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Cortical Deafness Cannot Account for the Inability of Japanese Macaques to Discriminate Species-Specific Vocalizations

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Bilateral ablation of the superior temporal gyrus in Japanese macaques results in a significant hearing loss (cortical deafness) as well as in an inability to discriminate between two types of their "coo" vocalizations. A two-part investigation was conducted to determine whether the hearing loss may itself affect the ability to discriminate vocalizations. First, four normal Japanese macaques were tested for their ability to discriminate coos which were filtered to simulate the effect of a cortical hearing loss. Second, four Japanese macaques with bilateral superior temporal gyrus lesions were tested for their ability to discriminate coos which were amplified and equalized to compensate for each animal's hearing loss. All four normal macaques were able to discriminate the filtered coos easily whereas compensating for the operated monkeys' hearing losses did not improve their performances. It appears that the inability of monkeys with bilateral superior temporal gyrus lesions to discriminate conspecific vocalizations is not simply due to the accompanying hearing loss, but is a separate auditory disorder.

INTRODUCTION

The study of cerebral lesions in human patients has shown that the neural mechanisms involved in speech are located predominantly in the left hemisphere. In particular, lesions of the left temporal lobe result in an inability to understand speech. This deficit, part of a syndrome referred to as Wernicke's aphasia, is associated with a cortical region located in the posterior portion of the superior temporal gyrus of the left hemisphere, i.e., Wernicke's area (e.g., Benson & Geschwind, 1969).

The existence of a lateralized cortical speech reception mechanism in

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humans has led to a search for a similar mechanism in other species, particularly nonhuman primates (e.g., Denenberg, 1981; Hamilton, 1977). Several years ago, there appeared evidence that Japanese macaques (*Macaca fuscata*) may have undergone specialization of the left hemisphere for the perception of their vocal communications. Specifically, Japanese macaques show a consistent right ear advantage in the discrimination of two types of their "coo" vocalizations (e.g., Petersen et al. 1984; Petersen, Beecher, Zoloth, Moody, & Stebbins, 1978); types that are acoustically similar, but have different meanings (Green, 1975). This right ear advantage for the perception of species-specific vocal communication sounds resembles that shown by humans for the perception of speech sounds (Kimura, 1961, 1967). In humans, the 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 Wernicke's area, which is located in the left hemisphere. Thus the presence of a right ear advantage in Japanese macaques suggested that they have a left hemisphere specialization for the perception of species-specific vocalizations. As a consequence, damage to this area would be expected to impair the macaques' ability to discriminate their vocalizations.

Recently, we have been studying the effects of temporal lobe lesions on the ability of Japanese macaques to discriminate two types of their coo vocalizations (Heffner & Heffner, 1984, 1986a). Using the same stimuli previously used to demonstrate their right ear advantage we found that left unilateral ablation of the superior temporal gyrus consistently resulted in an initial impairment in the ability to discriminate the vocalizations with the animals unable to regain normal performance for 5 to 15 days. In contrast, right unilateral ablation had no detectable effect on the discrimination. This difference, which was observed in five left and five right hemisphere cases, could not be attributed to differences in lesion size or postoperative recovery time. As a result, it was concluded that the Japanese macaque possesses a left hemisphere specialization for the perception of vocal communications and that ablation of the left superior temporal gyrus produces a deficit which may be analogous to sensory aphasia.

The fact that the monkeys with left hemisphere lesions regained normal performance on the coo discrimination was attributed to the right hemisphere mediating the discrimination in the absence of the left. This conclusion was based on the finding that subsequent ablation of the right superior temporal gyrus completely and permanently abolished the ability to discriminate the coos. While such evidence would seem to conclusively demonstrate the cortical nature of the discrimination, it was complicated by the discovery that the bilateral lesions also resulted in deafness.

An initial effect of the bilateral lesions was to render the animals totally unable to respond to sound. While the animals began to recover their

hearing within a few weeks, their pure tone audiograms never returned to normal even a year after surgery (Heffner & Heffner, 1986b). In humans, this type of hearing loss has classically been referred to as "cortical deafness" (e.g., Bramwell, 1927; Clark & Russell, 1938) and has been described by more recent investigators (e.g., Jerger, Weikers, Sharbrough, & Jerger, 1969; Lecours, Olivier, Bérubé, & Lacroix, 1983; Leicester, 1980; Rousseaux & Devos, 1983; for a recent review, see Heffner & Heffner, 1986b). Thus the question arises as to whether the inability of the monkeys with bilateral lesions to discriminate coos might have been due in part to difficulty in hearing them.

