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Effect of Auditory Cortex Ablation on Localization and Discrimination of Brief Sounds

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SUMMARY AND CONCLUSIONS

1. Dogs with bilateral auditory cortex lesions were tested on their ability to localize and discriminate brief sounds. In each test the animals were required to approach one of two goal boxes in order to indicate their response.

2. The results showed: *a*) that the operated animals could not solve the localization tasks when the goal boxes were located more than 125 cm away, but could solve the task if the goal boxes were located closer to the animal; *b*) that the operated animals could successfully discriminate brief bursts of click trains (i.e., 100/s versus 10/s, 0.3 s duration) even when required to indicate their discrimination by moving to goal boxes located 250 cm away, in spite of the fact that they could not successfully localize these sounds under similar conditions; *c*) that the operated animals tracked the source of a continuous sound instead of localizing it in a normal manner.

3. It appears that the deficit in sound localization resulting from cortical ablation is not due to any impairment in auditory attention or memory. Furthermore, the deficit cannot be ascribed to an inability to make a spatial response to an auditory cue. Instead, the deficit may be the result of a disconnection of the sound-localization mechanism from the motor mechanism necessary for some, though not all, behavioral responses.

INTRODUCTION

Bilateral ablation of auditory cortex has long been known to impair the ability to localize sound (13, 14). Recently, however, it has become apparent that the degree of the impairment varies as a function of the response which the animal is required to make to a localizable sound. For example, following bilateral auditory cortex ablation, monkeys are totally unable to locate the source of a brief sound by walking to it; yet the same animals are able to indicate the direction of the sound source by pressing a lever located on the same side of the animal as the sound source itself (9). Furthermore, cats, opossums, and monkeys deprived of auditory cortex are able to indicate the direction of a sound source by making a reflexive response (2, 10, 16, 21). These results indicate that auditory cortex ablation does not disrupt all of the responses to a localizable sound source but, instead, only some. Therefore, the cortical deficit in sound localization does not appear to be a strictly sensory impairment.

Because auditory cortex ablation disrupts some responses to a localizable sound and not others, the differences between these various responses have been analyzed in the hope of determining the nature of the sound-localization deficit. Such analyses have yielded several possible ways in which the ability to localize may be disrupted. First, it has been noted that cortical ablation appears to have less effect on those responses which can be completed either before or immediately after the sound is turned off. This observation suggests that the animals may have suffered some sort of auditory amnesia such that they are unable to remember the source of a sound long enough to complete a more protracted response, such as walking to the source of a sound (1, 9, 13, 15). The preceding observations also support a second possibility—namely that the animals

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have difficulty in attending to auditory stimuli (9, 14). Though similar to the auditory amnesia explanation, this explanation suggests that the animals may be more susceptible to distractions on auditory tasks and become distracted when required to respond after the sound has been turned off. A third potential explanation explains the deficit in terms of an auditory-motor disconnection. According to this interpretation, auditory cortex ablation may result in a sound-localization deficit because of a surgical separation of the mechanism for detecting sound direction (in the brain stem) from the motor mechanism necessary for the performance of some responses (e.g., walking to the sound source), but not for other responses (e.g., reflexive responses) (9, 15, 16).

The present report presents the results of experiments designed to evaluate these three alternative explanations. In this report we present evidence indicating that dogs with lesions of auditory cortex do not suffer any impairment of auditory memory or attention sufficient to account for the sound-localization deficit. Furthermore, it appears that while these animals are able to perform certain localization tasks, they do not appear to solve them in the same manner as a normal animal.

METHODS

Subjects

In all, six normal dogs (*N-2, N-7, N-13, N-14, N-20, N-22*) and three dogs with bilateral auditory cortex ablations (*B-6, B-9, B-10*) were used in this study. The dogs were mongrels ranging in size from 4 to 10 kg. They were housed in rooms with free access to food and were trained with water reward. Three of the normal dogs (*N-2, N-7, N-13*) and all three of the operated dogs had received previous training in a two-choice auditory discrimination.

Surgical and histological technique

Prior to sound-localization training, aseptic surgery aimed at bilateral ablation of auditory cortex was performed on dogs *B-6* and *B-10*, with *B-9* receiving a two-stage lesion. For surgery, the animal was initially anesthetized with Surital (Parke-Davis) administered intravenously, followed by methoxyflurane administered via an endotracheal cannula as required to maintain a deep level of anesthesia. The animal's head was shaved and washed, the scalp opened, and the temporal muscle dissected with a cautery. With the edges of the temporal muscle retracted, a portion of the cranium overlying the temporal lobe was removed, the dura retracted, and the cortical tissue removed by subpial aspiration.

Following the removal of cortical tissue, the muscle was sewn together and the scalp incision closed. Each animal was given 300,000 U of penicillin G. Behavioral testing for sound localization was begun 5–6 mo after surgery and after the animals had received training on an unrelated auditory discrimination.

Following completion of behavioral testing, the dogs were sacrificed with a lethal dose of pentobarbital and perfused with isotonic saline followed by 10% formalin. After perfusion was complete, the outer and middle ears were routinely examined for evidence of damage or disease. The brains were removed and embedded in gelatin for frozen sectioning. Each brain was sectioned at 33 μm in a frontal plane beginning anterior to the lesion and continuing until just posterior to the lesion. Every eighth section was stained by the cresyl violet technique except in the vicinity of the medial geniculate, where every fourth section was stained. These sections were then used to reconstruct the limits of the cortical lesion and to plot the retrograde degeneration in the medial geniculate and surrounding nuclei.

Behavioral technique

The animals were trained and tested daily in an automated sound-localization chamber based on a design described in detail elsewhere (20). Briefly, the chamber consisted of a 10 x 10 foot (3 x 3 m) room containing two goal boxes and a center water spout and contact plate (Fig. 1). The goal boxes (15 x 15 x 70 cm) each contained two loudspeakers and a water spout connected to a water reservoir via an electrically operated valve. A heavy iron plate attached to the bottom of the box served both as a contact plate and as a weight to keep boxes upright. The room was carpeted and the walls and ceiling were draped with burlap to reduce sound reflections.

