Effect of Bilateral Auditory Cortex Lesions on Sound Localization in Japanese Macaques

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SUMMARY AND CONCLUSIONS

1. The ability of four Japanese macaques (*Macaca fuscata*) to localize sound was determined after bilateral ablation of auditory cortex. The animals were given two tests: a "midline" test in which they had to discriminate noise bursts presented from a loudspeaker located to the left from identical noise bursts presented from a loudspeaker located to the right of midline, and a "hemifield" test in which both loudspeakers were located in their right hemifield.

2. Both of the tests were administered by the use of two different behavioral tasks: a conditioned-avoidance task in which the animals were trained to make or break contact with a water spout to indicate the location of a sound source, and a two-choice task that required the animals to walk to the source of the sound.

3. The results of both the conditioned-avoidance and the two-choice tasks demonstrated that the animals were able to perform the midline discrimination although their localization acuity was reduced. However, the animals had great difficulty in learning to walk to the source of a sound in spite of the fact that they had received previous sound-localization training in the conditioned-avoidance task. This difficulty suggested that the monkeys no longer associated the sound with a location in space.

4. The results of both the conditioned-avoidance and the two-choice tasks demonstrated that the animals were unable to discriminate the locus of a sound source when both loudspeakers were located in the same hemifield.

5. Bilateral ablation of auditory cortex results in both sensory and perceptual deficits. The presence of sensory deficits is indicated by the decreased acuity in the left-right discrimination and the inability to discriminate between two loudspeakers located in the same hemifield. The deficit in the perception of the locus of sound is indicated by the difficulty in learning to approach the source of a sound, an ability which normal monkeys exhibit without training.

6. There appear to be species' differences in the effect of auditory cortex lesions on sound localization. Although cortical lesions result in a sound-localization deficit in several species of primates and carnivores, they have little or no effect on rats.

INTRODUCTION

The physical analysis of the two chief binaural cues involved in sound localization (Δt and Δfi) initially takes place in the lower brain stem. Accordingly, auditory neurons sensitive to the location of sound can be found in the superior olivary complex, lateral lemniscus, and the superior and inferior colliculi (e.g., Irvine 1986). Nevertheless, ablation of auditory cortex results in a dramatic and permanent disruption in the ability to localize sound (e.g., Heffner 1978; Heffner and Masterton 1975; Jenkins and Merzenich 1984; Kavanagh and Kelly 1987; Neff et al.

1956). Because the physical (i.e., sensory) analysis of locus cues takes place at subcortical levels and is not disrupted by cortical ablation (Cranford 1979; Masterton and Diamond 1964), the question arises as to the basis of the cortical deficit.

The idea that the cortical deficit might not be sensory in nature first arose from the observation that auditory cortex lesions in cats reduce, but do not abolish, reflexive head movements toward an unexpected sound (Beitel and Kaas 1971; Thompson and Masterton 1978; Thompson and Welker 1963). It was supported by the observation that decorticate opossums can indicate the direction of a sound source by making a nonspatial response (Ravizza and Masterton 1972). These results taken together were interpreted as indicating that auditory cortex ablation does not disrupt all of the responses to a localizable sound source. This led to the suggestion by Ravizza and Masterton (1972) that auditory cortex lesions result in an "auditory-motor" impairment that disrupts some, but not all, responses to a localizable sound source.

The auditory-motor hypothesis was supported by subsequent studies that showed that bilateral auditory cortex ablation impairs the ability of monkeys to perform some, but not all, localization tasks (Heffner and Masterton 1975, 1978). Specifically, rhesus monkeys were able to indicate the direction of a sound with near-normal acuity either by pressing levers or by making a nonspatial response that consisted of ceasing to drink whenever a sound was presented on their left side while continuing to drink if the sound came from their right side. However, the animals were unable to locate the source of a brief sound by walking to it, the same task that Neff and his colleagues originally used to demonstrate the cortical deficit.

Although these results provided strong support for the idea that the cortical-sound–localization deficit was the result of a disconnection of the sound-localization mechanism from the motor mechanism necessary for some, but not all, behavioral responses, the issue was not entirely settled. One question that remained was how to predict which motor responses would be affected by cortical ablation. That is, there was no basis for predicting the effect of the cortical lesions on sound-localization performance in different tasks.

Recently, we have been investigating the effect of cortical lesions on the detection and discrimination of sound in Japanese macaques (Heffner and Heffner 1984, 1986a,b, 1989a–c, 1990b). During the course of these experiments we took the opportunity to reexamine the effect of bilateral auditory cortex lesions on the localization of sound.

The results of this investigation have led us to revise our views concerning the auditory-motor hypothesis and to restrict its application to explaining the fact that auditory cortex lesions may abolish the ability to make a learned response to the locus of a sound while leaving the unconditioned head-orienting reflex relatively intact. With regard to learned responses, it now appears that the reason animals with cortical lesions are able to indicate the direction of a sound source, but have great difficulty learning to walk to it, is that they retain the sensory ability to discriminate between sounds arising from different locations while losing the perception that the sounds are associated with locations in space.

METHODS

The general design of the study was to compare the sound localization performance of four monkeys that had received bilateral auditory cortex lesions with that of normal monkeys. A key feature of this study is that the animals were tested for their ability to perform two types of sound-localization discriminations and that each discrimination was tested twice with the use of different behavioral tasks. The two discriminations consisted of a "midline" test in which the animals were required to discriminate between a sound source located to the left of their midline from a sound source located to the right, and a "hemifield" test in which they were required to discriminate between two sound sources located within the same auditory hemifield (in this case, the right hemifield). Both tests were administered using a "conditioned-avoidance" task, which required them to make a nonspatial response, and a "two-choice" task, which required the animals to walk to the source of the sound. Thus the animals were given four basic tests of their sound-localization ability in the following order: midline conditioned-avoidance, midline two-choice, hemifield two-choice, and hemifield conditioned-avoidance.

Subjects

Altogether seven, 7-yr-old (adolescent) male Japanese macaques (*Macaca fuscata*), which had been born and reared in a free-ranging colony (Arashiyama West Institute), were used in this study. The four operated animals, referred to as A, B, C, and D, had previously been used in studies of the effect of cortical ablation on hearing and on the perception of primate vocalizations in which they were referred to as *M-207*, *M-214*, *M-267*, and *M-337*, respectively (Heffner and Heffner 1989a, 1990b). The three other monkeys, referred to as E (*M-231*), F (*M-286*), and G (*M-291*) were normal controls. All animals were individually housed in primate cages with free access to food and were trained with water reward.

Each monkey was weighed daily to monitor its health and deprivational level. The ears of each animal were examined during and after testing to ensure that they were free of damage or disease. Auditory-evoked potentials were recorded from each operated animal at the end of the experiment to provide further evaluation of their peripheral hearing (Hood and Heffner 1989).

Surgical and histological procedures

SURGERY.   Auditory cortex was ablated first in one hemisphere and then in the other hemisphere 6–16 wk later. For each surgery the monkey was initially sedated with ketamine (5 mg/kg) and given 0.5 mg of atropine sulfate and 100 mg of Lincocin (Upjohn). This was followed by halothane administered via an endotracheal cannula as needed to maintain deep anesthesia. The animal's head was shaved and washed, the scalp was opened, and the temporal muscle on one side was dissected with a cautery. With the edges of the temporal muscle retracted, the portion of the cranium overlying the sylvian fissure was removed, the dura retracted, and the superior temporal gyrus removed by subpial aspiration. Aseptic procedures were followed throughout surgery.

After removal of cortical tissue, the lesion was packed with Gelfoam (Upjohn) to minimize subsequent distortion of the gyri, and Gelfilm (Upjohn) was placed over the opening and under the edges of the cranium to minimize adhesions of the overlying tissue with the pia. The temporal muscle was then apposed and sutured; a topical antibiotic powder (Neo-Predef, Upjohn) was applied, and the scalp incision was closed with silk suture. The animal was placed in a cage located in a dark, quiet room and given acepromazine as needed to minimize discomfort.

HISTOLOGY.   After completion of behavioral testing the monkeys were deeply anesthetized with pentobarbital sodium and perfused with isotonic saline followed by 10% Formalin. The brains were removed, photographed to aid cortical reconstruction, and prepared for frozen sectioning. The brains were sectioned in the coronal plane at 40 μm, and two sets of sections at 200-μm intervals were stained: one with thionin and one with Protargol (Sterling). These sections were then used to reconstruct the lesions and resulting thalamic degeneration.

Behavioral tests

It is of interest to note that once the animals had recovered from the surgery, they showed no obvious visual or motor deficits. Indeed, to most observers, the animals were indistinguishable from normal, and laboratory tests were required to reveal their auditory abnormalities.

Three different behavioral apparatus were used. The midline conditioned-avoidance test was conducted with the animal seated in a primate chair; the midline and hemifield two-choice tests were conducted with the animal moving freely in a room, and the hemifield conditioned-avoidance test was conducted with the animal in a specially constructed wire cage. The tests are described in the order in which they were given.

MIDLINE CONDITIONED-AVOIDANCE TEST.   *Behavioral equipment.* A standard primate chair was modified to accommodate a double water spout. This spout consisted of two standard sipper tubes mounted parallel and close enough (1 cm apart) so that a monkey could comfortably place its mouth on both spouts. The two spouts, which were electrically isolated from each other, were connected to a contact switch that detected when an animal placed its mouth on them. One of the spouts was attached via plastic tubing to an electrically operated water valve and constant-pressure water reservoir. Using the double water spout eliminated the need to tie an animal's foot to a metal plate to complete the circuit for the contact switch, thus permitting an animal greater freedom of movement. Mild electric shock was provided by a shock generator connected to the two spouts. A 60-W light was mounted above the chair and the entire apparatus was located in a double-wall sound chamber (2.7 × 2.5 × 2.0 m), the walls and ceiling of which were lined with egg-crate foam to reduce sound reflection. A microcomputer was used for behavioral programming.

