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EFFECTS OF TEMPORAL AND FRONTAL CORTICAL LESIONS ON AUDITORY DISCRIMINATION IN MONKEYS

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EVIDENCE has been accumulating in recent years which suggests strongly that cortical areas outside the primary sensory projection areas play an important role in the perceptual functions of monkeys. Thus, it has been found that bilateral inferotemporal lesions produce an impairment in visual discrimination learning (Chow, 1952; Mishkin, 1954; Mishkin and Pribram, 1954), and that posterior parietal lesions impair somesthetic discrimination learning (Pribram and Barry, 1956). Of considerable theoretical and methodological importance is the fact that these relationships tend to be mutually exclusive, i.e. the temporal lesion seems to produce little or no change in somesthetically guided behaviour and the parietal lesion little or no change in visually guided behaviour. These findings lead to the expectation that other sensory modalities may also have "non-primary" cortical areas with which they are uniquely associated. This paper reports the results of a preliminary search for such an area in audition. The area selected for study comprises that portion of the posterior "association" cortex which lies between the areas implicated in vision and somesthesis. The hypothesis tested is that ablating this posterior temporal region without damaging the adjacent primary acoustic area will produce impairment in auditory discrimination learning.

Two other related aims are incorporated in the experimental design. In the first place an attempt is made to test further the proposition that the posterior cortical foci already discovered serve functions that are modality specific. To this end animals with inferotemporal lesions were included in the study in order to determine whether such lesions would indeed fail to produce deficit in auditory discrimination learning. Secondly, an attempt is made to investigate the findings of Ades and his associates (Stewart and Ades, 1951) and Blum (1952) that dorsolateral frontal lesions,

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dinarily associated with impairment in a special class of problem-lving (delayed-response-type) behaviour, produce deficit also in per-rmance on certain auditory tasks. Animals with dorsolateral frontal ions are included in the present study in order to permit a comparative timate to be made of the effects of frontal as opposed to the effects posterior cortical lesions.

Material and Methods

Subjects.—The subjects were 15 rhesus monkeys (*Macaca mulatta*). 6 were tested post-operative learning; the other 9 were tested for post-operative retention.

In the *post-operative learning group* there were 2 subjects in each of the three operative egories: posterior temporal (PT), inferotemporal (IT), and lateral frontal (LF). the 6 subjects, 4 (IT–164, IT–178, LF–168, LF–171) had previously received post-rative testing on a visual discrimination. The others (PT–287, PT–285) were naive.

In the *post-operative retention group* there were 3 subjects in each of the three rative categories. One animal was in each operative category (IT–249, PT–248, F–228) had received pre-operative training on another auditory problem which it d failed to learn. 8 of the 9 animals were operated two to five days after reaching e standard on the auditory task described below. The ninth animal (LF–275) was en a pre-operative retention test thirteen days after reaching the standard. After learning this animal was given an LF lesion and included in the LF retention group. e-learning trials for all subjects were begun on the tenth day following operation.

Surgical procedures.—Animals were anæsthetized with Nembutal and surgery was nformed under strict aseptic procedure. The lateral frontal and posterior temporal reas were exposed by turning a large bilateral bone flap (anteriorly for the frontal and steriorly for the temporal exposures) on the left temporal muscle. The inferotemporal rea was exposed by removing temporal bone. Cortical tissue was removed by subpial action. Silk was used in suturing successive layers of tissue.

On completing the experiments animals were sacrificed and the brains were removed r histological processing. After the brains were serially sectioned and stained with ionine, the limits of the lesions were determined by microscopic examination and nstructed graphically, and the thalamus was studied for evidence of retrograd generation.

Fig. 1 shows such reconstructions, together with representative cross ctions and thalamic sections, for the five PT lesions. In general these sions extended from the lunate sulcus, posteriorly, to the tip of the intraparietal sulcus, anteriorly; and from the intraparietal sulcus, dorsally, to the tip of the inferior occipital sulcus, ventrally. All the sions spared the supratemporal plane of the Sylvian fissure and there is no evidence of retrograde degeneration in the medial geniculate bodies. However, four of the five PT lesions produced degeneration in the central portions of the lateral geniculate bodies, probably as a result of unintended damage to the radiation fibres below the cortex. Degeneration in portions of the inferior and lateral nuclei of the pulvinar is due, according to Chow (1950), to ablation of the posterior temporal and inferior parietal regions.