A thirsty animal began a trial by placing its feet on the floor plate and its mouth on the center water spout (mounted on a pipe 40 cm high), which closed a contact circuit. The front part of the plate was covered with an insulating rubber mat so that the animal could make contact and start a trial only if its hind feet were on the plate, thus aligning its head with the two goal boxes. Once contact had been made with the center spout, a click or train of clicks was emitted from a loudspeaker located in one of the goal boxes. If the animal approached the goal box from which the clicks had come and made contact with the water spout protruding from it, a water reward was automatically dispensed through the water spout and a correct response was recorded. If the animal approached and licked the spout protruding from the box which had been silent, no reward was given and the room lights were momentarily turned off. After either response, the animal had to return to the center spout and make contact in order to start a new trial.

Details of stimulus

The clicks were produced by 0.1-ms square waves which were amplified and sent to oval loudspeakers (15.25 x 6 cm) mounted in the goal boxes. Two pairs of matched speakers were used, with each box containing one member of each pair. The pairs had been matched by human observers for click quality, and testing revealed that the dogs could not discriminate between them when the angle between the boxes was less than the animal's threshold. The purpose of having two pairs of speakers was to allow the second pair to be used to determine if an animal had learned to discriminate the first pair of speakers on the basis of the quality of the click. Though many such checks were made during the course of the experiment, no discrimination based on click quality instead of click locus was ever discovered.

Three types of stimuli or stimulus arrangements were used: *1*) A "continuous" click train which consisted of a 10/s train of clicks, which came on when the animal made contact with the center spout and did not go off until the animal made contact with a spout in one of the goal boxes. *2*) A "limited" click train which consisted of a 10/s train of clicks, which came on when the animal made contact with the center spout but which went off as soon as the animal broke contact with the center spout. This limitation prevented the animal from tracking the sound or from using head movements, i.e., scanning, to locate the direction of the sound. *3*) A "single click" in which only one click was emitted when the animal made contact with the center spout.

Details of training

Because the animals had been accustomed to drinking from water spouts prior to the study, training was relatively uncomplicated. The experimenter entered the sound-localization room with a thirsty dog and pointed toward the center water spout. The animal would lick the center spout, thus receiving a water reward and initiating a trial. The experimenter would then point to the goal box from which a 10/s click train was being emitted, and the dog would lick the spout protruding from that box. This procedure would be repeated for 5 or 10 min, after which the experimenter would leave the room. Unless a dog was unusually timid or insufficiently thirsty, it would respond on its own without further training. After 5–10 sessions, the animal was usually performing about 200 trials during the 1-hr sessions. By this time the water reward at the center spout was discontinued so that the animal would begin its response to the goal boxes immediately on presentation of a stimulus.

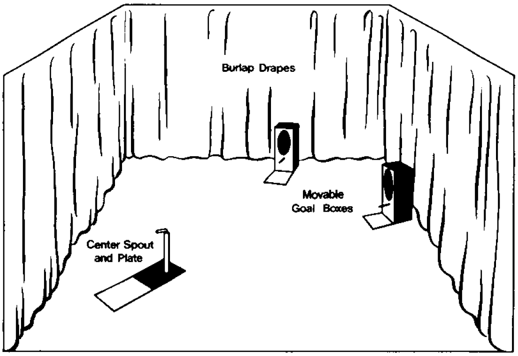

FIG. 1. Sound-localization room used to test animals. Dogs were required to initiate a trial by standing on the floor plate and licking the center water spout, thus positioning themselves equidistant from and facing toward the goal boxes. Animals would then respond to the goal box from which a sound had been emitted by moving to that box and licking the water spout which protruded from it. Variations in the arrangement of the room included moving the goal boxes closer to the center water spout, removing the loudspeakers from the goal boxes and locating them apart from the goal boxes, and placing a sound-transparent partition between the goal boxes extending from the center water spout to the far wall (see text for details).

Details of testing

Throughout training and testing, the locus of the sound source was determined by a quasi-random sequence (4) or by a random sequence. During all of training and most of testing, a correction procedure was used such that following an error, the correct side did not shift. This strategy was used to prevent the animal from responding predominantly to one side by forcing it to respond to the other side in order to get a reward. Since in order to be correct an animal had only to alternate its response following an error, these correction trials were not used in the computation of an animal's performance.

The tests which the animals received are divided into six sections, the details of which are best described as the results unfold. In brief, the tests involved either the localization of a sound in which the distance to the sound source and/or goal box was varied or else the discrimination of two different click trains.

RESULTS

Anatomical results

The probable locus and extent of auditory cortex in the dog is known from the electrophysiological studies of Tunturi (for a review, see Ref. 22) and the retrograde degeneration studies of Sychowa (19). According to these studies, primary auditory cortex is located in the middle ectosylvian gyrus with secondary auditory areas located in the anterior and posterior portions of the ectosylvian gyrus. In addition, the pattern of thalamic degeneration which occurs following cortical ablation suggests that the anterior and posterior sylvian gyri, which lie ventral to primary auditory cortex, have anatomical connections similar to those of the analogous area in the cat (cf. Ref. 13, 19).

