

*CONTROL OF RESPONDING BY THE LOCATION OF SOUND:
ROLE OF BINAURAL CUES*

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In auditory localization experiments, where the subject observes from a fixed position, both relative sound intensity and arrival time at the two ears determine the extent of localization performance. The present experiment investigated the role of binaural cues in a different context, the sound-position discrimination task, where the subject is free to move and interact with the sound source. The role of binaural cues was investigated in rats by producing an interaural imbalance through unilateral removal of the middle auditory ossicle (incus) prior to discrimination training. Discrete trial go-right/go-left sound-position discrimination of unilaterally incudectomised rats was then compared with that of normal rats and of rats with the incus of both sides removed. While bilateral incus removal affected binaural intensity and arrival times, the symmetry of sound input between the two ears was preserved. Percentage of correct responses and videotaped observations of sound approach and exploration showed that the unilateral rats failed to localize the sounding speaker. Rats with symmetrical binaural input (normal and bilaterally incudectomised rats) accurately discriminated sound position for the duration of the experiment. Previously reported monaural localization based upon following the intensity gradient to the sound source was not observed in the unilaterally incudectomised rats of the present experiment. It is concluded that sound-position discrimination depends upon the use of binaural cues.

Key words: auditory discrimination, localization, binaural cues, rats

In order to interact effectively with sound sources in the field, it is necessary that an animal be able to respond to the position of the source relative to itself. This requirement has led to the evolution of at least two behavioral characteristics that are controlled by the position of sources. Rats (for example) orient to, approach, and explore novel sources of low-intensity auditory stimuli (Harrison, 1983), and these animals have also evolved the ability to acquire, in one trial, discriminations of the position of sources under seminaturalistic conditions (Harrison, 1979, 1981). In addition, these animals have evolved the ability to respond to the position of a source in the presence

of echos (pseudosources) (Hoeffding & Harrison, 1979; Kelly, 1974a, 1974b).

Localization has been extensively investigated and it is widely accepted that localization depends upon interaural time and intensity differences (Durlach & Colburn, 1978). There are, however, other cues correlated with the position of a sound source. There is an intensity gradient from the source to the animal, detectable when moving to and from the source. This is a monaural cue. If the animal remains fixed but rotates its head, the resulting pattern of sound provides both monaural and binaural cues to source position. It has been shown that monaural animals can respond to the position of a sound source (Casseday & Neff, 1975; Masterton, Jane, & Diamond, 1967).

The primary purpose of the present experiment was to investigate the role of binaural cues in performance of a sound-position discrimination task. The role of binaural cues was investigated by producing an interaural imbalance by removing the middle auditory

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ossicle (incus) from one ear prior to training on the discrimination. Interruption of the human ossicular chain at the incus produces about 40 dB attenuation of sound at the affected ear when the tympanic membrane remains intact, as in the present experiment (Anklesari, 1963; Bauer, 1958, 1964; Elbrond, 1970). For incudectomised rats, such a reduction in sound intensity at the operated ear certainly would produce an extreme binaural imbalance in sound input, and thus the opportunity to evaluate the importance of binaural cues in sound-position discrimination.

In addition, two comparison groups were observed: unoperated control rats and bilaterally incudectomised rats (both incudes removed). Bilateral removal of the incus will change hearing equally on both sides and hence not destroy the symmetry of binaural cues.

METHOD

Subjects

Six male albino rats of the Sprague-Dawley strain, obtained from Charles River Breeding Laboratories, served as subjects. At the age of 4 weeks the middle auditory ossicle (incus) of either one ear (2 unilateral rats) or both ears (2 bilateral rats) was removed surgically. The remaining 2 rats were unoperated. All subjects were 100 days old at the start of the experiment and were maintained at approximately 75% of their free-feeding weights.

Surgery

Removal of the incus was performed under chloral hydrate anesthesia. The middle ear was approached via the external auditory meatus. With a sharp microscalpel, the dorsal attachment of the tympanic membrane to the bony ring was freed and the membrane flap turned down. After visualization of the auditory ossicles through a speculum placed in the meatus, the incus was gently freed from its attachments to the malleus and stapes and was removed, leaving the stapes footplate intact in the oval window. Gelfoam was placed in the middle ear, the tympanic membrane flap was repositioned at the bony ring, and additional Gelfoam was placed externally. Recovery was

uneventful, the tympanic membrane healing satisfactorily, and there was no postoperative evidence of infection. Light microscopic evaluation of the inner ears of three additional incudectomised animals did not reveal any surgery-related abnormalities.