The IT and LF lesions both resembled lesions made in a large number

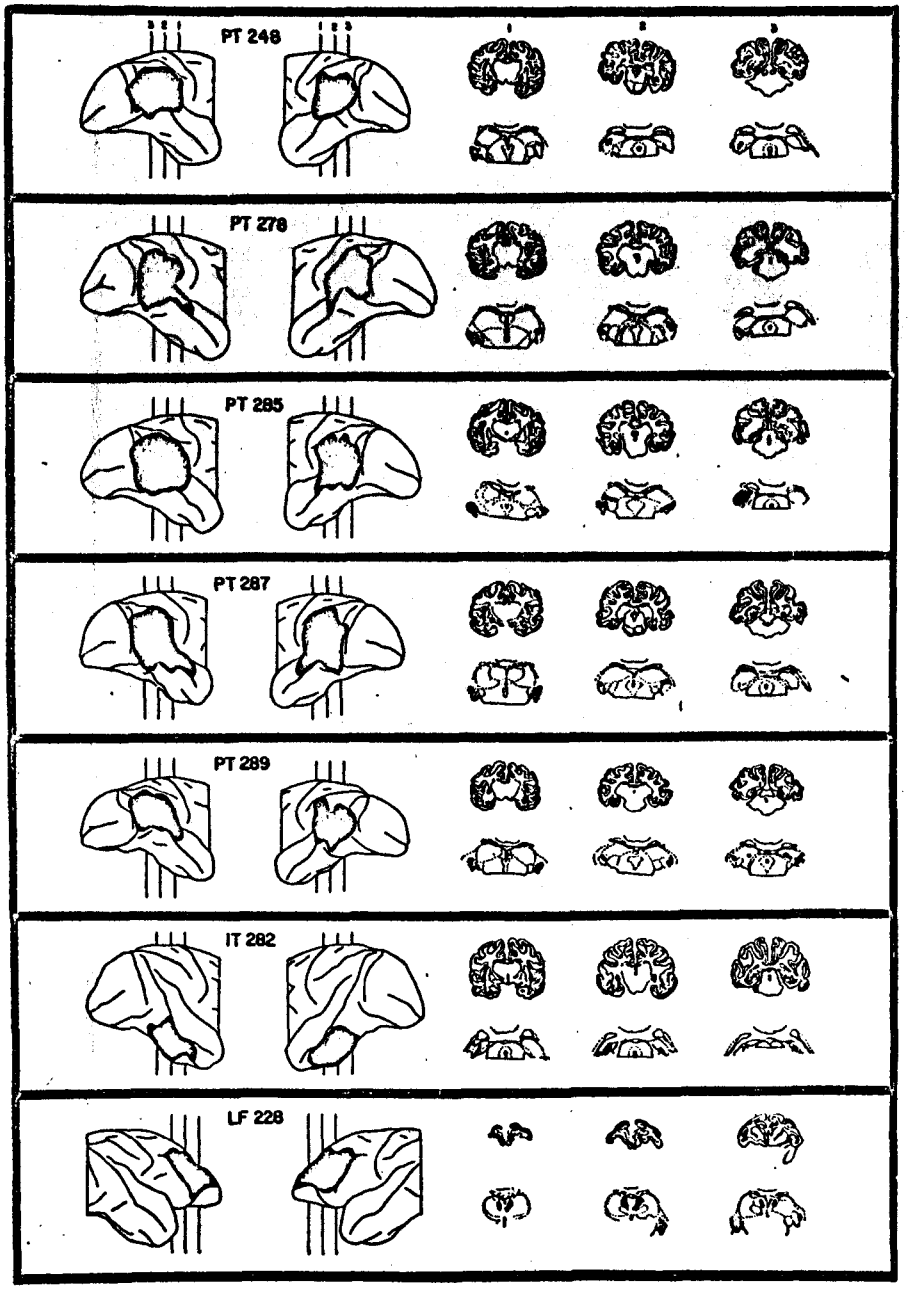

FIG. 1.—Reconstructions of lesions in all PT brains, and one IT and one LF brain. Representative cross sections and thalamic sections are shown to the right.

of studies from this laboratory (e.g. Pribram and Mishkin, 1956). For purposes of comparison with the PT lesions, reconstructions of one inferior temporal and one lateral frontal lesion are included in fig. 1. The IT lesion extended dorsally to include the inferior bank of the superior temporal sulcus and ventrally to include the fusiform area. The pole was spared anteriorly while the tip of the inferior occipital sulcus marked the posterior limit. Retrograde degeneration was found in the posterior portions of the medial pulvinar. The LF lesion extended posteriorly to the arcuate sulcus (including its anterior bank), dorsally to the longitudinal fissure, and ventrally to the lateral lip of the orbital surface. Both banks and the depths of the sulcus principalis were removed. The medialis dorsalis nucleus was largely degenerated.

