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Cerebral Mechanisms Involved in Ipsilateral Eye–Hand Use in Split-Brain Monkeys

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Seven chiasm-forebrain-split monkeys (*Macaca nemestrina*) were trained to perform, through one eye, a variety of visual discrimination problems by pushing with one hand the correct one of two black and white patterns presented simultaneously side by side. After learning with the first hand was completed, the other hand was tested and the extent of transfer was recorded. No transfer or savings was apparent on the average when the contralateral hand was trained first. By contrast, there was complete transfer to the contralateral hand when the ipsilateral hand was trained first. Two normal and three chiasm-split controls exhibited high-level transfer regardless of the order of the manual training. Training through one eye, paired first with one hand and then the other, in split-brain monkeys did not reduce the learning rates with the second eye. The evidence indicates that the corpus callosum is important for certain voluntary visually guided movements involving the use of a given hand across the midplane of the visual field. Eventually, control of ipsilateral extremities on a particular problem approached that of monkeys with the corpus callosum intact. It is proposed that this improvement in ipsilateral control involves ipsilateral motor participation in combination with motor regulatory mechanisms of the hemisphere contralateral to the sensory input.

Introduction

Splitting the cerebral commissures and optic chiasm in monkeys isolates a primary visual area from a primary motor area. Such surgical interruptions would, seemingly, create problems in the visual control of ipsilateral eye–hand movements. Recent investigations involving this question reveal inconsistent results. Some studies on split-brain monkeys claim little or no coordinational deficits (1, 9) while others stand in marked contrast and claim there are persistent indications of a visual-motor impairment (3, 4,

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12). Split-brain cats reportedly show no deficit in motor control of either upper forelimb when vision is restricted to one eye (11). On the other hand, recent testing of commissurotomized humans has indicated that pronounced deficits exist in ipsilateral sensory-motor combinations (5, 6, 7).

In the present study split-brain monkeys were trained visual discriminations monocularly accompanied with forced change of the hand used in response. An attempt is made to ascertain the nature and quality of ipsilateral hand performance in such testing situations.

Materials and Methods

Five female and five male monkeys (*Macaca nemestrina*) were used throughout all testing and training procedures. The animals were self-trained in an automated apparatus specifically designed and developed for the testing of split-brain monkeys. The apparatus consisted of a triangular-shaped box which permitted the experimenter to control eye and hand use and produced a minimum restriction of the visual field or arm movement or both. The unit was clamped onto the back of the monkey's home cage. The visual problems were projected onto two translucent screens by means of a one-plane projector unit. The stimuli consisted of simple geometric symbols or letters and numbers which were equalized for brightness. These patterns were automatically changed according to a predetermined pseudorandom schedule that advanced only if the animal made a correct response. The latter procedure proved to be a simple and efficient way to break position preferences that would characteristically appear during the initial training. Correct responses were rewarded with a food pellet delivered automatically in a trough immediately below the screens. Generally, the automated testing apparatus was on for 12 hours a day and the animals were free to work as often as they wished. Criterion was established at 90% correct over 80 trials. Some animals would work through the four eye–hand combinations within 24 hours of testing, while others took from 4–8 days.

For the most part, animals would be exposed to a visual problem monocularly in one of two possible eye–hand combinations. Upon reaching criterion, a change of hands was imposed until criterion was again reached. This was followed by exposing only the untrained eye and then by controlled hand use. In this manner, all intrahemispheric and interhemispheric eye–hand combinations were tested.

All operated animals have been killed and examined except for BRJ, BRN and DPK. All had a complete midline section of the optic chiasm, corpus callosum, and anterior commissure except WNL, which had some crossed extrafoveal fibers intact. Functionally the section was considered complete in WNL, however, for the animal never displayed interocular transfer of visual discriminations trained to one eye following section of the corpus callosum.

Results

No major impairments were detected in any of the animals using either ipsilateral or contralateral eye–hand combinations in reaching for food.

