Heffner, H.E. & Heffner, R.S. (1994). Lateralization of the perception of communicative vocalizations in Japanese macaques. In J.R. Anderson, J.J. Roeder, B. Thierry, & N. Herrenschmidt (Eds.), *Current Primatology, Vol. III, Behavioural Neuroscience, Physiology and Reproduction* (pp. 1-8). Strasbourg: Universite Louis Pasteur.

CURRENT PRIMATOLOGY

VOLUME III

Behavioural Neuroscience, Physiology and Reproduction

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Lateralization of the perception of communicative vocalizations in Japanese macaques

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The most prominent evidence for lateralization in the human nervous system is the location of the speech areas in the left hemisphere. In particular, the cortical area involved in the recognition of speech appears to be located in the posterior portion of the superior temporal gyrus of the left temporal lobe. Thus, lesions which involve this area typically result in a deficit in the ability to understand speech, part of a syndrome referred to as Wernicke's aphasia (e.g., Benson & Geschwind, 1969).

The existence of a speech reception mechanism in the left hemisphere of humans has led to the question of whether there might be a similar mechanism in nonhuman primates. Some years ago there appeared evidence that the left hemisphere of Japanese macaques (*Macaca fuscata*) was specialized for the perception of their vocal communications. This evidence came from the observation that Japanese macaques show a right-ear advantage in the discrimination of two types of their "coo" vocalizations (Petersen et al., 1978; Beecher et al., 1979); types that are acoustically similar, but have different behavioral meanings (Green, 1975).

The right-ear advantage for the perception of species-specific vocal communication in Japanese macaques resembles that shown by humans for the perception of speech sounds (Kimura, 1967). This right-ear advantage is explained by the fact that the output of each ear is sent primarily to the contralateral hemisphere (e.g., Glendenning & Masterton, 1983). As a result, information from the right ear reaches Wernicke's area, which is located in the left hemisphere, more directly than information from the left ear which, according to human split-brain studies, goes first to the right hemisphere and then to Wernicke's area via the corpus callosum (Zaidel, 1986). Whether the right-ear advantage is the result of information from the right ear reaching Wernicke's area first or because the right ear connections are more robust (e.g., qualitatively or quantitatively superior) is unknown. However, regardless of the mechanism, the result is that there is a small but reliable advantage for

reporting verbal information received by the right ear in a dichotic listening task.

The presence of a right-ear advantage in Japanese macaques suggests that, like humans, 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 and, indeed, this appears to be the case. Using the same coo vocalizations used to demonstrate the right-ear advantage, we have been studying the effects of temporal lobe lesions on the ability of Japanese macaques to discriminate their vocalizations (Heffner & Heffner, 1984, 1986, 1989). The results of these studies indicate that left unilateral ablation of the superior temporal gyrus consistently results in an initial impairment in the ability to discriminate the vocalizations. In contrast, right unilateral ablation has no detectable effect on discrimination ability.

The left hemisphere deficit, however, is not permanent and the monkeys regain normal performance after 5 to 15 days. This recovery of function may be due to two factors. First, it is apparent that the right hemisphere can mediate the coo discrimination. This conclusion is based on the observation that subsequent ablation of the right superior temporal gyrus completely and permanently abolishes the ability of the monkeys to discriminate the vocalizations. Second, although the coos themselves are acoustically complex, the behavioral task in which the animals discriminate 7 examples of one coo from 8 examples of another is one which normal monkeys learn quite easily (Heffner & Heffner, 1986). Because Japanese macaques are reported to have 7 different types of coo sounds as well as 9 other classes of sounds (cf. Green, 1975), it may be that a more demanding discrimination is required to demonstrate any permanent effect of left unilateral lesions. Indeed, given that in humans the left hemisphere superiority for the recognition of verbal stimuli is a matter of degree (e.g., Hellige, 1990), it is not surprising that the right hemisphere of macaques should be capable of mediating a relatively simple discrimination.