Animals *B-9* and *B-10* underwent surgery aimed at bilateral removal of primary and secondary auditory cortex, while *B-6* underwent surgery aimed at bilateral removal of only primary auditory cortex. Figure 2 illustrates the cortical lesion and thalamic degeneration in *B-6* and *B-10*. In *B-6*, the middle ectosylvian gyrus including the depths of the middle suprasylvian and ectosylvian sulci was completely removed or undercut bilaterally. In addition, most of the rostral and caudal portions of the ectosylvian gyrus were also removed, though the depths of the suprasylvian and ectosylvian sulci in these areas were spared. Degeneration in the medial geniculate was complete in the ventral division (cf. Ref. 12), while the dorsal and caudal divisions were spared. Moderate degeneration was found in the ventral quarter of dorsal lateral geniculate and light degeneration in the right pulvinar. In *B-10*, the entire ectosylvian gyrus including the depths of the ectosylvian sulcus was removed or undercut with the exception of the extreme anterior and ventral tips. The sylvian gyrus was

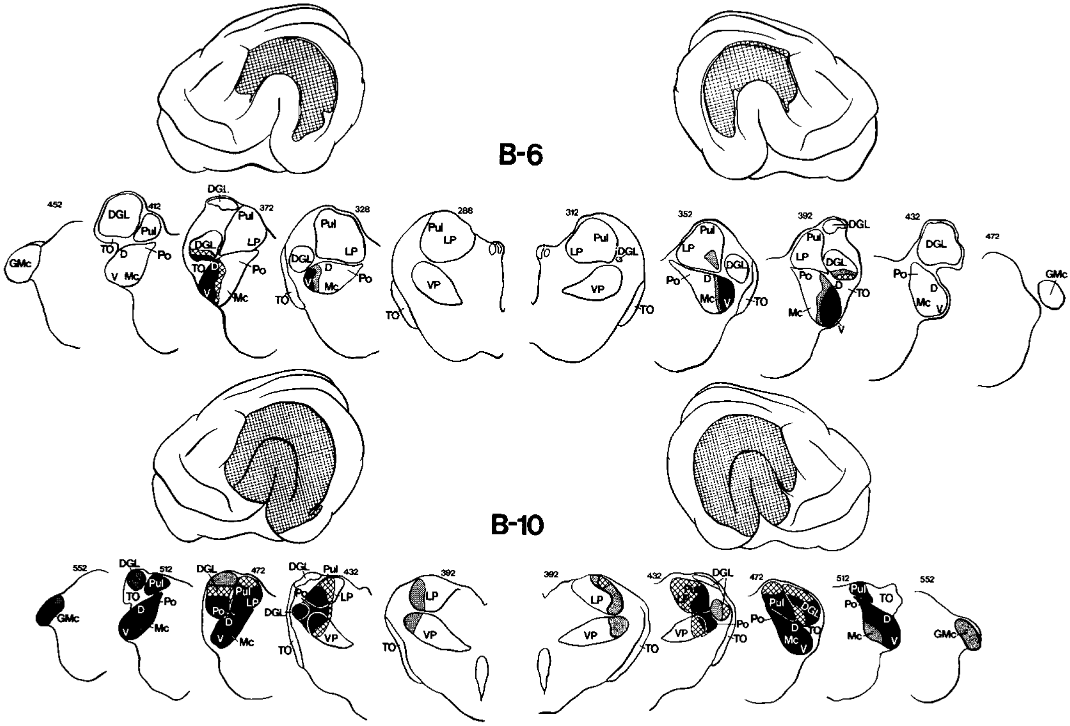

FIG. 2. Cortical reconstruction and medial geniculate degeneration of dogs *B-6* and *B-10*. Area of the cortical lesion is indicated by crosshatching. Area of complete degeneration is blackened, severe degeneration is hatched, and moderate degeneration is stippled. D, dorsal division of the medial geniculate body; DGL, dorsal lateral geniculate nucleus; GMc, caudal division of the medial geniculate body; LP, lateral posterior nucleus; Mc, magnocellular division of the medial geniculate body; Po, posterior group; Pul, pulvinar nucleus; TO, optic tract; V, ventral division of the medial geniculate body; VP, ventroposterolateral nucleus.

similarly totally removed. The anterior and middle portions of the principle division of the medial geniculate were completely degenerated, with moderate degeneration in caudal tip. The posterior group was completely degenerated and the magnocellular portion of the medial geniculate was completely degenerated anteriorly and at least moderately degenerated throughout the rest of the nucleus. In other portions of the thalamus, pulvinar, lateral posterior, ventral posterior, and dorsal lateral geniculate were partially degenerated bilaterally. The lesion in *B-9* was similar though slightly larger than the lesion in *B-10*.

In summary, primary auditory cortex was removed bilaterally in *B-6*, while the primary and secondary auditory areas were removed bilaterally in *B-9* and *B-10*. This distinction between the two types of lesions may be important for two reasons, which will be seen more clearly as the behavioral results unfold. First, the animal with the lesion confined to primary auditory cortex (*B-6*) exhibited the same pattern of deficits as did the other two operated animals. Second, throughout testing the degree of these deficits appeared to be less severe in *B-6* than in the other two animals. As will be discussed later, these results suggest that while total removal of both primary and secondary auditory areas results in a more severe deficit in sound localization than do smaller lesions, the removal of primary auditory cortex alone may be sufficient to produce the classic deficit in sound localization.

Behavioral results

The behavioral results described here are concerned with the analysis of the sound-localization deficit resulting from bilateral ablation of auditory cortex. But before describing these results it should be noted that each of the operated animals as well as three of the normal animals (*N-2, N-7, N-13*) previously received extensive training and testing in the discrimination of natural sounds (7, 8). Thus, not only were the animals highly experienced observers, but their ability to discriminate sounds using auditory cues other than locus cues had already been demonstrated. Therefore, the failure of the operated animals on some of the tasks described here cannot be attributed to a generalized inability to cope with the motor, intellectual, emotional, or motivational requirements of the tests but, instead, demonstrate much more specific deficits.

1. SOUND LOCALIZATION: DISTANT SOUND SOURCE AND GOAL BOX. In the first test the animals were required to locate the source of clicks emanating from goal boxes placed 60° apart and 250 cm in front of the center spout. Figure 3*A* shows that the normal animals were easily able to locate the correct goal box when either a continuous 10/s click train, a limited 10/s click train, or a single click was used as the stimulus. The operated animals were also able to locate the correct box when the continuous click train was used, though their scores were lower than normal. However, when the click train was turned off as soon as the animal broke contact with the center water spout (i.e., the limited click train), the animals' performances fell abruptly, with one animal totally unable to solve the discrimination. Furthermore, none of the operated animals proved able to localize a single click.

