

# Contribution of Auditory Cortex to Sound Localization in the Monkey (*Macaca mulatta*)

HENRY HEFFNER AND BRUCE MASTERTON

*Psychology Department, Florida State University, Tallahassee, Florida 32306*

THE ANALYSIS OF the two chief binaural cues for the direction of the source of a brief sound ( $\Delta t$  and  $\Delta fi$ ) probably takes place in the superior olivary complex (cf. ref 2, 6-8, 10, 12, 21, 22, 24). Nevertheless, ablation of auditory cortex results in a dramatic and permanent disruption in the ability to localize sounds (15, 16, 20, 25). Since it is also known that auditory cortex ablation does not, in itself, abolish the ability to discriminate either  $\Delta t$  or  $\Delta fi$  (11), the question arises: What is the basis of the cortical deficit?

The idea that the cortical deficit may not be sensory in nature can be derived from Thompson and Welker (27), Beitel and Kaas (1), and Ravizza and Masterton (19): either cats or opossums can indicate the direction of a sound source by a reflexive response even after bilateral ablation of auditory cortex. These results, when combined with the previous ones, show that auditory cortex ablation does not disrupt all of the responses to a localizable sound source but, instead, only some. Therefore, the strictly sensory capacity for sound localization itself may not depend on auditory cortex.

The present report is the first in a series based on experiments exploring the behavioral contributions of auditory cortex in the rhesus monkey (*Macaca mulatta*). In this report we present evidence that monkeys with lesions that include primary auditory cortex bilaterally can indicate the direction of the source of a click with a learned (i.e., nonreflexive) response, but they cannot locate (i.e., move to) the source. This dissociation of abilities shows that the deficit in sound localization that results from audi-

tory cortex ablation depends not on the sensory requirements of the task, but on the motor requirements; and therefore, it suggests that the role of auditory cortex in sound localization is probably not sensory nor perceptual but, rather, audiomotor or associative.

## METHODS

In all, seven monkeys (labeled *A*, *B*, *C*, *D*, *E*, *F*, and *G*) were used in the series of experiments. This report focuses on the behavioral results of four—one normal monkey (*D*) and three with bilateral ablations of auditory cortex (*A*, *C*, and *G*). The chief behavioral results are based on these animals' performance on two sound-localization tasks in which the sensory requirements were identical but the motor requirements were distinctly different.

### *Surgical, electrophysiological, and histological technique*

After preoperative training and testing on a battery of auditory discriminations, aseptic surgery aimed at bilateral ablation of auditory cortex was performed on monkeys *G* and *C*. In monkey *A*, a bilateral ablation was performed before any behavioral training or testing. For surgery, the monkeys were initially anesthetized with Sernylan (Bio-ceutic Laboratories, Inc.) administered intramuscularly (2 mg/kg) followed by pentobarbital sodium administered intravenously as required to maintain a deep level of anesthesia. The animal's head was shaved and washed, the scalp opened, and the temporal muscle dissected with a cautery. With the edges of the temporal muscle retracted, a portion of the cranium overlying the Sylvian fissure was removed, the dura was retracted, and the cortical tissue removed by subpial aspiration.

Following the removal of cortical tissue, the muscle was sewn together and the scalp incision closed with silk thread. Each animal was then given 300,000 U of Bicillin (Wyeth) in-

tramuscularly and returned to its home cage. Behavioral testing was begun 5–18 days later when the animal was judged to be well enough to undergo the water deprivation necessary for behavioral training.

**ELECTROPHYSIOLOGY AND HISTOLOGY.** Following completion of behavioral testing and before sacrifice, the remaining cortex was explored with a gross electrode for auditory evoked responses. For these observations, the animals were again anesthetized with Sernylan followed by pentobarbital, and the brain was exposed. The cortex adjacent to the lesion was then explored with silver-ball or tungsten electrodes for signs of activity evoked by loud clicks presented to the contralateral ear. Thirty-two evoked responses were summed on a signal averager and traced on an X-Y plotter. In each case, the general activity level of the cortex was monitored by recording the response in postcentral cortex to shocks to contralateral forepaw. Following these observations, the monkeys were sacrificed with a lethal dose of pentobarbital and perfused with isotonic saline followed by 10% formalin.

After perfusion was complete, the outer and middle ears were routinely examined for evidence of damage or disease. The brains were removed and embedded in egg yolk for frozen sectioning (5). Each brain was sectioned at 33  $\mu\text{m}$  in a frontal plane beginning at the anterior tip of the temporal lobe and continuing posteriorly past the caudal end of the lesion. Every 9th and 10th sections were stained by the Weil and cresyl violet techniques, respectively, except in the vicinity of the medial geniculate where every 4th and 5th sections were stained. These sections were then used to reconstruct the limits of the cortical lesion and to plot the retrograde degeneration in the medial geniculate and surrounding thalamic nuclei.

### *Behavioral tests*

Two tests were used to assess the ability of the monkeys to localize the source of a brief sound. For convenience in discussion we have given these tests distinctive names: the indication test and the location test. In the indication test, the monkey was required to press a lever on either its right or left side in response to clicks emanating from loudspeakers on either its right or left side. When the animal pressed the appropriate lever, it received a reward of water. In contrast, the location test required the monkey to walk to one of two loudspeakers which was, or had been, emitting clicks. When the animal contacted a water spout beneath the speaker from which the sound had come, it received a water reward.

**INDICATION TEST.** *Details of behavioral equipment.* A standard primate chair was modified to accommodate a water spout (mounted directly in front of the monkey's mouth) and two telegraph keys within easy reach to the left and right of the monkey. The water spout was connected to a calibrated water bottle with rubber tubing interrupted by an electrically operated valve which allowed a measured amount of water to be dispensed as reward. The monkey was required to place its mouth on the water spout before a sound was presented.

The primate chair was carefully positioned for each test session so that the water spout (and therefore, the monkey's head) was equidistant from the loudspeakers. Thus, the water spout served three purposes: 1) to deliver the reward; 2) to position the animal's head; and 3) to provide a so-called "observing response," which allowed the monkey to begin its own trials (23).

All training and testing on the indication task took place in an IAC 1202A sound chamber whose walls and ceiling were lined with loose burlap to reduce sound reflections.

*Sound-production equipment.* Clicks were produced by passing 100- $\mu\text{s}$  rectangular pulses through an attenuator and then to one of several speakers. Pairs of loudspeakers (one of each pair to the left and one to the right) were suspended from a perimeter bar of 88-cm radius at ear level to the monkey.

To reduce the possibility that an animal might distinguish between speakers by the quality of the sound rather than by their location, the pairs of speakers were matched by human observers on the basis of the quality and intensity of the clicks they produced. Eventually, each pair of speakers was also subjected to a quality test by the monkeys themselves. The results of these tests (to be described below) provided further assurance that any differences in click quality that might have existed were not sufficient to provide an alternative cue.

The intensities of the clicks were equated at an arbitrary level which was judged adequate to human observers. Subsequent testing indicated that the clicks could be localized easily by normal monkeys and that their intensity could be attenuated by 40 or 50 dB before their localization performance deteriorated. Thus, click intensity was well within a normal monkey's hearing range and at least 40 dB SPL above their click-detection threshold.

*Training procedure for indication task.* The monkey was placed in the primate chair for daily sessions approximately 30–45 min long.

During these sessions the animal was exposed to discrete trials, each of which began with the monkey initiating a presentation of the stimulus by mouthing the lick spout, and ended with a response, either correct or incorrect, to one of the two levers. On the average the monkeys usually administered between 200 and 300 trials to themselves each session.

By placing its mouth on the spout, the monkey triggered the presentation of the stimulus—either a single click or a click train from one or another of the speakers. In the case of click trains, the train was presented until the animal either made a response or broke contact with the water spout. If the animal broke contact without responding, the stimulus was discontinued until contact was remade. Thus, a stimulus was only presented when the animal's head was properly positioned.

