

Effects of Ablations of Temporal Cortex upon Speech Sound Discrimination in the Monkey

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Ten monkeys were trained on two auditory discrimination problems of different levels of difficulty plus one visual pattern discrimination task. Bilateral cortical ablations were made of either the ventral portion of the superior temporal gyrus to the depth of the superior temporal sulcus in the midtemporal region, or of the primary auditory projection cortex of the supratemporal plane extending onto the insular cortex in the depths of the lateral fissure. Monkeys with bilateral ablations of inferior temporal cortex were included as controls. Post operative performance revealed a modality-specific deficit in audition for the midtemporal area, and an apparent inability to relearn a speech-sound discrimination after lesion of primary auditory cortex.

Introduction

The cortex of the temporal lobe of primates is classically conceived to play an important role in audition. This view is based on the undoubted connection of the cochlea through the medial geniculate nucleus of the thalamus to the supratemporal plane and is supported by clinical evidence of a variety of auditory disturbances after injury to the temporal lobe. However, when the experimental literature is examined there is a paucity of evidence as to just what functions in audition might be ascribed to the temporal cortex.

The problem is complicated by the fact that in subprimate mammals (cats), and even in monkeys, bilateral resections limited to the primary auditory cortex have produced at best transient defects. Only when the extent of resection includes a good deal of cortex beyond the primary auditory receiving area have lasting deficits been produced (8, 10, 11, 15, 19, 22, 23).

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brought to the laboratory at the same time each day for testing, when they could receive, as food reinforcements, as many as 50 190-mg CIBA banana-flake pellets. Aside from these reinforcements, however, all feeding took place in the home cage between 1 and 3 hours after the daily testing session.

The general test situation has been described in detail (7). Figure 1 is a drawing of the testing cage which was placed inside an audiometric testing booth located in a separate, quiet room, remote from all programming apparatus. The monkey initiated a discrimination trial by pressing lever X. Immediately, one of a particular pair of stimuli was presented through the loudspeaker, and a press on either lever A or lever B (as appropriate) was required for food reinforcement. This press terminated the stimulus and initiated a timeout of 6 sec during which the houselights were either dimmed (correct press) or extinguished (incorrect press). As the end of the time-out the houselights became bright, signalling to the monkey that a press on lever X would once again begin a trial.

For training and testing on the visual pattern discrimination, a separate apparatus (5, 17) was used, in which the desired pair of stimuli were simultaneously projected at random locations upon 2 of a possible 16 lucite panels placed in a 4×4 array. The monkey's task was to press the panel where the positive (reinforced) pattern appeared. Reinforcement

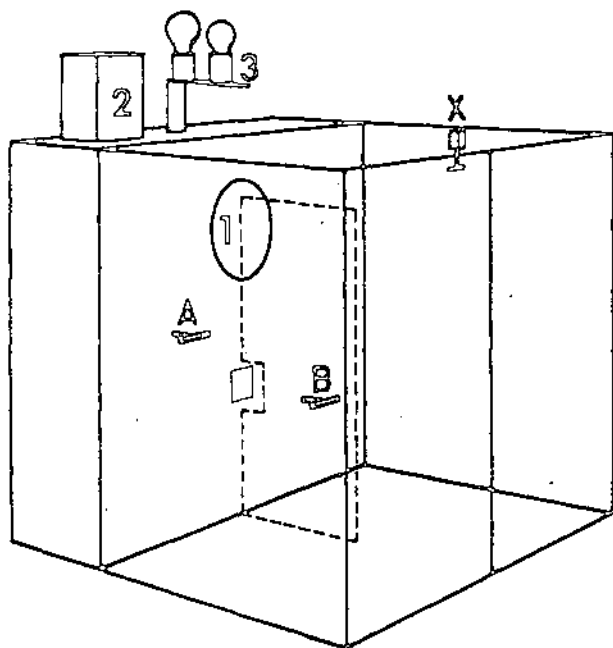


FIG. 1. Testing cage. Labeling for levers (A, B, and X), loudspeaker (1), pellet dispenser (2), and bright and dim houselights (3). (See also reference 7).

the boundaries of the primary auditory projection as determined in an earlier electrophysiological study (18).

