

STUDIES ON VISUAL LEARNING  
IN SPLIT-BRAIN MONKEYS

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Frontispiece. Subject BRS.



## ABSTRACT

The unity of perception and its divisibility were examined by a method of double learning. Polarized light and polarizing filters were used to present monkeys with two contradictory visual tasks simultaneously, one visible to each eye. Subjects were trained after surgical division of the visual pathways at the optic chiasm, and after the cerebral cortices were separated by cutting the corpus callosum. The distribution of learning between the two halves of the brain gave information about the location of visual learning, and about the relationship between visual attention and the intention to respond with a particular limb. Two subjects learned conflicting tasks simultaneously. In many tests, however, there remained some interaction between the two halves of the brain. This led to selective learning by one eye, the other eye remaining unretentive though it was open throughout training. In tasks involving brightness and color discriminations, there was significant interocular transfer of learning in spite of the surgery. It is concluded that the two surgically separated cerebral hemispheres may function independently in memorizing a visual pattern, but that there are also avenues for their communication. The motor system remains coordinated after split-brain surgery, although there is a tendency for preferential pairing of eye and hand of opposite sides of the body after surgery. Some visual tasks were found to involve interhemispheric processes to a higher degree than others. Visual recognition of comparative size, requiring interocular comparison, was found to survive chiasm and callosum section.

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## CHAPTER I

### INTRODUCTION

In the mid 19th century an English physician named David Ferrier became interested in the effects of stimulation and ablation of the surface of the brain. He applied small electric shocks from an induction coil to points on the brain of a lightly anesthetized monkey and he noted responses in various parts of the body (1). The movements were unlike the reflex twitches or spasms which could even be obtained from an isolated spinal cord, and more elaborate than the movements following cortical stimulation which had been reported a few years before in the now classical paper of Fritsch and Hitzig (2); they were more like "bits of motor acts." For the first time a function of higher order, a fragment of voluntary behavior, had been located in one part of the cerebral cortex.

An era of "localizing" following this discovery. Maps were drawn up showing the distribution over the cortex of newly discovered areas for each of the senses of sight, hearing, smell and touch (3). Some believed that complex functions of intelligence were performed wholly among the cells of particular cortical regions. It became generally accepted that transcortical association was responsible for elaboration of perceptions and for sensory control of skillful movements. But attempts to locate these special mechanisms or to disrupt the associative links between them by

injury to chosen parts of the cerebral cortex failed again and again. At the end of the century the higher functions of intelligence, of "mind" in the sense of Charles Sherrington, remained as mysterious and elusive as ever (4,5).

Modern neurophysiology has probed deep into the brain and found signs of complex partnership between brain-stem and cortex. The latter can no longer be regarded as an autonomous seat of intelligence in which perceptions are formed and where skillful acts become directed according to learned associations. Massed nerve cells in the deep parts of the cerebral hemispheres and in the core of the brain-stem receive information from all parts of the central nervous system including the cortex. They have been shown to regulate the activity of cortical neurones, and to modulate the passage of information centralwards in sensory pathways (6,7).

Electrodes have been fixed to lie on the surface of the cortex or implanted deep inside the brains of fully alert subjects--animals performing psychological tests, or human beings answering questions and reporting their experiences. The results have indicated that learning involves the projection areas of the cortex in intimate reciprocal association with brain-stem circuits. Penfield has conceived a "centrencephalic integrating system" outside the cortex to help explain the stimulated episodes of recall or sensation reported by his human subjects, and to account for the effects of epilepsy (8).

But in general the electrophysiological results, either the recorded patterns of activity in single or massed neurones, or the effects of artificial electrical stimulation, have not been easily equated to normal functioning. The experiments which test for losses resulting from lesions to nervous tissue are at a disadvantage because of the bilateral symmetry of the brain. For almost every part lost or damaged there is a duplicate, mirror-image part ready to stand in its place. Valuable information has been obtained by carefully doubling the lesions so that both lateral halves of a chosen system are equally involved. But there are often doubts about the extent of removal. An ever-present difficulty concerns the capacity of the brain to compensate for injuries. This has continually confounded surgical analysis of intelligence.

Recently a new approach has opened a wealth of possibilities for surgical analysis of complex behavior (9); an approach that turns the doubleness of the brain to advantage. In this technique the two halves of the brain are split apart by surgical cutting of communications between them, and then psychological tests are applied to explore the partially isolated mechanisms of the two halves. In this way relationships between the cortex and lower centers, and the adaptive adjustment of brain processes can be studied closely.

Studies of split-brain subjects made in the past 5 or 6 years have shown that perceptual learning of complex discriminations in vision or touch may be kept in one half of the brain containing a cortical projection area while the other half remains in ignorance. But it has also been found that the brain stem contains a coordinated mechanism of response which is able to couple with a perceptual recognition process initiated in either cerebral hemisphere.

Of the commissural fibers which connect the two cerebral hemispheres of higher mammals, the greater number by far are aggregated in a massive bridge called the corpus callosum (10). It has been estimated that there are  $10^6$  nerve fibers in the corpus callosum of man (11). But, surgical section or congenital lack of this bridge has been found to result in remarkably slight defect in visual, somesthetic or motor coordinations of animal or human subjects.

The most extensive studies of human subjects have been made by Akeleitidis and Smith on cases which had received partial or complete section of the corpus callosum in the hopes of preventing spread of epileptic seizures from one half of the brain to the other. They have made tests of motor functions, of visual and tactile recognition of objects, letters and words, of the extent of the visual field, binocular depth perception and continuity of the combined visual fields of the two eyes, and of mirror-drawing and

stylus-maze learning (12-23). These and other studies have yielded results which are almost entirely negative (24). The only dependable indications of postoperative effects of callosum section have been occasional exaggeration of motor disabilities which were already present before surgery, and some exceptional reports of inability to recognize letters by their feel in the subordinate hand (25), or their appearance in the subordinate half-field (26,27). It is possible that such effects have always been due to injury to one hemisphere, rather than to dissociation of the subordinate from the dominant hemisphere. In an extensive recent review of experimental and clinical data concerning the functions of the corpus callosum Bremer, Brihaye and Andre-Balisaux (24) have weighed the reliable evidence and concluded that the callosum has no important role in perceptual integration and determination of motor skills, even in man where the dominance of one hemisphere would seem to make the integration via this commissure particularly imperative.

In the course of an investigation of the role of the corpus callosum in the interocular transfer of learning in the cat, Myers achieved the combined separation of sensory input pathways and interhemispheric commissures which results in a split-brain preparation (28-31).

Optic fibers from a portion of each retina cross to the other side of the brain and form the optic chiasm. Myers exposed the chiasm by drilling a small hole through



the roof of the mouth and through this hole he made a midline incision cutting all the crossed fibers (31). When cats with both chiasm and callosum cut were subjected to psychological tests of learning and retention through one eye at a time, it was found that all but the most difficult tasks would transfer substantially from one eye to the other, provided the posterior segment of the corpus callosum was left intact (32). This transfer of learning was immediately abolished when the posterior 1/3 of the callosum was cut (31,33).

Further experiments have rigorously tested the isolation of learning which follows combined chiasm and callosum section. Sperry, Stamm and Miner compared successive, completed learning of a single task by the two eyes and found no sign of savings in the second learning (34). Their cats did not even show a capacity to attend to the critical visual cues more efficiently when using the second trained eye. They simply learned the problem over again, did so in the same general way so that the two learning curves for each subject were remarkably alike. All the results supported the conclusion that two separate and rather equal visual learning mechanisms were produced in the brain of each operated cat.

Normal transfer of learning over the corpus callosum was shown by Myers and Sperry to result in the establishment

of a new engram in, or through mediation of, the untrained half of the brain (35,36). When the visual cortex of the trained hemisphere was removed, some process of reduplication of the engram in the other hemisphere allowed retention by the untrained eye, and the same retention of a transferred learning was found after the corpus callosum was cut between the hemispheres (37).

After chiasm and callosum section, cats appear to move with normal coordination and exhibit no confusion or other outward sign of the separated brain processes. The only easily detected loss is the expected slight lateral visual field defect due to loss of the crossing fibers (31). The indications are that the visual processes themselves are isolated somewhere in the parts of the two hemispheres which communicate through the posterior corpus callosum, and that processes determining motor functions, with which they are to be linked, remain distributed in both halves of the brain.

The cats of the above tests were trained with one or other eye covered by a rubber face-mask. They were trained to push open hinged doors, on which the visual cues were mounted, to obtain a morsel of food (29,31,38). The forward pushes with forehead or nose were roughly symmetric with respect to the axis of the body, and presumably both halves of the brain were involved. An equivalence of unilateral motor functions, which might be expected

to originate in one-half of the brain was reported for visual learning by Schrier and Sperry (39). They demonstrated that the chiasm-callosum sectioned cat could work with either paw when vision was restricted to one eye by a face-mask. Alternate forced periods of work with left and right paw allowed learning of both combinations with a given eye to proceed side by side. No superiority of learning by particular eye-hand pairs was observed. From this we may conclude that, while visual learning by one eye is contained within one hemisphere after chiasm and callosum section, the motor system necessary for controlled movements of the forelimbs is represented in, or connected with, both hemispheres.

Studies of the sensory processes and their elaboration, of perception and recall of meaning, have employed the split-brain in attempts to locate essential regions where learning and recall occur in each hemisphere. Extensive ablations may be performed in one half-brain without incapacitating the animal.

It has been possible to pare away cortical tissue and in this way to locate a center for analysis of touch sensations. Stamm and Sperry have shown that callosum-sectioned cats no longer show the normal intermanual transfer of learned differences in shape or texture of pedals pushed by the fore limbs without visual observation (40). Sperry then demonstrated that there was a relatively small

region in each hemisphere which is necessary and sufficient for tactile discrimination learning and retention by the forelimb of the other side of the body (41).

This limitation of the essential sensory analysis to a small piece of cortex receiving projection fibers has not been possible, however, in the case of visual learning. Sperry, Myers and Schrier (42) found that monocular deficits in visual coordination and retention followed removal of nonvisual cortex on one side of the chiasm-sectioned cats. The losses were more pronounced after subsequent sectioning of the corpus callosum. Two-, and three-stage removals of cortex revealed that both parietal and frontal regions were involved in visual processes. Gradual recovery of simpler visual functions occurred over many weeks of observation and some of the tasks which had been trained before surgery recovered; particularly simpler tasks which were learned more quickly by normal subjects. The cats were described as suffering impairment of the visual perceptual process itself rather than its motor expression.

The eye which is connected to the isolated visual projection area on one side of the split-brain may still be used alone for reflex placing reactions (42) and for withdrawal reflexes conditioned to a flashing light (43). These eye-limb coordinations have been found to survive even when the eye is used in combination with the limb that receives cortical innervation from the motor area of

the other, intact cerebral hemisphere. Some kind of inter-hemispheric coupling at sub-callosal levels may account for these results.

This possibility has been tested by making reciprocal ablations in the two hemispheres. Myers, Sperry and Miner have found that eye-paw coordinations survived removal of the frontal cortex with all of somatic areas I and II from one hemisphere, plus removal of the entire temporal, occipital and posterior parietal areas from the other hemisphere in cats with total section of the corpus callosum, optic chiasm, anterior and hippocampal commissures (41).

When interpreting this experiment it is necessary to remember that bilateral anterior ablations lead to paralysis and paresthesia of the limbs, and that animals with bilateral posterior ablations which include all of the occipital area make only the simplest visual discriminations, such as of brightness differences or of the movement of striped patterns. Further data on interhemispheric integrations, obtained with monkeys, is discussed below.

Experiments with split-brain monkeys have, to a large extent, replicated the various results obtained with cats (9). However, there are differences, particularly concerning the elaboration of the response, and there are indications that callosal communication is more efficient in the more highly evolved organism.

Dissociation of visual learning in the two hemispheres following chiasm and callosum section has been reported in brief communications from two laboratories. Sperry has described efficient interhemispheric communication of visual learning, involving brightness, size, color, 3-D shape and flat-pattern discriminations, after section of the chiasm, anterior commissure and anterior half of the corpus callosum. This transfer was abolished by subsequent cutting of the remaining part of the corpus callosum (44). Downer has found absence of interhemispheric communication for pattern and color discriminations after section of the chiasm and corpus callosum (45). In both cases the subjects were required to choose between small, visually distinct objects and to displace one of them by hand in order to obtain a food reward.

Downer claims that color discriminations were laid down on both sides when learned through one eye after chiasm section, as long as the callosum remained intact. Pattern discriminations on the other hand were said to be more often than not restricted to the side receiving sensory information by direct thalamic projection (45). However, in other studies cats have been found to transfer pattern discrimination learning across the corpus callosum (32), and the writer has observed efficient transfer of pattern discrimination learning in a monkey with approximately four square millimeters of the posterior corpus callosum intact.

Sperry trained opposing discriminations concurrently to the two eyes of split-brain monkeys and found no signs of interference. He observed that even temperamental effects (sulking) with a particular problem could be coupled exclusively to one eye and the half-brain functioning with it (44).

In a study of intermanual somesthetic transfer in split-brain monkeys, Glickstein and Sperry reaffirmed an earlier observation (44) that, though transfer was frequently blocked by callosum section, it could occur; and they discovered, furthermore, that transfer in one direction could be aided by unilateral damage to one somatic cortical area (46). This latter effect arose presumably because learning was forced to occur predominantly on the undamaged side, even when the ipsilateral hand (the one most affected by surgery) was in use. Glickstein and Sperry have drawn attention to the fact that general motor habits, including exploratory comparison of the stimuli, transferred to the untrained limb after callosum section, even in those cases when learning of the correct choice between critical tactile cues failed to be transferred. Transfer of somesthetic learning may be explained as due to the presence of uncrossed somesthetic sensory fibers which allow both limbs to have representation in each hemisphere.

An apparent conflict of interpretation has appeared in the reports to date of the relationship between the

processes of visual perception and regulation of limb movements in split-brain monkeys. Downer has reported a very strong tendency for spontaneous choice of the contralateral hand when vision is restricted to one eye (47). In most of his cases, 90-100% of voluntary moves made over tests of 300 to 700 trials in length were made with the right hand when the left eye was in use, and vice versa. Changes of limb use followed rapidly upon the change of vision from one eye to the other. In the few cases where an ipsilateral combination of eye and hand were used for a few trials, a preference for use of the same hand had already been clear when both eyes were open or before callosum section. Ipsilateral hand movements were described as "clumsy and awkward with much pawing and groping," and the impression was gained that the movements following an initial orientation to the response situation were "as if blind."

Tests with artificial restraint of one limb at a time revealed that ipsilateral combinations could become effective in performing the tasks on visual cues (47). After long training the movements became "surer, swifter and much less fumbling," in all cases, but the proficiency always fell behind that for the other eye. This slow improvement was found to be similar to that seen in recovery of function following ablation of the precentral (motor) gyrus of the cerebral cortex.



Sperry has reported that the monkey will use either hand to perform visual discriminations, even though the visual input is restricted to one side. One case has been described in which, after removal of the arm area from the right side of the cerebrum and recovery of function of the left limb, the left eye and hand could be used together for good performance (48).

Perhaps the discrepancy shown by the two reports is a reflection of differences in technique. Specifically, attention may be drawn to the very different methods employed for restricting vision. Downer approximated the two trimmed eye-lids together with surgical thread and allowed them to remain continuously closed together for periods of some weeks. His subjects were therefore forced to use monocular vision with a particular eye continuously for this length of time. Sperry's experiments were performed with restriction of vision only at the time of viewing of the stimuli. The subjects were free to use both eyes, except during each trial when they voluntarily placed the head behind a single eye-hole and peered out at the otherwise invisible response situation and visual cues (9).

The question of sensory-sensory association which is fundamental to understanding of mechanisms of perception and stimulus recognition has been approached by training monkeys tasks which require combined discrimination of visual and somesthetic differences so that the decision in one modality

is "conditional" on the stimulation of the other. The correct choice of an object to be moved by hand must be made in these tests on the basis of both feel and appearance of the object (48,9).

Monkeys, first trained with the right eye and left hand, learned the same task with left eye and right hand without any sign of transfer of learning. However, once this second training was completed both ipsilateral eye-and-hand combinations performed with high level of retention and only a little hesitancy during the first several trials.

When the somesthetic area was removed from one hemisphere, it was found that visuo-somesthetic discriminations were retained for the unaffected limb working in combination with either eye. The ipsilateral combination of eye and limb, requiring linking of function between the hemispheres, reached criterion within 50 trials. Six weeks after the ablation, as soon as the hand contralateral to the lesion was recovered sufficiently for tests to be performed with it, retention was found to be complete with either eye, but only after a preliminary fluctuating performance for the first 3 days with the ipsilateral combination (48).

We have reported above the survival of visuo-motor coordinations following reciprocal lesions in the two hemispheres of split-brain cats, and pointed out that this result suggests an interhemispheric integration through the brain stem. There seems to be no other way to account for

the present results in which there is modification by visual processes contained in one hemisphere of processes thought to be confined to the other hemisphere by callosum section.

The degree to which the cerebral hemispheres may interact or cooperate in learning after the corpus callosum has been sectioned is still uncertain. Most of the tests of learning have indicated that sensory processes are isolated. Contradictory discriminations have been used to test the independence of the two halves of a split-brain during learning. Myers trained cats conflicting visual pattern discrimination tasks in seriatim (29-31), and Sperry trained monkeys to learn such tasks concurrently; with 5 or 10 trials to one eye, then as many to the other eye, and so on, alternately (44,48). The same has been done with the two paws on reverse tactile discrimination problems (40,46). In no case was evidence of confusion or frustration observable in the behavior of the subjects.

Myers has shown that normal transfer through the corpus callosum may be suppressed by presentation of conflicting stimuli to the two hemispheres. Subjects trained with the chiasm sectioned, but with the callosum intact showed transfer of the general nature of a problem through the callosum, and suppression of callosal communication when two problems, different in detail and contradictory in general features, were trained with alternation between the two eyes (49). Myers has concluded that transfer of

information through the corpus callosum is continued, but is without effect at times when there is competition from information arriving directly through the geniculo-striate projection.

The present study was designed to obtain further information about the distribution of visual learning and, at the same time, to investigate the mechanism of eye-hand coordination in split-brain monkeys. The independence of visual learning in the two hemispheres after chiasm and callosum were sectioned was tested by presenting two contradictory tasks simultaneously, one to each eye. These tasks required perception of differences between paired visual stimuli and both tasks converged upon a single response situation in which either hand could be used for obtaining a reward.

The studies of Sperry and Myers have shown that contradictory discriminations may be learned and retained in the two halves of the split-brain regardless of the form of the response. But contradictory discriminations may be learned and retained by normal monkeys, provided there is some opportunity for the subject to switch his set for the interpretation of the stimuli one way or the other. It seems possible that in the case of the tests with split-brain animals the alternations of monocular training or testing periods, however brief, might provide cues which would allow the processes of recognition for the opposing

discriminations to be kept apart. On the other hand, if the perception processes for the two eyes are completely separated in the split-brain, it might be possible for two conflicting engrams to be acquired simultaneously.

It was planned to test this possibility directly; to follow the course of learning in both halves of the split-brain by measuring the retention by each eye as soon as a dependable criterion of learning with both eyes at once had been attained. A variety of visual tasks were chosen in an attempt to test the further possibility that some tasks would be more subject to interhemispheric mixing than others.

It was immediately noted that any disbalance of learning between the two halves of the brain could be correlated with the development of a habit for use of one particular limb. Thenceforth, careful record was kept of the use of the two hands in performance of responses and, in addition, tests were made with forced modification of habits which had become established freely.

Cases of simultaneous learning of two contradictory problems were observed, but gradually it became clear that the method could yield information about factors of learning which might lead one eye to ascendancy over the other. Finally, observations were being made in an attempt to understand the dynamics of the attention processes which

underly the learning, and to determine the way in which the visual choice arises in conjunction with an intention to move a certain way.

## CHAPTER II

### METHODS

#### General Methods

Monkeys were trained to push by hand on one of two small plastic screens placed side by side, and to make their choice of movement on the basis of simple differences between visual stimuli projected onto the screens.

Most subjects were trained after "split-brain" surgery. Nerve fibers which cross over from each eye to the other side of the brain were cut at the chiasm, and direct communication between visual areas of the cerebral cortices were eliminated by cutting of the corpus callosum and other commissures of the forebrain. Visual structures of the brain stem below the cerebral hemispheres were also separated in cases where additional surgery was performed to midbrain commissures.

The two parallel visual systems of the split-brain subjects were presented with different visual tasks simultaneously as a test of their independence during learning. This was accomplished by use of polarized visual stimuli viewed by the subject through polarizing filters.

While overlapping polarizers allow only a minute amount of light to pass when their polarization planes are crossed at right angles, filters of like orientation transmit light with slight loss. Differing pairs of stimuli,

polarized at right angles to one another, were superimposed upon the pair of plastic screens, and individual eye-windows of polarizing material, also oriented at right angles, caused each pair of stimuli to be visible to a different eye. In this way the split-brain subjects were presented with two visual discrimination tasks converging upon a single response.

In most of the experiments to be described, the two visual tasks presented at one time were mutually contradictory. In consequence, any common brain process associated with the recognition of the stimuli, and receiving component information from both retinas, would be annulled. When working on a trial the subject looked out with both eyes upon a simplified visual field consisting of a black surface in front of the eyes, a shallow metal shelf just below the level of the eyes, and above the shelf, set in the black surface, two squares of white plastic illuminated from behind. To this field seen equally by both eyes were added the differential pairs of polarized cues (see fig. 4).

When a particular task was presented for the first time, both eyes of the subject were left free to receive their respective stimuli, and both hands were free for responses. Training was continued in this way until a criterion of statistically significant learning had been achieved; then the distribution of visual learning processes between the two halves of the brain could be found by testing performance with each eye alone. If one eye was found



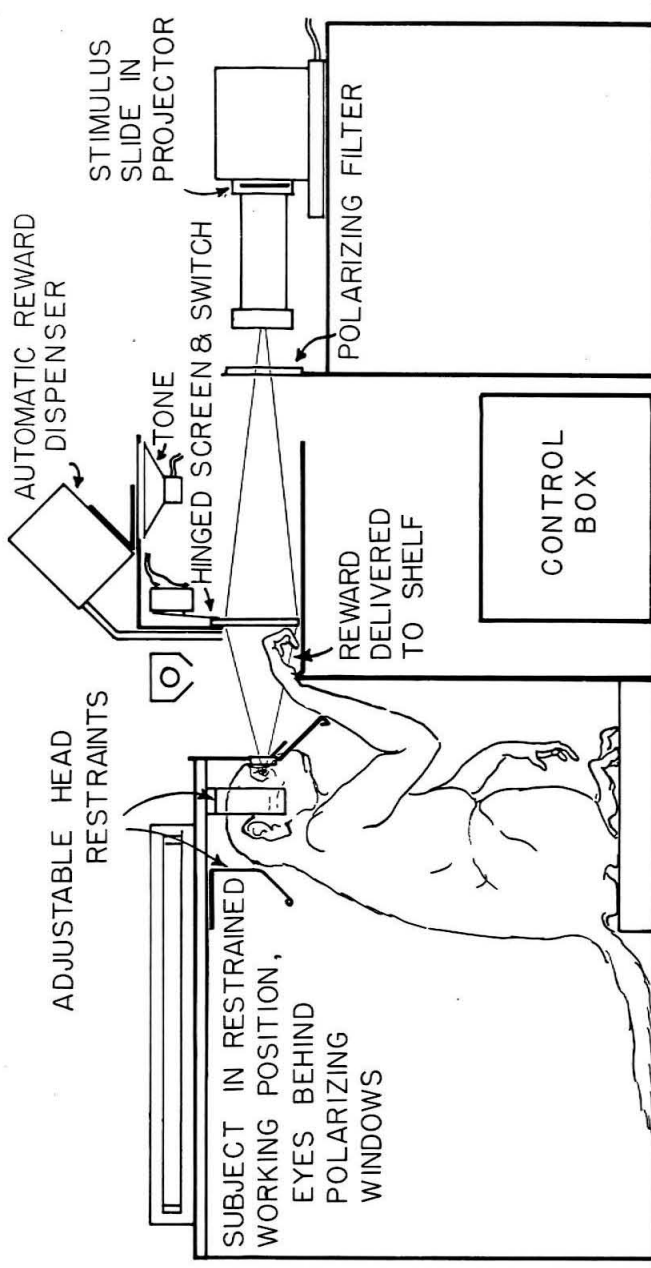


FIG. 1 - TRAINING BOX AND APPARATUS FOR PROJECTING POLARIZED STIMULI.

to have poor retention of the task to which it had already been exposed during binocular training, this eye was further trained alone until learning was complete. Finally, the effect of forced use of combinations of eye and hand other than those chosen voluntarily by the subject was studied, all combinations being eventually trained to criterion.