By pressing the lever located on the side from which the sound came, the animal received a small amount of water (0.5–1 ml) via the water spout. After 2 s another trial could be begun. Thus, by remaining in constant contact with the spout (as each of the monkeys usually did), an animal could administer trials to itself at a rate approaching one every 2 s. In contrast, if an incorrect response was made, a "time-out" interval ranging from 5 to 60 s was imposed, during which no trial could be initiated.

The side on which the stimulus occurred was determined by a quasi-random series. Assurance of the adequacy of this schedule in preventing the animals from using the schedule itself as a cue was provided later by the monkeys' chance performance on subthreshold trials and also by a series of specific control tests to be discussed below.

In order to minimize the probability of position habits (e.g., responding to one side only), the position of the sound was randomized only after a correct response. This procedure forced the monkey to break a position habit or suffer a long period without reward. As a result of this procedure, however, only trials following a randomization of the sound locus were true tests of sound-localization ability. Thus, the chief behavioral results are expressed as percentage correct localizations following a randomization of the locus of the sound source.

*Test procedure.* In the critical indication tests, the monkeys' acuity for the azimuth of a sound source was measured for clicks presented, first at a rate of 3/s and eventually for single clicks. The animals were tested at 11 angles of sound-source separation: 180°, 90°, 60°, 45°,

30°, 20°, 15°, 10°, 5°, 3.5°, and occasionally for control purposes, at 0°. In each instance the angle was centered on the animal's midline so that one speaker was one-half of the angle to the left and the other one-half of the angle to the right of the animal. For example, for 180°, one speaker was 90° to the left and the other speaker 90° to the right of midline. The 0° angle was obtained by placing the two speakers one above the other.

Three additional indication tests were given in order to explore the limits of the ability of the monkeys without auditory cortex. However, since each of these tests was only one or another variation of those just described, the details and reasoning behind their design can best be presented as the results of the earlier tests unfold.

*LOCATION TEST. Details of behavioral equipment.*

For the location test, the monkey was placed in a room in which two loudspeakers, two white lights, and two water spouts were mounted at one end. A third water spout was mounted on a post centered 1.7 m in front of the loudspeakers. The function of this center spout was to serve as an observing response for starting a trial and to position the monkey equidistant from, and facing toward, the loudspeakers.

To begin a trial, the monkey had to stand on a metal floor plate and lick the center water spout. This action completed an electronic circuit and initiated a trial. The floor plate was placed so that the circuit could be completed only when the animal was properly positioned relative to the loudspeakers. After beginning the trial the monkey had to walk to the speaker from which the sound had come and contact the lick spout beneath it. If it contacted the spout below the speaker that had emitted the sound, a reward of water was delivered.

It should be noted that this apparatus is nothing more than an automated version of the apparatus used by Neff in his original tests on cats (cf. ref 16, 26).

*Sound-production equipment.* The sound-generating equipment was the same as that used in the previous indication test. The two loudspeakers were also one of the matched pairs previously used in the indication test. Thus, the sound system was already known to produce clicks indistinguishable to the monkeys on the basis of quality alone.

*Training procedure for location test.* At the beginning of each session, the thirsty monkey was led into the room and its leash attached to a string on the wall behind the center water spout. Once it became accustomed to the room

it began to lick each of the water spouts to obtain water. When the center water spout was licked, the monkey received a drop of water and immediately a 6/s train of clicks was emitted from one of the speakers. If the monkey next licked the water spout below the activated loudspeaker, it was rewarded with water and the sound was discontinued. If the animal licked the water spout beneath the silent speaker, it received no water and the sound was discontinued. After either response, the monkey was required to return to the center water spout and lick it in order to receive water and initiate another trial. This procedure was learned by the normal and operated monkeys alike in less than seven sessions.

Once the animals had learned to lick the center water spout after responding to one of the two goal spouts, the water reward at the center spout was discontinued. The animals then learned to respond only to the correct goal spout; that is, the one below the speaker which had emitted the sound. When each animal had reached an 85% correct criterion, it was tested on its ability to localize click trains of various rates, and finally, a single click.

**Behavioral tests.** In the location tests, the ability to localize single clicks or click trains was determined at an angle of 60° only. In the first test, the stimuli were click trains of 6, 4, 3, or 1/s, which were turned on at the beginning of a trial and remained on until a response had been made. In the second test, only a single click was presented on each trial.

As a result of the performance of the operated animals on these two tests, three additional tests were eventually given. These tests are best described following the results of the earlier ones.

## RESULTS

### *Anatomical results*

The probable locus and extent of auditory cortex in macaque based on the cytoarchitectonic studies of Pandya and Sanides (17) and single-unit recordings of Merzenich and Brugge (13) are shown in Fig. 1. Reconstructions of the cortical lesions and the resulting retrograde degeneration in the medial geniculate are summarized in Table 1. Figures 2-5 show the lesions and thalamic degeneration in the two extreme cases, monkeys *A* and *G*. Although the three cases varied in several ways, for present purposes only two warrant special mention. First, primary auditory cortex (i.e., AI or Heschl's gyrus)

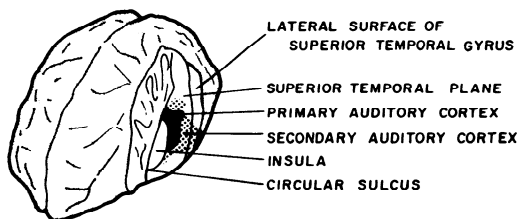


FIG. 1. Drawing of a rhesus monkey brain with the frontoparietal operculum removed to show the location of primary (blackened) and some secondary (dotted) auditory cortex. More secondary auditory cortex is buried in the circular sulcus bounding the insula (based on the work of Merzenich and Brugge (13) and Pandya and Sanides (17)).

was completely removed or undercut bilaterally in monkey *A* (Figs. 2 and 3), more than 90% removed bilaterally in monkey *C*, and in monkey *G*, was completely removed on the right side (Fig. 4), but only about two-thirds removed on the left side (Fig. 5). The bilateral damage to AI in monkey *G* is easily the smallest of the three because the lesion in its left hemisphere preserved a nonnegligible amount of AI just caudal to the insula. Therefore, monkeys *G*, *C*, and *A* approximate an ordered set increasing in degree of bilateral involvement of AI. This point will prove to be important as the behavioral results are described.

The second important way the lesions varied can be seen among the entries in Table 1 that summarize the resulting thalamic degeneration. The large lesion on the right in monkey *G* resulted in total degeneration of the entire medial geniculate. Detailed examination of this lesion (Fig. 4) shows that cortex was removed or undercut not only from Heschl's gyrus, but also from the rostral tip of the temporal lobe to the parietal operculum and the caudal tip of the insula. Therefore, it can be concluded that the total projection area of the principle (GMP) and magnocellular (GMm) divisions of the medial geniculate is a subset of this cortical area.

Turning now to monkey *A*, which had a complete ablation of AI bilaterally, severe degeneration appeared only in the rostral third of GMP and tapered caudally. The magnocellular division of the medial geniculate was preserved (Figs. 2 and 3).

TABLE 1. *Anatomical results*

	Animal:		C		G	
	Hemisphere:		L	R	L	R
<i>Cortical ablation</i>						
Primary auditory cortex	C	C	C*	C*	⅔	C
Secondary auditory cortex						
Rostral	N	N	⅓	N	⅔	C
Caudal	C	C	C*	C*	⅓	C
Medial	C*	⅔	⅓	⅓	C	C
Lateral	C	⅓	C	C*	C	C
Rostral tip of medial surface of temporal lobe	N	N	N	N	C*	C
Caudal tip of insula	N	N	N	N	N	⅔
Adjacent parietal border	N	⅓	N	N	⅓	C
<i>Retrograde degeneration</i>						
Medial geniculate principle division						
Rostral-dorsal	3	3	1	1½	0	4
Rostral-ventral	3	3	0	½	1	4
Middle-dorsal	3	2½	3	3	½	4
Middle-ventral	1½	2	0	0	3½	4
Caudal-dorsal	1½	0	½	½	3	4
Caudal-ventral	1	0	0	0	3	4
Medial geniculate magnocellular division	0	0	0	0	0	4
<i>Evoked response</i>	-	-	Yes	Yes	Yes	No

Cortical ablation: N = not removed; ⅓ = approximately ⅓ removed; ⅔ = approximately ⅔ removed; C\* = more than 90% removed; C = entirely removed. Retrograde degeneration: 0 = normal, no cell loss; 1 = slight degeneration, up to 30% cell loss; 2 = moderate degeneration, 30–70% cell loss; 3 = severe degeneration, 70–95% cell loss; 4 = total degeneration, 95–100% cell loss. Evoked response: yes = response obtained; no = no response obtained; - = sufficient recordings not possible.

