

Temporal Lobe Lesions and Perception of Species-Specific Vocalizations by Macaques

Abstract. Japanese macaques were trained to discriminate two forms of their coo vocalization before and after unilateral and bilateral ablation of the temporal cortex. Unilateral ablation of the left superior temporal gyrus, including auditory cortex, resulted in an initial impairment in the discrimination, but similar unilateral ablation of the right superior temporal gyrus had no effect. Bilateral temporal lesions including auditory cortex completely abolished the ability of the animals to discriminate their coos. Neither unilateral nor bilateral ablation of cortex dorsal to and sparing the auditory cortex had any effect on the discrimination. The perception of species-specific vocalizations by Japanese macaques seems to be mediated by the temporal cortex, with the left hemisphere playing a predominant role.

For a number of years primate vocal signals have been studied to determine what similarities they might have to human language (1). Recent evidence suggests that the neural mechanism mediating the perception of vocalizations by Japanese macaques may be similar to that mediating the perception of human speech. Specifically, Japanese macaques (*Macaca fuscata*) seem better able to discriminate between two forms of their "coo" vocalization with their right ear than with their left (2). This right-ear advantage for the perception of a species-specific vocalization resembles that shown by humans for the perception of speech sounds (3).

In humans, the right-ear advantage for speech perception is explained by the existence of an area in the left cortical hemisphere that is specialized for the perception of speech. Because of the contralateral representation of auditory space in the cortex (4), input from the right ear ascends through the auditory system directly to the speech reception area in the left hemisphere (Wernicke's area), while similar input from the left ear goes first to the right hemisphere before crossing over to reach the speech area. This direct access of the right ear to the speech area, as opposed to the indirect access of the left ear, is used to account for the superiority of the right ear in the perception of speech (3, 5). The presence of a right-ear advantage in the Japanese macaque, then, suggests that it may have a left-hemispheric specialization for the perception of species-specific vocalizations analogous to that found in humans.

The idea that monkeys possess an analog of Wernicke's area has important physiological as well as philosophical implications. Until now, however, there has been no direct evidence that the anatomical site of the neural mechanism in monkeys is the same as it is in humans. While a right-ear advantage suggests a specialization of the left side of the brain (6), it does not indicate whether

the area of specialization resides in the secondary auditory cortex as Wernicke's area appears to (7), or whether it is located elsewhere in the cerebral cortex or in some lower auditory center.

The purpose of this study was to determine the neuroanatomical basis of the right-ear advantage of Japanese macaques by use of an ablation-behavior technique. This was done by determining the ability of Japanese macaques to discriminate two forms of their coos before and after unilateral and bilateral ablation of the auditory cortex. In humans, similar damage to Wernicke's area results in an impairment in the ability to understand speech (8).

The 11 Japanese macaques used in this study were 5- to 7-year-old (adolescent) males that had been born and reared in a free-ranging colony. The monkeys were trained to discriminate two subtypes of their coo vocalizations in a conditioned avoidance task. The vocalizations used were the same sounds used in a previous study to demonstrate the right-ear advantage for this species (2). They consisted of seven so-called "smooth early (SE) high" and eight "smooth late (SL) high" coos.

A thirsty monkey was seated in a primate chair and trained to place its mouth on a water spout to receive a slow

but steady trickle of water (9). Initial auditory training consisted of presenting one of the SE coos at random intervals from 7 to 49 seconds apart over a loudspeaker (10). Each presentation consisted of playing the coo three times, following which a mild electric shock was delivered through the water spout and the room lights were momentarily turned off. After several stimulus presentations the animal learned to avoid the shock by breaking contact with the spout whenever the call was presented and return to the spout when the room lights signaled the end of the shock. The animal was then trained to distinguish between an SE and an SL call by presenting one of the two calls every 7 seconds, with the SE call presented randomly 25 percent of the time. Only SE calls were followed by shock. Once the animal had learned to break contact only when the SE call was presented, additional examples of both types of calls were presented until the animal had learned to discriminate the entire set of 15 calls. Thus, the animals demonstrated their ability to distinguish the two subtypes of coos by breaking contact with the spout after presentation of an SE coo and by maintaining contact after presentation of an SL coo.

After being trained, five monkeys received unilateral temporal lobe lesions that included all of the left primary and secondary auditory cortex, five other monkeys received unilateral lesions that included all of the right primary and secondary auditory cortex. The eleventh monkey received a unilateral lesion of the left superior temporal gyrus that spared part of the auditory cortex, but included the adjacent areas of the inferior parietal and preoccipital gyri (Fig. 1). Retesting on the discrimination was begun 3 to 11 days later. After being retested, six of the animals received similar lesions in the other hemisphere.