In investigating the contribution of cortical deafness to the deficit in coo discrimination, it has been demonstrated that not only do the animals recover sufficiently to be able to easily hear the coos in a simple detection task, but increasing the loudness of the coos does not improve their ability to discriminate them (Heffner & Heffner, 1986a). However, because of the nature of the hearing loss, these tests do not in themselves completely rule out the possibility that it may have added to the difficulty in discriminating the coos. Specifically, the hearing loss shown by these animals is not a constant decrease in sensitivity across all frequencies, but one which varies with frequency (see Fig. 1). Typically, the cortical hearing loss is smallest at low frequencies with the greatest losses in the midrange although peaks of sensitivity may occur at various frequencies. As a result, an animal's hearing loss may not only reduce the perceived loudness of the coos, but the unevenness of the loss may change the perceived spectrum of the coos rendering them more difficult to discriminate. Because research on the perception of coos by Japanese macaques has demonstrated that the harmonic structure of the calls is critical to their perception (May, Moody, & Stebbins, 1986), it is possible that such a hearing loss could affect the ability to discriminate them.

The purpose of this report is to present the results of a two-part investigation of the effect of the cortical hearing loss on the perception of coos. The first part consisted of determining whether the discriminatory ability of normal Japanese macaques is degraded when the coos are filtered to simulate the effect of a cortical hearing loss. The second part consisted of determining whether the discriminatory ability of Japanese macaques with bilateral superior temporal gyrus lesions is improved by equalizing the coos to compensate for their hearing loss.

METHOD

Subjects

Eight seven-year-old (adolescent) male Japanese macaques (*Macaca fuscata*) ranging in size from 8.5 to 11 kg were used in this study. The animals had been born and reared in a 58-acre outdoor primate colony (Arashiyama West Institute). The animals were individually housed in primate cages with free access to food and were trained using water as a reward.

The normal monkeys, whose numbers were 231, 286, 291, and 294, are referred to as monkeys A, B, C, and D, respectively. Each of these animals had received between 85 and 95 daily sessions of training on the discrimination of coos and 3 to 6 sessions on the detection of pure tones since arriving in the laboratory.

The operated monkeys, whose numbers were 207, 214, 267, and 337, are referred to as monkeys E, F, G, and H, respectively. Their preoperative training on the discrimination of coos consisted of 68 sessions for monkey E, 87 sessions for monkey F, 88 sessions for monkey G, and 118 sessions for monkey H. Each of these monkeys had received two-stage bilateral lesions which preliminary histological analysis indicated removed all of the superior temporal gyrus except the ventral tip (thus removing all of primary and secondary auditory cortex). The lesions had been completed 12 months (monkeys E and F) and 11 months (monkeys G and H) prior to beginning this study. Individual audiograms had been determined 4 weeks before this study was begun.

Behavioral Apparatus

A standard primate chair was modified to accommodate a "double" water spout. This spout consisted of two standard drink tubes mounted parallel and close enough (1 cm apart) that a monkey could comfortably place its mouth on both spouts. The two spouts were electrically isolated from each other and were attached to a touch switch which detected when an animal placed its mouth on them. One of the spouts was attached via plastic tubing to an electrically operated water valve and constant-pressure water reservoir. Mild electric shock was provided by a shock generator connected to the two spouts. A 60-W light was mounted above the chair and the entire apparatus was located in a sound chamber (2.7 × 2.5 × 2.0 m). A microcomputer was used for behavioral programming and stimulus generation.

Stimuli

The monkey vocalizations used in the discrimination were the same 15 coos previously used to demonstrate the effect of bilateral superior temporal gyrus lesions in Japanese macaques (Heffner & Heffner, 1984, 1986a). These vocalizations were originally recorded by Green (1975) and had been used by Petersen and his colleagues to demonstrate a right-ear advantage in Japanese macaques for the perception of vocalizations (e.g., Petersen et al., 1978, 1984). They consist of 7 so-called "smooth early (SE) high" and eight "smooth late (SL) high" coos. The coos are distinguished by the temporal position (i.e., either early or late) of the peak fundamental frequency in the frequency-modulation portion of the call. Furthermore, the SE coo is emitted by all ages and sexes and appears to be a "contact-seeking" call while the SL coo is produced primarily by estrous females seeking male consorts. The two types of coos are thus acoustically similar sounds with different meanings.