Finally, in the left hemisphere of monkey *G* in which the most caudal part of AI escaped ablation, the rostral part of GM was preserved (Fig. 5). Although no detailed conclusions regarding the projection pattern of Gmp onto auditory cortex can be made, these results, together with the anterograde studies of Mesulam and Pandya (14), indicate that the projection of Gmp is certainly not confined to AI alone, nor even to AI and the immediately adjacent area (note left lesion in monkey *A* in Table 1 and Fig. 3; also ref 19). Instead, the total projection area of Gmp seems to be bracketed by the large area removed on the right side in case *G* (Fig. 4) and the lesser, but still large, area removed on the left side in case *A* (Fig. 3).

The electrophysiological results were in agreement with the histological analysis. No response to clicks would be detected in the right hemisphere of monkey *G*, though small surface-positive responses (15  $\mu$ V, 7 ms latency) were detected in

parietal cortex immediately adjacent to the caudal tip of the Sylvian fissure. In monkey *C*, a small response (biphasic negative-positive, 10  $\mu$ V) was recorded in the right hemisphere when a concentric electrode was used to penetrate the caudal tip of the Sylvian fissure. This same procedure yielded a similar result in the left hemisphere. Though no click-evoked responses were obtained from either hemisphere of monkey *A*, this animal died before a complete set of records could be made.

In summary, the anatomical results show that the three monkeys received auditory cortex ablations ranging from a complete, bilateral AI case (monkey *A*), to a somewhat smaller bilateral case (monkey *C*), to a case (monkey *G*) with a massive lesion on one side and an incomplete ablation of AI and surrounding areas on the other. Because the behavioral results focus on the difference between the post-operative performances of each monkey

## CASE A Right

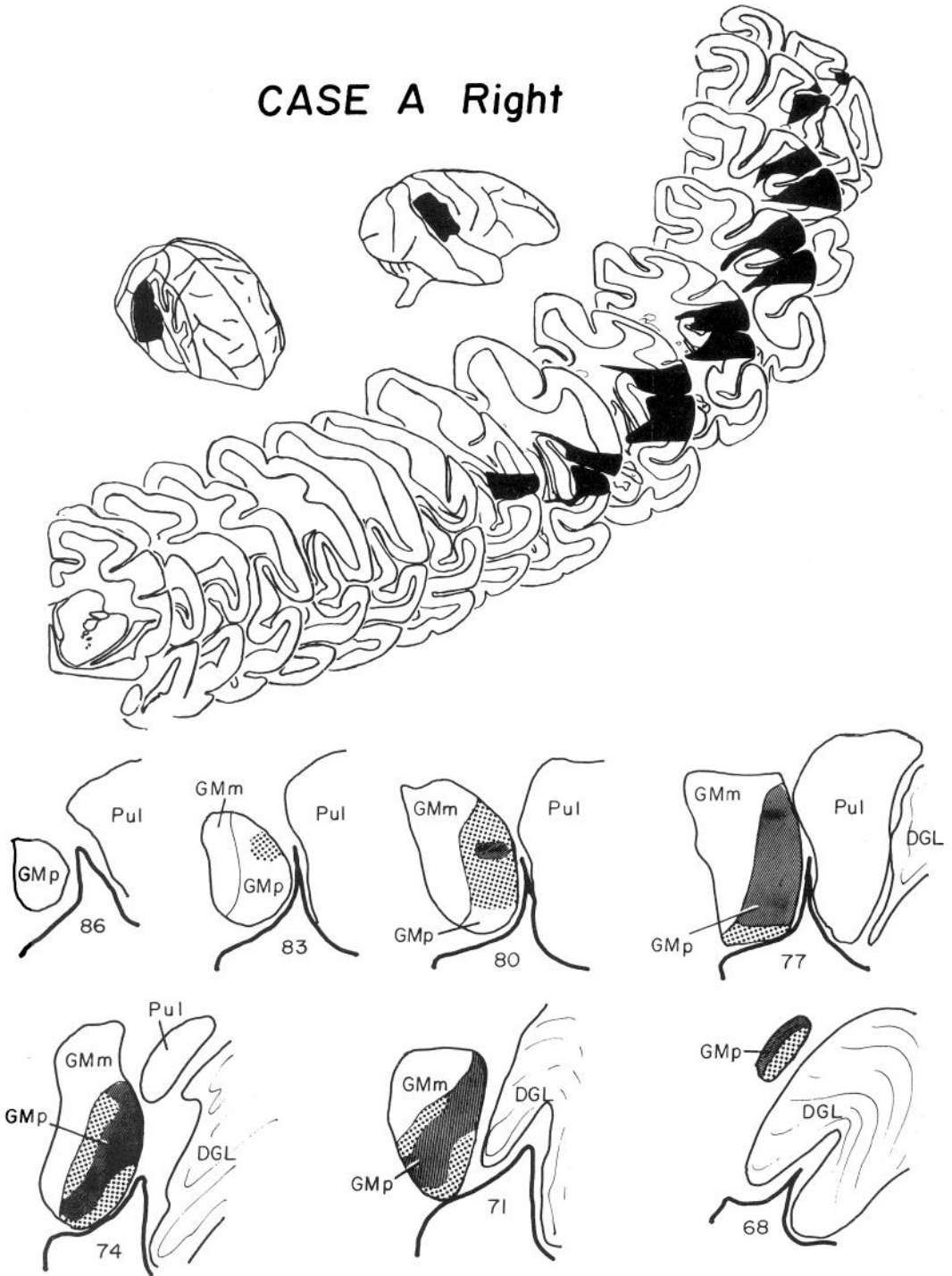


FIG. 2. Cortical reconstruction and medial geniculate degeneration in right hemisphere of monkey *A*. *Top*: reconstruction of cortical lesion. *Bottom*: retrograde degeneration in vicinity of medial geniculate from posterior to anterior. DGL, dorsal lateral geniculate; GMm, magnocellular division of the medial geniculate; GMp, principle division of the medial geniculate; Pul, inferior pulvinar. Area of severe degeneration is blackened; moderate degeneration, stippled.