Sound-production equipment. The same audio equipment was used in all of the tests. Broadband noise was produced by a Grason-Stadler noise generator (model 901A) and led to a programmable attenuator (Coulbourn S85-08). The signal was then split into left and right lines, and each line was connected to an equalizer (Symmetric Sound Systems EQ-3), mixer-amplifier (Coulbourn S82-24), and 3.5-cm dome loudspeaker (Long L15F). The loudspeakers were suspended at ear level from a perimeter bar

110 cm from the midpoint of a monkey's head when it was drinking from the spout. The noise was presented as either a 2-per-s train of 100-ms noise bursts or as a single, 100-ms noise burst, which were switched on at the mixer-amplifier with 0 ms rise-decay.

The noise was measured with a Brüel and Kjaer (B & K) sound-level meter (model 2203), ¼-in. (0.64-cm) microphone (B & K 4144), and an octave filter (B & K 1613) or band-pass filter (Krohn-Hite 3202). The spectra of the noise from the two speakers were matched by measuring their output at octave intervals from 31 Hz to 32 kHz and adjusting the equalizer accordingly. The overall intensity of the noise at the animals' ears was 58 dBA (60 dB SPL), which was at least 40 dB above their detection thresholds.

Training procedure. The monkeys had been previously trained to detect tones and discriminate monkey vocalizations with the use of this task (Heffner and Heffner 1989a, 1990b). Briefly, a thirsty monkey was rewarded for climbing into the primate chair and placing its mouth on the water spout by dispensing a steady trickle of water (3–4 ml/min) as long as the animal maintained contact with the spout. A 2-per-s train of 100-ms noise bursts was presented every 7 s for 3.6 s from either the left or right loudspeaker. The animal was trained to break contact with the spout whenever the noise bursts were emitted from the left speaker by following the noise bursts with a mild electric shock delivered through the spout. Breaking contact in this way allowed the animal to avoid the shock and served as an indication that the animal detected a shift in the locus of the sound source. To provide feedback for successful avoidance, the light mounted above the chair was turned on during shock delivery.

The level of shock was individually adjusted for each animal to the lowest level that would reliably produce an avoidance response. The mildness of the shock was empirically verified by observing that the animals never developed any fear of the water spout and returned to it without hesitation after receiving a shock.

Test procedure. Sound-localization thresholds were obtained first for a 2-per-s train of 100-ms noise bursts (8 bursts) and then for a single, 100-ms burst. The test procedure consisted of presenting stimuli from the left and right speakers in a quasi-random order with the probability of a left stimulus being 0.25. Stimuli from the left were followed by shock and are referred to as "warning" stimuli, whereas stimuli from the right were never followed by shock and are referred to as "safe" stimuli. A trial sequence consisted of presenting a stimulus every 7 s until either a warning stimulus was presented or until seven safe stimuli were presented. The end of a trial sequence was signaled by a 5-s pause in the presentation of stimuli. Thus stimuli were presented at 7-s intervals beginning 5 s after the previous trial sequence (e.g., 5, 12, 19, . . . 47 s).

The number of times in which a left (warning) stimulus occurred in a particular interval was adjusted so that, within a session, each of the seven intervals had the same probability (0.25) of containing a warning signal. This resulted in some sequences in which no warning signal occurred so that the probability of the seventh period containing a warning signal was also 0.25.

The response of an animal on each trial, i.e., whether it had made an avoidance response, was determined by noting whether the animal was in contact with the spout during the last 200 ms of the time period that contained the warning signal. Basing the response criterion on the last 200 ms allowed the animal sufficient time to break contact with the spout after presentation of the stimulus. An animal's responses to warning signals at a particular angle of speaker separation were averaged to obtain a "hit" rate. A measure of an animal's "false alarm" rate was obtained by recording the animal's response during the last 200 ms of the time periods that contained the safe signal. To reduce the effects of occasional pauses in drinking, a score for a particular time period

was automatically discarded if the animal was not in contact with the spout at any time during the 1 s immediately preceding that period.

Average hit and false alarm rates were determined separately for each angle of separation. The hit rate was then corrected for false alarms by the following formula: corrected hit rate = observed hit rate − (observed hit rate × false alarm rate) (Heffner and Heffner 1988). In trained animals this measure varies from 0 (failure to detect the tone) to 1 (perfect detection).

Thresholds were determined by reducing the angle of separation until performance fell to chance. Threshold was defined as the smallest angle that yielded a corrected hit rate of 0.50. Chance level was calculated by comparing the occurrence of responses during the safe and warning trials with the use of the binomial distribution.

MIDLINE TWO-CHOICE TEST. *Behavioral equipment.* Testing was conducted in a sound-proof chamber (2.7 × 2.5 × 2.0 m), the walls and ceiling of which were lined with egg-crate foam. Two loudspeakers and water spouts were mounted in a wooden box (2.5 × 0.3 × 0.9 m), which was placed along the wall of the chamber. The water spouts were mounted 60 cm above the floor and 2.1 m apart with the loudspeakers mounted 15 cm above the spouts. The water spouts were connected via plastic tubing to separate electrically operated water valves and constant-pressure water reservoirs. A contact switch was connected between each water spout and a metal plate (50 × 50 cm) located on the floor in front of the spout to detect when an animal licked a spout. A third water spout was mounted on a 70-cm post centered 1.7 m in front of the loudspeakers. The function of this center spout was to provide an "observing" response for starting a trial and to position the monkey equidistant from, and facing toward, the loudspeakers. The animal was monitored via closed-circuit television.

To begin a trial the monkey had to stand on a metal floor plate and lick the center water spout. 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 water 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 simply an automated version of the apparatus used by Neff in his original tests with cats (cf. Heffner and Masterton 1975; Neff et al. 1956; Thompson et al. 1974).

Training procedure. At the beginning of each session a 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 contacted, the monkey received water and immediately a 2-per-s train of 100-ms noise bursts was emitted from one of the speakers. If the monkey next contacted the water spout below the active loudspeaker, it was rewarded with water, and the sound was turned off. If the animal contacted the water spout beneath the silent speaker, it received no water, and the sound was turned off. After either response the monkey was required to contact the center water spout to initiate another trial.

Once the animals had learned to make the observing response, the water reward at the center spout was discontinued, and water was provided only at the spout below the active speaker. When each animal had reached an 85% correct criterion, it was tested on its ability to localize trains of noise bursts of various length and, finally, a single, 100-ms noise burst.

Behavioral tests. Throughout training and testing, the locus of the sound source was determined by a quasi-random sequence (Gellermann 1933). During all of training and most of testing, a

correction procedure was used such that after an error, the correct side did not shift. This strategy was used to prevent an animal from responding predominantly to one side by forcing it to respond to the other side to get a reward. Because an animal had only to alternate its response after an error to be correct, these correction trials were not used in the computation of an animal's performance. Chance-level performance was determined with the use of the binomial distribution.

The ability of the animals to localize single noise bursts or trains of noise bursts was determined at a fixed angle of 60°. In the first test an animal was required to localize a "continuous" stimulus that consisted of a 2-per-s train of 100-ms noise bursts, which was turned on at the beginning of a trial and remained on until a response had been made. The second test used a "limited" stimulus in which a 2-per-s train was turned on at the beginning of a trial and remained on only as long as the animal kept its mouth on the center spout. The final test used a "single" stimulus in which a single, 100-ms noise burst was presented on each trial.

HEMIFIELD TWO-CHOICE TEST. This test was identical to the midline two-choice test with the exception that the center spout and floor plate were turned 90° to the left. This placed the speakers in the animal's right hemifield at 55 and 125° from its midline when the animal licked the spout.

HEMIFIELD CONDITIONED-AVOIDANCE TEST. *Behavioral equipment.* The animals were tested in a cage specifically designed to be sound transparent and minimize reflections in the sound field. The cage was circular (90 cm high, 90 cm in diameter) and constructed of 1 × 2-in. (2.54 × 5.08-cm), welded-wire (2-mm) fencing. A double water spout was mounted in the front of the cage at a height that placed an animal's ears level with the loudspeakers. The two spouts were connected to an electronic contact switch that detected when an animal placed its mouth on them. One of the spouts was connected via plastic tubing to an electrically operated water valve and constant-pressure water reservoir. Mild electric shock was provided by a shock generator connected to the two spouts. The animal entered through a door in the rear of the cage. A 60-W light was mounted above the cage, and the cage was placed on 30-cm-high legs in a double-walled sound chamber (2.7 × 2.5 × 2.0 m), the walls and ceiling of which were lined with egg-crate foam to reduce sound reflection.

Training procedure. An animal was initially trained on a midline discrimination with the use of a 2-per-s train of 100-ms noise bursts. This was done to accustom the animal to the cage as well as to recheck the animal's midline performance. Thus the training procedure was identical to that described in the midline conditioned-avoidance test.

Test procedure. Before commencing with the hemifield tests, thresholds for localization around midline were obtained by the use of the 2-per-s train of noise bursts. As before, the animal was trained to break contact with the spout when the sound came from the left of midline and to maintain contact if the sound came from the right of midline. The resulting thresholds were the same as those obtained with the animals in the primate chair, indicating that there were no significant differences between the two arrangements.

The ability of an animal to discriminate sound sources within its right hemifield were determined by placing one loudspeaker at a fixed angle in the right hemifield. The other speaker was then placed at various locations to the left of this speaker, and the discrimination ability of the animal was determined. As before, only sound from the left-most speaker was followed by shock. The right loudspeaker was placed at three different positions in the right hemifield: 45, 90, and 135° to the right of midline. The animal's performance was calculated in the same way as in the midline conditioned-avoidance test.

RESULTS

Anatomic results

The locus and extent of auditory cortex have been studied in the rhesus macaque by evoked response (Woolsey and Walzl 1982), microelectrode recordings (Merzenich and Brugge 1973), cytoarchitectural analysis (Galaburda and Pandya 1983; Pandya and Sanides 1973), and by tracing thalamocortical connections (Mesulam and Pandya 1973). Because Japanese and rhesus macaques are closely related and their brains are similar in appearance, information from these studies is useful in locating auditory cortex in the Japanese macaque.

