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The Neurobehavioral Study of Auditory Cortex

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Introduction

The use of ablation-behavior experimentation to study auditory cortex began during the second half of the 19th century when it was discovered that sensory and motor functions could be localized to different parts of neocortex. Since that time, our views on the role of auditory cortex have gradually evolved as the results of new studies have added to, or revised, previous findings. Sometimes new findings have met with general acceptance; at other times, they have been accompanied by controversy, and the view that prevailed at the time has not always been the correct one. The purpose of this chapter is not only to present our views of the function of auditory cortex, but to describe how we arrived at them.

History

19th Century

During the first half of the 19th century, it was generally believed that the cerebral hemispheres were the seat of consciousness, although, contrary to the claims of the phrenologists, the various functions were not localized to specific areas (e.g., James, 1890). This view was based primarily on the ablation studies of Pierre Flourens, who claimed that the cerebral lobes were "... the seat of sensations, perception and volition", and that the degree to which these

functions were affected depended on the size of the lesion, with total removal of the lobes resulting in a total deficit (Flourens, 1824). However, Flourens' work was conducted primarily on birds and the cerebral lobes of birds are not homologous to the neocortex of mammals. Thus, Flourens' generalization of his results from birds to mammals is an early example of the pitfalls encountered in generalizing results obtained on one species to others.

The strong anti-localization views held by early researchers was a reaction to the localizationist claims of the phrenologists. Indeed, phrenology played such a prominent role in the early study of cerebral cortex that well into the 20th century, Charles Sherrington was still giving a relatively detailed discussion of the theories of Franz Gall (Sherrington, 1926). As a result, 19th century researchers were cautious about making claims regarding the localization of function in the cortex. The first serious inkling that functions were localized in the cortex came from the work of Paul Broca, who described a patient with a frontal lobe lesion that all but abolished the ability to speak—interestingly, Broca noted in his paper that his placement of the “seat of the faculty of language” differed from that of the phrenologists, which he likely did as a way of distancing himself from them (Broca, 1861). However, it was the publication by Fritsch and Hitzig (1870) of their results of electrically stimulating cortex in the dog that finally convinced researchers that different functions could be localized in the cortex. (It may be noted that Fritsch and Hitzig were not the first to electrically stimulate cortex and much of their paper is devoted to attempting to explain the negative results of others, as well as the ablation results of Flourens.)

Following on the work of Fritsch and Hitzig, a number of researchers began to search for the various functional areas they expected to find in the cortex, including an auditory area. One of the leading localizationists in this search was a British physician, David Ferrier, who conducted a series of experiments to find auditory cortex in monkeys (for references, see H. E. Heffner, 1987; James, 1890). The standard procedure at that time was to initially identify a functional area by electrical stimulation. Once an area had been delineated, it was then removed surgically to see if that particular function was abolished. Thus, Ferrier began by electrically stimulating cortex and looking for an auditory startle response, which he found when he stimulated the posterior two thirds of the superior temporal gyrus (Fig. 1; Ferrier, 1875). The next step was to surgically remove that area and, based on Flourens' view that the cerebral lobes were the seat of consciousness, it was expected that such lesions would completely abolish hearing (e.g., James, 1890). Ferrier found that bilateral ablations that included the superior temporal gyrus did indeed render monkeys unresponsive to sound. In addition, unilateral lesions resulted in a lack of response to sounds presented to the ear contralateral to the lesion, a phenomenon Ferrier demonstrated by plugging the ipsilateral ear.

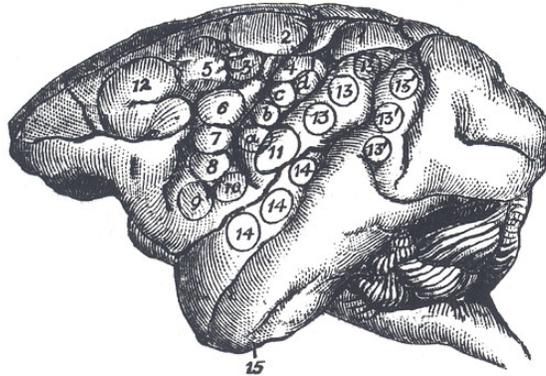


Figure 1: Auditory cortex in the macaque brain (14) as defined by David Ferrier (1875).