The performance during training was recorded as sequences of movements, each made by a particular hand to a particular response screen and scored as correct or incorrect.

Notes were made of the eagerness with which the response was made, the hesitancy of the subject in choosing a response, any ineffective gestures made by either hand to the screens, and the reaction by the subject to success or failure when this reaction was particularly emotional. A one-way glass window in the side of the training box made it possible to observe all movements of the subject closely.

### Apparatus

The aim of providing simultaneous, but different, stimulation of the eyes required that the subjects were to be trained in a box which limited their access to the visual stimuli. For this purpose they were made accustomed to working with the head placed in a fixed position, and only in this voluntarily assumed position could they see the stimuli, gain visual control of responses, or obtain reward. (See fig. 1.)

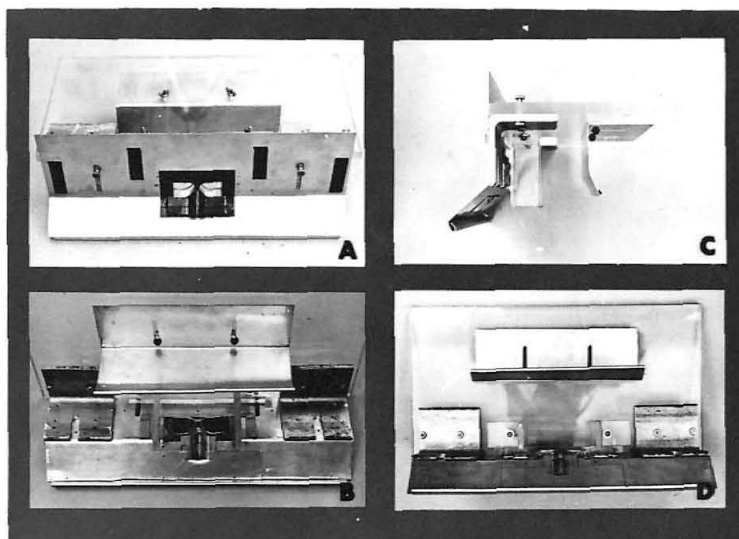


FIG. 2 - FRONT OF TRAINING BOX TO SHOW EYE-HOLES  
AND HEAD-RESTRAINTS

A- FROM IN FRONT  
B- FROM BEHIND

C- FROM THE SIDE  
D- FROM DIRECTLY BELOW

When looking at the stimuli, as in figure 1, the subject was placed with each eye 5 mm. behind a small spectacle-like window (see figs. 2,3). In this way the paths of vision of the two eyes were separated. Stimuli mounted as standard 2" x 2" slides were back-projected onto two white plastic screens at 5-6" directly in front of the eyes, and easily visible to both of them. Without moving from position, the subject could reach through a horizontal space to push one or the other screen, and, if the correct side had been chosen, a switch behind the screen caused delivery of a peanut onto a shelf in front of the screens. A small partition between the screens prevented double pushing by a hand aimed at both screens.

Simultaneous presentation of different stimuli to the eyes was made possible by polarization of the light between the projectors and the screens. Polarizing material mounted in thin plastic sheet in front of the projectors polarized the stimulus figures before they were focussed on the screens. The latter were made of an opal plastic, 1/16" thick, chosen for minimum depolarization of the light pattern.\* A second pair of polarizing filters, one in front of each eye, allowed control of vision. If the planes of polarization of a projector-filter and of an eye-filter were parallel, a slight reduction in intensity of the projected image occurred, but it remained plainly visible.

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\* See p. 29 .

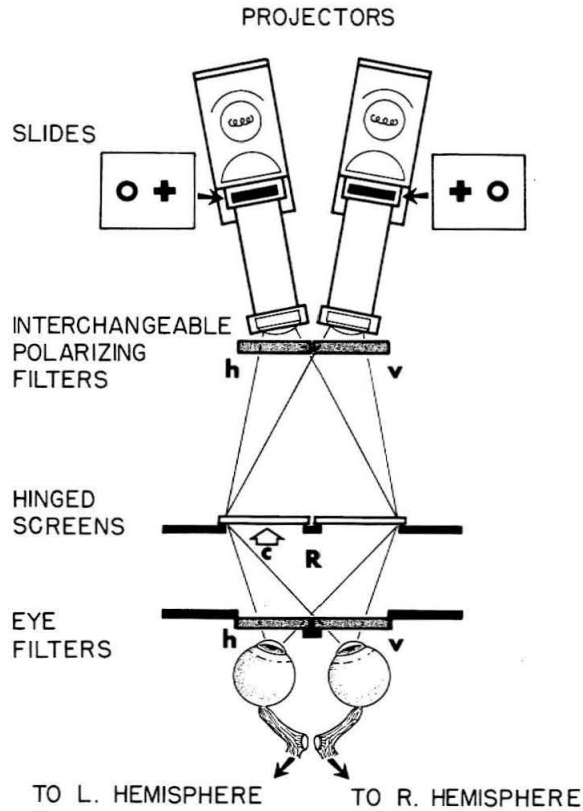


FIG. 3 - PLAN OF PROJECTION APPARATUS.

**h** & **v** HORIZONTAL & VERTICAL POLARIZING FILTERS  
 STIMULI PROJECTED AS IN FIGURE 4  
 CORRECT PUSH MARKED **c** REWARD DELIVERED AT **R**

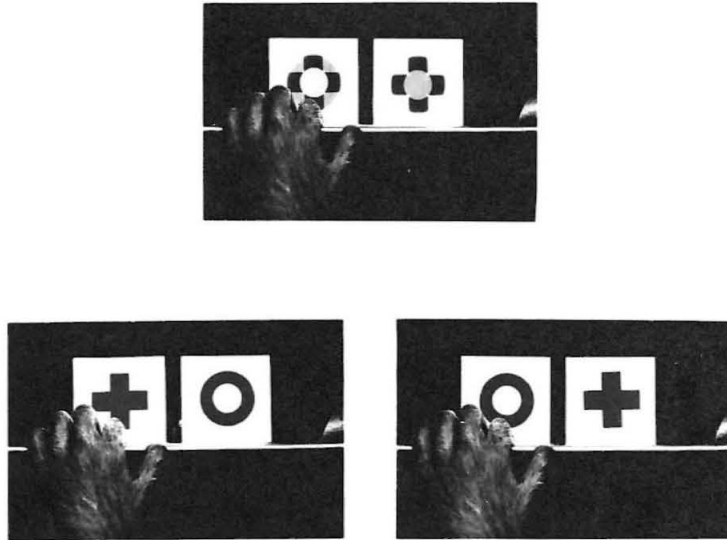


FIG. 4 - STIMULI OF TASK C AS SEEN BY SUBJECT.  
TRIAL IN WHICH LEFT SIDE REWARDED.

ABOVE - OVERLAPPING STIMULI SEEN WITHOUT POLARIZATION.  
BELOW - WITH POLARIZING FILTERS.  
LEFT - BY L. EYE ; RIGHT - BY R. EYE.

If, however, the filters were a crossed pair, all but a very small part of the projected light was blocked. In this case a figure could then be made invisible to the eye by a low level of unpolarized background illumination. Thus the relative orientation of projector-filters and eye-filters could determine which eye would see the stimuli from a particular projector (figs 1 and 3).

Two sets of a pair of stimulus figures were projected with equal brightness of total illumination, so as to overlap on the screens with one figure of each pair on each screen. The two sets were mutually contradictory. If, for instance, one set from one projector presented a cross on the left and a circle on the right, the other, from the second projector, showed the circle on the left and the cross on the right. Each set was visible to only one eye, left or right, depending upon the plane of polarization of the projector-filter relative to the filter in front of the eyes. When the projector-filters were interchanged in accordance with a standard schedule of alternation for side of rewarded response, the stimulus pairs were simultaneously reversed for each eye (figs. 3 and 4).

A note on leakage of light through  
crossed polarizing filters

The filters used were made of Polaroid HN 32 mounted between 1/32" thick laminated plastic. These, when crossed, have a transmittance between 0.0003 and 0.000,01 for visible light. The light is specially modified on passage

through the filters since there is higher transmittance in the blue-violet region. A bright white light appears purple when viewed through the crossed polaroids.

When a pattern of light of the contrast of brightness used in these experiments is projected through such a filter onto a screen of the white plastic material used (Plexiglas #W-2067), and this is viewed in a darkened room through a sheet of polaroid oriented at right angles to the pattern of light emitted from the screen, a faint bluish ghost of the pattern is visible. This becomes invisible when even a low level of unpolarized overlapping illumination is added. When a second pattern is projected, the threshold of visibility of the ghost is further reduced.

Thus, when two patterns of light are vertically polarized and the other horizontally polarized, are both projected at comparable levels of illumination so as to overlap on the plastic screens, only one is visible through a filter oriented parallel to it.

### Training

#### Preliminary training

Familiarization of each subject with the restrained head position began with the rear head-barrier removed and the side barriers widely separated (fig. 2). Food placed on the shelf in front of the eyes enticed the subject to look out and also to reach up through the arm space while looking. The screens were then placed in position and the relationship



between depression of one of the screens and delivery of reward was soon discovered. Automatic cut-off of the reward after each push caused the subjects to learn rapidly that only one push at a time would be effective.

The warning tone (cf. fig. 1) was soon introduced as a cue to effective response, and then the visual stimuli of the first problem were projected onto the screens.

#### Binocular training of the contradictory visual tasks

In each daily training session, 50 to 100 trials were presented as rapidly as the animal would work without becoming excited or satiated with the reward. Each group of ten successive trials include 5 rewarded on the left side, and 5 rewarded on the right.

#### The criterion of learning

A criterion of correctness, better than the 0.025% level of probability by chance, was set by training until twenty successive trials (two groups) included 2 or fewer errors. Experience shows that a monkey has learned and will normally retain a task trained to this level of correctness. No overtraining beyond this level preceded the monocular tests.

#### Monocular tests for retention, and monocular training in absence of retention

Upon attainment of the above criterion, with both eyes free to see the stimuli, each eye was tested alone.

Monocular attention was forced by placing a small blackened metal flap over one window immediately in front of one eye. In general, the eye of the opposite side of the body to the limb chosen for response was tested first; then, after 10 or 20 trials, the other eye was tested in a similar way.

In all cases, training with one eye alone required presentation of only one pair of stimuli in each trial. Under these circumstances only one projector was employed in each trial.

Although restriction of vision to either eye would sometimes cause a drop of performance to below criterion, at least one eye rapidly became as effective alone as when both eyes were open. This most-retentive eye was regarded as the one to which attention had been directed during binocular learning. In some cases the second eye performed with equal efficiency with the reverse task. Usually its performance was immediately inferior, and in this event training was continued until the criterion of correct performance had again been attained. Subsequent tests depended upon the course of performance as will be described in the presentation of the results.

#### Control of training

Trials were presented with irregular alternation of the side rewarded according to the principle laid down by Gellerman for two-choice discrimination training (50). It was impossible for the subject to attain a significant

correlation of performance with reward except by attending to and learning the visual stimuli.

Spurious visual cues were eliminated by interchange of the projectors from time to time, exchange of slides bearing the stimulus figures, and like methods of control.

Auditory cues of change of stimuli or reward were prevented by use of silent mercury switches for shift of reward, or for interchange of the projectors where this was used for reversal of the cues in monocular training. The reversal of polarization planes of the projector-filters was accomplished with almost no sound, and false, reversed moves were used to check this out as a source of learned information. In no case was evidence obtained of attention to this cue.

Control switches, operated by the experimenter in the inter-trial interval, enabled each trial to be set up with proper distribution of stimulus figures and appropriate connection of the reward circuit. Upon depression of a start switch by the experimenter, both projectors were turned on and the reward circuit, controlling the automatic peanut vendor, was completed. Simultaneously, a low-pitched warning tone alerted the subject to the possibility of making a response. Any move made by the subject which caused depression of either switch behind the two response screens immediately resulted in the disconnection of the whole circuit and further pushes were without effect until a new trial was set.

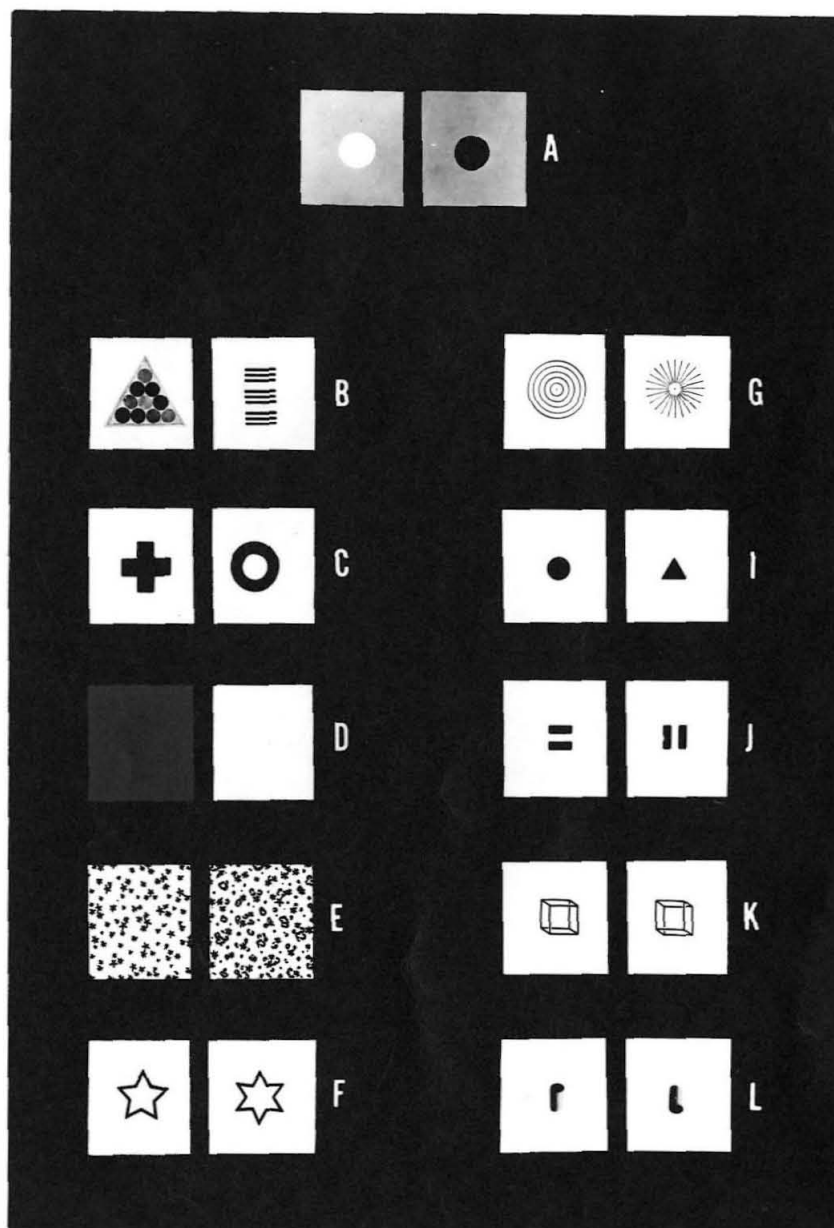


FIG. 5 - THE VISUAL STIMULI. 1/3 - SCALE.  
(STIMULUS ON LEFT IS CORRECT FOR LEFT EYE)

### Visual Stimuli

The stimuli were projected with the aid of a standard 300 watt 2" x 2" slide projector placed as shown in figure 1.

In the following account of results each discrimination task is referred to by one of the letters A through O. The tasks are shown, with stimuli in proportion to the size they were actually projected, in figure 5.

Task A.--Two, half-inch diameter, transparent, plastic push-buttons mounted in a transparent plastic surround, and illuminated from behind. Both buttons and surround were covered with sheet polarizing filter. When viewed through one or other eye window of the training box, the buttons appeared as one black and the other white in a grey surround half-way in brightness between the two. These relative brightnesses were determined by the orientation of the polarizing material relative to the eye filters.

Task B.--Relatively complex and distinct colored patterns. A blue triangle, bordered with a yellow line, and containing red, purple, green and dark blue spots was coupled with a stack of green, orange, red and blue horizontal bars.

Task C.--A black cross and a black circle of equal area.

Task D.--Uniform differences in illumination. The level of light on one response screen was reduced by insertion of a Kodak Wratten Neutral Density Filter No. 96 over half the projected field of light. A filter of density 1.00, with 10% transmittance, was used.

Task E.--Scattered small figures forming overall patterns differing in composition. In one, irregular curved lines were added to the common pattern of irregular, different-sized stars. The patterns were approximated in overall brightness.

Task F.--Black outline stars with equal area; one with 5 points, the other with 6.

Task G.--Orthogonal, concentric patterns of fine black lines. Concentric circles and radiating lines.

Task H.--Uniform blue and orange illuminations. The hue was determined with Kodak Wratten Filters No. 44A and No. 23A, respectively. Brightnesses were balanced for human vision by addition of Kodak N.D. No. 96, with 80% transmittance, to No. 23A.

Task I.--A black circular spot and a black triangle of equal area.

Task J.--Horizontal and vertical pairs of rectangular lines.

Task K.--Two line drawings representing two Necker Cubes which normally give rise to ambiguous illusions of

three-dimensional orientation. Each figure was made unambiguous by breaks in certain of the lines which favored the appearance of one or other of the two possible interpretations.

Task L.--Photographs of grey cylinders, illuminated from one side and tilted in two diagonal directions, with top or bottom nearest to the subject.

Task M.--Yellow and green uniform illuminations. Kodak Wratten Filters No. 9 (plus N.D. No. 96 with 40% transmittance) and No. 57.

Task N.--Green and violet uniform illuminations. Kodak Wratten Filters No. 11 and No. 32 (plus N.D. No. 96, transmittance 63%).

Task O.--Yellow and blue uniform illuminations. Kodak Wratten Filters No. 8 (plus N.D. No. 96, transmittance 16%) and No. 46.

The dominant wavelengths of the color filters, when used in conjunction with an incandescent tungsten source, are as follows:

Task	Filter	Color	Dominant Wavelength m $\mu$
H	44A	Blue	492
	23A	Orange	606
M	9	Yellow	583
	57	Green	531
N	11	Yellow-Green	553
	32	Violet	531
O	8	Yellow	581
	46	Indigo Blue	475

### Surgery, Recovery and Postmortems

#### Surgery<sup>\*</sup>

Barbiturate anesthesia was administered after ether induction, by both intrapleural and intramuscular injections.

Aseptic technique was used throughout, and close visual control of the operation was obtained with the aid of a wide angle binocular microscope with coaxial illumination. The head of the subject was held firmly tied in a moulded plastic frame fitting to the contours of the lower jaw.

An elliptical bone segment, approximately 4 cm x 3 cm was removed from the skull, extending rather more down the

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\* The surgery was performed by Dr. H. L. Arora with methods developed by Dr. R. W. Sperry.



left side than to the right of the midline. A longitudinal incision was made in the dura to the left of the sagittal sinus, and deflected towards the falx cerebri. For exposure of the commissures, the left cerebral hemisphere was gently retracted a few mm, and cutting was carried out with small knives and fine glass suction tubes with sharp tips. The field of operation was kept clear of blood and cerebrospinal fluid by suction. A specially constructed speculum allowed separation of the two halves of the cerebrum and visualization of all phases of the surgery, including cutting of the optic chiasm at the base of the brain and separation of the superior colliculi. In conclusion, the dura was sutured loosely with surgical silk, the bone flap was replaced and held in place, without pressure on the cerebrum, by wire sutures, then muscular layers and scalp were approximated and sutured together.

Antibiotics were administered upon completion of surgery.

#### Post surgical recovery and abnormalities consequent to surgery

As a rule, abnormal consequences of surgery, such as weakness, lack of responsiveness, transient minor paralyses or seizures, were over by the end of the first week after the operation. The following points require special attention.

Subjects CHC, BRS and IGR all showed slight weakness of the right side and a tendency to turn head and eyes to the right, and to circle to the right when walking in the first postoperative week. CHC and IGR suffered Jacksonian type seizures of the right leg, arm and face on the 4th and 6th days respectively. The next day, in each case, the seizures were absent and thereafter there was steady recovery with attainment of apparently normal use of all limbs and good vision within the following week.

Subject HDN was first operated upon in the usual way for section of callosum and chiasm. After signs of interocular transfer of pattern and color discrimination learning, a second operation was performed 7 months later. A small portion of the extreme posterior edge of the corpus callosum approximately 5 sq. mm in area was found intact. Corpus callosum and optic chiasm were re-separated, and further surgery was performed to divide the posterior commissure and separate the superior colliculi.

After operation to the midbrain structures, subjects JNY and HDN showed characteristic signs which have since become recognized as characteristic of this extended split-brain surgery. In this condition the eyes appear wide open, slightly protuberant and with somewhat dilated pupils. There is generally a trembling of the eyes which takes the form of an oscillatory see-saw nystagmus, one eye moving up while the other moves down and vice versa.

This movement varies in intensity and appears most pronounced when the subjects are staring vacantly with apprehension, and least pronounced when they are concentrating visual attention on some visual task. The tremor has a frequency of about 5 oscillations per second; there are associated trembling movements of the eye-brows and head when the nystagmus is most severe.

These effects persist long after surgery; subject JNY has protruding eyes with see-saw movements 16 months after surgery.

Both JNY and HDN showed weakness and a certain ineptness in coordination when free in a large cage after the midbrain surgery, but when in familiar situations they were capable of competent and apparently normal behavior.

Subject HDN was considerably less alert and learned poorly after the second operation, though tasks learned before this surgery were retained perfectly. It was noted 3 weeks after the operation that HDN walked vaguely and gently about a large exercise cage. Visual fixation appeared poor; peanuts could be seen and picked up but with rather more than usual concentration.

The subject miscalculated the position of perches in the cage when forced to move quickly, and stumbled. Nervous threatening gestures were made to the experimenter and the head twitched, usually cocked to the left meanwhile. The face was generally expressionless and a wan monotonous

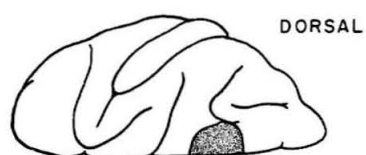
call was made when the monkey was left alone. In the training box this subject showed less alertness but more compulsive activity than before the operation, and made submissive or aggressive faces and gestures often accompanied by grunting noises to the mirror formed by the one-way-vision glass front. Frequently the hair of the shoulders and arms was erected.

At the time of sacrifice, 8 months after the second operation it was noted that the right pupil (6 mm diameter) was somewhat more dilated than the left (4 mm).

