FURTHER BEHAVIORAL ANALYSIS OF PARIETO-TEMPORO-PREOCCIPITAL CORTEX

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FURTHER BEHAVIORAL ANALYSIS OF PARIETO-TEMPORO-PREOCCIPITAL CORTEX[1]

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According to currently available evidence, the cerebral isocortex contains two large sectors which have few direct afferent connections (via the thalamus) with extracerebral structures: an anterior or frontal sector and a posterior or parieto-temporo-preoccipital sector. The sectors, often referred to as "associative" or, more recently, as "intrinsic" (14, 19), have been the subject of a number of investigations (1, 2, 4, 15, 18, 21, 22) which have demonstrated that they serve different behavioral functions. Experimental literature, based on studies of the monkey, suggests that the parieto-temporo-preoccipital sector (subsequently referred to as PTO) may be further subdivided into areas serving separate functions: thus, the evidence points reliably to a temporal focus implicated in visual processes, and less reliably to a parieto-preoccipital focus in somesthesis (6, 7, 10). The present study attempts to provide further evidence regarding the possibility of such functional localization within the PTO cortex.

An extensive study by Blum *et al.* (2) showed that large parieto-temporo-preoccipital lesions in the rhesus monkey resulted in decrement in performance of problems involving both visual *and* somesthetic discriminations. Since the animals in this group showed consistent and lasting impairment of visual discrimination and only transient impairment in somesthesis, these functions were considered dissociable. The question arose as to whether smaller lesions might produce a deficit in one type of discrimination or the other, depending on the locus of the lesions. A series of studies (4, 11, 12, 17, 18) involving visual discrimination tasks, but no measure of somesthetic performance, implicate the temporal cortex. Blum, in addition to a number of previous workers (see 1 for references), found a relationship between parieto-preoccipital cortex and somesthetic function but reported no test of visual performance.

On the basis of these studies it is predicted that a lesion in one of these areas will produce performance decrement in one modality only, rather than producing a nonmodality-specific decrement in discriminatory performance. In addition, extending the parietal lobe resection to include the medial surface might result in a greater decrement in somesthetic discrimination than has been observed to date.

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METHODS

Subjects. Five immature rhesus monkeys (*Macaca mulatta*) were divided into two operated groups. Two of the animals (T-44, T-45) received inferotemporal lesions, and three (P-46, P-48, P-49) were given parieto-preoccipital lesions.

Test procedures. Tests included tactile and weight discriminations presented in a modified Wisconsin general testing apparatus. In addition, postoperative observations were made of ataxia, visual fields and discrimination of food from nonfood objects (as described in 15). In the visual test, the stimulus figures consisted of a white plus sign (positive) with bars 2 inches long and three-eighths inch wide and a white ring, three-eighths inch wide and with an outside diameter of 2 inches, each painted on a black 2 and seven-eighths inches square of one-eighth inch masonite. These squares were used as covers of 1 inch holes located 10 inches apart in a sliding tray. The apparatus was modified to exclude vision in the somesthetic tests. Auditory cues were eliminated by use of rubber-lined cups and by randomizing the noise of baiting. The stimuli for the tactile test consisted of a plus sign (positive) and a ring of the same plane dimensions as described above for the visual stimuli. These figures were cut from 0.25 inch masonite and glued to masonite plaques. The holes in the testing board were surrounded by a square frame of masonite into which the plaques fitted snugly. This frame prevented the animals from lifting a plaque by the edge and thus forced contact with the stimulus figures at each trial. As an additional precaution, 0.25 inch holes were drilled in two diagonal corners of each plaque and finishing nails were driven through these holes into the testing board so that 1 inch of the nail was left protruding. This device forced the animals to lift the plaques directly upward, providing an arbitrary criterion for a nonvisual response—if an animal lifted the incorrect plaque so far that it cleared the tops of the nails, the response was scored as incorrect even though the animal then dropped it without apparently "seeing" it. This arbitrary criterion of response was necessary since the animals showed a strong tendency to lift up and examine the stimulus figures visually. The period of orientation for this problem was considerably longer than for the visual discrimination, and had to be done in gradual steps, using plaques with neutral rectangles as "handles." At first the animals were trained by degrees to lift the neutral plaques off the nails under visual guidance; then a low barrier was introduced and the gap between the raised opaque screen and the barrier gradually reduced. When visual selection of the plaques was no longer possible (as checked by human observers and by the observation of the behavior of the subjects), the neutral plaques were replaced by the stimulus figures and scoring was begun.

