ROLE OF AUDITORY CORTEX IN THE PERCEPTION OF VOCALIZATIONS BY JAPANESE MACAQUES

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INTRODUCTION

Ever since the latter half of the 19th century when it was discovered that sensory and motor functions could be localized in the cerebral cortex, the role of the cortex in auditory processing has been studied by observing the effects of brain damage in both humans and animals. Initially, it was envisioned that the study of experimental lesions in animals would provide a basis for inferring cortical functioning in humans. This was based on the fact that lesions in animals could be precisely controlled thus avoiding the complications which arise when analyzing the effects of lesions which are either too small to result in distinct deficits or else are too large and result in multiple deficits which may be difficult to differentiate (e.g., Ferrier, 1876b). Indeed, the utility of animal research was soon demonstrated when ablation studies narrowed the search for auditory cortex in monkeys to the posterior two thirds of the superior temporal gyrus (Ferrier 1876a).

Yet despite early successes, studies of auditory processing in humans and animals have for the most part been pursued independently with little interaction between the two fields (see Neff et al., 1975). Two factors have contributed to this state of affairs. First, the study of the effects of auditory lesions in humans and animals has occasionally resulted in contradictory findings. The primary example of this is the question of whether cortical lesions result in a hearing loss. Although a number of cases of "cortical deafness" following bilateral temporal lobe lesions have appeared in the clinical literature, the failure (until recently) to find significant hearing losses in animals cast doubt on the validity of the human results and led animal researchers to believe that the cortex did not play a role in the detection of sound (e.g., Masterton and Berkley, 1974; for reviews, see Heffner and Heffner, 1986b, 1990c).

A second factor contributing to the separation of human and animal studies has been the difference in the focus of their investigations. While animal research has concentrated on

the role of cortex in the discrimination of the physical aspects of sounds (e.g., frequency, intensity and temporal discriminations), much of the human research has been directed to
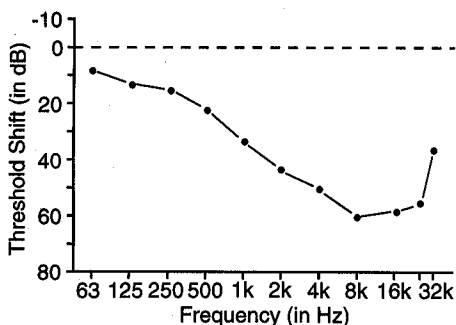

Figure 1. Average increase in pure-tone thresholds following complete bilateral auditory cortex lesions in 4 Japanese macaques. The dashed line at zero is the preoperative hearing level of the animals. Note that the hearing loss is small at low frequencies, gradually increases in the mid-frequency range, and then declines at the high frequencies, a characteristic which presumably reflects the proportion of cortical neurons responding to the different frequencies (modified from Heffner and Heffner, 1990c).

the study of the role of the cortex in the perception of speech. Although there has long been great interest in the possibility that the neural mechanisms underlying the perception of vocalizations in non-human primates might bear some similarity to that underlying human speech perception, the actual amount of research on this topic has been small (cf. Steklis and Raleigh, 1979).

Functional Similarities Between Macaque and Human Auditory Cortex

In the last few years, however, two findings have appeared which demonstrate that there are close similarities between humans and other primates, particularly macaques, with regard to cortical auditory processing. First, studies of cortical lesions in Japanese macaques have demonstrated that bilateral lesions of auditory cortex result in a hearing loss similar to the cortical deafness observed in humans (e.g., Jerger et al., 1969). Specifically, bilateral lesions of the superior temporal gyrus in macaques result in a substantial and permanent hearing loss as demonstrated by pure-tone audiometry (Fig. 1; Heffner and Heffner, 1986b, 1990c). Furthermore, the pattern of the hearing loss is similar to that often observed in humans in that it is greater at middle frequencies than at low frequencies (the degree of loss at high frequencies in humans has not been determined) (Leicester, 1980; Michel and Peronnet, 1980). This finding may reflect the fact that there are more cortical neurons tuned to middle than to low and high frequencies (e.g., Merzenich et al., 1976) with the result that removal of the cortical influence on the lower auditory system, which mediates the detection of sound, is in proportion to the cortical frequency representation. Moreover, research on macaques has extended what is known about cortical deafness by revealing that unilateral

lesions result in a small, but reliable hearing loss in the ear contralateral to the lesion (Heffner and Heffner, 1989c).