Although Ferrier's findings met with initial acceptance, this soon changed. One source of doubt was the finding by Luciani that temporal lobe lesions did not produce permanent absolute deafness in dogs—Ferrier's response to this was that there were species differences and dogs would not show the same degree of impairment as monkeys and humans (see Heffner, 1987). However, a more serious problem was the failure of Edward Schäfer and his colleagues in 1889 to replicate Ferrier's results in monkeys. Although Schäfer's initial results appeared to support Ferrier's, a later series of cases failed to show deafness following bilateral lesions of the superior temporal gyrus. Ferrier's response was that Schäfer's lesions were incomplete, though he eventually was willing to concede that cortical lesions might not cause total deafness. However, in the opinion of William James, it was Schäfer's failure to find total deafness in monkeys that was the more important of the two results, by which James implied that auditory cortex was probably not located in the superior temporal gyrus of monkeys. [In contrast, James felt that the work on sensory aphasia definitely indicated that auditory cortex in man was located in the temporal lobe, particularly the posterior two thirds of the superior temporal gyrus, which he labeled as "Wernicke's Area" (James, 1890, p. 39, Fig. 11).]

The reason for William James favoring Schäfer's negative results lay in the view that "...the *loss* of [a] function does not necessarily show that it *is* dependent on the part cut out; but its *preservation* does show that it is *not* dependent: and this is true though the loss should be observed ninety-nine times and the preservation only once in a hundred similar excisions." (James, 1890; p. 43; emphasis in the original). Indeed, this rule still applies today, assuming, of course, that the difference in results is not due to differences in the lesions. Thus, a hundred years elapsed before it was discovered that Ferrier was correct: ablation of auditory cortex in primates *does* result in a hearing loss, the failure of Schäfer to find such a deficit was probably because his lesions were incomplete,

and not all species show a cortical hearing loss (H. E. Heffner & Heffner, 1990a).

Middle 20th Century

It has been noted that the modern era of auditory neurobehavioral studies dates to the late 1940's, when Dewey Neff and others returned from the armed forces to set up experimental laboratories (Masterton, 1997). Together with their students, they began to use the ablation-behavior method to study the auditory system. A major advance in their work was that, where previous studies had looked at an animal's *unconditioned* response to sound, animals were now trained to detect and discriminate sounds using conditioning procedures. Thus, after pretraining and testing of auditory discriminations, using carefully controlled auditory stimuli, circumscribed lesions were made and postoperative testing of the same discriminations was conducted. Another advance was the careful histological verification of the lesions along with a description of the resulting thalamic retrograde degeneration added by Irving Diamond, a substantial improvement over the gross verification of lesions conducted during the 19th century.

Frequency discrimination. The 1940's witnessed advances in the electrophysiological study of the brain and it was soon discovered that auditory cortex could be divided into different areas, many of which were tonotopically organized (for a well-known summary, see Woolsey, 1960). To many researchers, the tonotopic arrangement suggested that auditory cortex was necessary for the discrimination of frequency and ablation studies were soon performed to test that hypothesis (e.g., Butler & Neff, 1950; Evarts, 1952). Although most studies found that cortical lesions did not abolish frequency discrimination, Meyer and Woolsey (1952) reported that cats with large auditory cortex lesions were no longer able to discriminate frequency. This finding resulted in some controversy and the search for an explanation of the discrepancy focused on differences in the behavioral and stimulus presentation procedures (Neff et al., 1975).