Apparatus

The experimental chamber was a wire-cloth cage (26 cm wide, by 30 cm long, by 20 cm high) situated inside a large enclosure (approximately 1 m square). Two response levers were mounted on the front wall of the chamber, equidistant (7 cm) from the vertical centerline of the wall. Two Radio Shack Super Tweeter speakers were hung one behind each lever, facing into the chamber. Sound was conveyed to a point directly above each response lever by a metal funnel affixed to the front of each speaker. Carnation sweetened condensed milk (milk to water ratio, 1:3) was delivered as the reinforcer via a dipper feeder located on the back wall. During each session the chamber was illuminated by a 28-V house-light mounted at the center of the chamber ceiling. The first discrimination session was videotaped without additional illumination, using a Sony videotape recorder.

The auditory stimulus was wide band noise with a fast rise-decay time, delivered in repetitive pulses of 0.5 s on and 0.5 s off, repeating for the duration of a trial. Acoustic measurements were made using a Bruel and Kjaer ¼-inch condenser microphone calibrated with a Bruel and Kjaer pistonphone (4220). The stimulus contained all frequencies from 4.5 kHz to 50 kHz, with approximately equal energy at each frequency, and approximately matched the hearing range of the rat.

The acoustic signal was adjusted to an intensity of 77 dB (SPL), reference 20 $\mu\text{N}/\text{m}^2$, for unoperated and unilateral rats, and to 87 dB (SPL) for the bilaterally incudectomised rats, as measured from a point 0.5 cm from the speaker opening. The intensity of the stimulus was raised for the bilaterally incudectomised rats to partially compensate for their elevated thresholds. The intensity used, 87 dB (SPL), was the maximum that could be obtained from the equipment. The intensity at

all points within the chamber was above the auditory intensity threshold of normal rats (Harrison & Turnock, 1975).

Procedure

The procedure consisted of two parts: (1) preliminary magazine and lever training, and (2) discrimination training. All subjects were trained first to drink milk at the magazine, and then to press both levers (speakers unplugged). When the response rates on both levers were judged stable and equal, the speakers were plugged in and discrete go-right/go-left sound trials were presented in random order from the left and right speakers. During any trial, a response on the lever contiguous with the sounding speaker (correct response) was reinforced and started the next intertrial interval. A response on the other, noncontiguous, lever (error) produced only the next intertrial interval. On any trial, the sound stimulus remained on until the animal pressed one of the two levers. The intertrial interval averaged 45 s. Intertrial-interval responses had no consequence unless made within 5 s of trial onset; such responses delayed trial onset for an additional 5 s (prolong). Sessions terminated after 40 trials. The experiment was conducted for 10 sessions.

RESULTS

The principal data recorded were the percentage of trial responses that were spatially contiguous with the sounding speaker (percentage correct responses). In order to provide a baseline against which to assess the effects of introducing acoustic stimuli, data collected during the last day of preliminary training consisted of the percentage of correct responses with the speakers unplugged and no sound actually presented. As expected, the percentage of correct responses during the no-sound baseline session was near 50% for all subjects.

Sound trials were introduced at the beginning of the first discrimination-training session. As can be seen from the lower panel of Figure 1, the unoperated subjects made 97% and 100% correct responses during the first

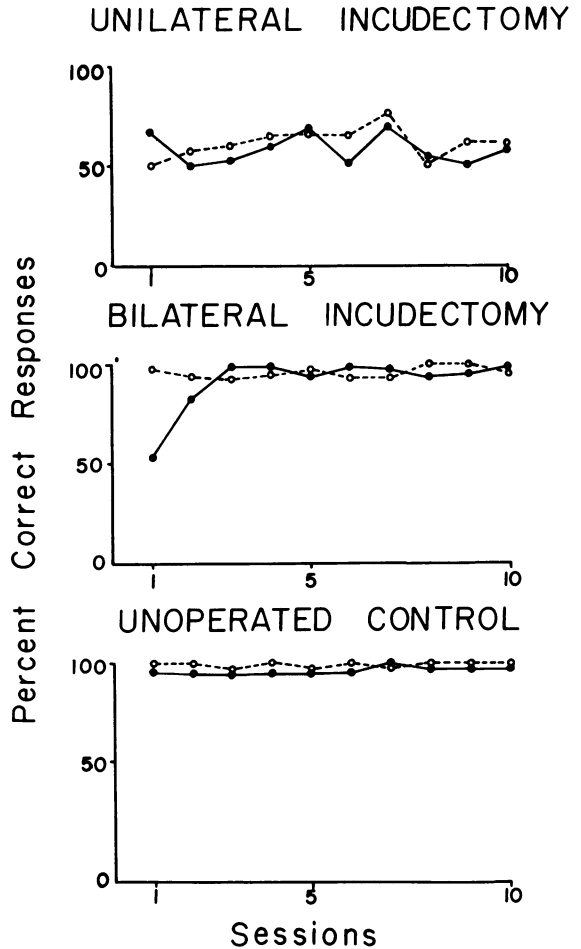


Fig. 1. The percentage of correct responses plotted for each session of the sound-position discrimination. Each panel displays the performances of 2 rats. The sound was first introduced at the beginning of Session 1.

session and maintained an asymptote of nearly 100% correct for the duration of the experiment.

