

## Effects of Commissurotomy on a Preoperatively Learned Visual Discrimination

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Three normal pigtail monkeys (*Macaca nemestrina*) were trained to perform a visual discrimination problem by pushing with a finger on the correct one of two black and white patterns presented simultaneously side by side. Use of right and left hands was equalized by forced alternation every twenty trials. When the monkeys had learned the discrimination and were performing at high level with each of the four possible eye-hand pairs, the optic chiasm and cerebral commissures were sectioned in the midline. The postoperative performance with the different eye-hand combinations indicated that the acquired memory in all three cases had been laid down in one hemisphere only.

### Introduction

Previous split-brain studies with cats and monkeys indicate that the memory for perceptual and motor learning in which the sensory or motor components have been lateralized to one of the separated hemispheres is generally confined to that one hemisphere (12). On the other hand, when the same kind of learning proceeds in the presence of an intact corpus callosum, the typical result is reported to be a double set of engrams, one in the directly trained hemisphere and a second established in the opposite hemisphere via the callosal fibers (2, 9). From these and related findings it has been inferred that a major function of the corpus callosum in these animals is to keep the two hemispheres equated and up-to-date with respect to the acquisition of new cortical engrams. It is clear that this is not uniformly true of the human brain where language functions especially are strongly lateralized. The following experiment reveals that in the monkey, also, the presence of an intact corpus callosum during

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learning does not necessarily result in the laying down of a double set of engrams.

### Materials and Methods

Three male (DXZ, SCH, VHT) pigtail monkeys, *Macaca nemestrina* weighing about 3 kg, and without previous laboratory experience, served as subjects. Training and testing were carried out in an apparatus that permitted the experimenter to control eye and hand use and that produced a minimum restriction of the visual field and arm movement or both. The subject was unrestrained except by the dimensions of the box and voluntarily placed himself in the working position. The visual stimuli, a black cross and a circle on white backgrounds, were back-projected onto two translucent screens. Following a correct response, a reward was discharged into a trough immediately below the screens by means of an automatic feeder.

The training schedule consisted of one session of eighty trials per day 5 days a week. Preoperative training involved free use of both eyes with forced alternation of hand shifted every twenty or forty trials so that at the completion of each training session both hands had been used for an equal number of trials. The stimuli were equated for brightness and were shifted from right to left on a pseudo-random schedule.

The criterion for learning was set at eighteen correct trials out of twenty. After the problem had been fully learned under binocular conditions, the various eye-hand combinations were tested separately for knowledge of the task. Monkey DXZ was overtrained 300 trials while SCH and VHT received no overtraining. Monkey SCH was temporarily used on another problem that involved presentation of the plus-zero stimuli simultaneously and contradictorily to each eye. None of these variations in preoperative procedure seemed to have a significant effect on the results.

All three cases then underwent surgery that included complete section of the corpus callosum, anterior commissure and midline section of the optic chiasm in a single operation carried out by exposure and retraction of the right hemisphere. Following surgery (2-4 weeks), the animals were tested for retention of the discrimination in the four eye-hand combinations indicated in Fig. 1. All animals are currently being used on further experiments. It will be obvious, however, that the findings and their implications for the present study are such that they would not be significantly changed even if the surgical sections did prove to be incomplete.

### Results

The performance curves for the pre- and postoperative training are shown in Fig. 1. Monkey DXZ had moderate paralysis in the left arm for 2-3 weeks after surgery which for the most part disappeared coincidentally with his high score for that hand. His initially poor performance is probably attributable to this deficiency, for during this period he appeared to be incapable of well-monitored hand movements in the testing situation. The other animals had no major motor impairments though they both had transient mild seizures on the left side during the first 2 weeks after surgery. It is clear that criterion was reached with only one intrahemispheric eye-hand combination in all three cases. Performance with the other eye-hand combination revealed either mnemonic (L. eye-R. hand) or coordinational (L. eye-L. hand, R. eye-R. hand) deficits, the latter of which will be discussed below.

Additional visual discriminations learned after the surgery with the same training procedure also tended to be laid down initially in one or the other hemisphere rather than both. The hemisphere that learned faster in the postoperative task was not necessarily the same one that had learned preoperatively. For example, SCH learned a second problem first with his right hemisphere and a third faster with the left hemisphere. Animal VHT learned two additional problems more quickly with the left hemisphere. An older animal, PKY, used on another related experiment, also exhibited this same kind of fluctuation in hemispheric performance. Throughout the right-left shifts in the lateralization of learning proficiency none of the animals showed any change in their natural right hand preference in their everyday activities.

The motor proficiency of right and left hand in the training situation followed a characteristic pattern in all animals according to which eye was exposed. For the most part intracortical eye-hand combinations (L. eye-R. hand, R. eye-L. hand) in all instances were fast and exact in their movements. Intercortical combinations were comparatively slow and clumsy. Hand movements under these latter conditions typically resulted in the fanning out of the fingers. This deficit was more pronounced when the task involved a pairing of the unpreferred hand and the eye ipsilateral to it. It is of interest that when both eyes were opened, DXZ and VHT had no difficulties in responding at criteria with either hand.

