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DEFICITS IN ROUGHNESS DISCRIMINATION AFTER POSTERIOR PARIETAL LESIONS IN MONKEYS[1]

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Although the role of the posterior parietal cortex in the mediation of somesthetic behavior has been studied extensively, there has been little agreement as to the effects of lesions in sensory tasks (Blum, Chow, & Pribram, 1950; Ettlinger & Wegener, 1958; Glees & Cole, 1954). The nature of deficits in performance (Blum, 1951), the permanence of deficits (Ruch, Fulton, & German, 1938), and even the presence of any deficit independent of ataxic symptoms (Pasik, Pasik, Battersby, & Bender, 1958) have all been questioned. Nonetheless, previous studies from this laboratory (Pribram & Barry, 1956; Wilson, 1957) gave results that implicated this cortical area in somesthetic discriminative behavior. Defective performance on difficult somesthetic tasks with sparing of the learned ability to perform easier tasks was one result. Modality specificity of the defect was another; performance of "similar" tasks that depended solely on visual cues was unaffected. These results suggested that with more quantitative techniques the current discrepancies could be resolved. The following study was initiated in order to assess the amount of difficulty that monkeys with posterior parietal lesions would experience in making tactile discriminations and the effects of this lesion on the factors that contribute to difficulty. Thresholds of roughness discrimination were used as indicators of performance. By obtaining a number of threshold measurements, based on judgments of different grades of sandpaper, differences in performance could be related to two factors that determine behavior: rate of learning and final capacity.

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METHOD

Subjects

Eight immature naive cynomolgus monkeys, weighing between $3\frac{3}{4}$ and $4\frac{3}{4}$ lb. at the start of the experiment, were randomly divided into an experimental group and a control group after completion of preoperative testing.

Apparatus

The *S*s were trained in a testing cage, the front of which had vertical bars spaced $2\frac{1}{2}$ in. apart. This cage was placed in a light-tight box with an opaque sliding panel. When the panel was lowered, *S* was presented with two cues separated by a 2-in. space situated 8 in. above the floor of the testing cage. These cues consisted of 2-in. lengths of wooden doweling, 1 in. in diameter, cut in half, mounted flat side down and covered on all exposed surfaces with sandpaper.

Each manipulandum could be pushed, on a slide, against a spring of $\frac{3}{4}$-lb. tension for a stroke of $1\frac{1}{2}$ in., after which it locked. A food cup, in which a quarter of a peanut could be placed, was then revealed under the slide. The manipulanda were constructed so that each could be readily and firmly attached to the left or right slide. Signal lights, visible only to *E*, were activated by microswitches after movements of the manipulanda. The apparatus had the advantage that when *S* reached out of its cage, its tactile field contained only the two manipulanda. Thus, there were no obstructions in the testing space and the required response movements were such that they could be made even by monkeys with considerable ataxia.

Procedure

Surgery. The monkeys in the experimental group received one-stage bilateral resections of the parieto-preoccipital cortex. The surgical procedure and extent of the lesions which had produced somesthetic deficits in previous studies (Pribram & Barry, 1956; Wilson, 1957) were reproduced as closely as possible. The cortical area removed extended from the intraparietal sulcus to the lunate sulcus, and inferiorly to the superior temporal gyrus. Care was taken to include the whole precuneal gyrus on the medial aspect of the brain. The animals were not sacrificed pending ongoing experiments, and histology will be reported in a future publication. Reconstructions of similar ablations can be found in a previous study (Wilson, 1957).

Testing. In order to obtain thresholds for roughness discrimination, it was first necessary to teach the *S*s a roughness discrimination. Commercial grades of sandpaper, of 24, 36, 50, 80, 120, 180, and 280 grains/inch, formed the stimulus magnitude scale. The coarsest sandpaper in the series (24) was opposed to the smoothest (280) in the preliminary training, and was consistently rewarded. Initial trials were given in the light, and the animals were allowed to correct wrong choices until they went freely to both left and right sides. Noncorrection technique was then employed. Gradually, the room illumination was decreased until finally the *S*s made their choices in complete darkness on the basis of somesthetic cues. The *S*s quickly learned to feel both stimuli and then push back the correct block far enough to reach the peanut reward. The position of the correct stimulus was alternated in a random sequence (Gellermann, 1933). The sandpaper blocks were concealed between trials by the sliding barrier between the testing cage and the apparatus. Auditory cues resulting from changing the blocks and baiting the foodwells were equalized. The sandpaper on each of the stimulus blocks was renewed frequently. The *S*s were trained to a criterion of 90 correct responses in 100 consecutive trials.