Although the exact boundaries of auditory cortex can be difficult to define, both cytoarchitectural and electrophysiological studies have indicated that there is a central core area (primary auditory cortex) and a surrounding belt region of secondary auditory fields. Primary auditory cortex lies in the depths of the sylvian fissure on the middle one-third of the superior temporal plane and is surrounded by four secondary auditory fields. In addition electrophysiological, anatomic, and behavioral evidence indicates that all of the superior temporal gyrus including the rostral portion may have auditory functions (Heffner and Heffner 1989b; Merzenich and Brugge 1973; Mesulam and Pandya 1973; Pandya and Sanides 1973).

Although precise placement of auditory lesions requires prior electrophysiological mapping, the pattern of thalamic degeneration that follows cortical ablation gives a useful picture of the extent of a lesion (for details, see Heffner and Heffner 1986b). Ablation of primary auditory cortex results in severe degeneration of the anterior two-thirds of the principal division of the medial geniculate (GMp) with no noticeable degeneration in the magnocellular division (GMmc) or in the suprageniculate nucleus (SG). Ablation of the primary and surrounding secondary auditory fields results in severe degeneration throughout GMp with the exception of the caudal tip, and partial degeneration of GMmc and SG. Finally, ablation of the entire superior temporal gyrus results in total degeneration of all of GMp including the caudal tip, with severe degeneration in GMmc and SG.

EXTENT OF THE LESIONS. Cortical reconstructions are illustrated for all four monkeys, and thalamic degeneration is illustrated for the largest and smallest lesions (Figs. 1–3). The lesions were confined to the superior temporal gyrus and differed primarily in the involvement of the rostral tip of the gyrus. All of the animals appeared to have complete lesions of the primary and surrounding auditory fields with the possible exception of *monkey C* in which part of the rostral auditory field on the left side may have been spared (Fig. 2).

Behavioral results

Sound localization testing was begun 13–15 mo after surgery. By this time the animals had been given detailed audiograms and had been tested for their ability to discriminate monkey vocalizations (Heffner and Heffner 1989a, 1990b). Thus the animals were highly experienced observers having received >300 training and test sessions
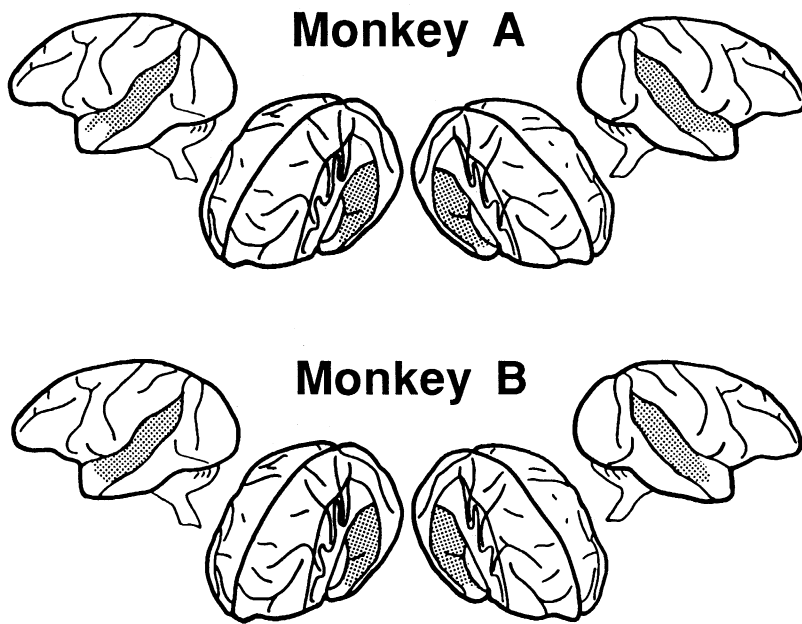
Monkey A

Monkey B

FIG. 1. Cortical reconstructions for *monkeys A* and *B* showing surface views and views of the superior temporal plane with the parietal operculum removed. Locations of lesions are indicated by stippling.

each. The following is a description of the performance of the animals on the four sound-localization tests.

MIDLINE CONDITIONED-AVOIDANCE TEST. *Training.* Each of the monkeys was familiar with the conditioned-avoidance task having received prior training on the detection of tones and the discrimination of monkey coos. However, none of them had received any previous pre- or post-operative training on sound localization.

The monkeys were initially trained to discriminate between two loudspeakers separated by 90° with the use of a 2-per-s train of noise bursts. Figure 4 illustrates the best performance on a block of 10 trials for the four operated and two normal animals (*monkeys E* and *F*) during the first five training sessions. As can be seen, the operated animals had no difficulty in learning the discrimination. Although the operated monkeys did not always perform as well as the normal animals, all of the animals were able to perform the discrimination successfully in the first session. As will be seen, the ease with which the operated animals learned this task is in contrast to their performance on the two-choice task.

Test results. The ability of the monkeys to discriminate sounds coming from their left hemifield from those coming from their right is shown in Fig. 5. The operated monkeys were able to perform the discrimination by the use of either a 2-per-s train of noise bursts (Fig. 5A) or a single, 100-ms noise burst (Fig. 5B). Although some of their scores were occasionally as high as those of the two normal monkeys (E and F), the operated animals' thresholds were elevated and their asymptotic performances were generally lower than normal. Of the four animals, the monkey with the largest lesion (*monkey D*) had the poorest performance both in terms of asymptotic performance and threshold. Thus, although the operated animals could perform the discriminations, the cortical lesions resulted in elevated thresholds and reduced asymptotic performance in the ability to discriminate between sounds emanating from the two hemifields.

The present results are in agreement with those of two previous studies on the effect of auditory cortex lesions in monkeys (Heffner and Masterton 1975, 1978). These studies showed that Rhesus monkeys were able to make a left-right discrimination of click trains and single clicks when tested with a conditioned suppression task, similar to the avoidance task used here, or a two-choice task in which they had to press one of two levers to indicate the hemifield from which a sound came. As in the present study, the rhesus monkeys were able to perform these discriminations at reduced but near-normal levels.

MIDLINE TWO-CHOICE TEST. This test yielded two important points. The first concerns the animals' ability to learn the task, the second concerns their eventual ability to perform the discriminations.

Training. The initial performance of the operated monkeys was obviously abnormal. Whereas the normal monkey (*monkey G*) quickly learned to walk to the source of a 2-per-s train of noise bursts, the operated monkeys had great difficulty in learning this task.

At the beginning of training the animals were brought into the test chamber and permitted to drink from the water spouts to familiarize them with the test arrangement. The operated monkeys were given two to three sessions to familiarize themselves, whereas the normal monkey was given only one. The animals were then trained on the auditory discrimination by the use of a continuous train of noise bursts that came on when they contacted the center spout and went off when they contacted one of the two goal spouts.

The learning curves of the animals illustrate the degree of difficulty that the operated monkeys showed in learning the task. As shown in Fig. 6, the operated monkeys took 11–12 sessions to learn the discrimination. In contrast, the normal monkey learned the task in 15 min.