2. SOUND LOCALIZATION: NEAR SOUND SOURCE AND GOAL BOX. In this test the goal boxes were moved to 20 cm in front of the center spout (while maintaining the 60° separation) so that instead of having to walk to the goal box, the dog needed only to turn its head to reach the water spout. The results of this test (shown in Fig. 3*B*) demonstrate that moving the goal boxes closer to the center spout had a dramatic effect on the performance of the operated animals. First, the animals were able to localize the limited click train at a comparatively high level of performance, though not as well as normal animals. Second, all three operated animals were able to localize single clicks at levels well above chance though, again, their performance levels were obviously below normal. From these results, though, it is clear that under certain circumstances animals with bilateral auditory cortex lesions can demonstrate an ability to localize very brief sounds.

In moving the goal boxes closer to the center spout, two major changes were made. First, the loudspeakers were now closer to the animal and second, the response spouts were also closer. To determine whether the proximity of the loudspeakers or the response spouts (or both) was the crucial fac-

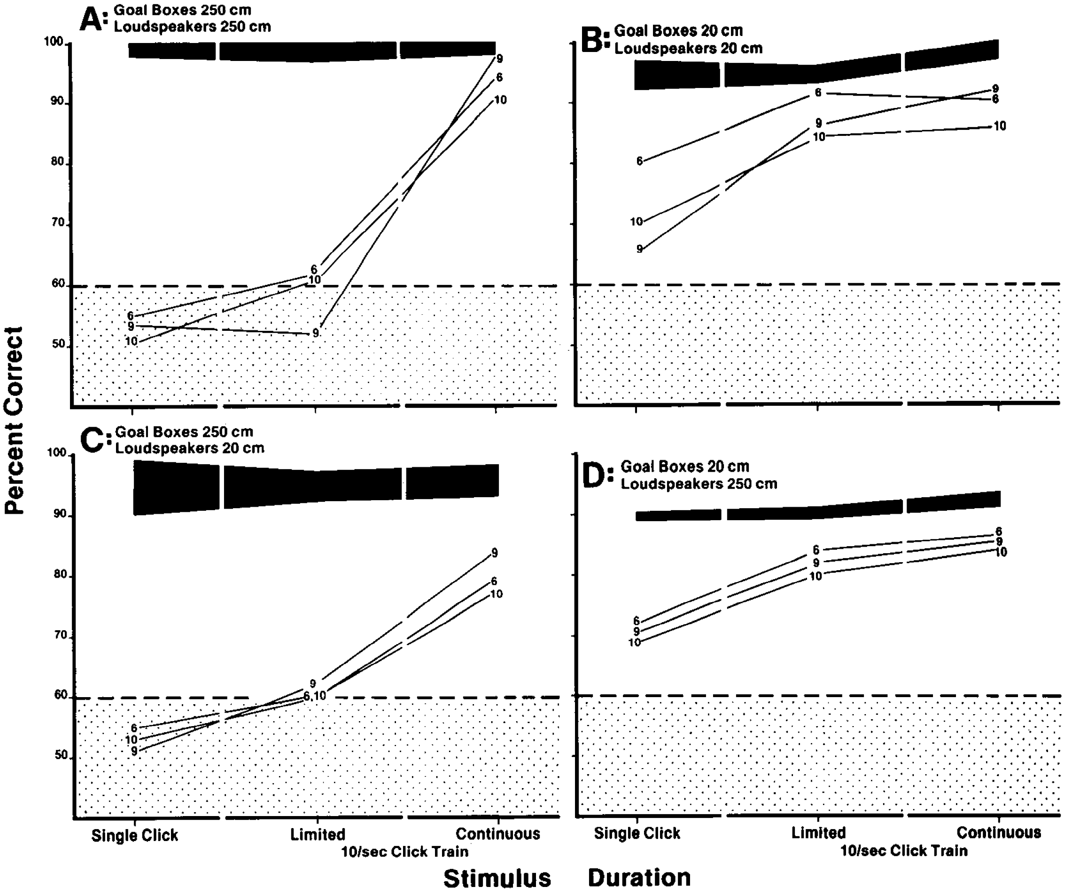

FIG. 3. Performance of the three animals with auditory cortex lesions (*B-6*, *B-9*, and *B-10*) on four sound-localization tasks. *A*: goal boxes and loudspeakers located 250 cm from the center spout. *B*: goal boxes and loudspeakers 20 cm from center spout. *C*: goal boxes 250 cm and loudspeakers 20 cm from center spout. *D*: goal boxes 20 cm and loudspeakers 250 cm from center spout. Three stimuli were used: a single click, a limited 10/s click train which was turned off when the animal broke contact with the center spout, and a continuous 10/s click train which remained on until the animal responded at one of the goal boxes. Blackened areas above indicate the range of performance for three normal dogs, while stippled areas below indicate chance performance. Note that all the operated animals performed successfully when the goal boxes were located 20 cm from the center spout, but not when they were located 250 cm away, regardless of the location of the loudspeakers.

tor, the next two tests were given in which the speakers and goal boxes were set at different distances.

3. DISSOCIATION OF LOUDSPEAKERS AND GOAL BOXES. In these two tests the loudspeakers were mounted on stands so that they could be placed independently of the goal boxes. Though the goal boxes and loudspeakers were now located at different distances, they were always located at the same angle of separation (i.e., 60°). Thus when the goal boxes were located 20 cm from the center spout the speakers were located 250 cm behind them, and vice versa. This dissociation of the sound source from the response could be expected to adversely affect performance itself. However, as a comparison of Fig. 3*C* and *D* with 3*A* and *B* shows, not only did the normal animals have little difficulty in performing these tests, but even the operated animals could still solve the task when the continuous click train was used.