That procedural differences accounted for the different results was suggested by R. F. Thompson in Woolsey's laboratory (Thompson, 1960). The main difference between the two procedures was that Neff's group required animals to respond to a change in the frequency of an ongoing train of tone pulses; Meyer and Woolsey, on the other hand, required animals to discriminate a train of tone pulses in which the last pulse differed in frequency from the preceding pulses from another train in which all the tone pulses were the same frequency. Thompson found that although operated animals could detect a change in frequency when tested with Neff's procedure, they failed to respond differentially to the two tone trains in Meyer and Woolsey's procedure. Because the animals responded equally to both pulse trains (i.e., their false positive rate increased), he concluded that removal of auditory cortex interfered with their ability to inhibit a response to the non-target or neutral stimulus.

Neff and his colleagues, however, had a different interpretation (e.g., Neff

et al., 1975). They focused on whether the sounds to be discriminated were presented against a background of silence (Meyer and Woolsey's task) or whether there was an on-going signal with the animal simply required to detect a change in the signal (Neff's task). Specifically, they proposed that neural habituation takes place when a neutral stimulus is presented for some time and that changing to a new frequency then elicits a larger neural response to which an animal with an auditory cortex lesion is able to respond (Neff, 1960; Neff et al., 1975). This formulation, which came to be known as the "Neff Neural Model", was more a description of what the auditory system did in the absence of auditory cortex, than a theory of what auditory cortex did.

Our current views differ from both previous ones. With the development of advanced behavioral techniques, we now know that although cortical lesions result in increased frequency discrimination thresholds, they do not abolish the ability of an animal to respond to tone trains that differ in frequency (Harrington, R. S. Heffner, & H. E. Heffner, 2001). The fact that both Meyer & Woolsey (1952) and Thompson (1960) were unable to get their animals to perform was because a go/no-go procedure gives little control over an animal's false positive rate with the result that an animal may adopt the strategy of responding to both the target signal and the neutral signal when a task becomes difficult (H. E. Heffner & R. S. Heffner, 1995). Thus, auditory cortex lesions do not abolish simple frequency discrimination regardless of whether the animals are trained to detect a change in frequency or to discriminate between two different frequencies (Cranford, 1979)

Tone patterns. A second line of inquiry concerned the role of auditory cortex in discriminating tone patterns, an investigation that was prompted by the discovery that visual cortex played a role in the discrimination of visual patterns (Neff, et al., 1975). For example, cats were tested before and after auditory cortex ablation for their ability to discriminate a "low-high-low" set of tones from a "high-low-high" set (where low might be 800 Hz and high 1000 Hz). A number of studies were conducted using a variety of tone patterns, each with a well-defined rationale (for a review, see Elliott & Trahiotis, 1972). However, this line of research did not yield any new insights into the function of auditory cortex. Part of the problem was that normal animals sometimes had difficulty discriminating the tone patterns, making the inability of an animal to discriminate them after cortical ablation difficult to interpret; that is, did the cortical ablation abolish the ability to discriminate a particular pattern or did the general effects of the lesion just make the task a little more difficult. Thus, although one can make a compelling rationale that analogous anatomical structures, such as auditory and visual cortex, might have analogous functions, this line of reasoning did not meet with success in this case.

Sound localization. One line of research that did lead to an important finding was the study of the role of auditory cortex in sound localization. Specifically, Neff and his colleagues demonstrated that cats with bilateral auditory cortex lesions were unable to walk to the source of a brief sound, i.e., one too brief to be scanned or tracked (Neff, Fisher, Diamond, & Yela, 1956).

They considered this to be a perceptual deficit, i.e., a loss of auditory space, as opposed to a sensory deficit, such as an increase in sound localization thresholds, an interpretation that has been borne out by subsequent research.

