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EFFECTS OF CIRCUMSCRIBED CORTICAL LESIONS UPON SOMESTHETIC AND VISUAL DISCRIMINATION IN THE MONKEY[1]

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Attempts at functional parcellation of the posterior associative cortex have yielded some evidence that the parieto-preoccipital area is concerned with the mediation of somesthetic discrimination (1, 2, 8, 9, 11). However, the evidence from previous studies has not been unequivocal. In order to demonstrate an unambiguous deficit in tactile discriminative behavior after lesions in this area, the following conditions were set up to obviate difficulties of previous interpretations:

1. It must be shown that such a deficit reflects a loss in ability to utilize somesthetic cues and does not merely reflect a difficulty in orientation in space or in manipulation of the stimulus objects.

2. The effects of brain lesions upon retention as opposed to the effects on initial learning must be established in order to determine whether or not any performance decrements which may occur can be attributed solely to amnesia for specific somesthetic habits.

3. "Double dissociation of function" (12) must be shown, both to prove that a given area is concerned with somesthesis alone and to show that the tests used are valid indicators. Thus, the effects of a given lesion upon at least two tests specific to different modalities must be studied, and the effects of at least two lesions upon the same test must be studied.

4. In order to insure an adequate sampling of behavior within a modality, several tests which are presumed to measure the same function should be given. In this way, factors of order, difficulty, and interval between operation and test can be evaluated and some indication of consistency of effect obtained.

5. Histological verification of lesions should be available in order to specify the relation between the locus and extent of lesion and a given performance as exactly as possible.

METHOD

Subjects

Eight experimentally naive, immature, rhesus monkeys, weighing between 3¾ and 5½ lb. at the beginning of the experiment, were used. These were divided into two operative and two testing groups on the basis of their preoperative scores. One animal died as a result of the operation; therefore, its results are not included.

Operative Procedures

All operations were done in one stage under Nembutal anesthesia given intraperitoneally.[2] For the parietal lesion, an osteoplastic bone flap was turned. After the brain was exposed, the lesion was produced by subpial aspiration using a small-gauge sucker. Cautery was used sparingly to seal major vessels, and wounds were sutured in anatomical layers. After completion of postoperative testing, the animals were sacrificed.

Site of Lesions

An attempt was made to approximate the extent of lesions reported by H. Pribram and Barry (9), which were based on a neuronographic analysis of the monkey brain by K. Pribram and MacLean (10). In the case of the parietal lesion, this included cortex which had not been regarded as important for somesthetic function prior to the study by Pribram and Barry. The parietal resection extended from the intraparietal sulcus to the lunate sulcus, and inferiorly as far as the superior temporal gyrus. The medial extent included the whole precuneal gyrus. The inferotemporal lesion comprised the ventral occipitotemporal portions of the temporal lobe which have been shown to be important in the mediation of visual behavior (7). All lesions were bilateral.

Procedures for verifying the locus of lesions have been described previously (7). In Figure 1 are shown the relevant cross sections and serial reconstructions of that brain in each lesion group which sustained the minimal ablation. Additional cortex removed in the remaining animals in each lesion group is also indicated on the same diagram.

[1] This study was supported by a grant from Contract DA-49-007-MD-401 of the Department of the Army. It summarizes material contained in a thesis submitted to Yale University, in 1955, in partial fulfillment of the requirements for the degree of Doctor of Philosophy, and reported at the 1955 meeting of the American Psychological Association, San Francisco. The author is grateful to Drs. Burton S. Rosner, Karl H. Pribram and Frank A. Beach under whose guidance the experiment was done. The author is also in debt to Dr. William A. Wilson, Jr. for advice and criticism.