The physical characteristics of the coos have been described in detail elsewhere (e.g., Petersen, 1981). Briefly, the coos have an average fundamental onset frequency of 625 Hz (ranging from 500 to 750 Hz) with an average peak frequency of 865 Hz (ranging from 600 to 1350 Hz). The harmonic structure of the calls is such that all the significant energy is below 4 kHz.

The vocalizations were digitized at a 20-kHz sample rate, edited to remove the background noise which preceded and followed the coos on the tape recording, and stored on computer disk for direct digital-to-analog playback. For standard presentation, the sounds were played back through a bandpass filter (100 Hz to 5 kHz) to reduce low-frequency noise and prevent aliasing, an amplifier, and a high-fidelity loudspeaker (Acoustic Research 3a) located 1.5 m in front of the primate chair. The standard coos were presented at an average level of 55 dB above threshold as previously determined on normal monkeys (Heffner & Heffner, 1986a).

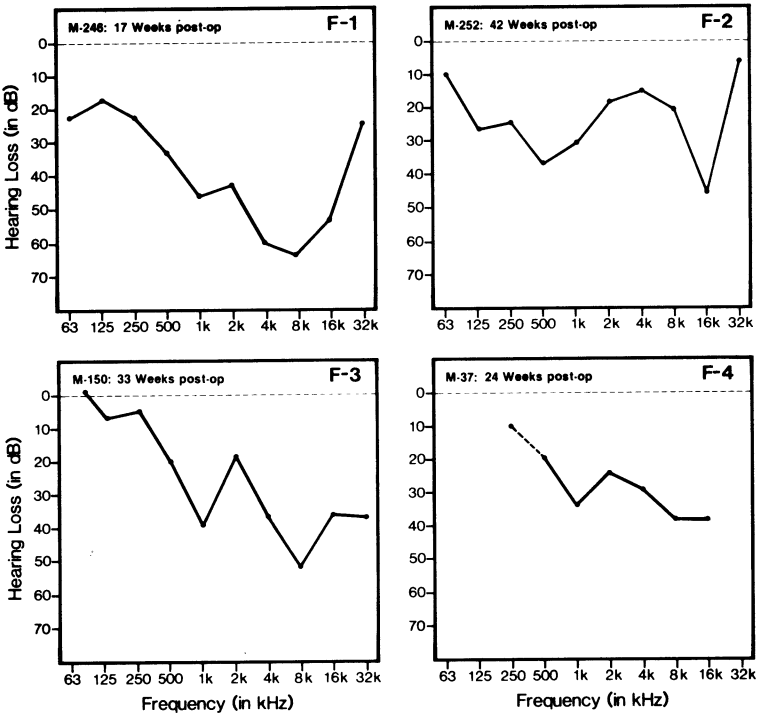

FIG. 1. The audiograms of four monkeys with bilateral auditory cortex lesions on which were based the four filter settings used to simulate the effect of a cortical hearing loss (from Heffner & Heffner, 1986b). Dashed line in F-4 indicates that the 240-Hz threshold was based on a point taken 52 weeks post-op.

(A) Simulating a cortical hearing loss. Filtered coos were used to simulate the effect of four different cortical hearing losses (Fig. 1) which had previously been observed in four animals with bilateral superior temporal gyrus lesions (Heffner & Heffner, 1986b). The coos were filtered by passing the electrical signal through two equalizers (Symmetric Sound Systems, Model EQ-3) using the frequency bands which spanned the frequency range of the coos. These bands were centered at 270 Hz, 360 Hz, 490 Hz, 640 Hz, 850 Hz, 1.1 kHz, 1.5 kHz, 2.0 kHz, 2.7 kHz, 3.6 kHz, 4.9 kHz, 6.4 kHz, and 8.5 kHz. The amount of attenuation for each band was determined by referring to the corresponding frequency of the particular audiogram being approximated (see Fig. 1) and attenuating by the amount of the hearing loss. This procedure was used to generate four separate sets of equalizer settings, referred to as F-1, F-2, F-3, and F-4, which matched the four hearing losses shown in Fig. 1 as closely as possible.

