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The Role of Macaque Auditory Cortex in Sound Localization

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Bilateral ablation of auditory cortex in macaques results in both sensory and perceptual deficits. The sensory deficit is indicated by increased thresholds for left-right locus discriminations and an inability to discriminate locus within either the left or right hemifield. The perceptual deficit is indicated by the observation that the monkeys no longer appear to associate a sound with a location in space. Unilateral auditory cortex ablation results in an inability to discriminate locus within the hemifield contralateral to the lesion. It is not known whether unilateral lesions also result in a perceptual deficit.
Key words: *auditory cortex, lesions, macaques, primates, sound localization.*

INTRODUCTION

The modern study of the function of auditory cortex began in the latter half of the 19th century when it was established that sensory and motor functions were localized to specific areas of the cerebral cortex. One of the primary methods used to determine the function of a cortical area was the ablation-behavior method. This method consisted of determining the effects of discrete cortical lesions in animals on their sensory and motor behavior. By carefully observing the effects of cortical lesions on the detection of sound, early researchers were able to demonstrate that auditory cortex lies within the superior temporal gyrus of macaques (1). However, further testing of the effect of cortical lesions on hearing had to await the development of behavioral procedures for assessing the sensory abilities of animals.

The first half of the 20th century witnessed the growth in our understanding of operant and classical conditioning. One result was the development of techniques for assessing the ability of animals to respond to sensory stimuli (2, 3). Ablation studies using conditioning procedures began to appear in the 1930s and by the late 1940s it was discovered that auditory cortex lesions in cats result in a deficit in sound localization (2, 4).

At present, auditory cortex is most commonly studied with electrophysiological and anatomical methods. However, behavioral tests of animals with cortical lesions can give us clues to the function of auditory cortex which cannot easily be obtained with other methods. For example, ablation studies have revealed that the role of auditory cortex in sound localization is not the same in all mammals. While auditory cortex lesions result in an obvious sound-localization deficit in primates and carnivores, there is no apparent deficit in a rodent such as the Norway rat (5).

Of those animals which have been studied, macaques are of particular interest due to their neurological similarities to humans. Thus, the purpose of this paper is to describe the role of auditory cortex in sound localization based primarily on the results of ablation-behavior experiments with Japanese macaques (*Macaca fuscata*).

LOCUS OF AUDITORY CORTEX IN MACAQUES

The locus and extent of auditory cortex have been studied in the rhesus macaque by evoked response, microelectrode recordings, cytoarchitectural analysis, and by tracing thalamocortical connections (5). 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.

Both cytoarchitectural and electrophysiological studies have indicated that there is a central core area, referred to as primary auditory cortex, and a surrounding belt region of secondary auditory fields (Fig. 1*A*). Primary auditory cortex lies in the depths of the Sylvian fissure on the middle third of the superior temporal plane and is surrounded by at least four secondary areas. In addition, electrophysiological, anatomical, and behavioral evidence indicates that all of the superior temporal gyrus including the rostral portion may have auditory functions (6).

EFFECT OF BILATERAL AUDITORY CORTEX LESIONS

The effect of bilateral auditory cortex lesions (Fig. 1*B*) on sound localization is two-fold. First, there is a sensory deficit in that a) the ability to make left-right locus judgements is reduced, and b) the ability to discriminate between two sound sources within a hemifield is abolished. Second, there is a perceptual deficit in that although animals are able to make

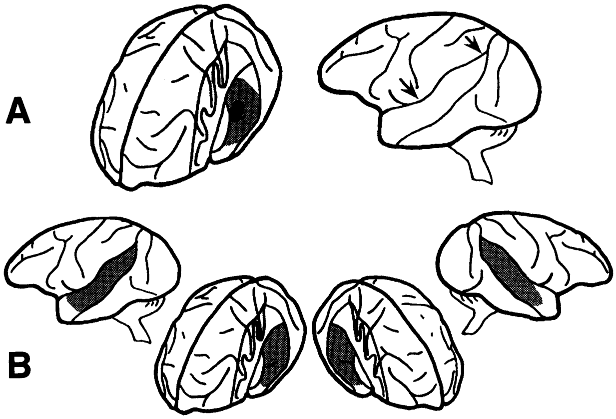

Fig. 1. (*A*) Drawing on the left is of a Japanese macaque brain with the frontoparietal operculum removed to show the location of primary (*blackened*) and secondary (*shaded*) auditory cortex (modified from ref. 6). Drawing on the right shows the lateral surface with *arrows* marking the approximate limits of primary and secondary auditory cortex. (*B*) Cortical reconstruction of a typical lesion, indicated by *shading* (modified from ref. 5).