Training procedure.—The auditory task consisted of training subjects to discriminate a white noise from a pure tone of 1,000 cps. These stimuli were generated by a Grayson-Stadler twin-oscillator unit, and were delivered through a 6 in. speaker placed horizontally 1 ft. above the testing cage. The intensity of the stimuli was set at 16 db. on the instrument, a value which was estimated to be 35–40 db. above the noise level of the testing room.

During the experimental session the animal was placed in a cage in a sound-proofed room which also contained a ventilator that served as a masking-noise generator. All stimulus and reward events were controlled automatically by relay and timing equipment in an adjoining room.

The discrimination was established according to a set of contingencies described elsewhere (Weiskrantz, 1957, Section V). Briefly, the stimuli were presented successfully in a predetermined balanced sequence which was varied daily. Each stimulus had a duration of 5 seconds unless the animal turned it off sooner by pressing a panel mounted on the front of the cage. If the stimulus was white noise the animal could obtain a pellet of food by pressing the panel. If the animal did not press during the white noise, but allowed it to go off automatically after the 5 seconds, then the white noise was repeated on succeeding runs until the animal did turn it off and received the reward. Conversely, if the stimulus was a 1,000-cps. tone the animal could obtain food only by *refraining* from pressing the panel. If the animal turned off the 1,000-cps. tone it was repeated on succeeding runs until the animal let it go off automatically, at which time a food pellet was delivered. Each food delivery was accompanied by a light over the food dish (located below the panel) which remained on for 2·5 seconds. There was an interval of 5 seconds between the termination of one stimulus and the beginning of the next unless the animal was rewarded, in which case there was a 5-second interval between the end of the reward period and the presentation of the next stimulus.

Twenty noise and twenty tone trials were delivered daily, excluding

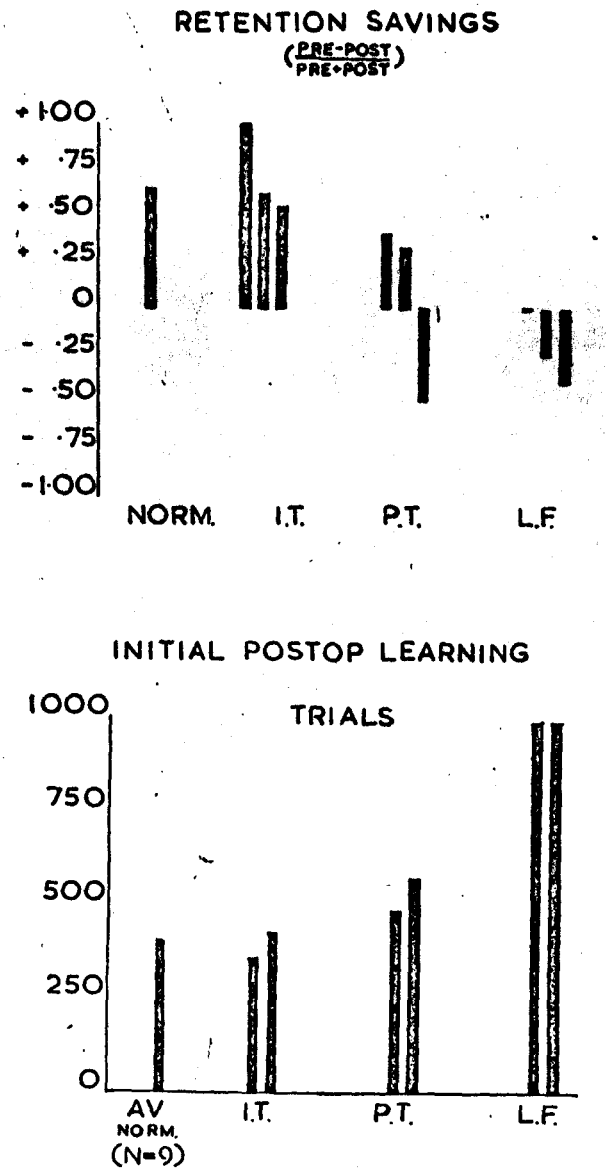

FIG. 2.—Pre-operative and post-operative learning and performance scores.

re-runs after errors, until the animal achieved 90 per cent correct out of the 40 daily trials on two successive days.