The remaining five monkeys (175, 177, 182, 261, and 262) received resections of the cortex buried within the superior temporal sulcus. Rhesus monkeys have a considerable expanse of such cortex, some of which makes a second "island" of gray matter buried within the sulcus. In all five subjects this cortex was ablated as was that of the superior bank of the sulcus; additionally, in three subjects the inferior bank of the sulcus was removed.

Recovery from the surgical procedures was, without exception, uneventful.

Testing for retention of the discrimination habits, one at a time and in their original training order, was begun following a 2-week post-surgical recovery period. Two consecutive daily sessions were devoted to each problem. After 6 days, relearning sessions were given for one task at a time, preserving the original order, until postoperative performance had reached preoperative levels or, failing this, until the number of postoperative trials was at least twice that required for original learning.

The effects of cortical ablations upon postoperative discrimination ability were determined for each animal by dividing preoperative minus postoperative by preoperative plus postoperative trials-to-criterion ($A-B/A+B$). This analysis yields a value which lies between +1.00 (no deficit in retention) and -1.00. The case wherein preoperative and postoperative trials-to-criterion are equal is represented by 0.00, while a value of -0.33 indicates that the animal required twice as many trials to relearn as were necessary for original learning.

At the end of the experiments, the animals were deeply anesthetized with Nembutal and killed by cardiac perfusion with normal saline followed by 10% formalin. The fixed whole brains were sectioned in the coronal plane at 50- μ thickness, and every tenth section stained with aniline thionine. Site of lesion was verified histologically for each animal by the method of serial reconstruction. Figures 2, 3, and 4 show that the loci of ablations for each of the three groups are accurate and essentially nonoverlapping. A minor exception concerns the cortex of the inferior bank of the superior temporal sulcus (generally regarded as part of inferior temporal cortex), which is totally spared in both inferotemporal operates, though removed in two of the five members of the midtemporal lesion group. Although there is noticeable variation in size of lesion within midtemporal and supratemporal groups, variations in bilateral symmetry for any given animal is gratifyingly small. Retrograde thalamic degeneration of all but the posterior tip of the medial geniculate body was evident

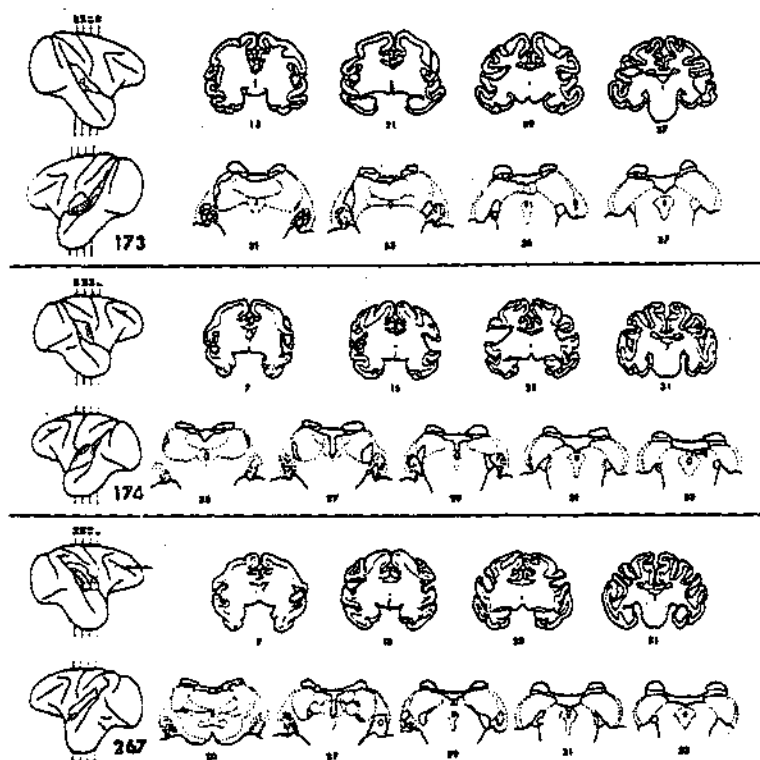


FIG. 3. Serial reconstructions for three monkeys with bilateral ablations of the supratemporal plane. Retrograde thalamic degeneration restricted to anterior three-fourths of parvocellular division of *nucleus geniculatus medialis*.

the nucleus medialis dorsalis of subject 267. Degeneration in the thalami of both of the other lesion groups centered on the pulvinar nucleus; the posterior tip for those monkeys with inferotemporal lesions and a mid-portion in the monkeys with midtemporal removals. No degeneration was noted in the medial geniculates of any of these seven subjects. A moderate amount of lateral geniculate degeneration occurred in subject 175 following a midtemporal lesion but no deficit occurred in the visual task.