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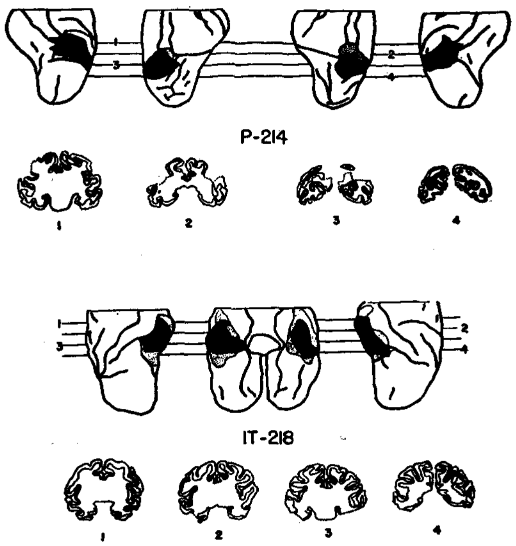

FIG. 1. Reconstructions of lesions. Lateral and medial views of parietal lesions are shown above cross sections numbered accordingly. The inferotemporal lesions are shown in lateral and ventral views. The black area indicates the extent of the minimal lesion in each operate group. Stippled area denotes additional cortex removed in remaining animals in each group.

Apparatus

Since disorientation and apparent unwillingness to move the limbs are symptoms commonly reported following parietal lesions, it is possible that performance decrements found previously could be attributed in part to these factors. In this experiment an electromechanical infrared scanning device (4) was used to observe the monkeys while they performed the somesthetic tests in darkness. Since visual cues were completely excluded in this way, a testing situation could be set up in which the animal could orient itself easily with respect to the stimulus objects without complicated motor responses such as reaching over barriers (1, 2, 9) or into bags (3).

The scanning device was set up in front of a wooden barrier, which could be raised to expose a shelf to the monkey. To facilitate apprehension of the stimuli, the edge of the shelf farther from the monkey was elevated from the horizontal plane. Lucite containers, $2\frac{9}{16}$ in. square and $\frac{1}{2}$ in. deep with easily removable covers, were painted a flat black and secured to the shelf. Stimulus figures were painted on or fixed to the lids of the boxes, which the animals were trained to lift. The monkeys reached directly through the bars of the testing cage to reach the boxes on the shelf, and the response in darkness to the somesthetic stimuli was thus identical to the response in the light to the visual stimuli.

Tests

Each animal received four tests, two visual and two somesthetic, with each modality tested at two levels of difficulty. The difficulty of a given test is defined as the relative number of trials to criterion for an intact animal. The stimuli used for each discrimination are described below, the easier test in each modality being described first.

Visual ┘ *vs.* ┌. A left facing L and the same figure rotated through 180° were made into unpainted wooden figures with outside dimensions of $1\frac{7}{16}$ in. and $1\frac{15}{16}$ in., $\frac{1}{2}$ in. wide, and $\frac{3}{8}$ in. high. These were attached to the black Lucite covers of the stimulus boxes so that the animal touched the stimulus figures before removing the box covers. The left-facing L was made positive for the monkey.

Visual cross vs. square. A cross with equal arms, $1\frac{7}{8}$ in. long and $\frac{3}{8}$ in. wide was painted white on one box cover. On the other, an outline square of $1\frac{1}{2}$ in. outside dimensions, and $\frac{5}{16}$ in. wide was painted in white. The cross was made positive.

Somesthetic ┘ *vs.* ┌. The same stimulus figures were used as in the first visual test, but the monkey was forced to discriminate them by touching them in the dark. The left-facing L was again positive.

Somesthetic length. Pieces of wooden doweling, $\frac{1}{2}$ in. in diameter, were attached horizontally to the covers of the stimulus boxes. The positive one was $1\frac{7}{16}$ in. long, the negative one was $2\frac{7}{16}$ in. long.

Training Procedures

On the visual tests, the correct box was baited with $\frac{1}{4}$ peanut, and 50 trials per day were given to each animal. On the somesthetic tests, the correct box was baited with $\frac{1}{2}$ peanut, the smallest amount which the animal could find quickly in the dark, and 30 trials per day were given each animal.

In the visual test, the monkey was scored wrong and was not rewarded for that trial if it touched the incorrect stimulus box. In the somesthetic tests, *S* was permitted to feel both box covers, and a trial was scored wrong only if *S* removed the incorrect cover. The position of the correct box was alternated from right to left in accordance with a balanced testing schedule (6). In the beginning of the testing, when the animals tended to perseverate on one side, correction trials were given until the animal gave up the place habit. In the correction procedure, if the animal opened the incorrect box, the barrier was lowered and immediately raised so that *S* had the opportunity to go to the other gox.