Previous animal studies, which used rats, cats, ferrets, and dogs, did not find a hearing loss following cortical ablation, apparently because cortical deafness does not occur in these species. The fact that cortical deafness has so far been observed only in humans and macaques suggests that it may be peculiar to primates (for reviews, see Heffner and Heffner 1986b, 1990c). Thus, by using macaques, it has been possible not only to verify the clinical observations of cortical deafness following bilateral temporal lobe lesions, but to extend these findings by demonstrating that unilateral lesions result in a hearing loss in the contralateral ear - a result which clinical studies had been unable to demonstrate conclusively (Heffner and Heffner, 1990b).

The second finding indicating a similarity between humans and macaques is that macaques possess a "cortical mechanism" for the perception of their species-specific vocalizations that is lateralized to the left hemisphere. That is, Japanese macaques have been shown to have a right ear advantage for the perception of two forms of their "coo" calls (e.g., Petersen et al., 1978). Furthermore, left, but not right, auditory cortex lesions have a marked, although transient, effect on their ability to discriminate these calls (e.g., Heffner and Heffner, 1986a). These results suggest that Japanese macaques have a specialization of the left temporal lobe analogous to that in humans for the perception of speech (i.e., Wernicke's area). Thus, it is possible to use macaques to study the role of the cortex in the perception of species-specific vocalizations and, perhaps, to generalize the results to the study of speech perception in humans.

In short, there appear to be important similarities in the role of the cortex in humans and Japanese macaques. Not only does the cortex of both species play a similar role in the detection of sound, but both possess a left hemisphere specialization for the perception of species-specific vocalizations. It is this latter aspect of cortical functioning which is the topic of this chapter.

PERCEPTION OF VOCAL COMMUNICATIONS BY JAPANESE MACAQUES

For over a hundred years it has been known that lesions of the posterior portion of the superior temporal gyrus of the left hemisphere in humans almost invariably result in the inability to understand language (for reviews, see Geschwind, 1965; Passingham, 1979). This fact has been used to support the idea that there is a cortical area specialized for the perception of language that, in most people, is located in the left temporal lobe (e.g., Wernicke, 1874; Geschwind, 1965). Language, however, can be viewed as an example of species-specific communication (e.g., Steklis and Raleigh, 1979) and its mechanism is unlikely to have arisen de novo with humans. Thus, the question arises as to whether other primates possess a similar cortical specialization for the perception of their vocal communications and whether that mechanism might also be lateralized to the left hemisphere.

Right-Ear Advantage in Macaques

Some years ago, there appeared evidence that the left hemisphere of Japanese macaques (*Macaca fuscata*) is specialized for the perception of species-specific communication sounds. This evidence came from the work of Petersen and his colleagues who studied the ability of Japanese macaques to discriminate two forms of their "coo" vocalizations (e.g., Petersen, 1981; Petersen et al., 1978). Briefly, they trained monkeys to

discriminate seven "smooth early high" (SE) coos from eight "smooth late high" (SL) coos using a go/no-go procedure. These coos are distinguished by the temporal position of the peak fundamental frequency in the frequency-modulation portion of the call. The two types of coos are acoustically similar, but appear to have different meanings the SE coo is emitted by both sexes and is a "contact-seeking" call, whereas the SL coo is produced primarily by estrous females seeking male consorts (Green, 1975). When the monkeys were trained to discriminate the coos, which were presented through headphones, Petersen found that the Japanese macaques showed a consistent right-ear advantage. Because other species of macaques failed to show a right-ear advantage when trained to discriminate the Japanese macaque coos, it was concluded that this effect was specific to the species whose vocalizations were being discriminated (Petersen, 1981; Petersen et al., 1978). Indeed, recent evidence has suggested that rhesus macaques may show a right-ear advantage when tested with their own species-specific vocalizations (Hauser and Andersson, in press).