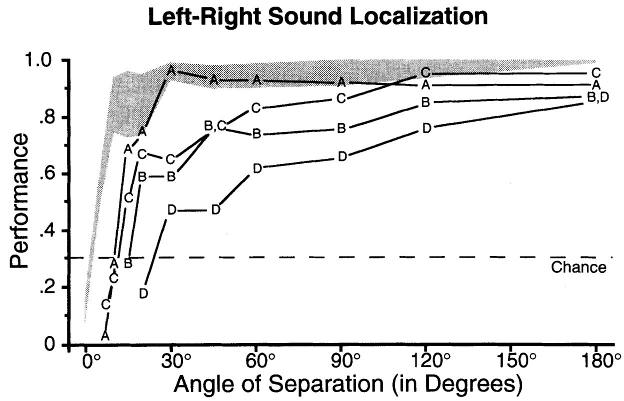

Fig. 2. Ability of four monkeys with bilateral auditory cortex lesions (A, B, C and D) to perform a left-right sound-localization discrimination in a conditioned avoidance task (modified from ref. 5). The stimulus was a single 100-ms noise burst. Range of performance of 2 normal monkeys is indicated by shading. The increased thresholds of the operated animals indicates a sensory deficit.

left-right judgements, albeit with reduced acuity, they no longer naturally associate the sounds with locations in space.

Sensory deficit

The sensory nature of the cortical sound-localization deficit has been demonstrated using a conditioned avoidance procedure (5). Briefly, a thirsty animal is placed in a primate chair or cage and allowed to drink from a water spout. Water is dispensed from the spout at a slow rate as long as the animal maintains contact with it. The act of drinking not only provides the basis for the animal's discriminatory response, but also fixes its head in the sound field.

An animal's ability to perform a left-right locus discrimination can be determined by training it to break contact with the water spout whenever it hears a sound from its left. This is done by emitting a brief sound (e.g., a 100-ms noise burst) from a loudspeaker on its left side and following it by a mild electric shock delivered through the water spout. Sounds emitted by a loudspeaker on the right side, on the other hand, are not followed by shock and the animal quickly learns to break contact when it hears a left sound while maintaining contact when it hears a right sound. This difference in response to left and right sounds is then used to indicate that the animal can discriminate the sounds based on location. Thresholds are determined by moving the two loudspeakers closer together, keeping them centered on the animal's midline, until the animal can no longer discriminate between them.

The ability of an animal to discriminate between two loudspeakers within a hemifield can be determined in the same manner as the left-right discrimination except that both loudspeakers are located in the same hemifield. Testing begins with one loudspeaker placed on either side of midline (e.g., 90° left and right) with thresholds determined by keeping the right loudspeaker at 90° right and moving the left loudspeaker towards it and across midline until the animal's performance falls to chance. The animal is trained to break contact when the sound comes from the left-most loudspeaker while maintaining contact when the sound comes from the right-most loudspeaker.

The effect of bilateral ablation of auditory cortex on the ability to make a left-right locus discrimination is shown in Fig. 2. As can be seen, the operated monkeys retained the ability to localize a single, 100-ms noise burst. Although the scores of the operated animals occasionally overlapped those of two normal animals, the operated animals' asymptotic performances are generally lower than normal and their thresholds are elevated. The fact that all four of the monkeys with auditory cortex lesions had elevated thresholds is interpreted to mean that they had suffered at least a mild sensory impairment.

A more dramatic sensory impairment, however, is evidenced by the performance of the animals when attempting to localize sound within a hemifield. As shown in Fig. 3, the ability of the operated monkeys to localize a train of 2/s noise bursts declined rapidly as the left-most loudspeaker was moved into the right hemifield. Indeed, this is not a simple threshold shift as the performance of the animals was independent of