Bilateral lesions, on the other hand, permanently abolish the ability of the monkeys to discriminate the two sets of coos indicating that this particular discrimination is a cortically-dependent task. Indeed, the cortical deficit is so severe that the animals are generally unable to discriminate between even a single pair of coos. That auditory cortex is necessary for this task is of special interest - although cortical ablation is known to affect a number of auditory discriminations, most are only partially disrupted and the animals show only

increased thresholds or decreased performance levels (Heffner & Heffner, 1990b). The coo discrimination, however, is unique in that although it is very easy for normal monkeys, it cannot be performed by monkeys with bilateral auditory cortex lesions.

The discovery of a discrimination which requires auditory cortex presents an opportunity to study the process by which information is sent to the cortex - specifically, the relative contribution of the ipsilateral and contralateral auditory pathways. It is generally accepted that information from an ear is sent primarily to the opposite hemisphere. However, the question arises as to how much information is also sent to the ipsilateral hemisphere. In the case of Japanese macaques, this can be answered by removing the superior temporal gyrus in one hemisphere and testing the ability of the animal to discriminate coos presented to each ear separately. Whereas the animal would be expected to perform the discrimination at normal or near normal levels when the coos were presented to the ear opposite the intact hemisphere, the degree to which it could discriminate coos presented to the ear on the same side as the intact hemisphere would reflect the ability of the ipsilateral pathway to send information to the cortex. Thus, the purpose of this study was to assess the relative efficacy of the ipsilateral and contralateral auditory pathways by determining the effect of unilateral lesions on the ability of Japanese macaques to discriminate coos presented to each ear.

Methods

Subjects

Four male Japanese macaques (*Macaca fuscata*) were used in this study and are referred to as M-291, M-294, M-352 and M-395. The animals were individually housed in primate cages with free access to food and were trained using water as a reward.

Surgery

Following preoperative training and testing, the monkeys received unilateral lesions of either the left (M-294 and M-395) or right (M-291 and M-352) superior temporal gyrus (for details of the surgical procedure, see Heffner & Heffner, 1986). Placement of the lesions was verified by magnetic resonance imaging.

Acoustic stimuli

The vocalizations used in this discrimination were the same 15 coos previously used to demonstrate the effect of unilateral and bilateral auditory cortex lesions in Japanese macaques (Heffner & Heffner, 1984, 1986). These vocalizations were originally recorded by

Green (1975) and had been used to demonstrate a right-ear advantage in Japanese macaques (for details of the coos, see Beecher et al., 1979). They consist of seven "smooth early high" (SE) and eight "smooth late high" (SL) coos. The coos are distinguished by the temporal position (i.e., either early or late) of the peak fundamental frequency of the frequency-modulation portion of the call and are emitted by the monkeys in different behavioral situations. These vocalizations were digitized using a microcomputer and presented through insertion earphones in either of two stimulus configurations: 1) a coo was presented either to the left or right ear only, and 2) a coo was presented to both ears with one ear receiving the coo 384 μs earlier and 15 dB louder than the other ear. In Japanese macaques this configuration results in a "lateralized" auditory image which is perceived as a sound presented only to the ear receiving the early, louder stimulus (Heffner, unpubl. obs.).

Behavioral procedure

The details of the behavioral procedure are described elsewhere (Heffner & Heffner, 1986). Briefly, a monkey was trained to climb into a primate chair and place its mouth on a water spout. This was accomplished by providing a steady trickle of water (3-4 ml per min) as long as the animal maintained contact with the spout. Coos were then presented and the animal was trained to break contact with the water spout whenever one of the SE coos was presented in order to avoid a mild electric shock delivered through the spout. Presentations of SL coos were never followed by shock and the animal learned to maintain contact with the spout when any of the SL coos were presented.