The difficulty experienced by the operated monkeys was surprising. These animals had easily learned to perform a sound-localization discrimination in the conditioned-
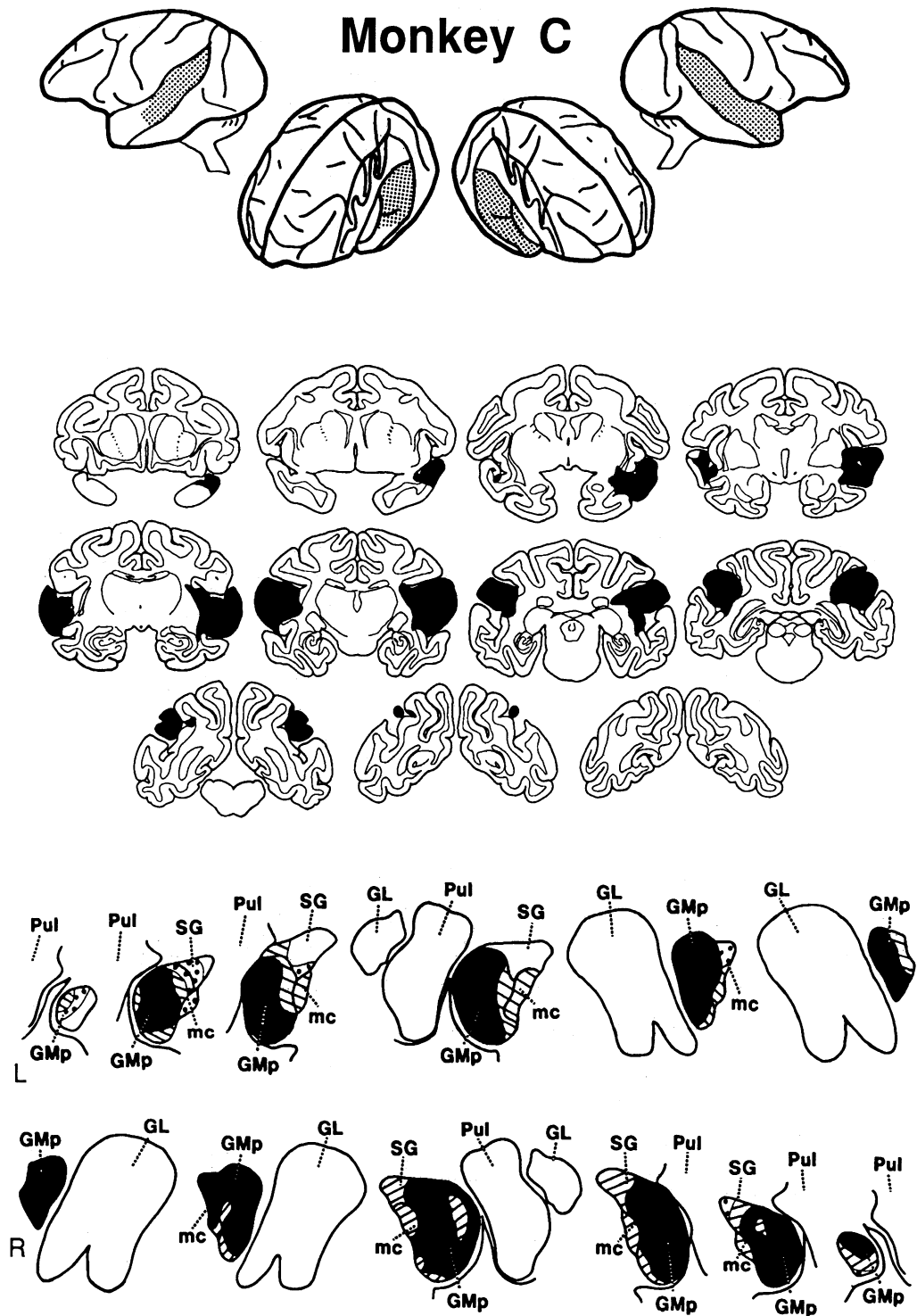
FIG. 2. Cortical reconstruction and medial geniculate degeneration for *monkey C*. This animal had the smallest bilateral lesion because of sparing of the rostral tip of the left superior temporal gyrus. *Top*: reconstruction of cortical lesion (▨) showing surface views and views of the superior temporal plane with the parietal operculum removed. *Middle*: coronal sections 3.6 mm apart with ablated areas shown in black. *Bottom*: retrograde degeneration in the vicinity of the medial geniculate. Left thalamic sections (*top*) are shown posterior to anterior, whereas the right sections (*bottom*) are anterior to posterior. Thalamic sections are 600 μm apart. GL, dorsal lateral geniculate; GMp, principal division of the medial geniculate; mc, magnocellular division of the medial geniculate; Pul, pulvinar; SG, suprageniculate nucleus. Blackened area indicates total degeneration, 95–100% cell loss; hatched area indicates severe degeneration, 70–95% cell loss; stippled area indicates moderate degeneration, 30–70% cell loss.
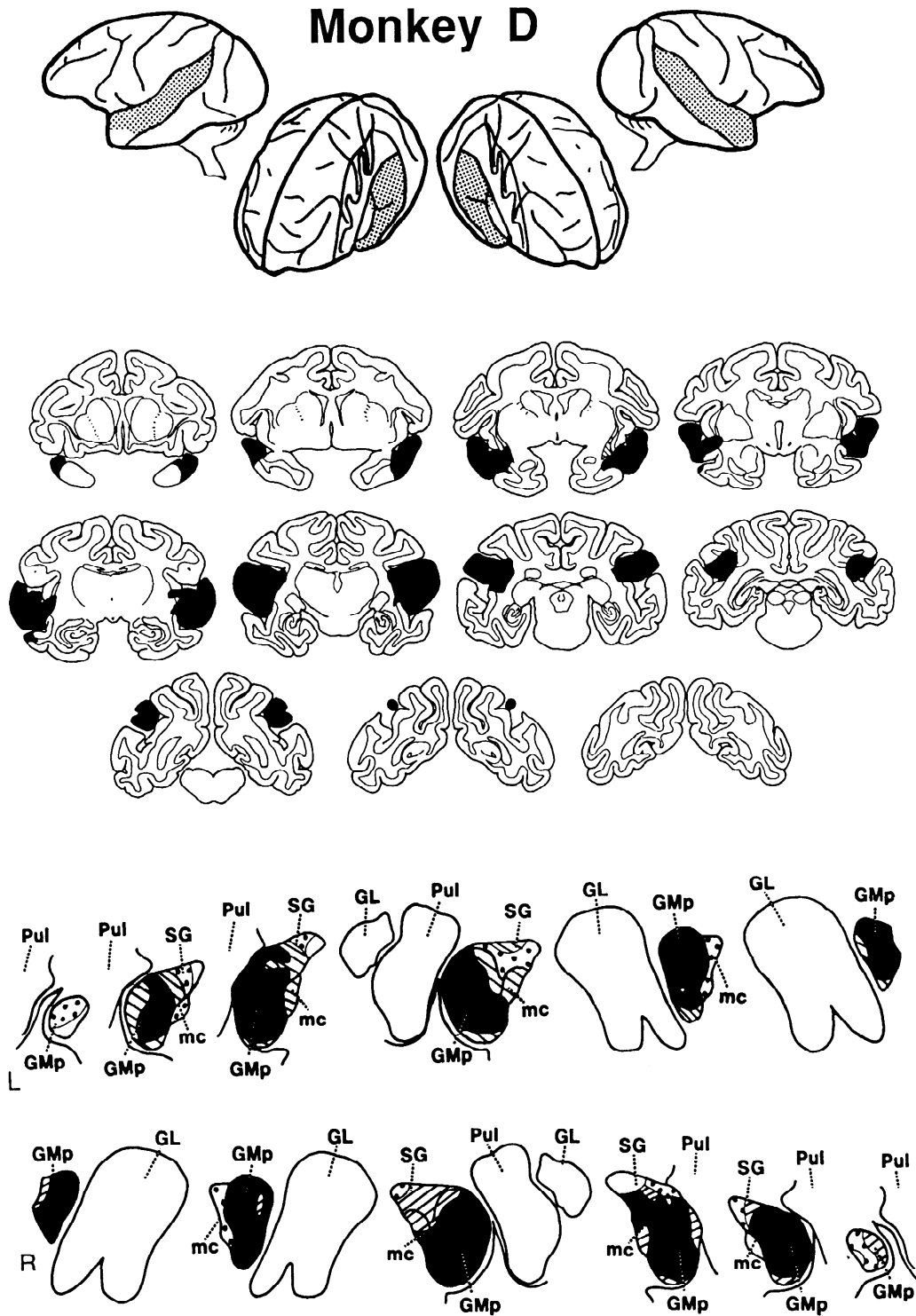
FIG. 3. Cortical reconstruction and medial geniculate degeneration for *monkey D*. This animal had the most complete bilateral lesion. (See Fig. 2 for key.)

avoidance task (cf. Figs. 4 and 6). Furthermore, they had received over 25 sessions of training and testing on sound localization in the conditioned-avoidance task immediately before starting training in the two-choice task. Thus, although they had previously demonstrated near-normal ability to perform a left-right discrimination in the avoidance task and were well practiced in discriminating locus, they had great difficulty in learning to associate the sounds

with the water spouts. It was as though they were being required to make an arbitrary association between a sound and a locus in space.

Eventually the animals did learn the task and were able to perform consistently at a level ∼90% correct. However, even after >1,000 training trials, they never performed as well as the normal animal.

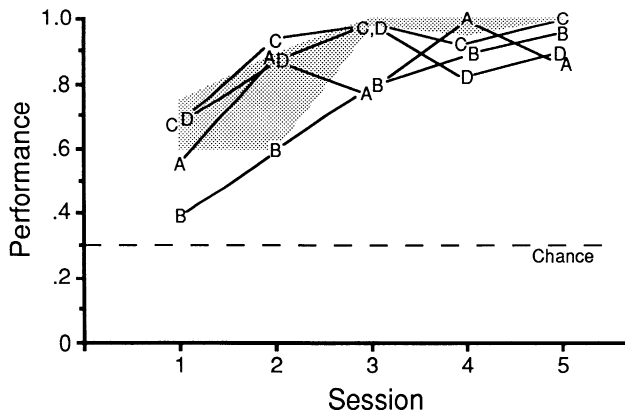*Test results.* After the animals had learned to perform

FIG. 4. Learning curves of 4 monkeys with bilateral auditory cortex lesions (A, B, C, and D) in the midline sound localization conditioned-avoidance task. Note that animals had no difficulty learning the discrimination. Range of performance of 2 normal monkeys is indicated by stippling. Stimulus was a continuous 2-per-s train of noise bursts emitted from loudspeakers located 45° to the left and right of midline (90° total separation).

the task, they were tested for their ability to discriminate single noise bursts as well as a 2-per-s train, which was turned on only while an animal had its mouth on the center spout (the limited stimulus). As shown in Fig. 7, three of the four monkeys were able to perform both of these discriminations above chance level.

This result suggests that this task is a difficult but not impossible task for operated animals to perform. Indeed, the one consistent finding is that all of the operated monkeys had great difficulty in learning to locate the source of even a continuous sound. As a result it is difficult to avoid the possibility that all of the monkeys would have eventually learned to locate the source of a brief sound had they been given more time.

The fact that the lesions did not abolish the ability of most of the monkeys to walk to the source of a brief sound has led us to reexamine the auditory-motor hypothesis that states that the cortex provides a necessary link between the physical analysis of sound and the motor mechanisms necessary for some responses. In addition, the great difficulty that all the operated monkeys had in learning to walk to the source of a continuous sound suggested to us that they had suffered a perceptual deficit in sound localization.

HEMIFIELD TWO-CHOICE TEST. On completion of midline testing, the center spout was turned so that the two loudspeakers would be centered in an animal's right hemifield when the animal licked the spout. The results of this test showed that none of the animals could discriminate between two loudspeakers located 60° apart when both speakers were in the same hemifield (Fig. 8). This inability could be demonstrated not only with a brief stimulus, i.e., the single, 100-ms noise burst, but with much longer-duration stimuli as well. Specifically, the monkeys were unable to localize the limited stimulus that consisted of a 2-per-s train of 100-ms noise bursts that was presented as long as an animal maintained contact with the center water spout —typically 2-3 s and occasionally as long as 10 s. In fact, it was not unusual for a monkey to break contact with the center spout, look at the goal boxes, and then remake con-

tact thus turning the sound on several times before leaving the center spout to make a response. Nevertheless, the act of licking the center spout positioned the monkey's head so that both loudspeakers were in its right hemifield whenever the noise bursts were presented, and the animals were unable to perform the discrimination regardless of the duration of the stimulus.

