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SOMAESTHETIC ALTERNATION, DISCRIMINATION AND ORIENTATION AFTER FRONTAL AND PARIETAL LESIONS IN MONKEYS

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Eight naïve monkeys were trained on non-visual tests of alternation and discrimination. These animals were also taught to perform a test of orientation with or without visual control. Four animals then received bilateral frontal excisions and three (of four) animals survived bilateral removal of the posterior parietal region. Following surgery, all frontal operates were found to be severely impaired on the somaesthetic alternation test. The parietal operates, on the other hand, were unimpaired on this test though all gave evidence of defective orientation in space. Some implications of the results are discussed.

Introduction

Monkeys with bilateral antero-lateral frontal lesions have repeatedly suffered impairment on two tests when their performance is compared with that of either unoperated controls or of monkeys having cortical lesions elsewhere. These tests have been named Delayed Response and Spatial Alternation. The procedures involved in each test have been described, and the findings comprehensively reviewed, by Chow and Hutt (1953). For the present study it is of especial relevance that a normal animal could pass adequately on both of these tests in their customary form by responding, at least *prima facie*, solely to visual cues. The question therefore arises whether failure on these two tests by monkeys with frontal lesions can be attributed to a specifically visual disorder.

In one investigation by Blum (1952) the traditional form of the delayed response test was modified by the substitution of auditory for visual spatial cues. Blum's findings are not, however, strictly comparable with other results, since the two sounds he used, namely a bell and a buzzer, differed most probably in pitch and intensity as well as in location.

The aim of the present study was first, to establish whether or not monkeys with frontal lesions show impairment on a test of alternation which cannot be passed by responding to visual cues. A deficit on this test would suggest that a specifically

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visual disturbance does not form the basis of the previously demonstrated consequences of frontal lesions. In the second place, it was intended to examine the effect of frontal lesions upon the somaesthetic discrimination of monkeys in order to determine what relationship might exist between discrimination and alternation performance. Finally it was planned to include a quantitative evaluation of the finding of Glees and Cole (1953) and Wilson (1957) that spatial orientation in monkeys following bilateral posterior parietal lesions is improved by the exclusion of vision.

Method

Subjects

Eight previously untrained macaques were the subjects of this study. Their weights ranged from 3½ to 6½ lb. at the beginning of training. On the basis of their scores on a preliminary somaesthetic discrimination they were divided into two balanced operative groups. Subjects F1–F4 were given antero-lateral frontal lesions, the remainder (P1–P4) received parieto-preoccipital lesions. One animal (P4) died as the result of operation, leaving post-operative results available only for seven animals.

Operations

Sub-pial aspirations were carried out by means of a small-guage sucker bilaterally in one stage under intraperitoneal Nembutal anaesthesia. Especial care was taken to remove all grey matter from the depths of the sulci included within the limits of the lesions. The frontal lesions were designed to extend forwards from the arcuate sulcus over the entire lateral surface. The frontal poles were amputated in one piece within an arc of about 1·5 cm. radius from their tips, but both medial and orbital surfaces were otherwise spared. The parieto-preoccipital lesions were intended to involve the region between the intraparietal and lunate sulci, extending inferiorly to the superior temporal gyrus and medially over the whole precuneal gyrus.

Histological procedures

Following completion of testing the animals were anaesthetized and their brains perfused with formalin, removed and prepared for histological study. Serial coronal sections of 50 μ thickness were cut and every tenth section was stained with thionin. Reconstructions of the lesions of animals F1 and P1 are presented in Figure 1, together with representative cross-sections through areas of cortical resection and thalamic degeneration. Comparable data for the remaining operates are available, but have not been presented since the lesions and associated degeneration in these animals are similar in all essential respects to those of animals F1 and P1. There is some degeneration in the lateral geniculate bodies of all of the parietal operates, but this is somewhat less extensive in the case of animals P2 and P3 than for animal P1.