The response of an animal on each trial (i.e., whether it had made an avoidance response) was determined and a measure of performance was recorded for each session using the formula: *performance = hit rate - (false alarm rate x hit rate)*, where hit rate is the percentage of avoidance responses when SE coos were presented, and false alarm rate is the percentage of avoidance responses when SL coos were presented. This measure proportionately reduces the hit rate by the false alarm rate and varies from 0 (no hits) to 1 (100% hit rate with no false alarms)(for a discussion of this measure, see Heffner & Heffner, 1988).

The ability of a monkey to discriminate coos presented separately to each ear was determined by presenting one of the 15 coos every 7 seconds to either the left or right ear. Both the coo and the ear to which it was presented were determined with a quasi-random schedule. The response of an animal to the coos was determined separately for each ear and an overall performance measure was calculated for each ear on each session. During a typical session, the SE coos were presented 2-3 times and the SL coos 6-8 times to each ear. The ability to discriminate coos presented to both ears, but with a time and intensity difference (i.e., the lateralized stimuli) was determined in a similar fashion.

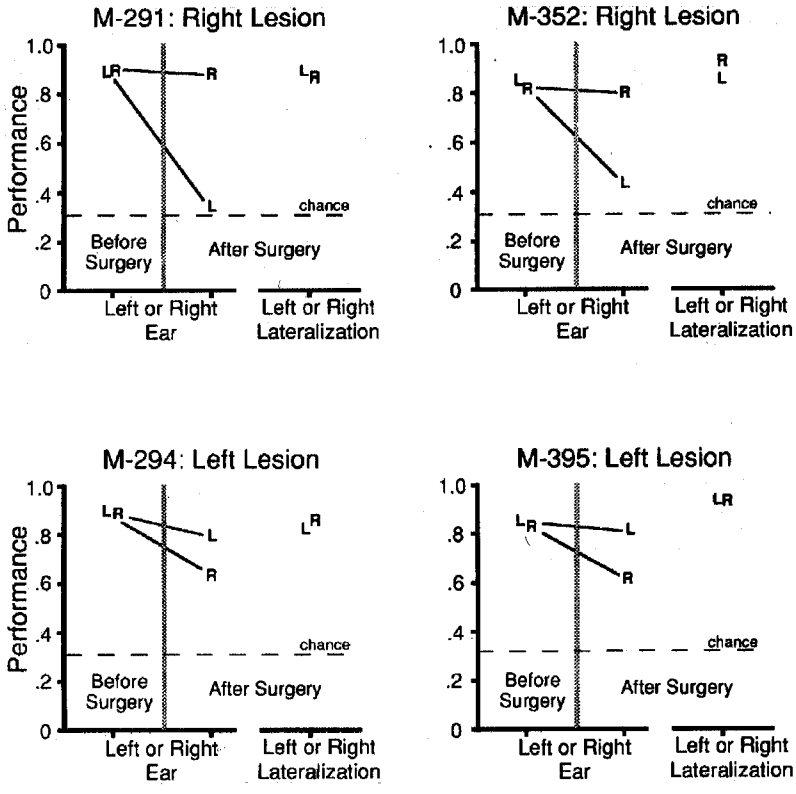

Fig. 1. Pre- and postoperative ability of the four monkeys to discriminate coos presented to the left and right ear as well as postoperative ability to discriminate coos lateralized to the left or right side. L and R indicate left and right respectively. After surgery, the animals showed a significant deficit in discriminating coos presented to the ear opposite the lesion. However, there was no deficit in discriminating the lateralized coos. (Each data point represents the average for 10 sessions. Dashed line indicates .01 chance level of performance.)

Results

Although the lesions did not completely abolish the ability of the monkeys to discriminate coos presented to the ear opposite the lesion, they did result in a large and permanent decrement. In addition, there appeared to be a slight decrease in performance for the ear opposite the intact hemisphere. However, the lesions appeared to have no effect on the discrimination of the lateralized coos.

