aggregates in AVCN. Whether the concept might also prove applicable to aggregates of neurons elsewhere in the auditory system remains undecided. We suggest that the technique of masking a central electrical stimulus with a peripheral sensory stimulus is a precise and useful tool for the study of sensory neural organization in the behaving animal.

CHRISTOPHER J. FREDERICKSON
Program in Psychology and Human Development, Mail Station GR 4.1, University of Texas at Dallas, Box 688, Richardson 75080
GEORGE M. GERKEN
Program in Communication Disorders and *Callier Center for Communication Disorders, University of Texas at Dallas, 1966 Inwood Road 75235*

References and Notes

1. J. E. Rose, *Neural Mechanisms of the Auditory and Vestibular System*, G. L. Rasmussen and W. F. Windle, Eds. (Thomas, Springfield, Ill., 1960), p. 116; E. F. Evans and P. G. Nelson, *Exp. Brain Res.* **17**, 402 (1973).
2. J. M. Goldberg and W. E. Brownell, *Brain Res.* **64**, 35 (1973); E. D. Young and W. E. Brownell, *J. Neurophysiol.* **39**, 282 (1976).
3. G. M. Gerken, *Brain Res.* **17**, 483 (1970).
4. The assumption that competitive activation underlies perceptual masking is supported by investigations of the masking of one pure tone by a second pure tone. In that "tone-on-tone" paradigm, perceptual masking is maximal when signal tone and masker tone are the same frequency. Because of the resemblance between the form of the tone-on-tone masking functions and the form of tuning curves of individual neurons, the masking functions are called psychophysical tuning curves [L. A. Christovich, *Biophysics (U.S.S.R.)* **2**, 714 (1957); A. J. Small, *J. Acoust. Soc. Am.* **31**, 1619 (1959)]. Psychophysical tuning curves have also been obtained with animals [T. McGee, A. Ryan, P. Dallos, *ibid.* **60**, 1146 (1976)]. In the present work, we have adapted the masking paradigm to the study of anatomic questions; with our procedure the target population of neurons under study is selected not indirectly by the pitch of a test tone, but directly, by the placement of the stimulating electrode.
5. G. M. Gerken and D. Sandlin, *J. Acoust. Soc. Am.* **61**, 602 (1977).
6. Ten transitions from hit to miss or from miss to hit were required in order to calculate a threshold. The final calculation was an interpolation between the two intensities 1 db apart which spanned the 50 percent detection point. Other restrictions and procedures for the calculation of threshold were identical with those given in Gerken and Sandlin (*5*).
7. These were animals experienced in detecting electrical stimulation. Initially, there is a decrease in detection threshold [G. M. Gerken, in *Handbook of Sensory Physiology*, W. D. Keidel and W. D. Nedd, Eds. (Springer-Verlag, New York, 1975), vol. 5, p. 431], but later the threshold stabilizes. During the experiments reported here, threshold decreased by 1 to 2 μa and this decrease was compensated for in the experimental designs.
8. Stimulation intensities were 15.8, 14.1, and 22.4 μa for cats 188, 216, and 220, respectively. In silence, those stimuli were detected by the animals on 85 to 100 percent of the trials.
9. Electrode tip locations were confirmed by examination of serial sections (50 μm) stained alternately for Nissl substance (thionin) or myelin (Weil). In agreement with others [N. Y. S. Kiang, D. A. Godfrey, B. E. Norris, S. E. Moxon, *J. Comp. Neurol.* **162**, 221 (1975); K. K. Osen, *ibid.* **136**, 453 (1969); J. R. Brawer, D. K. Morest, G. C. Kane, *ibid.* **155**, 251 (1974)], we have taken as an anteroventral subdivision of the nucleus the region lying rostral, dorsal, and slightly medial to the interstitial zone of entrance and bifurcation of the acoustic nerve. The electrode tip of cat 188 was found at the ventral border of AVCN, adjacent to the interstitial zone, the electrodes of cats 216 and 220 were more dorsally situated within AVCN.
10. F. H. Lewy and H. Kobrak, *Arch. Neurol. Psychiatry* **35**, 839 (1936); I. Sando, *Acta Oto-Laryngol.* **59**, 417 (1965); K. K. Osen, *Arch. Ital. Biol.* **108**, 21 (1970).
11. J. E. Rose, R. Galambos, J. R. Hughes, *Bull. Johns Hopkins Hosp.* **104**, 211 (1959); G. Moushegian, A. Rupert, R. Galambos, *J. Neurophysiol.* **25**, 515 (1962); N. Y. S. Kiang, R. R. Pfeiffer, W. B. Warr, A. S. N. Bockus, *Ann. Otol. Rhinol. Laryngol.* **74**, 463 (1965); A. R. Moller, *Q. Rev. Biophys.* **5**, 59 (1972).
12. B. M. Clopton, J. A. Winfield, F. L. Flammino, *Brain Res.* **76**, 1 (1974).
13. J. B. Ranck, Jr., *ibid.* **98**, 417 (1975).
14. Supported in part by research grant NS08612 from the National Institute of Neurological and Communicative Disorders and Stroke. We thank Eileen McClintock and Dick Sandlin for their assistance.