That the inability of the monkeys to perform above chance was due to both speakers being located in the same hemifield was demonstrated with the continuous stimulus. In this condition the sound came on when an animal contacted the center water spout and stayed on until it responded to one of the goal boxes. By turning to approach the speakers, the animals placed the speakers in the left and right hemifields and changed the task to a midline discrimination. As shown in Fig. 8, three of the four monkeys performed well above chance on this discrimination. However, one of the monkeys (monkey D) was unable to perform even this discrimination.
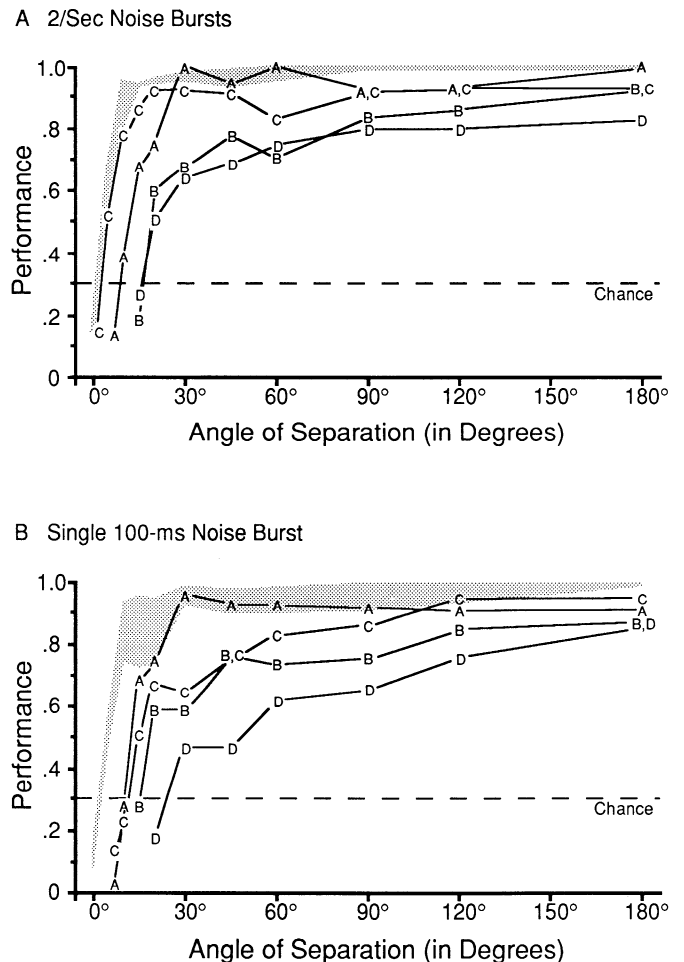
The inability of monkey D to discriminate the continu-

A 2/Sec Noise Bursts

B Single 100-ms Noise Burst

FIG. 5. Performance of 4 monkeys with bilateral auditory cortex lesions (A, B, C, and D) on a midline sound-localization discrimination with the use of the conditioned-avoidance task. Range of performance of 2 normal monkeys is indicated by stippling. Note that operated animals could discriminate either a 2-per-s train of noise bursts (top) or a single noise burst (bottom) when 2 loudspeakers were located to the left and right of midline, although asymptotic performances and thresholds were usually below normal levels.
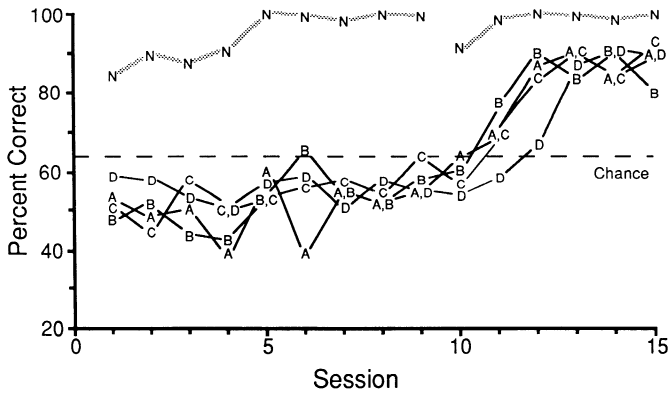
FIG. 6. Learning curves of 4 monkeys with bilateral auditory cortex lesions (*A, B, C,* and *D*) in the midline, sound-localization, two-choice task. Performance of a normal monkey is indicated by N. Note that operated monkeys had great difficulty in learning to walk to the source of a continuous sound, whereas the normal monkey demonstrated its ability in 15 min. Stimulus was a continuous 2-per-s train of noise bursts. (Normal monkey was required to localize a single noise burst after session 9.)
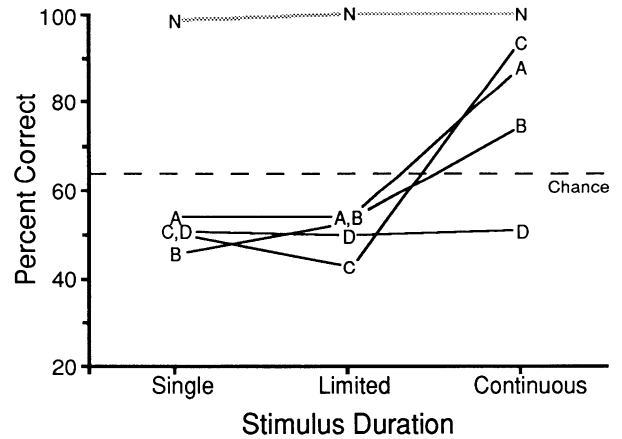

FIG. 8. Asymptotic performance of 4 monkeys with bilateral auditory cortex lesions (*A, B, C,* and *D*) on the hemifield, sound-localization discrimination with the use of the two-choice task. Performance of a normal animal indicated by N. Note that none of the operated animals could discriminate between brief sounds when both loudspeakers were located within the same hemifield.

ous stimulus is in contrast to the previous test in which it out performed all of the other animals. During midline-locus tests, it was noticed that *monkey D* would contact the center spout and then proceed without hesitation to one of the goal spouts when the sound was a limited or continuous pulse train. This suggested that the animal was responding to the initial noise burst and was not attempting to scan or track the sound. In contrast, the other monkeys often hesitated before beginning toward the goal spouts. The strategy of responding to the initial noise burst enabled *monkey D* to perform the midline task when the stimulus duration was reduced to a single, 100-ms noise burst. However, this same strategy worked against the animal in the hemifield test. Instead of hesitating at the beginning of a continuous

FIG. 7. Asymptotic performance of 4 monkeys with bilateral auditory cortex lesions (*A, B, C,* and *D*) on the midline, sound-localization discrimination with the use of the two-choice task. Performance of a normal animal indicated by N. Stimulus was either a single, 100-ms noise burst, a "limited" 2-per-s train of noise bursts that stayed on as long as the animal had its mouth on the observing spout, or a continuous 2-per-s train that stayed on until the animal made a response. Note that most of the operated monkeys could discriminate between brief sounds when 2 loud-speakers were located to the left and right of midline, although none of the animals could perform at normal levels.

stimulus, *monkey D* proceeded immediately to one of the goal spouts. Because the initial sound was always in the right hemifield it is not surprising that the animal tended to respond to the goal spout on the right regardless of the source of the sound. Thus this monkey's strategy of responding to the initial noise burst enabled it to perform well when single noise bursts were used in the midline test but prevented it from solving the hemifield test when a continuous stimulus was used.

HEMIFIELD CONDITIONED-AVOIDANCE TEST. Immediately after the two-choice tests, the monkeys were tested on their ability to discriminate sounds within their right hemifield with the use of the conditioned-avoidance task. Because the localization of sounds in a hemifield relies heavily on monaural spectral cues (e.g., Musicant and Butler 1984), the animals were tested in a wire cage specially designed to minimize surfaces that would obstruct or reflect the sound. Before commencing the hemifield test, the animals' midline thresholds were briefly rechecked to ensure the comparability of these results with those of the midline test in which the animals were placed in a monkey chair.

Training. The animals were initially retrained to make a left-right discrimination by the use of the 2-per-s train of noise bursts. This was done both to acclimate them to the new cage and to verify their midline thresholds. Determination of the animals' asymptotic performances and a brief recheck of their thresholds gave the same results as in the previous midline conditioned-avoidance test. Once the comparability of the data obtained with the monkey chair and cage had been established, hemifield testing was begun.

Test results. Hemifield tests were conducted by placing one loudspeaker at one of three locations in the right hemifield (either 45, 90, or 135° to the right of the animal's midline). The animal was then tested on its ability to discriminate between sounds coming from that loudspeaker and a second loudspeaker placed at various locations to the left of the fixed speaker. In each case the stimulus was a 2-per-s train of noise bursts.
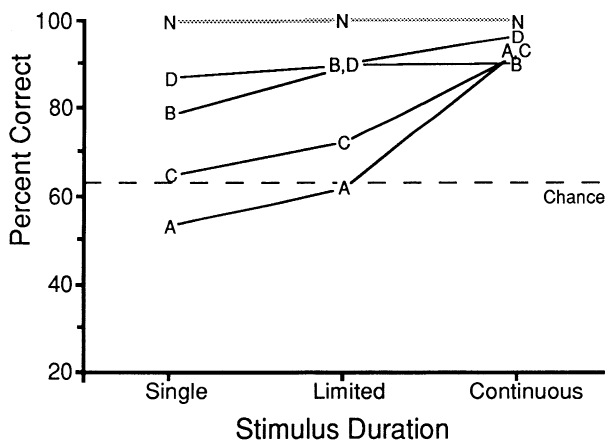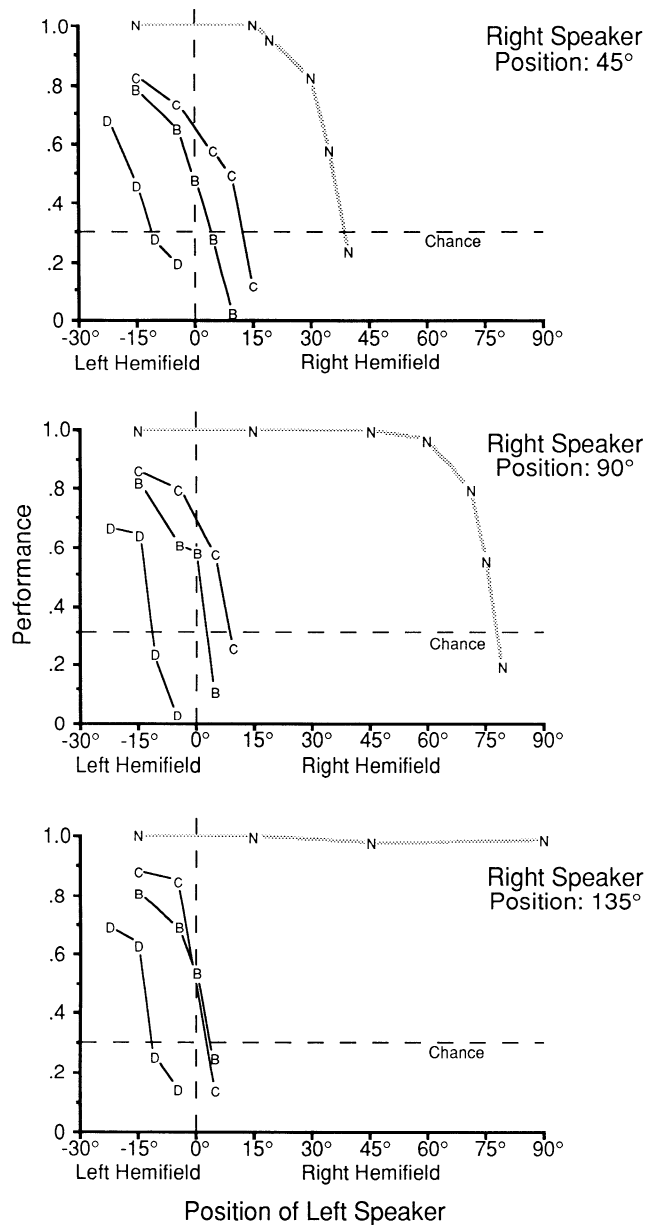
FIG. 9. Ability of 3 monkeys with bilateral auditory cortex lesions (A, B, and C) to discriminate a 3.6-s train of 2-per-s noise bursts in the conditioned-avoidance task. Performance of a normal animal indicated by N. One loudspeaker was placed at either 45° (top), 90° (middle), or 135° (bottom) to the right of an animal's midline, whereas the other speaker was placed at various locations to the left of the first speaker. Note that operated animals' performances fell to chance when both loudspeakers were located within the same hemifield.