Independence of Hemispheres. Training one contralateral eye–hand pair

TABLE 1

Performance of Split-Brain Animals on Visual Discriminations Trained Sequentially to All Four Eye–Hand Combinations[a]

A

	First eye		Second eye	
Animal	Contra.	Ipsi.	Contra.	Ipsi.
GRT	120	560	200	840
FNR	160	40	80	720
FKY	160	160	240	1000
	Total 440		Total 520	
	Ipsi.	Contra.	Ipsi.	Contra.
SQY	320	120	200	0
FNR	760	0	560	0
FKY	1440	40	2240	0
	Total 2520		Total 3000	

B

	First eye		Second eye	
Animal	Contra.	Ipsi.	Ipsi.	Contra.
FNR	1080	520	320	40
SQY	440	360	920	80
FKY	520	1600	1040	0
	Total 2040		Total 2280	
	Ipsi.	Contra.	Contra.	Ipsi.
FNR	680	0	840	0
DPK	1160	0	1080	2240
FKY	1040	0	1080	800
	Total 2880		Total 3000	

[a] Scores refer to number of trials to criteria. Each animal was exposed to the same visual discrimination during training of its four eye–hand combinations.

in chiasm-callosum sectioned animals to criteria, followed by training the ipsilateral hand to criteria, did not appear to influence the learning rate of the second contralateral eye–hand pair (Table 1A). The same result is also evident if one compares the two ipsilateral eye–hand pairs. In the following analysis of eye–hand learning rates, therefore, the data obtained from the training of each eye will be pooled.

Training Contralateral Then Ipsilateral Eye–Hand Pairs. Forced training of contralateral eye–hand pairs to criteria does not enable the ipsilateral hand, in split-brain monkeys, to perform immediately at criteria. From Table 2 it can be seen that while there is a wide variability in performance of the homolateral hand, there is generally no trend to savings (median savings = — 33%). There is complete savings in normal and chiasm-sectioned animals.

TABLE 2

IPSILATERAL EYE–HAND PERFORMANCE FOLLOWING TRAINING OF CONTRALATERAL HAND[a]

Animal	Experience problem no.	Contra.	Ipsi.	% Savings
FGO (normal)	2	360	0	100
BRJ (chiasm)	1	400	0	100
BRN	1	640	120	81
WNL	2	480	0	100
BRN	3	80	0	100
BRN	4	40	0	100
FKY (split)	1	80	120	— 33
GRT	1	40	960	— 96
FNR	1	1080	520	52
DPK	1	1080	2240	— 50
GRT	2	120	560	— 79
GRT	2	200	840	— 76
FKY	3	160	160	0
FKY	3	240	1000	— 76
FNR	3	840	0	100
FKY	4	520	1000	— 50
FKY	5	1080	800	25
FNR	5	80	720	— 88
FNR	5	160	40	75
SQY	6	440	360	18
WNL	General experience	240	80	66
				Med. sav. — 33%

[a] Scores refer to trials to criteria. Total visual discrimination experience is also noted.

The shape of the learning curve for the ipsilateral hand, however, is not necessarily similar to that of the contralateral. From inspection of the learning curves it was clear that individual animals differed widely. For example, GRT was very poor at learning with an ipsilateral eye–hand pair and rarely rose above a chance level; SQY most always began training at a high level with her ipsilateral hand although she never performed immediately at criteria; FNR demonstrated varied ability ranging from poor to excellent.

Use of the ipsilateral hand appeared not to improve markedly after continued training with several different visual problems, if that hand's performance was compared to the contralateral hand's score on the same task. Evidence for this comes also from an animal who was manually trained on a series of visual discriminations with forced alternation of hand use every twenty trials. The testing box and procedure were similar to the one described above with eighty trials presented per day, 5 days a week. Four problems were presented to the left eye and three to the right. The percentage savings to the ipsilateral hand were — 83, — 21, 0, 0, — 65, 100, — 100, in that order. These results again suggest that a marked increase in proficiency of ipsilateral sensory-motor combinations does not occur.

Training Ipsilateral Then Contralateral Eye–Hand Pairs. Contrary to the foregoing, training ipsilateral eye–hand combinations to criterion first, enables the contralateral eye–hand pair to perform immediately at criterion in all the animals (Table 3).