Apparatus

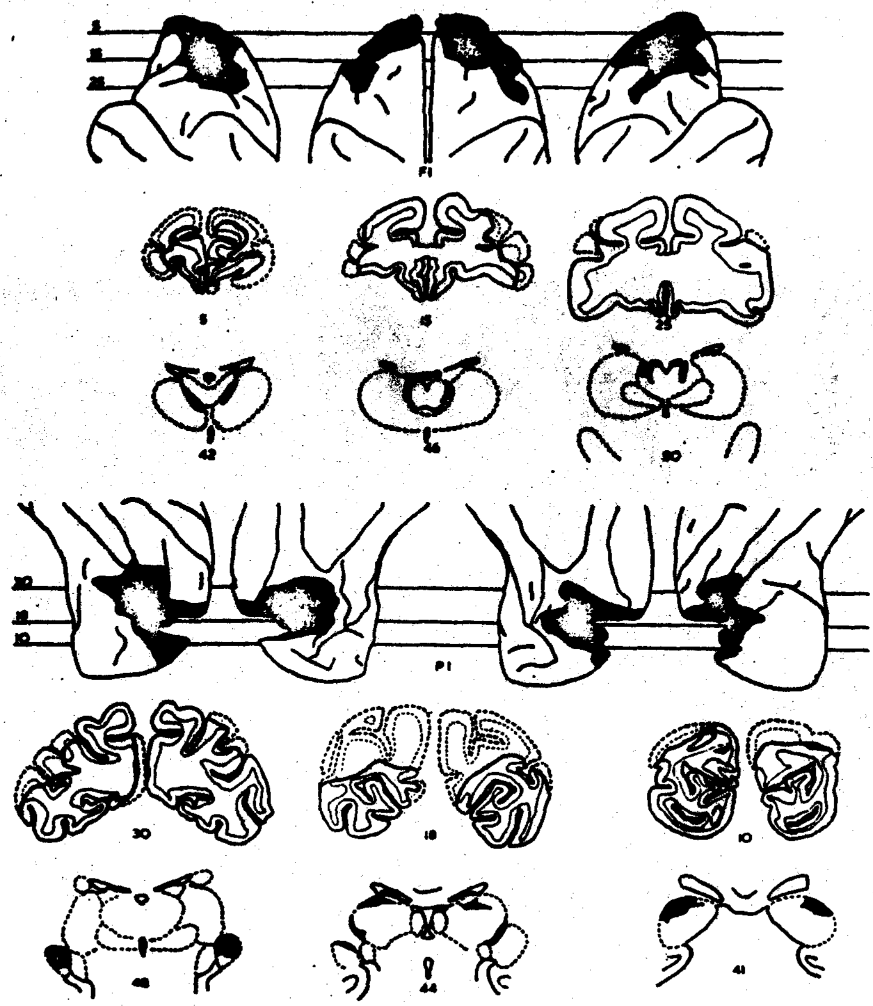
An improved model of the infra-red scanning device described by Cox and Kruger (1955) was used in conjunction with a modified Wisconsin general testing apparatus situated in a light-proof room. The animal was trained to jump into a cage having horizontal bars 2 in. apart. The opaque screen in front of this cage could be lowered to expose a horizontal shelf. The cues and reward containers were attached to this shelf which the monkey could explore by reaching through the bars of the cage. The scanning device permitted the experimenter to resolve detail in two areas on the shelf, measuring 2 in. × 2 in. and 12 in. apart, when the illumination was too low for ordinary vision. Observation of the monkey's hand in close proximity to alternative cues was thus made possible even in total darkness. In removing the lid of either of two food containers the monkey operated a microswitch, so that one of two 6 v. bulbs, set 12 in. distant from the centre of the shelf, lit up on the same side as the response. This signalled that a definite choice had been made, bringing the trial to an end if the response was incorrect or providing light for the animal to find the reward for a correct choice.

Tests

All animals were trained to a fixed criterion on tests of somaesthetic alternation, somaesthetic discrimination and orientation. Informal tests of field defect, spatial and topographic orientation, discrimination between edible and inedible objects and of emotional reactivity were also carried out.

Alternation test; two wooden food cups, $2\frac{3}{16}$ in. square and $\frac{1}{4}$ in. deep, were symmetrically attached to the shelf with their centres 3 in. from the cage and 6 in. distant from the middle of the shelf. A metal ashtray and a tobacco tin fastened to the lids served as cues in object alternation. For spatial alternation two identical 1-in. lengths of wooden rod ($\frac{1}{4}$ in. diameter) were fixed vertically to the centres of the otherwise plain lids.