In the weight discrimination task, the apparatus was identical to that described above except for the stimulus figures, which were two gray cylindrical vials, measuring 2.25 inches high by 1 inch in diameter. Both vials, fitted with plastic screw caps, were placed on their sides and wired to masonite squares. The vials were oriented parallel to the barrier with caps always pointing toward the animal's left. The positive vial was filled with a mixture of buckshot and glue, and weighed approximately 156 g. The negative vial was empty and weighed 21 g. The criterion of response was the same as that described for the tactile discrimination.

All animals were given the discrimination training in the order: visual, tactile, weight. Delayed self-correction technique was used; criterion performance consisted of 90 per cent correct on 100 consecutive trials. Two weeks following the attainment of criterion the animals were tested for retention in the order: visual, tactile, weight, to one animal in each group (P-48 and T-45); weight, tactile, visual, to another animal in each group (P-46 and T-44). The third monkey (P-49) in the occipito-parietal group received two preoperative retention tests, each given in the order: visual, tactile, weight. Two weeks postoperatively, after informal tests of extent of visual field, food-nonfood discrimination and ataxia, retention procedures were repeated in the order of the preoperative retention tests.

Following these procedures all animals were tested for initial learning of a somesthetic length discrimination. A 3 inch strip of 0.5 inch dowelling served as positive and a 2 inch strip as negative cue. Technique and criterion were those used in the other discriminations.

Surgical and anatomical procedures. The lesions were based on the classification of cortical regions as delineated by strychnine neuronography (16). Specifically, the resections were designed to approximate the occipitotemporal and the parieto-occipital regions: the former (referred to subsequently as "inferotemporal") duplicated lesions previously described as producing decrement in visual discrimination performance (14); the latter (parieto-preoccipital lesions) were intended to involve an area extending anteroposteriorly from the intraparietal to the lunate sulcus, inferiorly to the superior temporal gyrus, and