After all *S*s had learned the initial discrimination, it was possible to test their ability to discriminate between the various grades of sandpaper.[2] The method of constant stimuli was adapted to this situation by using the 280 grade sandpaper as the standard or comparison stimulus and pairing it with one of the rougher grades, 36, 50, 80, 120, 180, as the variable stimulus. Since the *S*s had been trained to choose the coarser sandpaper in the initial 24 vs. 280 discrimination, the variable stimulus was correct in each pair. The variable stimuli were presented in random order and the number of right-left positions was balanced for each stimulus. The five variable stimuli were presented 10 times each with the standard stimulus on one testing day. The 50-trial set was repeated three times so that each *S* judged each stimulus 30 times against the 280 standard.

Each of the five variable stimuli was then paired with the 24 sandpaper as the standard. Each stimulus was presented 10 times on each of three testing days in the manner described above. In this case, the standard stimulus was always correct since the 24 sandpaper was coarser than any of the variable stimuli. Before starting each test series, *S* was given trials on the initial 24 vs. 280 discrimination to insure understanding of the problem.

After completion of the initial training and the 24 and 280 threshold problems, four monkeys chosen randomly were given posterior parietal ablations. At least two weeks was allowed for recuperation, and then all *S*s, normal and operated, were tested on the initial training problem 22 days after the last preoperative test. All monkeys were then tested on the threshold series with the 280 standard, then on the stimuli with the 24 standard. Three sets of 50 trials were run in the same way as preoperatively. Approximately 2½ months after operation two additional sets of 50 trials on both threshold problems were given to all monkeys.

Treatment of data. Thresholds were determined graphically in the usual manner. The number of correct responses to each grade of sandpaper when paired with a given standard stimulus was cumulated. The percentage of correct judgments was plotted as a function of the logarithm of the stimulus (log grains/inch). The log stimulus value which was responded to at the 75% correct level was determined by graphical interpolation. The difference between this value and the standard stimulus gave a measure of the difference limen, or that difference in log grains/inch which *S* could discriminate correctly 75% of the time.

[2] All monkeys except N-538 and N-548 took part in preliminary tests to determine the appropriate range and number of stimuli.

Results

After operation the *S*s with parietal lesions displayed none of the symptoms which have been noticed previously after lesions in this area. Neither ataxic symptoms nor visual disturbances were observed immediately after operation. There was also no apparent spatial disorientation.

When tested after the operative interval, all *S*s showed perfect retention of the initial 24 vs. 280 discrimination. The parietal group made a few more errors in reaching the criterion, but this group as well as the normal reached 90% correct responses in 100 consecutive trials immediately.

Table 1 gives the difference limens for the two groups pre- and postoperatively, expressed in logarithmic units of the stimulus. Before operation, there was no significant difference between the mean threshold values of the two groups. On the first postoperative threshold determination with 280 as standard, the normal group reduced its DL from .35 to .18 while the operated group's DL increased from .45 to .50. After further experience with the stimuli on the second postoperative

TABLE 1

Mean Difference Limens for Normal and Operated Monkeys

Comparison Stimulus	Group	Preoperative M	Preoperative σ	Postoperative I M	Postoperative I σ	Postoperative II M	Postoperative II σ
280	Parietal	.45	.23	.50	.31	.34	.11
	Normal	.35	.11	.18	.06	.16	.03
24	Parietal	.31	.09	.33	.04	.31	.04
	Normal	.38	.10	.33	.05	.28	.08

threshold determination, the operated animals improved their DL to a mean of .34 while the normal group further reduced its mean DL to .16. When the variable stimuli were compared with the 24 standard stimulus, changes in threshold were similar. The normal *S*s improved their performance while the operated group remained at essentially the same level. Results of a repeated-measurements analysis of variance of threshold changes (McNemar, 1955, pp. 332–5) yielded one significant main effect, that of the lesion (Groups) tested against Subjects ($p < .01$). The only other significant effect is the Subject by Comparison-Stimulus interaction ($p < .05$). The fact that no significant interaction was found for Groups by Tests suggests that the effect of the lesion was constant as the postoperative interval and the animals' experience increased. It is possible that with further testing the parietal group's performance would approximate the normal performance; however, after several months of testing the parietals' improvement is clearly inferior to the normals'.

The behavior of the two groups may also be compared by considering their responses to each of the variable stimuli on successive testing days. Figure 1 shows the learning curves for three of the five stimuli, which result when the percentage of correct responses to each sandpaper is plotted as a function of the amount of practice. The break in the curve represents the operative interval. It is interesting to note that the first postoperative test does not reveal the poorest performance by the operated animals. It can be seen that as experience with the stimuli increased, the operated *S*s reached equal or better performances on the easy discriminations, i.e., when the difference between standard and variable was great, but that their level of performance deteriorated compared with the normal group when the discriminations were difficult.