FIGURE 1



Reconstructions of brains of animals F1 and P1, and representative cross sections through areas of cortical damage and thalamic degeneration. Black indicates the extent of the cortical removal in the surface views and of thalamic degeneration in the appropriate cross sections.

Somaesthetic discrimination test: the same cups were used in the three versions of this test. However, in the one case identical equilateral triangles, cut out of wood $\frac{5}{16}$ in. thick with sides 1 in. long, were attached to the two lids so that they could be rotated about their centres. Each lid always remained on the one side, but one triangle was presented to the animal erect, the other inverted (i.e. one angle directed towards the animal). The inverted triangle was the positive cue for all animals. In the second form of the discrimination test the longer one of two lengths of wooden rod (measuring $2\frac{7}{16}$ in. and $1\frac{1}{4}$ in.

respectively) indicated the presence of reward. The rods were fixed to the lids in the frontal plane and had a diameter of ½ in. For initial post-operative somaesthetic discrimination learning a cross (2 in. × 2 in. × $\frac{7}{16}$ in.) and an inverted T (2 in. × 2 in. × ⅞ in.) both of wood ½ in. thick, served as the alternative cues. Whichever form an animal selected on its first trial was adopted as the negative cue throughout. Thus the cross (i.e. non-preferred) was rewarded for animals F1, F4 and P2, while the inverted T was positive for the remainder.

Test for orientation: a peg-board was fitted to the shelf so that its front edge was separated by ½ in. from the cage. This board, measuring 14 in. × 6½ in., contained three rows each of seven holes. Wooden pegs of ½ in. diameter fitted snugly into these holes so that they projected 1½ in. above the surface of the board. The centres of the two food cups were again 3 in. in front of the cage, but (being separated by the intervening peg-board) they were 8½ in. from the middle of the shelf. The two lids of the cups were identical, being those used also for spatial alternation. The absence of pegs to either side of the middle of the board indicated to the animal the presence of a reward in the covered cup on that side.

Training procedures

Animals were given 40 trials per day and tested on five or six days each week. The standard reward for a correct response consisted of ¼ peanut except in the test of object and spatial alternation, when ½ peanut was provided. Supplementary food was given immediately after testing in sufficient quantities to maintain good nourishment and health. Training was continued on all tests until the animal reached the criterion of 90 per cent. correct in 100 consecutive trials. The last 100 trials are not included in the test scores, according to convention. Auditory cues were eliminated from the test procedure by the presence of a continuous masking noise and by balancing the noise of baiting. Non-correction procedure was adopted throughout except in the case of severe position habits during the initial learning of any habit, and in the alternation test. If the animal responded to one side on ten consecutive trials the positive cue and reward were maintained on the alternate side until the animal went there on three consecutive occasions. Such positional corrections were counted as trials. In object alternation the tobacco tin and ashtray were presented in a random left-right sequence with about 5 seconds interval in between trials. Correct response consisted of choosing that object which had not been rewarded on the previous trial, irrespective of the object's position. In case of error the opaque screen was interposed only for an instant, following which the animal was permitted to correct its choice. In spatial alternation both cups (identical lids) were baited on the first trial. Correct response thereafter consisted of choosing the cup on the side which had not been rewarded on the preceding trial. Trials were separated by about 5 seconds. If the animal removed the wrong lid, the opaque screen was interposed, the lid replaced and the animal given a further trial. This correction procedure was continued until the animal made the correct response. The first trial of a test session (both cups baited) and correction trials at alternation were not counted towards the total of 40 daily trials. The position of the positive cue in the discrimination and orientation tests was randomized in accordance with a balanced (Gellerman) schedule.