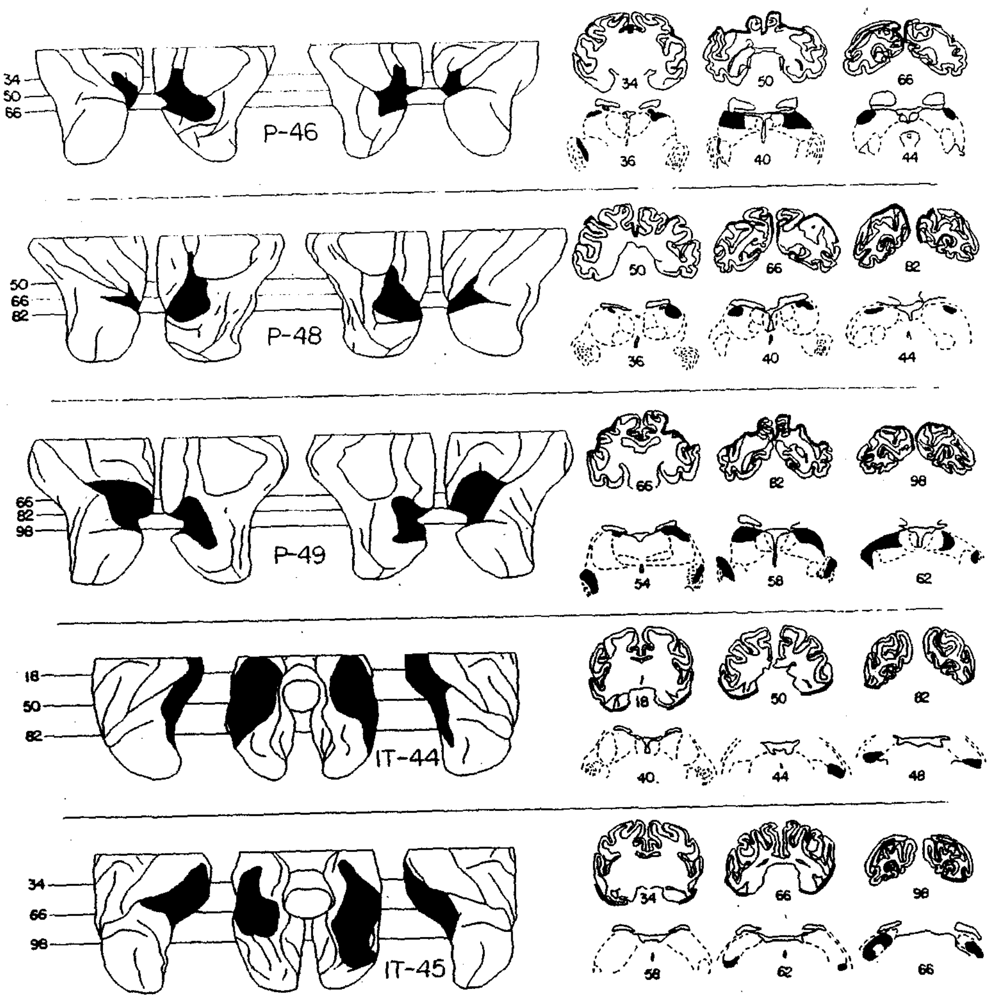

FIG. 1. Reconstructions of parieto-preoccipital (P-46, P-48, P-49) and inferotemporal (IT-44, IT-45) lesions indicated in black on medial and lateral surface reproductions of each hemisphere. Black also indicates lesion in representative cross sections through hemisphere and retrograde degeneration in thalamic sections. For description of lesions and of thalamic degeneration, see text. Visual and somesthetic discrimination scores made by animals with these lesions appear in Table 1.

medially to involve the entire precuneal gyrus. All resections were single-stage, bilateral, subpial operations. Following completion of testing, the animals were sacrificed, their brains perfused with formalin, removed and prepared for histological study. Reconstructions were made from serial sections and appear in Fig. 1, together with representative cross sections through the lesion and through the thalamus.

RESULTS

The anatomical findings in animals with inferotemporal lesions confirm those described previously (11, 12). The resections include the basal isocortex of the temporal lobe, the inferior and middle temporal convolution, and extend posteriorly to include the ventro-anterior portion of the occipital lobe.

The temporal polar cortex is spared, as are the allocortical formations. The lesion corresponds roughly to the occipitotemporal region as defined by neuronographic studies (16). Thalamic retrograde degeneration is limited to the posterior inferior portion of the n. pulvinaris. The ventrolateral portion of the n. geniculatus lateralis is minimally involved in only one animal (IT-44); the other inferotemporal animal shows no such degeneration.

The lesions of the parieto-preoccipital animal extend from the lunate sulcus posteriorly to the intraparietal sulcus anteriorly. Laterally, these resections reach a variable distance but are limited to the dorsal portion of the hemisphere. Medially, the entire precuneus is involved, as is the posterior portion of the cingulate gyrus (corresponding to parieto-preoccipital region, cf. 16). Thalamic degeneration is found in the n. anterior ventralis, the n. lateralis dorsalis, and in the lateral portion of the n. pulvinaris, confirming earlier reports (2, 3, 5, 20). In addition, two of the parieto-preoccipital monkeys (P-46 and P-49) show considerable degeneration in the n. geniculatus lateralis.