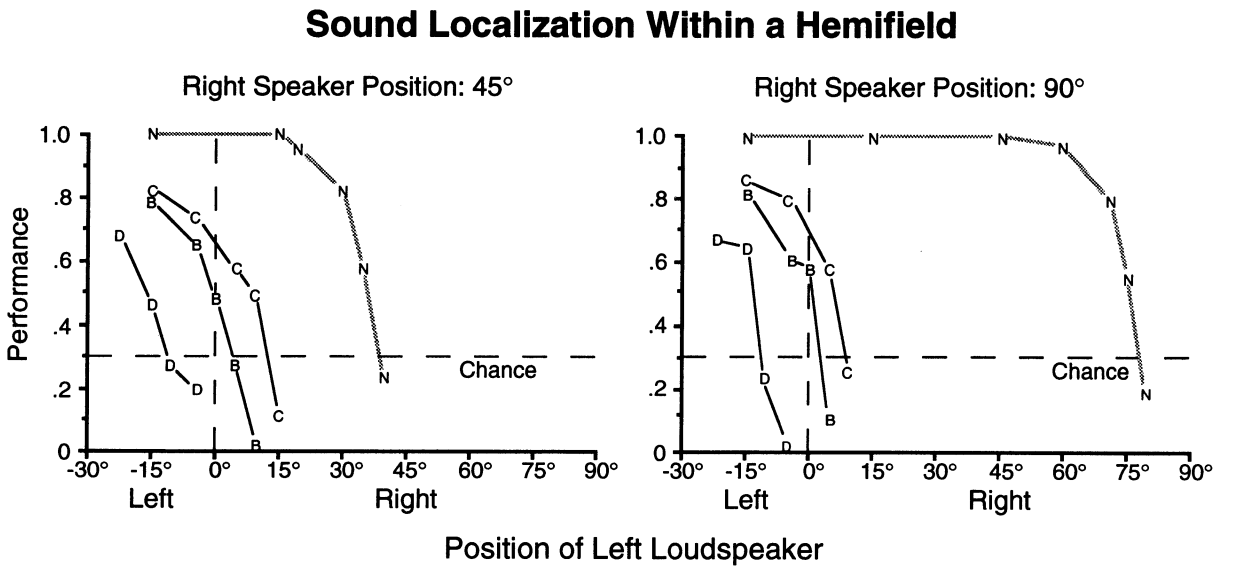

Fig. 3. Ability of three monkeys with bilateral auditory cortex lesions (B, C and D) and one normal monkey (N) to perform a localization discrimination within the same hemifield using a conditioned avoidance task. One loudspeaker was placed at either 45° or 90° to the right of midline with the other loudspeaker placed at various locations to the left of the first loudspeaker. Note that the operated animals' performances fell to chance when the left-most loudspeaker was moved into the right hemifield regardless of the location of the right-most loudspeaker (modified from ref. 5).

the position of the right-most speaker. That is, the operated animals fell to chance as the left-most loudspeaker was moved to the midline regardless of whether the right-most loudspeaker was at 45°, 90°, or even 135° (not shown). Thus, bilateral ablation of auditory cortex results in a collapse of the auditory hemifields such that although the animals were able to discriminate sounds arising in the left hemifield from those arising in the right hemifield, they were virtually unable to discriminate the locus of sounds arising within a hemifield.

Perceptual deficit

The perceptual nature of the cortical sound-localization deficit has been demonstrated by using a procedure in which the animals indicate the direction of the sound source. One such procedure is a two-choice task in which the animals walk to the source of a sound (5). In using this procedure with monkeys, a thirsty animal was placed in a small room containing three water spouts, a "center" spout and two "goal" spouts (Fig. 4). The animal was trained to place its mouth on the center spout, an act which positioned it in front of the two goal spouts 60° apart and 1.7 m away. Making contact with the center spout initiated a trial in which a sound was presented from a loudspeaker located above one of the goal spouts. The animal was then trained to walk to the source of the sound and lick the water spout located below the loudspeaker that had emitted the sound in order to receive a water reward. After collecting the reward, the animal returned to the center spout in order to initiate a new trial. A response to the incorrect spout, however, was not rewarded, but was followed by a short wait or "error time out" before the animal could begin a new trial. An animal was first trained to walk to the source of a 2/s train of 100-ms noise bursts that stayed on until the animal made contact with one of the goal spouts. Ultimately, the animal was required to localize a single 100-ms noise burst.

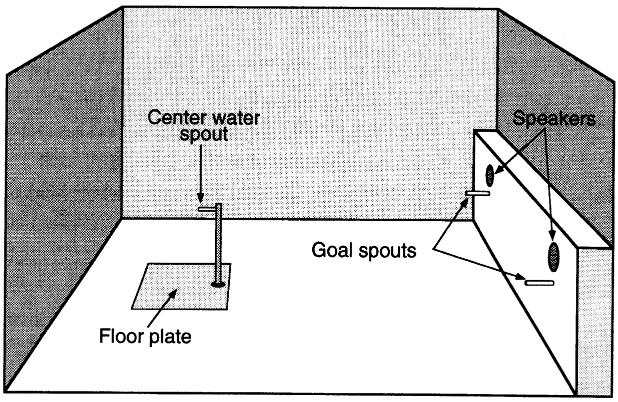

Fig. 4. Semi-schematic drawing of the sound chamber used to test the ability of monkeys to walk to the source of a sound. An animal would initiate a trial by standing on the floor plate and licking the center water spout, thus positioning it equidistant from and facing toward the goal spouts. It would then respond by walking to the loudspeaker from which a sound was coming and placing its mouth on the water spout beneath it.