17 March 1977; revised 30 June 1977

Receptive Fields of Auditory Neurons in the Owl

Abstract. *The influence of sound location on the responses of auditory neurons in the forebrain of the owl (*Tyto alba*) was studied directly by using a remotely controlled, movable sound source under free-field, anechoic conditions. Some auditory neurons demonstrated well-defined receptive fields that were (i) restricted both in elevation and in azimuth and (ii) relatively independent of the intensity and the nature of the sound stimulus. The majority of the fields were located frontally and contralateral to the recording site.*

The ability to localize sound sources in space is vital to the survival of many animals and represents one of the most important functions performed by the auditory system. Most neurophysiological studies on sound localization have dealt with the responses of auditory neurons to interaural time, phase, and intensity differences, by using a closed system in which sound reaches the eardrums through hollow ear-bars (*1*). Although this method permits the accurate control of dichotic stimulus parameters, it cannot directly reveal the attributes that auditory neurons might exhibit in response to sound sources in real space (*2*).

We have studied directly the influence of sound location on the responses of telencephalic auditory neurons in the barn owl (*Tyto alba*), a species known for its sound localization abilities (*3–5*). Using a movable sound stimulus under free-field anechoic conditions, we have found auditory units with well-defined receptive fields (*6*) that were restricted both in elevation and in azimuth and that were relatively independent of the intensity and the nature of the sound stimulus.

Five owls were used in these experiments (*7*). Anesthesia was induced with an intramuscular injection of Ketamine (4 mg per kilogram of body weight) and was maintained at a light level by repeated injections as necessary. The experiments were carried out in an anechoic chamber (3 by 3 by 5 m) (*8*). Sound stimuli, including clicks, tone bursts, frequency modulation, and band-filtered noise, were delivered from a 5-cm speaker (*9*) that moved in azimuth along a semicircular track 2 cm wide and 2 m in diameter. The track could be rotated to provide changes in speaker elevation. Azimuth and elevation were controlled independently by two stepping motors located outside the chamber. Thus the speaker could be moved to any point on a sphere of radius 1 m centered at the owl's head, except for a 20° sector blocked by a supporting post for the owl. The owl was positioned within the sphere by using retinal landmarks, so that the intersection of the owl's visual and median planes corresponded to 0° elevation, 0° azimuth of the speaker (Fig. 1) (*10*).

Auditory units were recorded with glass-insulated tungsten electrodes from the primary auditory projection area in the owl's telencephalon, field L. The statements made in this report are based on the response properties of 213 units out of 314; the 101 units excluded from this report responded only to complex stimuli such as finger snapping, sandpaper grating, or whistling. Although these units displayed definite and often quite small receptive fields, they could not be driven by our electronic sounds and therefore could not be accurately mapped.

The procedure for mapping auditory receptive fields was as follows. After a single unit had been isolated, its approximate receptive field was determined by the experimenter's entering the chamber and making sounds at various positions. The experimenter would then leave the chamber and position the movable speaker at the appropriate location. The best sound for driving the unit and the unit's threshold for that sound were determined. While using the best sound at 10 db above threshold, we moved the speaker in elevation and azimuth to locations where the unit failed to respond.

The coordinates of these locations defined the unit's receptive field borders (Fig. 1). When possible, receptive fields were also mapped with higher intensities and different sounds. Once the receptive field boundaries had been established, peristimulus-time histograms were collected of the unit's responses to stimuli presented at different locations within its receptive field.

Auditory units in field L could be segregated into three categories on the basis of the effect of sound location on their responses: (i) space-independent units, (ii) space-preferring units, and (iii) space-dependent units. Space-independent units (33 percent) responded to sound stimuli regardless of location; most of these units responded best to low-frequency tonal stimuli (< 3 khz). Space-preferring units (52 percent) responded best to sounds located in a particular area of space (preferred area), but the borders of their receptive fields were poorly defined and they varied considerably with sound intensity; the azimuths of their receptive fields expanded by at least 25° following a 20-db increase in sound intensity. Space-dependent units (15 percent) responded only when a sound was located within a well-defined receptive field, the borders of which were distinct and expanded by 20° or less to a 20-db increase in sound intensity.