This finding is correlated with a transient but marked visual field defect in these animals. These two subjects were unreactive to visual threats for approximately five days, after which reactivity gradually reappeared. Visual field testing was unsatisfactory in the parieto-preoccipital animals because of their ataxia which is described below. Inferotemporal animals showed no detectable visual field defect. All with parieto-preoccipital lesions chose peanuts rather than nonfood objects in the food-nonfood discrimination test as did one of the inferotemporal animals (IT-45). The other inferotemporal animal (IT-44), on the initial postoperative test, took two nonfood objects after first selecting the peanuts; thereafter, no nonfood objects were picked up. Neither of the inferotemporal monkeys was ataxic. However, those with parieto-preoccipital lesions were so severely ataxic for one week postoperatively that they used their mouths to grasp a peanut. Ataxia gradually receded so that by one (P-46) to four (P-48) months postoperatively no past pointing or awkwardness of movement persisted. No animal changed the hand preferred in performing the somesthetic tasks as a result of surgery—yet three (P-48, P-49 and T-44) changed the hand used to per form the visual discrimination task. No changes in temperament were noted.

I. Visual discrimination

As can be seen in Table 1, the subjects required from 200 to 410 trials to learn the discrimination originally. Preoperative retention scores ranged from 0 to 70. Postoperatively, both animals with inferotemporal lesions were still scoring chance at 500 trials, whereas all subjects with parieto-preoccipital lesions reached criterion immediately.

II. Somesthetic discrimination

The tactile and weight tests are discussed together since there were no reliable differences in any animal's pre- or postoperative performance that could be ascribed to a difference between the somesthetic tasks. As can be seen in Table 1, the subjects required from 400 to 720 trials to learn these tasks originally. Preoperative retention scores ranged from 0 to 250. Postoperatively, the inferotemporal animals attained criterion in fewer trials than in preoperative retention, averaging 60 trials. The parieto-preoccipital animals, on the other hand, on the first somesthetic task given postopera-

Table 1. Pre- and postoperative learning and retention scores on visual (VD), tactile (TD), weight (WD) and length (LD) discriminations. Scores indicate number of trials taken to reach a criterion performance of 90 per cent in 100 consecutive trials. Postoperative scores indicate retention except in the case of length discrimination which was presented to all animals postoperatively only. 1000F indicates chance performance after 1000 trials had been given. Arrows represent order in which the pre- and postoperative retention tests were given.

Animal		VD	TD	WD	LD	Lesion
P-46	original learning	380	580	410		
	preop. retention	0	0	40		Parieto-preoccipital
	postop.	0	0	460	1000F	
P-48	original learning	220	520	480		
	preop. retention	10	60	0		Parieto-preoccipital
	postop.	0	120	170	1000F	
P-49	original learning	200	720	530		
	preop. retention I	0	250	150		Parieto-preoccipital
	preop. retention II	0	0	40		
	postop.	0	350	10	1000F	
IT-44	original learning	210	450	410		
	preop. retention	10	50	100		Inferotemporal
	postop.	500F	0	70	350	
IT-45	original learning	410	400	490		
	preop. retention	70	70	20		Inferotemporal
	postop.	500F	50	0	260	

tively, required more trials to reach criterion than during the preoperative retention test irrespective of whether this was a tactile or a weight discrimination (with an average of 330 trials). P-48, alone, showed a deficit as well on the second test given. However, all subjects reached criterion performance on each of the somesthetic tasks within 460 trials, a score well within the range of preoperative learning. In initial learning of the somesthetic length discrimination, the scores of the inferotemporal monkeys (T-44 and T-45) were 320 and 260 trials, respectively. All parieto-preoccipital monkeys, on the other hand, were performing at chance after 1000 trials. Thus, in initial postoperative learning, in contrast to retention, the parieto-preoccipital animals failed in this task to reach criterion performance.

Conversely, initial postoperative learning of a visual pattern discrimination was found, in another study, to be markedly impaired for inferotemporal as compared with parieto-preoccipital animals (13). All subjects of the current experiment were also tested in initial postoperative learning of delayed alternation: their scores (mean 360, range 120–430) did not differ significantly from each other or from those of a control group of 14 subjects (13) which had not been operated on.

