

ity of neurons to synthesize or assemble materials necessary for growth. Alternatively, growth-inducing substances may not be so readily elaborated or perhaps the target cells may be less able to accept new innervation. In the case of sympathetic CA fibers, the diminished growth may be related in part to a reduction in the number of blood vessels in the dentate molecular layer (9). However, the reduction in vascular supply is not as great as the reduction in fiber growth, so other factors are probably involved.

Age-related differences in reactive fiber growth may have functional significance. In some instances reactive synaptogenesis appears to underlie recovery or retention of normal function after damage to the central nervous system, but in other instances it seems to cause or contribute to abnormal behavior. In the aged brain we would expect this process to operate not only in cases of severe damage, such as that induced in our study, but also in the replacement of connections lost as a result of the natural aging process. If the new connections can replace the old functionally, then reactive synaptogenesis may be regarded as a compensatory mechanism that counteracts the ill effects of aging. A reduction in growth capacity with age would therefore be detrimental. On the other hand, if the new connections interfere with normal function, reactive synaptogenesis would be harmful and the aged brain would benefit from a diminished growth capacity. Such issues are in need of direct evaluation and must await a more complete understanding of the significance of reactive synaptogenesis. In any case, our finding that neuronal circuitry appears more rigid in old animals needs to be taken into account in considering the end result.

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#### References and Notes

1. C. W. Cotman and G. S. Lynch, in *Neuronal Recognition*, S. Barondes, Ed. (Plenum, New York, 1976), p. 69; C. W. Cotman and J. V. Nadler, in *Neuronal Plasticity*, C. W. Cotman, Ed. (Raven, New York, 1978), p. 227.
2. R. Y. Moore, A. Bjorklund, U. Stenevi, in *The Neurosciences: Third Study Program*, F. O. Schmitt and F. G. Worden, Eds. (MIT Press, Cambridge, Mass., 1974), p. 961.
3. ———, *Brain Res.* **33**, 13 (1971).
4. J. C. de la Torre and J. W. Surgeon, *Histochemistry* **49**, 81 (1976).
5. L. A. Benevento and F. F. Ebner, *J. Comp. Neurol.* **141**, 157 (1971).
6. K. R. Brizzee, B. Kaack, P. Klara, in *Neurobiology of Aging*, J. M. Ordy and K. R. Brizzee, Eds. (Plenum, New York, 1975), p. 463.
7. Lesions of the fimbria-fornix disrupt several pathways, among which are the connections be-

tween the two hippocampi. The commissural projection which arises in the CA3-CA4 region of one hippocampus and projects to the contralateral hippocampus with specific terminations in the inner one-third of the dentate molecular layer and also strata radiatum and oriens of regio superior and regio inferior [T. W. Blackstad, *J. Comp. Neurol.* **105**, 417 (1956)]. A lesion of the fimbria-fornix also produces degeneration in the septal nuclei because the hippocampal and subicular pyramidal cells project to different parts of the septal area [L. W. Swanson and W. M. Cowan, *J. Comp. Neurol.* **172**, 49 (1977)]. Finally this lesion also removes the adrenergic in-

nervation to the hippocampal formation arising from locus coeruleus because some of these fibers enter the hippocampal formation through the fimbria [R. Y. Moore, in *The Hippocampus*, R. L. Isaacson and K. H. Pribram, Eds. (Plenum, New York, 1975), vol. 1, p. 215].

8. R. Loy and R. Y. Moore, *Exp. Neurol.* **57**, 645 (1977).
9. C. W. Cotman and S. W. Scheff, in *Mechanisms of Ageing and Development*, B. L. Strehler, Ed. (Elsevier Sequoia SA, Lausanne, Switzerland, in press).

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## Center-Surround Organization of Auditory Receptive Fields in the Owl

**Abstract.** *The spatial receptive fields of specialized auditory units in the midbrain of the barn owl (Tyto abla) contain two functionally antagonistic areas: an excitatory center and an inhibitory surround. The response of these units represents the balance of acoustic activation of the two areas, which in turn depends upon the location, intensity, and spectral content of the sound stimulus.*

The barn owl (*Tyto alba*) derives spatial information from sound signals accurately enough to capture small prey in total darkness. Recently a specialized auditory region in the midbrain of the owl has been implicated in spatial analysis of sound stimuli (1). Neurons in this region, which respond to sounds from restricted areas of space (receptive fields) are arranged systematically according to the location of their receptive fields so that they form a physiological map of auditory space. We now describe another space-dependent response property of these units that further supports their implied function in spatial analysis of sound: their receptive fields are subdivided into spatially separate excitatory and inhibitory areas similar to the center-surround receptive field organization described for other sensory systems.