The animals were first adapted to the test situation and to responding in the dark by training on an easy somaesthetic discrimination test (cube *vs.* cylinder). Scores to criterion ranged from 140 to 350 trials. They were next trained on the orientation test so that any transient disturbance of orientation might become manifest on the first post-operative test. Half of the animals (F1, F4, P1 and P4) learnt this test in the light (i.e. visual cues were available and animals were not required to touch the pegs), the remainder were given exactly the same stimulus display, but in darkness. In both cases six pegs were initially removed from either the left or right side of the board. The empty holes were situated in the front two rows to either side of the middle one of the seven columns. The animals were taught to go to the cup on the side of the empty holes. When the animal had reached criterion on this stage, only four pegs were removed (again from the front two rows but leaving the outside pair intact). Although performing better than chance no animal was able to meet the criterion on this stage within 500 trials. The aim of eventually teaching the animals to respond to the absence of only one peg to either side of the midline was therefore abandoned. All animals were retrained to respond to the absence of six pegs, and the trials given in the four-peg situation were discounted.

Animals F1, F2, P1 and P2 were next trained to discriminate in the dark between the upright and inverted triangles. Only one animal (P2) passed on this test within 2,000 trials. The best animal amongst the remainder (P1) achieved 71 per cent. correct in the last 100 trials. Animals F1, F2 and P1 were therefore taught the length discrimination. Thus each animal of these four reached criterion on only one form of the somaesthetic discrimination test pre-operatively. Finally all these four animals (F1, F2, P1 and P2) were trained on spatial alternation in darkness.

The remaining four monkeys (F3, F4, P3 and P4) attempted somaesthetic object alternation after passing on the orientation test. However, no animal met the criterion within 2,000 trials. Their scores over the last 100 trials were 40, 58, 53 and 56 per cent. correct respectively. They were all therefore trained on spatial alternation (in the dark) and finally on the somaesthetic length discrimination.

After each animal had passed on three tests (in addition to the preliminary adaptation test) it was allowed 14 days' rest and then retrained on each of the three tests in the same order as they were passed originally. This phase of training was called pre-operative retention testing. The animal then received its lesion and was allowed 14 days for recovery. Informal testing (e.g. for field defects) was done during this period. Thereafter the stage of post-operative retention consisted of retraining each animal once again on each of the three tests in the same order as before. If, however, any animal failed to regain the criterion in less than the maximum score for all the animals on that test *during pre-operative retention*, its performance on the next remaining test(s) was assessed before the former was eventually completed. Re-training was continued only for 1,000 trials post-operatively on the alternation test. Finally, after varying periods of rest and 5–6 months after operation, all animals were taught a new somaesthetic discrimination (cross *vs.* inverted T).

Results

Informal observation after operation revealed striking differences between the animals with frontal and parietal lesions. The frontal operates made purposeless slow movements with their limbs as soon as they recovered from the anaesthetic. Within 2–6 hours these limb movements had merged into the typical picture of hypermotility and pacing. Any kind of pre-operative avoidance (e.g. aversion of the gaze) was replaced by fearlessness bordering on the aggressive. All four animals with frontal lesions took food within 6 hours of recovery from the anaesthetic, although a tendency to manipulate tactually and then discard some food items persisted for periods of 2–14 days. There was no evidence of field defect nor of disorientation. Two of the parietal operates on the other hand were transiently blind (for a period of two days in the case of P2), and all three surviving animals showed severe visual disorientation (in the sense of Holmes, 1919) as soon as reactivity to visual stimulation returned. This disorientation was manifest in gross inaccuracies in jumping and reaching. Such an animal will not infrequently strike its face against an obstacle or miss its objective in jumping by a foot or more. All three parietal operates preferred to accept food in their mouth (even so inaccurately) instead of in their hand following the operation. No inaccuracies in bringing the hand to the mouth were observed. Difficulties in finding the way between the home and test cages were tentatively attributed to this disorientation, which persisted during the six months' period of observation despite some improvement. The extent of field defects could not be reliably ascertained in these animals, but all three were able to discriminate between edible and inedible objects without error on the twelfth post-operative day. A further effect of the parietal lesions was to greatly increase the fear and withdrawal responses in all animals for periods of 21 days or more. Thus P3 would not spontaneously move from the furthest corner of its cage for 11 days. For 36–48 hours after the operation no parietal operate would eat so that recourse was had to force-feeding. No animal in this study reversed its hand preference as a result of operation.