The total numbers of intertrial-interval responses per session, a measure of the sound versus no-sound discrimination, are shown in Figure 2. These responses declined from the baseline (no sound) level of approximately 600 responses per session to approximately 20 responses per session, and remained at that level.

The results observed in each of the two unilaterally incudectomised subjects were quite different. Both rats exhibited near chance levels of the percentage of correct responses on the first session and remained at

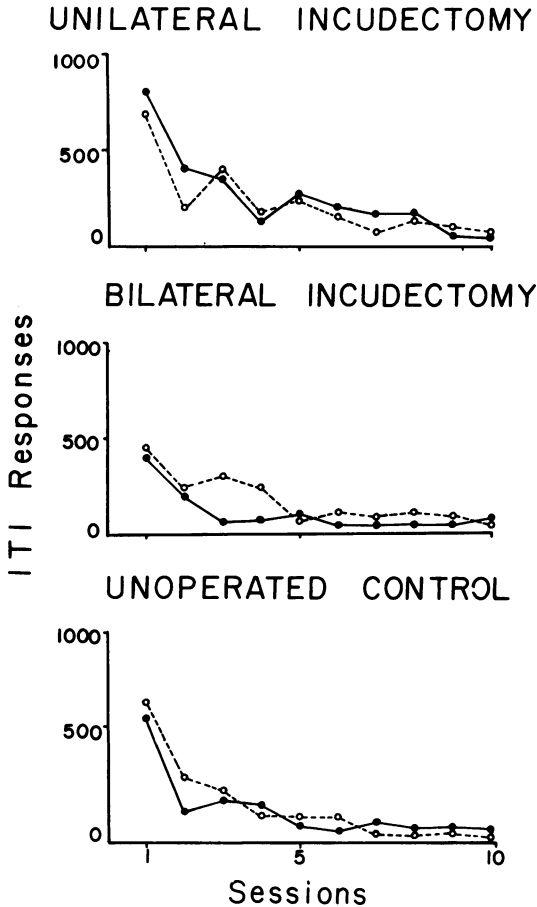


Fig. 2. The number of intertrial-interval responses plotted for each session of the sound-position discrimination. Intertrial-interval responses were never reinforced. Each panel displays the performance of 2 rats.

that level for the duration of the experiment (top panel of Figure 1). Like the unoperated control subjects, both unilateral rats decreased their frequencies of intertrial responses from a baseline of approximately 800 responses per session to approximately 20 responses per session (top panel of Figure 2).

The bilaterally incudectomised rats reached asymptotic levels of correct responding that were similar to those of the unoperated control subjects (middle panel of Figure 1). One bilateral subject acquired the discrimination in one trial and the second bilateral subject reached asymptote in Session 3. Intertrial-interval responses decreased in the same fashion as the first two groups (middle panel of Figure 2).

Videotaped observations of the first session

also revealed differences between unoperated and bilateral rats on the one hand, and the unilateral rats on the other. Unoperated rats vigorously approached and explored sounding speakers during the first few trials of the first session, in the manner described by Harrison (1979). Bilateral rats showed approach and exploratory behavior similar to that of the unoperated subjects. Unilateral rats, however, did not react to sound onset by approaching either speaker, nor was exploratory behavior directed toward either speaker during the first sound trials when the sound was novel.

DISCUSSION

The failure of the unilaterally incudectomised rats to acquire the sound-position discrimination is not attributable to subthreshold stimuli. One ear was normal in each of these rats, and the decline in intertrial-interval responding (the measure of the sound versus no-sound discrimination) was the same as that found in normal animals.