Post-mortem examination of the  
extent of surgery

Three subjects have been sacrificed and examined for surgical effects. All were perfused with 10% formalin immediately upon death following administration of a lethal dose of barbiturate. The brains were carefully removed, examined grossly, then blocked for histological preparation and microscopic examination when there was doubt concerning the extent of the surgery. The results were as follows:

CHC.--The corpus callosum, anterior and hippocampal commissures and optic chiasm were found to be completely severed. The massa intermedia was found separated in the anterior half but fully intact in the posterior half. No attempt had been made to separate the two halves of the thalamus at surgery. The right fornix had been injured in surgery and was degenerate. The incision in the chiasm



DORSAL



MEDIAL

$\frac{1}{x2}$

FIG. 6 - EXTENT OF LESION IN LEFT  
HEMISPHERE OF SUBJECT HDN.

was near the midline but veered slightly to the right at the posterior aspect.

No injuries were noted on the surface of the brain.

IGR.--The corpus callosum, anterior and hippocampal commissures and optic chiasm were found to be perfectly sectioned. The chiasm was divided exactly in the midline. Three tiny lesions, made by the drill during removal of the bone plate, were noted in the cortex; but these were obviously of inconsequential dimensions.

HDN.--The corpus callosum, anterior hippocampal habenular and posterior commissures and optic chiasm were sectioned, and the superior and inferior colliculi were separated by an incision extending down to the third ventricle, and posteriorly to a point just anterior to the trigeminal decussation.

A large lesion (fig. 6), apparently caused by retraction of the left hemisphere and postoperative infection of the brain, had produced an excavation in this hemisphere extending from just anterior to the pre-central motor area for the right foot and down into the cingulate gyrus, completely removing the cortex of the supplementary motor area of Woolsey, et al. (51). The corpus callosum was absorbed, and a hydrocephalic condition had distended all cerebral ventricles. Sections through the thalamus revealed that nuclei had suffered displacement, but that they had apparently lost little tissue.

It has been noted above that HDN had certain abnormal signs after this operation, which were not seen by other cases with similar surgery. These may largely be accounted for by the losses of cortical tissue from the medial face of the left hemisphere. The effects produced by experimental ablation of one cingulate gyrus have been reported by Showers and Crosby (52). They noted the following effects:

Deviation of the head, neck, eyes and tongue towards the side of the lesion.

Lowered body temperature and piloerection over the face, neck, trunk and upper extremities.

Dilation of the pupil of the eye contralateral to the lesion.

The animals remained alternately sleepy and hyperkinetic for about 4 days. They remained more active than others in the colony and were more vocal, more aggressive and less fearful.

These observations bear many points of correspondence with the postoperative behavior of HDN described on pages 40 and 41.

The Subjects

The seven monkeys used are referred to in the text by three-letter abbreviation of their names. Their different characteristics are summarized in Table I.

TABLE I

<u>Name</u>	<u>Species</u>	<u>Sex</u>	<u>Lbs. Weight*</u>	<u>Personality</u>
MLN	R	m	14	Young and lively. Cooperative.
ELZ	C	f	12	Tame and gentle. Had been house-pet.
CHC	R	m	8	Young and excitable.
IGR	R	m	20	Robust. Serious. Became aggressive.
BRS	R	m	17	Eager and excitable.
HDN	R	m	15	Large but timid. Changed by surgery (cf. p. 40).
JNY	R	m	11	Young, quiet and shy. Cooperative.

R = Macaca (Rhesus) mulatta;

C = Macaca (Cynamolgus) irus.

m = male

f = female

\* Taken at the end of the experiments.



## CHAPTER III

### RESULTS

#### Introduction

Two factors were measured as quantitative indices of behavior. The number of correct moves, or of errors made in each group of 10 trials, indicated how accurately the subject could choose between the visual stimuli. The distribution of correct moves and incorrect moves between the hands, and the relative amount of use made of each hand, averaged over a number of trials, could be obtained as information about the brain mechanisms of visuo-motor coordination.

In the following, the changes of visual choice will be recorded as numbers of trials correct in each group of ten, and given in the form of learning curves, or as numbers of errors made in each group of 10 trials and tabulated. Each measure was taken from the initiation of a particular training, at the beginning of a new task or new condition of vision, until criterion had been reached. In tables of errors, those errors made during the 20 criterial trials will be omitted. They number 0, 1 or 2 in accord with the definition of criterion used (cf. p. 30 ).

Motor performance is reported as numbers of correct and incorrect moves made by each hand in each group of 10 trials, or as sums or percentages derived

from these numbers. Figures show the distribution of errors and correct moves between left and right hands, and the changes which occur during learning or retention testing.

## Section I

### Performance of normal subjects

Fig. 7 shows the course of learning by a normal, naive subject, MLN, under conditions in which both eyes were presented the same stimuli in each trial. Task C, requiring discrimination between a black cross and a black circle, was used (cf. fig. 5).

For the first few days of training the subject was nervous and could not be worked for more than 10-50 trials in any one session. During this time many consecutive pushes were made by the left hand to the left response screen; a "position preference" which enabled escape from choice between the visual cues. While a position habit persists, each group of 10 trials includes 5 in which reward is obtained.\*

After 200 trials there was a period of learning which, however, did not last. The learning curve fluctuates uncertainly and there is occasional reappearance of a position preference. Criterion was attained after a total of 750 trials by a sudden reappearance of learning.

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\* A position preference is defined as occurring when a group of 10 successive trials contains only pushes to one of the two screens.

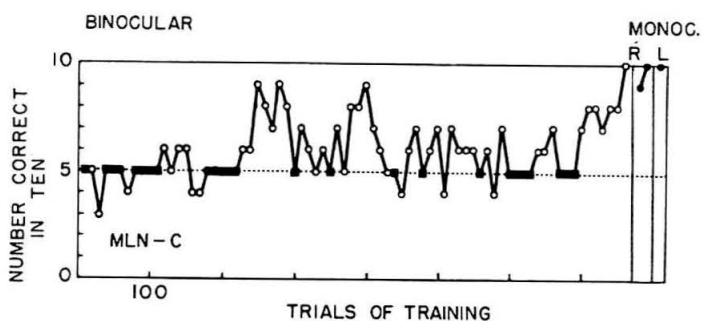


FIG. 7 - NORMAL LEARNING.

### Explanation of Figures.

The following conventions were used in the learning curves of figures 7 to 14:-

Each subject is represented by a three-letter symbol as in the text, and this is followed by a letter indicating the task presented. e.g. MLN-C means, "performance by subject MLN on Task C".

Each point represents one group of ten trials.

- ..... = random choice; 5 trials correct in each group of 10.
- = binocular performance with contradictory stimuli.
- = monocular performance.
- R = right eye.
- L = left eye.
- = performance with a position preference; see p. 47.

In figure 13, the task is described with the stimulus correct for the left eye given first. Thus, "Grey vs. White" means, "Grey correct for the left eye, White correct for the right eye".

Subsequent tests revealed that both eyes had perfect retention of the task when used individually.

Although all moves during learning were made with the left hand, the right hand could be used with either eye for perfect performance; when a barrier was placed across the left half of the arm-slot preventing use of the left hand, the following two trials were prolonged, with a few frustrated moves by the left hand and signs of nervousness and confusion. However, by the third trial no attempt was made to use the left hand, and thenceforth either hand could be used without difficulty.

The reaction to contradictory overlapping pairs of stimuli by normal subjects varies with past experience. Naive animals were no more disturbed by the contradictory cues than by the unfamiliarity of the whole situation. But, when experienced subjects were presented contradictory stimuli, after they had learned to use similar stimuli for directing their responses, there were signs of frustration.

The above subject, MLN, was immediately bewildered by overlapping polarized pairs of stimuli presented after learning and made a few nervous responses, then stopped work.

One case (ELZ) was first trained to choose a black push-button as correct and to reject a white button (task A), then was presented with contradictory pairs of

stimuli to the two eyes. Thus the correct button in each trial now appeared black, as before, to the right eye, but white to the left eye (cf. fig. 5).

The initial binocular learning was normal and there was perfect retention by both eyes as in the case of MLN. The curve for performance with contradictory ones (fig. 8) shows that learning could occur, but that only periodically, during long exposure to the situation, could choices be made accurately.

The fluctuations of performance do not show correspondence with the daily training sessions. A few interspersed monocular tests of 6 trials each indicate that good performance occurred when the left eye was inattentive. The right eye shows good retention throughout. Apparently temporary escape from the conflict could be obtained by inattention to the eye which suffered reversal of cues.

At first the subject was greatly disturbed by the frustrating stimulation and became obviously tense and nervous each period of superior performance. The temperamental displays included jumping, making of faces to the reflecting glass in the front of the training box, biting at wrists and ankles, and sulking with back turned to the eye-windows and screens. When she was sulking an offered peanut would be pointedly rejected.

In both the above cases, and in other tests of normal subjects, the use of a particular limb was

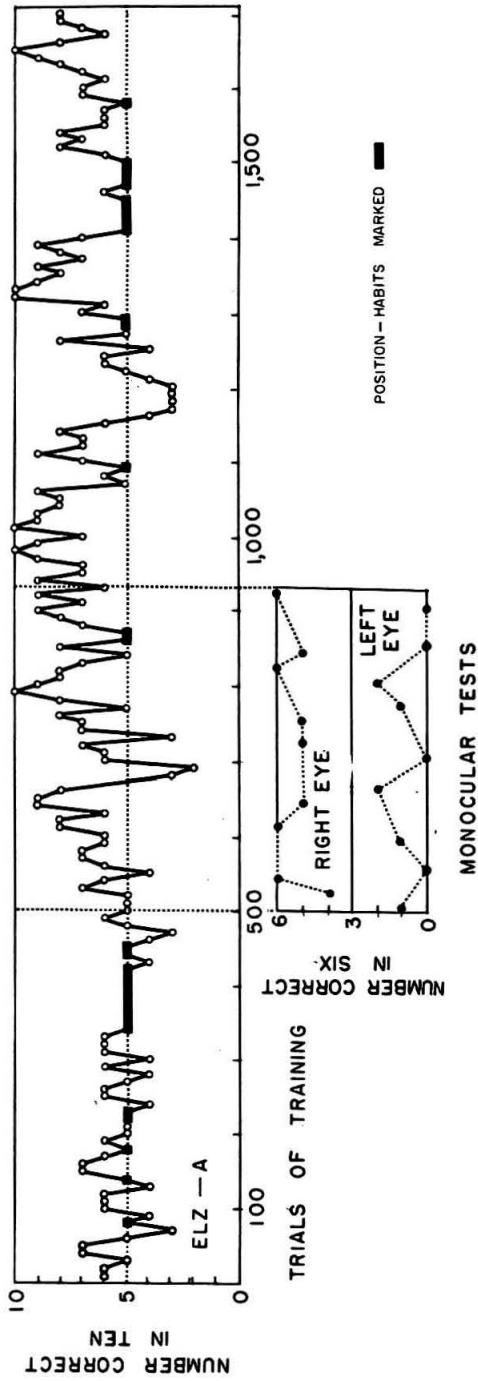


FIG. 8 - NORMAL SUBJECT WITH CONFLICTING STIMULI.  
SEE TEXT.

consistent, except occasionally at times of confusion or excitement. After reaching cautiously with either hand when first introduced to the training box, and when food inducements were laid in front of the response screen, the subject came to prefer a hand for response which thereafter was always used for pushing. Peanuts were picked up by either hand from the metal shelf to which they were delivered.

#### Summary and conclusions for Section I

Visual discrimination learning by a normal subject proceeded with an initial period in which random responses may be regulated by position preferences. These even recurred after there was a period of improved score indicative of learning. The final learning of the visual cues was rapid and a steady high level of choice was maintained thereafter.

Both eyes exhibited perfect retention of the visual task immediately learning was completed.

Although a particular limb was chosen for learning when both hands were free to work, the previously unused hand could be brought to work for perfect performance immediately the preferred hand was restrained. There was a brief confusion as hands were exchanged for the first time.

Contradictory overlapping pairs of cues cause little disturbance to a naive animal when presented one

to each eye. Such stimuli are discouraging to, and avoided by a subject previously trained to choose between the same cues without contradiction.

A normal subject may learn to pay attention to one eye and so resolve a conflict of visual stimulation introduced after normal training, but this restriction of attention is maintained poorly and involves considerable emotional strain. Periodic improvement of performance due to resolution of conflict alternates with periods of collapse in which random choices supervene.

## Section II

### Tests for double visual learning in split-brain subjects

Differences between subjects with the forebrain commissures cut,\* and those with additional surgery to the commissures of the roof of the midbrain\*\* make it convenient to consider these two groups of subjects separately.

A. Subjects with chiasm and forebrain commissures cut.--In Figures 9 and 10 are shown the results of four complete experiments with three subjects, CHC, IGR and BRS.

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\*The corpus callosum, anterior commissure, hippocampal commissure were cut, but the habenular commissure was left intact.

\*\*The posterior commissure and anterior 2/3 of the roof of the midbrain including all direct connections between the superior colliculi, as well as the habenular commissure, were cut in addition to the above forebrain structures.



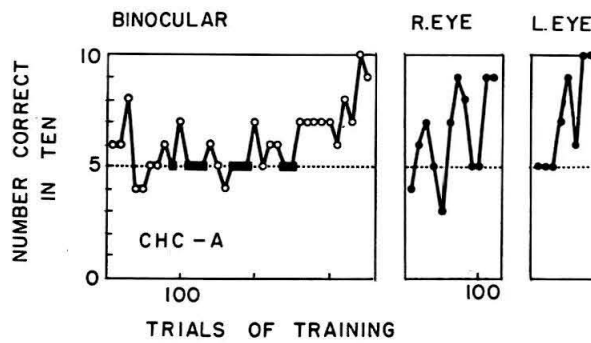


FIG. 9 - DOUBLE LEARNING, SUBJECT CHC.

POSITION HABITS MARKED ■

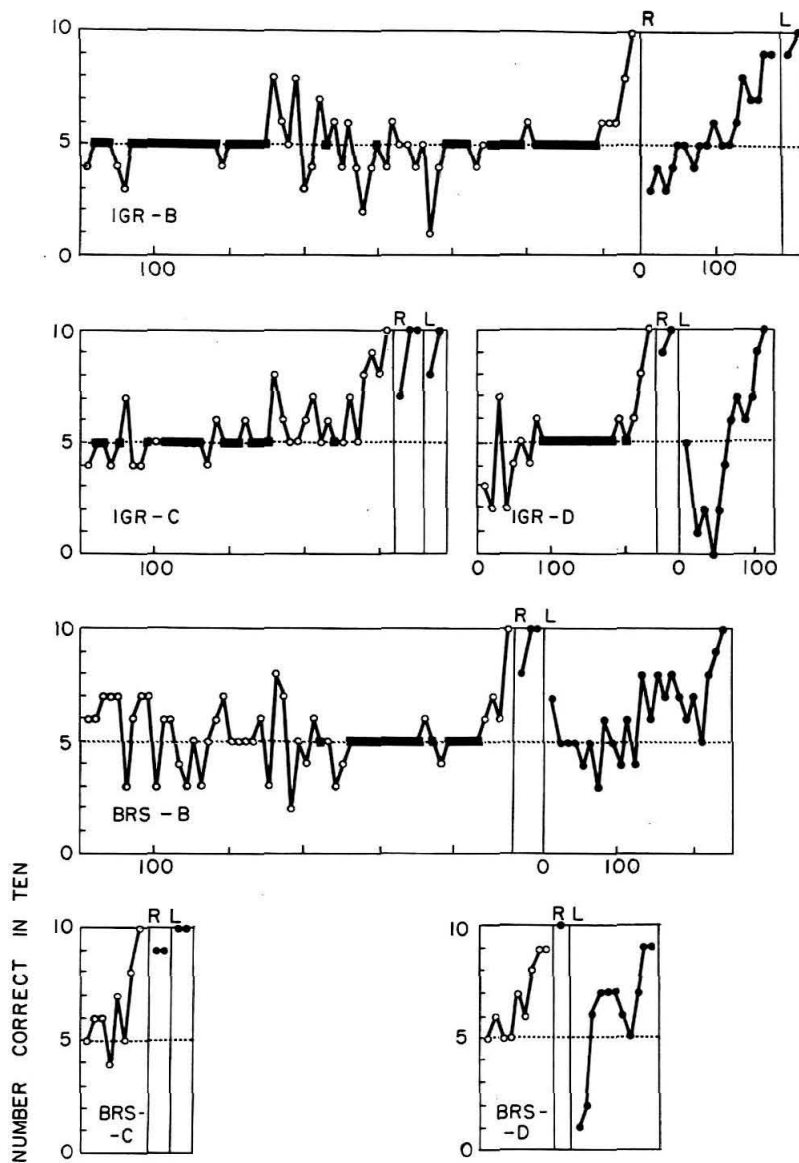


FIG. 10 - LEARNING OF SUBJECTS IGR AND BRS WITH TASKS B, C & D.

Table II summarizes the error scores to criterion of learning for IGR and BRS over a series of 14 tasks, and presents them in the order in which they were given to the animals.

This data will be considered, first, as information concerning the presence or absence of conflict during binocular training; and second, for such evidence of independent learning or interaction of learning as may be obtained from the monocular retention tests.

The learning curves of Figures 9 and 10 present features which serve to distinguish some of them from similar learning curves obtained with normal subjects as shown in Figures 7 and 8, pages 48 and 51. As in the case MLN there are periods of erratic performance, followed or preceded by steady periods in which the score remains at 5 correct in 10, and finally rapid rise to criterion. However, the flat portions, revealed by the performance record to reflect maintained position preference (cf. p. 47) may be more prolonged in the split-brain learning.

IGR falls into long runs of 100 trials with unbroken position preference while learning Tasks B and D. Later it will be shown that retention of these two tasks was distinguished from retention of Task C by signs of interocular conflict and suppression of use of one eye (cf. p. 63). Of the remaining binocular learning curves, those for Tasks E and F also showed brief runs (of 50 and

TABLE II

Number of errors made in attaining the criterion of two or fewer errors in 20 trials ( $p = 0.025\%$ ). **Binocular training with contradiction, and subsequent monocular retention tests for two subjects.** (Errors made during the two criterial groups of trials are omitted.)

SUBJECTS				TASKS	
<u>IGR</u>		<u>BRS</u>			
Binocular	Right Eye	Left Eye	Binocular	Right Eye	Left Eye
367	60	0	272	0	88
180	3	0	27	0	0
110	1	60	28	0	42
70	5	58	23	15	17
87	0	44	38	3	60
11	0	37	-	-	-
8	2	58	15	0	19
11	0	24	8	4	21
-	-	-	6	0	48
8	6	7	2	0	0
35	0	49	-	-	-
11	0	35	2	0	10
14	0	24	0	0	5
-	3	3	-	6	12
B - Spotted triangle-Stripes both colored. C - Cross-Circle. D - Grey-White. E - Patterns of small figures. F - 5 and 6 pointed stars. G - Concentric-Radial lines. H - Blue-Orange. I - Black spot-Black triangle. J - Horizontal-Vertical pairs of lines. K - 2 directions of Necker Cube. L - Photographs of tilted cylinders. M - Yellow-Green. N - Green-Violet. O - Yellow-Blue.					

40 trials, respectively) in which a position preference was shown.

BRS, a more rapid learner throughout the tests, shows position preferences of up to 50 trials in length with Task B (fig. 10) and only very brief ones of 30 trials or less, in Trials E, F and H subsequently.

When performing on these tasks, the split-brain subjects, though possibly a trifle vaguer in attention, showed remarkably little indication of disturbance from the double stimulation.

Table II shows a progressive reduction in the number of errors which occurs with both subjects over the series of tasks presented. Irregularities in the course of the progressive reduction in errors presumably reflect the obvious inequalities in difficulty of the tasks used (cf. fig. 5). Throughout the training BRS was a more rapid learner, and few or no errors were made by this subject at the end of the series of tasks. At this stage the subject approached the first trial of a new task with care and concentration and, in as few as one trial had mastered the choice and retained the learning perfectly. Thus, highly efficient performance is possible after the visual mechanism has been divided by surgery. In the final tasks (G through P, excluding J which was not presented, and L which was a particularly difficult

task) subject IGR began to learn immediately each new task as presented, and attained criterion with 15 or fewer errors.

Monocular retentions by the two eyes tested individually after completion of learning with both eyes open.--Figures 9 and 10 and Table II show that wide differences in the retention of learning by the two eyes may follow binocular training.

As would be expected, there is always one eye which retains knowledge of the task previously presented to it. It will be explained later how it was possible to predict which of the two eyes would be the most retentive from the use of the limbs in binocular training. Therefore the test of retention by this favored eye could be made immediately criterion had been attained with binocular training and before testing of the less favored eye (cf. p. 102).

When the blackened eye-flap was placed a short distance in front of the presumed least-attentive eye to completely block vision of the stimuli and response situation for that eye, the subject was always at least momentarily disturbed. Probably this disturbance reflects the change in visual attention required. The least attentive eye may have been little used for learning, but throughout binocular training it appeared to look at the

training situation, and was used for guiding hand movements, for example, when a peanut was to be obtained from a place where it could not be seen by the other eye. As a rule, upon moving to respond in the first trial of training with restricted vision, the subject started back and made attempts to scrape away the cover from the eye-window.

For the most part, one particular eye was favored as the most retentive throughout the series of tests. Almost all tests show very few or zero errors in monocular tests with the right eye (Table II). In the case of IGR there was a shift from preferred use of the left eye in the learning of Task B. This shift at the beginning of training indicates that the consistent preference for use of one eye may not reflect an original and inflexible asymmetry in the brain.

a) Strong retention by both eyes; simultaneous learning.--Almost perfect retention by both eyes, immediately after learning with both eyes open had been completed, occurred with IGR and BRS when working with Task C. This is shown in Figure 10.

The data of Table II show that such equal learning was exceptional, but that in two other cases, namely with Tasks E (BRS only) and K, near equal retention scores were obtained for the two eyes (see fig. 11). Task E required choice between rather confusing patterns as will be seen from reference to Figure 5. Binocular tests made

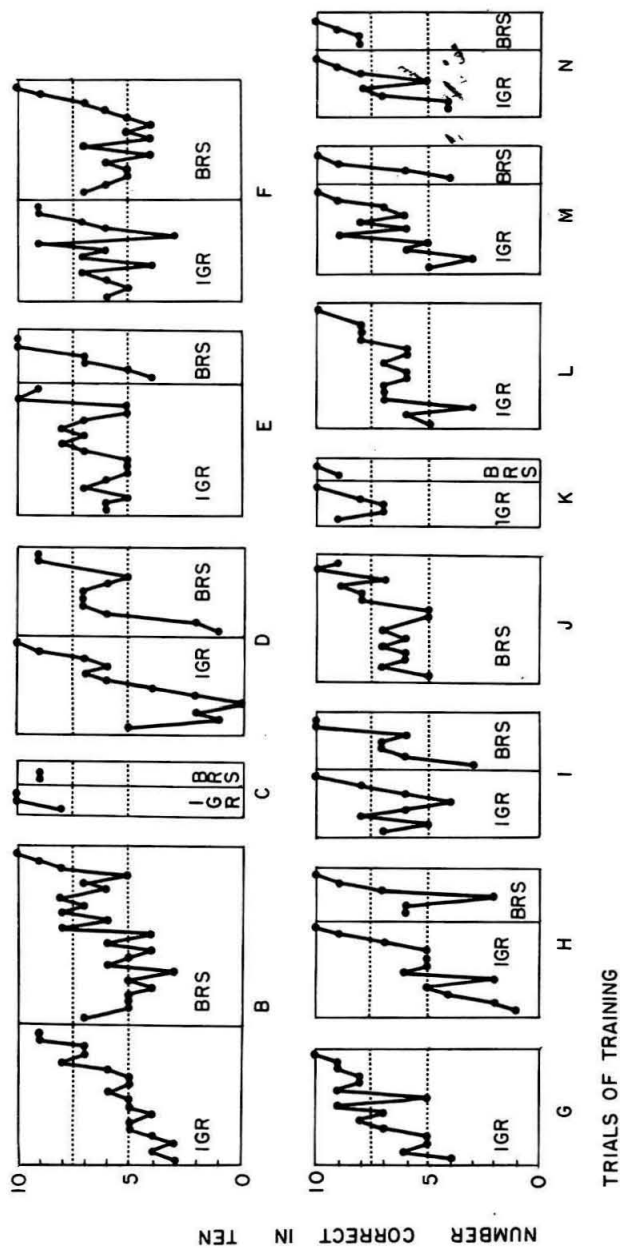


FIG. 11 - LEARNING OF LEAST RETENTIVE EYE. SUBJECTS IGR AND BRS. TASKS B TO N. EACH POINT REPRESENTS TEN TRIALS.



after criterion had already been attained showed that retention of this task was unusually poor, and for 2 or 3 consecutive days of training after criterion had been attained there was a period of relearning with both eyes open before performance reached criterion once again.