When the loudspeakers were 20 cm from the center spout and the goal boxes located 250 cm away, the performance of the operated animals paralleled their performance when both loudspeakers and goal boxes were located 250 cm away (cf. Fig. 3*A* and *C*). In this test the animals could perform successfully when the click train was kept on until they completed their response, but they could barely perform above chance when the limited click train was used, and fell to chance entirely when the stimulus was a single click. In nearly all respects the performance of the operated animals in this situation parallels the results of test 1 in which both the goal boxes and loudspeakers were located 250 cm away from the center spout.

In contrast, placing the goal boxes 20 cm from the center spout and the loudspeakers 250 cm away did result in an improvement in performance (Fig. 3*D*). With the goal boxes close to the center spout, the operated animals were able to discriminate all of the stimuli, including single clicks, at a level well above chance. Thus, it appears that it is the proximity of the goal boxes and not the loudspeakers which was the crucial factor in the performance of the animals with bilateral auditory cortex ablation.

4. SOUND LOCALIZATION: EFFECT OF DISTANCE. Once it had been determined that the operated animals could localize single clicks when the goal boxes were 20 cm away, the performance of the animals on the single click localization task was determined with the goal boxes placed at various distances from the center spout, but always 60°apart. It was found in this test that the performance of the animals decreased as the goal boxes were moved further away from the center spout (Table 1). The performance of the two animals with larger lesions (*B-9* and *B-10*) fell to chance when the goal boxes were 50 cm away. However, the performance of the animal with the smaller lesion (*B-6*) remained above chance until a distance of 125 cm had been reached.

SUMMARY OF TESTS 1–4. All three of the animals with bilateral auditory cortex ablations were unable to locate the source of a single click when the goal boxes were located 250 cm away from the starting point. This result was obtained even in the case of *B-6* in which primary auditory cortex was ablated while a large part of the secondary auditory areas were spared. However, all three of the animals were able to solve the task at a level well above chance when the goal boxes were placed 20 cm from the starting point—a change which allowed the animals not only to make their response in a shorter period of time, but to make it using a simpler motor response (i.e., turning their head instead of moving their body to reach the goal boxes). When tested on their ability to localize single clicks with the response boxes located at various distances from the center spout, it was found that the performance of the two animals with the larger lesions (*B-9* and *B-10*) fell to chance at a distance of 50 cm, while the performance of the animal with the smaller lesion (*B-6*) remained above chance until a distance of 125 cm had been reached. In addition, it was found that the operated animals were generally better able to localize a 10/s click train which was turned off when they broke contact with the center spout (limited click train) than a single click. This result suggests that a stimulus of longer duration is slightly easier to localize even if scanning and tracking movements are not permitted. It should be noted, however, that in each of the above tests the operated animals were clearly inferior to the normal animals in localizing any of the sounds, regardless of the duration of the sound.

TABLE 1. *Ability of dogs with bilateral auditory cortex lesions to localize a single click as a function of distance to goal box*

	Distance to Goal Box, cm				
Dog	10	20	50	125	250
B-6		80	64	60*	55*
B-9	73	65	54*		54*
B-10	77	70	56*		51*

Values are percentages correct, based on at least 100 trials. All testing was conducted at 60° separation. * Chance performance ($P > 0.01$).

These first four tests demonstrate that following bilateral ablation of auditory cortex, dogs are unable to locate the source of a brief sound in one situation yet can perform successfully in another situation. As was mentioned previously, several hypotheses have been offered in order to explain this phenomenon. The following tests were, therefore, directed at the problem of determining which explanation might best account for the behavior of the operated animals.

5. DISCRIMINATION OF BRIEF CLICK BURSTS. The ability of the animals to succcessfully perform the sound-localization task when the response boxes were located close to the starting point, but not when they were further away, could be accounted for by the attention and memory hypotheses (1, 9, 13, 15). According to these explanations, an animal with bilateral lesions of auditory cortex is able to localize a brief sound, but is either unable to store this information (amnesia) or is distracted before it can respond on the basis of the information (attention deficit). As a result, such an animal might be able to successfully solve the task if it could respond immediately after the sound had been presented, but would be unable to remember the locus of the sound source long enough to make a response which took several seconds to complete.

The following test was designed to determine if the three operated animals suffered some sort of general inability to attend to or remember auditory stimuli, which could account for their failure to discriminate the locus of a sound when the goal box was located 250 cm away from the starting point. In this test the goal boxes were placed 60° apart and 250 cm in front of the center spout, as in the first sound-localization test. However, the stimuli were presented via a loudspeaker placed 250 cm in front of the center spout (i.e., midway between the two goal boxes). When an animal made contact with the center spout a burst of either 100 or 10/s clicks was emitted for 0.3 s, and the animal was required to respond to the left goal box when the 100/s click train was presented and to respond to the right goal box when the 10/s click train was presented. It is important to note that all three operated animals had previously been tested on their ability to localize these two click bursts when the goal boxes were placed 250 cm away. Not one of the operated animals was able to perform at a level above chance. Therefore, this test was designed to determine if animals with bilateral auditory cortex lesions could discriminate sounds which they could not locate when tested in the same manner.

If the operated animals had suffered some sort of general auditory amnesia or inability to attend to brief sounds, then it would be expected that they would not be able to discriminate the brief 100 and 10/s click bursts when required to respond to goal boxes located 250 cm away from the starting point. As Fig. 4 illustrates, however, not only were the operated animals able to discriminate these brief sounds, but their performances, for the first time in this series of tests, fell within normal limits. That is, the animals were able to attend to these brief sounds long enough to discriminate them and were able to remember which sounds had been presented long enough to respond to the appropriate goal box. Furthermore, this test demonstrates that the animals were able to make a spatial response (i.e., moving to the goal boxes) to an auditory stimulus. Therefore, the failure of these animals to localize brief sounds when the goal boxes were placed 250 cm away cannot be ascribed to either a general amnesia for brief auditory stimuli or to an inability to attend to brief sounds. Nor, for that matter, can it be due to an inability to make a spatial response using auditory cues.