The results on the formal tests are presented in Tables I to IV. The four frontal animals had required up to 830 trials to reach the 90 per cent. criterion during initial learning of the somaesthetic spatial alternation test, but none exceeded 64 per cent. correct after 1,000 post-operative trials. On the other hand the scores of the remaining

TABLE I

NUMBER OF TRIALS TO CRITERION ON THE SOMAESTHETIC SPATIAL ALTERNATION TEST

Animal	*Pre-op. learning*	*Pre-op. retention*	*Post-op. retention*
F1	400	180	1,000 + (50 per cent.)
F2	720	160	1,000 + (61 ,, ,,)
F3	830	440	1,000 + (64 ,, ,,)
F4	810	60	1,000 + (52 ,, ,,)
P1	240	160	150
P2	910	70	170
P3	710	130	40

1,000 + indicates that the animal failed to reach criterion in 1,000 trials. Figures in brackets indicate per cent. of correct responses in the last 100 trials. Animal P2 was trained at each of the three stages to a criterion of 80 per cent. correct

TABLE II

NUMBER OF TRIALS TO CRITERION ON THE SOMAESTHETIC DISCRIMINATION TEST

Animal	*Pre-op. learning*	*Pre-op. retention*	*Post-op. retention*
F1	640	70	420
F2	820	190	670
F3	760	110	40
F4	610	40	0
P1	370	110	30
P2	610	0	60
P3	770	200	30

Animal P2 was trained to discriminate between triangles; the remainder were trained to discriminate between lengths.

TABLE III

NUMBER OF TRIALS TO CRITERION ON THE VISUAL AND SOMAESTHETIC ORIENTATION TEST

Animal	*Form of test*	*Pre-op. learning*	*Pre-op. retention*	*Post-op. retention*
F1	Visual	410	150	110
F2	Somaesthetic	1,270	330	420
F3	Somaesthetic	520	300	20
F4	Visual	500	100	430
P1	Visual	610	10	280
P2	Somaesthetic	1,860	190	1,200
P3	Somaesthetic	710	430	660

TABLE IV

NUMBER OF TRIALS TO CRITERION ON THE NEW SOMAESTHETIC DISCRIMINATION TEST ADMINISTERED POST-OPERATIVELY (CROSS *vs.* INVERTED T)

Animal	*Trials*	*Animal*	*Trials*
F1	280	P1	170
F2	380	P2	70
F3	460	P3	400
F4	370		

three animals following parietal lesions fell easily within the range of all the pre-operative retention scores on this test. Animals P1 and P3 actually required fewer retention trials after than before operation. During initial learning of the alternation habit some animals persisted in selecting the incorrect side during several consecutive corrections following an error. Such perseverative errors during correction trials were as a rule associated with position habits. However, not a single instance of perseveration occurred during pre-operative retention testing. Impaired alternation in the frontal operates was accompanied by a striking increase in the amount of response perseveration. Thus a frontal operate would repeat its incorrect choice (i.e. go to the previously correct side) on up to 20 consecutive trials before making the alternate response. This perseveration was manifested to some degree following the majority of incorrect responses, irrespective of laterality, during the first 200–300 post-operative alternation trials. It persisted despite improvement throughout testing. Thus the incidence of perseveration following an incorrect response is 58·9 per cent. in respect of 192 errors during the first 100 trials, and 30·9 per cent. in respect of 173 errors during the last 100 of 1,000 post-operative alternation trials for the four frontal animals combined. Three or more corrections were required in 37·5 per cent. of errors during the first 100, and in 8·1 per cent. during the last 100 trials. There was little if any increase following frontal lesions in the incidence of position habits, except during the first 200 trials of F4.