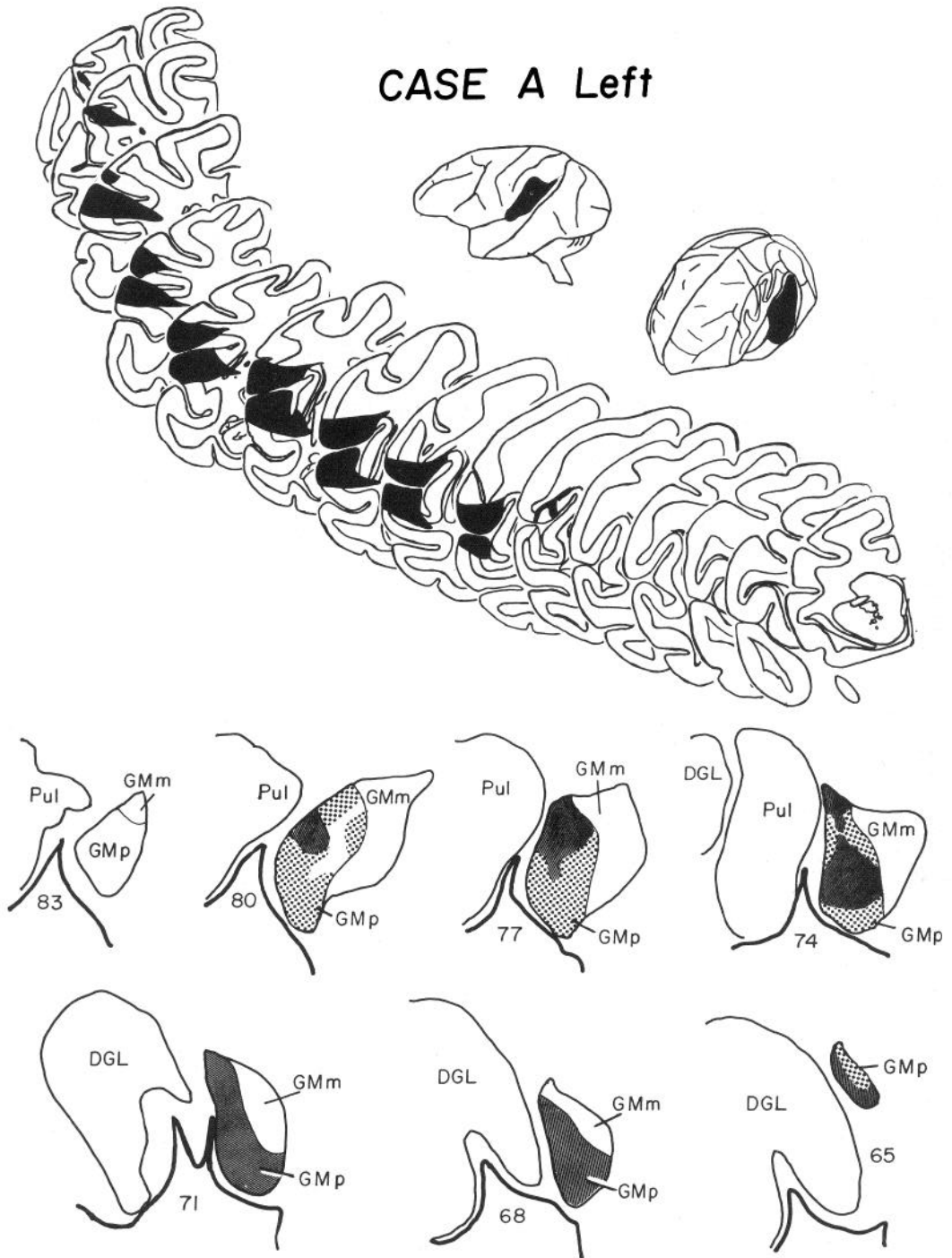


FIG. 3. Cortical reconstruction and medial geniculate degeneration in left hemisphere of monkey A. See Fig. 2 for abbreviations.

## CASE G Right

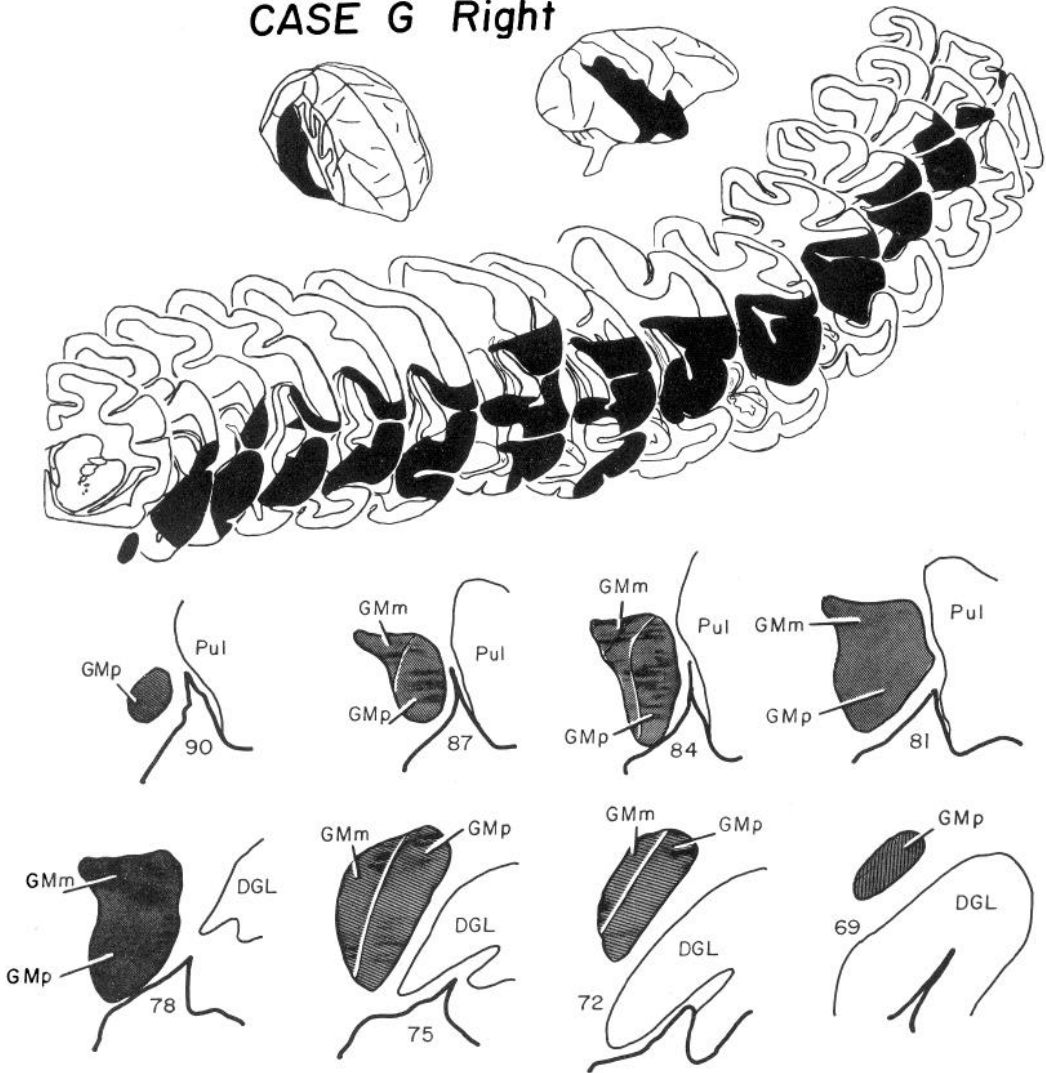


FIG. 4. Cortical reconstruction and medial geniculate degeneration in right hemisphere of monkey G. See Fig. 2 for abbreviations.

in the two different behavioral tasks (rather than on a difference between preoperative and postoperative performance), this gradation of the involvement of AI in the lesion allowed the assessment of the contribution of AI to the nonsensory aspects of the two tasks. As the behavioral results are described, it will be seen that the degree of dissociation of the ability to locate a sound source from the ability to indicate the direction of the sound source corresponds to the degree

of bilateral involvement of AI in the lesions.

#### Behavioral results

The behavioral results described here are concerned primarily with four tests: the localization of a single click or a click train in each of the two behavioral situations. But before describing these results in detail, it should be noted that each of the monkeys discussed here was subjected to a battery of 29 different psychophysical