The results of this test are shown for one normal monkey (monkey E) and three operated monkeys (Fig. 9; monkey A could not be coaxed into the cage and therefore was not tested). As these results show, the performance of the normal monkey declined when the left speaker was brought to within 30° of the right speaker.

In contrast, the performance of the operated monkeys was unrelated to the angle separating the two speakers. Instead, their performance fell to chance whenever the left speaker entered the right hemifield. Because the deficit was

apparent even with the 3.6-s duration click train, shorter-duration stimuli were not used. Had the animals developed the strategy of breaking contact and turning their heads each time a sound was presented and immediately returning to the spout if the sound was not from the left-most speaker, they probably could have performed the discrimination. However, the animals never developed this strategy; they either maintained constant contact or else broke contact each time any sound was presented. Thus, like the two-choice hemifield test, the conditioned-avoidance test demonstrated that the animals lacked the ability to discriminate between two sound sources located in the same hemifield.

Perusal of Fig. 9 indicates that one animal, monkey C, was occasionally able to perform above chance when the left speaker was 5 or 10° inside the right hemifield. Although it is not possible to positively determine the reason, there are at least two possible explanations for this slight but statistically significant ability. First, monkey C had the smallest lesion, and it is not impossible that it retained some residual ability. That lesion size may be a factor is supported by the fact that the performance of the animal with the largest lesion (monkey D) consistently fell to chance well before the left speaker crossed the midline.

A second possibility is that monkey C's head was not always perfectly aligned. Indeed, the monkeys often tried to turn their heads so that the speakers would fall in different hemifields, and it was occasionally necessary to adjust the position of the cage to precisely align their heads with the speakers. Thus we do not find this animal's sporadic ability sufficient to contradict the general rule that ablation of auditory cortex in macaques abolishes the ability to discriminate sounds arising from different locations within a hemifield.

DISCUSSION

The results of this study can be briefly summarized as follows: first, bilateral ablation of auditory cortex abolishes the ability to discriminate the locus of a sound source when the sources are in the same hemifield. This deficit applies to both brief- and long-duration sounds and can be demonstrated with both the conditioned-avoidance and two-choice tasks. Second, auditory cortex ablation reduces but does not abolish the ability of monkeys to discriminate the locus of two sound sources when one source is in the left and the other is in the right hemifield. Although it is more difficult for operated monkeys to learn to discriminate the locus of brief sounds in the two-choice task, there is no fundamental difference between the results of the conditioned-avoidance and two-choice tasks. Finally, the fact that the operated monkeys can discriminate left and right sounds but have difficulty in learning to walk to the source of a sound suggests that they retain the sensory ability to discriminate between left and right sounds while losing the perception of auditory locus.

In the following discussion we address the issue of the nature of the sound-localization deficit, the effect of task variables on localization performance, and the effect of cortical ablation on sound localization in different species.

Nature of the sound-localization deficit

The cortical sound-localization deficit, first noted by Neff and Yela in 1948, was described in detail by Neff and his colleagues in 1956. They found that bilateral auditory cortex lesions resulted in a severe deficit in the ability of cats to walk to the source of a sound in a left-right, two-choice task. One of the issues addressed by them was the nature of the deficit, that is, whether it was a learning, attention, or sensory deficit. Since then, additional explanations have been proposed as further studies have appeared. Of the two major explanations that have been advanced, one is that the cortical lesions result in an auditory-motor deficit, the other that they result in a deficit in the ability to perceive the spatial qualities of sound. The following discussion examines each of these explanations.

LEARNING HYPOTHESIS. One of the first possibilities considered by Neff and his colleagues was that the cortical lesions might have resulted in an inability to associate an auditory signal with a food reward, i.e., that the animals had an auditory-learning deficit. They rejected this possibility because cats with cortical lesions could learn to associate a buzzer with the availability of food, demonstrating that the sound-localization deficit was not the result of a general auditory-learning deficit. Nor is it a learning deficit specific to sound localization, as monkeys in the present study were able to learn to associate a sound with a locus as long as there was only one sound source in each hemifield. Thus learning per se does not appear to play a role in the deficit.

ATTENTION-MEMORY HYPOTHESIS. A second possible explanation offered by Neff and his colleagues (1956) was that ablation of auditory cortex may have resulted in a deficit in attention. They defined attention as ". . . the ability of the animal not only to orient towards the signal but to keep its activity directed appropriately until the final response . . . has been made." Because this definition requires that the animals maintain their attention after the auditory signal is turned off, it includes a memory component.

Although they were unable to rule out the possibility of an attention or memory deficit, it has been shown that these factors do not account for the deficit. Specifically, dogs with bilateral auditory cortex lesions were trained on a two-choice task (similar to the one used in this study) in which they had to walk from a center water spout to one of two goal water spouts (Heffner 1978). This study found that the animals were able to discriminate a 10-per-s from a 100-per-s train of clicks even when the clicks were turned off before the animals left the center water spout. Thus the animals could both attend to the auditory stimulus and remember it long enough to make a correct response.

The results of this study provide additional grounds for rejecting the possibility of an attention or memory deficit. In the two-choice task, three of the monkeys were eventually able to perform the midline discrimination with the use of brief sounds including single noise bursts. That is, they could attend to the stimulus, associate it with a response, and remember which stimulus had been presented long enough to complete the response as long as the two stimuli were presented in different hemifields. Thus the deficit is not one of attention or memory but is specific to the ability to localize sound.

AUDITORY-MOTOR HYPOTHESIS. The concept of an auditory-motor impairment after bilateral auditory cortex ablation was first proposed by Ravizza and Masterton (1972). They had found that, although removal of all neocortex in opossum resulted in a decrease in sound-localization acuity for the discrimination of left and right sounds, it did not result in as severe a deficit as that found in cats. After first noting that this could be the result of species differences in the contribution of auditory cortex to sound localization in cats and opossums, they pointed out that there were potentially important differences in the behavioral techniques used to measure localization in the two species. Specifically, the cats were tested with a two-choice task that required them to make a spatial response to a sound, i.e., walk to its source, whereas the opossum was tested with a conditioned-suppression task that made use of a nonspatial response, i.e., ceasing to drink. This difference in tasks suggested the possibility of an auditory-motor impairment in which the ability to make a spatial response to a sound was virtually abolished while the ability to make a nonspatial response was only minimally affected.

The auditory-motor hypothesis received subsequent support from a study of the effect of cortical lesions on the ability of rhesus monkeys to localize sound (Heffner and Masterton 1975, 1978). This study found that bilateral auditory cortex lesions reduced, but did not abolish, the ability of monkeys to perform a left-right–hemifield discrimination by pressing one of two levers to indicate the direction of the sound source. In addition the monkeys, like opossums, were able to discriminate locus with the nonspatial conditioned suppression response. However, when the monkeys were required to walk to the source of a brief sound, two of the three monkeys were unable to do so. Because the one monkey that could perform the task had the smallest bilateral lesion, it was concluded that complete auditory cortex lesions abolish the ability to move to the source of a brief sound.

In this study, we concluded that auditory cortex lesions do not abolish the ability to move to the source of a brief sound. Because this conclusion reverses that of the previous study, it is necessary to carefully compare the two studies to explain this change in our interpretation.

The methods used in this and previous two-choice midline tests on monkeys were very similar. In both studies, the monkeys were required to localize brief sounds separated by 60° by moving 1.7 m to a goal box. Although one might argue that the 100-ms noise burst used in this study is easier to localize than a single click used in the previous study, this difference is probably minor. One important difference between the two studies, however, was the size of the lesions—those in this study were larger than any of the lesions in the previous study. Specifically, the lesions in this study included more of the rostral portion of the superior temporal gyrus and resulted in greater degeneration throughout the GMp, particularly in the caudal tip.

The results of the two studies are also similar—in both the results were mixed. In the previous study two of the three animals could not locate the source of a brief sound, and in this study one of the four animals could not locate the source. However, in contrast to the previous study the performance of the present animals did not appear to be related to the completeness of the lesion. In fact, in this study the animal with the largest lesion also had the best performance.

Our conclusion, then, is that monkeys with bilateral auditory cortex lesions have great difficulty in performing a left-right, sound-localization discrimination by moving to the source of a brief sound. However, because most monkeys do eventually perform this task, it does not seem that their deficit is best described as an auditory-motor disconnection. Instead, we propose that the monkeys do poorly for two reasons. First, they have elevated thresholds, which makes the discrimination somewhat more difficult than normal. Second, and more importantly, they have lost the perception of auditory locus. Thus their poor performance is due to the fact that they are being required to make a spatial response to sounds that have no normal spatial meaning for them and are, in addition, somewhat more difficult to distinguish.