The right-ear advantage of Japanese macaques for the perception of their coos may be analogous to that shown by humans for the perception of speech sounds (e.g., Kimura, 1961, 1967). The human right-ear advantage is explained by the fact that input from each ear is dominant in the contralateral hemisphere. As a result, input from the right ear will predominate in the left hemisphere where, in most people, Wernicke's area is located. Thus, speech sounds presented to the right ear have an advantage over those presented to the left ear when competing for analysis in Wernicke's area. Accordingly, the presence of a right-ear advantage in Japanese macaques suggested that they might also have a left hemisphere specialization for the perception of their vocal communications.

Once it had been established that Japanese macaques have a right-ear advantage, the next step was to examine the effect of unilateral temporal lobe lesions on the perception of their vocalizations. If the monkeys possessed a left hemisphere specialization then one would expect left hemisphere lesions to have a greater effect than right hemisphere lesions on their perception of the coos.

Effect of Cortical Lesions on the Perception of Coos

Some years ago, we began to investigate the effect of superior temporal gyrus lesions on the ability of Japanese macaques to categorize their vocalizations using the same stimuli that Petersen and his colleagues used to demonstrate the right-ear advantage (Petersen, 1981; Petersen et al., 1978). In our study, the monkeys were preoperatively trained to classify examples of the two types of coos presented from a loudspeaker placed in front of them using a conditioned-avoidance procedure. Briefly, a thirsty monkey was seated in a standard primate chair and accustomed to drinking out of a water spout mounted on the chair. Initial auditory training consisted of presenting one of the SE coos at random intervals from 7 to 49 sec apart. Each presentation consisted of playing the coo three times, following which a mild electric shock was delivered through the water spout. After several stimulus presentations, the monkeys learned to avoid the shock by breaking contact with the spout whenever the coo was presented and to return to the spout after the shock had been presented.

The animals were then trained to distinguish one SE coo from one SL coo by presenting one of the two coos every 7 sec. Because only the SE coo was followed by shock, the animals learned to break contact whenever they heard the SE coo, but to maintain contact whenever the SL coo was presented. Note that in this initial training, only one example of each type of coo was used and, at this point, the monkeys could distinguish between them on the basis of any number of physical differences such as frequency, intensity, or duration.

Once an animal had learned to break contact only when the SE coo was presented, additional examples of both types of coos were presented until the animal had learned to discriminate the entire set of 15 coos. Thus, the animals demonstrated the ability to distinguish the two types of coos by breaking contact with the spout following presentation of an SE coo and maintaining contact after presentation of an SL coo. This task could not easily be accomplished by discriminating on the basis of some physical aspect of the sounds because each of the two sets of coos contained individual coos which varied noticeably in duration, intensity, spectrum, etc. Although the animals could conceivably have memorized each of the 15 coos, this strategy would be expected to increase the difficulty of the task as

Figure 2. Drawing of a Japanese macaque brain indicating the location of primary auditory cortex and the surrounding auditory fields (also referred to as secondary auditory cortex). Left: view with the parietal operculum removed to show the location of primary (blackened) and the surrounding auditory fields (stippled). Right: lateral view; arrows indicate the extent of auditory cortex which is buried within the depths of the Sylvian fissure. STG, superior temporal gyrus (drawings based on the electrophysiological study of Merzenich and Brugge, 1973).

more examples were added. However, just the opposite occurred the discrimination appeared to become easier as more examples were added. That is, while learning to discriminate the first pair of coos took an average of 6.8 sessions, learning the next 6 pairs (plus one additional SL coo) took only an additional 25.9 sessions, with one animal learning the additional coos in only 10 sessions. Moreover, the monkeys did not forget the discrimination and could successfully perform it even after a hiatus of over 3 months. Thus, the monkeys' performances suggest that they were performing a biologically simple discrimination in spite of the fact that the stimuli were acoustically complex signals.