6. TRACKING TEST. The ability of the operated animals to discriminate brief sounds in a task which required them to move to goal boxes located 250 cm away rules out the possibility of a general auditory amnesia as an explanation for the deficit in sound localization. However, it does not rule out the possibility that the animals may have suffered a memory deficit specific to the localization of sound. For example, it is possible that the animals retained the ability to remember which sound had been presented while losing the ability to remember where the sound had come from.

If the sound-localization deficit is primarily the result of such a specific memory deficit, then an operated animal would be expected to normally localize a sound which stayed on until the animal completed its response. However, there is reason to believe that animals with bilateral auditory cortex ablation do not localize even continuous sounds in the same manner as normal animals, but that they instead track the sound (e.g., Ref. 15, 17). Indeed, during sound-localization tests employing a continuous click train, it was noticed that while the normal animals almost always began moving toward the correct goal box, the operated animals appeared to begin their response by moving toward one of the goal boxes at random and if it were the incorrect or silent goal box, they would usually veer away from it and respond to the other goal box.

To quantify this observation, the animals were required to localize a continuous 10/s click train emitted from goal boxes which were located 60° apart and 250 cm in front of the center spout (as in test 1). However, a sound-transparent partition (constructed of 0.5-inch hardware cloth on a wooden frame 90 cm high) was placed between the goal boxes extending from the center spout to the far wall. The purpose of this partition was to enable the experimenter to unambiguously determine the animal's initial response, that is, the goal box toward which it took its first step. Since the animal was allowed to turn around and cross over the center plate to the other side of the partition, providing it had not already made contact with a response water spout, the animal's initial response could differ from its final response.

The results of this test, shown in Fig. 5, illustrate that the normal animals nearly always started out in the direction of the correct goal box. Since the animals were allowed to retrace their steps and respond on the other side (provided they had not already responded to the goal box on the initial side), all of the normal animals were 100% correct on their final response. In contrast, only one of the three operated animals (*B-6*) was able to perform at a level above chance on its initial response and even in this case, performance was relatively poor. In most cases in which the animals initially approached the incorrect goal box, the animals turned back and crossed over to the correct goal box without contacting the incorrect water spout. As a result, their final response scores are all well above chance.

The results of this test indicate that unlike the normal animals, the operated animals were unable to determine the locus of a continuous sound until they had moved closer to the goal boxes. This finding suggests that the operated animals were tracking the sound by moving about the sound field in order to determine where the sound was more intense—a behavior which has been observed in cortically ablated animals by others (15, 17). Such behavior is inconsistent with the hypothesis of a memory deficit, which would predict that the animals would perform normally at least until the sound was turned off. Thus, it does not appear that the sound-localization deficit is the result of an impairment in memory specific to the localization of sound.

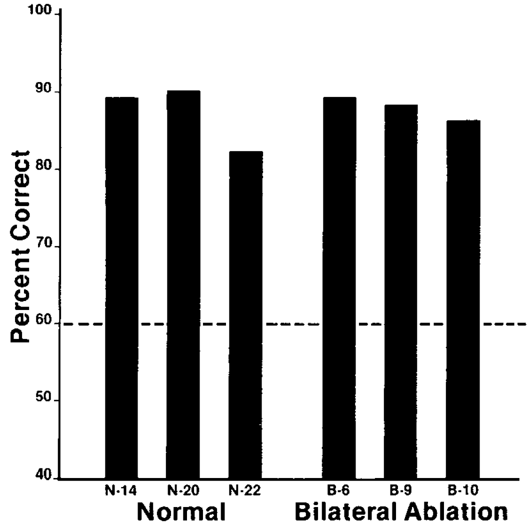

FIG. 4. Performance of three normal and three operated animals on the discrimination of 0.3-s bursts of 100/s and 10/s click trains. Animals were trained to respond to the left goal box when the 100/s click burst was presented and to the right goal box when the 10/s click burst was presented. Both goal boxes were located 250 cm away from the center spout. All the operated animals were able to discriminate these stimuli at normal levels of performance even though they were unable to localize them under similar conditions. Dotted line indicates chance level of performance.

7. ANALYSIS OF LOCALIZATION PERFORMANCE. At this point it became apparent that we had no indication that the animals were able to localize sounds in the same manner as normal dogs. When presented with sounds of long duration the animals appeared to track instead of localize, and when presented with brief sounds the animals could successfully solve the task only if the goal boxes were moved close to the animal. Even in the latter case, however, the operated animals were clearly inferior to the normal animals (cf. Fig. 3*B*, *D*). In order to obtain more information on their performance we reanalyzed our data to determine if there were any further clues concerning the way in which the operated animals were