(B) Compensating for a cortical hearing loss. The coos for the operated monkeys were equalized and amplified to compensate for their hearing losses, as closely as possible, across frequency. The equalizer settings for each animal were based on the hearing loss of an animal's best ear, which was the left ear for monkeys E and H and the right ear for monkeys F and G (Fig. 2). Because of the severity of the hearing losses, it was not possible to produce a level equivalent to zero hearing loss without causing distortion. Thus, the hearing losses were equalized across frequency to a "flat" hearing loss (from

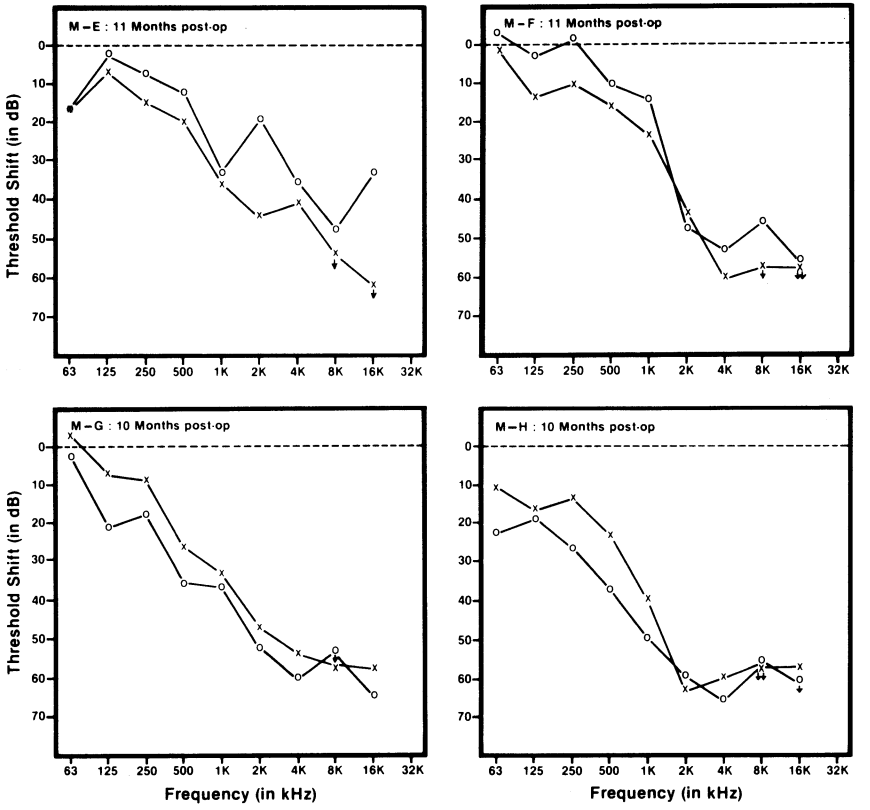

FIG. 2. Audiograms of the four monkeys with bilateral auditory cortex lesions (E, F, G, and H) used in this study. Threshold points are plotted relative to each animal's preoperative audiogram with (X) indicating left ear and (0) indicating right ear. An arrow indicates that an animal was unable to respond to a tone at maximum intensity.

270 Hz to 8.5 kHz) of 17 dB for monkey E, 5 dB for monkey F, 13 dB for monkey G, and 24 dB for monkey H.

Procedure

An avoidance procedure was used in which a thirsty monkey was seated in the primate chair and trained to place its mouth on the water spout, an action which fixed its head in front of the loudspeaker. This was accomplished by providing a steady trickle of water (3–4 ml/min) as long as the animal maintained contact with the spout. The SE coos were arbitrarily designated as the "warning" stimuli and the monkeys were taught to break contact with the spout whenever an SE coo was presented.

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 and the overhead light was momentarily turned on. After several stimulus presentations the animals learned to avoid the shock by breaking contact with the spout whenever the coo was presented and to return to the spout when the light signaled the end of the shock.

The animals were then trained to distinguish one SE coo from one SL coo by presenting one of the two coos every 7 sec, with the SE coo presented randomly 25% of the time. Only the SE coo was followed by shock. 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 animals 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 any SE coo (i.e., a "warning" signal) and by maintaining contact after presentation of any SL coo (a "safe" signal).