In a later study, Masterton and Diamond (1964) investigated the effect of bilateral auditory cortex lesions in cats on the discrimination of binaural clicks. Although their results are sometimes *mis*interpreted as indicating that the lesions abolished an animal's ability to discriminate binaural clicks, what they showed is that, unlike normal animals, the operated animals did not generalize from a single click to the left or right ear to binaural clicks in which the left or right ear received the leading sound. In other words the animals had a perceptual deficit in which they no longer equated binaural clicks (which differed in their time of arrival at the two ears) with single clicks. The perceptual nature of the cortical sound-localization deficit has also been supported by additional studies that have demonstrated that although carnivores and primates with bilateral cortical lesions retain some ability to discriminate left sounds from right sounds, they no longer associate the sounds with locations in space (H. Heffner, 1978; H. E. Heffner & Heffner, 1990b).

Latter Part of the 20th Century

Beginning in the mid 1960's, R. Bruce Masterton made several methodological and theoretical contributions to the study of auditory cortex. One was to improve on the regimen of behavioral methods used to assess the effects of lesions. Although postoperative testing would begin with a repetition of the preoperative tests, it now included further intensive and extensive testing to circumscribe any deficit that might be present, or to illustrate the absence of ancillary deficits over a wide variety of discriminations (Masterton, 1997).

Testing methods. Detailed testing of animals with cortical lesions was facilitated by the use of advanced testing procedures. The method of "conditioned suppression" was borrowed from the behavioral psychologists (Estes & Skinner, 1941), by way of James C. Smith of Florida State University, and adapted for auditory testing (H. E. Heffner & Heffner, 1995). This method simply requires an animal to drink from a water spout and break contact with the spout whenever it hears a particular sound (or a different sound). Not only does it fix an animal's head within the sound field, but it requires little cognitive ability on the part of the animal, making it well-suited for testing brain-damaged and other difficult-to-test animals.

Another important factor was the automation of testing procedures, which both removed the experimenter from direct contact with the animal, a potential distraction to the animal, and dramatically increased the number of trials that could be obtained. For example, the original sound-localization procedure used by Neff involved placing an animal in a start box, presenting a sound from behind the correct goal box, releasing the animal, and then physically returning the animal to the start box after it had made its response (Neff et al., 1975). Automating this procedure by having the animal begin a trial by placing its mouth on a "start" water spout and then contacting "goal" spout to indicate its

response not only fixed the animal's head in the sound field at the beginning of each trial, but increased the number of trials that could be obtained in a session from 20 to over 200 (Thompson, Heffner, & Masterton, 1974).

The delineation of a deficit involves multiple and detailed tests. Although postoperative testing always begins with a repetition of the preoperative test, it is necessary to include additional tests to determine the nature of a deficit or to rule out the possibility that an animal is using alternative strategies to solve a task. In addition, ablation/behavior studies typically include control tests to demonstrate that an observed deficit is not due to any attention, motivation, cognitive, or motor disorder. Thus, for example, such control tests have established that the cortical deficits observed using the conditioned suppression procedure are not the result of any reduction in fear conditioning (H. E. Heffner & Heffner 2003). [On the other hand, the possibility that the reduced fear response observed following lesions of the amygdala (and other sites) may be due to a hearing loss has never been ruled out. Not only does the possibility exist that such lesions themselves may cause a hearing loss, but the lesions are made stereotaxically and the earbars used to position an animal's head in a stereotaxic device are known to rupture the eardrums.]

Evolutionary approach. Influenced by Irv Diamond at Duke University, Masterton brought an evolutionary approach to the study of auditory cortex. Arguing that the functions of auditory cortex might differ between animals at different levels of a phyletic scale, he proposed to determine the evolution of auditory cortex in man's lineage. This would be done by determining the effects of cortical ablation in animals selected for their neurological similarity to various ancestors of man. The animals he chose were the Virginia opossum (marsupial), the hedgehog (insectivore), the Malaysian tree shrew (believed at the time to be a primitive primate), the bushbaby (a prosimian), and macaques (monkey) (see Figure 1 of Masterton, Heffner, & Ravizza, 1969).