Two measures of localization were available in the present experiment. The first was the percentage of correct responses, and the second was the approach to and exploration of only the sounding speaker for the first trials of the first discrimination session when the stimuli were novel. By both measures the unilaterally incudectomised rats failed to localize, while the normal and the bilaterally incudectomised rats did localize the sounding speaker. The immediate implication of the failure of the unilateral rats to localize is that the interaural intensity cues produced by the operation prevented localization. It has been shown by direct measurement at the pinna in rats that, beyond about 2° azimuth, interaural intensity differences are adequate to support localization of sounds above about 4 kHz (Harrison & Downey, 1970). Presumably, the imbalance of interaural intensity cues resulting from the unilateral operation was one factor preventing localization. The removal of the incus on one side is also likely to produce an imbalance on interaural time cues. In the normal ear, sound is transmitted to the cochlea via the ossicular chain and the oval window. After re-

removal of the incus, transmission is via the air in the middle ear cavity and the round window. Although the quantitative time of transmission of the sound to the cochlea by the two different pathways in the rat is not known, it is almost certain that there is a difference. This difference may also have been a factor preventing localization.

Bilateral removal of the incus will affect the auditory intensity threshold of both ears. However, the intensity of the sound reaching the cochlea and also the time of transmission through the middle ear will be symmetrically changed, leaving the effective binaural localization cues little affected.

It is possible that the sounding speaker could be localized by monaural cues. Analysis of the position of the sound could be performed monaurally, for example, by homing (Jenkins & Masterton, 1979) or by tracking (Heffner, 1978) maneuvers—that is, by moving about the sound field within the sound intensity gradient from the sounding speaker (the sound would be at maximum intensity close to the speaker outlet). The unilaterally incudectomized subjects in the present experiment did not use the available intensity gradient from the speaker, but other species under different experimental conditions have been observed to do so (Heffner, 1978).

Thus we conclude that the performance of normal rats in sound-position discrimination experiments is based upon binaural cues (Harrison, 1979).

REFERENCES

- Anklesaria, D. M. (1963). The dislocated incus. *Journal of Laryngology and Otology*, **77**, 528-532.
- Bauer, F. (1958). Dislocation of the incus due to head injury. *Journal of Laryngology and Otology*, **72**, 676-682.
- Bauer, F. (1964). Fixed stapes or interrupted ossicular chain? *Journal of Laryngology and Otology*, **78**, 408-414.
- Casseday, J. H., & Neff, W. D. (1975). Auditory localization: Role of auditory pathways in brain stem of the cat. *Journal of Neurophysiology*, **38**, 842-858.
- Durlach, N. I. & Colburn, H. S. (1978). Binaural phenomena. In E. Carterette & M. Friedman (Eds.), *Handbook of perception: Vol. 4. Hearing* (pp. 365-455). New York: Academic Press.
- Elbrond, O. (1970). Defects of the auditory ossicles in ears with intact tympanic membrane. *Acta Otolaryngologica* (Suppl. 264).
- Harrison, J. M. (1979). The control of responding by sounds: Unusual effect of reinforcement. *Journal of the Experimental Analysis of Behavior*, **32**, 167-181.
- Harrison, J. M. (1981). Effects of age on acquisition and maintenance of a location discrimination in rats. *Experimental Aging Research*, **7**, 467-476.
- Harrison, J. M. (1983). Effects of age on some behavioral characteristics of novel auditory stimuli in the rat. *Experimental Aging Research*, **9**, 35-39.
- Harrison, J. M., & Downey, P. (1970). Intensity changes at the ear as a function of the azimuth of a tone source; a comparative study. *Journal of the Acoustical Society of America*, **47**, 1509-1518.
- Harrison, J. M., & Turnock, M. T. (1975). Animal psychophysics: Improvements in the tracking method. *Journal of the Experimental Analysis of Behavior*, **23**, 141-147.
- Heffner, H. (1978). Effect of auditory cortex ablation on localization and discrimination of brief sounds. *Journal of Neurophysiology*, **41**, 963-976.
- Hoeffding, V., & Harrison, J. M. (1979). Auditory discrimination: Role of time and intensity in the precedence effect. *Journal of the Experimental Analysis of Behavior*, **32**, 157-166.
- Jenkins, W. M., & Masterton, R. B. (1979). Sound localization in pigeon (*Columba livia*). *Journal of Comparative and Physiological Psychology*, **93**, 403-413.
- Kelly, J. B. (1974a). Localization of paired sound sources in the rat: Small time differences. *Journal of the Acoustical Society of America*, **55**, 1277-1284.
- Kelly, J. B. (1974b). Studies of stereophonic hearing in the albino rat. *Journal of the Acoustical Society of America*, **56** (Suppl.), 39-40.
- Masterton, B., Jane, J. A., & Diamond, I. T. (1967). Role of brainstem auditory structures in sound localization. I. Trapezoid body, superior olive, and lateral lemniscus. *Journal of Neurophysiology*, **30**, 341-359.

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