Table 1 summarizes the experimental procedure. The visual ┘ *vs.* ┌ discrimination test was given first to all animals. All monkeys were then trained on the somesthetic ┘ *vs.* ┌ discrimination, which utilized the same stimulus figures. The room illumination was gradually decreased and the monkeys learned to reach for and touch the stimulus boxes in the dark. After 10 to 20 transition trials, all monkeys tested easily in darkness and were well oriented with respect to the placement of the boxes and to the location of the peanut inside.

Two potential parietal (P-216, P-214) and two p-tential temporal (IT-218, IT-219) operates comprised Group A and were trained on the somesthetic length discrimination preoperatively. They were given the visual cross *vs.* square discrimination test postoperatively as new learning. Group B included the other

TABLE 1

Order in Which Tests Were Given for Each Group of Animals

Task	Group A P-216, P-214, IT-218, IT-219	Group B P-227, P-240, IT-238
Preoperative learning	Visual ⌋ *vs.* ⌐ Somesthetic ⌋ *vs.* ⌐ Somesthetic length	Visual ⌋ *vs.* ⌐ Somesthetic ⌋ *vs.* ⌐ Visual cross *vs.* square
	14 day interval	
Preoperative retention	Somesthetic length Somesthetic ⌋ *vs.* ⌐ Visual ⌋ *vs.* ⌐	Visual cross *vs.* square Somesthetic ⌋ *vs.* ⌐ Visual ⌋ *vs.* ⌐
	Operation 14 day interval	
Postoperative retention	Somesthetic length Somesthetic ⌋ *vs.* ⌐ Visual ⌋ *vs.* ⌐	Visual cross *vs.* square Somesthetic ⌋ *vs.* ⌐ Visual ⌋ *vs.* ⌐
Postoperative new learning	Visual cross *vs.* square	Somesthetic length

monkeys in each operative group (P-227, P-240, IT-238); they were trained on the visual cross *vs.* square preoperatively and were given the somesthetic length discrimination test as postoperative new learning.

After each monkey had completed training in the preoperative series, a two-week interval was allowed to elapse. Following this, retention trials were given in order to get an estimate of the amount of forgetting to be expected from the postoperative recuperative period apart from the effects of the lesion. Immediately after the retention trials, the animal was operated upon and allowed two weeks for recovery. Postoperative tests were then given in the same order as the preoperative retention tests, and the new learning tests were given last in each case. In order to pass a test, the animal was required to make 90 correct responses in 100 consecutive trials. If an animal failed to meet this criterion within 1,000 trials, no further trials were given on that test.

To evaluate the effects of both the order of presentation of the tests and the length of time since operation, the postoperative schedule was modified to some extent. If an animal failed to meet criterion on a test after it had been given 100 trials more than its own preoperative learning score on that test, it was given the rest of the postoperative series, including the new learning test. After completion of the other postoperative tests, testing was continued on the problems it had failed.

RESULTS

Qualitative Observations

There were marked differences in the gross behavior of the two operate groups immediately following operation and to a lesser extent throughout subsequent testing. All the parietal operates showed initial disruption of visual behavior, which contrasted with the apparently normal functioning of the temporal group. Apparent total blindness was observed in all the parietal operates for one to three days after operation, and P-227 and P-240 continued to ignore the left side of the visual field for several weeks. Visual field defects of this nature are frequent concomitants of parietal lobe resection (1, 5, 9) and are ascribed to invasions of the optic radiations underlying the cortex (see Fig. 1). While a recuperative period of two weeks proved to be sufficient time for recovery from most of these inadvertent effects of operation, P-227 and P-240 still had difficulty in visually guided behavior by the time formal testing was resumed. The first postoperative trials, therefore, showed a performance decrement which would presumably not have appeared if the procedure had been planned so that the animals could readjust to the marked visual field defect before formal visual testing was begun. After the first postoperative trials were given, an additional week was allowed P-227 for recovery, with IT-238 being treated the same way as a control. Testing was continued with P-240 in spite of its visual difficulty. After the additional week had elapsed, no gross visual defects were observed in either P-227 or P-240.