Preliminary training consisted of first teaching the animal to press the panel for reward, and then to press the panel only during the presentation of the white-noise stimulus. When the animal had reached a criterion

f responding to at least 40 out of 44 white noise presentations and of sponding not more than ten times in the "silent" intervals between ese 44 presentations, it was given the discrimination task using both ditory stimuli.

Results

Initial post-operative learning.—Post-operative learning scores are own graphically in the *lower* half of fig. 2. There is no overlap among e scores for the 3 operative pairs. The 2 IT subjects fall symmetrically either side of the control average (computed from the pre-operative rning scores of the 9 animals tested for post-operative retention). e PT subjects required more trials than the IT subjects. The LF bjects did not solve the problem within the 1,000 trials allotted.

Post-operative retention.—The retention scores are shown graphically the *upper* half of fig. 2. They are computed from the pre-operative d post-operative scores, listed in Table I, by the formula: No. of

TABLE I.—PRE-OPERATIVE AND POST-OPERATIVE LEARNING AND PERFORMANCE SCORES

Animal	*Pre-operative trials*	*Post-operative trials*	*Average performance 200 trials Post-criterion*
IT–249	280	80	95·5%
IT–282	280	0	95·5
IT–288	560	120	96·0
PT–248	200	600	92·0
PT–278	400	160	96·5
PT–289	880	440	88·5
LF–228	160	400	88·5
LF–283	360	360	87·0
LF–275*	(120)	200	92·0
C–275*	560	120	—

*This animal was first tested for pre-operative retention (*see* text).

re-operative trials minus No. of post-operative trials divided by the sum of pre-operative and post-operative trials. A score of zero would indicate that pre-operative and post-operative scores are the same; positive scores indicate savings in relearning while negative scores indicate retardation in relearning. The measure can vary from plus 1·0 to minus 1·0.

There is no overlap between the IT subjects (all of which showed a high positive retention score equivalent to that shown by the normal control) and either of the other two groups of operated animals. Of the

latter two groups, those with the LF operation were the more severely impaired. All their retention scores are negative indicating that all frontal animals required more trials to re-learn after operation than they had required initially. 2 of the 3 PT animals' scores, on the other hand, are positive. The last column of Table I lists the performance of each animal during the 200 trials immediately following the attainment of criterion. Although there is overlap among the three groups, the rank order in terms of average group performance is, again, IT, PT, and IF.

Discussion

Inferotemporal lesion.—Neither in initial learning nor in retention was there any suggestion of a difference between the animals with inferotemporal lesions and the normal controls. This finding provides new evidence for the hypothesis that inferotemporal lesions produce a behavioural deficit limited to discrimination learning in vision.

Lateral frontal lesion.—The results obtained with the animals with dorsolateral frontal lesions supports earlier findings of deficit in auditory discrimination learning following frontal damage. Both in initial learning and in retention all animals with lateral frontal lesions were severely impaired. Superficially, at least, such a finding falls outside the class of phenomena usually associated with lateral frontal lesions in monkeys, viz., deficit in delayed-response-type tasks.

Two lines of attack are evident for future research. Firstly, one might suggest that performance on auditory-discrimination tasks and on delayed-response tasks is impaired by lesions having independent and spatially separate foci, and that the lateral frontal lesion includes both. According to Sugar, French and Chusid (1948) there are strong connexions in monkey between the primary auditory cortex and area 8, a strip located at the posterior limit of the lateral frontal lesion. It would not be surprising to find a cortical area far removed from the primary acoustic area serving discrimination functions in audition. The inferotemporal region, which appears to fulfil such a role in vision, is quite distant from the striate cortex (although no analogous connexions between the striate cortex and the inferotemporal region are yet known).