Following training, five monkeys received lesions of the left superior temporal gyrus, which included primary auditory cortex and the surrounding auditory fields (Fig. 2), while 5 other monkeys received lesions of the right superior temporal gyrus. Analysis of the lesions indicated that primary and secondary auditory cortex was removed in each case as demonstrated by cortical reconstruction and analysis of the resulting thalamic degeneration (Heffner and Heffner, 1986a).

The behavioral results showed that right auditory cortex lesions had no noticeable effect on the discrimination (Fig. 3). That is, the animals with right hemisphere lesions were able to perform the discrimination at normal levels when tested within 3 to 8 days following surgery. On the other hand, left auditory cortex lesions consistently resulted in a noticeable, although transient, deficit in the ability of the animals to perform the discrimination. That is, when tested within 4 to 11 days after surgery, the performance of the animals with left hemisphere lesions was below preoperative levels for the first 5 to 15 sessions. This

difference between the effects of left and right auditory cortex lesions suggests that the left hemisphere in Japanese macaques is dominant for the perception of species-specific vocalizations.

The difference between the performances of the two groups suggests that the initial impairment shown by the left unilateral cases was not due to any general postoperative malaise. Nor did the difference appear to be due to such factors as amount of recovery time before testing, overall time between pre- and postoperative testing, or to differences in the size of the lesions (Heffner and Heffner, 1984, 1986a, 1989b, 1990a).

However, as noted, the left-hemisphere deficit for this task proved to be impermanent and these animals were able to regain preoperative performance levels within a few weeks. The discovery that the deficit is transient suggested two possibilities. The first is that the lateralization may not be as strong as that found in humans and that the right hemisphere possesses the ability to process vocal communications in the absence of the left hemisphere.
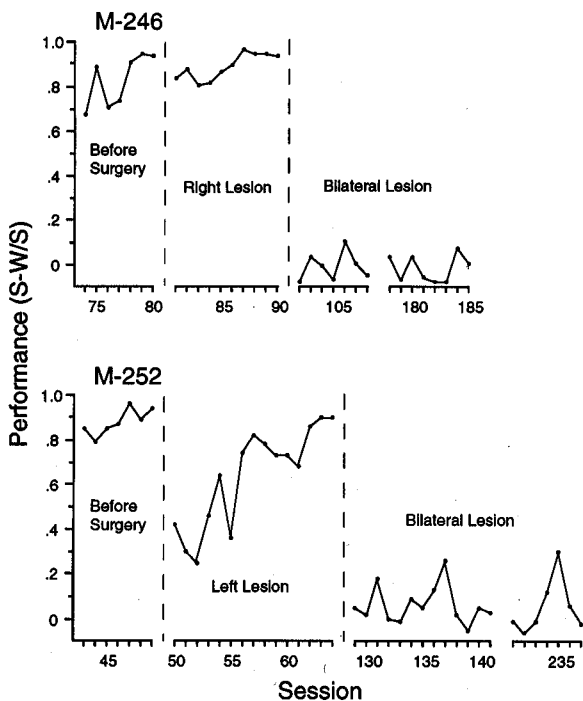

Figure 3. Effect of cortical ablation in two monkeys (M-246 and M-252) on the ability to discriminate the coo vocalizations. Performance on this task can range from 1.0 (perfect discrimination of the two sets of coos) to around 0 (failure to discriminate). Note that left, but not right, auditory cortex lesions result in a transient deficit. Bilateral lesions result in a permanent deficit which is still evident months after the surgery. S represents the average of the SL coo (safe) scores and W is the average of the SE coo (warning) scores (modified from Heffner and Heffner, 1986a).