An unstated assumption underlying this approach was that if auditory cortex was not necessary for a basic sensory function in animals lower on the phylogenetic scale, then it would not be necessary for animals that were higher on the scale. This assumption, however, resulted in an error. Because auditory cortex lesions have little or no effect on absolute thresholds in such animals as opossums, rats, and cats, it was firmly believed that the cortex played no role in the detection of sound in any species (e.g., Neff et al., 1975). As a result, reports of "cortical deafness" in humans following bilateral strokes were brushed off as the result of damage to non-auditory areas of cortex, i.e., cognitive deficits. This changed when it was discovered that bilateral auditory cortex ablation resulted in a hearing loss that could not be ignored (H. E. Heffner & R. S. Heffner, 1986a). Thus, auditory cortex in primates has extended its influence to include so basic a function as the detection of sound, which, because one sees substantial recovery of hearing over time, is probably due to the sudden removal of descending cortical input to lower auditory centers.

Sounds vs sound sources. The observation that in cats, at least, auditory cortex ablation seems to have little effect on the sensory aspects of hearing (e.g.,

sound detection, frequency and intensity discrimination), while it has a profound effect on the ability of an animal to locate the source of a sound, led to a distinction between the discrimination of sounds and the discrimination of sound sources (Masterton, 1992; 1993; 1997; Masterton & Diamond, 1973). A broader way of expressing this distinction is “sensation vs perception” with auditory cortex having a perceptual role. One opportunity to test this hypothesis arose when Bill Stebbins’ group at the University of Michigan demonstrated a right-ear advantage in Japanese macaques for the discrimination of two forms of their coo calls (e.g., Peterson et al., 1978). Drawing an analogy between monkey vocalizations and human speech, their finding suggested that the left cortical hemisphere of these monkeys was responsible for the perception of vocal communications.

The demonstration that bilateral ablation of auditory cortex in Japanese macaques permanently abolished their ability to discriminate the coo calls, with left (but not right) unilateral lesions results in a small, transient deficit demonstrated that, indeed, cortex was involved in this ability (H. E. Heffner & Heffner, 1986b). At this point, however, the deficit could be explained as either a perceptual or a sensory deficit. It would be a perceptual deficit if the animals were unable to discriminate the biological meaning of the coos. However, because the two classes of coos were physically different, one rising the other falling in frequency, there was always the possibility that the deficit was sensory in that the animals were unable to physically distinguish between the two types of coos. We now know that this deficit is sensory in nature, that bilateral auditory cortex ablation renders macaques being unable to determine if a sound is changing in frequency (Harrington et al., 2001). Thus, although we are reluctant to abandon the idea that auditory cortex is responsible for the perception of sound, this particular result is a sensory deficit.

Effects of Auditory Cortex Ablation

The following is a brief summary of the main effects of auditory cortex lesions on hearing. The citations are not exhaustive and additional studies can be found by consulting those referenced here. A comprehensive review of the pre-1975 studies can be found in the chapter by Neff et al. (1975).

Absolute sensitivity

In macaque monkeys, unilateral ablation of auditory cortex (the posterior two thirds of the superior temporal gyrus; Fig. 2) results in a definite, and often severe, hearing loss in the ear contralateral to the lesion (H. E. Heffner & Heffner, 1989). The initial hearing loss is followed by rapid, but incomplete recovery during the first month after surgery. A small hearing loss can still be seen 4 months later, although it is necessary to compare pre- and post-operative thresholds to conclusively demonstrate that a hearing loss exists. A unilateral cortical hearing loss undoubtedly occurs in humans, however, the rapid recovery

