Further work is in progress to explore the relationship between the carbonic anhydrase inhibition and Cs^{137} excretion.

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Double Visual Learning in Split-Brain Monkeys

Abstract. Split-brain monkeys (with forebrain divided) were trained to perform two contradictory visual tasks simultaneously, one task being presented to each eye. Usually one cerebral hemisphere dominated, but in some cases the two halves of the brain learned simultaneously. Contradictory color discriminations showed interference or transfer of learning until mid-brain commissures were also sectioned. The more extensive surgery failed to prevent transfer of simple brightness discriminations.

Recent experiments have shown that split-brain cats and rhesus monkeys, with midline section of the optic chiasm, corpus callosum, and hippocampal and anterior commissures, learn pattern discriminations presented to one eye but subsequently fail to remember them when the patterns are presented to the other eye (*1–3*). When successive monocular learning curves were compared, there was no indication that the learning with the second eye could benefit from the learning with the first eye (*4*). Animals sectioned in the optic chiasm and corpus callosum have also been found able to learn an opposite discrimination habit with the second eye without any sign of confusion or retardation of learning (*2*). They have been trained to perform two contradictory tasks concurrently by switching from eye to eye every few trials during training, and there has been no evidence of interaction between the processes of learning (*3, 5*).

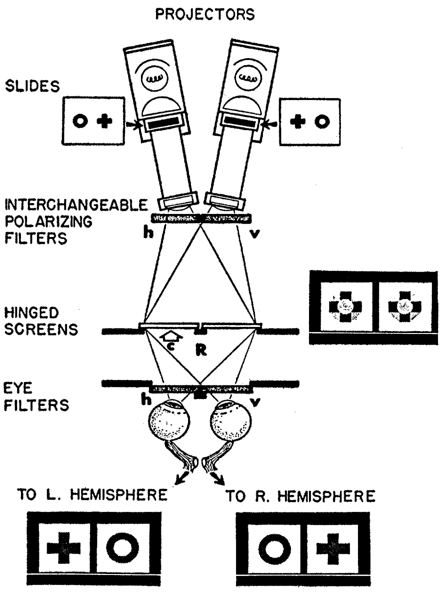

Fig. 1. Plan of the projection apparatus, with horizontal (*h*) and vertical (*v*) polarizing filters arranged to project +**o** to the left eye and **o**+ to the right eye. A correct response (*c*) to the left screen leads to automatic delivery of a reward at *R*. Diagrams of the screens as they appear without polarizing filters are shown to the right, and below they are shown as seen by left and right eyes through their respective filters. Intertrial reversal of the side of reward was accompanied by exchange of the filters in front of the projector.

The object of my study was to carry the analysis a step further. Can the concurrent learning of contradictory tasks proceed under conditions where both eyes receive the contradictory information simultaneously in each trial of training?

To test this question, a training apparatus was designed in which plane-polarized light and polarizing filters were used for the separation of stimuli to the two eyes. This apparatus, and the method of its use, are diagrammed in Fig. 1. Of the two pairs of patterns, one was polarized vertically, the other horizontally, and one pattern of each pair was rewarded consistently for a given eye throughout training, the rewarded figure for one eye being always the reverse of that for the other eye. The subject was trained to place its head in position at the sound of an alerting tone, and to respond by pushing one of the stimulus-bearing screens by hand.

Learning was allowed to proceed with both eyes open until a reliable criterion of learning (*6*) had been attained; then each eye was tested separately. When the performance with one eye did not show complete retention, training was continued with this eye alone until the criterion of learning was again satisfied.

Two subjects, with optic chiasm, corpus callosum, and anterior and hippocampal commissures cut (*7*), showed double learning, as in Fig. 2*A*, when presented with a black circle and a black cross equated for brightness. Both eyes retained knowledge of the discriminations as if there had been simultaneous learning of the contradictory choices. Moreover, as training proceeded, there was no sign of interference between rival learning processes. A normal control, in contrast, would not attend and showed signs of extreme frustration when confronted with the two overlapping pairs of stimuli after being trained to choose with reference to only one of them.

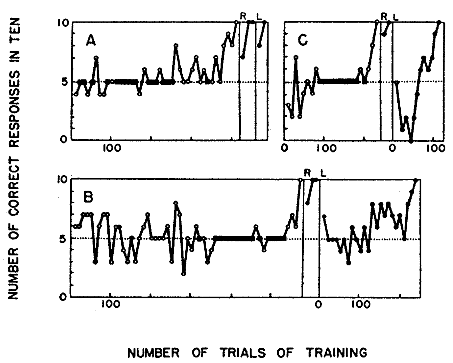

Fig. 2. Sample learning curves for three different tasks. *A*, Simultaneous learning of contradictory "circle vs. plus" discriminations by the two eyes. *B*, Monocular learning of another task, and interference of performance with the other eye. *C*, Monocular learning and interocular transfer of learning with contradictory brightness discriminations. Each hollow circle (binocular learning) or solid circle (monocular tests) represents ten trials. R = right eye test, L = left eye test. Position habits by which all ten trials of a group were made to one response screen, are shown by black horizontal bars.

However, in 12 out of 14 tasks given these animals the retention was not equal in the two halves of the brain. In these instances one eye learned ahead of the other, as if the latter had been somewhat inattentive during binocular training, even though it was open and directed to the screens in each trial. An example of this asymmetric performance is shown in Fig. 2*B*, which gives the learning of contradictory choices between two complex colored figures. In a series of nine pattern-discrimination tasks there appeared to be no simple correlation between the nature of the patterns and the restriction of learning to one eye, although variations in the learning were closely similar in the two subjects.