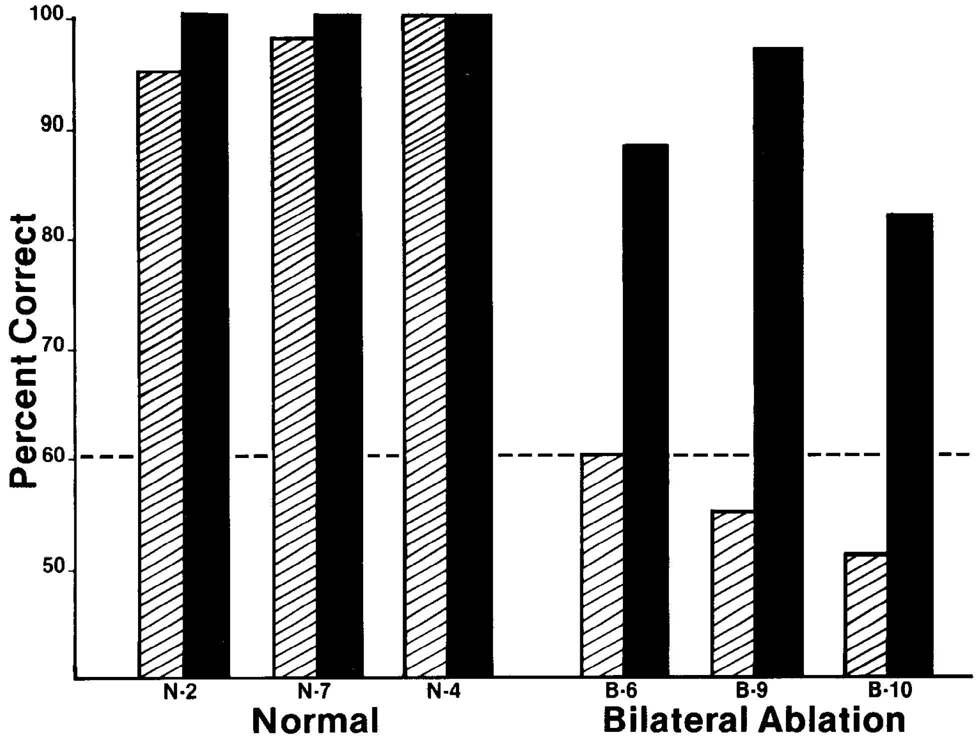

FIG. 5. Performance of three normal and three operated animals on the tracking test, which involved the localization of a continuous 10/s click train. The hatched bar indicates the percentage of trials on which an animal started toward the correct goal box, while the solid bar indicates the final response of the animal. Note that while all animals were eventually successful in locating the correct goal box, the operated animals did not usually begin their response in the correct direction. This result suggests that unlike the normal animals, the operated animals tracked the sound in order to determine its source. Dotted line indicates chance level of performance.

solving the localization task. We found one such clue in the ability of the animals to learn the 100/s versus 10/s click train discrimination.

In training the animals for the 100/s versus 10/s click train test, it was immediately noticed that the normal animals had much difficulty in solving the task. In contrast, the three operated animals had little difficulty in learning the task with each of the animals reaching a criterion of 90% correct (for two consecutive blocks of 20 trials) within 40 to 80 trials. The relative ease with which the operated animals learned to discriminate the two click trains can be seen in Fig. 6, which shows the number of errors in the first 50 training trials for this task (in which a continuous click train was used). In this task the operated animals attained overall scores for the first session of between 88 and 90% correct, while none of the normal animals was able to perform at a level above chance.

The difficulty encountered by the normal dogs in this task may have been related to the difficulty normally encountered in attempting to train an animal to make a spatial response to a nonspatial stimulus. Indeed, Konorski and his colleagues (3) have shown that dogs learn to approach the source of a sound much more readily than they learn to go left or right on the basis of frequency cues. In the present experiment this tendency was probably reinforced by the extensive sound-localization training which the dogs received. That this training may have interfered with learning the click-rate discrimination is suggested by the fact that prior to this training, the three normal dogs which failed to learn the discrimination received over 30 sessions in which the locus of the sound was the relevant cue, while the three normal dogs which ultimately learned the discrimination had received 10 or fewer such sessions. Thus, it is possible that the sound-localization training which the normal dogs received may have interfered with the learning of the click-rate discrimination.

That the three operated dogs had no such difficulty in learning the click-rate discrimination may possibily be due to two factors. First, if the animals were unable to perceive the spatial attributes of a sound source, then the more than 80 sessions of sound-localization training which each of the operated animals received would not be expected to have interfered with learning the click-rate discrimination. That is, if the experience which the animals received in localizing sounds was devoid of spatial meaning, then the training would not have been expected to adversely affect their ability to learn a nonspatial discrimination. Second, if the operated dogs had lost the ability to perceive the spatial attributes of sound and were, therefore, solving the sound-localization tasks on the basis of a nonspatial interpretation of the cues supplied by the brain stem or midbrain auditory nuclei, then such training might possibly have been expected to facilitate their learning a new nonspatial discrimination. Whether one or both of the above explanations accounts for the superiority of the operated dogs in learning to make a spatial response to a nonspatial auditory cue, it is apparent that in this test, as in the tracking test, we were unable to find any indication that the animals were solving the localization tasks in a normal manner.

DISCUSSION

The results show that dogs deprived of auditory cortex bilaterally are unable to demonstrate an ability to localize single clicks if they are required to walk to response boxes located, in this case, 125 cm or more away. Furthermore, presenting the animals with a brief burst of clicks which they are unable to track or scan (i.e., the limited click train) improves performance only marginally and the animals are consistently successful only when the sound is left on until they complete their response. These results are virtually identical to those found for monkeys with auditory cortex lesions (9) and agree well with the results of Neff and his colleagues (13) with cats.

However, moving the goal boxes closer to the animal results in a dramatic improvement in performance on the single click and limited click localization tasks. The operated animals were previously unable to perform the single click discrimination, whereas now they could perform consistently above chance when the goal boxes were sufficiently close. It appears that moving the goal boxes closer allowed the animals to demonstrate their ability to localize sound, indicating that they did not suffer from a strictly sensory impairment. This demonstration of the effect of the distance to the goal boxes on performance confirms the findings of others (15).

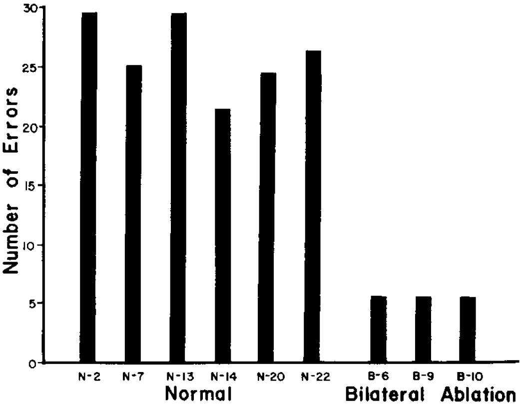

FIG. 6. Number of errors in the first 50 trials involving discrimination of a 100/s and a 10/s click train. The large number of errors made by the six normal dogs indicates that these animals had great difficulty in transferring from a sound-localization discrimination to a discrimination involving nonspatial cues. In contrast, the operated dogs had little difficulty in learning the nonspatial discrimination, and all three were performing well above chance after the first 50 trials. This result suggests that the sound-localization training which all nine animals had previously received interfered with the learning of a nonspatial discrimination only in the case of the normal animals.

