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INTERMANUAL STEREOGNOSTIC SIZE DISCRIMINATION IN SPLIT-BRAIN MONKEYS[1]

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7 pigtail monkeys were trained to perform an intermanual size discrimination and tested after split-brain surgery. Experiment 1 required Ss to pull the larger of 2 cylindric levers presented simultaneously, 1 by each hand. Postoperative scores for 2 Ss working with 4 lever pairs from 5 sizes were good initially, but declined gradually. Scores of 2 Ss working with 9 lever pairs from 10 sizes fell abruptly to chance level after surgery and remained there. Experiment 2 required Ss to use 1 hand to pull 1 of 2 levers that matched in size a lever presented to the other hand; postoperative scores from 3 Ss were at chance level, even with gross size difference. Evidently cross-communication of manual stereognostic size information was eliminated by the surgery.

Initial studies in split-brain monkeys indicated that disconnection of the hemispheres prevented contralateral transfer of visual, but not of somesthetic, learning (Sperry, 1958). Subsequent reports on somesthesia in primates (Ebner & Myers, 1962; Ettlinger & Morton, 1963; Gazzaniga, Bogen, & Sperry, 1963; Glickstein & Sperry, 1960; Myers & Henson, 1960) all agree that section of the callosum markedly impairs intermanual transfer, but they have not been consistent on the question of whether such transfer can be excluded completely by disconnection of the hemispheres. This issue is complicated and raises questions concerning the extent and functional proficiency of ipsilateral cerebral projections in the somesthetic pathways, and more specifically, questions concerning the variations to which these projections may be subject in different individuals and species, in the different somesthetic modalities, and in the different regions of the body, including the different axiodistal segments of the forelimb. These questions become critical when it comes to application of the split-brain preparation to the localization of memory and to the analysis of cerebral organization in general (Sperry, 1959, 1961).

The purpose of the present study was to explore further the extent to which manual stereognostic size information in monkeys might be confined to the contralateral hemisphere by cerebral commissurotomy. Recent observations (Trevarthen, 1963) have suggested that split-brain monkeys are able to select the larger of two circles presented simultaneously, one to each of the separated right and left visual half fields, and that cross-matching for color is also possible at a low level, even though trained visual discriminations for pattern and color in the same animals fail to transfer from one side to the other. In the present study this technique of simultaneous presentation with immediate cross-comparison was used along with simple size discriminations. In general the experiments were designed to favor the detection of any possible remnants of functional cross-communication of manual stereognosis after cerebral commissurotomy.

GENERAL METHOD

Subjects and Apparatus

A total of eight pigtail monkeys (*Macaca nemestrina*) 5–11 lbs. in weight served as *S*s in two experiments.

The apparatus has been illustrated elsewhere (Sperry, 1964, p. 43). It consisted of a working cage that permits control of the use of each eye and hand of *S*, plus a sliding unit for presentation of the levers to be discriminated by *S*. A set of 10 levers with 1⅜-in.-long handles made of hardwood cylinders sanded smooth and painted gray had varying diameters graded proportionately from 3⁄16 to 1¼ in. The levers were numbered from 1 to 10 according to their sizes in descending order.

For each trial two levers were mounted on the sliding unit with their centers 4¼ in. apart; *S*'s pulling of the "correct" lever released a peanut or

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candy which dropped into a food pocket centered below the levers, and a pull on the "incorrect" lever activated a buzzer to signal the error. Lock mechanisms made it impossible to pull both levers simultaneously, and the pulling of one lever automatically locked the other, thus allowing the *S* only one chance in each trial. The *E* was screened from *S*'s view during the intertrial manipulations by swinging doors that automatically opened when the unit was slid towards *S*, and closed after it was withdrawn.

Procedure

The experimental plan included the training of *S*s on an intermanual stereognostic size discrimination problem, followed by split-brain surgery, and then postoperative testing. Each *S* was trained or tested 5 days a week. For each session *S* was transported from its home cage to the experimental cage located in a separate soundproof room. Two levers of different sizes were presented in each trial. The left-right position of the correct lever was balanced in a pseudorandom schedule. Four variations of such schedules were used in rotation for consecutive sessions to prevent *S* from memorizing the sequences.