With the exception of P-216, the parietal operates showed other striking behavioral anomalies. Transient ataxia and limited use of limbs were noted during the recuperative period. Past pointing and inaccurate grasping for food in the right-left dimension were consistently observed in P-214, P-227, and P-240 for a month after operation. While no muscular weakness or incoordination was noted after the initial period, P-214, P-227, and P-240 had difficulty in making the spatial adjustments required for accurate jumping into a cage. This was evident both in the frequency with which the animals jumped to the right or left of the cage door, and in the difficulty which they had in grading the force of the jump appropriately. This deficit also showed up in the animals' inability to grasp the peanut in the stimulus box. While lookng at it, animals consistently reached to the right, left, or past it. When tested in darkness, they had no difficulty in finding the peanut and grasping it. While disorientation in free space persisted in P-214 and P-227 throughout testing, all the parietal operates were able to locate peanuts visually after several weeks.

Results of Tests

The test scores for each animal are shown in Tables 2 through 5. The criterion for a behavioral deficit on any postoperative performance was based upon the scores obtained by intact animals on the same test. Thus, any postoperative new learning score which fell outside the range of preoperative learning scores on that discrimination was considered a deficit. Similarly, any postoperative retention score which fell outside the range of preoperative retention scores on that test was considered a deficit.

All parietal operates showed deficits on the somesthetic length discrimination as measured by either retention of the habit or by learning (Table 2). Neither parietal monkey had difficulty in learning the postoperative visual cross *vs.* square discrimination. Retention tests given postoperatively to P-227 and P-240 showed initial decrement in performance on this test correlated with the marked visual field deficit described above (Table 3). This transient blindness disappeared with additional recovery time, and there was immediate and simultaneous attainment of criterion.

TABLE 2

Number of Trials to Criterion for Somesthetic Length Discrimination (1,000 F indicates that animal had not reached criterion after 1,000 trials).

Subject	Pre-operative Learning	Pre-operative Retention	Post-operative Retention	Post-operative Learning
P-216	374	10	373	—
P-214	441	0	1,000 F	—
P-227	—	—	—	1,000 F
P-240	—	—	—	642
IT-218	240	42	0	—
IT-219	579	65	37	—
IT-238	—	—	—	439

TABLE 3

Number of Trials to Criterion for Visual Cross versus Square Discrimination (1,000 F indicates that animal had not reached criterion after 1,000 trials).

Subject	Pre-operative Learning	Pre-operative Retention	Post-operative Retention	Post-operative Learning
P-216	—	—	—	193
P-214	—	—	—	468
P-227	250	0	41	—
P-240	390	0	347	—
IT-218	—	—	—	1,000 F
IT-219	—	—	—	1,000 F
IT-238	518	0	1,000 F	—

No temporal operate was able to reach criterion on the visual cross *vs.* square discrimination given either as a retention test or as new learning (Table 3). No temporal operate showed a deficit on the somesthetic length discrimination, either on retention or new learning (Table 2).

There is no overlap between the new learning scores on the somesthetic length discrimination for animals with parietal lesions (P-227, P-240) and the learning scores of all other animals (P-216, P-214, IT-218, IT-219, IT-238). This result is significant ($p < .05$) by a one-tailed Mann-Whitney test. Similarly, there is no overlap between the new learning scores for animals with temporal lesions (IT-218, IT-219) and learning scores for all other animals (P-216, P214, P-227, P-240, IT-238) on the visual cross *vs.* square discrimination. This result is also significant

TABLE 4

Number of Trials to Criterion for Somesthetic ⌟ versus ⌜ Discrimination (1,000 F indicates that animal had not reached criterion after 1,000 trials).