IGR shows markedly unequal learning of Task E though some errors were made by the right eye in attaining criterion. It is likely that the near equal retention shown by BRS reflected a temporary confusion of vision with the right eye which interfered with retention by this eye.

A more likely second case of equal retention by both eyes is provided with Task K. Here, however, both subjects were performing after the "learning set" described above had become well established. With such rapid binocular learning it is difficult to be sure that the two eyes learned at one time during the binocular training. However, one may say that inequalities of imposed monocular attention as were found for most tasks trained, did not follow binocular training of this task. A task which one might expect to be comparable, viz. recognition of the two photographs of cylinders with different orientation in a unilateral field of illumination (see fig. 5, L) was difficult for IGR and was retained by only one eye.

b) Unequal retention by the two eyes. Monocular attention to stimuli during binocular training.--

Table II shows that, in most cases, a considerable amount of training was necessary before the less retentive eye could be used for performance at the criterion level of proficiency.

All learning curves for the least retentive eye of subjects BRS and IGR are shown in Figure 11. They are grouped for comparison between the two subjects. Each point in these graphs represents the score for 10 trials, and the learning is shown complete in each case, from immediately after retention testing of the favored eye to criterion. Breaks between daily training periods are indicated.

Marked differences occur between the performance of the two subjects but, nevertheless, there are some definite similarities which may be singled out as evidence for common features of learning.

There is less of a decline in the number of trials or numbers of errors to criterion than has been described above for binocular performance (p. 58). Early in the series of tasks, the monocular learning by the least retentive eye is more rapid than was the corresponding binocular learning. This partial retention is clear from the error scores (Table II). Towards the end of training there are several instances where the least retentive eye

takes many more trials to learn a task than was taken during binocular training of the same task. (See IGR-G,H,I,M,N and BRS-F,I,J,M.) Nevertheless, there is a general decline of the number of trials needed to bring the unretentive eye to criterion level for comparable problems, and this partial learning set is most apparent in the case of the rapid learner, BRS. Task J forms a conspicuous exception.

Exceptionally rapid learning, indicating good retention by this eye, also, is shown for Tasks C and K as described above.

The longer learning curves in which 10 or more errors were made (IGR-B,D,E,F,G,H,I,L,M,N; BRS-B,D,F,H,I,J,M) cover a wide range of forms, and many do not resemble the binocular learning curves (cf. p. 56).

Position preferences are not shown. On the contrary, many of the curves show sudden shift in level of performance, and never remain at a given level for more than 30 consecutive trials. The learning curve for the right eye of CHC (cf. fig. 9) shows this repeated sudden rising and falling in a particularly striking way. Both sudden falls in performance occurred after 30 trials of training on two consecutive days and were correlated with signs of agitation of the subject. The training of the second day concluded with the two criterial groups of trials which thus appeared spontaneously, within the

training session. Inspection of Figure 11 will disclose that many of the sudden drops and rises of scores during learning occur within a single day's training and are not simply due to discontinuities of training. They are also to be seen in cases where the training was uninterrupted (cf. for example IGR-F,G,M,N).

A further special characteristic of certain monocular learning curves is the tendency for many groups of 10 trials to have a score between random and fully learned; that is to say 6, 7 or 8 were correct in these groups of trials. This tendency is seen as a flattening of the learning curves at this intermediate level of performance (e.g. IGR-E,L. BRS-B,D,J).

c) Negative correlations between choice and stimuli. Interocular transfer of learning.--In three cases the score of performance falls to a level in which there are as few as 3 correct choices in 20 consecutive trials ( $p = .001$ ). These are IGR-D, H; BRS-D. In one, IGR-D, the score falls to 0 correct in 10 ( $p = .0001$ ) and satisfies our criterion for perfect retention. But the retention is for the direction of choice to which the other, most retentive eye had been trained during binocular learning. Clearly the learning by the right eye was retained in some portion of the brain where it was accessible to the left eye when this was forced into

use. A weaker indication of transfer; a group of ten trials in which but 2 were correct ( $p = .04$ ) was also found in the case of BRS-H.

In all cases, even when transfer was most marked, there is rapid reversal, and the inappropriate responses are replaced by correct choices within 100 trials of training. Subsequently, tests reveal that the engrams appropriate to the two eyes remains distinct and unconfused. In both cases the retention by the right eye remains unaffected by the new learning of the left eye.

Later, unsuccessful attempts were made to demonstrate transfer of color discriminations with other comparable pairs of colors (tasks M,N,O). Possible brief negative correlations of choice shown by IGR when tested for retention of M and N fall far below significance.

The progressively rising curve of learning by the left eye in the case of IGR-B supports the possibility that the small negative correlations shown by the three first groups of 10 trials indicate some degree of interocular transfer. Possibly the information responsible for this doubtful transfer concerned the differences in color between the stimuli.

It is not possible to conclude that areas of color which are equal in brightness for a human are also equally bright to a monkey. In defense of the conclusion that color discrimination learning did transfer it may be

pointed out that brightness discrimination transfer had already been controlled when training Task D. Also, when tests were made (after completion of the training with Task H), in which the relative brightness of the orange and blue colors were altered by placing neutral density filters over one response screen at a time, the retention of discrimination according to color was unaffected.

#### Order of Difficulty for Equal Binocular Retention

If the number of errors made by the least retentive eye in attaining criterion reflects a competition between the two visual systems, there may be a correspondence between this number and the type of visual task presented for learning. Alternatively, the difficulty of monocular learning may reflect a state of adjustment which is independent of the visual stimuli.

When the number of errors is used as a measure of retention by the less retentive eye, the tasks can be put in order of increasing difficulty for subjects IGR and BRS, as in Table III.

Three tasks which are not common to the two subjects are circled. Corresponding tasks are placed opposite one another where the order of their occurrence in the lists permit, and only two exceptions, F and I, are found. These are both learned with relatively greater ease (relatively fewer errors) by IGR. The least readily

TABLE III

Tasks B to N Arranged in Order of Decreasing  
Error Score for Subjects IGR and BRS

<u>Errors to Criterion</u>		<u>Task</u>	<u>Description</u>
Subject IGR	Subject BRS		
79	88	B	Spotted triangle-Stripes both colored.
	60	F	5 and 6 pointed stars.
	48	ⓐ	Horizontal-Vertical pairs of lines.
60	42	D	Grey-White.
	21	I	Black spot-Black triangle.
58	19	H	Blue-Orange.
58	17	E	Patterns of small figures.
49		Ⓛ	Photographs of tilted cylinders.
44		F	5 and 6 pointed stars.
37		ⓖ	Concentric-Radial lines.
35	10	M	Yellow-Green.
24	5	N	Green-Violet.
24		I	Black spot-Black triangle.

retained task is B which was presented first, while the subjects were most naive in their performance. The following tasks D,H,E,M,N,K,C fall into an order which may well reflect the degree of interaction between visual processes in the brain. D and H are cases where significant transfer occurred. E was a complex pattern task which may have been discriminated as an overall texture difference, or even as a difference in overall brightness although an attempt was made to equate the patterns for this factor. M and N were successive color discrimination tasks learned without significant transfer. K and C were pattern discrimination tasks learned without transfer.

The standard Rank Order Correlation Coefficient for the relationship between the two sequences of decreasing error score is  $r_s = +0.8$ . This has a level of significance,  $\alpha = 0.004$ , which makes it highly probable that similar effects were produced in the two cases by corresponding tasks.

Both subjects showed a weak correlation between the order of the presentation of the tasks, and the order of decreasing error scores ( $r_s = +0.5$ ,  $\alpha = 0.1$ ; in each case). However, they were given the tasks in the same order for convenience of experimentation; therefore, it may not be said with confidence that the order of difficulty for monocular retention of the tasks is independent of the order in which they were given.



Comparison Between Learning with Both Eyes Open  
and Monocular Learning with the  
Less Retentive Eye

If choice between the two possible responses, to the left or to the right, were performed randomly, the distribution of frequencies for each score of correct trials in any ten attempted would fit the Binomial Distribution histogram. Deviations from this distribution occur for both binocular learning and for the monocular retention learning. These two distributions (fig. 12), summarize certain features of learning which have been described. The data from which the distributions were obtained are shown in Table IV.

We may describe the deviations from the Binomial Distribution as follows:--

1. Binocular learning shows an increase of frequency of mean scores above random, which effect is accompanied by a proportional reduction in errors. When learning begins, the position preference which has been found to be the main cause of groups of 10 trials in which 5 are correct, is abandoned. Presumably, before any learning has occurred there is a symmetrical distribution of frequency of scores with a high mean due to position preferences.

2. Monocular performance is not characterized by a concentration of scores about the mean value; the distribution of scores is skew towards higher scores.

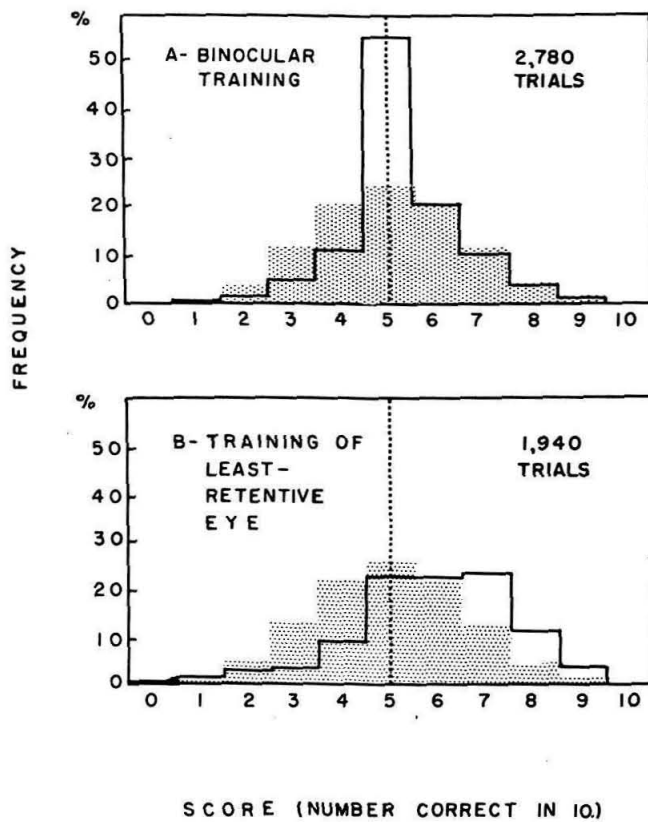


FIG. 12 - FREQUENCY DISTRIBUTIONS FOR SCORES.  
TOTALS FOR ALL TASKS LEARNED BY IGR AND BRS.  
BINOMIAL DISTRIBUTION OF RANDOM PERFORMANCE SHOWN GREY.

TABLE IV

Frequencies of Occurrence of Groups of Ten Trials  
in which the Number Correct is as Shown.  
(Criterial trials are excluded)

		<u>Number Correct in 10</u>											
		0	1	2	3	4	5	6	7	8	9	10	
Binocular Training													
	IGR	0	1	3	6	23	98	35	12	4	3	0	Total 185
	%	0	0.5	1.5	3.3	12.5	53	19	6.5	2.2	1.5	0	
	BRS	0	0	1	6	6	42	18	14	6	0	0	Total 93
	%	0	0	1.5	6.5	6.5	45	19	15	6.5	0	0	
SUM		0	1	4	12	29	140	53	26	10	3	0	Total 278
	%	0	0.4	1.5	4.3	10.5	50.6	19	9.4	3.7	1.1	0	
Monocular Training													
	IGR	1	2	4	5	10	28	25	26	13	6	0	Total 120
	%	0.8	1.7	3.3	4.2	8.4	23.3	20.8	21.7	10.8	5	0	
	BRS	0	1	2	2	8	15	18	19	8	1	0	Total 74
	%	0	1.4	2.7	2.7	10.8	20.3	24.3	25.6	10.8	1.4	0	
SUM		1	3	6	7	18	43	43	44	21	7	0	Total 194
	%	0.5	1.6	3.1	3.6	10.1	22.1	22.1	22.5	10.8	3.6	0	

This could merely be a reflection of learning. If so, the learning must be retarded by comparison with that of binocular performance. The average number of trials involved in learning to criterion by this single eye is high compared with binocular learning.

Alternatively, there may be some impediment to performance which leads to many scores which exhibit learning only partially. For example, if attention were distributed in half the trials to the eye which is covered, and if the eye in use were fully learned, then a score of 7.5 in 10 would be obtained on the average.

A swinging of attention of this kind may explain the flattening of monocular performance by the least retentive eye in regions where the score has between 6 and 8 correct in each 10 trials. A rapid alternation between the eyes would result in a flat score; a slow swinging, taking many trials for its changes of phase, would result in a rapidly rising and falling score ranging between levels near random (5 in 10 correct) to those near perfect (9 or 10 correct in 10). Such effects have indeed been observed, on occasion. (Cf. p. 64 and fig. 11.)

B. Subjects with additional surgery to the roof of the midbrain.--When brightness transfer was found with subjects IGR and BRS after surgical separation of the cerebral hemispheres, attention was turned to possible

connections between visual structures of the midbrain. Two subjects, HDN and JNY, were trained after the posterior commissure and the quadrigeminal plate, in addition to all the previously sectioned structures had been cut in the midline. JNY was used in tests of pattern and color discrimination, and both were trained brightness discriminations in an attempt to locate the sight of transfer for this task.\*

#### Color discrimination learning

Figure 13a, shows the course of learning when JNY was required to discriminate between blue and orange (task H). Binocular learning, with contradictory cues presented to the two eyes, was completed in 250 trials and 147 errors were made before criterion was attained. This learning compares well with that shown previously by IGR and BRS when these subjects were at a comparable state of experience in the training situation.

There was almost perfect retention by the right eye, only two errors were made in the single pre-criterial group of ten trials.

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\* Subject HDN was found to have a large additional lesion developed after surgery. This is described on p. 43.

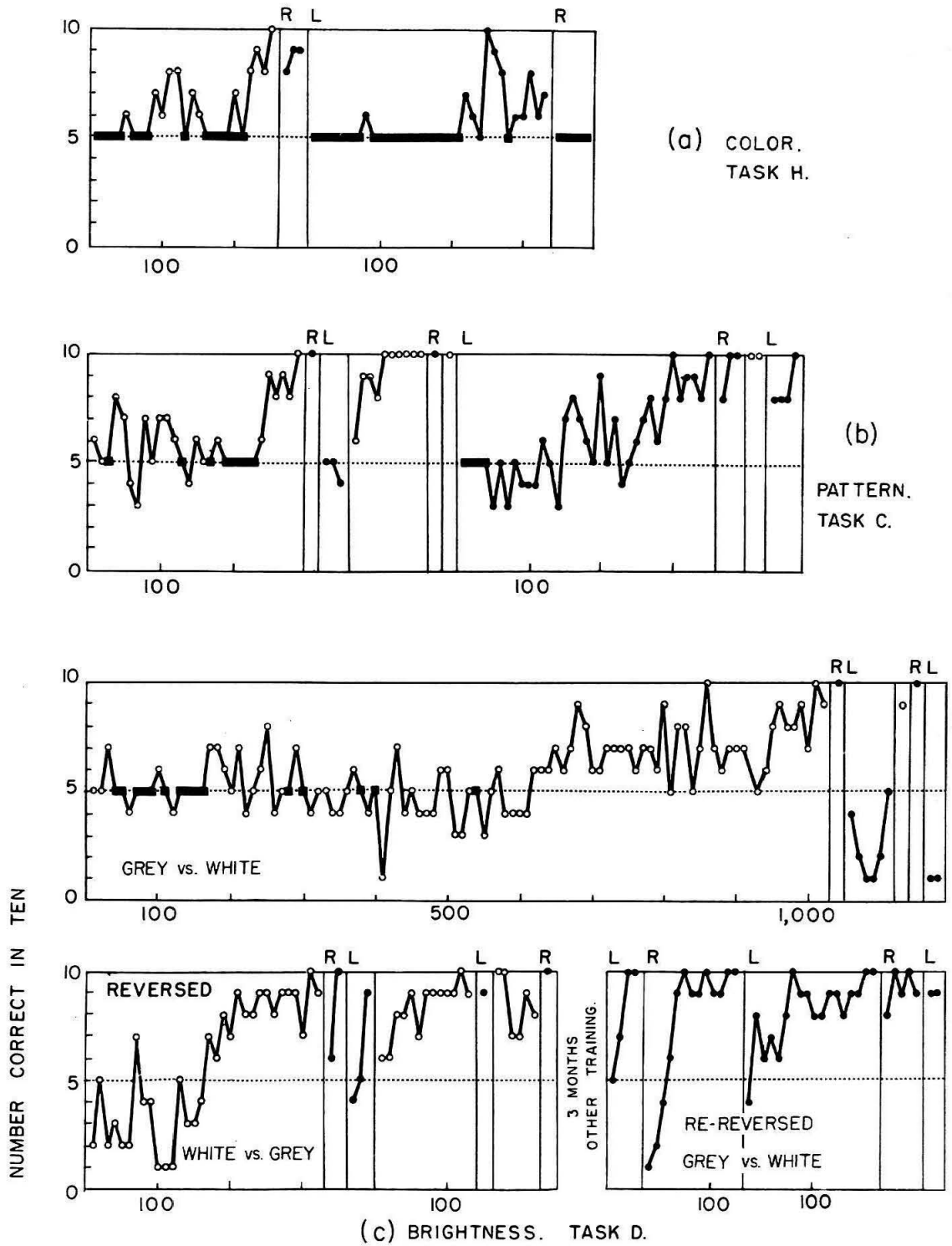


FIG. 13 — LEARNING OF SUBJECT JNY WITH MID-BRAIN ROOF SECTIONED.

The left eye, however, attained an unstable criterion after 200 trials, and in the first 200 trials the subject adopted an almost unbroken position habit to the left. During this training JNY became most discouraged and unwilling. There was, however, no sign of interocular transfer of learning. Subsequent to the training of the left eye, the right eye was inattentive and adopted a position preference to the right.

#### Pattern discrimination learning

Figure 13b shows learning by JNY with Task C in which it was required to discriminate between a black cross and a black circle (see fig. 5, p.33 ).

No unusual features distinguish the binocular learning which was completed in 300 trials, with 163 errors before criterion.

Once again, there was perfect retention by the right eye.

Performance with the left eye begins as if uninfluenced by previous exposure to the stimuli. When 30 trials of forced vision with the left eye alone were made immediately after learning had been completed with both eyes open, binocular retention was impaired. Presumably, there was a temporary inattention to use of the right eye. The learning by the left eye was erratic and prolonged. Criterion was attained in 300 trials,

with 152 errors, and retention was thereafter more unstable than in the case of either binocular or right-eyed performance.

#### Brightness discrimination learning (task D)

Both JNY and HDN showed remarkably poor learning of this seemingly simple task.

The tests with JNY are shown in Figure 13c, where it may be seen that binocular learning occupied 1000 trials and was wandering and erratic. 568 errors were made before criterion was reached.

Following this training the right eye was perfectly retentive and zero errors were made in satisfying the criterion.

Negative correlations of performance with the left eye with respect to the visual stimuli indicate interocular transfer of learning. The performance with the left eye fell within 20 trials and 18 errors were made in a further 20 consecutive trials ( $p = .0002$ ). The same high level of negative correlation was attained in a succeeding test of the left eye after the right eye had made 10 successive correct choices of the brightly lit screen ( $p = .001$ ).

The direction of the choice learned, in favor of choice of the bright screen and rejection of the dark one by both eyes, made it seem possible that a preference for the more brightly lit, more conspicuous side had led to spurious results. A double reversal test, in which both



eyes were trained the reverse of the tasks which had been presented in the first training, was given in an effort to obtain transfer of the opposite direction of choice. The results, shown in Figure 13d, were inconclusive. Binocular reversal learning began with fluctuating returns to the now negative choice, then climbed to criterion in 250 trials. Retention by the right eye of the new discrimination was not perfect, the first group of ten trials recording 4 errors. The left eye failed to reveal transfer of the reversed choice, and quickly regained the criterial level of performance, probably by retention of the engram transferred in the previous training. Subsequently, binocular performance and both monocular performances remained at high levels, indicating that, with the loss of transfer, the subject had become able to retain two contradictory engrams.

When tested three months later, however, after intervening experience with quite different and complex visual learning tasks, JNY gave evidence of transfer of choice of the less brightly lit screen in the opposite direction; i.e., from the left eye to the right eye (fig. 13d). Rapid learning by the left eye was followed by significant transfer to the right eye which was, however, soon reversed. Subsequently, both engrams were retained, retention being somewhat less efficient in the case of the left eye.

Comparable training with the second subject, HDN, gave the results shown in Figure 14. After 600 trials of training with both eyes and contradictory stimuli, in which the score was erratic and no significant learning occurred, monocular training of the right eye was attempted. An unsteady criterion was attained in 1000 trials, and the learning curve has features which compare closely with those described above for JNY (fig. 13c). In particular, there is a slow undulating change of the average level of response over which the sudden changes of level are superimposed.

When the left eye was tested with the reverse task, interocular transfer of learning occurred in the first 100 trials. In this period the learning curve swung wildly, dropping to the level at which 0 trials were correct in 10 ( $p = .0001$ ). Subsequently the learning undulated slowly below and above the mean level of 5 correct in 10 before learning occurred. Throughout, wide fluctuations obscured the course of the slower event. Twice, when approximately 700 trials of training with this eye had been completed, the score fell to 1 correct in 10 ( $p = 0.1$ ).