In the pretraining sessions the eyeholes on the experimental cage were unblocked so that *S* could see the levers and the food pocket. As soon as *S* learned to pull the lever and to retrieve food from the food pocket, visual guidance was reduced and then eliminated by gradual closing of the eyeholes with the occluders. Formal training started when the eyeholes were completely blocked so that *S* had to depend entirely on somesthetic cues to judge the size of the levers. After *S* reached a predetermined criterion of learning, it was overtrained for about 500 trials. Postoperative testing was started a few days after surgery.

Surgery

The *S* was anesthetized before surgery by intrapleural injection of pentobarbital sodium. A large oval skull plate was removed from over one hemisphere extending about 1.5 cm. across the midline. The dura was opened and reflected centrally to expose the one hemisphere up to the midline. The hemispheres were then parted gently by inserting first Gelfoam and then a laboratory-made separator. The large cerebral veins were usually left intact by working around and between them, as were also all but a few of the tiny vessels on and over the corpus callosum. All work between the hemispheres was carried out in clear view between the blades of the separator. The callosum, plus the anterior and hippocampal commissures, were sectioned with a fine aspirating needle the cutting tip of which was formed from a No. 27 hypodermic needle. Very weak suction was used, which was just strong enough to keep the cutting field clear. Except for the gross features of the surgery like the removal and the reposition of the skull plate, most of the surgery was carried out with the aid of a binocular stereoscopic microscope using magnifications of 6–16 times. Routine aseptic procedures were followed throughout.

EXPERIMENT 1A

Method

In Experiment 1 only the five even-numbered levers were used, No. 2 being the largest, No. 10 the smallest. Two levers were presented at each trial, each lever being accessible to only one hand of *S*. The correct response was to pull the larger lever of the pair.

Only two *S*s, Abn and Lnx, were used with this procedure because the results suggested a change in method as will be evident below.

Pretraining was started with levers No. 2 and No. 10 paired together. Gradually the size difference was reduced by steps, resulting in the final four pairs of 2-4, 4-6, 6-8, and 8-10. During formal training without visual guidance, the four pairs of comparisons were presented equally frequently according to schedule in each 32-trial session. The criterion of learning was 29 (91%) or more correct responses in one session.

Results

The *S*s gradually learned that only one of the two levers could be pulled in each trial, and that pulling a lever either yielded food, or caused a buzzing sound, depending on its relative size. Excluding pretraining, Abn reached criterion preoperatively in 26 sessions, and Lnx in 8 sessions. Their postoperative test scores are shown in Figure 1.

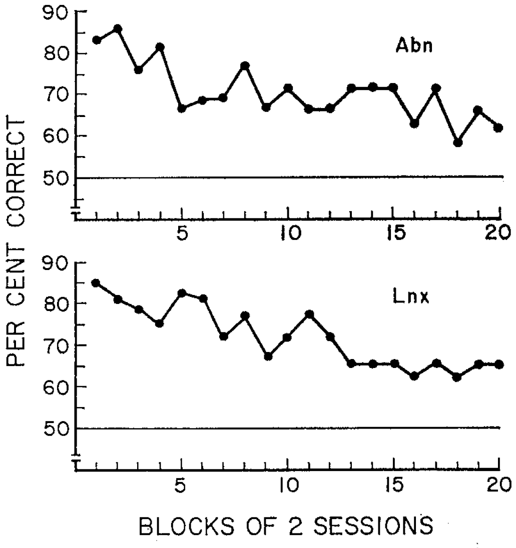

FIG. 1. Postoperative scores on the five-size paired-comparison problem.

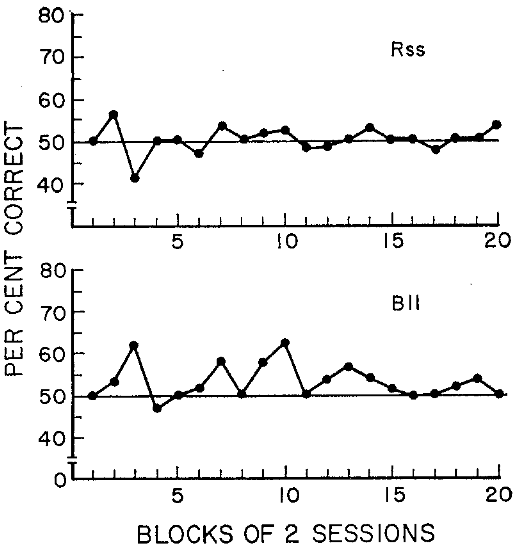

FIG. 2. Postoperative scores on the 10-size paired-comparison problem.