The second possibility is that there is in fact a permanent deficit following left unilateral lesions, but that the specific task used here is relatively undemanding and that a more stringent test is needed to demonstrate it.

Nevertheless, it is clear that the perception of vocal communications by Japanese macaques is a cortically-dependent task even if it is not as strongly lateralized as speech perception is in humans. This is demonstrated by the effect of bilateral ablation on the discrimination of the coos. As the examples in Fig. 3 indicate, when a second auditory cortex lesion is made in the other hemisphere, the animals are rendered totally and permanently unable to discriminate the coos (Heffner and Heffner, 1986a). This result supports the interpretation that the recovery of the monkeys with left auditory cortex lesions occurs because the right hemisphere is able to mediate the discrimination. However, once both auditory cortices have been removed, not only are the animals unable to discriminate the two sets of coos (i.e., all 15 coos), but they cannot even perform the task when it is made easier by reducing the discrimination to a single pair of SE and SL coos. Thus, removal of auditory cortex changes the discrimination from an acoustically complex yet biologically simple task to one that is both biologically and acoustically complex.

Although unable to discriminate the coos, the monkeys with bilateral lesions were still capable of making other auditory discriminations (Heffner and Heffner, 1986a). Not only were they easily able to detect the coos (their hearing loss was not total), but they could discriminate them from noise bursts. However, when tested on their ability to discriminate the coos from tones, they could easily discriminate the coos from 2 and 4 kHz tones, but had difficulty discriminating them from a 1 kHz tone and were never able to discriminate them from a 500 Hz tone. Because 500 and 1000 Hz are close to the fundamental frequencies of the coos which had beginning frequencies from about 500 to 750 Hz, this result suggests that the monkeys had a deficit in frequency discrimination.

Because numerous studies have demonstrated that monkeys with auditory cortex lesions retain the ability to discriminate frequency (Heffner and Masterton, 1978; Massopust et al., 1971), it is difficult to account for their failure to discriminate the coos from a 500-Hz tone in terms of a general inability to discriminate frequency. However, a characteristic of the coos is that they are frequency-modulated signals - that is, the fundamental frequency of a coo rises and then falls with the peak frequency occurring earlier in the SE coos than in the SL coos. This leads to the possibility that the deficit in discriminating the coos may be the result of an inability to discriminate rapid changes in frequency, a deficit that a typical frequency-discrimination task using comparatively long-duration tone pips might miss (cf. Heffner and Masterton, 1978). If so, then this represents another possible similarity between monkeys and humans as it has been suggested that the hemispheric specialization for speech perception in humans reflects left-hemispheric dominance in the processing of rapidly changing signals (Schwartz and Tallal, 1980).

It should be noted that the permanent deficit seen following a bilateral lesion does not appear to be a secondary result of a cortical hearing loss. This was demonstrated by a study in which monkeys with bilateral lesions were tested to determine if amplifying the coos would improve the animals' performances (Heffner and Heffner, 1989a). The results of this study showed that even if the different frequency bands of the coos were selectively amplified to compensate, as closely as possible, for each animal's individual hearing loss, the monkeys still could not discriminate the coos. Moreover, when normal monkeys were presented with coos which had been attenuated and filtered to simulate a cortical hearing loss, they were still able to discriminate the coos at normal levels. These two findings indicate that the loss in the ability to discriminate the coos which follows bilateral lesions cannot be explained in terms of a simple hearing loss.