The receptive fields of both space-preferring and space-dependent units were vertically elongate and ellipsoidal, and ranged in size from a minimum of 12° azimuth by 40° elevation, to a maximum of 260° azimuth by 300° elevation. The responsiveness of these units to stimuli delivered at different locations across their fields was not uniform: each field comprised an area of reliable responsiveness surrounded by a zone of sporadic responsiveness (Fig. 1). For units with small receptive fields, the area for a maximum response was geometrically centered in the receptive field. This was not the case for many large-field units, which responded best to stimuli located eccentrically in their fields.

Besides demonstrating a spatial response requirement, most of these units also preferred a particular type of sound. Thus, to excite most space-preferring and space-dependent units, both the spatial and the spectral properties of the sound had to be adequate.

The receptive fields of space-dependent units tended to be small, ranging in size from 12° to 42° (mean, 26°) in azimuth, and from 40° to 200° (mean, 80°) in elevation (Fig. 1). The receptive field borders of such units were sharp and could be reproducibly mapped to an accuracy of ±1°. At high sound intensities the borders were still sharp, although the fields tended to increase slightly in size; following a 20-db increase in stimulus intensity the increase in field size among these units ranged from 0° to 20° in azimuth and from 3° to 45° in elevation. Stimuli delivered outside a unit's field could not excite the unit even at high intensities. None of these units responded to tonal stimuli below 3 khz; 22 responded best to band-filtered noise, four to clicks, and seven to tones between 3 and 9 khz.

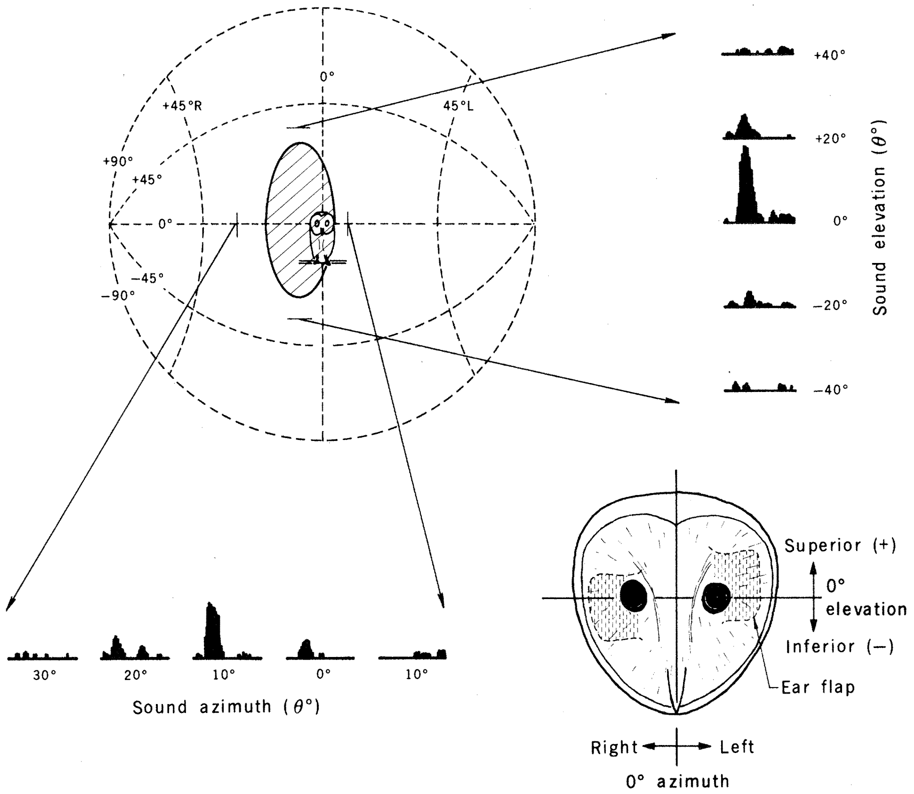

Fig. 1. The receptive field of an auditory neuron depicted from the observer's point of view. The owl is shown facing out from the center of the stimulus sphere (dashed globe), and the unit's receptive field (25° in azimuth by 62° in elevation) is projected onto the sphere (diagonally lined area). The unit was located in the owl's left hemisphere; its field dimensions were independent of stimulus intensity. Below and to the right are shown peristimulus-time histograms of the unit's responses to a sound stimulus presented at different locations within its receptive field. The stimulus was a 200-msec noise burst, 20 db above threshold, delivered once per second. Each histogram is a 500-msec sample and represents 16 stimulus repetitions. Notice the increasing response vigor as the sound source approaches the center of the unit's receptive field. The owl head in the lower right corner illustrates the alignment of the owl in the stimulus sphere and defines the nomenclature used for describing auditory space.