It was clear that disconnection of the hemispheres did not produce much immediate disruption of the performance. Both *S*s continued to pull the larger lever and their scores were only slightly below criterion. However, the scores gradually became worse instead of better, and dropped to about 65% correct after 40 sessions of testing. The decline in scores was accompanied by signs of increasing irritability in *S*s during the test sessions, and it seemed evident that their performance would not improve with further testing.

Postmortem examination showed the brains to be in good condition throughout, except for the intended lesions in the commissures, which were complete in both cases.

Discussion

The initial preservation of high scores after surgery in these cases is difficult to reconcile with the subsequent deterioration of performance. A possible explanation and the one deemed most probable is that the surgery was effective in eliminating cross-communication of the size information from the hands, but that high scores were maintained for a short time on the basis that both hemispheres had learned from preoperative training and overtraining that the No. 2 lever was always correct and No. 10 always incorrect and if each hand always promptly pulled the No. 2 lever and withdrew from No. 10, this in itself would give a score of 75% correct; the intermediate levers could also be responded to correctly if each hand reacted with a different degree of hesitancy according to the lever size encountered. The postoperative performance might thus be analogous to the cooperative efforts of two different individuals working together, each well trained but each having access to only one lever. The decline of scores during postoperative testing would be a natural consequence with cross-communication eliminated, since every erroneous identification of a lever would thereafter add confusion that could not be corrected without cross-comparison of the lever sizes.

EXPERIMENT 1B

According to the above interpretation it would become increasingly difficult to maintain high scores after commissurotomy if more levers were added to the series for paired comparison. Thus the whole set of 10 levers was used in this experiment.

Method

The procedure essentially followed that of Experiment 1A. Each *S* was first trained on the five-size set of 2-4, 4-6, 6-8, 8-10, until it reached the criterion of 29 or more correct responses in a 32-trial session. Then the 10-size series was used, and 36 instead of 32 trials were run in each session to keep a balanced schedule. The criterion of learning was 33 (92%) or more correct responses in one session.

Results and Discussion

Two *S*s, Bll and Rss, were used. When the 10-size series was substituted for the five-size set, there was no observable behavioral disturbance. Both *S*s continued to work as before; Rss reached criterion after 12 additional sessions on the new 10-size set, and Bll did so after 4 additional sessions.

As is shown in Figure 2, postoperative testing yielded chance-level scores from the beginning in both *S*s, and their performance failed to improve in 40 sessions.

Bll is still working on other problems. In postmortem examination of Rss' brain the commissurotomy was found to be complete except for the front edge of the anterior commissure and a small thread of fibers less than ½ mm. across at the anterior tip of the corpus callosum. The cortex was in good condition with no lesions detected. The results thus conform to the above explanation and support the hypothesis that the forebrain commissures are necessary for cross-communication of stereognostic size information from the two hands.

The possibility remained, however, that much larger differences in size than those employed in this experiment might yet be communicated through the subcortical commissures after callosal section. It is, of course, difficult to have both large size difference and also a long series. Therefore a different approach was used in the following experiment.

Experiment 2

To find out if cross-communication might be possible or easier with a large size difference between the levers, a matching-from-sample task was used in which *S* feels a sample lever with one hand and then selects a lever of the same size with the other hand. This method has an advantage over that of paired comparison in that there are no extreme sizes that are always correct or incorrect. Also, since only two different sizes are needed for the sample-matching task, a gross size difference can be used. This simplifies the discrimination and thus increases the possibility of detecting any remnants of cross-communication that might still be present after disconnection of the hemispheres.