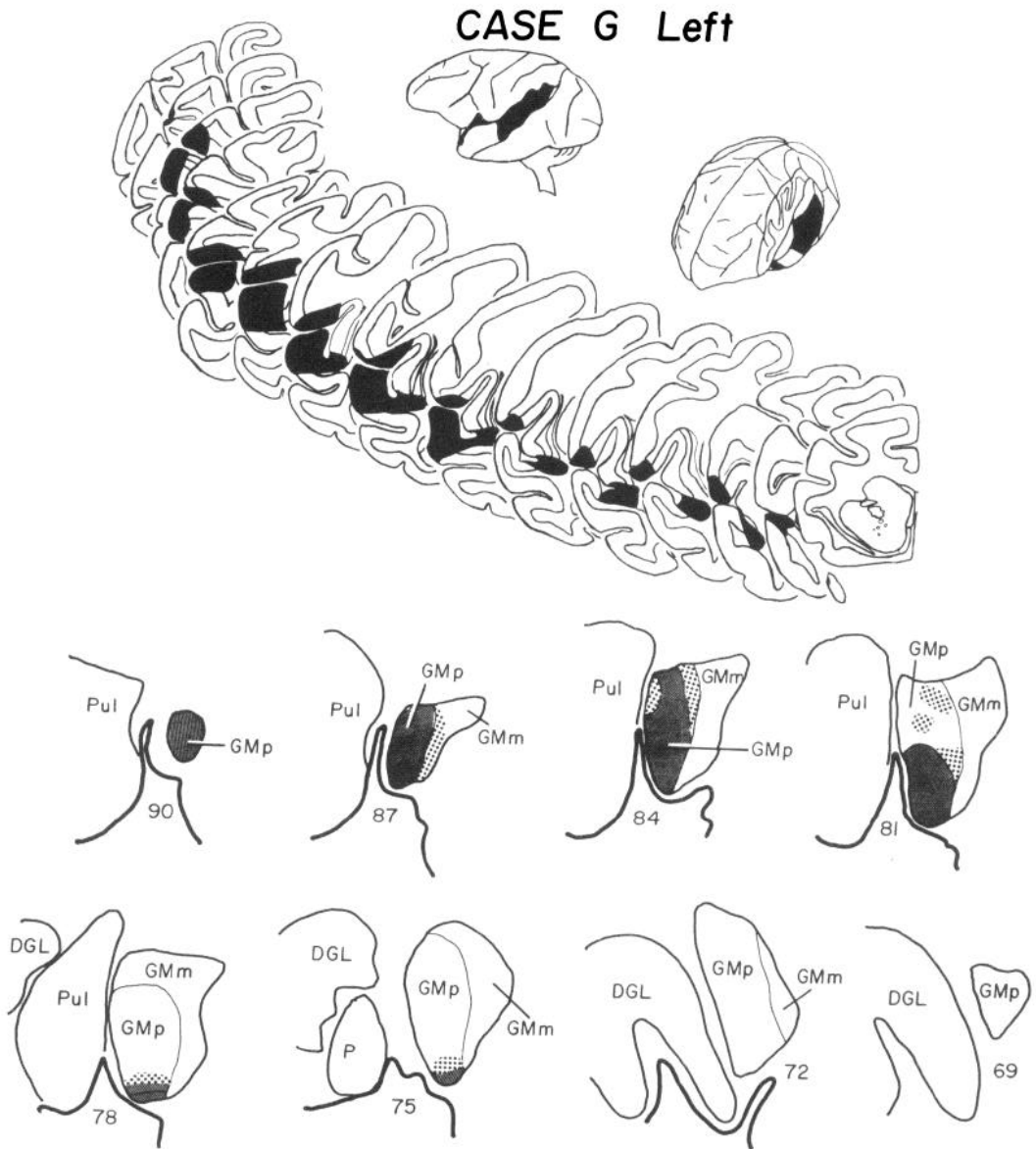


FIG. 5. Cortical reconstruction and medial geniculate degeneration in left hemisphere of monkey G. See Fig. 2 for abbreviations.

tests ranging from simple tests of absolute threshold for pure tones to tests of binaural lateralization using headphones. Although the results of these other tests are not directly relevant to the question of sound localization, it is important to note that each of the three operated monkeys performed normally on several other auditory tests, some having the same motor

requirements as the tests described here. This means that the lesions did not result in an impairment so general as to preclude successful performance on any behavioral task nor even on every auditory task. Therefore, the monkeys' failure on some of the tasks described here cannot be attributed to a generalized inability to cope with the motor, intellectual, emo-

tional, or motivational requirements of the tests but instead, demonstrate much more specific deficits.

**INDICATION TESTS: INDICATION OF DIRECTION OF SOURCE OF A 3/S CLICK TRAIN.** Figure 6 shows that the three monkeys with auditory cortex lesions were able to indicate the direction of the source of a click train even at small angles of separation. Although the performance levels of monkeys *A* and *C* were statistically lower than normal overall, their thresholds were either normal or near normal. The thresholds of six normal monkeys ranged between 3.75° and 5°, while the postoperative thresholds for monkeys *A*, *C*, and *G*, were 4.5°, 7.5°, and 4.5°, respectively. Thus, the lesions in monkeys *A* and *C* affected their overall performance. Nevertheless, there was no important change in their threshold for the direction of the source of a click train.

**INDICATION OF SOURCE OF SINGLE CLICKS.** Since the most critical test of truly binaural sound localization is the ability to localize a single brief sound (20), the results of the single-click localization test, shown in Fig. 7, are of special interest. The figure shows that the three monkeys with auditory cortex lesions were indeed able to indicate the direction of the source of a single click.

Furthermore, the threshold values of 7.25°, 7.5°, and 3.75° for monkeys *A*, *C*, and *G*, respectively, are very close to normal values which ranged from 4° to 7.5°. Thus, it appears that monkeys with auditory cortex lesions are able to indicate the direction of the source of a single click with normal thresholds.

Although none of the three monkeys showed a clear deficit in threshold acuity for the localization of single clicks, it is important to note that two of the monkeys performed the test only with difficulty. In Fig. 7 it can be seen that the two monkeys with the largest lesions of AI (monkeys *A* and *C*) had lower overall performance levels than either normal monkeys or the monkey with a part of AI remaining on one side (monkey *G*). Because monkeys *A* and *C* received thousands of practice trials both with single clicks and with click trains before receiving this test, it is doubtful that further testing would have resulted in significant improvement. Even after this extensive training, for example, the performance of monkey *A* was occasionally erratic, and on some sessions it failed entirely to perform above chance levels. Despite these difficulties in performing the task consistently, however, it is clear that the monkeys had the ability to indicate the direction of

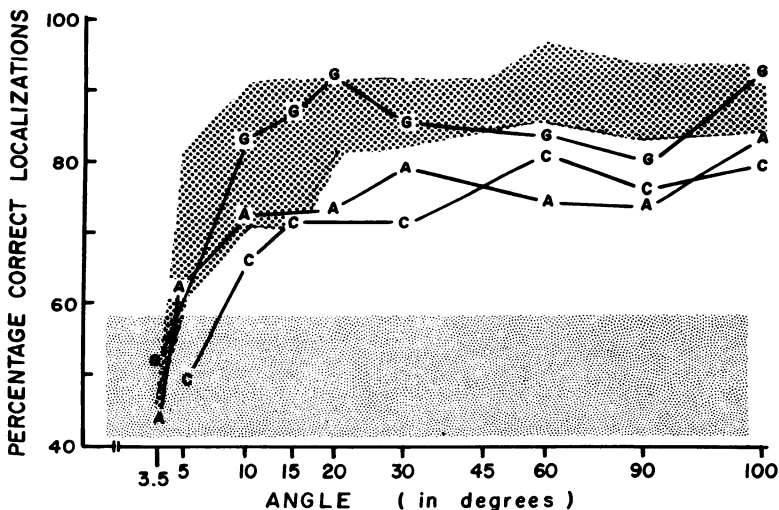


FIG. 6. Performance of three monkeys with auditory cortex lesions (*A*, *C*, and *G*) on the localization of a 3/s click train in the indication test. The range of scores for six normal monkeys is indicated by stippling. The gray area shows chance level of performance. Note dissimilarity of overall performance levels but similarity of thresholds.