The final learning occurred after addition of a  $\frac{3}{4}$ " spacer which prevented the clumsy movements made by this subject from displacing both screens in a single trial. This device, painted black, separated the two

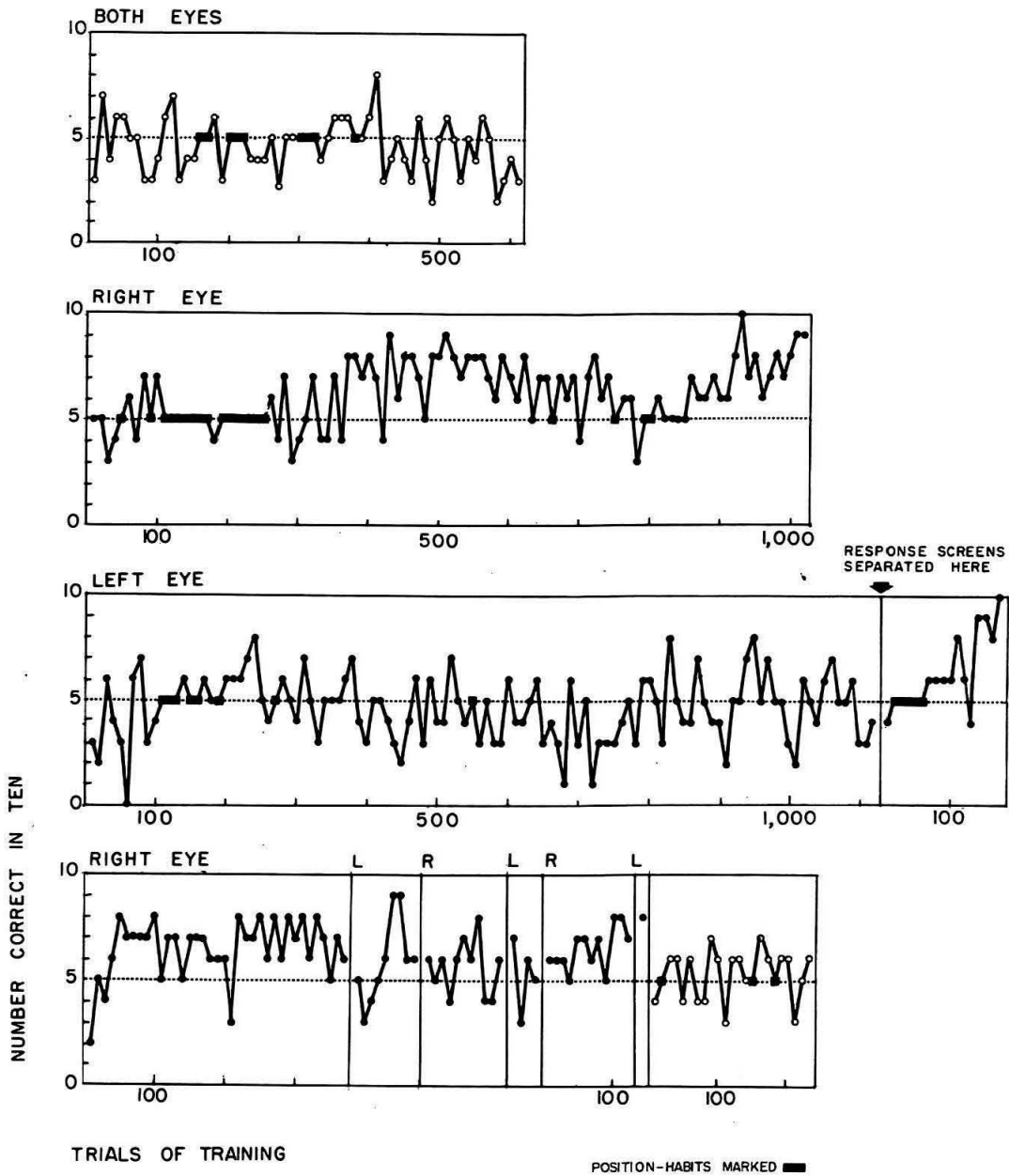


FIG. 14 - LEARNING OF SUBJECT HDN AFTER DIVISION OF FORE-BRAIN AND MID-BRAIN ROOF  
BRIGHTNESS DISCRIMINATION, TASK D. (SEE ALSO FIG. 6)

screens which appeared correspondingly reduced in width. The point at which this change was made is indicated in Figure 14, and it may be seen that performance was less erratic and that learning appeared to take place immediately. All following training with HDN was made with the screens so separated.

Immediately the left eye had been trained to criterion, tests were made with the right eye, and the first group of 10 trials gained a score of 2 correct moves ( $p = .04$ ). Thereafter performance remained strikingly steady at the intermediate 6-8 correct in 10 levels.

Alternated tests with the two eyes showed that transfer could be suppressed, and finally both eyes were able to perform at a level of 8 correct in 10. Nevertheless, the score for 100 trials of binocular training with separate contradictory stimulation of the two eyes showed no signs of retention on learning, but remained near the mean level.

#### Summary and conclusions for Section II

Split-brain subjects, with optic chiasm, corpus callosum, anterior, hippocampal and habenular commissures cut, show little abnormality in their free behavior. There is no clear sign of visual confusion or of malcoordination of movements. There is, of course, a deficiency in visual

field, a bilateral temporal hemianopia, which results from the elimination of crossed fibers at the chiasm. This effect presents little disadvantage to the animal after post-surgical recovery of normal vigor and adaptiveness.

When presented with two contradictory visual discrimination tasks simultaneously, split-brain subjects appeared, at first sight, to learn without conflict as if they were normal and learning but one task. Occasionally, however, position habits were more pronounced possibly because some degree of conflict did occur and learning was retarded by it.

Over a series of tasks, a "learning set," or progressive task-to-task shortening of learning was observed. Finally, the subjects became attentive to the discrimination of a new task immediately, and learned in less than 10 trials.

There were cases in which both eyes were almost equally retentive. Both subjects retained a pattern discrimination learning, requiring distinction between a circle and a cross (task C), in both halves of the brain immediately after monocular tests were made. The two halves of the brain had acquired the visual choice in both contradictory directions simultaneously in approximately the same number of trials as would have been required

for learning by one eye, or for normal learning by an unoperated subject. Similar double learning of a second, but more complex, figural discrimination (task K) occurred late in training. However, monocular retention tests revealed that learning was located most frequently in one-half of the brain during the presentation of contradictory tasks. For most of the tasks a single eye showed near perfect retention while the other eye required a considerable amount of training to attain criterion of learning. For each of two subjects, one particular eye, the right in both cases, was consistently most retentive. A shift in the use of eyes occurred at the beginning of learning with subject IGR, the left eye being most retentive for learning of the first task presented in this case.

In most cases where retention was unequal, the learning by the least retentive eye did not show the "learning set" described for binocular training. Towards the end of learning there were many cases where the forced monocular learning by the left eye took many more trials than was required in the learning of corresponding tasks when both eyes were open. A slight indication of improvement in learning by the less favored eye occurred towards the end of the series of tasks.

Position preferences shown in binocular learning were not apparent in learning by the less favored eye. Wide fluctuations of score occurred, and the criterial

level of performance was not maintained once first achieved. Emotional signs of excitement and of impatience or discouragement reveal a disorganization of those brain processes which, presumably, were responsible for learning in the preceding training with both eyes, and for retention by the most retentive eye alone.

Many of the learning curves with the least retentive eye show a high proportion of groups of trials with intermediate, partially retentive, score. Sometimes the learning curves show a tendency to form a plateau near the 7-8 correct in 10 level.

In four cases, significant interocular transfer of learning occurred. For Tasks D and H (brightness and color discriminations, respectively) both subjects, when forced to use the least retentive eye, performed with temporary reference to the engram acquired by the other eye. After training for no more than 100 trials, this inappropriate transferred memory was reversed, and then both eyes could be used for their respective, mutually contradictory tasks with consistent high scores. In subsequent training of comparable color discrimination tasks, there was no significant interocular transfer of learning.

When the tasks were arranged in order of the number of errors made in attaining criterion with the least retentive half of the visual mechanism, after the favored half had reached criterion while both eyes were open, both subjects showed a highly significant correlation between their performances. Both were trained in the same order and both show a weak correlation of error scores with the order in which the trials were presented.

The least quickly learned tasks were those in which interocular transfer led to a high proportion of errors in early groups of trials when the least retentive eye was tested alone. The highest error score was obtained, however, for the first task which forms an exception to this rule, although signs of weak interocular transfer were observed for this task, also.

The most quickly learned tasks were those involving pattern recognition, and possibly interpretation in terms of three-dimensional objects. Intermediate error scores were less consistently similar for the two subjects, but may reflect a partial transfer or interaction of the contradictory pairs of cues for tasks in which the discrimination required recognition of one character or quality which separated otherwise similar pairs of stimuli.



Analyses of the distributions of scores for binocular learning, and for monocular learning by the least retentive eye for the two split brain subjects IGR and BRS reveal differences in their deviation from the binomial distribution of random performance on a two-choice task (cf. p.70 ). It is concluded that position habits of binocular training serve to conserve errors before learning of the visual cues enables scores higher than the mean value to be obtained. The final learning is rapid and sustains high scores.

By contrast, monocular learning by the least retentive eye is slower and may be affected by a swinging of attention between the retentive, but blocked visual system and the now active system which has acquired the ability to choose a significantly high proportion of times correctly. Such competition for attention would result in a maintained depression of the score to intermediate levels. If rapid swinging of attention between the eyes occurred, the learning curves would remain flat at the 7-8 correct in 10 level; if the attention shift were less frequent, the score would also show shift between random and near perfect levels. Both types of performance curve were observed.

When surgery was extended to include separation of the superior colliculi, and the posterior commissure was cut as well as the forebrain commissures and optic chiasm, pattern and color discrimination learning was distributed in one half of the brain after binocular training with contradictory cues. There was no sign of interocular transfer of color discrimination learning.

In two cases there was pronounced transfer of brightness discrimination learning after midbrain surgery. Moreover, the initial learning was conspicuously slow and fluctuating as if some component of the mechanism for distinction between levels of luminous flux were damaged by the surgery.\* Conflict between the contradictory tasks does not give the explanation for this defect, as it was equally apparent for extended monocular training of a preferred eye. Reversal training demonstrated a limited ability for control of the transfer with practice. In one case this ability to separate vision by the two eyes was lost after 3 months of different training, but was quickly regained.

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\*One of the subjects (HDN) was found to have suffered extensive loss of brain tissue in one half. This injury may be partly responsible for poor learning but does not affect the conclusions about transfer of brightness discrimination learning.

### Section III

#### Habits of limb use and choice of response in split-brain monkeys when learning visual discrimination tasks

Throughout the learning tests which have been described, observations were made on the use of the limbs.

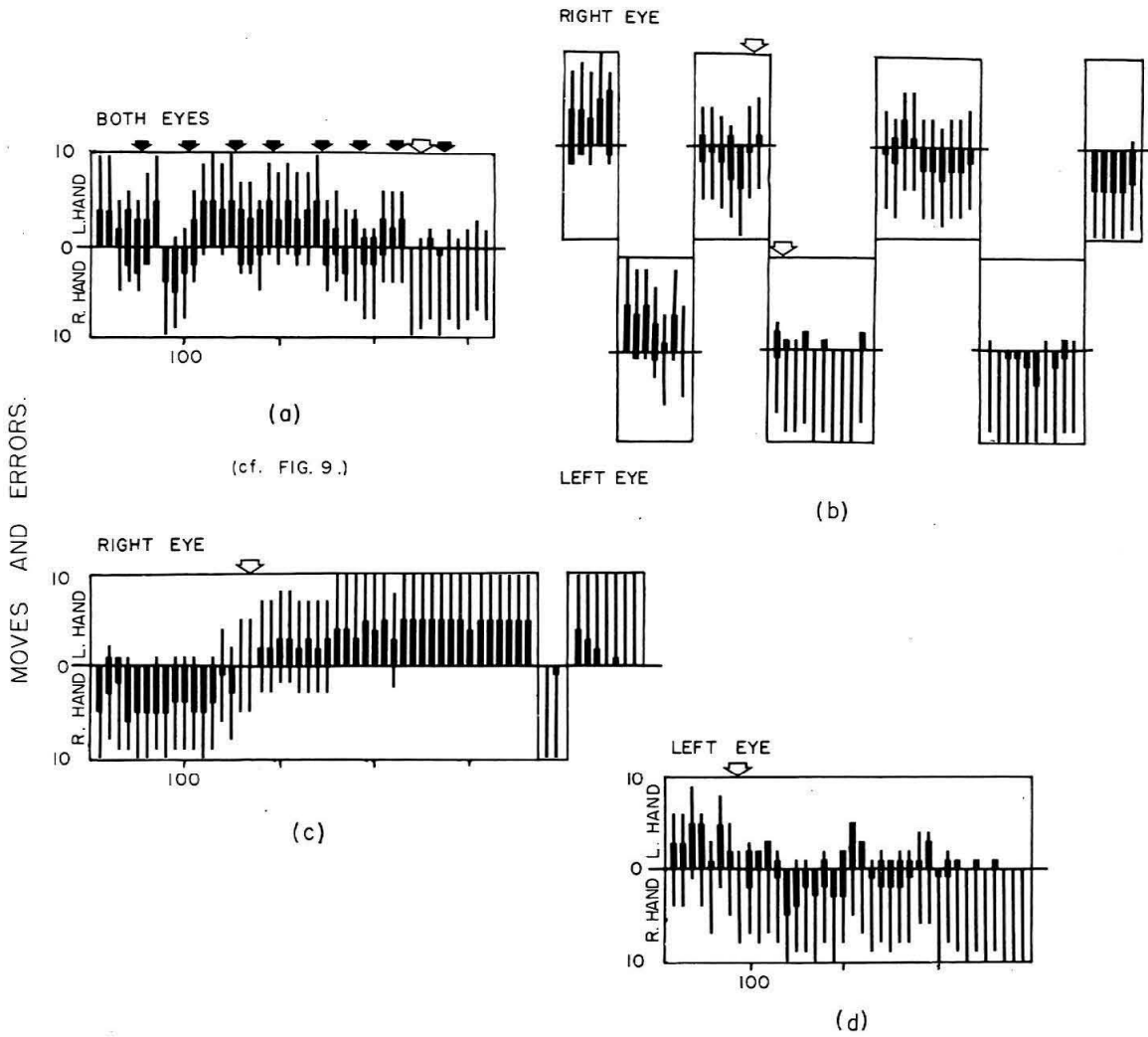
Split-brain subjects, like normal monkeys, tend to develop a preference for use of one particular hand. But this choice is not invariably maintained. Spontaneous changes of hands were noted at various stages in training, and it was found that these changes and the direction in which they occurred corresponded with events in the visual learning. For example, change of hands occurred most often at a time when changes in the score were taking place, either in the direction of learning, or towards a more erratic performance. Recurring preferences for paired use of either eye with the limbs of the opposite side of the body and interaction between these preferences and the tendency for consistent use of a particular limb were observed.

In the training of each task, after learning had been completed with both eyes individually, the hitherto free choice of a limb for responses was altered by insertion of arm barriers which restricted movement to a particular limb.

Before a new task was introduced, all combinations of eye and hand were brought to the criterial level of learned performance. The course of forced learning gave further information about the mechanisms underlying choice of a hand, and enabled comparison of the guidance of the two hands by a single eye and associated visual system.


A. Spontaneous changes of limb use during binocular and monocular training.--The distribution between the two hands of total moves made in each group of ten trials and of errors between the two hands, was followed from group to group of trials. The result for 3 subjects are shown in Figures 15 and 16.


The thick vertical black bars which lie across the line dividing left-hand moves from right-hand moves, are proportional in length to the number of errors made, and their position relative to the midline indicates how many of these errors were made by the left hand (above the line), and how many by the right (below the line). The distributions of all moves between the two hands in the groups of ten trials are indicated by the position of the thinner vertical lines.



TRIALS OF TRAINING

FIG. 15 — DISTRIBUTION OF ERRORS AND TOTAL MOVES BETWEEN HANDS.  
SUBJECT CHC.

END OF A DAILY TRAINING SESSION IN (a)  TOTAL MOVES

CRITERIAL PERFORMANCE  ERRORS

Use of the Limbs by Subject CHC when Learning Task A

(a) Learning with both eyes open and contradictory cues for the two eyes.--Limb use and the distribution of errors are shown for CHC-A in Figure 15. The first portion, a, of 350 trials, shows the changes which occurred spontaneously during training with both eyes open.

This subject was young and excitable and, particularly in the early training, moved feverishly and obviously without perfect control over choice of limbs for the response. During two days of preliminary training without polarized visual cues, CHC showed a tendency to push mainly with the left hand, and usually to the left button. But, occasionally the right hand would move and push at the button on the right side.

When the polarizing filters were placed in front of the eyes, causing the polarized response buttons to appear of differing brightness, but in opposite ways to the two eyes, the left hand remained dominant, and the score showed no evidence of visual learning. After 20 trial moves the right hand displaced the left to some degree and this change was accompanied by a slight but distinct improvement in the score. The first 2 changes of limb use show correspondence with the daily sessions of training which are indicated in Figure 15a, by vertical black arrows at the end of each day's training. Thereafter changes occur almost independently of the training schedule.

Significant correlation between the choice of moves and the visual stimuli occurs after 250 trials and continues until criterion is reached at 380 trials. In the intervening period, the right hand becomes more and more active, and finally 19 of the 20 criterial trials are performed with this hand. After criterion there is a drift towards use of the left hand, but almost no errors are made. This is suggestive of an effect on the choices made by the left hand of learning made first with the right.

Of the 211 trials made with the left hand in attaining criterion, 101 or 48% were errors. The right hand was responsible for 119 trials of which 38 or 32% were errors.

b) Learning with alternate use of right and left eyes alone.--Figure 15b shows the performance on tests given with alternate periods of training to the two eyes. These tests followed immediately upon the binocular training described above.

A first period of 50 trials with the right eye indicated poor retention; 27 or 54% of the attempts were errors. Of the 50 pushes, 43 or 86% were made with the left hand. The sudden shift of limb use is striking. In the immediately preceding 50 trials of binocular training but 20% were made by the left hand.

The change of limb use apparently left an effect on the following performance with the left eye alone. In 70 trials there was a gradual shift back from use of the left hand. In the first 40 trials many errors were made but then performance improved suddenly. At the conclusion of this first training of the left eye 10 trials were made without error ( $p = 0.001$ ), and half of these were made with each limb.

During the remainder of the alternations of eye use the performance with the left eye quickly attained a high level of retention in which 10.5% of errors were made over 200 trials. Of these 200 moves, 93% were made with the right hand. Meanwhile the performance with the right eye rose to a criterion after a total of 120 trials of training. Then, with increasing confusion of movements in which right hand became more and more dominant, performance fell to the 50% level of correctness once again. There is no doubt that a tendency to use the right hand came to over-shadow the learning by the right eye and finally prevented expression of this learning entirely. On the last 100 trials, 89 were made by the right hand, and with a total of 44 errors all made by the right hand.

A correlation between use of a limb and visual direction by the eye of the opposite side of the body is revealed by these results, and apparently the learning, made first by the left eye with the right hand, stabilizes



the use of the right hand. When the right eye was forced into use alone learning occurred only for the brief period in which the left hand asserted some prominence. Thereafter the increasing number of moves by the right hand brought poorer performance.

Presumably, the improvement of performance toward the end of binocular training, since it occurs with an increase of the use of the right hand, reflects learning by the left eye. The inferior performance by the left eye when in use alone probably reflects an interference by the 50 preceding trials of training with the right eye in which the left limb became dominant.

c) Extended training of the right eye (fig. 15c). --In more than 500 trials of training to the right eye alone, use of the right limb was gradually suppressed between the 100th and the 250th trials. The criterion of learning was satisfied at the intermediate point after 170 trials of this training, when 10 of the 20 moves in which no errors were made were performed by each hand. Thereafter no errors were made by the right hand. Once the contralateral left limb had finally reached full dominance, performance fell once again; in the final 200 trials a position preference appeared, and 46.5% of the moves were in error.

When, by insertion of a barrier to left hand moves (see fig. 19 , p.109), the right hand was forced to make all of 20 responses, only one error was made. Immediately afterwards, when the left hand is forced back into use, learning occurred and within 40 trials, the criterion was satisfied for the third time with use of the right eye.

Extended use of the right eye has here led to the replacement of the right limb by the left, thus demonstrating a second contralateral pairing tendency. But retention falls with increasing dominance of the left hand, until forced change of movement satisfies some requirement for learning by the left hand-right eye combination.

In the final phase of the right eye training (fig. 15c), in which the left hand had become responsible for execution of the adequate response in each trial, the movement fell into a stereotyped pattern. In each trial a move was made by the left hand to the left response button. Immediately after each false move, the right hand made a correcting push of the right button which, however, failed to gain the subject a reward. Thus we see that the activity of the left hand was undirected and the right hand, though unable to make moves before the left hand was able to discriminate correctly between the visual cues. Hence the immediate retention by the right eye when the moves of the left hand were excluded. Once attempts by the right hand were prevented in turn, the left hand perfor-

mance quickly improved to a criterion which remained more steady than any previous performance with the right eye.

d) Extended training of the left eye alone (fig. 13d).--As had come to be expected, return to the left eye after long training of the right eye left a residue of interfering habits which prevented immediate retention of the learning already achieved by the left eye. In the first 50 trials, 60% of the moves were made by the left hand, but the right hand readily regained dominance and in the 100th to 200th trials 84 were made with the right hand. A second criterion for performance with the left eye was gained at 70 trials, and performance steadily improved over the remaining 300 trials. In the total 380 trials, 90 or 24% were made by the left hand and of these 62% were errors. In 290 moves by the right hand there were 35 errors (12%).

#### Comparison of Subjects IGR and BRS with Different Tasks

An analysis of limb use similar to that made above for CHC, was made when IGR and BRS were learning a variety of visual tasks. The observations on use of limbs and distribution of errors between the two hands were made concurrently with the visual learning tests described in Section II (pp. 53-72 ). The visual stimuli (B through O) have been shown in Figure 5.

TABLE V  
Number of Correct and Incorrect Moves by Each Hand  
Under the Three Conditions of Vision.  
The 20 criterial moves have been excluded

Subjects	Tasks	BE				RE				LE			
		LH		RH		LH		RH		LH		RH	
		+	-	+	-	+	-	+	-	+	-	+	-
IGR	B	117	115	236	252	20	13	62	65				
	C	212	181	7	1								
	D	100	109		1					14	47	26	13
	E	75	65	5	5	5	5			79	46	13	12
	F	93	87							65	44	1	
	G	19	11							72	37	1	
	H	12	8							42	55		3
	I	9	11							36	23		1
	J	-	-	-	-	-	-	-	-	-	-	-	-
	K	12	8			14	6			23	7		
	L	55	35							90	50		
	M	20	10							38	31	17	4
	N	10	9	3	5					14	4	22	20
	O	-	-	-	-	5	5			1	1	6	2
BRS	B	298	272							118	88	4	
	C	12	9	21	18	8	2			16	24	32	18
	D	42	28							18	15	5	2
	E	17	23			15	15			31	28	32	32
	F	37	36	5	2	14	2	13	1	-	-	-	-
	G	-	-			-	-	-	-	3	9	17	11
	H	12	5	13	10					-	-	28	21
	I	11	8	1		6	4			33	18	59	30
	J	7	2	6	5					8	1	-	1
	K	8	2			-	-	-	-	-	-	-	-
	L	-	-	-	-	-	-	-	-	9	8	-	3
	M	-	-	-	-					10		6	4
CHC	A	110	101	81	38	32	24	27	19	12	8	9	

BE = Binocular training with contradictory cues.

RE = Forced use of the right eye alone.

LE = Forced use of the left eye alone.

LH = Left hand moves.

RH = Right hand moves.

+ = Correct moves; - = incorrect moves.

Moves made during binocular and monocular tests described in Section II are shown in Figures 16a-f, for Tasks B, C and D, and information about the performance on other tasks is shown in Figures 17 and 18.

The overall distributions of activity between the hands during learning for all tasks B-O are summarized in Table V for IGR and BRS together with similar data for CHC. The distributions of activity for the 20 criterial trials of binocular and left and right eye learning are presented in Table VI.