The midbrain region that contains these units is the lateral and anterior region of the auditory nucleus known as mesencephalic lateralis dorsalis (MLD), the avian homolog of the inferior colliculus. Because of the systematic arrangement of unit receptive fields in this region, it has been called the space-mapped region of MLD (2). The receptive fields exhibited by units in the space-mapped region have been classified as limited-field (L-F) receptive fields, to contrast them with other, less restricted field types.

Four barn owls were studied, each owl being prepared for long-term recording (2). The statements made here are based on the properties of 63 single units (3) that were located in the lateral and anterior portion of the MLD as confirmed by electrode track reconstructions. The experiments were performed in a large an-

echoic chamber (4). Conventional amplification and spike analysis equipment was used (1, 2).

Nearly all L-F units (60 of 63) had low ongoing discharge rates. Thus, in order to detect inhibitory effects of sounds presented in areas outside a unit's receptive field, two sound sources were required: one positioned inside the unit's receptive field to drive the unit (driving speaker), and a second to present test sounds at various locations outside its receptive field (roving speaker) (5). The position of the roving speaker was remotely controlled from outside the chamber. The speaker moved along a semicircular track to provide changes in sound-source azimuth, and the track itself rotated around a horizontal axis to provide changes in sound-source elevation. The sphere described by the movement of the roving speaker was 1 m in radius. The head of the anesthetized owl (6) was secured to a head holder and was centered within the speaker's sphere of movement so that the owl's median and visual planes corresponded to 0° azimuth and 0° elevation of the roving speaker (7). The driving speaker was also movable, but not by remote control.

The protocol for testing units was as follows. After a single unit had been isolated, the roving speaker was moved while emitting noise bursts (8) to the area of space to which the unit responded most vigorously. This area of space, which is sharply defined for L-F units, is called the unit's best area (1). The driving speaker was then manually positioned in the unit's best area, behind the roving speaker. The threshold of the unit to noise bursts from each speaker was measured; sound intensity values refer

to sound pressure levels with respect to these thresholds. The unit's receptive field was mapped with 20-dB noise bursts from the roving speaker. The speaker locations at which the unit just failed to respond marked the boundaries of its receptive field. After this initial procedure, the protocol varied depending on the experiment. In all cases, however, the measure of a unit's inhibition versus excitation was made by comparing control responses (to sound from the driving speaker alone located in the unit's best area), with test responses (to simultaneous sounds from the roving and driving speakers). Sound intensity from the driving speaker was normally set to the middle of the unit's dynamic range (5 to 10 dB above threshold). When test responses (number of spikes) were consistently less than control responses, the effect of the roving speaker was considered to be inhibitory; when they were greater, the effect of the roving speaker was considered excitatory.

When analyzed with a single sound source, the receptive field properties of L-F units appeared simple. The units responded to the onset of a sound presented inside their receptive fields if the sound contained frequencies between 5 and 9 kHz (the upper end of the owl's audible range), and they remained inactive when the sound source was located anywhere else. One remarkable characteristic of these auditory receptive fields was their insensitivity to large increments in sound intensity; the borders of nearly half of the L-F units changed in azimuth by  $\pm 2^\circ$  or less following a tenfold (20 dB) increase in sound intensity. This averages out to a mere  $\pm 0.1^\circ$  change per decibel of sound level increase. Insensitivity to changes in sound intensity of this magnitude cannot be explained by the directionality of the owl's ears (2, 9). Instead, some form of space-dependent neuronal processing must occur to prevent sound stimuli originating outside the unit's receptive field from exciting the unit.