Unilateral ablation of the left superior

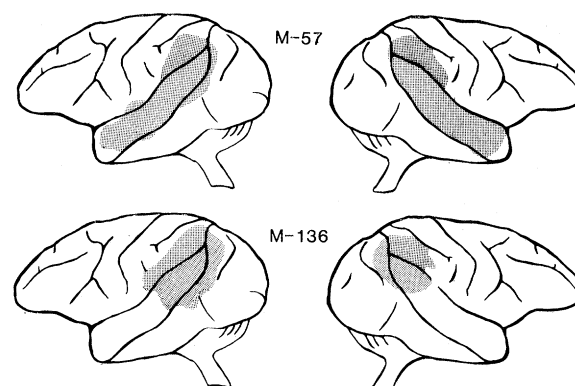


Fig. 1. Cortical lesions. The lesions of the auditory cortex (illustrated for M-57) included nearly all of the superior temporal gyrus and, in some cases, adjacent parietal and occipital cortex, resulting in complete degeneration of the medial geniculate. The lesions in M-136 included the dorsal part of the superior temporal gyrus and adjacent parietal and occipital areas, but spared part of auditory cortex on the left side and all of auditory cortex on the right side. The lesions were performed in two stages with testing between stages.

temporal gyrus, including the auditory cortex, resulted in an initial impairment in the ability to discriminate the coos (Fig. 2A). This impairment consistently occurred in all five left-hemisphere animals, which required from 5 to 15 training sessions (with an average of 10) before reaching preoperative performance levels. In contrast, unilateral ablation of the right superior temporal gyrus had no measurable effect on postoperative performance (Fig. 2B). All five right-hemisphere animals performed within normal preoperative levels on the first postoperative session, even when tested as soon as 3 days after surgery. Thus, the five monkeys with lesions of the left hemisphere consistently showed an initial impairment, whereas the five monkeys with lesions of the right hemisphere showed no impairment ($U = 0$, $P < 0.01$).

After the animals had reached normal performance levels, similar lesions were made in the other hemisphere in three of the left and two of the right unilateral monkeys. The bilateral lesions rendered the animals totally unable to perform the discrimination (Fig. 2, A and B). Even as long as 9 months after surgery, the ani-

mals were unable to reliably discriminate a single pair of coos. The superior temporal gyrus thus seems necessary for the discrimination of coo vocalizations by Japanese macaques.

The pattern of the deficits after the unilateral and bilateral lesions indicates the relative roles of the two hemispheres in the discrimination of the vocalizations. The observation that ablation of the left, but not right, superior temporal gyrus results in an initial deficit suggests that the left side plays a predominant role in the discrimination. The observation that subsequent removal of the right superior temporal gyrus permanently abolishes the discrimination suggests that the apparent recovery after a lesion on the left was due to the right hemisphere's mediating the discrimination in the absence of the left hemisphere. The

question of whether the right hemisphere can mediate the discrimination as proficiently as the left, however, must await the results of further testing.

In contrast to these bilateral lesions, a lesion that spared the ventral portions of the superior temporal gyrus, including part of the left and all of the right auditory cortex (Fig. 2C), did not cause any impairment. This result demonstrates (i) that the deficit shown by the other animals is not due to general cortical trauma and (ii) that the cortical area necessary for this discrimination does not lie immediately dorsal and lateral to auditory cortex.

These results demonstrate that the perception of species-specific vocalizations by Japanese macaques is mediated in the superior temporal gyrus. Furthermore, the left temporal lobe seems to play a predominant role in this perception. Such results are consistent with the notion that Japanese macaques possess an area analogous to Wernicke's area.

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9. A contact switch connected between the water spout and footplate was used to detect spout contact. Water was delivered through an electrically operated valve (about 6 ml/min) whenever the animal placed its mouth on the water spout. All testing was conducted in a burlap-draped acoustic chamber.
10. Initially the auditory stimuli were produced by playing tape-recorded coos. In later testing, the coos were digitized and reproduced by a microcomputer with a digital-to-analog converter.
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Fig. 2. The effect of unilateral and bilateral lesions on the discrimination of SE and SL coos, expressed as a ratio between the average time an animal remained on the water spout after an SL or safe (S) trial and an SE or warning (W) trial. Testing for the effect of the unilateral lesions was begun on postoperative day 11 for M-57 and on the postoperative day 8 for the other two animals. (A) The deficit shown by the monkeys with left superior temporal lesions (which included the auditory cortex) is illustrated for M-57. This animal required five sessions to reach preoperative performance levels while the other four animals with left lesions required 8 to 15 sessions. (B) In contrast, all five animals with right superior temporal lesions reached normal levels on postoperative day 1 of testing, as exemplified by M-150. The necessity of the superior temporal gyrus for this task is indicated by the fact that bilateral ablation totally and permanently abolished the ability to perform the discrimination. That the performance of animals with both left and right unilateral lesions fell to chance levels after a contralateral ablation demonstrates that they had received comparable lesions. (C) In contrast, neither left unilateral nor bilateral ablation of the dorsal part of the superior temporal gyrus and adjacent midtemporal, inferior parietal and preoccipital gyri had any effect on the discrimination (M-136).