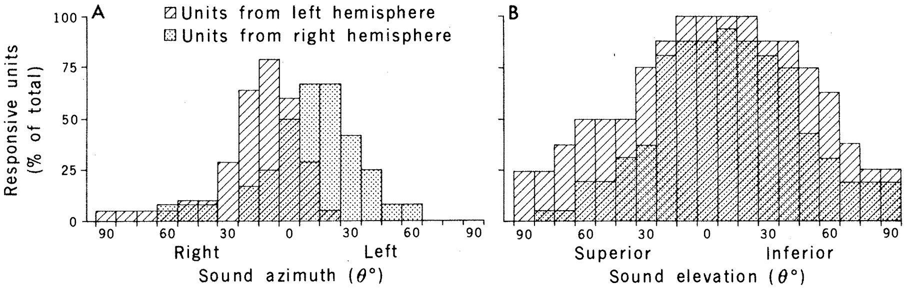

Fig. 2. The distribution of receptive fields of space-dependent units. The histograms represent the number of units (plotted as the percentage of the total) with receptive fields that include the designated azimuth (A) or elevation (B). Units recorded from the left and right hemispheres are shown separately.

Several observations can be made concerning the distribution of receptive fields of space-dependent units. (i) The majority (82 percent) of the fields were frontal, centered in azimuth within ±30° of the median plane and less than 20° superior to 30° inferior to the visual plane

(Fig. 2). Only three units had receptive fields that extended beyond ±50° in azimuth. In elevation, the centering appeared less restricted largely because of the elongate shapes of the receptive fields. Still, there was an unequivocal increase in the representation of auditory space around and just inferior to the intersection of the median and visual planes. (ii) The receptive fields of space-dependent units in each hemisphere demonstrated a strong contralateral bias with the greatest representation given to 0° to 20° contralateral (Fig. 2). Few fields extended farther than 15° ipsilateral. Thus the area of redundant representation in the left and right hemispheres was limited to ±15°, with the median plane receiving the greatest representation. (iii) Although there was a discernible tendency for space-dependent units from a single electrode track to have overlapping receptive fields, the trend was not strong enough to confirm a systematic representation of auditory space in field L.

Because the receptive fields of space-preferring units were poorly defined and expanded with increasing sound intensity, specific statements regarding their size and distribution are somewhat arbitrary. Nevertheless some generalizations can be made. Receptive field sizes of space-preferring units, measured at 10 db above threshold, tended to be large (typically greater than 40° in azimuth and 100° in elevation) although their preferred areas were often small (usually less than 30° in azimuth and 60° in elevation). The distribution of these receptive fields was similar to that of space-dependent receptive fields: primarily frontal with a strong contralateral bias.

The emphasis given by the owl's auditory system to the frontal area (±30° azimuth and +20° to −30° elevation) is not unlike that given by the visual system to the center of gaze: the number of units with receptive fields in this area is disproportionately large, and their fields tend to be small. Although the mechanism by which this "expansion of representation" is derived is necessarily different in these two sensory systems, the functional consequences may again be improved acuity and more detailed analysis of the stimulus. If so, then one would expect that the owl's spatial acuity for auditory stimuli would be maximal within the frontal area and would drop off rapidly as the sound source is located more peripherally, especially beyond ±50° in azimuth or elevation, where only units with large receptive fields are responsive.

Behavioral measurements have estimated the barn owl's auditory spatial acuity at less than 5° in both elevation and azimuth (*3–5*). Thus it is not surprising to find units with receptive fields that are restricted in elevation as well as in azimuth. However, the mechanism by which elevation tuning is achieved is less obvious than the binaural intensity or time cues that are likely to determine azimuthal tuning. Elevation sensitivity in mammals (particularly in man) is thought to be based on the elevation-dependent filter properties of the external ear (*11*). To be effective, such a mechanism demands both a wide-band noise stimulus and a broad range of frequency sensitivity. The owl, on the other hand, attains maximal spatial acuity when a target sound includes frequencies of only 5 to 9 khz and is quite accurate at localizing even a 7-khz pure tone (*4, 5*). Furthermore, although most of the units with small receptive fields were sensitive to noise bands, some were sensitive to tones and demonstrated marked elevation tuning when mapped with a tone burst stimulus. Clearly some other mechanism must be involved.