The receptive field properties of these units became more complex when more than one source of sound was present in the sound chamber. For example, ambient noise introduced by opening the chamber door could inhibit a unit's responses to an excitatory stimulus located within its receptive field. When the roving speaker was used as a point source of noise, its effectiveness in inhibiting the unit's response depended upon its location and the intensity and spectral content of the noise. In general the most effective area for inhibition (locations re-

quiring the least intensity to inhibit) was the area in front of the owl from approximately  $+50^\circ$  to  $-90^\circ$  in elevation, and from  $60^\circ$  to the left to  $60^\circ$  to the right (Fig. 1). This frontal area also corresponds to the owl's area of maximum sensitivity, due to the directionality of its ears (2, 9).

For any given unit, inhibition increased as the sound source moved in from the periphery and approached the borders of its receptive field (Fig. 1). As the source entered the unit's field, the effect of the noise changed from inhibitory to either neutral or excitatory within a few degrees of movement. This transition was dramatic for azimuthal speaker movements, whereas transitions in elevation tended to be more gradual. As the noise source moved away from the unit's receptive field, particularly beyond the frontal area, its inhibitory effect diminished. Thus, when the noise level was properly chosen, its inhibitory influence extended only a limited distance into the periphery, beyond which the noise had no effect (Fig. 1). Increasing the intensity of the noise, however, caused the inhibitory area to expand so that, at sufficiently high noise levels (20 to 35 dB), sound locations even behind the owl's head inhibited the units.

Although a unit's receptive field was surrounded by an inhibitory area, not all sectors of this inhibitory area were of equal potency. This was revealed by measuring the sound intensity (re threshold) necessary to completely suppress unit responses to a 20-dB noise burst from the driving speaker at four locations around the unit's receptive field. The areas just to the left or right of the unit's receptive field were the most effective for inhibiting 16 of the 20 units tested. Of the remaining four units, two were best inhibited by noise from above their receptive fields, and two by noise from below. The units inhibited best from below had unusually high receptive fields (best areas =  $+15^\circ$ ); the units inhibited best from above had low receptive fields (best areas =  $-45^\circ$ ,  $-70^\circ$ ).

In contrast to the usually equal inhibitory efficacy of noise to the right or left, the inhibitory efficacy of noise from above or below the receptive fields was typically asymmetrical (Fig. 1). Units with best areas higher than  $0^\circ$  tended (five of six) to be inhibited better from below; units with best areas lower than  $-25^\circ$  tended (8 of 13) to be inhibited better from above.

Tone bursts also inhibited these units, although in general the inhibitory effect