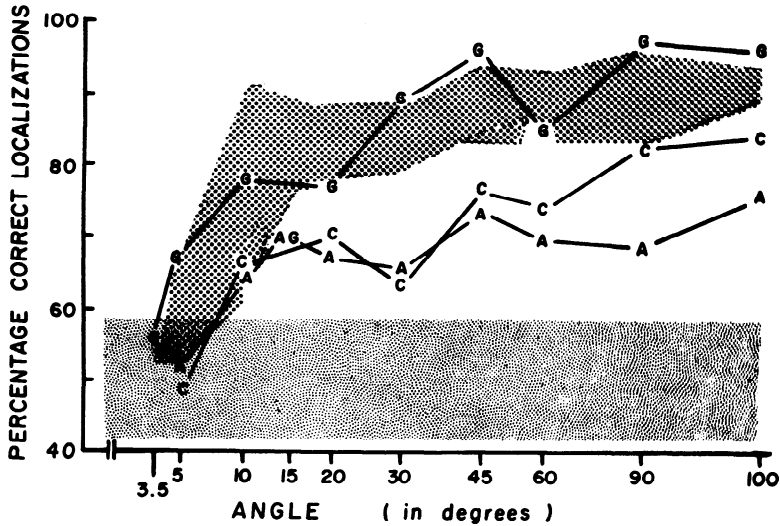


FIG. 7. Performance of three monkeys with auditory cortex lesions (*A*, *C*, and *G*) on the localization of a single click in the indication test. The range of scores for six normal monkeys is indicated by stippling. Gray area shows chance level of performance. Note dissimilarity of overall performance levels but similarity of thresholds.

the source of a single click with near-normal acuity.

**REVERSAL TEST.** Once it had been determined that the monkeys with auditory cortex lesions could indicate the direction of a sound source, further testing was conducted to determine if they might be solving the task in an unusual manner. One possibility which we considered was that the monkeys might not be localizing the sounds, but responding after comparing the sound on one trial with the sound on the preceding trial. That is, if the sound was judged by the animal to be the same as the one in the preceding trial, then the animal would make the same response which had been correct on the preceding trial. If, however, it sounded somehow different, then the opposite response would be made. While possible cues for such a discrimination might arise from differences in click quality resulting from the use of different speakers, the fact that no animal was able to perform successfully when the angle of separation was reduced to  $0^\circ$  indicated that such cues were probably not being used (see Figs. 6 and 7). However, the possibility remained that the animals might be using locus cues (i.e., binaural time and intensity differences) as the basis of their comparison. In this way the monkeys might be using

the differences in sensation resulting from the differences in locus to make a relative rather than an absolute discrimination.

In designing a test of this possibility, we reasoned that if the animals were making a comparison between successive stimuli as the basis of their responding, then it would make little difference whether a stimulus was associated with the lever located on the same side or on the opposite side from which the sound came. Accordingly, a test was given in which the monkeys were required to press the lever opposite to the direction of the sound source. Figure 8 shows the results of this test at  $180^\circ$  for monkeys *A*, *C*, and *G*. During the first half of the session, while the animals were required to respond to the lever on the same side as the sound source in the usual manner, all three animals performed above chance levels. However, during the second half of the session when the animals were required to respond to the lever opposite the sound source, the performances of all three monkeys changed abruptly. Two of the monkeys, *C* and *G*, made a series of incorrect responses and then stopped responding entirely, even though they had received only half of their daily water intake. Monkey *A* continued to respond, but performed at a level significantly below chance. Thus,

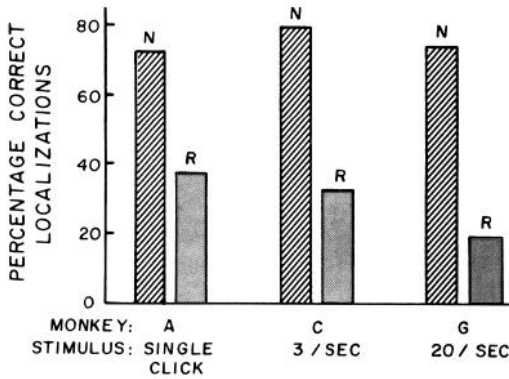


FIG. 8. Effect of left-right reversal on performance in the indication task. N: monkeys required to respond left to left stimulus and right to right stimulus. R: monkeys required to respond left to right stimulus and respond right to left stimulus. Note below-chance performance levels of each animal when required to reverse responses.

it can be concluded that the monkeys had made an association between the direction of the sound source and the direction of the levers and were not responding by comparing the stimulus on a particular trial with the stimulus presented on a previous trial.

Pursuing one step further the general question of whether the monkeys were responding to the locus of the sound source in the same way as normal monkeys, it should be noted that once an animal had relearned the task at one angle postoperatively, it immediately transferred its training to other angles of separation without a significant decrement in performance. Therefore, by several measures the animals responded as though the sounds emitted from one side had more in common with each other than they did with any of the sounds from the other side. This result suggests once more that the animals associated the left lever to sounds from the left and the right lever to sounds from the right. Therefore, there seems sufficient reason to believe that the operated monkeys, like normal monkeys, were responding to the "leftness" and "rightness" of the sound sources and were not merely associating arbitrary stimuli with arbitrary responses.

LEFT SOUND SOURCE VERSUS SILENCE. Although the performance of the monkeys with auditory cortex lesions did not appear to be qualitatively different from the per-

formance of the normal monkeys, monkeys A and C showed a quantitative decrement in overall performance. In an attempt to discover the nature of the difficulty, monkey A was presented with one final test. During one session in which monkey A was having difficulty on a 1/s click train at 60° separation, the right speaker was entirely disconnected. This procedure changed the test from a localization test to a nonspatial-click vs. no click—discrimination without changing the response requirements. The effect of this procedure was to raise the performance of monkey A to a level well above chance. When the right speaker was reconnected, the animal's performance immediately fell again to chance. This result suggests that monkey A's difficulty in the indication tests was not due to any simple sensory loss or motor impairment nor to an inability to link an auditory stimulus to a motor response. Instead, it appears that the difficulty lay in responding on the basis of the truly spatial aspects of the sound.

In summary, the results of the indication tests show that monkeys deprived of AI bilaterally retain the ability to perceive the direction of the source of a brief sound with near-normal acuity. However, they seem to suffer some sort of deficit in the ability to act on this perception.

#### Location tests

Whereas in the previous indication tests the monkeys responded by pressing one of two levers, the location tests required the animal to walk to one of two loudspeakers. Thus, in each of these tests the monkeys were required to locate the source of the sound rather than merely indicate the direction from which the sound came. In each of these latter tests, the angle of separation between the loudspeakers was fixed at 60°.

LOCATION OF SOURCE OF CLICK TRAINS. Once the monkeys had reached a training criterion, they were tested on their ability to localize click trains of progressively lesser rates (6, 4, 3, and 1/s). The results shown in Fig. 9 indicate that each of the monkeys could localize the click trains. However, the performance of the three monkeys with auditory cortex le-

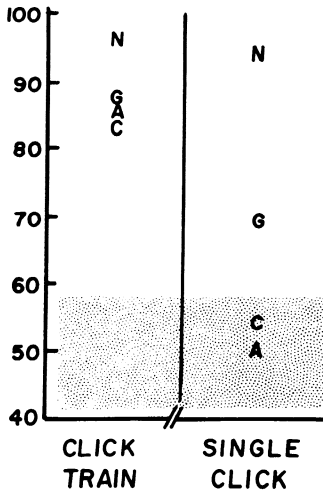


FIG. 9. Performance of normal monkey (*N*) and three monkeys with auditory cortex lesions (*A*, *C*, and *G*) on the location test. Though each monkey was able to discriminate click trains (left), all three monkeys with cortical lesions suffered a severe deficit in locating a single click (right). Cases *A* and *C* with the largest lesions were unable to perform above a chance level even after 1,000 training trials.

sions did not overlap the performance of a normal monkey. Postoperatively, the animals were barely able to maintain a performance level above 85%.

In one way, the results of this test are quite similar to those obtained in the previous indication tests (cf. Figs. 6 and 8). Comparing the performances of the animals for click trains at 60°, it can be seen that there is little difference between the performance levels achieved by the operated animals on the two tasks. Indeed, in each case the performance on the location task is slightly higher than on the indication task. This result is important because it indicates that the location task is certainly no more difficult than the indication task and, indeed, may even be easier for the monkeys to learn. Therefore, the inability of two animals to perform the location test to be described next cannot be construed as merely a secondary result of greater intellectual or motor demands.

**LOCATION OF SOURCE OF SINGLE CLICKS.** Because the monkeys had performed reasonably well on the click-train test, it was expected that they would have no more difficulty in localizing single clicks in

this test than they did in the indication test. Therefore, we were surprised to find that monkeys *A* and *C* were completely unable to locate the source of a single click.