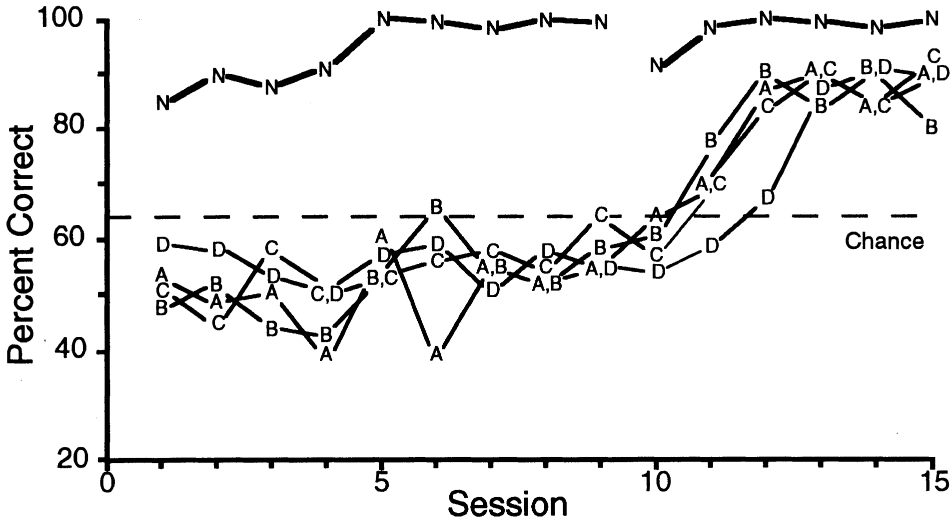

Fig. 5. Ability of four monkeys with bilateral auditory cortex lesions (A, B, C and D) to learn to walk to the source of a sound in the two-choice task (see Fig. 4) (modified from ref. 5). Performance of a normal monkey is indicated by the letter N. The operated monkeys had great difficulty learning this task suggesting that they had lost the normal association of sound with a location in space. The localization stimulus was a 2/s train of 100-ms noise bursts (after session 9, a single noise burst was used for the normal monkey).

The results of tests of four Japanese macaques with bilateral auditory cortex lesions illustrates the perceptual nature of the cortical sound localization deficit (5). The main finding was that the operated monkeys had great difficultly learning to approach the source of the sound even when the train of noise bursts stayed on until the animal made contact with the goal spout (Fig. 5). This difficulty occurred in spite of the fact that all of the animals were trained observers and had previously completed the conditioned avoidance sound-localization tests where they had demonstrated their ability to perform a left-right discrimination. However, none of the animals, including the normal control animal, had been previously required to walk to the source of a sound.

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 or three sessions to become familiar with the test apparatus, whereas the normal monkey was given only one. The animals were then trained to approach the source of a 2/s train of 100-ms 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 experienced in learning this task. As shown in Fig. 5, the operated monkeys took 11–12 sessions to learn the discrimination. In contrast, the normal monkey learned the task in less than one session (indeed, the animal was successfully performing the task within 15 min.). Eventually the operated animals did learn the task and were able to perform consistently at about 90% correct—as long as the sound was left on until they made contact with a goal spout. However, even after more than 1000 training trials, they never performed as well as the normal animal. Moreover, when the localization stimulus was reduced to a single noise burst, their performance declined with one animal unable to perform above chance levels.

The difficulty that the operated animals had in associating the sounds with the goal spouts adjacent to the loudspeakers cannot be attributed to a sensory deficit. This is because the monkeys had previously demonstrated their ability to perform a left-right locus discrimination in the conditioned avoidance task (see Fig. 2). Yet in spite of the fact that the animals possessed the ability to discriminate the sounds on the basis of locus, they had great difficulty in learning to walk to the source of the sound.

It should be noted that in the conditioned avoidance task, the animals were making a nonspatial response to the stimuli. That is, although the monkeys had to discriminate left sounds from right sounds, they had only to make a nonspatial response, that is, to break contact with the water spout, to indicate that they could make that discrimination—a response they learned without any difficulty. It is this difference in their ability to learn to make a spatial response, as opposed to a nonspatial response, that leads us to believe that they had lost the perception of auditory locus. In other words, the operated animals appeared unable to perceive an important biologically relevant feature of the sounds, namely, that the sounds came from specific locations in space.