Nor does this deficit appear to be due to any general impairment in auditory learning or memory. This is demonstrated by the fact that bilateral lesions, which abolish the ability to discriminate the coos, do not abolish the ability to discriminate other auditory stimuli, such as frequency and intensity. Therefore, it would appear that bilateral auditory cortex lesions

do not have any general effect on auditory learning or memory. Moreover, lesions which produce a specific short-term memory deficit in monkeys (i.e., superior temporal gyrus lesions which spare auditory cortex) do not abolish the ability to categorize the coos (cf. Colombo et al., 1990; Heffner and Heffner, 1989b). Finally, although the monkeys in our studies were tested with a conditioned-avoidance procedure, the results cannot be explained in terms of an inability of the animals to establish fear conditioning (LeDoux et al., 1984) since, as previously noted, the monkeys were able to condition to frequency differences using the same avoidance task. Thus, while the deficit could conceivably be the result of some sort of learning or memory deficit which affects some, but not all, auditory discriminations, there is currently little evidence for such a possibility.

Location of the Neural Mechanism

Given the discovery that bilateral removal of the superior temporal gyrus results in a total inability to discriminate the coos, the question arises as to whether smaller lesions might have the same effect. In order to address this question, it is first necessary to review what is known concerning the location of auditory cortex.
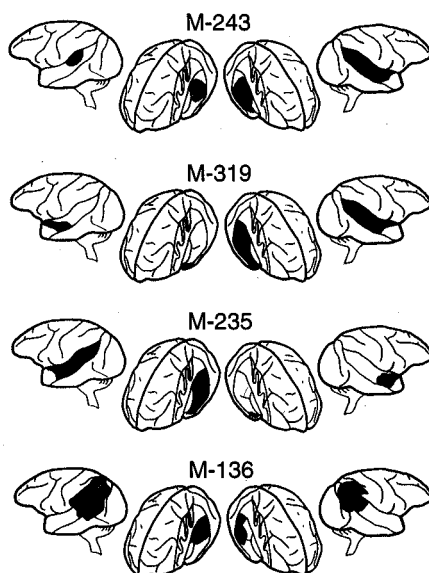

Figure 4. Cortical reconstructions for 4 monkeys which received partial lesions of the superior temporal gyrus. Shaded areas indicate the extent of the lesions. The lesions are arranged in descending order of their effect on the ability to discriminate the coos (cf. Fig. 5). Note that only M-243 showed a total and permanent deficit in the ability to discriminate the coos (modified from Heffner and Heffner, 1989b).

Although the exact boundaries of auditory cortex can be difficult to define, both cytoarchitectural and electrophysiological studies have indicated that there is a central core area (primary auditory cortex) and a surrounding belt of secondary auditory fields. Primary auditory cortex lies in the depth of the Sylvian fissure on the middle third of the superior temporal plane and is surrounded by four secondary auditory fields (Fig. 1; Merzenich and Brugge, 1973; for a review see Heffner and Heffner, 1986b). Other parts of the superior temporal gyrus also appear to be auditory. Auditory responses have been recorded on the
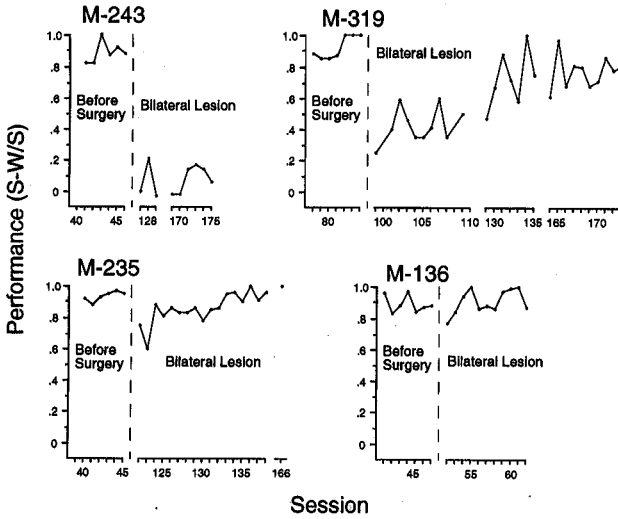