Monkey GRT was totally unable to learn a visual problem using an ipsilateral eye–hand combination. Other animals, however, on the average, showed no greater difficulty learning a visual discrimination with an ipsilateral eye–hand combination than with a contralateral (Table 1B).

Discussion

The findings show a marked difference between the ipsilateral and contralateral hand with respect to performing learned visual discriminations. No savings were observed on the average for the ipsilateral hand when it was tested for transfer following training of the contralateral hand whereas transfer was complete and immediate to the contralateral hand after first training the ipsilateral hand. The results from the present study also confirm the absence of interocular transfer on learned visual discriminations even after extensive over-training with both hands through one eye.

TABLE 3

CONTRALATERAL EYE–HAND PERFORMANCE FOLLOWING TRAINING OF IPSILATERAL HAND[a]

Animal	Experience problem no.	Ipsi.	Contra.	% Savings
DPK (normal)	1	320	0	100
DPK	2	640	0	100
FGO	2	880	0	100
WNI (chiasm)	1	1400	40	97
BRJ	2	280	0	100
FNR (split)	1	320	80	88
SQY	1	600	0	100
DPK	1	1160	0	100
FNR	2	760	0	100
FNR	2	560	0	100
FKY	2	1440	40	97
FKY	2	2240	40	99
SQY	3	1200	0	100
FNR	3	680	0	100
FKY	4	1040	0	100
FKY	5	1040	0	100
SQY	6	920	80	91
SQY	7	320	120	62
SQY	7	200	0	100
WNL	General experience	360	0	100
			Med. sav.	100%

[a] See footnote, Table 2.

The discrepancies that appear to exist in the present literature regarding the existence of an ipsilateral deficit are possibly explained by considering the method of testing for the deficit. Reports that claim no visual-motor deficits result following split-brain surgery in monkeys, chose the animal's ability to retrieve food as the criterion for good ipsilateral eye-hand function. Studies containing the contrary finding, however, observed the deficit when the animals were choosing between two different visual stimuli.

Reconciliation of the question of why split-brain monkeys demonstrate an ipsilateral deficit in a learning situation but not in reaching for food remains difficult. Related phenomena have been observed in humans and it has been suggested that the presence of two objects in the visual field offers to the observer two possible responses and that these two different motor patterns are competing within the observer for action (8). An incorrect response would thereby suggest that the trigger stimulus to the motor system released the wrong motor pattern. Explanations like this might well apply in the present experiment. However, other interpretations such as viewing the results in terms of hierarchical organization are just as likely at this point and cannot be ruled out.

Absence of the same ipsilateral impairment in the chiasm-sectioned controls suggests callosal involvement in the mediation of visually guided movements when the visual stimulus and motor response are centered in opposite hemispheres. The motor deficit seen in chiasm-callosum sectioned animals is reminiscent of similar difficulties observed in human patients with callosal section (5, 6, 7). In both cases the callosum appears necessary for the successful completion of certain sensory-motor activities.

The question still remains as to whether or not the ipsilateral deficit seen in a learning situation disappears with practice. There are strong indications from the present study that the deficit does remain, but the results are not conclusive.

While it is important to emphasize this demonstrated existence of an ipsilateral eye–hand deficit, split-brain monkeys do have, or can acquire, remarkably good control with ipsilateral eye–hand combinations. It is proposed that the control involves ipsilateral motor centers working in combination with the primary contralateral motor center of the other hemisphere. Once the movement is initiated and grossly directed toward the correct goal by the ipsilateral hemisphere, successful completion is dependent on the necessary motor-proprioceptive feedback systems that go on in the hemisphere which normally controls the responding hand.

That a great deal of the movement would be dependent on the participation of these feedback systems seems true from hemispherectomy data (10, 13). Also, monkeys with bilateral ablation of the motor and premotor areas do not recover control of their extremities while ablation of the motor area alone leaves the animal with considerable mobility (2). Again, as above, the importance of ipsilateral motor centers for initiating movement is indicated.

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