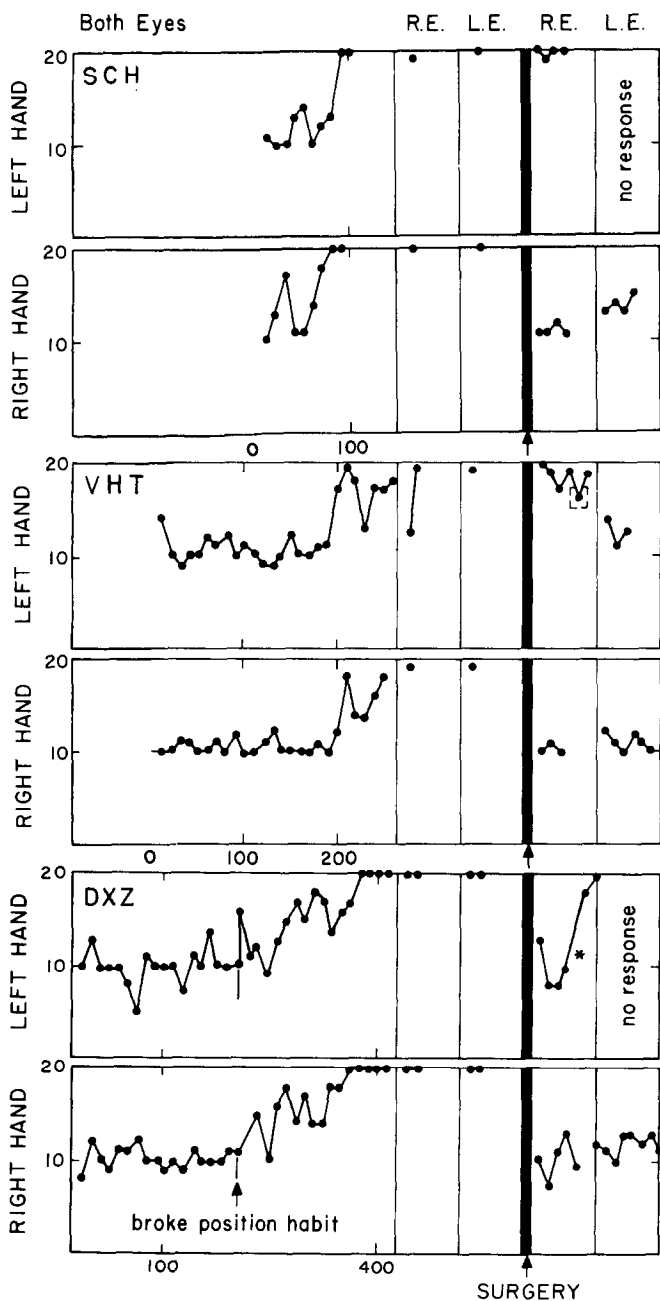


FIG. 1. Performance of SCH, VHT, and DXZ on cross vs circle pattern discrimination both before and after surgery. Number of correct trials in twenty on ordinate; number of trials of training, on abscissa. Asterisk (\*): animal had temporary paralysis of left hand after the operation.

### Discussion

The cortical engrams for visual discrimination learning in three normal, unoperated monkeys were shown by subsequent analysis with split-brain procedures to have been localized predominantly or entirely in one hemisphere. This lateralization of memory occurred consistently in all three cases tested despite the presence throughout learning of the intact corpus callosum and the optic chiasm, and even though bilateral symmetry in engram formation had been further favored by forced alternation in the use of hands, and also by overtraining through 300 trials prior to surgery in the case of DXZ. These findings contrast with earlier reports indicating that the presence of the corpus callosum during unilateral visual training in cats and manual tactile training in monkeys resulted in the establishment of a double system of memory traces, one in each hemisphere (2, 9). The present results suggest that in the normal monkey the memory for visual tasks tends to remain localized in one hemisphere, and when needed by the other, the mnemonic information is tapped via the corpus callosum.

This raises the puzzling question as to why, in the presence of the callosal fibers, the engrams for learning are laid down bilaterally in some cases and unilaterally in others. The present result is directly comparable to the effects of similar commissurotomy on language functions in man (5, 6) where speech is confined to one hemisphere even though the speech centers of the cortex are richly interconnected by callosal fibers in addition to the fact that either or both hemispheres have the capacity for acquiring language (3, 4). In the human brain, the cerebral dominance and lateral specialization presumably reflect some sort of asymmetry in anatomical organization. In these monkeys, however, the nonpredictable fluctuation from left to right hemisphere suggests that the lateral dominance is a matter of the transient dynamics of learning rather than a permanent feature of cerebral organization.

Previous reports have varied widely regarding the presence, extent, and duration of visuomotor deficits that exist when split-brain animals are obliged to use the hand ipsilateral to the exposed eye (1, 7, 8, 10, 11, 13). Split-brain cats with monocular exposure combined with forced alternation of paws learned visual discrimination problems equally fast with either paw (11). However, application of similar training procedures to naive split-brain monkeys, has now shown that a significant deficit exists in reaching criterional performance with the ipsilateral hand (7).

In the present case, all the animals were initially unable to perform at criteria postoperatively except with the left hand and right eye. With this contralateral combination, the response was characteristically swift and accurate. The same sort of good coordination was seen with the opposing eye-hand combination even though the correct choices were at chance level. When the hand ipsilateral to the retentive eye was used, the movements were clumsy and slow and the choices inaccurate. This lack of coordination which gradually disappears proved to be especially severe when the unlearned eye was paired with the ipsilateral hand. The very poor motor control seen with ipsilateral combinations in this situation is reminiscent of the apraxic difficulties seen recently in a human patient in whom the importance of the cerebral commissures for verbally triggered volitional movements of the extremities became strikingly evident following commissurotomy (5, 6).

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