Results

Acquisition of each of the three discriminations by all ten of the monkeys is shown by the data of Table 1. The two auditory tasks each required more trials to learn than did the visual pattern discrimination; discrimination of speech sounds took significantly more trials to master than did tone vs. noise. The greatest number of trials taken on any task was the

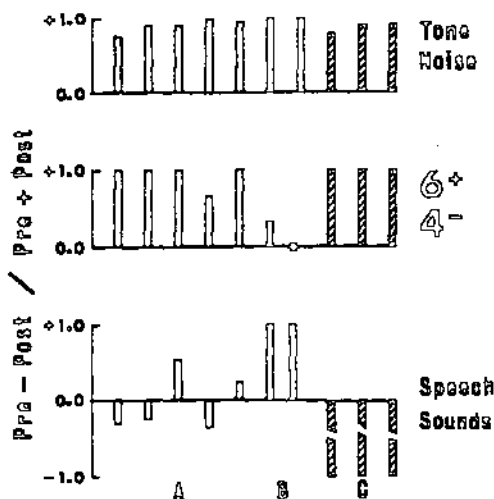


FIG. 3. Postoperative discrimination performance for ten monkeys on the three problems indicated on the right-hand margins of the bar graphs. A (open bars): five monkeys with midtemporal lesions; B (solid bars): two monkeys with inferotemporal lesions; C (hatched bars): three monkeys with lesions of the supratemporal plane.

(b) Bilateral ablation of the supratemporal plane, the cortical projection field of the medial geniculate body results in an apparently complete inability to relearn a conditional discrimination between the vowel sounds [i] and [u] when these are presented at equal duration, fundamental frequency, and over-all intensity. There is a transient, slight deficit in the retention of a similar conditional discrimination between tone and noise, and the retention of a visual pattern discrimination habit is totally spared.

TABLE 2

ABLATIONS OF AUDITORY ASSOCIATION CORTEX: PREOPERATIVE AND POSTOPERATIVE TRIALS-TO-CRITERION FOR FIVE MONKEYS

Subject	Task					
	Tone vs. noise		Speech sounds		Visual pattern	
	Pre	Post	Pre	Post	Pre	Post
175	1100	150	1750	3300	200	0
177	1050	50	2200	3300	150	0
261	1100	50	2200	650	100	0
262	1050	0	2650	5500	250	50
182	2050	50	1500	900	150	0

grates that pattern most likely remained the critical discriminative factor in post operative relearning.

Discussion

The finding that the deficit after resections of the supratemporal plane and the midtemporal cortex are specific to the auditory mode was expected from the results of the earlier studies which had led to the current undertaking. What was unexpected from a reading of the earlier results, however, was the fact that the lesions of primary auditory cortex produced complete inability to relearn a previously acquired auditory discrimination. The magnitude of this deficit stands in contrast to the more reversible difficulty experienced by the subjects with midtemporal lesions as well as that previously reported to follow resections of primary auditory cortex.

The grave difficulty experienced in speech sound discrimination by the subjects with primary auditory cortex resections is clearly a function of the spectral complexity of the stimuli. Bishop (2) has observed that those discriminations which have in the past been most disrupted by the lesions of primary auditory cortex have all involved the temporal order or duration of stimuli. The present results demonstrate a further class of acoustic signals for which the presence of primary auditory cortex is even more critical. A persuasive discussion supporting this interpretation has recently been advanced by Gersuni and his colleagues (9).

The severe but reversible deficit found to follow midtemporal resection can be interpreted to indicate that all of the auditory "association" cortex was not removed in making these lesions. Support for such an interpretation comes from the fact that a rough ranking of subjects on the basis of the amount of tissue removed and the amount of consequent degeneration in the pulvinar corresponds (with the exception of one reversal, 262 and 175) to the amount of difficulty experienced in relearning the speech sound task. Thus the order of damage is $175 > 262 > 177 > 182 > 261$. The order on the basis of behavioral deficit is $262 (2850) > 175 (1550) > 177 (1100) > 182 (-600) > 261 (-1550)$. The fact that monkey 262 showed the greatest deficit might be due to the forward location of the lesion although this is doubtful since monkey 261 has his resection in almost the same place. Most likely to account for the severity of the difficulty shown by monkey 262 is the fact that this subject was also the slowest to learn the task preoperatively.

