EFFECT OF AUDITORY CORTEX ABLATION ON FREQUENCY DISCRIMINATION IN MONKEY*

EDWARD V. EVARTS†

Yerkes Laboratories of Primate Biology, Orange Park, Florida

(Received for publication October 17, 1951)

TONOTOPIC ORGANIZATION of the auditory cortex has been demonstrated in the monkey (1, 5), the cat (9), and the dog (7). This organization has sug-gested that the auditory cortex in these animals may play a vital role in fre-quency perception and discrimination. In the cat, however, Meyer and Woolsey (6) have shown that small increments in frequency are still dis-criminated following bilateral ablation of auditory areas I and II. This work hows that in the cat, at least, tonotopic arrangement of the auditory cortex s not associated with localization of function with respect to tonal discrimi-ation. The present study was designed to discover whether frequency dis-rimination in the monkey depends upon the presence of the auditory cor-ex, or whether, as in the cat, discrimination between frequencies is unaf-ected by its ablation.

MATERIALS AND METHODS

ubjects. Four monkeys (*Macaca mulatta*) weighing from 2.5 to 3.0 kg. were used as imental subjects. Two of these subjects (M-3 and M-5) had been used in a previous udy on the effect of auditory cortex ablation on auditory-visual association (4), and were ained on the problem of frequency discrimination only postoperatively. The remaining vo subjects (M-19 and M-20) were without previous experimental experience; they were ven initial training preoperatively, and retrained postoperatively.

Training procedure. The problem on which subjects were trained required that they t up the cover of a food well in the presence of a tone of 350 cps, and refrain from aking any attempt to do so in the presence of a tone of 3500 cps. Subjects were placed a table behind an opaque screen which separated them from the experimenter and a ngle food well with hinged metal cover wired to deliver shock. A trial began with the unding of a tone, either 350 or 3500 cps. Five seconds later the opaque screen was evated, allowing the subject access to the food well. In the presence of the 350 cps tone, e subject was able to open the food well and remove a piece of banana; in the presence the tone of 3500 cps, he received a shock on touching the food well cover. On all trials, 10-second period was allowed for response; the sound stimulus was continued for this me. On trials accompanied by the lower frequency tone, an opening of the food well within e period allowed for response was scored as correct; failure to do so was scored as an ror. On trials accompanied by the higher frequency tone, any attempt by the subject to en the food well was scored as an error, while failure to make any such attempt was ored as correct. At the end of the 10 seconds allowed for response, the sound was termi-ted and the screen lowered; after a 5-second silent pause, a new trial began. The 350 and 00 cps tones followed a randomized sequence in successive trials. One session of 50 trials as given daily, and training was carried to a criterion of 80 per cent correct responses in e session.

The tonal stimuli were generated by a Sylvania audio oscillator, type 145, and de-

* This study was carried out under grant No. B-2C from the United States Public ealth Service to the Yerkes Laboratories of Primate Biology, Inc.

† Present address: Payne Whitney Psychiatric Clinic, The New York Hospital, New rk City.

livered to the subject by a loudspeaker suspended at a level with and three feet behind his cage. The two tones were of equal intensity; the 350 cps tone was approximately 50 decibels above human threshold. In all cases, controls were carried out in which the intensities of the two tones were systematically varied: the intensity of the 350 cps tone was lowered by 10 db and the intensity of the 3500 cps tone was raised by 10 db, thus presenting the 3500 cps tone at an intensity 20 db greater than that of the 350 cps tone; intensity variations in the opposite direction, *i.e.*, raising the 350 cps tone and lowering the 3500 cps tone by 10 db were also carried out. This variation in intensity of the tonal stimuli did not interfere with the correct performance of any subject. Though no determination of auditory acuity in the monkey at these frequencies has been made, Wendt's (8) data on thresholds at 256, 512, 2048, and 4096 cps may be interpolated to indicate that the intensity limen is approximately 6 db lower at 3500 cps than at 350 cps. This difference of 6 db is amply allowed for in the variations of intensity made in the intensity controls in the present study, justifying the conclusion that the discrimination between the tonal stimuli was made on the basis of difference in frequency.