Subject	Preoperative Learning	Preoperative Retention	Postoperative Retention
P-216	285	0	0
P-214	206	0	1,000 F
P-227	184	0	231
P-240	215	5	9
IT-218	229	0	0
IT-219	93	69	24
IT-238	88	0	0

TABLE 5

Number of Trials to Criterion for Visual ⌟ versus ⌜ Discrimination

Subject	Preoperative Learning	Preoperative Retention	Postoperative Retention
P-216	109	0	0
P-214	127	0	9
P-227	199	11	0
P-240	94	0	0
IT-218	285	0	0
IT-219	181	0	201
IT-238	160	0	0

($p < .05$) by a one-tailed Mann-Whitney test. Furthermore, inspection of Tables 2 and 3 shows that there is no overlap in the ranges of scores obtained by the two operate groups on retention of the somesthetic length discrimination or on retention of the visual cross *vs.* square discrimination.

The "easy" test in each modality was less discriminative of the effects of the two types of lesions in that only two of four parietals showed a deficit on the somesthetic ⌟ *vs.* ⌜ discrimination (Table 4), and only one of three temporals showed a deficit on retention of the visual ⌟ *vs.* ⌜ discrimination (Table 5). However, since no parietal operate showed a deficit on the "easy" visual test, and no temporal operate showed a deficit on the "easy" somesthetic test, these tests support the results of the two difficult tests, which did doubly distinguish the two operate groups.

The order in which the tests were presented postoperatively appears not to have affected the degree of deficit. P-216 and P-214 showed a decrement in performance on the somesthetic length discrimination, as would be expected if only the first postoperative test were affected (9). However, P-214 also failed to pass the somesthetic ⌟ *vs.* ⌜ discrimination, which was given second. Additional trials on the length discrimination after completion of the other tests failed to bring P-214 to criterion after 1,000 trials. P-227 and P-240 showed deficits in learning the same discrimination when it was presented as new learning after the other postoperative tests. Similarly, the visual cross *vs.* square was failed by the temporal operates whether it was the first postoperative test or given later. Neither length of time elapsing since operation nor serial position of the tests is sufficient explanation for these behavioral deficits in performance.

DISCUSSION

The pattern of failures on somesthetic tests shown by parietal operates demonstrates that there is a critical cortical locus for somesthesis in the parieto-preoccipital area. The fact that animals with lesions of this area have difficulty in learning habits based on somesthetic cues suggests that more than an amnesia for specific tests is involved. While it cannot definitely be stated that parietal lesions of this extent produce permanent disruption of behavior, the responses of the parietal operates after several months of recovery and after 1,000 trials of testing suggests that other neural substrates cannot easily substitute for the cortical area studied.

The double dissociation between somesthetic and visual functions further suggests that the integrity of the parieto-preoccipital area is required for normal performance of the somesthetic tasks used here, but not for performance of the visual tasks, and conversely, the integrity of the inferotemporal area is necessary for normal visual behavior as here defined and is not necessary for the somesthetic tasks.

The animals with the greatest deficit on the formal somesthetic tests also proved to have the most difficulty in orienting themselves and other objects accurately in space. The descriptions of the deficit in spatial orientation and on the formal somesthetic tasks are not enhanced by characterizing the latter as more "associative" simply because learning procedures were utilized to detect it.

The question does arise, however, as to the nature of this deficit. While the tasks chosen were capable of demonstrating difficulties in discriminative behavior only, it seemed from observation that the animal's capacity for receiving tactile stimuli was unimpaired. The parietal animal responded to an object placed in its hand as consistently as an inferotemporal or normal animal. It is suggested that the results of both parietal and inferotemporal lesions were limited to impairment of discriminative functions. These observations support a distinction between associative processes and primary sensory capacities, but are conclusive only in implicating the cortical areas studied as being important for the tests described. Having shown the dependence of somesthetic discriminative behavior upon the parieto-preoccipital cortex, it is now possible to explore further the dimensions of the resultant behavior.

SUMMARY

1. Circumscribed cortical lesions in monkeys produced behavioral deficits on tests of tactile discrimination.

2. The critical cortical locus for this behavior appears to include the parieto-preoccipital region, extending medially to include the precuneal gyrus.

3. Lesions of the inferotemporal region were correlated with consistent and prolonged deficits in utilization of visual cues.

4. This one-to-one relationship between site of lesion and functional deficit demonstrates dissociation of the area required for adequate performance of certain somatosensory discriminations from that required for visual discriminations.

5. The degree of deficit manifested was correlated with the difficulty of the tests as defined by number of trials taken to learn preoperatively.

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