In sum, the results of the experiment were encouraging to us since we are interested in using animal models to learn something about the organization of the neural mechanisms involved in the processing of complex auditory signals. Pointing out that the human patient with temporal lobe damage often suffers from an inability to understand speech

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In other sensory modalities resections of cortex beyond the primary receiving areas have been shown to interfere with discriminative behavior independent of any involvement of the primary sensory system. In the somatic mode the posterior parieto-occipital cortex is responsible (16, 25); in the gustatory mode the anterior temporal (polar) cortex appears to be involved (1); in the visual mode a great number of studies have shown the inferior temporal gyrus to be critical (3, 12, 13). On an earlier occasion Weiskrantz and Mishkin (24) made a partially successful attempt to locate an area of cortex with similar functions in the auditory mode. The results of their study indicate that a portion of the posterior midtemporal cortex might be implicated uniquely in auditory discrimination. They suggested that further investigation of this cortical area was warranted, and that the use of both auditory and nonauditory discrimination problems coupled with more suitable lesions might clarify the situation.

During the past decade the senior author has been successful in obtaining severe deficits in speech sound discrimination in cats after bilateral resections of their insular-temporal cortex (4). This suggested to us that perhaps the midtemporal lesions in the monkey had been placed too posteriorly to obtain the maximum effect.

The present study was therefore conceived: Just what would happen when bilateral resection was restricted to the primary auditory cortex but when tests comparable in complexity to those used in the cat experiments were given? And what would be the effect of midtemporal cortex resections (extending sufficiently anterior) on such tasks?

To accomplish an experiment which would answer these questions it was necessary to produce lesions which would not overlap. Also, as in the earlier study, comparison with the visual mode would rule out nonspecific effects so a control group of monkeys with inferior temporal cortex removals needed to be included—but, here as well, care had to be exercised not to overlap the extent of the resections with those meant to affect the auditory mode.

In short, answers were sought to two questions: Can the auditory functions of the temporal lobe be dissociated from those of other sensory modalities by locus of lesion; and can some difference between the effects of lesions of the primary and of its associated cortex be obtained within the auditory modality?

Methods

Ten adolescent rhesus monkeys (*Macaca mulatta*) whose average weight was 2.9 kg were used. They were individually home-caged and maintained on a daily diet of 12–16 standard-size Purina monkey chow pellets supplemented weekly with fresh fruit and vitamin extract. The animals were

(a peanut) was delivered at a centrally located food well. A press on either of the two illuminated panels produced a time-out of 6 sec. during which the stimuli were turned off, to be subsequently reprojected at new locations at the end of the time-out.

Pairs of stimuli, for the two auditory problems, were separately recorded on two channels of $\frac{1}{4}$ -inch magnetic tape which was made into loops for playback through the loudspeaker in the testing cage. Each loop, running at $7\frac{1}{2}$ inches/sec, contained four repetitions of each stimulus, spaced so they occurred regularly at a rate of 2/sec. For the tone vs. noise discrimination a 500 msec burst of an 800-Hz tone (rise and decay time 25 msec) was matched in over-all intensity at 72 db SPL with a noise burst (100 kHz low-pass) of similar duration and rise-decay time. As in an earlier study with cats (4), the vowel sounds [i] and [u] were used for the speech sound discrimination task. Over-all intensities were equal at 78 db SPL; the fundamental frequency of each stimulus was 136 Hz, and the durations of each were approximately 300 msec. Sonagrams and spectrograms of these stimuli have been published (6). The tapes were checked regularly and often by human listeners to detect loss of fidelity with use; although this was never found to be a critical factor, the tapes were routinely exchanged for fresh ones. In the visual pattern discrimination task, the numerals "6" (positive) and "4" (negative) were used. They were equated for brightness and area.

Discrimination training on each task was given in single daily sessions on consecutive days until a score of at least 45/50 correct (90%) had been achieved in two consecutive sessions. All monkeys learned the three tasks separately and in the same order, namely, tone vs. noise, speech sounds, and visual patterns. When all problems had been learned to criterion levels, each monkey was removed from the testing situation for 2 weeks, then tested for retention. If necessary, the monkeys were retrained to criterion level at this time before undergoing surgery.