Operations and anatomical procedure. Operations were carried out in two stages; aseptic precautions were observed and pentobarbital anesthesia was used. Tissue was removed by suction. Following operation, M-19 and M-20 were allowed a recovery period of 10 days before the start of postoperative training. M-3 and M-5, trained only postoperatively, received initial training on the problem of frequency discrimination two months following operation. At the completion of training, subjects were sacrificed by perfusion with saline and 10 per cent formalin. Histological procedure, methods of reconstruction of the cortical lesion, and criteria for degeneration in thalamic nuclei have been described previously (2).

RESULTS

Anatomical. In M-19 and M-20, the cortical lesions in both hemispheres extended along the Sylvian fissure from about 1.0 cm. anterior to the foot of the central fissure to the juncture of the Sylvian and superior temporal sulci, and for this extent included the inferior half of the insula, the inferior bank of the Sylvian fissure and the lateral surface of the superior temporal gyrus (Fig. 1). Retrograde degeneration in the parvocellular portion of the medial geniculate of both of these subjects was almost complete save in the caudal tip, where in all hemispheres the infero-medial portion of the nucleus was consistently spared (Fig. 1). On the basis of this extensive degeneration in the parvocellular portion of the medial geniculate, it may be said that the cortical ablations in M-19 and M-20 involved approximately 90 per cent of the auditory cortex bilaterally.

The cortical and thalamic lesions of M-3 and M-5 have been reported previously (4). In brief, auditory cortex ablation and medial geniculate degeneration in the right hemisphere of M-5 and in both hemispheres of M-3

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FIG. 1. Records of cortical ablations and degeneration in parvocellular portion of medial geniculate nuclei. In the reconstructions of cortical surface, complete excision is indicated by hatching, and partial destruction by stippling. Preservation of depths of sulci is indicated by interrupted lines. Positions of cross sections through lesions are indicated by numbered lines on surface drawings. In these cross sections, subcortical white matter is represented in solid black. Principal sulci are indicated. CE, central fissure; IP, intraparietal sulcus; LA, lateral (Sylvian) fissure; TS, superior temporal sulcus. Areas of degeneration in parvocellular portion of medial geniculate nucleus are indicated by solid black. Sections are arranged from anterior to posterior. LG, lateral geniculate; MG, parvocellular portion of median geniculate; PI, n. pulvinaris inferior; PL, n. pulvinaris lateralis.