Figure 9 shows the performance levels of the three cortical cases (*A*, *C*, and *G*) and a normal monkey (*N*). It can be seen that each of the cortical cases suffered a significant deficit. Furthermore, the degree of the deficit corresponds with the degree of the bilateral removal of AI. In contrast to the previous results, the performance levels of monkeys *A* and *C* remained at chance levels. Despite a thousand training trials, neither *A* nor *C* gave any sign of being able to locate the click source.

It is important to note that the large number of training trials for cases *A* and *C* were not amassed through mere repetition of a seemingly impossible task. Instead, we tried every device we knew in an attempt to bring forth performance above chance levels. For example, for fear they might give up trying to perform the task entirely, the animals were not allowed to perform at chance levels for long periods of time. Instead, periods of testing on click trains (a task they could perform reasonably well, see Fig. 9) were interposed from time to time. Later, when it became obvious that monkeys *A* and *C* were having extraordinary difficulty locating the source of a single click, they were tested with single clicks only in sessions where their level of performance for click trains was shown to be high. In spite of these special allowances, however, neither of the two monkeys was able to perform the discrimination successfully. Therefore, in contrast to normal monkeys and monkey *G* with a nonnegligible part of AI remaining, monkeys *A* and *C* showed the same sort of persistent deficit in localizing a sound source that Neff and his colleagues (16) and Riss (20) have shown to be the case with cats with comparable lesions.

#### *Further behavioral results*

In seeking a reason how the very same monkeys that could indicate the direction of the source of a brief sound would fail

completely to locate the source, we explored several diverse possibilities. In this and the following sections, we present the results of some further behavioral tests that served to narrow the range of plausible explanations.

**LOCATION OF SOURCE OF A LIMITED 6/s CLICK TRAIN.** One difference between the previous indication test that the monkeys without AI could perform and the location test that they could not perform is the necessarily longer delay imposed between the stimulus and the response in the location test. That is, in the indication test the response levers could be pressed immediately after the stimulus and usually were, well within 1 s. In the location test, however, the goal boxes were 1.7 m from the start point and the monkeys required about 7 s to respond. This difference in the time between stimulus and response led to the possibility that the inability of the two monkeys to localize the single click in the latter test might be due to some sort of memory deficit, i.e., they may have "forgotten" where the sound came from before they could complete their trek to the speaker. To determine if it was only the delay between the stimulus and the response that resulted in the deficit, monkeys *A* and *C* were given a test in which a 6/s click train was presented as long as the animal was in contact with the center water spout, but ended the moment the animal broke contact and began its response. With this arrangement, the delay between the offset of the stimulus and the response was the same as before, but the monkey could gain a longer exposure to the stimulus, if it chose, by remaining in contact with the center spout. Though the number of clicks an animal received obviously varied from trial to trial depending on the time it remained in contact with the spout, it usually ranged from 3 to 6 clicks for monkey *A*, and 6 to 12 clicks for monkey *C*. But for this test the critical feature was that the same delay occurred between the stimulus and the response as in the previous single-click test.

In this test, monkeys *A* and *C* performed much more poorly than they had on the continuous click trains before, but they finally managed to score just above

chance and, therefore, they performed better than they did with only a single click. This result suggests that there were at least two factors contributing to the failure of the animals to perform the single-click task. First, since increasing the number of clicks increased the probability that the animals would correctly locate the stimulus, the poor performance of the monkeys on the single-click test was due, in part, to the brevity of the stimulus. Second, since neither animal performed as well on this test as on the continuous click-train test, it follows that the inability of monkeys *A* and *C* to perform the single-click discrimination was also due in part to the delay between the stimulus and the response.

**ATTENTIVENESS TO AUDITORY STIMULUS.** Because there was an obvious decrement in performance for the animals deprived of AI (*A* and *C*) in both the indication and the location of click trains as well as a total inability for the location of single clicks, the possibility was entertained that the results might be explained by some sort of deficit in attentiveness.

During the location tests we had noticed that the two monkeys without AI (*A* and *C*) would occasionally fail to make sufficient contact at the center spout to start the trial and yet, even though no stimulus was presented, they would respond to one of the goal spouts nevertheless. Certainly no normal monkey, once trained, ever began its response without first receiving a stimulus. In an attempt to pursue the meaning of this curious behavior, we intentionally gave the animals a special test that included trials in which the auditory stimulus was not presented at all. This test was accomplished by presenting the usual 6/s train of clicks for the first 30 trials of a session, and then in the next 30 trials presenting no auditory stimulus whatever.

On the initial 30 trials in which the click train was presented, monkeys *A* and *G* performed above chance, while monkey *C* performed at chance. But more important for the present question, the average latencies were 7.2 s for monkey *A*, 8.9 s for monkey *C*, and 4 s for monkey *G* (Table 2). On the subsequent 30 trials in

TABLE 2. *Effect on latency of response of failing to present an auditory stimulus*

Monkey	6/s Click Train, s	No Auditory Stimulus, s
A	7.2	8.2
C	8.9	6.7
G	4.0	37*

\* Monkey G refused to continue responding after four trials.

which no auditory stimulus was presented, of course, all three of the animals performed at chance. However, the latency of monkey G (with a part of AI remaining) increased more than ninefold, while the latencies of monkeys A and C (without AI) were hardly changed at all. Indeed, monkey G, like a normal monkey, completely ceased to perform after only four trials. In marked contrast, monkeys A and C continued to respond for the full 30 trials without giving any sign (other than their chance performance) that the sound no longer occurred.

At first this result would seem to be unusually significant in that it suggests a degree of inattentiveness which might well have precluded successful performance on any auditory test. However, it should be noted that the animals were not given this test until after they had received more than a thousand trials in the location test. Therefore, it is not possible to tell whether their inattentiveness was a cause or an effect of poor performance. That is, the lack of attentiveness on the part of monkeys deprived of AI may have resulted from the long period of training and testing in which (to them) the auditory stimulus had proved to have very little value in signaling the location of the water reward. We will return to this point in the general discussion.

**INFLUENCE OF A VISUAL STIMULUS ON PERFORMANCE.** While the previous test indicated that the influence of the auditory stimulus on the behavior of monkeys A and C was comparatively weak, other observations suggested that nonauditory stimuli might have gained a stronger than usual influence. To investigate the potency of a competing stimulus on perfor-

mance, a test was given in which a visual stimulus was introduced along with the auditory stimulus (9).

As a visual stimulus, lights mounted above each of the goal water spouts were flashed at a rate of 3/s. The auditory stimulus was the usual 6/s click train. The two stimuli were presented at the beginning of a trial and continued until the animal made a response.

The test consisted of a single session divided into two parts. The first part consisted of 50 trials in which the light and sound cues were presented together, both signaling the correct response. The second part consisted of 48 trials in which the click train was presented on every trial and the light was presented on every fourth trial (i.e., a total of 12 sound-plus-light trials and 36 sound-alone trials). On these 12 test trials the competing stimuli were presented from opposite goal boxes. That is, if the clicks came from the left speaker, then the right light was flashed. On these trials the animal was rewarded for responding to either goal spout.

Table 3 shows that both animals performed well during the first part of the session when both light and sound indicated the correct response. Furthermore, on the 36 sound-alone trials in the second part of the session, the two monkeys scored 82 and 89% correct. On the 12 test trials when the light and sound stimuli were opposed, however, both animals went to the light more often than to the sound (C: 7 light, 5 sound; A: 11 light, 1 sound). Therefore, the results of this test illustrate the ease with which a nonauditory stimulus could influence the performance of the operated monkeys. Even though they had received hundreds of daily sessions in which sounds were the only relevant cues, it was possible to

TABLE 3. *Influence of a visual stimulus on performance of a sound-localization task*

Monkey	Stimulus Condition		
	Light and sound, %	Sound only, %	Light vs. sound
A	90	82	1/12 to sound
C	92	89	5/12 to sound

influence their performance quickly and significantly with a visual cue which had not previously been paired with reward. Clearly, this distraction by nonauditory cues or, alternatively, the willingness to give up responding to auditory cues, may also have been a factor in determining the performance of the monkeys on the sound-localization tests.