#### Binocular Learning

When first introduced to the training situation with Task B neither IGR nor BRS showed the wild fluctuations of limb use, which were seen with CHC (fig. 15a). Figure 16a, shows that IGR made two shifts of hand before criterion was reached and finally learned with the right hand. The two shifts at the beginning of training and again after 250 trials of training, as well as a partial shift toward use of the left hand at 400 trials of training, each accompanied some distinct change in the score (cf. fig. 15a, p. 89). In the intervening periods, most of the groups of ten trials were occupied by unbroken position preferences. In the first 40 trials most moves were made to the left screen by the right hand; later many groups were made up of pushes by the left hand to the left screen. Finally, before the terminal learning, many moves

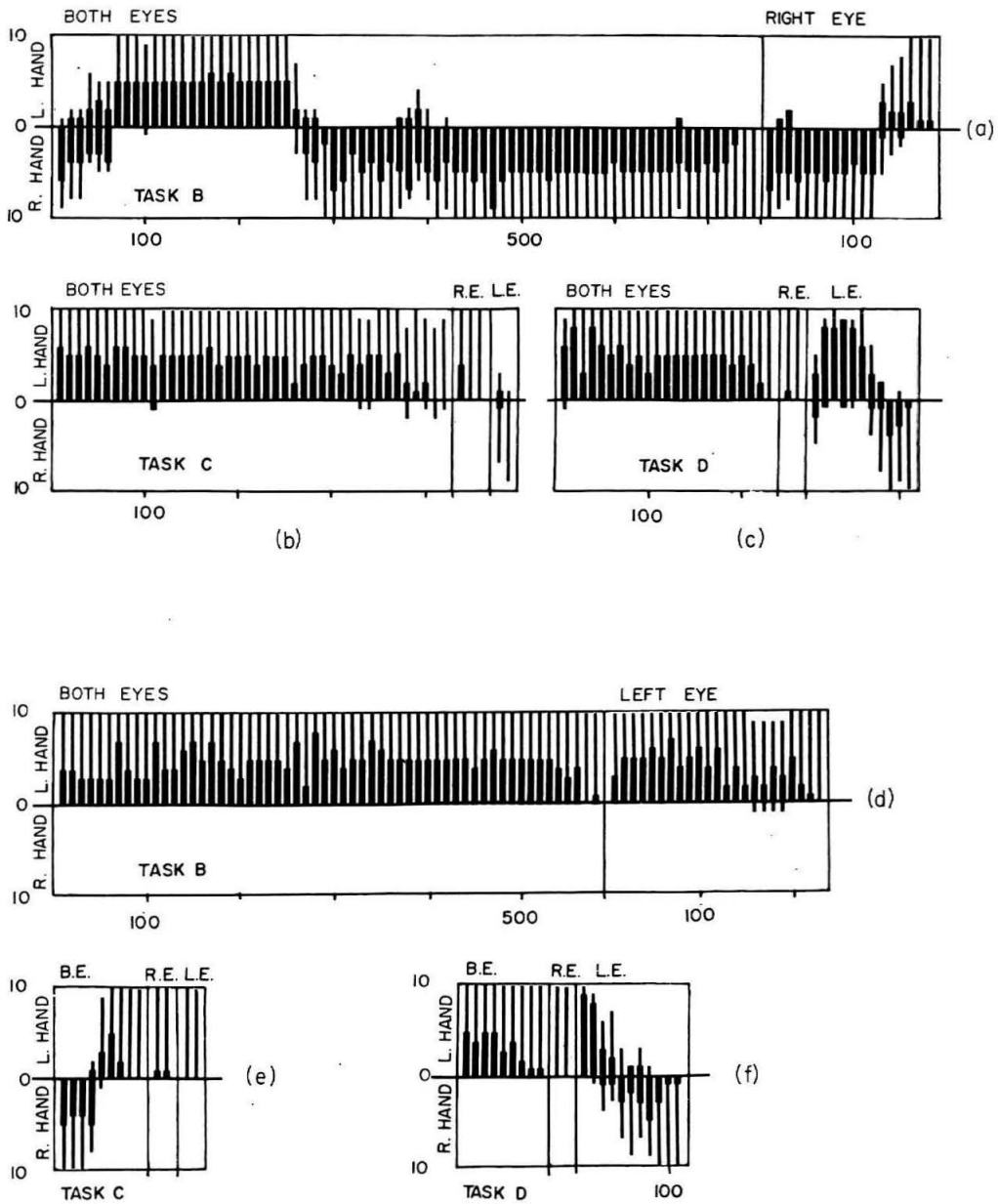


FIG. 16 - DISTRIBUTION OF ERRORS AND TOTAL MOVES BETWEEN HANDS.  
SUBJECTS IGR AND BRS, FIRST THREE TASKS. (cf. FIG. 10)

were made consecutively by the right hand to the right screen. These effects compare with the changes already described for CHC working with the right eye (cf. fig.15c, p. 89).

With the same Task B, BRS maintained an unbroken use of the left hand. A position preference appeared for the left screen shortly before the final learning occurred (fig. 16d).

In Task C (fig. 16b), IGR learned with the left hand almost exclusively, and in the following 10 tasks continued to be consistently left-handed. Likewise BRS was predominantly left-handed throughout the series of tasks when learning binocularly. These preferences are clear from Table V.

Some irregularities are to be observed in the records of BRS (cf. figs. 16e; 17c; 18e; for tasks C, F, J, H) and, to a less extent, in some of the learning of IGR (tasks E, fig. 17a; and N, fig. 18c). It is possible to relate these to the preceding learning in which modified use of eye or of limbs, or both, were used. Each task was trained close upon the concluding experiments with a previous task and, as will be described, tests were made with forced eye-hand combinations in each case.

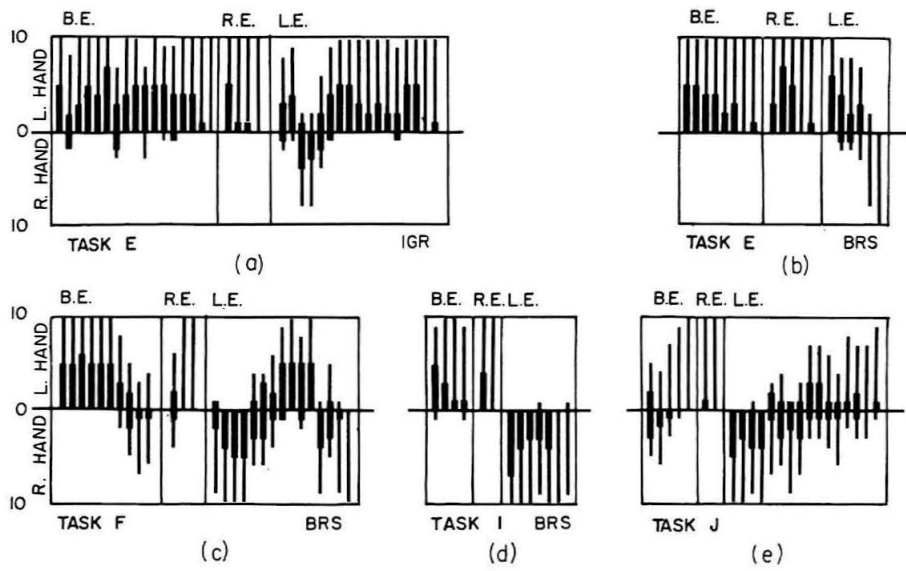
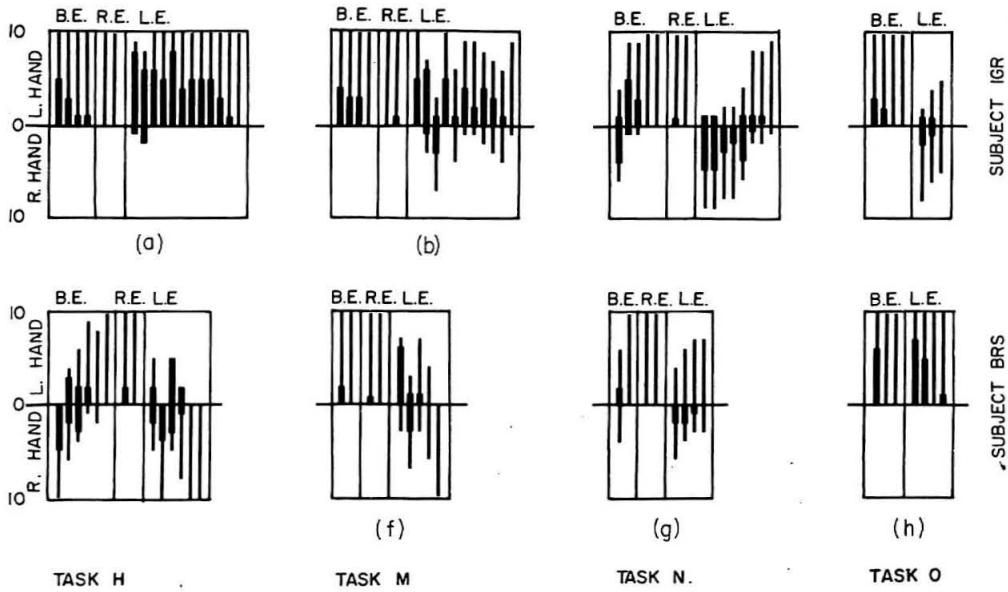


FIG. 17 - HAND USE OF IGR AND BRS ON VARIOUS TASKS. (cf. FIG. 11)





(cf. FIG. 11)

FIG. 18 - HAND USE OF IGR AND BRS ON BRIGHTNESS AND COLOR TASKS.

Visual Retention and Limb Preference

a) The dominant eye-hand pair.--Table VI shows that, except for the cases of IGR-B and BRS-F, binocular learning was completed with almost exclusive use of the left hand by both subjects. It has been shown with the aid of data summarized on Table II that almost all tasks were near perfectly retained by the right eye (cf. p.69 ). The most noticeable exceptions are IGR-B and BRS-E. In the former case there was perfect retention of learning by the left eye after binocular training and retention by the right eye.

Retention by the eye contralateral to a preferred limb was not immediately perfect in all tests. It was noted when discussing the results of CHC that training of the least retentive eye interfered with retention by the eye which was presumed to be active during binocular learning (cf. p.92 ). Training of the preferred eye was made without interruption as soon as binocular learning was completed. Nevertheless, there is some indication in many tests of a brief set-back in performance. Sometimes, apparently with more confusing tasks, this disadvantage of monocular attention was more marked; e.g. IGR-E, BRS-E (fig. 17a,b).

b) Forced use of the least favored eye and change of hands.--In many cases forced learning by the least retentive eye was accompanied by a shift of hand

TABLE VI

Distribution of Criterial Moves  
Between the Two Hands

	Task	LH	BE	RH	LH	RE	RH	LH	LE	RH
Subject CHC	A	1		19	10	10		9		11
	B			20	20					20
	C	18		2	20			4		16
	D	20			20					20
	E	20			20			20		
	F	20			20			20		
Subject IGR	G	20			20			20		
	H	20			20			20		
	I	20			20			20		
	J				-		-	-		-
	K	20			20			20		
	L	20			20			20		
	M	20			20			15		5
	N	20			20			17		3
	O	-		-	20			9		11
	B	20			20			20		
Subject BRS	C	20			20			20		
	D	20			20					20
	E	20			20			2		18
	F	7		13	20			1		19
	G	-		-	-		-	-		-
	H	18		2	20					20
	I	19		1	20			1		20
	J	16		4	20			16		4
	K	20			20			11		9
	L	-		-	-		-	-		-
	M	20			20			5		15
	N	16		4	20			14		5
	O	-		-	20			20		

BE = Both Eyes RE = Right Eye LE = Left Eye LH & RH =  
Left and Right Hands.

use, sometimes immediate, often gradual, towards the alternative side. In this way the second contralateral eye-hand pair was brought into effect spontaneously.

IGR showed such a shift in each of the first three Tasks, B, C and D (fig. 16a,b,c). The change of hands was made with Task B only after more than 200 trials of nervous and erratic moves by the right hand while the right eye was forced to use. The shift to the left hand is accomplished progressively in 40 trials during which the score fluctuates about an intermediate level halfway between random and fully learned. With Task C in which retention by both eyes was excellent (cf. p. 60), the shift of hands from left to right seen when the left eye was forced into use was rapidly accomplished. In the second group of 10 trials only one was made by the left hand.

In Task D a remarkable correlation was observed between negative performance, indicative of interocular transfer of learning (cf. p. 65), and continued use of the left hand. Coincident with the shift, after 60 trials of monocular training, there was a reduction in the percentage of errors. Within 30 trials the shift was completed and criterion was attained in the next 40 trials. We see here two results of the exchange of hands. First, the preferred contralateral pairing is

reestablished; and secondly, suppression is achieved of an inappropriate engram which was transferred from the right eye.

From Figure 16d,e,f, it may be seen that subject BRS reacted with less tendency to transfer hands. Tasks B and C were learned with only one brief suggestion (in B) of a shift to the inactive right hand. But again, a complete exchange was made for task D and a similar correlation of erroneous moves with use of the ipsilateral (left) hand was recorded. (See p. 65.)

In the learning of the remaining tasks IGR showed decreasing tendency to change from use of the left hand. Many tasks were learned with the ipsilateral combination of left eye and hand. A temporary exchange of hands is seen in Figure 17a, for learning of Task E by the left eye. Of the remaining tasks, only D, M, N, and O show change of hands (cf. figs. 17c; 18b,c,d, tables V and VI), and these are tasks involving brightness or color discrimination and which have relatively large error scores for the left eye.

BRS, is more inclined to use both limbs in later tasks, but does not invariably retain use of the contralateral limb for final learning to criterion. This is apparent from Table VI. Task J (fig. 17e) is learned after immediate shift to the contralateral hand and during a subsequent slow replacement of right hand moves by left

hand moves. Compare the learning by IGR of N with the left eye (fig. 18e). It is clear for BRS, as with IGR, that those tasks in which transfer occurs, or is presumed to be incipient (i.e., brightness and color discrimination tasks D, H, M, N, O), are the ones in which it is most likely there will be a shift to use of the right hand when the left eye is forced into use alone.

c) Interocular transfer of learning and use of the "least retentive" eye with the ipsilateral hand.-- Whenever a significantly higher than random proportion of errors are made by the subject when forced to use an eye which has been least favored by learning, these errors are made in large part by the ipsilateral hand. This leads to the excess of errors over positive choices in Table V for the left hand performance with the left eye for IGR-D, IGR-H, BRS-D, BRS-H and BRS-O. Frequently, as has been observed, this source of false moves becomes controlled when the subject exchanged hands. IGR-H and BRS-O (fig. 18a,h) form the only clear exceptions to this rule. Nevertheless, there is at first a definite excess of errors in these cases, too.

d) The relationship between visual learning and shift of limb use.-- It is most important to determine if any direction can be given to the relationships between limb performance and visual discrimination learning. Does the visual process proceed to a given stage of completion,

and then call upon a particular limb for execution of chosen, directed responses? Or is it that the general stimulation first causes an ipsilateral limb to become active, and then visual attention and learning of the discrimination occur in consequence of the developed limb activity?

Some information bearing upon this point may be obtained from the performance figures.

In those cases where change to a contralateral limb occurs during training of the unretentive eye, the first group of trials in which the limb is newly active contain a proportion of errors close to that which would occur if the visual discrimination were as yet unlearned. This is apparent for example in the following cases:

Fig. 16a,c.     IGR-B, IGR-D

Fig. 16e,f.     BRS-C (binocular learning) BRS-D

Fig. 17a,c,d.   IGR-E, BRS-F, BRS-I

Fig. 18c,e.     IGR-N (binocular)

BRS-H (both binocular and left  
eye learning)

Comparisons may be made with the delayed learning of CHC with the right eye and left hand (cf. fig. 15c, p.89 ). In this case, however, the apparently blind activity of the contralateral limb does not begin immediately, and persists for a long period of training.

In contrast, a spontaneous return to use of a contralateral limb, after learning has been already accomplished for the eye in use, may be accompanied by a very few errors. This is shown three times by CHC; first at the end of binocular training, again with use of the left eye in the period of alternating monocular training (fig. 15a,b, p. 89) and finally when the left eye is brought back into use after extended training of the right eye alone (fig. 15d, p. 89).

B. Special features of ipsilateral eye-hand association.--It has been observed that subject CHC was unable to sustain good learned visual discrimination performance during extended training when the right hand was active under direction of the right eye (figs. 15b,c, p. 89). Likewise the left eye and left hand work together badly in this case (fig. 15b,d). Not only do these ipsilateral pairs exhibit defect of learning and retention, but the proportion of errors appears to vary erratically although use of the ipsilateral limb in each case was voluntary.

Compulsory use of the ipsilateral limbs during monocular training has been studied with IGR and BRS. As in previous experiments, monocular attention was forced by placing a blackened metal flap over the alternative eye window. Limb use was altered by insertion of a horizontal shelf across one half of the arm slot of



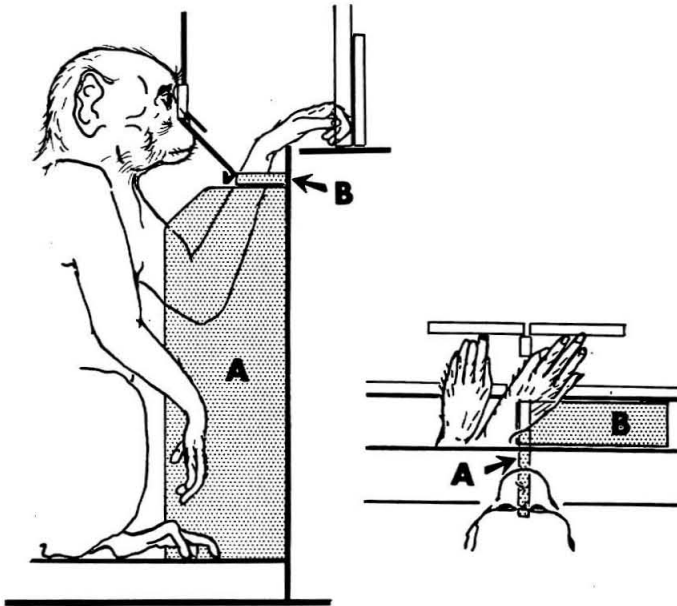


FIG. 19 — CONTROL OF LIMB-USE.

**A** VERTICAL PARTITION

**B** BARRIER PREVENTING USE OF  
RIGHT HAND

LEFT HAND SHOWN PUSHING TO L. & R.

the training box. A central vertical piece which separated the elbows of the subject and made "cheating," by reaching with a preferred hand from the other open side of the arm slot to the response screens, impossible. These insertions for control of limb use are shown and explained in Figure 19.

Training with ipsilateral pairs of eye and hand led to results shown in Figure 20. The two subjects were trained to criterion for each combination once criterial performance had been attained for binocular and monocular learning with free hand use. Thus each half-brain had been proven to have knowledge of the task presented to it.

In spite of this previous training, retention by either eye with forced use of the limb of the same side of the body was uncertain for both subjects in Task B. When learning had occurred preferentially with the left eye and right hand (IGR-B), the left eye and hand performed very badly together, high levels of performance being attained only three times and for 10 or 20 trials over a total of 300 trials of training. Position habits stood instead of discriminative performance, and the improvements when they did occur were sudden, as if recall had occurred all at once. A total of 140 or 47% of errors were made in the 300 trials. Rather fewer errors (35%) were made in a similar erratic performance with the right eye-hand pair.

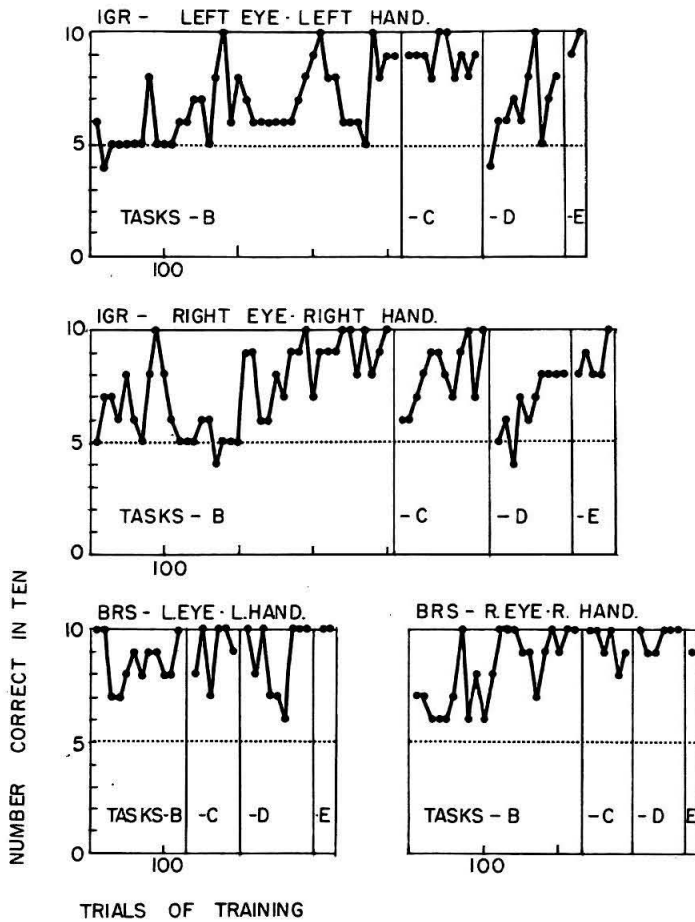


FIG. 20 - IPSILATERAL EYE - HAND PAIRS.

In the case of BRS learning Task B, however, retention was relatively strong with the left eye-hand pair. In the first 100 trials 17% of errors were made by the left pair while 31% of errors were made by the right pair.

These differences in ability may reflect the different use of the hands by the two subjects. IGR learned Task B mainly with the right hand, while BRS showed a preference for learning with the left hand. In the subsequent three tests the ipsilateral performance remains uncertain and there are sudden losses of ability to choose correctly, but there is a clear improvement overall, and by the fifth task each subject appears to have gained control of ipsilateral eye-hand performance.

It was noted that when forced to use an ipsilateral eye-hand pair for learning or for execution of a previously learned task, split-brain animals invariably appear more uncertain and make the movement with less control. They frequently fumble and seem unable to direct the hand accurately. Nevertheless they are able to manipulate familiar objects, such as peanuts, with little sign of difficulty. The periodic fall of performance from high levels of choice to near random levels is reminiscent of the erratic curve observed for the normal subject, ELZ, working with conflicting visual cues. Similar swings of the learning curve have been noted for monocular learning by the least

retentive eye of split-brain subjects trained with conflicting visual tasks (cf. p. 85). Here, however, the conflict leading to poorer performance may not be purely a consequence of convergence of visual processes.

It has been noted, in the tests with subjects CHC, IGR and BRS, that learning by the least retentive eye frequently occurs with the ipsilateral hand. If an exchange of hands occurs towards a contralateral eye-hand combination, this is quickly followed by learning and erratic performance ceases. It seems that the inability to execute choices arises from some conflict within, or intimately connected with, the motor sphere; an uncertainty about the form of the response which must be resolved before learning and stable retention may occur. It is of interest to note that even spontaneous choice of an ipsilateral hand for use with a given eye, presumably when there is a strong preference for the limb in question in any circumstance, may result in a poor performance and slow learning (for example, see learning of CHC-A with the right eye, fig. 15c; and of IGR-E with the left eye, fig. 17a).

C. Limb use in two subjects with additional mid-brain surgery.--The subjects JNY and HDN, which were trained subsequently to surgery extended to the roof of the midbrain (see p. 73), both showed consistent preference for use of the left hand. JNY never changed hands from left to right

spontaneously, even when transfer of brightness discrimination was observed with use of the left eye (p. 76). A restlessness, during which the right hand came close to the response screens and made gestures as if to respond, occurred on one or two occasions when the left eye was used for inappropriate, transferred guidance of response.

HDN, like IGR and BRS, did show a spontaneous shift of performance on occasions when attention was forced to the left eye and transfer of learning occurred. This is shown in Figure 21 where the weak tendency to change across to use of the right hand was strengthened by a period of 250 trials of forced use of the right hand. In this period, which is indicated in the figure, many moves were made to the right response screen, and this position preference was broken occasionally for periods in which weak negative choices based upon the transferred engram were made. The forced right-hand training occurred, as may be seen in the figure, shortly after a spontaneous shift in this direction had taken place.

Towards the end of training of the left eye, after more than 1000 trials in which no learning occurred, a spacer was inserted between the response screens to simplify the task as well as to control clumsy hand movement (see p. 78). This change immediately resulted in a brief reversion to use of the left hand and then the right hand was again brought into use and significant learning followed.