Relation of deficit to lesion

Before turning to an evaluation of these results, it is of interest to note the extent of the lesion necessary to produce a deficit in sound localization. In the present study, primary auditory cortex was completely removed bilaterally in animal *B-6* while a large portion of the secondary auditory areas were spared on both sides. The fact that this animal was unable to perform the single click localization test when the goal boxes were 250 cm away is consistent with the results of at least two previous studies. First, monkeys with lesions of primary auditory cortex were unable to walk to the source of a single click which was located 170 cm away (9). Second, cats with lesions confined to AI have been shown to be deficient in their perception of binaurally presented clicks (11), indicating that such lesions are sufficient to disrupt the perception of the locus of a sound source.

Nor do these results disagree with those of Neff (13) and Strominger (18) who have found that ablation of AI does not completely impair the ability to localize sounds. Throughout testing the performance of *B-6* was superior to that of the animals with larger lesions. Not only was the animal able to perform the single-click localization task at a greater distance than the other animals, but it also seemed more adept at performing the limited click-train task. As a result, it is quite likely that *B-6* would have been able to perform successfully in the task used by Neff and his colleagues which employed both a longer duration sound (e.g., five 0.5-s presentations of a buzzer) and a shorter distance to the goal boxes (3 feet or 90 cm). The test used in the present study may well be more sensitive to the presence of a sound-localization deficit, thus accounting for the failure of *B-6* on this test.

Auditory attention or memory deficit

Turning now to the different explanations of the deficit, it has been suggested that an inability to attend to or to remember brief sounds may account for the inability of the animals to approach the source of a brief sound (1, 9, 13, 15). Indeed, it could be argued that the animals in the present study could not remember where the sound came from or else were distracted before they could move to goal boxes located 250 cm away, although they could remember long enough to respond when the boxes were only 20 cm away. However, the results of the 100/s versus 10/s click train discrimination demonstrate that the localization deficit cannot be explained in terms of a general inability to attend to or remember brief sounds. In the click-rate discrimination, the animals were not only required to discriminate brief sounds, but they were required to respond by moving to one or the other of the goal boxes, which were located 250 cm away. The ability of the operated animals to discriminate sounds that they could not localize and to do so by moving to the goal boxes after the sound had been turned off rules out the possibility of any general amnesia or deficit in attention for auditory stimuli.

Though the animals appeared to have suffered no general auditory amnesia or impairment of attention, the next question concerns the possibility that they suffered an impairment specific to sound localization. For example, the animals may have been unable to remember the locus of a sound though their memory of the other parameters of sound (e.g., frequency, intensity, timbre) may have been unimpaired. However, such an argument must assume that the animals were capable of normally localizing sound, for it is difficult to argue for a specific memory deficit if there is nothing to forget. Yet we were unable to detect any sign that the animals ever solved the localization tasks in a normal manner. For example, the results of the tracking test indicate that the operated animals did not normally localize a continuous sound. If the animals had only suffered an amnesia specific to sound localization, it would be expected that the animals would localize sounds normally until they forgot the locus. Yet, when presented with the task of localizing a continuous sound, in which memory presumably would not be a factor, the animals did not demonstrate an ability to normally localize sound, but instead apparently solved the task by tracking the sound. This result suggests that the operated animals may have been incapable of normally localizing sound and that their deficit stemmed not from an inability to attend to or remember the locus of a brief sound, but from an inability to determine the locus of a sound source in the same manner as a normal animal.

Auditory-motor disconnection

It has previously been suggested that bilateral ablation of auditory cortex may result in a surgical separation of the sound-localization mechanism from the motor mechanism necessary for some, though not all, behavioral responses (9, 15, 16). The idea of analyzing cortical deficits in terms of a disconnection syndrome is not new (5, 6) and may be helpful in explaining the results of the sound-localization experiments. From this point of view, the mechanism for detecting sound direction (in the brain stem) is viewed as being disconnected from the motor mechanism necessary for the performance of the task when the goal boxes are located comparatively far away, but that some connection remains which enables the animals to perform successfully (albeit poorly) when the goal boxes are located near the starting point. This line of reasoning would also apply to the ability of operated animals to press levers or to make reflexive responses on the basis of the locus of a sound source (2, 9, 10, 16, 21).

Though we know of no line of evidence which would specifically refute the idea of an auditory-motor disconnection, this explanation is as yet incomplete. In particular, it is still necessary to determine a basis for predicting which responses to a localizable sound will be affected by cortical ablation and which will not. For example, the determining factor may be the extensiveness of the muscle groups required for the motor program, the length of time necessary to complete the response, or both.

Before assuming that the ability of an operated animal to perform a particular localization task is due to the survival of direct connections between the auditory system and the particular motor system involved in the behavioral response, another possibility must be considered. If cortical ablation separates the sound-localization mechanism from some, but not all of the motor mechanisms, it is possible that the surviving motor responses to locus cues may be used indirectly as a means of solving some of the sound-localization tasks. For example, it is known that cats without auditory cortex retain the ability to indicate the direction of a sound source by means of an unconditioned orienting reflex (2, 21). This reflex, then, is a motor response that survives cortical ablation and that could possibly serve as the source of cues to solve some of the other sound-localization tasks. For example, it may provide kinesthetic feedback, which could serve as a cue in shock avoidance and conditioned suppression tasks. The idea that the operated animals might learn to use a secondary cue, such as reflex orientation, is not new (11). Nor is the use of such an indirect and subtle cue incompatible with results which show that, even at best, the animals are never able to perform at normal levels. Indeed, with the advent of sensitive behavioral tests capable of detecting the slightest abilities, such a possibility must be considered.

In spite of any uncertainty concerning the means by which animals with auditory cortex lesions are able to make some responses to the locus of a sound, it appears that the cortical deficit in sound localization is not a strictly sensory deficit, nor does it appear to be due to an impairment in memory or attention or in the ability to make a spatial response to an auditory cue. Furthermore, it appears that the auditomotor interpretation may prove to be of use in the investigation of the role of the cortex in hearing.

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