Figure 5. Effect of restricted superior temporal gyrus lesions on the ability to discriminate the coos. See Fig. 4 for drawings of the lesions. Note that only M-243 was completely unable to perform the discrimination (modified from Heffner and Heffner, 1989b).

superior temporal plane rostral to the secondary fields and on the lateral surface of the superior temporal gyrus indicating that there are at least two other auditory fields (Merzenich and Brugge, 1973). In addition, data on the cytoarchitectonics and cortical connections of the auditory fields suggests that all of the superior temporal gyrus with the exception of the caudal (posterior) end, which receives no significant projections from the medial geniculate, may have auditory functions (Galaburda and Pandya, 1983; Mesulam and Pandya, 1973).

The effect of restricted bilateral lesions on the ability to discriminate the coos was determined using 4 animals (Heffner and Heffner, 1989b). In this study, 3 of the monkeys received a large lesion of the superior temporal gyrus in one hemisphere followed by a

restricted lesion of the superior temporal gyrus in the other hemisphere (Fig. 4). Because unilateral lesions do not result in a permanent deficit, any effect would be the result of removing the same region on both sides, i.e., the functional lesion would be that area which was removed in both hemispheres. The functional lesions received by the 4 monkeys were: primary and secondary auditory cortex was removed in M-243, a portion of the superior temporal gyrus rostral to the primary and secondary auditory fields was removed in M-319, the rostral portion of the superior temporal gyrus outside the primary and secondary auditory fields was removed in M-235 (resulting in a similar, though slightly smaller functional lesion than in M-319), and the superior temporal gyrus caudal to primary and secondary auditory cortex and the immediately adjacent parietal, occipital, and temporal area were removed in M-136.

The results of this study showed that only the monkey in which primary and secondary auditory cortex were removed bilaterally (M-243) had a complete and permanent deficit. As shown in Fig. 5, M-243 was unable to discriminate the coos when tested during the first week after surgery. This monkey was then given training with single pairs of coos, but at no time was it able to discriminate even one SE coo from one SL coo despite weeks of training. The animal was then retested on the full set of 15 coos for seven more sessions, during which it again failed to discriminate them.

The two animals with bilateral ventral lesions that spared auditory cortex on one side were successfully able to discriminate the coos when first tested 5 days (M-235) and 10 days (M-319) after surgery. However, although M-235 quickly reached normal levels of performance, M-319, with a larger lesion, was initially unable to perform at normal levels. Although M-319's performance gradually improved, it was never able to perform consistently at preoperative levels and appears to have suffered a minor but permanent impairment. The results of the fourth animal, M-136, demonstrate that a lesion that bilaterally removes the area of the superior temporal gyrus posterior to auditory cortex has little effect on the discrimination.
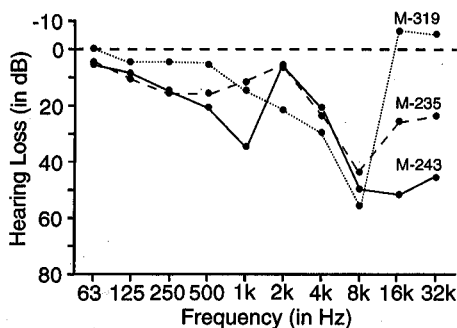

Figure 6. Effect of restricted superior temporal gyrus lesions on pure-tone thresholds. Dashed line at zero is the average hearing level for normal macaques. Note that although all three of the monkeys had a hearing loss, only M-243 was unable to discriminate the coos (cf. Fig. 5) (Data from Heffner and Heffner, 1989b).