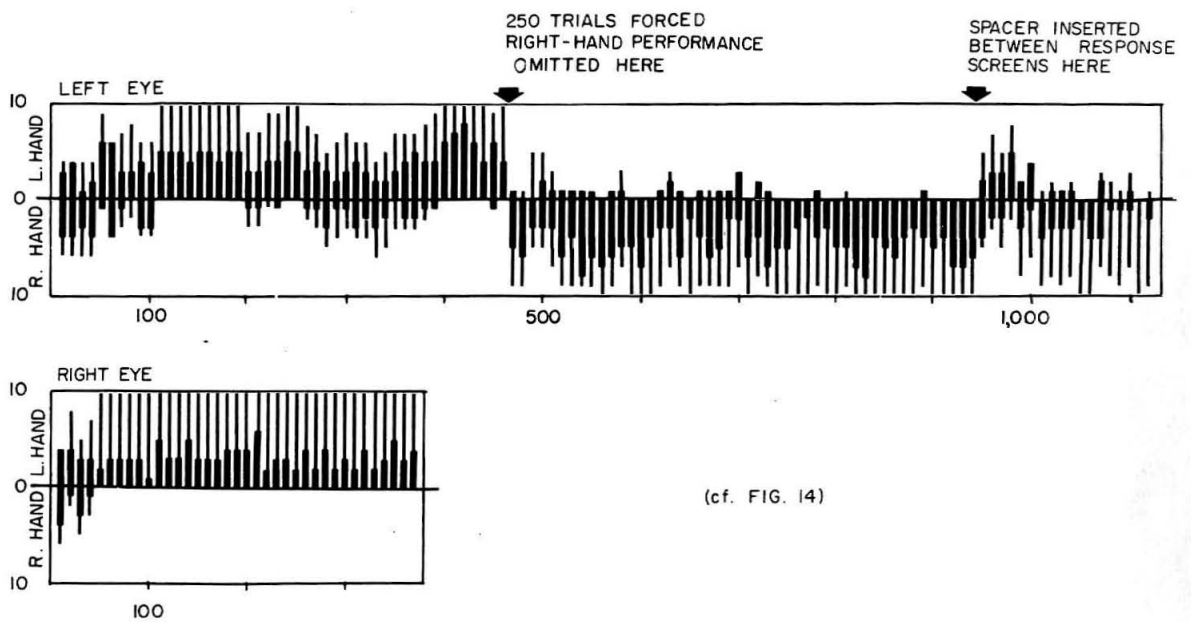


FIG. 21 - HAND USE OF SUBJECT HDN; BRIGHTNESS DISCRIMINATION.

When a switch was made to use the right eye, a weak transfer occurred in the first group of 10 trials which were half right-handed. The left hand then immediately gained all responses, and 300 trials were performed at an intermediate level which indicates partial retention.

### Summary and conclusions for Section III

Careful observation of the distribution of hand movement between the limbs has revealed that there is a strong tendency for split-brain animals to develop a preference for a particular hand as normals have been found to do. But the division of the brain reduces the stability of a choice, and spontaneous changes of limb use were observed when both limbs were free to respond. These changes were found to be closely related to the balance of visual learning between the two eyes.

Subject CHC (fig. 15) showed spontaneous exchange of hands several times in the course of binocular learning with contradictory stimuli. This suggests an inability to develop a habitual use of one limb. Nevertheless, learning was correlated with increased numbers of moves by the right hand and finally a right-hand-preference developed coincidentally with the attainment of a criterial score. When monocular tests were made it was found that the learning during binocular training was best retained by the left eye.



During a period of alternated monocular tests with left and right eyes, the right hand was at first active with the left eye, and vice versa. The contralateral combinations appeared spontaneously following restriction of vision to one or other eye. Gradually, near perfect retention was sustained by the left eye, and the right hand came to dominate even when the right eye was forced to use. There was a corresponding deterioration of score with the right eye.

It is concluded that activity of a given limb is associated with learning and retention by the contralateral eye and furthermore, that limb preferences are refractory to change. Extended alternation of monocular vision by the two eyes leads to retention of one limb at the expense of visual function by the eye of the same side of the body.

When training was continued over many trials with the right eye alone, the left hand became active supplanting the right, and the score showed an improvement. Then uncontrolled movement led to a fall of the score. Left hand pushes were apparently distracted while the right hand regained activity. Forced use of the hands one at a time was followed by the improvement for both combinations with the right eye. A return once more to the left eye was accompanied by a spontaneous shift to the right hand. Errors were made while the left hand remained most active.

On the basis of these observations, subsequent training was made to include forced training of all eye-hand pairs which were not spontaneously active. Comparisons were made between spontaneous and forced eye-hand associations.

Fluctuations of limb use in binocular training were less in evidence for subjects IGR and BRS over a series of tasks (figs. 16,17,18). However, position preferences, possibly indicative of a degree of conflict in choice of a limb, were conspicuous before final learning. In almost every case, learning was accomplished with dominant use of one hand. Early in the series of tasks, IGR showed a shift of dominance from right to left hand. Thereafter both subjects remained primarily left-handed when trained with both eyes open. Interference effects were noted to result from forced training patterns of tasks preceding one in which free choice of limbs was measured. These effects are evidence of the slow equilibration changes of limb habits which have already been referred to.

In almost every case there was good visual retention by the eye contralateral to the limb chosen for execution of the final trials in binocular learning. Since most binocular tests were learned with use of the left hand, this implies that visual retention by the right

eye was complete. The left eye, however, showed various degrees of retentiveness as has been described in Section II.

When a survey was made of the behavior following restriction of vision to the least retentive eye, a tendency was observed for use of the hands to change, and so a second contralateral association was formed. This tendency showed a decrease as the subjects became more practiced in working and learning with all eye-hand combinations. More definite change of hands was found to occur with certain tasks, particularly those in which there was interocular transfer of visual learning. The two subjects differed in their tendency to exchange hands, the younger (BRS) being both more versatile and quick to change.

Whenever interocular transfer was observed as a significantly proportion of errors in the early choices by the least retentive eye, these errors were made predominantly by the ipsilateral hand. Exchange of hands frequently led to a control of errors.

When a shift to a contralateral limb occurred for the first time in the new training of a particular eye, the first groups of trials during the shift contained approximately half of the errors indicating that learning had at this stage still no effect. A spontaneous return to use of a contralateral limb after learning has occurred may, however, be accompanied by almost no errors. There-

fore it is concluded that, though visual learning may be expressed immediately upon change of hands, a shift of hand use may occur before learning takes place. The change of limb use may, in fact, be regarded as a causal factor in visual learning. Moreover, since no evidence of previous visual learning was obtained for the least preferred eye on several occasions, it is concluded that this eye was truly inactive with respect to reception of the visual cues during binocular training.

Performance with forced use of eye and hand of the same side of the body was, in early tasks, most erratic and inefficient; even though both eyes had been shown to know their respective directions of choice. There appeared to be a slight advantage in favor of the ipsilateral eye-hand pair which included the dominant limb. The ipsilateral performance improves over the series of tasks until, by the fifth task, little training is needed for a critical level of retention to be attained. However, at no time does ipsilateral performance remain for extended periods as efficient as that for contralateral eye-hand associations.

Over all the tests of visuo-motor association, the impression was gained that visual learning is dependent upon equilibration within the motor sphere; or,

rather, upon determination of a form of response by forces which do not include visual recognition of the correct cue projected on one of the response screens.

Subjects with midbrain roof divided, in addition to separation of the hemispheres and section of the chiasm, showed substantially the same results as described above. There was, nevertheless, in two cases, a greater refractoriness in use of limbs. In one case a preferred limb was used exclusively, even for performance with the ipsilateral eye. The alternative limb was, however, brought eventually into efficient use when the preferred limb was restrained. In the second case, the least preferred hand became spontaneously active during slow learning of a brightness discrimination by the least retentive eye after interocular transfer of learning had taken place. This shift was stabilized by a period of forced use of the least preferred hand alone.

## CHAPTER IV

### DISCUSSION AND CONCLUSIONS

We have presented the results of thirty-two experiments in which split-brain monkeys were simultaneously confronted with two contradictory visual tasks, one seen by each eye. In all cases at least one of the tasks was learned in approximately the same time as a normal subject would take to learn either one of them and there was little or no sign of conflict. There were six cases in which the two eyes appeared to learn simultaneously, the most significant of these occurring when two chiasm-callosum sectioned monkeys were required to make a discrimination between two simple and distinct patterns early in their training. In the majority of the tests, however, one eye was distinctly superior in retention, the second eye remaining to some extent naive at the end of the learning with both eyes open.

After completion of the binocular training and of the monocular retention tests, the less retentive eye was forced into use alone. It was found that some visual problems were acquired more quickly in this second training than they had been when both eyes were open. Pattern discrimination tasks differed in the ease with which both

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\*Task C: circle versus cross.

eyes could be trained to retain their respective contradictory interpretations simultaneously. There were other cases in which learning by the dominant eye during binocular training transferred to the second eye so that the subject showed preference for the unrewarded stimulus when forced to use this eye alone.

At the conclusion of every experiment, whether there had been transfer of learning or not, each eye retained its respective problem. A double memory, comprising two equal but opposite components was held in the two halves of the brain. In the circle versus cross test mentioned above, this double memory was completed by a process of simultaneous learning in both halves of the brain, as if each eye was connected to an independent and intact brain. Previous experiments which were reviewed in the introduction have indicated that two visual systems more or less equal and complete in their learning capacity, are created by split-brain surgery. Although the output of the trained split-brain is usually a single habit, a uniform general method of response by a chosen hand, the double learning mechanism may include duplicate components of such intrinsic features of learning as attention, motivation, expectancy and preparation to respond in a particular direction.

Signs of inattention or of shifting attention were observed in tests with one eye at a time. In those cases where one eye was superior to the other in learning the performance with the second, less retentive eye did not suggest that it was merely lagging in an independent way. It was, rather, as if this eye had an active selection imposed against it by some internal process of choice which remained in operation for a time when the eye was forced to see the stimuli. The subject sometimes showed signs of temporary excitement and confusion when vision by the dominant eye was blocked, and the performance often fell at once to a low level. Thereafter learning always did occur in time, and, as we have said, a coexistence of the contradictory learning traces could eventually be established in every case. At the same time there were characteristic signs that this forced learning with the least preferred eye was imperfect, presumably because of the persisting effects of attentional or other kinds of set favoring choice of the dominant eye.

Periods of negative preference due to interocular transfer of learning were brief. The contradiction of choice implied in the lack of reward which followed restriction of vision caused subjects either to abandon choice based on visual cues for a time, or, more characteristically, to quickly reverse choice so that the responses became appropriate and rewarded. After this



reversal of choice both contradictory memory traces were retained separately by the two halves of the brain. Hence we must assume that the visual learning mechanisms of brightness discrimination for the two eyes, though overlapping, are still capable of separate use. Evidently they are not completely convergent.

Where unbalanced learning was not accompanied by outright transfer of meaning from eye to eye, one may assume a subliminal conflict between the two contradictory pairs of stimuli because of partial overlap of the perception mechanisms; that this conflict led, in turn, to an internal adjustment consistently in favor of the use of a visual system of one eye. We have proposed a tentative working hypothesis which distinguishes discriminations showing interaction from those for which learning proceeds independently in the two visual systems of the split-brain (cf. p. 67). Interaction was found, on the basis of a small population of tests, to be more likely when the paired figures to be discriminated belonged to one generalized class (e.g. stars) but differed in one limited dimension (number of vertices). More distinct figures with larger, more redundant descriptions and fewer common features (e.g. cross and circle) may be recognized by independent processes confined within the two hemispheres and contradictory discriminations of this kind do not interact to produce confusion of the

perception processes. Theoretical considerations of economy and efficiency in perception processes make such a classification in terms of the description of the stimuli attractive.\*

Empirical evidence that common features of pairs of figures to be discriminated may form a bridge for inter-hemispheric communication in the split-brain is provided by the experiments reported in Appendix II (p.148). Two split-brain animals which had previously acquired the two contradictory discriminations between a circle and a cross simultaneously, and therefore separately, in the two halves of the brain, were shown to be capable of comparing the sizes of circles received separately by the two eyes. The correct response here requires some manner of convergence of information from the two eyes defining the size of each circle. If such sensory-sensory association of complementary inputs is possible, it seems likely that interaction would occur between contradictory inputs to the two eyes to produce conflict within perception and learning processes.

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\* Cf. for example, hierarchical response mechanisms outlined by MacKay in his description of an intelligent automaton (53).

At the present stage of knowledge, however, a more significant correlation with the inequalities of learning by the two eyes is provided by the symmetry of the response, and arises as a result of sensory motor association processes. As has been pointed out in the introduction (p. 8 ), use of the forelimbs for response offers opportunity for asymmetric involvement of brain parts in processes of sensory-motor association. Split-brain monkeys have a bias for visual attention by the eye contralateral to the limb which is habitually used for response (cf. p. 116). This bond between eye and hand of opposite sides of the body is a consequence of surgery and follows from the anatomy of the motor regulating structures; in particular, the crossing of the efferent pathways in the brain stem. That this is, however, a bias rather than a rigid sensory-motor association of eye-hand pairs is indicated by those cases where ipsilateral eye and hand have learned freely, and by the pattern of learning when less preferred combinations of eye and hand are forced into use (cf. pp. 105 and 108).

The observed development of motor habits and the changes which follow from various experimental alterations of behavior may be summarized as follows.

1. All other things being equal, there is developed a preference for use of a single limb for responses as learning begins. Later, if there is no change in the

nature of the task, this limb is used exclusively for responses. Learning of new things is more rapid after this habit is set, and remains so as long as it is not disturbed.

2. When both eyes have connections to separate halves of the cerebrum and when incompatible visual tasks are presented, both may become coupled with a learning change and both may be subsequently effective alone in directing the response. If one eye only learns, it is the one which is connected to the half of the brain also possessing more connections to the limb chosen for response.

3. Attempts made to alter conditions of stimulation, or to change the hand used by the subject for response, reveal a refractory habit to which the subject is strongly committed unless extensive training has been given in alternation of hand use. This stubbornness is seen even when a change would result in a more favorable contralateral combination of eye and hand. The habit to make a complete set of response movements with a particular hand is seen when responses are made in absence of critical ones, e.g. when the cue-tone for a trial is presented while both eyes are covered by opaque flaps.

4. This refractory habit does, however, change spontaneously in time when a previously inactive ipsilateral eye is forced into use by covering the preferred eye. When

first presented with the unknown or misjudged task associated with the hitherto "inattentive" eye, the inappropriate responses are made with the preferred hand according to established habit. Then, through a phase of disorganized, often emotionally charged behavior, there frequently emerges a modified habit in which the alternative limb becomes more active. Subsequent to this change of habits, not before, there is a change of visual guidance indicative of visual learning. Sometimes the new visual learning appears without change of limb use; but even in this case, there is a period of disorganization and reorganization of response before learning is stabilized.

5. As a rule, additional learning is required to enable coupling of either hand with either eye, but all four combinations of eye and hand may learn. The split-brain subjects were eventually able to retain both contradictory visual tasks, one known by each eye, in every experiment, and could perform well immediately vision was restricted to one eye regardless of which hand was used for responding.

In seeking for an explanation of these effects one may assume an internal brain process in the form of a preparatory set to respond in a specified manner while the general conditions of stimulation are not opposed to such a response. This central set acquires strength by

a learning process which improves prediction of sensory cues associated with the response. Thus the form of response in the present experiments is not regulated by the critical visual cues until an attention process, predicting their occurrence and form with sufficient accuracy, is developed as an additional modification of the central preparatory set.

An asymmetric preparation for response by one arm is first associated with visual expectancy in one eye. But the central set still has access to visual projections of both eyes and, moreover, it contains elements which enable equivalence relationships to be set up between the two limbs.

Theories of sensory function and of learning have frequently postulated a central preparation to respond in a particular way. Latent patterns of central facilitation have been considered to explain the reflex reactions of invertebrates and primitive vertebrates after surgical manipulation of sensory-motor correspondences (54,55), the influence of "preparatory set" in acquisition of conditioned responses (56), and particularly the psychological effects of human perception and consciousness (57,58,59). Last century Helmholtz (60) emphasized that a psychological preparatory set, based upon previous experience and attributed meaning derived from experience, was essential to the perception of sensations in any particular form.

Recently MacKay (53) has formulated a theoretical model of perception and learning which utilizes matching and error detection between an hypothesis formed in conjunction with response organization, on the one hand, and the incoming sensory information, on the other.

Such a theory may be used when considering the way in which the brain resolves conflict between contradictory tasks where the two visual systems overlap. We may suppose that, when confusion of choice arises from convergence of the two contradictory sets of stimuli at certain points within the brain, the learning process "feels its way" to automatic selection of other points which are identified with one eye and therefore with one evolving hypothesis of choice. Furthermore, when such a selection in favor of use of one eye in learning takes place, it is prejudiced to occur so as to associate a contralateral eye and hand pair. These internal selections frame the perception of a particular stimulus and so determine the course of subsequent behavior. Helmholtz has summarized an essentially similar kind of interpretation as follows:

When considering opposite stimuli in rivalry, nothing in our sense perceptions can be recognized as sensation which can be overcome in the perceptual image and converted into its opposite by factors that are demonstrably due to experience. (60, p. 13)

In the forced tests which followed spontaneous learning of a particular visual task by a split-brain monkey we have found deficiencies of performance by ipsilateral pairs of eye and hand (cf. p.108). While highly significant correlations between hand moves and the visual stimuli may be reached from time to time with such pairs, there are frequently periods when the moves are awkward, hesitant and misdirected. Often the score drops suddenly from high levels of efficiency to near random choice and returns equally quickly to high levels shortly afterwards. Sometimes there is maintenance of an intermediate, half-learned level of performance which is relatively steady for as many as 100 trials.

As an explanation of this peculiar performance, in which poor choices are made even after it has been proven that the eye which is in use has access to a perfectly efficient engram for correct choice between the stimuli, let us assume that a fluctuation of attention between the eyes causes periodic blindness, and that in the blind periods moves are made at random. If there was an even 50:50 alternation of active vision between the two eyes, and if the choices were made correctly whenever the uncovered eye were attentive, then a score averaging 75% correct would be obtained over many trials. The speed of the swinging of attention between the eyes would determine the coarseness of fluctuations to be observed in the learn-



ing curve. A sufficiently slow alternation would produce a periodic rise and fall between random performance and near perfect choice.

No conclusive, direct evidence is available regarding this hypothesis, but there are some interesting indications of periodic phenomena. Comparison may be made with the very slow oscillations observed for the normal subject when presented with contradictory pairs of stimuli to the two eyes; here it was found that periodic inattention to one eye allowed temporary resolution of the conflict from time to time (cf. p. 50).

A simple test for alternation of visual attention is reported in Appendix I, p. 146. After learning of both contradictory directions of choice was completed, one pair of stimuli was reversed. Thus both eyes came to see the same stimuli and the one chosen as correct would be correct by reference to the learning of one eye only. These results suggest that a periodic switching of visual choices between the eyes could, in fact, occur.

It is perhaps unlikely that alternation of vision would occur when one eye was covered by a black metal flap, but some comparable alternation between equivalent systems in rivalry, as between expectancy for choice by one eye or the other, might lead to a memory blank for the free eye in a proportion of trials.

Use of the term "rivalry" is suggested by the occurrence of numerous fluctuations called rivalries in human subjective awareness. Alternation of rival perceptions, both within and between modalities of stimulation, are common features of consciousness when two equally valid but alternative and incompatible patterns of information are supplied at one time. Perhaps best known are effects which occur under particular conditions of restricted stimulation where the perception process is no longer free to choose between, or combine alternative configurations of the stimuli. The misnamed "retinal rivalry" has long been known to occur when two incompatible (unfusible) visual stimuli are simultaneously presented, one to each eye, as through a stereoscope, or with abnormal convergence of the two visual fields (60). There is a regular swinging of perceptions; first one stimulus is visible, then there is a spasmodic change after about 2-5 seconds and the second one is seen, and so on back and forth. Sometimes only part of the field, often a meaningful "unit," is affected by the spontaneous change. Interocular rivalry like this is also seen with superimposed polarized stimuli seen by a normal subject through crossed polarizers in the same way as the monkeys receive their stimuli in the experiments we have been discussing. Presumably the normal animals, such as ELZ (p. 50), experienced the interocular swinging of vision in the same way.

When an ambiguous figure, for example, the famous Necker Cube\* is seen by one eye, there is a similar periodic alternation of the two rival "interpretations." The phenomenon is certainly not restricted to conflict of information between two separate sense organs.

Fluctuations in awareness are compellingly apparent when human subjects suffer alterations of the visual field with prisms (61), or are placed in special situations where they are deprived of normal stimulation (62). Ditchburn, Riggs and others have described fluctuations of awareness when stimuli are stabilized on the retina by abolition of the effects of the natural eye tremor, or grosser eye movements directed by attention (63,64). The visibility factor, defined by Ditchburn as "the percentage of time a given stimulus is seen," is a delicate measure of the dynamic processes behind the awareness. Ditchburn and Pritchard (65) have shown that the fluctuations may involve central changes as well as retinal inhibitory processes.

All of these dynamic effects in presence of conflicting or abnormal stimuli are exceedingly sensitive to any factors which may tip the balance in favor of one rival perception and so resolve the conflict. If one of two visual stimuli giving interocular rivalry is suddenly

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\*As in Task K, fig. 5 , p. 33, but without the breaks in the lines.

moved, it is immediately clearly visible for a protracted time and the alternative stimulus is not seen. If one of the two has some meaning in or interest for the subject, it is seen for most of the time; also it has a larger visibility factor if presented as a stabilized retinal image (66). Changes in the perceptions of subjects adapting to prisms often occur when movements are made, or when they are intended. And so on.

These effects in human subjective awareness may well provide close analogues for the variations of visual functions observed in split-brain monkeys, though the rivalries may find origin more remote from the projection system carrying the critical visual stimuli, at deeper levels, and may concern the preparatory adjustments discussed above, which are shown as readiness to respond with use of one or other limb.

If one accepts any possibility of an alternation of attention between the two eyes, it becomes necessary to admit that there may not be true simultaneous attention when both eyes are learning together over a period of training. There may be alternative use of one eye at a time, as in interocular rivalry, and yet the learning gains of the two eyes may remain equal. This question could be resolved by use of tachistoscopic methods in which

test stimuli are presented to one or other eye for times which are brief enough to lie within one single attention span.

Turning finally to anatomical questions raised by the results obtained with double contradictory stimulation, let us consider the passage of information from one eye to the other which causes interocular transfer of learning.

The known visual system of the monkey or of man includes fibers carrying information from the retina to the superior colliculi and the pretectal nuclei of the midbrain, and to the lateral geniculate nuclei of the thalamus. Most fibers from the latter nucleus apparently pass on to the striate cortex of the posterior occipital pole of each hemisphere. These structures are the only ones in which orderly topographic preservation of retinal relations is preserved to a recognizable degree (67,68).

Recently, evidence has been obtained of inter-hemispheric transfer of brightness discrimination learning in chiasm-callosum sectioned cats (69). Chiasm-callosum sectioned monkeys, with the roof of the midbrain sectioned in addition so as to separate all direct connections from the optic nerve, also transfer brightness discrimination learning strongly (cf. p. 76). One must conclude that unknown avenues of communication are involved. Possibly brightness discrimination learning takes place exclusively

or preferentially in brain stem regions, or there may be a reference to visual structures of either side from such regions, centrifugally.

It has long been suspected that brightness discriminations can be performed in regions remote from the cortex. Lasley (3) found retention of a brightness discrimination habit after removal of the occipital cortex on both sides of the brain of the rat. Other studies have shown that reactions to differences in luminous flux persist in higher mammals after the striate cortex has been ablated (70,71).