Figure 1 shows the averaged data for each of the 4 monkeys for the three conditions. The preoperative ability of the animals to discriminate coos presented separately to each ear represents the average scores for the 10 sessions immediately prior to surgery. By this time, each animal had received

extensive training (over 100 training sessions) and consistently scored .80 or better for each ear. Because the right-ear advantage for this task is apparent only during the initial acquisition of the discrimination (Moody et al., 1990), no right-ear advantage would be expected by this time.

Following surgery, each of the animals showed a consistent and permanent decrease in the ability to discriminate coos presented to the ear opposite the lesion. The deficit is illustrated in Figure 1, which shows the average of the 10 most recent sessions for the monkeys (conducted 9 to 11 months after surgery). The degree of the deficit varied and was larger in the two animals with right hemisphere lesions; whether or not this is due to differences in lesion size is not known at this time. Although all of the animals were able to perform above chance, the performance of M-291 would occasionally fall to chance levels on individual sessions. In addition, each animal showed a decrement in performance in the ear opposite the intact hemisphere which decreased with time, but was still apparent 9-11 months after surgery (Fig. 1).

Finally, when the lateralized coos were presented to both ears with a time and intensity difference which normally results in the perception of a single image in the ear receiving the earlier and louder stimulus, there was no consistent side difference (Fig. 1). Indeed, although preoperative data on this task are not available, the relatively high performance of the animals suggests that this task was not affected by the lesions.

Discussion

These results have a direct bearing on our views of the organization of the auditory system with regard to the pathway from the ear to the cortex. First, the demonstration of a major deficit in discriminating coos presented to the ear opposite the lesion supports the accepted view that information from each ear is sent primarily to the opposite hemisphere. It should be noted, however, that the exact anatomical pathway by which input travels from the ear to the opposite hemisphere is by no means certain. Although the classical view holds that the primary auditory decussation is at the level of the superior olivary nuclei, there are (at least in the cat) no less than 14 decussations in the auditory system (Hutson et al., 1991).

The fact that the animals could still discriminate coos presented to the ear opposite the lesion, although at reduced performance levels, demonstrates that there is also a route by which input to one ear can reach the ipsilateral cortex. As with the crossed pathway, however, the exact route is unknown.

Indeed, given the large number of auditory decussations, it is quite possible for input to cross back and forth before reaching the cortex.

It was also noted that the animals showed a small but persistent decrease in performance for discriminating coos presented to the ear opposite the intact hemisphere. Although additional cases are needed to establish the reliability of this observation, it suggests that the two hemispheres work in close coordination. Thus, removal of the auditory area of one hemisphere may compromise the performance of the auditory area in the other.

Finally, Phillips and Gates (1982) have proposed that the dominant input to a hemisphere is not from the contralateral ear, but from the contralateral sound field. In other words, sounds originating in one hemifield are represented in the opposite hemisphere even though the sound reaches both ears. Indeed, this appears to be true in the case of sound localization as a unilateral lesion primarily disrupts the ability to localize sound in the hemifield opposite the lesion (e.g., Heffner et al., 1992).

However, previous work has indicated that the role of the cortex in the detection of sound is organized in terms of the ear, not the hemifield (Heffner & Heffner, 1990a), and the results of the lateralized coos indicate that the same applies to the identification of sound. That is, if information reaching the two ears is sent primarily to the hemisphere opposite the hemifield in which the sound is perceived to originate, then the monkeys should have shown a deficit when the coos were lateralized to the ear opposite the lesion. The fact that there was no such deficit indicates that the intact hemisphere was receiving information by a direct route, i.e., from the ear receiving the delayed and less intense coo. Thus, assuming that the lesions do not affect the way in which the brainstem routes binaural information, these results indicate that information regarding the identification of a sound which reaches both ears is sent to both hemispheres even if the sound is lateralized to one hemifield.

Acknowledgments

This work was supported by NIH grant R01 NS30539. The research protocols used here were reviewed and approved by the University of Toledo Institutional Animal Care and Use Committee.