Interestingly, 3 of the monkeys showed a hearing loss following bilateral lesions. As shown in Fig. 6, M-235, M-243, and M-319 each showed a hearing loss that followed the same general pattern as that shown in Fig. 2 for monkeys with large superior temporal gyrus lesions. However, their hearing losses were not as severe evidently due to the fact that their lesions were smaller. Moreover, the hearing losses of these 3 animals are similar to each other, with the exception of frequencies above 8 kHz, yet only one of them, M-243, was unable to discriminate the coos. The fact that two of the monkeys showed a hearing loss, but were still able to discriminate the coos supports the conclusion that the deficit in the discrimination of the coos cannot be accounted for by the hearing loss - because the coos did not contain any energy above 8 kHz, the difference in the audiograms above this point was not a factor. This conclusion is further supported by the fact that increasing the intensity of the coos to compensate for M-243's hearing loss did not improve its performance. The fact that a superior temporal gyrus lesion can result in a hearing loss without abolishing the ability to discriminate the coos demonstrates that these two deficits can be partially dissociated.

In summary, removal of primary auditory cortex and the surrounding auditory fields in both hemispheres abolishes the ability to discriminate the coos. In contrast, lesions of the superior temporal gyrus that include bilateral removal of areas rostral or caudal to auditory cortex, but spare auditory cortex on one side, have little or no effect on the discrimination. Although we cannot rule out the possibility that the neural mechanism for the perception of species-specific vocal communications may be located outside the superior temporal gyrus and that the deficit observed in M-243 may be caused by the disruption of auditory input from auditory cortex to that area, this study demonstrates that the deficit may be produced by small lesions restricted to the middle third of the superior temporal plane.

CONCLUSION

The perception of vocal communications by Japanese macaques is a cortically-dependent task which is lateralized to some extent to the left hemisphere. This fact suggests that macaques possess a cortical mechanism analogous to the cortical speech perception mechanism in humans which, although predominately an unilateral mechanism, does appear in bilateral form in some individuals (e.g., Courtois et al., 1983). Given the current state of knowledge concerning the cortical mechanism in macaques, there are at least three questions which need to be addressed.

The first question concerns the degree to which the mechanism is lateralized to the left hemisphere. As previously noted, although left hemisphere lesions result in an immediate deficit in categorizing the coos, the right hemisphere is eventually able to mediate the task at normal levels. While this result may indicate that the mechanism is only weakly lateralized to the left hemisphere, it may also be a reflection of the simplicity of the task itself. That is, the coo classification task used so far employs only 15 sounds and the animals typically receive several months of preoperative training using these sounds. Thus, a more demanding task might well reveal a permanent deficit following left hemisphere lesions. For example, the task could be made more difficult by presenting competing stimuli to the two ears using headphones as well as by including additional examples of coos to which the monkeys have not been exposed preoperatively.

The second question concerns the nature of the deficit, that is, whether the permanent deficit seen following bilateral lesions is specific to vocal communications or whether it represents a general deficit in the discrimination of the physical parameters of sound.

Although it is well established that auditory cortex ablation does not abolish the ability to discriminate frequency, intensity, or the temporal aspects of sound, few studies have examined these abilities using stimuli which mimic natural sounds such as vocalizations. Thus, although the ability to discriminate the frequency of long duration sounds may be normal, cortical ablation may affect the ability to perform such a discrimination on a short or rapidly changing sound (e.g., Symmes, 1966). Furthermore, a number of these studies were performed on carnivores and it is now apparent that the effects of cortical lesions in primates and carnivores may differ a significant finding for which we as yet have no explanation (e.g., Heffner and Heffner, 1986b).

The third question concerns the issue of whether the cortical deficit is "species-specific". As demonstrated by Petersen and his colleagues, although other species of macaques, such as *Macaca nemestrina* and *Macaca radiata*, can learn to categorize Japanese macaque coos, they do not show a right-ear advantage (e.g., Petersen, 1981). This result suggests that macaques process the vocalizations of other species differently from those of their own species. If so, then it might be expected that non-Japanese macaques would not show a deficit following left hemisphere lesions and, perhaps would not show a deficit following a bilateral lesion.

ACKNOWLEDGEMENTS

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