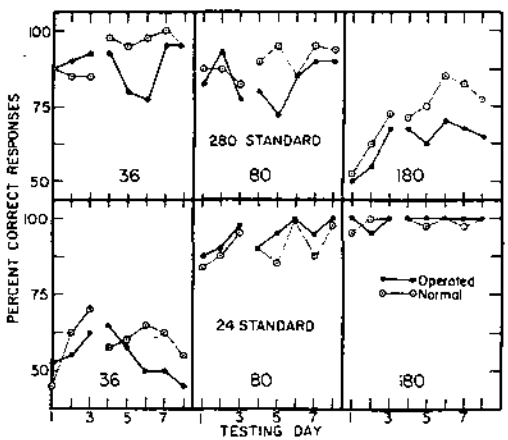

FIG. 1. Scores for normal and operated groups on successive testing days for 3 stimulus comparisons, upper curves for 280 standard, lower curves for 24 standard. The break in the curves represents the operative interval.

The 24 threshold determinations reveal better performance by the operated group than do the 280 determinations. Nonetheless, on the most difficult comparison, 24 vs. 36, the operated animals show a performance inferior to that of the normals as they do on the difficult discriminations with the 280 standard.

DISCUSSION

Comparison of the normal and the parietally operated groups on pre- and postoperative thresholds shows that the operated group performed more poorly. Had the operated animals' thresholds been compared with their own preoperative thresholds, it would have been concluded that they were functioning at a normal level. However, it is seen that simply with repetition the normal animals were able to improve their thresholds, and thus the effect of the lesion becomes apparent. This is another demonstration that discrimination may show improvement with practice even though no new stimulus-response learning seems to be involved (Ghent, Weinstein, Semmes, & Teuber, 1955). This is a type of perceptual learning (Gibson & Gibson, 1955) in which the animal is presumably learning more about what constitutes the stimuli in the situation. A further analysis of this type of behavior can be made by considering separately the kinds of factors which determined the threshold values. Improvement in discrimination can then be considered to be both a function of the difficulty of the task and the amount of practice. The operated group responded as well as did the control group on easy problems but remained at an inferior level of performance on difficult ones. On the other hand, the operated group did show an increment in performance on the less difficult discriminations after practice. Therefore, the deficit can best be described as some decrement in the level that performance can reach, i.e., loss in capacity to resolve differences between stimuli.

This conclusion could make unnecessary the interpretation of an earlier study (Wilson, 1957) which suggested an associational deficit unrelated to loss of capacity for resolving or differentiating stimuli. In that case, trials to criterion was the index of deficit and there was no possibility of assessing separately the learning and capacity factors (except insofar as the behavior of the operated monkeys gave no indication of any gross sensory defects apart from disorientation in space). However, the deficit postulated here to account for the inferior performance of the operated group is not of the same order as the ataxic symptoms which Pasik et al. (1958) suggest underlie deficits on somesthetic tasks. These kinds of symptoms, had they been observed, would be expected to affect all the differentiations equally, while the present study shows selective effects on difficult discriminations. Simple "memory" loss can be ruled out for the same reason. Thus, when tasks are easy or when a great deal of overtraining has taken place, as in the usual trials-to-criterion problem, significant deficits in performance may not be observed—especially when the preoperative performance is taken as a base line. The results of this study are in agreement with those of other studies which show that difficulty of task and overtraining must be considered in assessing the effects of lesions on performance (Mishkin & Hall, 1955; Orbach & Fantz, 1958).[3]

In conclusion, the results of this study suggest how previous discrepant findings can be reconciled. If sufficiently sensitive measures of behavior are used, and if factors of difficulty of task, amount of practice, and the meaning of criterional measures are assessed, the presence or absence of behavioral deficits can be accounted for. For example, Pasik et al. (1958) concluded that there was no deficit on tactile intensity discrimination after parietal lesions when they found unaltered performance on a 480 vs. 120 sandpaper discrimination. Since this represents a log stimulus difference of .60, which is greater than the DL of the parietal animals in this study, it is clear that no deficit should be observed. Ghent et al. (1955) have shown the importance of such analyses in a study of somatosensory abilities in man, and Mishkin and Hall (1955) for visual discrimination in the monkey. When such results are taken into account, the role of the posterior parietal cortex in somesthesis seems to be firmly established. Direct comparison of effects of lesions in primary somatosensory cortex and posterior "associational" cortex should further the understanding of somesthetic structures and functions in terms of classical psychological categories.

[3] An uncontrolled factor in this study lies in the possibility that *S*s responded to auditory cues resulting from feeling the sandpaper. While *E* was not aware of the presence of any auditory cues, *S* may have been, and in this case, the specificity of the deficits produced would be open to question.

Summary

1. A graded series of sandpapers was opposed to two standard sandpaper stimuli in order to measure roughness thresholds in four monkeys which underwent posterior parietal lesions and in four monkeys which acted as normal controls.

2. Postoperative thresholds for the operated group remained the same while the normal group showed an improvement in performance characteristic of perceptual learning.

3. Analysis of responses to each sandpaper showed that the parietals improved only on easy discriminations while the normals improved on both easy and difficult ones.

4. This is further evidence for the importance of the posterior parietal area in somesthetic behavior: the deficits in performance produced appear to be related to capacity factors rather than to so-called associational processes.

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