An expected preference for the use of eye and hand connected with the same hemisphere appeared with the asymmetric learning. As a rule, it was the eye contralateral to the limb chosen for response which was superior. Furthermore, when vision was subsequently restricted to the unpreferred eye, there often resulted, after 10 to 20 trials, a spontaneous exchange of hands. Nevertheless, preferences for using motor and visual areas of the same hemisphere were not invariable. An eye and a hand of the same side would occasionally be chosen for execution of previously learned responses, or for new learning.

Both subjects showed interference effects indicating transfer of learning when they were working on tasks which involved recognition of color or brightness differences. Figure 2*C* shows the case of a brightness-discrimination test in which there was good retention with the right eye. The significantly-below-chance performance with the left eye indicates interference on this side from the learning on the right side. Training with the left eye alone led to reversal of the transferred habit in 100 trials. Closely similar results were obtained with the second monkey on the same brightness discrimination task. These findings are in accord with the recent report of Meikle and Sechzer on the transfer of easy brightness discriminations with cats sectioned in the optic chiasm and corpus callosum (*8*). They are also to be compared with the survival of a simple visual conditioned response, after extensive midline surgery, reported by Voneida and Sperry (*9*).

Both these subjects also showed definite transfer of a blue-orange discrimination, although they failed to show transfer when they were subsequently trained to comparable color discriminations.

Further tests with an additional two monkeys, in which the posterior commissure, habenular commissure, and rostral two-thirds of the quadrigeminal plate had been sectioned (*7*), failed to show transfer of this same color discrimination learning. Tests for brightness-discrimination transfer in the two latter cases revealed, first, a seeming impairment in the ability to learn this task, and later, a pronounced but transitory transfer effect in spite of the more extensive surgery.

The occurrence of simultaneous learning in these experiments suggests that two relatively independent perceiving and attending processes can be sustained simultaneously in the separated hemispheres of the split-brain monkey. The alternative possibility, that this double visual learning depends upon a rapid switching of attention from eye to eye during the binocular training, suggests that further tests, with tachistoscopic presentation of stimuli, should be made. In cases where unequal learning occurs, some central processes, possibly associated with the selection of the mechanism of response, may confine the learning to one visual system (*10*).

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6. A criterion was set at the $p = 0.002$ level. This is satisfied if all trials in a group of ten are chosen correctly, or if two successive groups of ten trials contain but one error each.
7. Postmortem examination of the brains of two subjects, one with forebrain commissures sectioned and the other with the midbrain connections cut in addition, showed that surgery was complete. The two remaining cases have been kept for further experimental work.
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10. This report is a condensation of part of my doctoral dissertation for California Institute of Technology. Financial support was received from a National Science Foundation grant, G-3438, and from the Arthur McCallum Fund of California Institute of Technology. Dr. Harbans L. Arora performed all the surgery.

14 November 1961

Early Experience and Sexual Behavior in the Domestic Chicken

Abstract. Newly hatched chickens were imprinted to one of two moving objects. From the fifth day of life on, the chickens were injected with male sex hormone. When later presented with a choice between the two objects, they addressed induced sexual responses to the object to which they were imprinted.

By manipulating the environment of a bird, it is possible to cause it to respond to biologically inappropriate objects (*1*). Manipulations have always included exposure of the bird to the object during very early life (for nidifugous birds during the critical period for following), as well as prolonged contact with the object during adolescence. It has not, therefore, been possible to determine whether the relevant learning takes place during a particular period of the bird's life or whether the learning is dependent merely on length of contact with the object. It has not been demonstrated that either imprinting on an artificial model or lack of experience of their own species during the critical period will produce abnormal fixations or prevent normal sexual development (*2*).

My experiment was designed to compare induced sexual behavior of birds imprinted within the critical period with that of birds given the same treatment outside the critical period.

Male chickens were placed in individual 3-by-1½-by-2-foot boxes containing a light, food and water trays, a gauze-covered one-way observation panel, and a rotating arm which carried a suspended model around a circle 14 inches in diameter. The chicks were placed in the boxes as soon as they had dried in the incubator (approximately 12 to 18 hours after hatching) and remained in the boxes except for daily removal for an intramuscular injection of 0.5 mg testosterone propionate (*3*) in 0.1 ml sesame oil from the fifth day of life on. The model was half a cellulose toilet float, 4½ by 1½ inches, painted blue or yellow. The model traveled for ½ minute, was still for 2 minutes, then moved for ½ minute, and so on. Lights were on for 10 hours a day, during which time the model, if present, traveled according to schedule.

Each chick was observed for four periods of 1½ minutes at 2-hour intervals each day; observation periods were scheduled so that the model moved during the middle of the period. Every 10 seconds a bird's position was scored as less than or more than 4 inches from the model, giving a total of 40 records per bird per day. Thus a bird which was within 4 inches of the model at each observation would score 40 for that day.

On days 19 and 20 both the yellow and the blue models were placed in the box 1 foot apart, the chick's sexual behavior was observed for 10 minutes, and then the models were removed. An estimate was made of the number and direction of treads during each minute of observation.

Three experiments were run, the first

Table 1. Following and treading scores of different groups of chicks exposed to a model during the critical period for imprinting (group 1), after the critical period (group 2), or during both periods (group 3).

Group	No. of birds trained on		Model in box on days	Following scores		No. of birds treading training model
	Yellow model	Blue model		Mean	Range	
Group 1	5	6	2– 9	28.0	24.0–34.0	9
Group 2	5	5	10–17	4.5	0.1–13.1	1
Group 3	6	6	2–17	25.7	19.8–31.5	9