#### DISCUSSION

The results show that monkeys deprived of all (or virtually all) of AI bilaterally are unable to locate the source of a brief sound. Nevertheless, these same monkeys are able to indicate the direction of the sound source and can do so with normal acuity. Therefore, it appears that the basis of the cortical deficit in sound localization observed in previous studies (e.g., ref 15, 20) cannot be due to a simple impairment in the strictly sensory aspects of the ability to localize a sound source. Furthermore, since the same monkeys that fail the click-location test were capable of high levels of performance when a visual cue was introduced, it follows that there was no general nor pervasive intellectual, motivational, emotional, or motor difficulty which may have prevented a high level of performance on the sound-location task. In order to account for the inability to locate a single click, therefore, it is necessary to focus on the differences in the nonsensory requirements of the indication and location tests.

Though there are several obvious differences between the two tests, it is important to note that each turns on differing motor requirements rather than on differing sensory or motivational requirements. That is, the stimuli and rewards presented in each of the two tests were virtually identical. On the motor side, however, the monkeys were required to walk to the sound source in the location task while they had only to press a lever on the same side as the sound source in the indication task. We think it is the correspondence between the success and failure of the monkeys with this difference in the clearly motor requirements of the two tasks that leads to the most plausible explanation for the deficit observed here and also for the

deficits in sound localization resulting from ablation of auditory cortex observed in the past (cf. ref 16, 19, 20).

#### *Auditory-motor segregation*

There are at least three potential explanations that seem to fit all of the evidence from this and the many previous studies of the effect of auditory cortex ablations on sound localization. First, auditory cortex ablation may result in a sound-localization deficit because of a surgical separation of the mechanism for detecting sound direction (in the brain stem) from a motor mechanism (under cortical control), which is necessary for the performance of the location task but not necessary for the indication task. This cortically dependent motor mechanism might be necessary for the location response because of either the more extensive muscle groups involved in the motor program, the longer time span, or both.

At present, we know of no experimental facts or line of argument that contraindicate this possible explanation. It is also in agreement with the conclusions of Thompson and Welker (27) and of Beitel and Kaas (1) who showed that cats without auditory cortex retain the ability to indicate the direction of a sound source by an unconditioned orienting reflex. At the same time, it is also compatible with the results of Neff and his colleagues (16), of Riss (20), and of Strominger (25) who have shown that cats deprived of auditory cortex are unable to locate the source of a sound.

This explanation is similar to one proposed by Ravizza and Masterton (19) and Ravizza and Diamond (18), in the first case, to explain the retention in decorticate opossums of the ability to indicate the direction of a sound source; and in the second case, to explain the loss in bushbabies and hedgehogs of the ability to locate a sound source. It remains attractive mostly because of its simplicity and directness in suggesting further research.

#### *Auditory amnesia*

A second possible explanation of the deficit found in the location test hinges



only on the extra length of time it takes an animal to respond in that task. The longer interval of time required by the location response leads to the possibility that the monkeys may have suffered some sort of a specifically auditory memory deficit—perhaps the perceptual image of the sound source decays before the response can be completed, as suggested as a possibility by Ravizza and Diamond (18). Although we prefer to include this kind of explanation within the class of auditory-motor deficits just described, it is not impossible that auditory cortex serves sound localization as a short-term memory bank alone. In such a case, a mechanism quite different from the one previously described is suggested.

The possibility of a specifically auditory amnesia following temporal lobe ablation in rhesus monkeys has been suggested before as an explanation of deficits having nothing whatever to do with sound localization (3, 4). In those studies, it was shown that either unilateral or bilateral ablation of auditory association cortex (i.e., non-AI) results in an impairment in performance of a task in which the animals had to respond to a pair of sounds on the basis of the order or sequence in which the sounds were presented. However, since it is known that cats, and now monkeys (case *G*), with large unilateral auditory cortex ablations retain the ability to locate sound sources (16, 25), the short-term memory deficit suggested by Dewson and his colleagues (3, 4) either may be of a somewhat different nature from the one observed here, or it may be more easily detectable by their test than it is by a sound-location test. One way to decide whether an auditory amnesia alone can explain a monkey's inability in the location test would be to introduce a mandatory delay between the stimulus and response in the indication test. If it were a fast-decaying image alone that was the basis of the sound-location deficit, then one would expect a failure on a delayed-response indication test, too.

#### *Auditory inattentiveness*

A third possible explanation of the deficit found in the location task is that

the animals suffered an impairment in their ability to attend to auditory stimuli. Indeed, this notion has been suggested before (e.g., ref 9, 16) and it is also an obvious explanation for two of the secondary results obtained in the location tests. First, monkeys *A* and *C*, with bilateral AI lesions, continued to respond even though the auditory stimulus was turned off. In contrast, a normal monkey and the monkey with a relatively large amount of AI remaining (monkey *G*) soon refused to respond entirely. This result indicates that monkeys *A* and *C* certainly were not using the sound in exactly the same way as the others. Furthermore, the monkey entirely without AI (monkey *A*) proved to be easily distractable by a visual stimulus even in the presence of a familiar auditory stimulus. Thus, it is not impossible that one effect of ablation is to impair auditory attentiveness to the point where a monkey becomes so easily distracted by nonauditory stimuli that it cannot remain focused on an auditory task.

Although we are well aware that a deficit in attention has also been cited as an explanation for other neurological signs of cortical damage and cannot be completely ruled out here, we are inclined to believe that a general inattentiveness to auditory stimuli is not the best explanation of the deficit in the click-location test. Our reasoning relies on the many other auditory tasks at which the operated monkeys were successful and, most important, on their successful performance on the indication tests included here. If one wishes to explain the location deficit as due to inattention, it is necessary to argue that the attention demanded by the location task is somehow different from the attention demanded by the indication task. It is difficult to see how the notion of attention can remain useful if it must be divided into a large number of specific attentive processes, one for each set of behavioral tasks for which a dissociation of deficits might be found.

In lieu of such a sweeping explanation, we think it is more likely that the inattentiveness to sound and the distraction by light are probably the effect of the deficit in the location test rather than the cause

of it. As mentioned previously the inattention to the sound could well have resulted from the thousands of training and testing trials in which, to the monkeys, the sound had proved to have little value in signaling the location of the water. Their prompt use of the light, when it was presented, then may not have been a distraction or even an alternative signal, but instead the only signal which reliably indicated the locus of the water reward.

However, it is necessary to note that the monkeys were subjected to more potential distractions throughout training and testing in the location test than in the indication test. The comparatively long delay between the click and the response in the location test could have served to increase the possibility of extraneous stimuli distracting an animal before it had made its response. Thus, while we are reluctant to accept the interpretation that the deficit is the result of inattentiveness, we are unable to rule it out as a possibility.

Other than our reluctance to accept an attention deficit as an explanation, it is difficult to choose between the other interpretations at this time. Nevertheless, in view of an operated monkey's ability to indicate the direction of a sound source despite its inability to locate it, the idea that the role of auditory cortex in sound localization is merely sensory or perceptual seems no longer possible to defend.

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## SUMMARY

Monkeys with lesions of auditory cortex were tested for their ability to localize the source of brief sounds. Although those deprived of primary auditory cortex bilaterally were able to indicate the direction of a sound with near-normal acuity, they were unable to locate its source. This dissociation of abilities suggests that the role of auditory cortex in sound localization is not so much sensory or perceptual as it is auditomotor or associative.

Thus, sound localization joins loudness, pitch, and most other traditional attributes of sound as dimensions whose discrimination does not depend on auditory cortex. The question would now seem to turn to whether or not auditory cortex is necessary for any sensory discrimination whatever.

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H. Heffner is a Public Health Service Predoctoral Research Fellow.

Present address of H. Heffner: Bureau of Child Research, Parsons State Hospital & Training Center, Parsons, Kansas 67357.

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