For surgery, the animals were anesthetized (Nembutal: 36 mg/kg, iv) and bilateral cortical ablations were made by subpial aspiration under aseptic conditions. Two monkeys (263 and 265) received restricted resections of the inferior temporal gyrus—the lesion differing from the usual in that inferior bank of the superior temporal sulcus was completely spared. Despite this, sufficient tissue was removed to make a lesion of a size comparable to that of the others. Three monkeys (173, 174, and 267) received resections of the supratemporal plane extending onto the insular cortex. This lesion was made by gently separating the lateral fissure and packing with cottonoid until most of the cortex buried within the fissure could be readily visualized. The attempt was made to remain well within

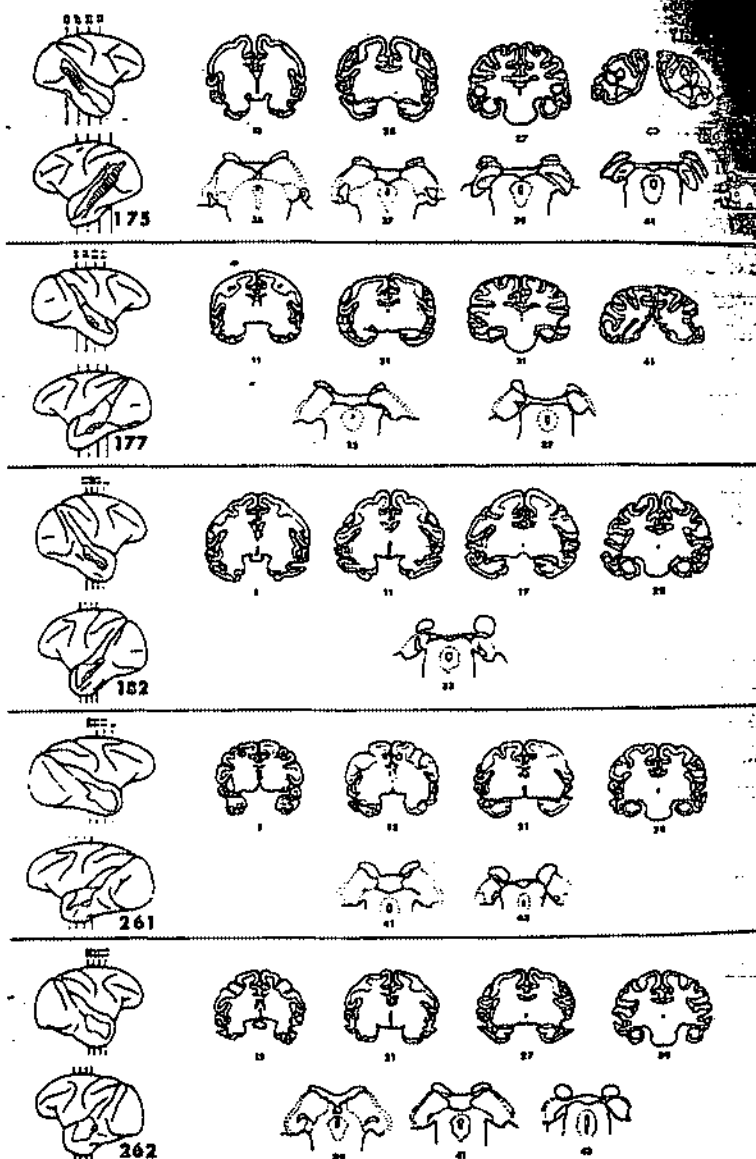


FIG. 2. Serial reconstructions for five monkeys with bilateral ablations of the banks of the superior temporal sulcus. Numbered cross-sections (above) show depth of cortical removal and (below) retrograde thalamic degeneration in *nucleus pulvinaris*.

in all three of the monkeys with lesions of the supratemporal plane. In addition, lateral and ventral parts of the pulvinar were affected in two of the subjects (173 and 174) and a patch of degeneration appeared in