Another possibility, however, is that the lateral frontal lesion is interfering with a *single* class of behaviour. While the theoretical task of uniting auditory discrimination learning and delayed-response-type learning appears formidable, certain lines of experimental approach may be suggested. For example, one possible critical difference between the auditory discrimination task employed here and the standard discrimination situation say, in vision, in which frontal animals perform successfully, concerns the spatial relationships between the stimuli and the responses. The visual task involves discriminanda having definite spatial locations and these frequently conform to the spatial aspects of the responses. In

the present auditory task the stimuli had only an indefinite locus which was moreover completely unrelated to the spatial aspects of the responses. How, then, would frontal animals perform on the auditory analogue of the visual task? The standard discrimination situation might be approximated by the use of the Klüver pull-in technique. Pulling in either of two spatially separated food containers, each with its own speaker, would produce one of two auditory signals emanating from that container. Successful performance by frontal animals on such an auditory task would suggest, as one possibility, that frontal animals are impaired not in auditory discrimination learning, *per se*, but rather on tasks in which there are no close or well-defined spatial and temporal relationships between the stimuli and the responses.

Posterior temporal lesion.—Both in initial learning and in retention a slight deficit was evident in all 5 PT animals as compared with the 5 IT animals. While the result can only be considered as preliminary it is comparable to the early results which helped to establish a relationship between an extra-striate cortical area and visual functions, and therefore more intensive investigation is justified. A larger range of auditory problems and the effects of lesions of smaller areas within the posterior temporal region should be studied. Finally, the question as to the specificity of the deficit must receive further investigation. Clearly, greater significance would accrue to the slight but positive results of the present study if it could be demonstrated that animals with posterior temporal lesions showed no deficit in visual or somesthetic discrimination learning.

Comparatively little work has been reported on the effects of temporal lesions on aurally guided behaviour in monkeys. Such evidence as does exist suggests that damage limited to the primary auditory cortex is ineffective in producing "permanent" loss in auditory discriminations, but larger lesions encompassing auditory area I, II, and III (although these are variously defined) do result in permanent loss of at least some types of discriminations (Evarts, 1952; Jerison and Neff, 1953). Similar findings have been reported for cats (Diamond and Neff, 1957; Meyer and Woolsey, 1952), and dogs (Allen, 1945). In relating the present work to these earlier findings two comments must be made. Firstly, traditional research has generally been preoccupied with the search for cortical areas which are *critical* for audition. Findings of post-operative "amnesia," or retardation in re-learning, therefore, while common, have not received close examination. The interpretation has probably been made that while auditory habits can be abolished other equipotentials areas could assume auditory functions without a significant reduction in sensitivity. The studies of the effects of inferotemporal lesions on vision, however, suggest a different interpretation. What has been labelled "amnesia," in fact, might be associated with the imperfect retention normal animals often show (*see* fig. 2, top) plus a permanent impairment in the ability to acquire

discriminations. Such impairment would be reflected in slower learning; not necessarily in *failure* to learn, and would become evident only with further post-operative testing, making full allowance for improvement which normal control animals show when given a series of new discriminations (Harlow, 1949).

Secondly, research on the effects of inferotemporal lesions on visually-guided behaviour strongly suggests that the impairment is a function of the difficulty of the task. Therefore, conclusions that cortical lesions disturb auditory "pattern" discriminations but no frequency discriminations are premature since the former tasks were almost certainly the more difficult ones (Diamond and Neff, 1957). Indeed, the fact that it is possible to interpret a different study as indicating that cortical lesions interfere with frequency but no intensity discriminations (Meyer and Woolsey, 1952), suggests that difficulty of task rather than any special dimension of the auditory stimulus is the significant parameter.

SUMMARY

15 animals subjected to bilateral lesions in the inferotemporal region, the posterior temporal region, or the lateral frontal region were tested either for initial post-operative learning or for post-operative retention, of a simple auditory discrimination between white noise and a 1,000-cps. tone. It was found that inferotemporal animals were not impaired, posterior temporal animals were slightly impaired, and lateral frontal animals were severely impaired on this task. The results were the same for initial learning and for retention.

These findings are discussed with respect to the assertions that lesions in the inferotemporal region are modality specific in their effects; that there is a posterior temporal region which bears analogous relation to audition that the inferotemporal region does to vision; and that the effects of anterior dorsolateral frontal lesions on behaviour require re-evaluation.

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