Evidence has been obtained recently of essential participation of the interpeduncular nucleus, posterior hypothalamus and tegmentum in brightness discrimination learning and retention in the rat (72). All of these structures lie ventral to the ventricle and have not been separated by operations performed in the midline to date.

Both subjects with chiasm and callosum sectioned showed transfer of visual learning in the first color discrimination task presented to them. Subsequent color tests failed to show transfer but did show signs of the interaction between the learning of the two eyes. As has been pointed out on p. 66, there will remain some doubt concerning the transfer data until the experiments are repeated with randomization of brightness differences which may have been responsible for the transfer.

At present it is known that colored visual effects are produced by stimulation of the human visual cortex (8), and that differential reappearance of color vision occurs at the borders of scotomata following cortical lesions in the striate area (73). De Valois (74) has demonstrated components of color analyzing mechanism in the lateral geniculate of the monkey by recording from single units with microelectrodes during controlled stimulation of the retinal receptor-cells with light. No direct connections between the lateral geniculates are known to exist--all projections from this nucleus are thought to go to the cortex (68). We have seen how, in the absence of connections between visual analyzing areas, two visual learning processes can occur together, separately bound within the two hemispheres, even when the stimuli seen by the two eyes are contradictory in behavior import for the subject. Separate, double visual-learning of distinct black patterns on white by split-brain subjects falls in line with the usual concept that pattern-recognition processes are located in the visual cortex. Blindness over portions of the visual field results from striate lesions in humans (75), and elements of pattern recognition processes have been observed in the striate cortex of the cat (76). It is known, moreover, that more complex pattern recognition tasks require additional regions of the cortex remote from the striate areas, as well (75).

However, when interaction of learning by the two eyes is indicated, and particularly when the two hemispheres compliment one another in a single perceptual process (cf. p.125), it is necessary to conclude that pattern-recognition and learning involve regions remote from the cortex. There are two different possible ways this could occur.

The complexity of visual functions as well as the additional visual connections known for lower vertebrates offers opportunity for speculation that the brain stem of mammals performs as yet unknown elements of visual learning. Fish are known to learn color and pattern discriminations in absence of the cerebellum and forebrain lobes, presumably in the superior colliculi of the mid-brain where the connections of visual fibers are greatly elaborated (77). Certain pattern recognition elements have been shown to occur in the colliculi of the frog (78). Furthermore, there are known visual fibers in these forms which pass vertically to structures of the brain stem and which therefore are not separated by split-brain surgery (79,80). On the other hand, there is now ample evidence that central integrative processes may link various remote parts, including the specialized cortical "analyzers."

The nature of these associations is at present a mystery. When it is solved we will be in a better position to understand how some learning processes may be



separated in the split-brain, while others remain partly convergent, and we will also possess at least a partial understanding of the way in which the response is evoked and how it comes to be directed by the significant stimuli as a result of learning.

Taken as a whole, the results of this study leave us with new evidence of the central integrative processes which have been postulated repeatedly to explain effects of perception and learning. It has been known for some time that one may not predict the location of learning processes from knowledge of the classical projection systems, either sensory or motor, as they enter or leave the cerebral cortex. We find that the formation of a response has a role in determining perception, and there are indications that perception processes may be in rivalry between the two halves of the split-brain under certain conditions. Motor processes which define the general form of the response can take place in structures that remain integrated after split-brain surgery. Presumably, this undivided motor system has closely associated with it those structures which bridge the gap between the two halves of the split-brain, and so enable interhemispheric associations, or even complete transfer of learning, to occur.

REFERENCES

1. Ferrier, D. Proc. Roy. Soc. Lond. (1874-75) 23, 409-432.
2. Fritsch, G. and Hitzig, E. Arch. f. Anat. Physiol. und. wiss. Mediz. (1870) 300-332.
3. James W. The Principles of Psychology (1890) Henry Holt & Co., New York.
4. von Bonin, G. Some Papers on the Cerebral Cortex (1960) Charles C. Thomas, Springfield, Ill.
5. Lashley, K. S. Brain Mechanisms and Intelligence (1929) Univ. Chicago Press, Chicago, Ill.
6. Lindsley, D. B. Handbook of Experimental Psychology (1951) S. S. Stevens (ed.), John Wiley & Sons, New York, 473-516.
7. Jasper, H. H., Gloor, P. and Milner, B. Ann. Rev. Physiol. (1956) 18, 359-386.
8. Penfield, W. and Rasmussen, T. The Cerebral Cortex of Man (1950) New York.
9. Sperry, R. W. Science (1961) 133, 1749-1757.
10. Bremer, F. Res. Rpt. Assoc. Nerv. Ment. Dis. (1958) 36, 424-448.
11. Bailey, P. and von Bonin, G. The Isocortex of Man (1951) Univ. Illinois Press, Chicago, p. 301.
12. Akelaitis, A. J. Amer. J. Psychiat. (1941) 97, 1147-1155.
13. \_\_\_\_\_. Arch. Neurol. and Psychiat. (1941) 45, 788-796,
14. \_\_\_\_\_. Arch. Neurol. and Psychiat. (1942) 48, 914-937.
15. \_\_\_\_\_. J. Neuropath. and Exp. Neurol. (1943) 2, 226-262.
16. \_\_\_\_\_. J. Neurosurg. (1944) 1, 94-101.
17. \_\_\_\_\_. Risteen, W. A., Herren, R. Y. and Van Wagenen, W. P. Arch. Neurol. and Psychiat. (1942) 47, 971-1007.

18. Bridgman, C. S. and Smith, K. U. J. Comp. Neurol. (1945) 83, 57-68.
19. Smith, K. U. Science (1951) 114, 117-120.
20. \_\_\_\_\_. J. Comp. Physiol. Psychol. (1952) 45, 66-72.
21. Smith, K. U. and Akelaitis, A. J. Arch. Neurol. and Psychiat. (1942) 47, 519-543.
22. Smith, K. U. and Bridgman, C. S. (1942). See reference number 24.
23. Van Wegenen, W. P. and Herren, R. Y. Arch. Neurol and Psychiat. 44, 740-759.
24. Bremer, F., Brihaye, J. and Andre-Balissaux, G. Arch. Suisses de Neurol. et de Psychiat. (1956) 78, 31-79.
25. Trescher, J. H. and Ford, F. P. Arch. Neurol. and Psychiat. (1937) 37, 959-973.
26. Dandy, W. E. Arch. Surg. (1936) 33, 19-46.
27. Maspes, P. E. Rev. Neurolog. (1948) 80, 100-113.
28. Myers, R. E. and Sperry, R. W. Anat. Rec. (1953) 115, 351-352.
29. Myers, R. E. Unpublished Doctor's Thesis. University of Chicago (1955).
30. \_\_\_\_\_. Science (1955) 122, 877.
31. \_\_\_\_\_. Brain (1956) 79, 358-363.
32. \_\_\_\_\_. J. Comp. Physiol. Psychol. (1955) 48, 470-473.
33. \_\_\_\_\_. Arch. Neurol. (1959) 1, 74-77.
34. Sperry, R. W., Stamm, J. S. and Miner, N. M. J. Comp. Physiol. Psychol. (1956) 49, 529-533.
35. Myers, R. E. and Sperry, R. W. Fed. Proc. (1956) 15, No. 436.
36. \_\_\_\_\_. Arch. Neurol and Psychiat. (1958) 80, 298-303.
37. Sperry, R. W. The Central Nervous System and Behavior. (1959) M. A. B. Brazier (ed.) Josiah Macy Foundation, New York, p. 220.

38. Sperry, R. W., Miner, N. M. and Myers, R. E. J. Comp. Physiol. Psychol. (1955) 48, 50-58.
39. Schrier, A. M. and Sperry, R. W. Science (1959) 129, 1275-1276.
40. Stamm, J. S. and Sperry, R. W. J. Comp. Physiol. Psychol. (1957) 50, 138-143.
41. Sperry, R. W. J. Neurophysiol. (1959) 22, 78-87.
42. Sperry, R. W., Myers, R. E. and Schrier, A. L. Quart. J. Exp. Psychol. (1960) 12, 65-71.
43. Voneida, T. J. and Sperry, R. W. Anat. Rec. (1961) 139, 283.
44. Sperry, R. W. Anat. Rec. (1958) 131, 297.
45. Downer, J. L. de C. Fed. Proc. (1958) 17, 37.
46. Glickstein, M. and Sperry, R. W. J. Comp. Physiol. Psychol. (1960) 53, 322-327.
47. Downer, J. L. de C. Brain (1959) 82, 251-259.
48. Sperry, R. W. The Central Nervous System and Behavior. (1959) M. A. B. Brazier (ed.), Josiah Macy Foundation, New York, 387-392.
49. Myers, R. E. J. Comp. Physiol. Psychol. (1959) 52, 6-9.
50. Gellerman, L. W. J. Genet. Psychol. (1933) 42, 206-208.
51. Woolsey, C. N. et al. Res. Rpt. Assoc. Nerv. Ment. Dis. (1952) 30, 238-264.
52. Showers, M. J. and Crosby, E. C. Neurology (1958) 8, 561-565.
53. MacKay, D. M. Automata Studies (1956). C. E. Shannon and J. McCarthy (eds.), Princeton University Press, Princeton.
54. Mittelstaedt, H. Naturwissen (1949) 36, 90-91.
55. von Holst, E. and Mittelstaedt, H. Naturwissen (1950) 37, 464-476.
56. Sperry, R. W. J. Comp. Physiol. Psychol. (1950) 43, 482-489.

57. MacKay, D. M. Brit. J. Psychol. (1956) 47, 30-43.
58. Held, R. J. Nerv. Ment. Dist. (1961) 132, 26-32.
59. Teuber, H. L. J. Nerv. Ment. Dist. (1961) 132, 32-40.
60. von Helmholtz, H. L. F. Treatise on Physiological Optics (1925) Vol. s. J. P. C. Southall (ed.), The Optical Society of America.
61. Kohler, I. Sitzber. Oesterr. Akad. Wiss. phil.-hist. Kl. (1951) 221, 1-118.
62. Heron, W., Doane, B. K. and Scott, T. H. Canad. J. Psychol. (1956) 10, 13-18.
63. Ditchburn, R. W. and Ginsberg, B. L. Nature (Lond.) (1952) 170, 36-37.
64. Riggs, L. A., Ratliff, F., Cornsweet, J. C. and Cornsweet, T. N. J. Opt. Soc. Amer. (1953) 43, 495-501.
65. Ditchburn, R. W. and Pritchard, R. M. Quart. J. Exp. Psychol. (1960) 12, 26-32.
66. Pritchard, R. M., Heron, W. and Hebb, D. O. Canad. J. Psychol. (1960) 14, 67-77.
67. Polyak, S. L. The Retina (1941), Univ. Chicago Press, Chicago.
68. Brindley, G. S. Physiology of the Retina and Visual Pathway (1960), The William and Wilkins Co., Baltimore.
69. Meikler, T. H. and Sechzer, J. A. Science (1960) 132, 734-735.
70. Klüver, H. Biol. Symp. (1942) 7, 253-299.
71. Smith, K. U., Kappauf, W. E. and Bojar, S. J. Gen. Physiol. (1940) 22, 341-357.
72. Thompson, R. and Massopust, L. C. J. Comp. Physiol. Psychol. (1960) 53, 488-496.
73. Bender, M. B. and Kanzer, M. M. Brain (1939) 62, 404-421.
74. DeValois, R. L. J. Gen. Physiol. (1960) 43, 115-128.

75. Teuber, H. L. Handbook Physiol. (Neurophysiol.) (1960) 3, 1595-1668.
76. Hubel, D. H. and Wiesel, T. N. J. Physiol. (1959) 148, 574-591.
77. Arora, H. L. (unpublished).
78. Maturana, H. R., Lettvin, J. Y., McCulloch, W. S. and Pitts, W. H. J. gen. Physiol. (1960) 43, 129-175.
79. Herrick, C. J. The Brain of the Tiger Salamander (1948), Chicago Univ. Press, Chicago.
80. Ariëns Kappers, C. U., Huber, G. C. and Crosby, E. C. The Comparative Anatomy of the Nervous System of Vertebrates Including Man (1960), Hafner, New York.

APPENDIX I

Test for Fluctuation of Attention

Between the Two Eyes

One test was made with a split-brain subject in which contradiction for choice of response by the two eyes was invoked by reversal of one pair of stimuli. This reversal cancelled the disagreement of the visual cues but caused conflict of the habit to respond to a particular screen.

While the test was in progress, both eyes were open and both could see the same two stimuli, a circle and a cross, projected in the same way on the two response screens in each trial of the test. Previously the left eye had been fully trained to choose the cross as correct, while the right had learned always to choose the circle. A peanut was given whichever side was chosen and the disposition of the stimuli on the screens was varied in the usual way.

On the assumption that choice of a side indicated visual direction by the eye for which the symbol chosen was correct, the following series was observed over 50 trials. (L = choice by the left eye; R = choice by the right eye.)

Imposed left-  
eye vision

RRRRRRRRRR	LLLLLLLLLL	LL RRRRR L RR LL RRRRRRR L RRRRRRR L RR		
10	20	30	40	50

The left hand was used, by choice, for the response, and at first all choices were as if made by the R eye only. Then 10 trials of imposed L eye vision, with the R eye blocked, were perfectly chosen, and were followed by an irregular alternation of L and R choices in which the frequency of R gradually increased.



## APPENDIX II

### Interhemispheric Sensory Association

#### In Split-Brain Monkeys

The experiments described in the preceding account were concerned with enforcing separation of visual learning by use of contradictory discrimination tasks. The two eyes were simultaneously presented with two tasks which, though they required the same responses, had to be kept apart at the sensory level if discriminative learning were to occur.

A different method may be used to study the extent to which the two surgically separated visual structures may cooperate or associate in the guidance of learned responses.

A preliminary experiment has been completed with three subjects in which two circles of different sizes were separately projected to the two eyes with the aid of the polarized-filtration technique. Each circle of the pair was projected onto one of the response screens in the same apparatus as was used for studies of double learning of contradictory tasks.

During preliminary training without polarized filtration and separate input to the eyes, both eyes learned to choose the larger circle independently of variations in the absolute size of the circles. Several

pairs were presented in a randomized order and these included common sizes. In this way control was achieved of possible recognition by the subject that a given size was always correct. Monocular training in which both members of the pair were visible, subsequently assured that both eyes had learned to choose the larger circle. Then the two circles of any pair presented in a trial were made separately visible to the two eyes by insertion of appropriate polaroid filters.

The three subjects, JNY, IGR and BRS, were trained for this experiment after the work described in the previous account. They were split-brain subjects which had surgery as described on p. 53. JNY was a case with the roof of the midbrain incised in addition to the forebrain commissures and chiasm. BRS and IGR were cases in which the forebrain commissures alone were cut along with the chiasm.

The results are shown in Figure 22. Binocular learning in each case was followed by somewhat inferior performance with the individual eyes. Both BRS and IGR learned preferentially with the right eye, and in the case of IGR the left eye required a considerable amount of training before reasonably good performance was obtained.

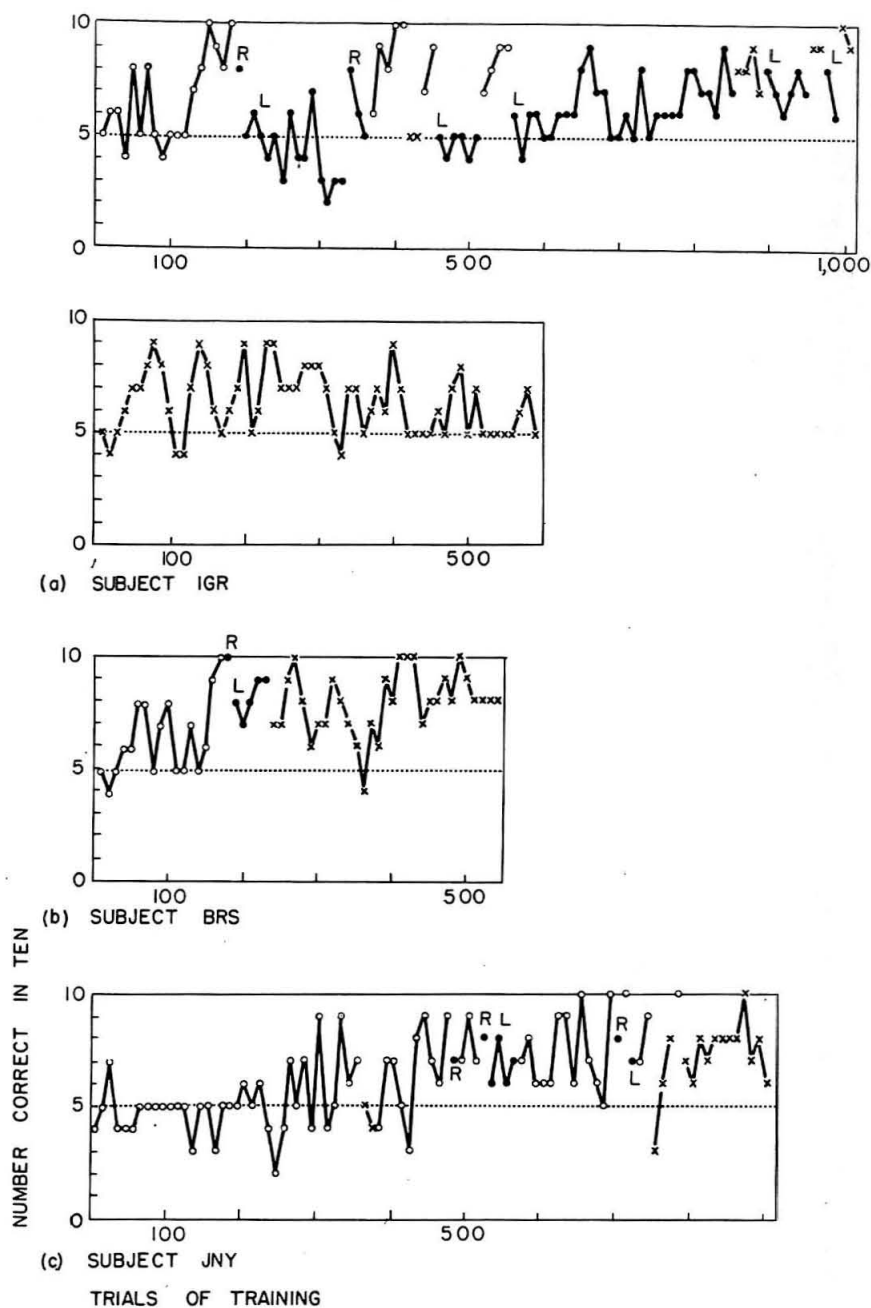


FIG. 22 - COMPARISON OF CIRCLE SIZES.

- BOTH EYES OPEN, EACH SEES BOTH CIRCLES.
- ONE EYE OPEN.
- ×—× BOTH EYES OPEN, EACH SEES ONE CIRCLE.

When separated vision was enforced JNY and BRS showed an immediate drop of performance, which, however, was soon overcome at least temporarily. The level of binocular performance by IGR followed the slow course of learning by the left eye. In every case this task was retained poorly with separated vision. Extended training of IGR shows a wide fluctuation of the level of correctness of choices and finally after 400 trials a position preference for the left side was developed, almost all moves being made by the left hand.

Nevertheless it is clear that some comparison enabling estimates of the relative sizes of the two circles is possible between the two visual systems of the brain, even when all known direct commissures have been severed. This result is in contrast to those studies with split-brain subjects which have demonstrated the separation of the two visual learning systems by the surgery.

### APPENDIX III

#### The Distribution of Learning Between the Two Halves of the Brain when Both Hands are Used Equally for Responses

When it had become clear, after 5 tasks had been learned by subjects IGR and BRS, that simultaneous learning in both hemispheres was an unlikely event, and that monocular learning was correlated with preferential use of one hand for responding, an attempt was made to equalize the use of the two halves of the brain by forcing the subjects to use both hands during learning. The results obtained discouraged the use of this method for obtaining simultaneous learning, but at the same time they showed interesting special features which are recorded here.



Use of both hands equally in each group of 10 trials was forced by placing a spacer, resembling B in Figure 19, midway in front of the two screens and across the top of the vertical partition, A. This spacer eliminated pushes by the left hand to the right screen, or by the right hand to the left screen. Thus, for 10 correct moves in each group of 10 trials, the subject was forced to make 5 pushes with each hand, the hands alternating according to the program for alternation of side of reward.

Results for subject IGR

First, a task was presented which required discrimination between a circular annulus and an elliptical annulus. Both eyes were presented the stimuli, the circle rewarded for the left eye and the ellipse rewarded for the right eye as described on pp. 20 ff.

In the beginning, after an initial unsuccessful attempt to use the left hand incorrectly for 200 trials, the right hand was used exclusively, and the score remained at 5 correct in 10. Then the left hand became more active while the score gradually improved. In the third group of 100 trials, 75 moves were made by the right hand; these included 24 errors. There was but one error in the 25 left-hand moves. In the next 60 trials there were 5 errors as the two hands became equally active.

A monocular test of 20 trials with the left eye contained 15 correct moves; 13 moves were made by the right hand, including 4 of the 5 errors. Twenty similar trials with the right eye alone showed a complimentary shift toward greater activity by the left hand which, in reciprocal fashion, made 13 moves with 4 out of a total of 5 errors.

On a second task, requiring discrimination between the patterns  and , binocular learning was completed in 100 trials. There was a shift from left hand moves towards equal use of both hands. In 100 trials with

the left eye alone the score was 68 correct. There were 14 errors in 47 moves by the left hand, and 18 errors in 53 moves by the right hand. With the right eye, in 100 trials, there was again a score of 68 correct; and there were 20 errors in 59 moves by the left hand, and 12 errors in 41 moves by the right hand.

For this second task, the tendency for use of the contralateral limb with vision of one eye at a time is shown to be weaker. In both tests with this subject, good binocular retention was followed by poorer performance with either eye alone. To some extent, however, these monocular tests did show simultaneous retention of the contradictory tasks by the two eyes.

#### Results for subject BRS

When tested with the circle-ellipse task described above, subject BRS, already adept at working with all combinations of eye and hand (cf. pp. 58 and 110), obtained a perfect score in the first 10 trials. However, when forced to perform with the left eye alone he scored 5 correct in 10 as the right hand became inactive. After 100 trials of forced performance with the left eye, the score with either right eye alone or with both eyes remained between 4 and 6 correct in 10. At first both hands became active with the binocular testing, but the score did not improve, and then, after 100 trials the left hand made all moves for a second 100 trials. Thereafter, the

right hand was gradually used for increasing numbers of correct pushes, and perfect performance was reattained in a further 50 trials. When monocular tests were made again it was found that this re-learning had occurred through use of the right eye alone and the left eye remained unretentive.

With the second task (as described for IGR), BRS learned with both eyes open in 20 trials, making but one error. The right eye showed perfect retention. With the left eye, the subject was unable to choose correctly for 180 trials, but in this case the right hand became the more active; only 26 responses were made with the left hand. With the left eye alone, criterion was reached in a further 60 trials as the left hand became more active.

Thus, after training on 5 tasks with full use of the hands, and after some forced use of the less preferred combinations of eye and hand, subject BRS was strongly biassed in favor of learning with the right eye, even when both hands were forced into equal activity during rapid learning with both eyes open. In this case, the experiment with forced use of both hands demonstrates the capability which a split-brain subject may show for use of a single preferred eye with either hand in learning or retention of a pattern discrimination task (cf. pp. 126 ff.)



In contrast, the results described for subject IGR suggest that forced use of both hands may, in other cases, tend to equalize function of the two eyes at the expense of perfect use of either eye alone.

It would be of interest to repeat these experiments with separate tachistoscopic presentation of visual stimuli to the two eyes. In this way it might be possible to obtain more precise information concerning the effect of alternate choice of limbs for response upon use of the eyes for learning or retention.