References

Beecher, M.D., Petersen, M.R., Zoloth, S.R., Moody, D.B. & Stebbins, W.C. (1979). Perception of conspecific vocalizations by Japanese macaques. *Brain Behav. Evol.* 16: 443-460.

Benson, D.F. & Geschwind, N. (1969). The alexias. In Vinken, P.J. & Bruyn, G.W. (eds.), *Handbook of clinical neurology, Vol. 4*, North-Holland, Amsterdam, pp. 112-140.

Glendenning, K.K. & Masterton, R.B. (1983). Acoustic chiasm: Efferent projections of the lateral superior olive. *J. Neurosci.* 3: 1521-1537.

Green, S. (1975). Variation of vocal pattern with social situation in the Japanese monkey

(*Macaca fuscata*): A field study. In Rosenblum, L.A. (ed.), *Primate behavior, Vol. 4*, Academic Press, New York, pp. 1-102.

Heffner, H.E. & Heffner, R.S. (1984). Temporal lobe lesions and perception of species-specific vocalizations by macaques. *Science* 226: 75-76.

Heffner, H.E. & Heffner, R.S. (1986). Effect of unilateral and bilateral auditory cortex lesions on the discrimination of vocalizations by Japanese macaques. *J. Neurophysiol.* 56: 683-701.

Heffner, H.E. & Heffner, R.S. (1989). Effect of restricted cortical lesions on absolute thresholds and the discrimination of species-specific sounds by Japanese macaques. *Behav. Neurosci.* 103: 158-169.

Heffner, H.E. & Heffner, R.S. (1990a). Effect of bilateral auditory cortex lesions on absolute thresholds in Japanese macaques. *J. Neurophysiol.* 64: 191-205.

Heffner, H.E. & Heffner, R.S. (1990b). Role of primate auditory cortex in hearing. In Stebbins, W.C. & Berkley, M.A. (eds.), *Comparative perception, Vol. II*, Wiley, New York, pp. 279-310.

Heffner, H.E., Carroll, B.A. & Kovach, D.R. (1992). Effect of unilateral ablation of auditory cortex on sound localization by macaques. *Abstracts of the Fifteenth Meeting of the Association for Research in Otolaryngology* 15: 52.

Heffner, R.S. & Heffner, H.E. (1988). Sound localization in a predatory rodent, the northern grasshopper mouse (*Onychomys leucogaster*). *J. Comp. Psychol.* 102: 66-71.

Hellige, J.B. (1990). Hemispheric asymmetry. *Ann. Rev. Psychol.* 41: 55-80.

Hutson, K.A., Glendenning, K.K. & Masterton, R.B. (1991). Acoustic chiasm IV: Eight midbrain decussations of the auditory system in the cat. *J. Comp. Neurol.* 312: 105-131.

Kimura, D. (1967). Functional asymmetry of the brain in dichotic listening. *Cortex* 3: 163-178.

Moody, D.B., Stebbins, W.C. & May, B.J. (1990). Auditory perception of communication signals by Japanese monkeys. In Stebbins, W.C. & Berkley, M.A. (eds.), *Comparative perception, Vol. II*, Wiley, New York, pp. 311-344.

Petersen, M.R., Beecher, M.D., Zoloth, S.R., Moody, D.B. & Stebbins, W.C. (1978). Neural lateralization of species-specific vocalizations by Japanese macaques (*Macaca fuscata*). *Science* 202: 324-327.

Phillips, D.P. & Gates, G.R. (1982). Representation of the two ears in the auditory cortex: A re-examination. *Int. J. Neurosci.* 16: 41-46.

Zaidel, E. (1986). Callosal dynamics and right hemisphere language. In Leporé, F., Ptito, M. & Jasper, H.H. (eds.), *Two hemispheres, one brain*, A.R. Liss, New York, pp. 435-459.