Elevation tuning in the barn owl might be achieved by comparing relative sound intensity at the two ears in the manner conceived for determining sound azimuth. Elevation-dependent intensity disparities result from a vertical asymmetry in the location of the owl's ears [the left ear is higher than the right ear (Fig. 1) (*3–5*)], the direction of maximum sensitivity for the right ear being 10° to 15° higher than that of the left ear (*12*). Thus, a binaural elevation cue is available to the owl. It remains to be shown, however, that this mechanism is the one responsible for the elevation tuning of single units.

ERIC I. KNUDSEN, MASAKAZU KONISHI
JOHN D. PETTIGREW
Division of Biology, California Institute of Technology, Pasadena 91125

References and Notes

1. For reviews of neurophysiological studies on sound localization, refer to S. D. Erulkar, *Physiol. Rev.* **52**, 237 (1972); M. Konishi, in *Recognition of Complex Acoustic Signals* (Dahlem Konferenzen, Berlin, 1977).
2. Space-dependent responses of auditory neurons have been demonstrated by using hand-held speakers [E. F. Evans, in *Ciba Foundation Symposium on Hearing Mechanisms in Vertebrates* (Churchill, London, 1968); A. R. A. Sovijärvi and J. Hyvärinen, *Brain Res.* **73**, 455 (1974)]. The existence of auditory receptive fields has been indicated by studies on multimodal neurons [B. G. Wickelgren, *Science* **173**, 69 (1971); F. Morrell, *Nature (London)* **238**, 44 (1972); U. C. Dräger and D. H. Hubel, *J. Neurophysiol.* **38**, 690 (1975)].
3. R. S. Payne, *J. Exp. Biol.* **54**, 535 (1971).
4. M. Konishi, *Am. Nat.* **107**, 775 (1973).
5. ——, *Am. Sci.* **61**, 414 (1973).
6. By analogy to its connotation in contemporary visual research, the term "receptive field" will refer to the area of space within which a sound stimulus can influence the firing of an auditory unit.
7. A recording chamber was implanted over field L in each owl, an arrangement that allowed repeated recording over a period of 8 months.
8. The chamber was free of standing waves resulting from reflection; sound attenuation followed the inverse-square law throughout the length of the chamber.
9. Sound intensity was calibrated with a 2.5-cm condenser microphone (Bruel and Kjaer) at the position where the owl would be located. The frequency response of the 5-cm speaker was flat from 4 to 10 khz. Variations in sound intensity as a function of speaker location were less than ± 2 db except in a small area directly beneath the owl.
10. The highly pigmented pecten oculi in each eye, which is plainly visible ophthalmoscopically, provided a convenient landmark for aligning the owl's head. The visual plane is the horizontal plane containing the projection from each area centralis through the nodal point of the eye to the horizon. In the barn owl, the visual plane is located 8° to 10° below the plane containing the projections of the superior limbs of each pecten into space. The owl's visual plane was adjusted by monitoring the projection angle of the superior limbs of the pectens. The median plane was aligned by positioning the owl so that its pectens projected symmetrically on either side of the 0° azimuth plane.
11. M. B. Gardner and R. S. Gardner, *J. Acoust. Soc. Am.* **53**, 400 (1973); J. Hebrank and D. Wright, *ibid.* **56**, 1829 (1974).
12. That the owl exploits this elevation-dependent intensity disparity is indicated by behavioral experiments in which one ear was plugged during sound localization. Under these conditions the owl commits consistent vertical errors (*5*).
13. We thank C. Adams for constructing the speaker carriage system, E. Akutagawa and G. Blasdel for technical assistance, and A. J. Hudspeth for critically reviewing the manuscript. This work was supported by an NIH postdoctoral fellowship (5 F32 NS 0552902) to E.I.K., an NSF grant (BMS 75-19180) to M.K., and a Spencer Foundation grant to J.D.P.

7 June 1977; revised 29 August 1977

Neoplastic Skin Lesions in Salamanders from a Sewage Lagoon Containing Perylene

Rose and Harshbarger (*1*) reported that tiger salamanders living in a sewage sedimentation lagoon had a high incidence of neoplastic skin lesions (including cancer) and suggested a chemical etiology for these neoplasms. In a search for a chemical agent, they reported 300 parts per million of perylene and a trace of benzopyrene (isomer not given) in this lagoon's sediment. They suggested that the source of perylene was related to jet aircraft activity on a nearby runway. We believe that this is not the correct source of perylene in this lagoon.

The presence of a single polycyclic aromatic hydrocarbon (PAH), rather than a complex mixture, usually indicates a natural source rather than anthropogenic input (*2*). In fact, high concentrations of perylene (and the absence of other PAH) have been reported for a number of sediments: Saanich Inlet,