure along with a slight transverse lesion in the anterior portion of the callosum, however, eliminated communication on three additional problems. LDR showed no indication of communication but was run on only one problem post-operatively. It is of interest to note that the posterior-half section of the callosum in LDR seemed sufficient to produce the impairment in ipsilateral eye–hand performance previously observed in monkeys with total cerebral commissurotomy [1]. Further experimentation along these general lines was stopped when at this time similar results were reported by Black and Myers [2].

3.3. *Experiment 3: Rôle of temporal lobe*

The functional interrelationships of the anterior commissure and posterior one-fifth of the corpus callosum in interhemispheric communication was further analyzed in two animals. LDR underwent a left unilateral temporal lobe transection. In this operation the lateral surface of the left temporal pole was exposed and a cut was made parallel to the vein of Labbé from the lateral fissure to the inferior surface of the temporal lobe. With the aid of a dissecting microscope the cut was extended down to the depths of the lateral fissure and then in a ventro-medial direction below the lateral geniculate through the medial surface of the hippocampus and hippocampal gyrus. The aim of the section was to effect a complete disconnection of temporal cortex from pre-occipital cortical structures.

Postoperative training revealed a complete and total incapacity for learning new visual discriminations on the transected side which in effect was an incapacity to perform the discrimination known by the other half-brain, thereby indicating no interhemispheric communication had occurred (Table 3). Presence of the anterior commissure in this case suggests that whatever information the anterior commissure transmits in order to enhance interhemispheric communication remains isolated and appears useless in the opposite, partially disconnected, temporal lobe.

Table 3. Visual discrimination learning with unilateral temporal lobe transection*

Animal	Problem	Eye–Hand Used	
		RELH	LERH†
LDR	Ǝ/d	600	>1200
	Λ/⅂‡	440	>2680
		LELH†	RERH
RST	L/X	680	80
		RELH	LERH†
	F/2	120	640

* Score refers to trials to criterion.
†Operated side.
‡ 6 months postoperative; at this stage also had right hemisphere frontal lesion.

After similar temporal lobe surgery RST proved able to perform visual discriminations. Performance was impaired, however, indicating again and confirming an earlier report [3] that interhemispheric integration carried out through the corpus callosum is far less efficient than intrahemispheric combinations.

4. DISCUSSION

The results indicate that the interhemispheric communication of two-dimensional visual discriminations of the type used in the present experiment is not immediate in chiasm-sectioned monkeys, but can eventually occur at a high level. Moreover, indications are that once a chiasm-sectioned animal is proficient at cross-hemisphere communication, posterior section of the callosum will temporarily abolish this communication. However, upon continued training on additional problems, surgical section of the anterior commissure is necessary to eliminate completely interhemispheric communication of this type. For example, SNK, after learning to transfer interocularly with a chiasm section, temporarily lost this ability following a posterior callosal section. Additional training, however, resulted again in good communication but further surgery involving sectioning of the anterior commissure permanently abolished all of the cross-communication.

The lack of immediate interhemispheric communication under the present test conditions of visual learning in the callosum-intact chiasm-sectioned monkey is at variance with previous reports [4, 5], using other training and testing procedures. It remains unclear whether this discrepancy reflects a general difference in the capacity of the corpus callosum for initial and later visual transfer, or whether our findings should be attributed to differences in the complexity of the visual tasks employed in the present experiment as contrasted with earlier ones. It is also possible that subtle attentional mechanisms need to be activated in order to engage the relevant central brain systems or areas for interocular performance of this kind.

The persistent and lasting inability of LDR to perform a discrimination through the left eye following transection of the left temporal lobe suggests that the potential stabilizing influence of the remaining temporal lobe is eliminated by a posterior cut in the callosum. These results are in basic agreement with an earlier report [6] and show further that a posterior half-section alone rather than total callosotomy is sufficient to cause the deficit. At the same time RST showed only the mild impairment in visual learning characteristically seen in unilateral temporal lobectomized monkeys with the callosum intact. The differing extent of callosal section between these two animals suggests that the fibers responsible for this kind of interhemispheric integration course through the posterior portion of the callosum, but perhaps anterior to the splenium.

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Résumé—Des interventions partielles et variables portant sur la ligne médiane chez des singes ont révelé plusieurs caractéristiques de communications interhémisphériques de discrimination des modèles optiquement appris. Les résultats montrent à la fois que la communication interhémisphérique de l'information visuelle chez l'animal avec commissures intactes n'a pas besoin d'être immédiate et que lorsque cette communication survient la transmission implique des composantes commissurales spécifiques du télencéphale.

Zusammenfassung—In Affenversuchen wurden an verschiedenen Stellen mittelliniennahe Hemisphärenverbindungen partiell operativ unterbrochen. Es zeigte sich dabei, dass mehrere Arten interhemisphärischer Wechselbeziehungen für die Unterscheidungsfähigkeit optisch erlernter Handlungsmodelle bestehen. Aus den Ergebnissen liessen sich zweierlei Folgerungen ziehen: einmal, dass Versuchstiere mit intakten kommissuralen Verbindungen bei Weitergabe optischer Informationen an beide Hemisphären keinen direkten Zugangsweg benötigten, und dann, dass eine kommunikative Wechselbeziehung, die auf diese Weise zustande kam, für die interhemisphärische Verbindung spezifischer Vorderhirnkommissuren bedurfte.