It appears, then, that the auditory-motor hypothesis is no longer needed to account for the difference in the ability of operated monkeys to learn to perform a spatial-versus-nonspatial response to the locus of a sound. However, it may still be useful in characterizing the differential effect of cortical lesions on reflexive as opposed to conditioned responses to the locus of a sound. Specifically, auditory cortex ablation in cats results in a sound-localization deficit similar to that in monkeys—the animals have severe difficulty performing a two-choice midline discrimination, and they are unable to localize within a hemifield (Jenkins and Masterton 1982; Jenkins and Merzenich 1984; Neff et al. 1956).

In contrast, bilateral auditory cortex lesions do not abolish the cat's head-orienting reflex to sounds (Beitel and Kaas 1971; Thompson and Masterton 1978; Thompson and Welker 1963). Specifically, lesions which include AI, AII, Ep, and SII have no effect on the occurrence or accuracy of head orientation, whereas larger lesions that extend ventrally to include insular and temporal cortex only reduce the probability that a cat will orient normally to a sound. That is, an animal with a large lesion will occasionally fail to orient to the proper hemifield, and its response latency will be unusually long. However, more often than not the animal will orient to the correct hemifield and will do so with normal latency and accuracy. Thus the orienting response demonstrates that the animal is not only able to determine the hemifield in which the sound occurs but is able to localize accurately within the hemifield.

The fact that reflexive head orientation to the source of a sound survives cortical ablation, whereas the ability to perform a nonreflexive response is lost, suggests that these two types of responses may be subserved by different pathways. As noted by Thompson and Masterton, the results of orientation experiments indicate that ". . . we are left with the notion of a sensorimotor pathway that bypasses auditory

cortex but which is either turned on or off by auditory cortex at any particular moment" (Thompson and Masterton 1978). Because the orienting response directs the gaze to the source of a sound—a purpose which evidently requires a rapid response—it appears that it has a separate motor output from the brain stem mechanism that determines locus. Thus these results suggest that the auditory-motor hypothesis may be a valid explanation for the difference in the effect of cortical lesions on reflex orientation to sound as opposed to the ability to make a learned response to the locus of sound.

SENSORY DEFICIT.   The results of the present study suggest that auditory cortex ablation results in sensory as well as perceptual deficits that affect the ability to localize sound. The sensory aspect of the cortical deficit is apparent in two features of the animals' abilities. First, it is a general finding in both primates and carnivores that bilateral ablation results in a decrease in sound-localization acuity in simple left-right discriminations (Heffner and Masterton 1975, 1978; Kavanagh and Kelly 1987). This reduced acuity is seen in the present monkeys that had increased thresholds in discriminating the locus of continuous as well as single noise bursts (Fig. 5).

The second demonstration of a sensory deficit is the virtually complete inability of the animals to discriminate between sounds arising within the same hemifield even at large angles of separation. This observation is in agreement with those of previous studies that examined sound localization within a hemifield after unilateral or bilateral auditory cortex ablation (Jenkins and Masterton 1982; Jenkins and Merzenich 1984; Kavanagh and Kelly 1987; Thompson and Cortez 1983). Furthermore, this inability can be demonstrated in the conditioned-avoidance task—a simple task in which the animals need only detect a difference between two stimuli. Thus there appears to be a definite sensory component to the cortical sound-localization deficit.

PERCEPTUAL DEFICIT.   The performance of the animals on the midline-localization tests in this study suggests that there is a perceptual component to the deficit as well. The animals were clearly able to discriminate sounds in the left hemifield from those in the right, and they had little difficulty learning to do so in the conditioned-avoidance task that required them to make a nonspatial response. Yet in spite of this prior training, the operated monkeys had great difficulty in learning to walk to the source of a sound (cf. Fig. 6). It is this difference in their ability to learn to make a spatial, as opposed to a nonspatial, response that leads us to believe that they had lost the perception of auditory locus.

That the loss of the perception of locus should affect the ability to make a spatial response can be explained by the normal response of animals to sound (cf. Harrison 1984, 1988). It has been well established that not only do normal monkeys rapidly learn to approach a sound source but that they have a natural bias to approach the source of a sound that signals the availability of food (Downey and Harrison 1972; Harrison et al. 1977). In an experiment in which monkeys were trained to press one of two buttons to obtain food, it was found that the animals consistently ap-

proached and responded to the button adjacent to the sound source even though responding to either button produced a food reward (Downey and Harrison 1972). Whether this bias is innate or the result of experience is unknown. However, it does demonstrate both the salience of locus and the propensity for normal monkeys to approach a sound source.

On the other hand, it is noticeably more difficult to train animals to make a spatial response to a nonspatial stimulus. In experiments with dogs, it has been demonstrated that animals take longer to learn to make a spatial response to sounds that differ in quality than it does to sounds that differ in location (e.g., Lawicka 1969). Thus we suggest that animals with auditory cortex lesions may have great difficulty in approaching the source of a sound simply because they no longer perceive the locus of the sound. As a result, a task that normal animals have little difficulty learning because of the natural association of sound with a location in space, becomes a difficult and arbitrary task for animals with cortical lesions.

It should be emphasized that the inability to perceive the locus of a sound was not a temporary effect of the lesions. The animals were not tested on sound localization for more than a year after surgery, during which time they were constantly exposed to sounds in their environment. As their vision was not noticeably affected by the lesions, they had ample opportunity to associate sounds in the environment with their sources. The fact that they had not regained this ability by the time they were tested suggests that they had permanently lost the ability to perceive the locus of a sound source.

The idea that the cortical sound-localization deficit is perceptual in nature is not new. In a now classic study, Masterton and Diamond (1964) determined the effect of cortical lesions on the ability of cats to discriminate clicks presented separately to each ear via headphones. Their results indicated that bilateral auditory cortex ablation did not abolish the ability of the animals to discriminate between a click presented to the left ear from a similar click presented to the right ear. Nor did it abolish the ability to use the time-of-arrival cue to discriminate left- and right-lateralized clicks. However, the lesions did result in a total loss of *transfer* between the two tasks. This result indicated that the animals had lost the equivalence between a click to one ear and a pair of clicks to both ears, which a normal animal would lateralize to one ear. Thus they concluded that auditory cortex ablation results in an inability to perceive the spatial attributes of a sound source.

A similar conclusion was reached by Jenkins and Masterton (1982). They suggested that a cat with a unilateral auditory cortex lesion may solve a midline-locus task by learning to discriminate between localizable sounds versus nonlocalizable sounds. That is, sounds arising from the hemifield contralateral to the lesion would be devoid of spatial meaning whereas those arising from the ipsilateral field would be easily localizable. In applying this reasoning to the effect of bilateral lesions, we suggest that a sound arising from one hemifield, although devoid of locus, is still different in some way from the same sound arising from the other hemifield. Given the fact that locus information

is segregated by hemifield above the level of the superior olivary complex, there are numerous opportunities for the nervous system to make use of this information in a discrimination test without attaching a percept to it (e.g., Glendenning and Masterton 1983).

It should be noted, however, that there is not complete agreement on the issue of a perceptual localization deficit. Specifically, Kavanagh and Kelly (1987) have argued that the ability of animals with cortical lesions to perform a left-right discrimination indicates that they have retained the perception of left and right auditory space and that their sound-localization deficit is therefore sensory in nature. By their criterion, then, the monkeys in this study did not have a loss of the perception of locus. Although one cannot totally rule out the possibility of a strictly sensory deficit, we believe that the evidence from the studies of monkeys and cats indicates that animals can lose the ability to identify the spatial location of a sound and still be able to discriminate left sounds from right sounds. Just how they perceive the difference between the sounds is at this time unknown.

In conclusion, we suggest that bilateral ablation of auditory cortex in carnivores and macaques results in both sensory and perceptual deficits. The sensory deficits are indicated by the reduced sound-localization acuity seen in left-right discriminations and by the total inability to discriminate locus within a hemifield. The perceptual deficit is a loss of the normal association of a sound with a location in space and is indicated by the difficulty that operated monkeys have in learning to approach the source of a sound.

Behavioral assessment of the sound localization deficit

Over the years a variety of tasks have been used to assess the effect of cortical lesions on sound localization. These tasks have differed from each other in terms of the type of response made by an animal (i.e., conditioned versus unconditioned, spatial versus nonspatial) as well as the number of sound sources and their location in the hemifields. As the previous discussion has noted, the apparent effect of a lesion on an animal's performance may vary with the task. Although such variation may at first appear confusing, it is actually very helpful in determining the nature of the cortical deficit. One example of this is the demonstration of a perceptual deficit by the fact that operated monkeys have difficulty learning to make a spatial response to the locus of a sound while easily learning to make a nonspatial response; another example is the relative lack of effect of cortical lesions on reflex head orientation. Thus a complete assessment of the effect of a lesion on sound localization requires a battery of tests.

In choosing these tests it is necessary to consider the effect of the number of sound sources and their location in the hemifields. Although the original sound-localization test devised by Neff and his colleagues used three sound sources, the number of sound sources was reduced when it was found that two sound sources located symmetrically around the midline were sufficient to demonstrate the cortical sound-localization deficit in cats (Neff et al. 1956).

Yet this arrangement, with one source in the left and the other in the right hemifield, does not reveal the inability of animals with unilateral lesions to localize sounds in the contralateral hemifield, (cf. Jenkins and Masterton 1982; Strominger 1969). However, it is not the number of sound sources but their location that is important in demonstrating the inability to localize within a hemifield. Specifically, it is possible to determine an animal's ability to localize within a hemifield with only two sound sources as long as both of them are located within that hemifield. This point was first demonstrated with ferrets by Kavanagh and Kelly (1987) and is supported by the results of this study (cf. Fig. 9).

Indeed, it may be preferable to test an animal's hemifield-localization ability with only two sound sources, as operated animals in a multichoice task may develop a response bias to a particular sound source that raises their performance at that location. Such a bias makes it appear that they can localize sound in part of the hemifield (i.e., that they have a "sigoma"), when in fact they are probably unable to localize sounds anywhere within that hemifield (for a detailed discussion of this problem, see Jenkins and Masterton 1982). Thus a test in which two sound sources can be moved about within the hemifields is sufficient, and sometimes preferable, for testing an animal's sound-localization ability.