Discussion

The results of this study support the hypothesis that circumscribed lesions within the PTO sector produce performance decrements which are modality-specific. The often described impairment of visual discrimination which follows inferotemporal resections has been confirmed. Such decrement is not accompanied by a loss in somesthetic discrimination performance. On the other hand, parieto-preoccipital resection resulted in a deficit on somesthetic discrimination and no impairment on the visual task (in spite of invasion of the geniculostriate system and the resulting "field defect" in these animals). There is no overlap between scores of the two groups. Additional support for a dissociation of effects following the two lesions is provided by the results of the initial learning experiment: the failure of the parieto-preoccipital animals to learn a somesthetic discrimination (length) that the inferotemporal ones learned readily.

On the other hand, the extensive parieto-preoccipital resection failed to produce as severe a deficit in somesthetic discrimination performance as did the inferotemporal resection in visual tasks. Furthermore, two of the three parietal-preoccipital monkeys performed immediately at criterion the second somesthetic task administered postoperatively. These results, in somesthesis, are similar to those obtained in vision in earlier experiments involving temporal lobe lesions (9, in reference to Klüver). More recent studies have shown that the decrement of visual discrimination performance following inferotemporal resections is a function of the difficulty of the task for control animals (11, 18). What looks like positive transfer of training seems to occur only when those tasks which are "less difficult" are used (9). The rather high initial preoperative learning scores in the somesthetic discriminations used in the current experiment could be a reflection of the intricacy of the procedure rather than the difficulty of the discrimination of the cues. Thus, reaching through a slit, necessitating awkward handling of the cues, might serve to mask the relatively easy discriminations involved. Elimination of these extraneous factors would permit the use of tasks more difficult with respect to the cues used; comparison with results obtained in vision with inferotemporal resections would then be facilitated.

Lashley has suggested that the impairment in vision following temporal lobe resections might best be understood in terms of interference with "comprehension of the total training situation" or "attitude to compare stimuli" (8, 9). The results of the current experiment make it necessary that this, or a similar, concept be modified to subsume modality specificity or interference with *visual* comparisons of stimuli since the temporal animals showed no such loss in somesthetic performance. However, the variables of postoperative time, general visual experience, as well as stimulus generalization must be experimentally analyzed before an explanation in such terms may be invoked. The failure of the parieto-preoccipital animals in the initial learning of a somesthetic discrimination, as well as the obvious comparisons of stimulus objects which these same subjects make before responding, contradicts the assumption that the deficit in discrimination performance in either modality is a function of failure to "compare."

In conclusion, it seems established that separate loci within the PTO systems serve vision and somesthesis. The relationship between the inferotemporal locus and vision has previously been established and many of the variables determining this relationship have been uncovered. The evaluation of the importance of the parieto-preoccipital locus in somesthesis has not been as intensively investigated as yet; the current experiment provides a base for further analysis of this relationship with the use of revised techniques.

Summary

1. The present study was undertaken to provide further experimental evidence to support the conception that the primate parieto-temporo-preoccipital cortex may be subdivided into areas serving separate functions.

2. To this end, visual and somesthetic discrimination performance of animals with parieto-preoccipital resections was contrasted with such performance of those with inferotemporal resections.

3. Monkeys with inferotemporal resections consistently failed the visual, and showed no impairment in the somesthetic, discriminations. Conversely, monkeys with parieto-preoccipital resections showed a decrement of retention in the somesthetic task initially administered, and showed no impairment in the visual discrimination.

4. However, the performance of visual discrimination by animals with inferotemporal lesions remained at chance level, whereas the performance of somesthetic discrimination by parieto-preoccipital animals reached criterion in approximately the same number of trials as had been required preoperatively to learn the task. Furthermore, there was little deficit of postoperative retention in the somesthetic task administered second. On the other hand, initial postoperative learning of a length discrimination was never accomplished by these animals. It is suggested that these latter results are a function of the ease or difficulty of the discrimination and of the intricacy of the somesthetic procedure used.

5. Thus, in spite of the less severe deficit in somesthetic than in visual discrimination obtained in the present experiment, the results support the hypothesis that circumscribed lesions within the parieto-temporo-preoccipital sector produce performance decrements which are modality-specific.

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