The final test procedure consisted of presenting 3.5-sec trials once every 7 sec (i.e., with a 3.5-sec intertrial interval). Each trial was either an SL (safe) trial or an SE (warning) trial. SE trials occurred randomly from 1 to 7 trials after the previous warning trial with occasional "catch" trials inserted in which a safe stimulus was presented on the seventh trial. The number of warning trials given in each of the trial periods was adjusted so that each trial period had the same probability of being a warning trial (which was .25). A typical session consisted of the presentation of 21 to 35 warning trials and 63 to 105 safe trials.

The response of an animal on each trial, i.e., whether or not it had made an avoidance response, was determined by noting whether the animal was in contact with the spout during the last 200 msec of the trial. Basing the response criterion on the last 200 msec of the trial allowed the animal sufficient time to break contact with the spout following presentation of a warning stimulus. The details of determining spout contact were as follows: The duration of spout contact during the last 200 msec of each trial was measured in 20-msec increments. This generated a number from zero to 10 where zero indicated no contact, 10 indicated contact during all 10 of the 20-msec periods, and an intermediate number indicated intermittent contact.

The scores for a session were averaged separately for each of the 15 coos and rank-ordered to allow a detailed comparison of the relative performances. An overall measure of performance was calculated by taking the average of the SE and SL scores and calculating a performance ratio with the formula: $(S - W)/S$ where S is the average of the SL (safe) scores and W is the average of the SE (warning) scores. In a trained animal the measure ranged from 1.0 (indicating good discrimination of the SE and SL coos) to 0 (indicating failure to discriminate).

The statistical reliability of the scores was evaluated two ways. First, chance probability for a session was calculated by comparing the occurrence of responses during the safe and warning trials using the binomial distribution (e.g., Hays, 1963). Second, the scores for the individual coos were rank-ordered and the Mann–Whitney U test (Siegel, 1956) was used to determine the probability that the two groups of coos were being responded to differently.

RESULTS AND DISCUSSION

Simulating a Cortical Hearing Loss

The four normal monkeys were given three sessions of the standard coos followed by five sessions of the filtered coos and three final sessions with the standard coos. As shown in Fig. 3, all of the animals easily discriminated the standard coos despite the fact that several weeks had elapsed since they had last received training on this task. Indeed, it has been demonstrated that training can be discontinued for up to 3 months with no serious decrement in performance (Heffner & Heffner, 1986a). Thus while the coos are acoustically complex stimuli, the ease with which the monkeys discriminated them indicates that they are biologically simple.

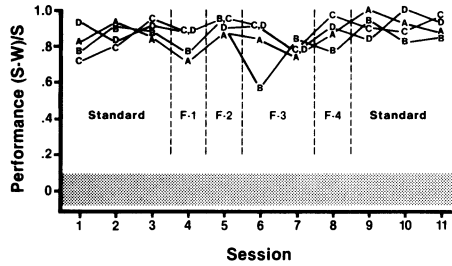

FIG. 3. Performance of the four normal monkeys (A, B, C, and D) on the discrimination of standard and filtered coos. Shaded area indicates the average performance, plus and minus one standard deviation, of four monkeys with bilateral auditory cortex lesions on the discrimination of standard coos (from Heffner & Heffner, 1986a).

In evaluating the performance of the monkeys on the filtered coos, it is necessary to consider the effect of lesions on the coo discrimination. Bilateral ablation of the superior temporal gyrus typically results in a complete and permanent inability to discriminate the coos. As a result the animals' scores range near zero even nearly a year after surgery. The performance of the four operated monkeys (taken from Heffner & Heffner, 1986a) whose audiograms were used to generate the filter settings (Fig. 1) is indicated by the shaded area in Fig. 3. The average score for these monkeys was .01 (standard deviation = .09) and the highest score ever achieved was .30. As previously mentioned, left (but not right) unilateral superior temporal gyrus lesions result in an initial impairment on this task. Although right hemisphere lesions have no noticeable effect, left hemisphere lesions result in a transient impairment in which the animals' scores fall to .40 or lower and then gradually improve to normal (Heffner & Heffner, 1986a).

Turning to the performance of the normal monkeys, it is apparent that their performance in no way resembles that of operated monkeys. In only one normal case did an animal's performance drop noticeably (monkey B, F-3). However, even this score (.57) did not overlap with that of the operated monkeys and the animal's score returned to normal on the following session. Although it is possible that a detailed analysis might reveal slight a decrement in performance due to filtering, it is clear that the filtering used here had less effect on the animals' performances than either a left unilateral or a bilateral superior temporal gyrus lesion (cf., Heffner & Heffner, 1986a).