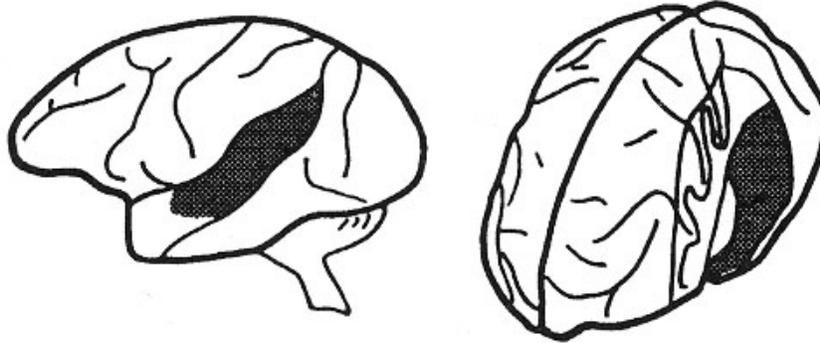


Figure 2: Typical lesion of auditory cortex in the Japanese macaque (blackened area), encompassing the posterior two-thirds (or more) of the superior temporal gyrus.

of sensitivity and the lack of pre-morbid audiograms for such patients has prevented it from being conclusively demonstrated.

The hearing loss that results in macaque following bilateral ablation of auditory cortex is much more severe than the combination of two unilateral hearing losses. (H. E. Heffner & R. S. Heffner, 1986a; 1989; 1990a). Indeed, an animal may initially be totally unresponsive to sound, especially if auditory cortex in both hemispheres is ablated at the same time. The animals show substantial recovery during the first 1-2 months after surgery, at which time the hearing loss becomes moderate. Although little recovery is seen during the next year or so, recent work indicates that thresholds do continue to improve with additional recovery observed 3-5 years later (Harrington, 1999; 2002). Control tests have indicated that the threshold shift cannot easily be accounted for by non-sensory factors such as attention or vigilance (H. E. Heffner & Heffner, 1990a). Cortical hearing loss following bilateral auditory cortex damage is well established in humans (e.g., Jerger, Weikers, Sharbrough III, & Jerger, 1969; for a review, see H. E. Heffner & R. S. Heffner, 1986a).

A significant cortical hearing loss has only been demonstrated in humans and macaques; no cortical hearing loss has been noted in opossums or rats and only small hearing losses have been noted in cats, dogs, and ferrets (R. S. Heffner & Heffner, 1984; H. E. Heffner & Heffner, 1986a; Kavanagh & Kelly, 1986; Ravizza & Masterton, 1972). So far, the survey of different species is too small to reach any conclusions as to which animals might show cortical deafness, although the undoubtedly simplistic hypothesis that it will be found only in gyrencephalic species comes to mind.

Although the recovery of hearing seen in primates could be due to other cortical areas compensating for the loss of auditory cortex, this seems unlikely to us. Not only are there relatively few cortical neurons outside of classical auditory cortex that respond to auditory stimuli (e.g., Romanski & Goldman-Rakic, 2002), but for them to assume new functions would likely disrupt their

ability to perform their normal ones. Instead, it seems more likely that the cortical hearing loss is due to the sudden removal of descending cortical input to lower auditory centers with the lower centers gradually adapting to the loss. Thus, one might expect neural responses in the lower auditory centers to be initially depressed following auditory cortex ablation.

Intensity discrimination

Auditory cortex lesions do not abolish the ability of carnivores or primates to discriminate intensity (Neff et al., 1975). However, recent research suggests that there may be some effect of cortical lesions on intensity discrimination thresholds in primates, depending on the direction of the intensity change (Harrington, 2002). Specifically, bilateral ablation results in, at most, a slight rise in thresholds for detecting an *increase* in intensity, whereas thresholds for detecting a *decrease* in intensity are noticeably raised. Higher than normal thresholds for an intensity decrement can also be observed in unilateral cases for sounds presented to the ear opposite the lesion. The observation that auditory cortex lesions result in raised thresholds for detecting a decrease, but not an increase, in threshold brings to mind the Neff Neural model, which, as previously discussed, states that animals without auditory cortex can detect an increase in neural activity.