Differences between the two operate groups are less consistent on the somaesthetic discrimination tests. Again all parietal operates relearnt their pre-operative discrimination following operation within the range of pre-operative retention scores (P1 and P3 actually required fewer trials for post-operative than for pre-operative relearning). However, while two of the frontal animals, F3 and F4, likewise showed improved retention post-operatively, the remaining two, F1 and F2, were not able to regain criterion after the operation within the range of trials required during pre-operative retention. For this reason and because both nevertheless reached criterion in fewer trials after the operation than during initial learning (i.e. showed 34 and 18 per cent. saving respectively), animals F1 and F2 may be said to display a "retention defect." An analysis of comparison behaviour (i.e. trials on which the animal touched one or both cues before making its choice) and of the incidence of position habits failed to reveal any differences between the records of F1 and F2 on the one hand and those of the remainder on the other. The test performance of F1 and F2 is best described as exceptionally variable, and it is noteworthy that F1 reached 83 per cent. correct during post-operative trials 21–120 and that F2 made only 16 errors in the 100 trials beginning with the 360th post-operative trial. As will be seen from Table IV, the learning scores of the two operate groups overlapped on the new post-operative somaesthetic discrimination (cross *vs.* inverted T). The mean number of trials to criterion is 373 for the four animals with frontal excisions, as compared with 213 for the three animals with parietal resections.

Before operation animals F1, F4 and P1 all regained criterion on the test of *visual* orientation within 150 trials. Both F4 and P1 required more than 150 trials to relearn this discrimination after operation, but fewer trials than for original acquisition of the habit. On the *somaesthetic* form of the orientation test the maximum pre-operative retention score for animals F2, F3, P2 and P3 was 430 trials. This score was exceeded during post-operative testing only by P2 and P3, though both animals regained the criterion in fewer trials than they required during original learning. Combining these results for *both* forms of the test, one frontal and all three parietal operates are found to have a "retention defect." This impairment can not be attributed to the order of testing after operation. Not only were *all* animals retrained first on this test following operation, but some continued to fail for up to three weeks and 770 trials when they returned to this test after passing on the other two tests. Nevertheless it could be argued that mechanical difficulties interfered with the execution of the responses of the parietal animals during the first 150–200 post-operative trials. Thus, for example, P2 required 50 minutes to complete the first 40 trials (somaesthetic form of test). At first she frequently reached through inappropriate bars of the cage and missed the peg-board entirely. Even when she succeeded in exploring it, as all the animals continued to try to do, she had difficulty in finding, grasping and lifting the lid of her choice so that on occasion she eventually shifted to the incorrect cup. Inaccuracies in the sagittal plane (mainly over-reaching) were more severe than in the coronal plane, with no selective differences as between right and left. Both hands were equally affected. This disability was similar both in the light and dark. It varied in severity from animal to animal, and most probably ceased to interfere with the purely *executive* aspects of testing after some 200 trials in all cases.

Discussion

The results of the present study indicate that bilateral antero-lateral frontal lesions, but not parietopreoccipital lesions, impair the performance of monkeys on a non-visual test of spatial alternation. This severe impairment persisted within the limits of 1,000 post-operative trials. What light then do the present findings throw upon the nature of the so-called frontal lobe deficit? In the first place the possibility has not, admittedly, been excluded that frontal lesions have as their consequences a multi-modal impairment of a particular kind. Thus it could still be argued that where delayed response or alternation tests are presented in the light a disorder of visual function forms the basis for the deficit in frontal operates. On the other hand a specifically kinaesthetic disorder might be claimed to underlie the impairment on delayed response and alternation regardless of the presence or absence of supplementary visual (or auditory) cues. Nevertheless, in view of the outcome of other investigations (e.g. Pribram and Mishkin, 1956) taken in conjunction with the present results, the disturbances in frontal monkeys are most plausibly regarded not as related to one or more sensory systems but as being of a supra-modal order. Their precise nature, however, or even their unitary character has not been established in the present study. It should be pointed out that the successful performance by three of the frontal operates on the orientation test does not necessarily contraindicate Campbell and Harlow's (1945) opinion that ". . . . failure to establish firmly an association between the position of the correct stimulus and the implicit food reward and to differentiate these cues from the rest of the test situation . . ." constitutes the essential source of difficulty in delayed response for frontal operates. For in the orientation test dissimilar cues are present at the moment of choice. The significance of the excessive response perseveration (which has previously aroused comment) likewise remains obscure, although this kind of stereotyped behaviour may merely be one *consequence* of the animals' inability to respond successfully under certain conditions.