Compensating for a Cortical Hearing Loss

The four operated monkeys were tested for their ability to discriminate standard and equalized coos in 44 sessions given over a period of 2

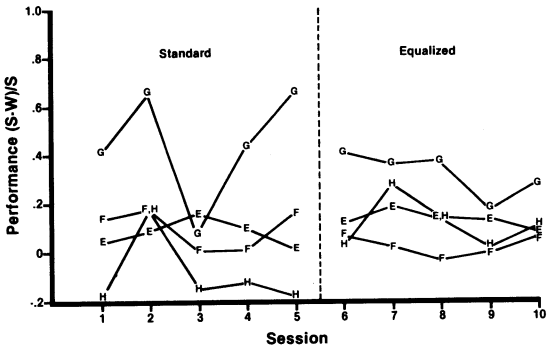

FIG. 4. Performance of the four monkeys (E, F, G, and H) with bilateral auditory cortex lesions on the discrimination of standard coos and coos which had been equalized to compensate for individual hearing losses (see Fig. 3). All scores for monkeys E, F, and H were at chance levels for both conditions while the scores for monkey G did not improve when the coos were equalized.

months. During this time the animals received training on individual pairs of coos as well as testing on the entire set of 15 coos. In evaluating their postoperative performance it should be noted that in their original preoperative training, these animals had achieved a performance of .80 or better in only 21 to 28 sessions.

Analysis of the performances of the animals during this period failed to show any reliable differences between the standard and equalized coos. This result is best illustrated by the performance of the animals during the last 10 sessions of testing (Fig. 4). Of the four monkeys, three (monkeys E, F, and H) were never able to perform above chance either when the standard sounds were presented or when they were equalized in an effort to compensate for their individual hearing losses ($p > .05$, binomial distribution and Mann–Whitney U).

The fourth animal, monkey G, showed a somewhat different pattern of responding. This animal was able to perform above chance ($p < .01$), although below preoperative levels, in 4 of the 5 sessions with standard coos (falling to chance on session 3). Similarly, monkey G was able to perform above chance on 3 of the 5 sessions of equalized coos, falling to chance on sessions 9 and 10. Whether this monkey may have been discriminating the stimuli on a different basis (such as frequency or intensity) or whether its partial recovery was the result of a smaller lesion remains to be determined by further behavioral and histological analyses. Nevertheless, the results of this animal, along with those of the other three operates, supports the conclusion that amplifying the coos to equalize the hearing loss does not improve performance over that achieved with the standard stimuli.

CONCLUSIONS

Until recently, it was generally believed that auditory cortex ablation had little or no permanent effect on pure-tone thresholds in any species, humans included (Neff, Diamond, & Casseday, 1975). We now know, however, that not only do macaques have a dramatic and persistent hearing loss following large bilateral lesions of the superior temporal gyrus (Heffner & Heffner, 1986b), they also have a hearing loss following more restricted lesions (Heffner & Heffner, 1987), and they have a small but distinct contralateral hearing loss following unilateral lesions (Heffner & Heffner, 1986c). While these effects were noted in the 19th century (e.g., Ferrier, 1876; for a review, see Heffner, 1987), they were overlooked by modern studies of nonprimates (which do not have as dramatic a hearing loss) and by studies of primates which tested hearing at low frequencies where the hearing loss is smallest (for a review, see Heffner & Heffner, 1986b). Thus, it should be noted that the animal literature is no longer in conflict with the results of clinical studies which found deafness in humans following bilateral lesions of the superior temporal gyrus.

Given the existence of cortical deafness, it is necessary to rule out the possibility that a perceptual deficit resulting from a cortical lesion might be confounded by an accompanying hearing loss. In the case of the permanent inability of Japanese macaques to discriminate coos following bilateral superior temporal gyrus lesions, it does not appear that the cortical deafness which also results from such lesions can account for the deficit. As the present results indicate, normal monkeys have little or no difficulty discriminating coos which have been filtered to approximate the effect of a cortical hearing loss. Furthermore, attempting to compensate for a cortical hearing loss by amplifying and equalizing the coos does not improve the performance of operated animals. These results indicate that the inability of the monkeys to discriminate the coos following bilateral lesions cannot be explained simply as an inability to adequately hear the coos. Instead, it appears that the ability of monkeys to discriminate vocal communication sounds is directly dependent on the integrity of the cortex.

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