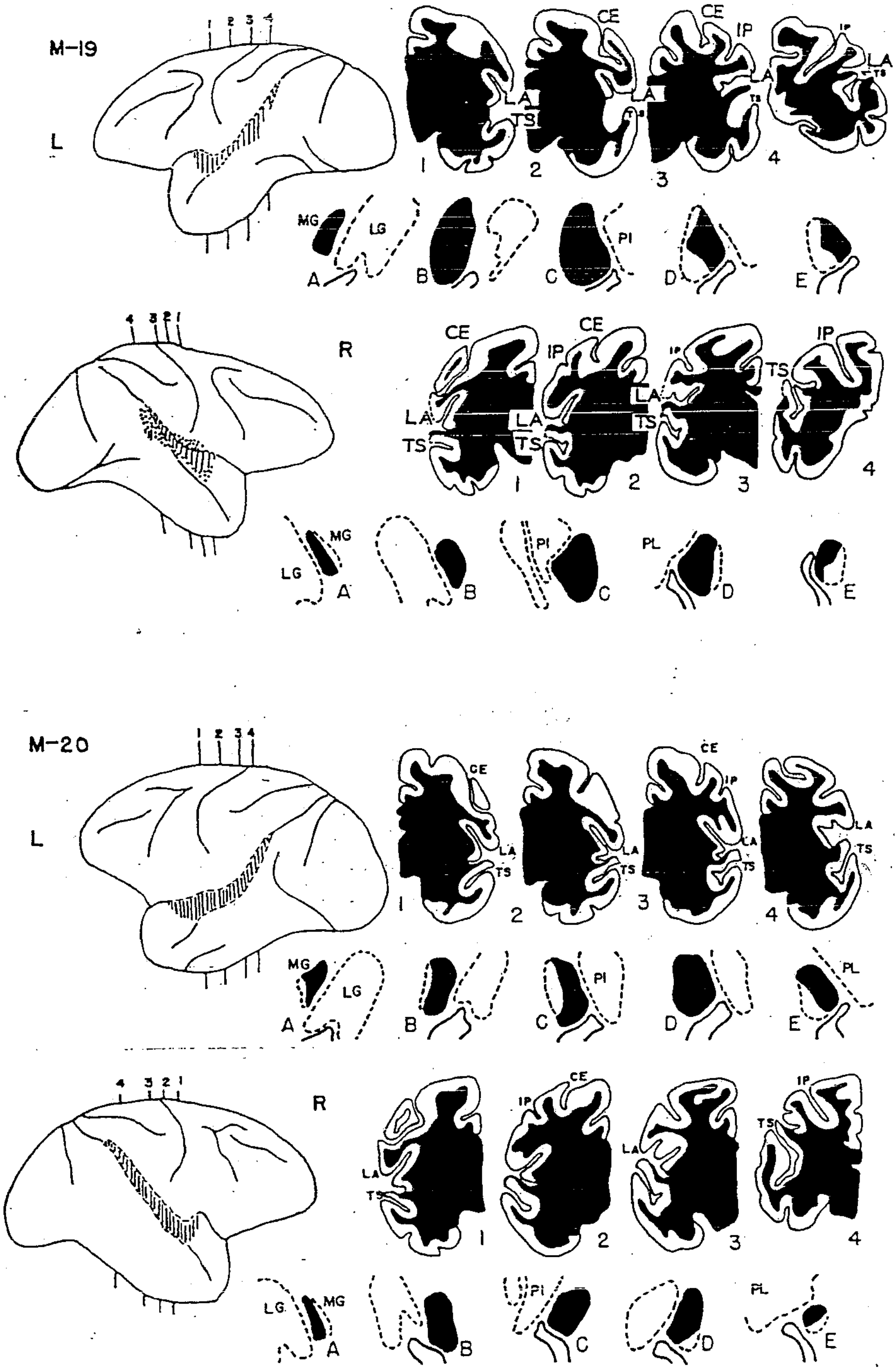

FIG. 1

were almost complete. In the left hemisphere of M-5, the cortical lesion failed to involve a large part of the posterior half of the inferior bank of the Sylvian fissure, and only 20–30 per cent of the medial geniculate body was degenerated.

Behavioral. Subjects M-19 and M-20 were trained preoperatively to discriminate between tones of 350 and 3500 cps (Table 1). Following operation, M-20 made 70 per cent correct responses in the initial training session, and in the following session met the criterion of 80 per cent correct responses. Though M-20 failed to meet the criterion in the initial session, his performance in this session differed from chance at the 0.01 level of confidence, showing that there was not even temporary loss of the ability to discriminate between the two frequencies. M-19 performed at chance levels in his initi postoperative session, and required 350 trials to meet the criterion of correct responses. Even in his first 50 trials, however, this subject showed a greater latency of response in attempting to open the food well on trials accompanied by the 3500 cps tone as compared to the latency of response on trials accompanied by the tone of 350 cps. Throughout postoperative training, this subject's errors took the form of hesitant taps on the corner of the food well cover in the presence of the higher tone, while on the trials accompanied by the tone of lower frequency, the subject opened the food well quickly and vigorously. Thus, though this subject met the criterion in only 50 fewer trials postoperatively than preoperatively, his behavior indicated that he was reacting differentially to the two frequencies within the first session of postoperative training.

Table 1. Initial preoperative learning and postoperative retention in M-19 and M-20. Initial postoperative learning in M-3 and M-5

Subject	Preoperative		Postoperative	
	Trials	% Correct	Trials	% Correct
M-19	400	55	350	54
M-20	650	54	50	70
M-3	Trained only postoperatively		550	57
M-5	Trained only postoperatively		752	53

Trials and errors are for training up to but not including the 50 trial session in which the subject met the criterion of 80% correct responses in one session.