Frequency discrimination

Auditory cortex ablation results in increased frequency discrimination thresholds in some species. The work of Massopust and his colleagues demonstrated reliable increases in discrimination thresholds in monkeys following cortical lesions (e.g., Massopust, Wolin, & Frost, 1970), a result that has been supported by subsequent research (H. Heffner & Masterton, 1978; Harrington et al., 2001). Cats also appear to have increased thresholds following cortical lesions (Cranford, 1979). On the other hand, cortical ablation does not appear to have any effect on frequency discrimination in rats (Kelly, unpublished doctoral dissertation). It has been demonstrated that chemical inactivation of auditory cortex by the application of muscimol temporarily causes rats to fail to respond on a frequency discrimination task (Talwar, Musial, & Gerstein, 2001); however no control tests were conducted so it is not known if the results are due to an auditory, attentional, cognitive, or motor deficit (H. E. Heffner & R. S. Heffner, 2003).

In what may be a related phenomenon, Whitfield (1980) found that auditory cortex lesions abolished the ability of cats to perceive the pitch of complex tones, a pitch referred to as the “missing fundamental.” However, of the 13 animals in the study, only 2 were able to learn the discrimination preoperatively. As a result, it is possible that the effect was due to the cortical lesions increasing the difficulty of an already difficult task. However, the question of whether auditory cortex is necessary for the perception of the missing fundamental is important and it would be worth replicating this study with advanced behavioral procedures.

Frequency change

In monkeys, auditory cortex ablation abolishes the ability to determine if a sound is changing in frequency. Specifically, the animals can no longer discriminate a steady tone from one that is rising or falling in frequency (Harrington, et al., 2001; Harrington, 2002). Because the animals can still discriminate frequency, it is necessary to test them in a way that prevents them from solving the task on the basis of absolute frequency. This is done by requiring the animals to discriminate swept tones from steady tones with the frequency of the steady tone varied from trial to trial. In addition, the range of frequencies of the steady tones must span the frequency range of the swept tones. It should be noted that normal monkeys easily learn this discrimination when tested with the method of conditioned suppression; on the other hand, an attempt to test this discrimination using a go/no-go procedure failed because the procedure lacked sufficient control over the animals' false positive rates (May et al., 1988).

The inability to determine if a sound is changing in frequency is a profound deficit that would be expected to render an individual unable to make much sense of the auditory world. This deficit may also occur in cats as cortical lesions are known to impair the ability to discriminate a rising from a falling swept tone; that the discrimination was not abolished may be due to the fact that an animal tested on rising versus falling tones may resort to using absolute frequency as a cue by attending just to the beginning or ending portion of the signal (Kelly & Whitfield, 1971). Whether a deficit may be found in rodents is not known; a study of the effect of cortical lesions on the discrimination of frequency sweeps by gerbils presented only group data with relatively large variance so it is not known if the deficit occurred in all of the animals (Ohl, Wetzell, Wagner, Rech, & Scheich, 1999).

Sound localization

Unilateral lesions of auditory cortex result in a complete inability to discriminate the locus of a sound in the hemifield opposite the lesions, an effect that has been demonstrated in both macaques and squirrel monkeys (H. E. Heffner, 1997; H. E. Heffner, & R. S. Heffner, 2003; Thompson & Cortez, 1983). Some residual ability to localize sound in the contralesional hemifield remains for sound sources within about 15E of midline. Bilateral ablation appears to be the sum of two unilateral lesions. Although an animal can distinguish left sounds from right sounds, it shows no awareness of the location of the sound source (H. E. Heffner & R. S. Heffner, 1990b).

Among the other species that have been tested, ferrets, cats, and dogs appear to have the same cortical sound localization deficit as monkeys (H. Heffner, 1978; H. E. Heffner & R. S. Heffner, 1990b; Kavanagh & Kelly, 1987; Neff et al., 1975). On the other hand, cortical lesions do not appear to affect the ability of laboratory rats or wild wood rats to localize sound. The studies of opossums, hedgehogs, and bushbabies with cortical lesions were not sufficiently

detailed to determine whether the animals were localizing sound sources as opposed to just discriminating left and right sounds (H. E. Heffner & Heffner, 1990b).