In considering the present findings on the somaesthetic discrimination tests it may be recalled (in connection with the retention defect of animals F1 and F2) that a proportion of frontal operates has not uncommonly failed on tests of visual discrimination (cf. Chow and Hutt, 1953). The unimpaired retention by the parietal operates (as assessed by reference to the range of the pre-operative retention scores of all seven animals) is less readily accounted for in view of the findings of Pribram and Barry (1955) and of Wilson (1957). However, when only those of their data which pertain to tests administered both pre- and post-operatively are considered, the defect consequent upon lesions confined to the posterior parietal and pre-occipital regions is seen to be both variable (four out of their seven parietal operates failed to show impairment on one out of two tests) and mild (only two out of seven animals required more trials for post-operative than initial learning on one or both tests). The findings of Glees and Cole (1953) in two parietal operates, and the comprehensive investigation of Blum (1951) are broadly in accord with this view (although the lesions in their animals did not extend as far on to the medial surface as do those from this laboratory). A new discrimination learnt initially after operation has, on the other hand, been generally found to be impaired more severely than one learnt pre-operatively. Since the range of learning scores by unoperated but otherwise comparable control animals on the new post-operative discrimination (cross *vs.* inverted T) has not been ascertained, it cannot be claimed that the parietal operates are unimpaired on this test. It has nevertheless at least been demonstrated that the performance of the parietal operates is not inferior on this test to that of the animals with frontal ablations. In connection with the demonstrated relationship between test difficulty and severity of post-operative impairment it is noteworthy that the discrimination retained successfully after operation by P2 (the triangles) was so difficult that three animals were unable to master it within 2,000 trials before operation. Thus the present results underline the need for further inquiry into the effects of posterior parietal lesions.

A number of investigators (Glees and Cole, 1953; Pribram and Barry, 1955; Wilson, 1957) have referred to defective visual orientation in monkeys with parietal lesions. Ferrier wrote in 1886 of a monkey given bilateral lesions of the angular gyrus: "On the fourth day (after operation) some indications of returning vision were observed, but the animal never during the whole period of its survival—over two months—regained perfect vision, but always exhibited some uncertainty or want of precision in its endeavours to seize things offered it, or to pick up minute articles of food from the floor, such as currants or grains of corn" (p. 282). In the present study, orientation both with and without visual guidance was assessed quantitatively, and parietal operates were found to be selectively impaired on both forms of the test. However, no quantitative data concerning this phenomenon are known to be available elsewhere in the literature dealing with sub-human behaviour, so that confirmation of the present findings is required.

The peg-board test differs from other discrimination tests chiefly in that the positive and negative cues are immediately adjacent to one another. The location of the alternative cues is also not identical with the location of the two food cups. The exceptionally high initial learning scores of two animals on the somaesthetic form of the orientation test partly resulted from the animals' neglect to explore the peg-board for many trials. However, all of the animals re-tested on this version after operation at once attempted to touch at least one end of the board before reaching for either food cup. It is not clear whether the parietal operates experienced difficulty in differentiating between the positive and negative cues, or in relating discriminated cue differences to the choice of cups, or in some other aspect of the task. The evidence from an analysis of comparison behaviour (i.e. instances on the somaesthetic version where an animal touched both ends of the board before selecting a cup) is not helpful. The number of such comparisons did not materially change as a result of operation. It may, however, be relevant that both P2 and P3 went to the incorrect cup after comparing both cues more frequently following than before operation (in 21·7 per cent. instead of 12·5 per cent. of comparisons). In any case the impairment of the parietal operates on the formal orientation test (a "retention defect" in all 3 animals) resolved at a time when they were still lacking full precision in reaching for food. Also it is noteworthy that this deficit was manifested both in the light and dark, contrary to expectations based on previously reported observations on reaching. The orientation test may not therefore be revealing the same disturbance as was apparent to informal observation. Even more tenuous, but deserving of further investigation, is the supposition of a relationship between the demonstrated consequences of parietal lesions in monkeys and the clinical symptomatology of visual disorientation so carefully analysed by Holmes (1919) in cases of parietal injury.

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