Method

Two extending bars were added to the sliding unit used in Experiment 1 so that a third "sample" lever could be mounted either to the right or to the left of the two "choice" levers. A removable partition was also added to make the sample lever accessible only to one hand while the two choice levers were accessible only to the other hand (see Figure 3).

Levers No. 3 and No. 7, with diameters of ⅞ in. and ⅜ in., respectively, were used. Each session consisted of 40 trials, in which a lever of either size was presented as the sample in half of the trials.

Each *S* was first trained to feel the sample lever with its left hand and to palpate the two choice levers and pull the matching one with the right hand. After *S* had reached a criterion of 35 (88%) or more correct responses in one session under the two-hand condition, it was trained to perform the same size matching using one hand, by feeling first the sample and then the two choice levers in succession. All three levers were made accessible to one hand by removing the partition between them, and the other hand was restrained by closing the appropriate armhole of the experimental cage. The left hand and then the right hand were each trained under the one-hand condition until each had reached criterion. (When the *S* was using the right hand alone, the sample lever was shifted to *S*'s right side.) Thereafter *S* was again trained under the two-hand condition, after which it underwent surgery.

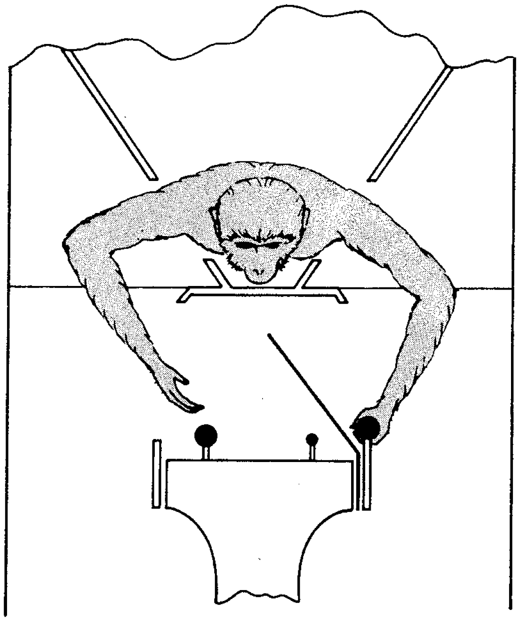

Fig. 3. Schematic drawing of the two-hand working condition in the size-matching problem.

Postoperative testing was carried out with the two-hand condition, followed by tests under the one-hand condition, first with the left and then with the right hand. Following reestablishment of good performance with each individual hand, the two-hand condition was resumed, and after a few sessions two levers with even larger size differences (levers No. 2 vs. No. 9, 1 in. vs. ¼ in.) were used.

Each change in the training and testing conditions was introduced with open eyeholes for a few trials to facilitate *S*s' adaptation to the new mode of operation, but the trials with visual guidance were not counted in the formal record.

Results

Four *S*s, Jss, Lcy, Ptr, and Vlt, were used. Pretraining for this size-matching problem