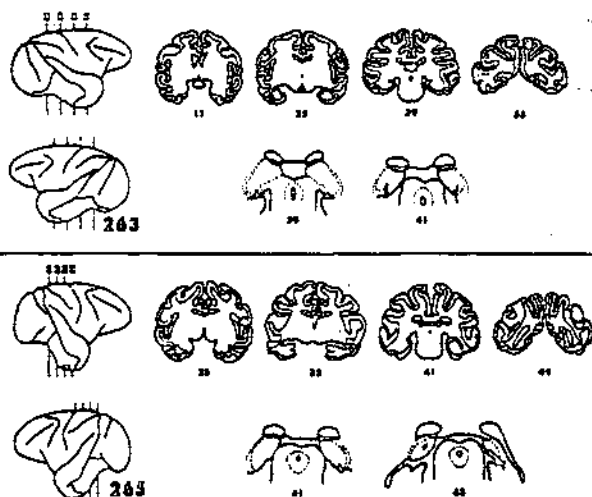


FIG. 4. Serial reconstructions for two monkeys with bilateral ablations of the inferotemporal cortex. Retrograde thalamic degeneration located in nucleus posterior.

3800 needed by one monkey to learn speech sound discrimination, while the fewest number of trials needed to reach criterion was 100 (two monkeys) on visual pattern discrimination.

A clear-cut double dissociation of effect (21) between locus of cortical lesion and discrimination task is demonstrated by Fig. 5. The dissociation is apparent not only between sensory modalities but within the auditory modality as well. The following results support this general statement.

(a) Bilateral ablations of the cortex buried within the superior temporal sulcus which receives no direct projection from the medial geniculate body results in a severe though reversible deficit in the retention of the ability to make a conditional discrimination between two vowel sounds. This same lesion leaves retention of the ability to make a similar conditional discrimination between tone and noise virtually unaffected. Likewise left intact is the ability to make a simultaneous discrimination between two visual patterns.

TABLE I
ORIGINAL LEARNING. TRIALS-TO-CRITERION FOR TEN MONKEYS

Task	Mean	Range	SD
Tone vs. noise	1365	850-3000	285
Speech sounds	2185	1300-3800	445
Visual pattern	180	100-300	31

TABLE 3
 ABLATIONS OF PRIMARY AUDITORY PROJECTION CORTEX: PREOPERATIVE
 AND POSTOPERATIVE TRIALS-TO-CRITERION FOR THREE MONKEYS

Subject	Task					
	Tone vs. noise		Speech sounds		Visual pattern	
	Pre	Post	Pre	Post	Pre	Post
173	1300	150	1900	3100 ^a	150	0
174	3000	150	3800	7750 ^a	300	0
267	1050	50	2750	6000 ^a	250	0

^a No relearning: mean scores on final 500 trials (ten sessions) between 49 and 88% correct.

(c) Bilateral partial ablation of inferior temporal cortex results in a reversible deficit in the ability to make a simultaneous discrimination between the numerals "6" and "4." There is no deficit in the retention of auditory discrimination habits, a finding also noted by Weiskrantz and Mishkin (24).

When the animals had reached criterion on speech sound discrimination, an additional experiment was performed. The speech sounds [i] and [u] produced by a female speaker (fundamental frequency: 212 Hz) and constrained by the same characteristics of intensity, duration, and rate as for the usual male-voice stimuli, were presented for a single 50-trial session, either before or after surgery, was the score lower than 86% correct on this task (three monkeys, of course, were never tested postoperatively on this problem). This is strong indication that the pattern of the speech sound was learned rather than any particular constituent. Lack of postoperative deficit in this control experiment further demon-

TABLE 4
 ABLATIONS OF VISUAL PROJECTION CORTEX: PREOPERATIVE AND
 POSTOPERATIVE TRIALS-TO-CRITERION FOR TWO MONKEYS

Subject	Task					
	Tone vs. noise		Speech sounds		Visual pattern	
	Pre	Post	Pre	Post	Pre	Post
263	1100	0	1300	0	100	50
265	850	0	1800	0	150	150

sounds, Neff (14, p. 271) wrote: "In order that a direct comparison may be made with the results of animal studies, it is desirable that tests of temporal patterns of tones or other acoustic signals, excluding speech, be carried out with human patients." As indicated by the results of the present study, the obverse of Neff's statement is equally important: The use of speech and speech-like discriminative stimuli in animal studies will materially contribute to our understanding of auditory function in man.

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