Given what we currently know about the role of cortex in sound localization, a complete test would consist first of an assessment of an animal's orientation reflex to sound. This would be followed by the determination of thresholds for left-right (midline) and hemifield discriminations by the use of two sound sources. The animals could be required to make either a spatial or a nonspatial response keeping in mind that a perceptual deficit might cause them difficulty in learning to make a spatial response. Finally, the way an animal perceives sound can be revealed through the use of transfer and equivalence tests (cf. Masterton and Diamond 1964).

Species differences

It has recently become apparent that there are large species differences in the effect of auditory cortex lesions on hearing. The first demonstration of this fact came from the work of Kelly and his colleagues who showed that, in contrast to their effect on carnivores and primates, cortical lesions have very little effect on the ability of the albino rat to localize sound (Judge and Kelly 1983; Kelly 1980; Kelly and Kavanagh 1986). As a result, it is necessary to assess the degree to which species may differ to avoid unnecessary confusion regarding the role of the cortex in hearing.

Over the years 11 different species have been used in studies of the effect of cortical lesions on sound localization. Because of variation in behavioral methods and the difficulty in making comparable lesions, the results of these studies are not always easy to compare. Nonetheless, it is clear that there are significant differences in the effect of cortical lesions on sound localization.

It is tempting to speculate that these differences may reflect variation in the importance of sound localization to the various species. Indeed, the fact that mammals vary in their reliance on sound localization is indicated by the fact that there are significant species differences in normal sound-localization acuity (e.g., Heffner and Masterton 1990). Furthermore, the results to date are not inconsistent with the notion that the cortical deficit is greatest in those animals with good sound-localization acuity. However, at the present time the sample of mammals that have been examined is too small to draw any specific conclusions. Furthermore, species differences in the effect of cortical lesions are not limited to sound localization but are also found in the detection of sound—auditory cortex lesions in humans and macaques result in a severe hearing loss, whereas similar lesions in carnivores have only a small effect on detection (cf. Heffner and Heffner 1986b, 1990b; Kavanagh and Kelly 1988). Thus it may eventually be necessary to address the issue of the importance of hearing in general to different species.

Nor is it likely that the results are due to the nature of the stimuli used in localization experiments. It has been noted elsewhere that most natural sounds are brief broadband sounds, such as snaps and thumps, and that such sounds are important because they usually signal the presence of other animals in the environment (Masterton and Diamond 1973). Because most studies of sound-localization ability have employed abrupt broadband sounds such as clicks and brief noise bursts, there is reason to believe that the animals were tested with sounds that their nervous systems evolved to detect and localize.

PRIMATES. Ablation of auditory cortex has been shown to affect the ability to localize sound in the five species of primates that have been tested. The most detailed testing of primates has been conducted with rhesus and Japanese macaques, and it would appear that the cortical deficit in these two species is the same (Heffner and Heffner 1990a; Heffner and Masterton 1975, 1978; Wegener 1973). Thus, as previously described, bilateral ablation in macaques results in a reduction in the ability to perform a left-right discrimination, an inability to discriminate locus within a hemifield, and a loss of the perception of auditory locus.

Two other species of primates that have been studied are the squirrel monkey (a new world monkey) and the bushbaby (a prosimian). Unilateral auditory cortex ablation in the squirrel monkey results in a severe deficit in localizing sound in the contralateral hemifield (Thompson and Cortez 1983). This result suggests that squirrel monkeys suffer the same deficit as macaques. A study of the effect of bilateral auditory cortex lesions in bushbabies showed them to be only moderately affected by bilateral lesions when tested in a multichoice task with the use of six sound sources (Ravizza and Diamond 1974). Whether their remaining ability to localize sound represents a species difference or is the result of incomplete lesions is unknown because lesion reconstructions were not published. However, the fact that the animals did show some decrement in performance indicates that cortex does play a role in sound localization in prosimians.

Finally, although a number of studies have looked at the ability of brain-damaged patients to localize sound, the

effect of auditory cortex lesions on sound localization in humans is far from clear. This is because the size and location of the lesions is largely unknown—a fact that probably accounts for much of the variation found in clinical studies (e.g., Hecaen and Albert 1978). Indeed, it is unlikely that any patient with complete bilateral auditory cortex lesions has ever been examined, as such a person would not only have a severe hearing loss but would be incapable of responding to verbal instruction.

Nevertheless, we know that auditory cortex lesions in humans disrupt the ability to localize sound. This was demonstrated by Sanchez-Longo and his colleagues who found that unilateral temporal lobe lesions impaired sound localization in the hemifield contralateral to the lesion (Sanchez-Longo et al. 1957; Sanchez-Longo and Forster 1958), a result that has been confirmed by subsequent studies (for reviews, see Bisiach et al. 1984; Neff et al. 1975; Walsh 1957). In addition, Jerger and his colleagues demonstrated impaired sound localization in a case of bilateral temporal lobe lesions (Jerger et al. 1969). Although the patient had sufficient speech comprehension to indicate that the cortex was by no means disconnected from auditory input, his perception of locus was abnormal in that stationary sound sources appeared to move. This observation not only demonstrates the importance of auditory cortex for sound localization in humans but may also illustrate a perceptual consequence of the remaining cortex attempting to compensate for the damaged or malfunctioning area. However, there does not appear to be any description of the effects of complete unilateral or bilateral auditory cortex lesions in humans. This is unfortunate as such a study could answer the question of how the perception of locus changes after a lesion—a question that is difficult to answer using animals.

In summary, it appears that auditory cortex ablation in primates results in an impairment in the ability to localize sound. Although the effect of complete auditory cortex lesions in humans has not been systematically investigated, it is probably similar to that seen in macaques.

CARNIVORES. The effect of cortical lesions on sound localization has been studied more often and in more detail in cats than in any other animal (cf. Neff et al. 1975). As previously noted, bilateral ablation of auditory cortex in cats results in a severe deficit in the ability to perform a left-right discrimination and a loss of the perception of auditory locus. In addition, unilateral ablation results in an inability to localize sound in the contralateral hemifield, and restricting such lesions to a particular band of frequencies within primary auditory cortex abolishes the ability to localize those specific frequencies (Jenkins and Masterton 1982; Jenkins and Merzenich 1984).

Studies using dogs and ferrets indicate that these animals have a similar cortical deficit. Bilateral ablation of auditory cortex in dogs resulted in an inability to locate the source of a sound in a left-right discrimination if the source was 125 cm or more from the starting position (Heffner 1978). Like cats, dogs could perform the discrimination above chance if the goal boxes were placed close to the starting position.

In a detailed study of ferrets, Kavanagh and Kelly (1987)

found that unilateral lesions result in an inability to localize sound in the hemifield contralateral to the lesion. Furthermore, although bilateral lesions restricted to primary auditory cortex resulted in minimal impairments in left-right localization, large lesions that included the areas ventral to primary auditory cortex produced severe impairments in even this task.

In summary, carnivores appear to suffer the same cortical sound-localization deficit as monkeys. They are unable to discriminate between sound sources located in the hemifield contralateral to a lesion; they are impaired in their ability to perform a left-right locus discrimination, and they appear to lose the perception of auditory locus.

RODENTS. In contrast to primates and carnivores, bilateral ablation of auditory cortex in the albino rat has very little effect on sound-localization ability. This was first noted by Kelly (1980), who found that bilateral ablation had little effect on a two-choice, left-right discrimination in which the animals had to approach the source of the sound. This lack of effect was verified in a subsequent study that involved a three-choice task in which the third sound source was located on the midline (Kelly and Kavanagh 1986). Furthermore, although rats do not appear to localize sound within a hemifield as readily as other animals (Kavanagh and Kelly 1986), they are able to perform a seven-choice localization task in which multiple sound sources are located in both hemifields and neither unilateral nor bilateral lesions have any large effect on their ability (Judge and Kelly 1983). Because macaques and carnivores are severely impaired on similar tasks, Kelly and his colleagues have concluded that cortical lesions in rats do not result in significant deficits in the ability to localize sound.

The lack of a significant deficit in the albino rat is supported by a study that looked at the effect of bilateral cortical lesions on the ability of wild rats to localize sound (Heffner 1981). In this study, two wood rats (*Neotoma floridana*) were tested in a seven-choice task that required them to approach sound sources that were located from 90° left to 90° right at 30° intervals. The results showed that although the rats could not localize a 500-ms noise burst as accurately as normal animals, they were still able to reliably localize noise bursts as short as 100 ms in duration. This finding suggests that the results of Kelly and his colleagues are not specific to albino rats and that rats do not lose the ability to localize sound within a hemifield. Instead it appears that cortical lesions in rats do not result in the severe sound-localization deficits seen in primates and carnivores. Whether the lack of a cortical sound localization deficit is common among rodents or is found only among certain species is as yet unknown.

OTHER SPECIES. The two other species that have been examined are the hedgehog, an insectivore, and the Virginia opossum, a marsupial. Hedgehogs were tested in a six-choice apparatus in which they were required to walk to the source of a sound (Ravizza and Diamond 1974). The results showed that although the animals were unable to localize brief noise bursts as accurately as normal, they were still able to localize above chance. Thus the effect of bilateral cortical ablation in the hedgehog is similar to that in

rats in that it results in a performance decrement but does not abolish their ability to localize sound.

The effect of cortical lesions on sound localization in a marsupial was examined by Ravizza and Masterton (1972). They tested the ability of opossums to perform a left-right discrimination in which the animals were trained to break contact with a water spout whenever they detected a change in the locus of a sound. The results indicated that although the animals suffered a loss of acuity, they retained the ability to discriminate left sounds from right sounds. However, without further information it is not possible to determine the degree of the opossum's deficit. That is, opossums may be like cats and monkeys in that they retain the ability to perform a left-right discrimination while losing both the perception of auditory locus and the ability to discriminate sound sources within a hemifield. On the other hand, they may be like rats, which suffer only a minor decrement in performance.

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