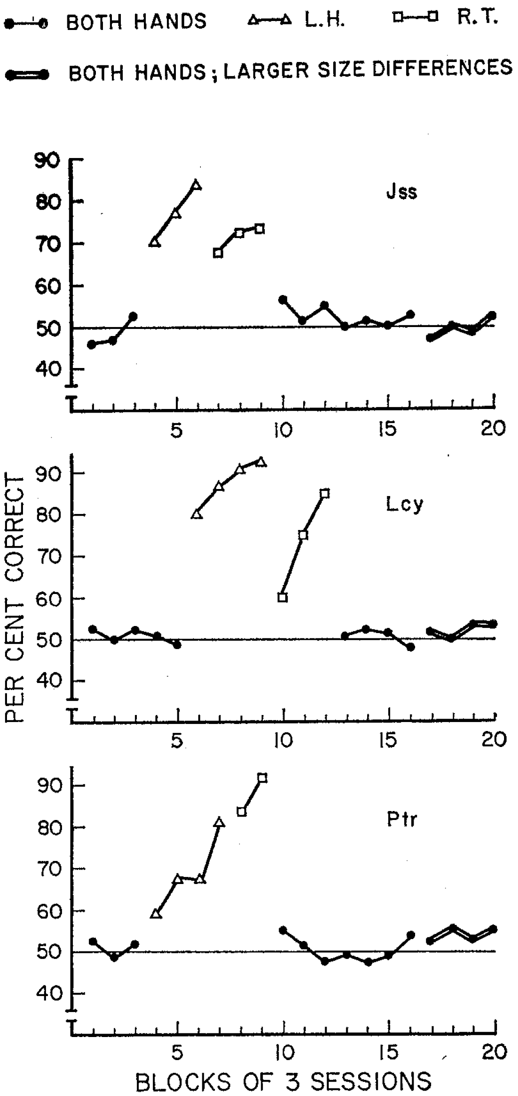

FIG. 4. Postoperative scores on the size-matching problem.

took longer than had that for the size-comparison problem in Experiment 1. The main difficulty was to get *S*s to feel the sample lever with one hand and to do the testing and pulling with the other hand. Once *S*s acquired the routine and the concept of matching, which took 1–6 wk., elimination of visual cues and shifting from the two-hand to the one-hand conditions were no problem. Usually no more than five sessions were required to reach criterion under a new condition.

The postoperative scores of Jss, Lcy, and Ptr are presented in Figure 4; Vlt became sick before surgery and later died at a veterinary hospital. As indicated in Figure 4, the scores of size matching between the two hands fell abruptly to chance level after surgery. This poor performance was often accompanied by reluctance to continue working that had to be overcome by occasional extra rewards between trials. The scores under the two-hand condition never exceeded the chance level, not even after the diameter difference of the levers was increased to ¼ vs. 1 in. By contrast, when using one hand alone, all three *S*s were able to perform well either immediately or after rapid improvement. Therefore *S*s' failure in cross-matching between the two hands could not be ascribed to forgetting, loss of interest, or unilateral engrams.

Jss is still alive, participating in another experiment. Postmortem examination of the two other *S*s showed the commissurotomy to be complete in Ptr. In Lcy there remained a thread of fibers about 1 mm. in diameter at the anterior tip of the corpus callosum. Also the front one-third of the anterior commissure was intact. No significant cortical lesions were found in the brains.

GENERAL DISCUSSION

Section of the cerebral commissures in Experiment 2 clearly abolished *S*s' capacity to cross-match for size from one to the other hand. At the same time it left intact, with little or no impairment, the ability to perform the same size matching with either hand alone. In conjunction with Experiment 1, the combined results offer strong evidence that section of the neocortical commissures prevents the central cross-integration for intermanual size discrimination. The critical sensory cues from each hand would thus appear to be effectively confined to the one (contralateral) hemisphere.

It should be emphasized, however, that this conclusion applies only to manual performances in which the critical sensory cues arise solely from the hand and not from higher segments of the arm. Significant differences in the amount of bilateral projection of somesthesia have been found for various parts of the body in human *S*s. The upper segments of the arms, axial structures, and particularly the head and neck tend to have increasing bilateral representation which permits cross-integration despite disconnection of the hemispheres (Gazzaniga, Bogen, & Sperry, 1963, 1965). The intermanual transfer of somesthetic discriminations observed occasionally in previous studies with split-brain monkeys (e.g., Glickstein & Sperry, 1960; Sperry, 1958) may now be understood primarily in terms of sensory cues from proximal bodily structures commonly involved in many manual activities.

It should be noted further that the present data do not exclude cross-integration of certain simpler categories of hand stimulation like the mere presence or absence, onset or cessation, of a stimulus.

The qualifications mentioned above warn against generalization of the findings of the present study. Nevertheless, the demonstration that stereognostic size information from the hand can be effectively confined by cerebral commissurotomy to one hemisphere makes possible more intensive analysis of the cerebral mechanisms for perception, learning, and memory in split-brain monkeys.

The results from the five-size paired-comparison experiment have alerted *E*s to some of the dangers involved in using the paired-comparison method with a small series of stimuli. Recognition of possible alternative strategies dependent on absolute size may modify some of the prior interpretations based on this method (Robinson & Voneida, 1964; Trevarthen, 1962, 1963, 1965). The advantages of the cross-matching technique over that of cross-comparison in this regard are evident.

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