The remaining two subjects (M-3 and M-5) were trained only postoperatively (Table 1). Both of these subjects reached the criterion of correct responses in roughly the same number of trials as the subjects who were trained preoperatively. Their behavior in the test situation showed no apparent deviations from the behavior of M-19 and M-20 in their preoperative training. Thus, the initial learning of M-3 and M-5 showed no apparent difference from the initial learning of the two normal subjects.

Discussion

The data from this study show that auditory cortex ablation causing degeneration of 90 per cent of the medial geniculate nuclei bilaterally does not interfere with initial learning of a frequency discrimination, and that such an ablation need not disrupt a frequency discrimination learned preoperatively. Of the two subjects trained preoperatively, one (M-19) required almost as many trials to reach the criterion postoperatively as were required for initial learning. As has been noted, however, the criterion of a correct response required that the subject make no attempt whatever to open the food well, any contact by the subject with the electrically charged food well cover being scored as an error. M-19, whose initial postoperative level of correct responses did not differ significantly from chance, showed certain signs of retained ability to discriminate frequencies immediately following operation; the latency and character of his responses were different on trials accompanied by the lower frequency as compared to the higher frequency one. It would appear that the postoperative amnesia that occurred in M-19 was a function of some factor other than specific loss of the ability to discriminate between the two frequencies. This conclusion is supported by immediate postoperative retention of the frequency discrimination in M-20, whose cortical and thalamic lesions were quite similar to those in M-19.

The failure of extensive ablation of the auditory cortex to produce a significant deficit in initial learning or postoperative retention of a frequency discrimination is difficult to reconcile with the strict tonotopic organization that has been demonstrated by the recording of evoked potentials from the auditory area. The complete disappearance of neurons from 90 per cent of the medial geniculate body makes it difficult to postulate that the seat of frequency discrimination is in that structure. It may be that more extensive cortical ablation would result in loss of the ability to discriminate between frequencies. Meyer and Woolsey (6) have shown that, in the cat, frequency discrimination is not affected by any lesion including less than somatic area , Ep, and auditory areas I and II, but that combined destruction of these four areas does prevent discrimination of small increments of frequency. This finding suggests that either the four areas whose combined ablation leads to a deficit in frequency discrimination make up a cortical field whose components function equipotentially with respect to frequency discrimination, or that the operative deficit was the function of a more general deterioration in the experimental situation.

The question of the functional significance of the small remnant of auditory cortex which was not ablated in the subjects of the present study is one which affects any conclusions which can be made concerning the role of the auditory cortex in frequency discrimination. It is possible that this small remnant was of great functional importance. The location of the cortical ..., however, makes it almost certain that the cortical areas receiving impulses initiated by frequencies of 350 and 3500 cps were ablated. Licklider and Kryter (5) have found that lower frequencies are represented in the antero-lateral and higher frequencies in the postero-medial portion of the monkey's auditory area. Only the extreme postero-medial extent of the auditory area was spared in the subjects of the present study. This area includes the depths of the Sylvian fissure at its posterior end and a small part of the contiguous parietal operculum. That the parietal operculum is part of the auditory cortex has been shown by Chow (3), who recorded evoked potentials from the ventral surface of the parietal operculum following acoustic stimuli. Licklider and Kryter (5), using tonal stimuli from 125 to 8000 cps, found that the 8000 cps tone gave rise to evoked potentials in the area of auditory cortex which was not ablated in the present study. The remainder of the auditory cortex, including the area representing frequencies of 350 and 3500 cps, was undoubtedly removed. This fact allows the definite conclusion that, within the cortical field of projection of the medial geniculate nucleus, areas delimited as receiving specific frequency projections do not play an essential role in the discrimination of these frequencies.

Summary

Ablation of the auditory cortex in the monkey (*Macaca mulatta*) has been shown to be without effect upon initial learning of a frequency discrimination, and to result in either temporary amnesia or no deficit whatever when such a discrimination has been learned preoperatively. These findings demonstrate that tonotopic organization within the auditory cortex of the monkey is not associated with localization of function with respect to tonal discrimination.

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