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. It has been well established that not only do animals rapidly learn to approach a sound source, but that they have a natural inclination to do so (7). In an experiment in which rhesus macaques were trained to press one of two buttons to obtain food, it was found that the animals consistently approached and responded to the button adjacent to the sound source even though responding to either button produced a food reward (8). 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 nonspatial stimuli. 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 (9). Thus, it is suggested that animals with auditory cortex lesions may have great difficulty in approaching the source of a sound simply because they no longer perceive it in an actual location in space. 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.

In conclusion, it appears that bilateral ablation of auditory cortex in 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.

EFFECT OF UNILATERAL AUDITORY CORTEX LESIONS

The effect of unilateral auditory cortex lesions on sound localization has also been determined using the conditioned avoidance procedure (10). Specifically, Japanese macaques were trained to maintain contact with a water spout when a 100-ms noise burst was presented from a loudspeaker located in a fixed location and to break contact when the noise burst was presented from a loudspeaker located either left or right of the first loudspeaker. The ability to localize sound in each hemifield was assessed by placing the fixed loudspeaker at each of eight locations: directly in front (0°) and in back (180°) of the animal, and off to each side at ±30°, ±60° and ±90° from midline.

The results of this test indicated that the four monkeys with unilateral auditory cortex lesions were able to localize sound within the hemifield on the same side as the lesion. However, their ability to localize within the hemifield on the side opposite the lesion was severely affected. Specifically, the animals were unable to discriminate between the two loudspeakers when both of them were, on average, more than 18° inside the affected hemifield (Fig. 6). This finding suggests that the animals have a "sigoma," that is, an area in which they are unable to localize sounds (11).

These results indicate that unilateral ablation of auditory cortex in macaques affects the ability to localize sound in the hemifield contralateral to the lesion while localization in the ipsilateral hemifield remains unaffected. This finding is consistent with the

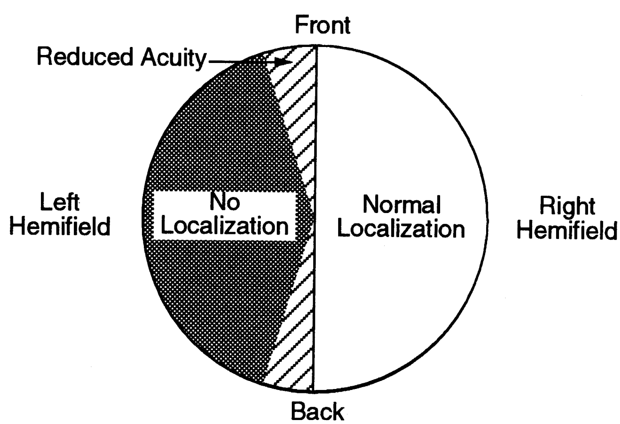

Fig. 6. Effect of a right unilateral auditory cortex lesion on sound-localization ability in the lateral hemifields. Such a lesion renders an animal unable to distinguish between two sound sources when they are located within the *shaded* portion of the left hemifield (i.e., the hemifield contralateral to the lesion). An animal is, however, able to discriminate the two sound sources in the contralateral hemifield if one loudspeaker lies near midline (*hatched segments*). Localization within the right (ipsilateral) hemifield is unaffected.

observation that most neurons in auditory cortex that are sensitive to locus respond to locations in the contralateral hemifield. However, the ability to localize within the hemifield opposite a lesion is not abolished through the entire hemifield. Instead, there appears to be a segment of this hemifield adjacent to midline in which sound-localization ability is reduced, but not abolished (Fig. 6). One explanation of this observation is that the intact hemisphere preserves some localization ability in the affected hemifield. This explanation is consistent with the finding that cortical neurons which respond to locations in the ipsilateral hemifield, are usually sensitive to locations near midline (12).

Comparing the deficits following unilateral auditory cortex ablation with those following bilateral ablation suggests that the bilateral deficit may be the sum of two unilateral deficits. That is, bilateral ablation results in a sensory deficit in that sound-localization ability is abolished within, but not between, the left and right hemifields. With regard to the perceptual deficit, the effect of the bilateral lesions suggest that animals with unilateral lesions would lose the perception of sound in space in the hemifield contralateral to their lesion whereas their ability to perceive locus in the ipsilateral hemifield would remain normal. Whether this is the case remains to be determined.

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