Some effects of partial lesions of auditory cortex

In macaques, it has been suggested on the basis of electrophysiological evidence that the identification of complex sounds is processed in the rostral portion of auditory cortex and that the localization of sounds in space is processed in the caudal portion (e.g., Rauschecker & Tian, 2000). To test this hypothesis, three Japanese macaques with complete auditory cortex lesions in one hemisphere received lesions in the other hemisphere that were restricted either to the rostral, core, or caudal areas of auditory cortex (Harrington, 2002). The animals were then tested on both their ability to determine if a sound was changing in frequency and to localize sound in the left and right hemifields. It was found that lesions of either the rostral or core portions of auditory cortex result in an inability to determine if a sound is changing in frequency whereas a lesion of the caudal portion had no effect. On the other hand, the rostral lesion appeared to have no effect on sound localization in the contralesional hemifield whereas the other two lesions resulted in threshold shifts, with the caudal lesion resulting in the largest shift (unlike complete unilateral lesions, none of the restricted lesions completely abolished sound localization in the contralesional hemifield). Thus, there appears to be some support for the idea that different portions of auditory cortex have different functions and further investigation on additional animals appears warranted.

In cats, the significance of the tonotopic arrangement of auditory cortex for sound localization has been investigated by compromising the blood supply to restricted frequency bands in primary auditory cortex (Jenkins & Merzenich, 1984). The results indicate that such lesions impair the ability of an animal to localize pure tones that fall within an affected frequency band in the hemifield contralateral to the lesion. This is an important finding, one that deserves to be replicated. Among the questions that remain to be answered are whether the results apply only to the very short duration (40 ms) pure tones used in the study or whether the same deficit would be found with longer duration tones and with narrow-band noise.

Concluding Comments

Given the present state of our knowledge, there are a number of directions for further research. One would be to explore species differences in the function of auditory cortex. As has been noted, the results of auditory cortex lesions can range from little or no effect, as in the rat, to the dramatic effects found in macaques. Not only would a knowledge of species differences shed light on the evolution of auditory cortex, but it would help avoid the problems that can arise with attempts to combine the results from one species with those of another, a

procedure that can result in an “auditory chimera” (H. E. Heffner & Heffner, 2003). A second line would be to determine the effect of ablating areas outside of classical auditory cortex where some neurons are known to respond to auditory stimuli, such as the prefrontal cortex of primates (e.g., Romanski & Goldman-Rakic, 2002). We expect that such lesions would have subtle effects and, as previously noted, we are doubtful that those areas would be able to compensate for the loss of auditory cortex.

A third line of research, one that will certainly give interesting results, is the use of chemicals or cooling to reversibly inactivate auditory cortex (e.g., Talwar et al., 2001; Lomber, 1999). One of the main advantages of this technique is the ability to determine the effect of different lesions in the same animal, and to repeat the lesions, thus reducing the effects of individual differences between animals due to motivation, skill-level, and other non-auditory factors. Another advantage is that it is possible to observe the immediate effects of a lesion before any compensation has occurred. For example, partial ablation lesions of an auditory area that impair an ability, but do not abolish it, may be due to compensation by the remaining cortical tissue. With ablation lesions, it is generally necessary to wait several days for the animal to recover from the effects of the surgery, especially the damage to muscle tissue overlying the skull, the after-effects of the anesthesia, and swelling of the brain, although in some cases it is possible to test an animal 24 hrs after surgery. The use of reversible lesions will also involve the use of intensive and extensive testing with control tests designed to rule out alternative explanations. Every advance in our views came about through investigations involving multiple experiments; although an individual experiment may provide new information, it must be replicated and tested in different ways to insure that it is correctly interpreted. And should the results of reversible lesions differ from those of ablation studies, it will be necessary to make a direct comparison between the two types of lesions under the same experimental conditions.

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