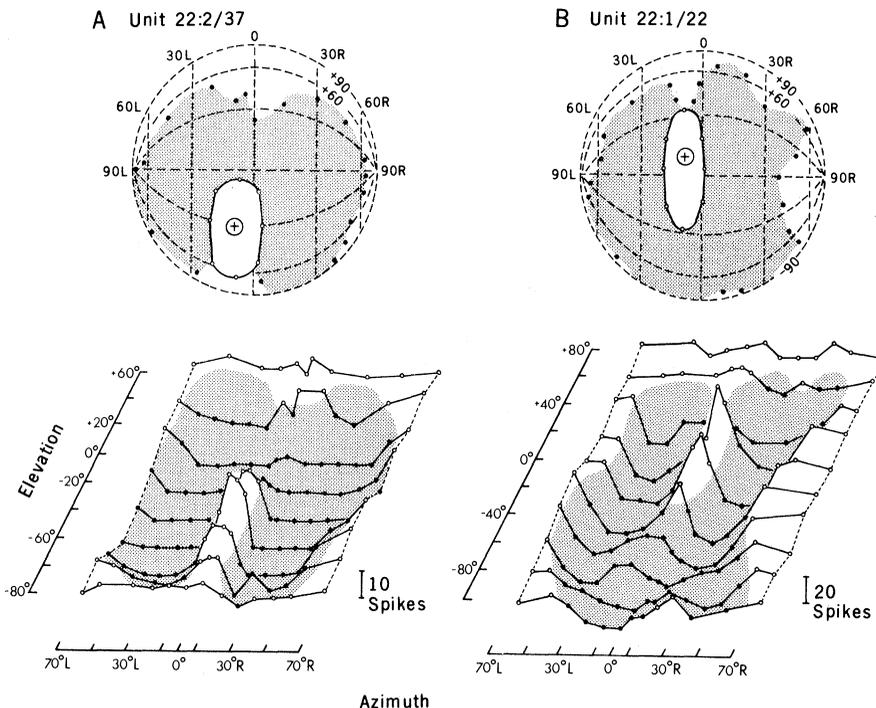


Fig. 1. Center-surround receptive field organization of two limited-field units in the MLD of the barn owl. Inhibitory areas are stippled; best areas are marked by a +. These fields were measured through use of 5-dB noise bursts from the driving speaker and 10-dB noise bursts from the roving speaker. A 5-dB increase in the noise level from the roving speaker caused the inhibitory areas to completely encircle the excitatory areas and to encompass large areas behind the owl's head. Above are the projections of the fields onto spherical coordinates of auditory space. Below are three-dimensional plots of the units' response to ten noise bursts (Y dimension) as a function of the roving speaker's location (X and Z dimensions) plotted on linear coordinates. Both units were recorded in the anterior lateral portion of the right MLD.

was weaker (Fig. 2). The range of frequencies contributing to inhibition was wide, typically spanning frequencies of 3 to 10 kHz. The area of space within which a tone burst could inhibit a unit varied with the frequency of the tone. The inhibitory areas of some frequencies extended well inside the borders of the receptive fields (as mapped with noise bursts), whereas other frequencies were inhibitory only in areas distant from the receptive fields. Because of the frequency-dependent variations in the inhibitory areas, the spectrum of inhibiting frequencies sometimes changed from one speaker location to another. For any given speaker location, however, the inhibitory spectrum was largely independent of sound intensity. Consequently, unit frequency-response curves (Fig. 2) measured with different speaker locations were often qualitatively different; inhibitory frequencies at one location being neutral or excitatory at another.

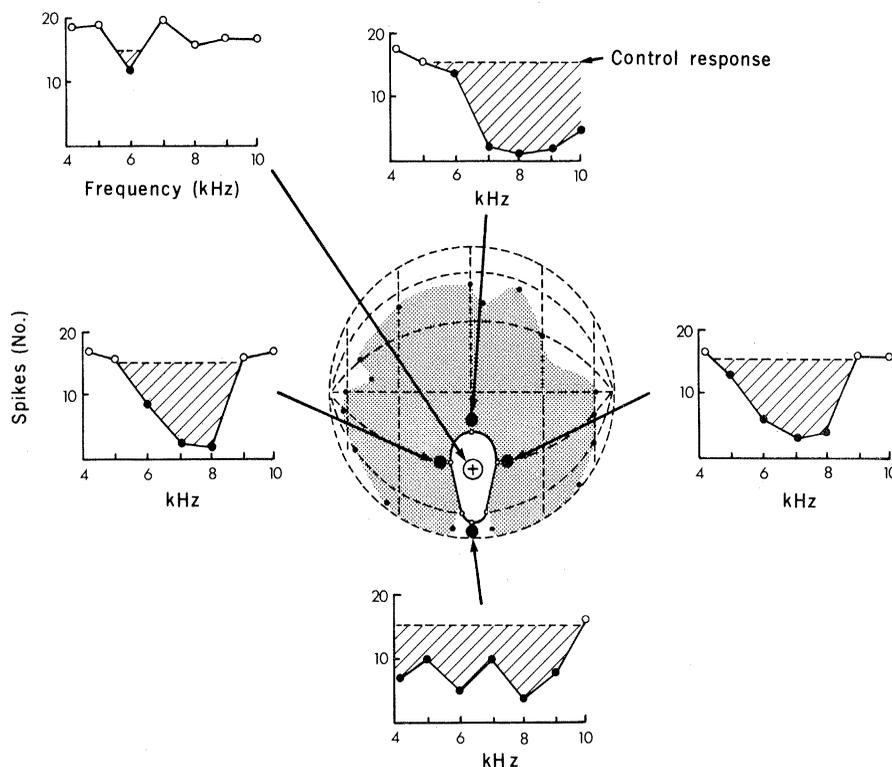


Fig. 2. Space-dependent frequency response properties of a limited-field unit in MLD. In the center of the figure, the receptive field of the unit, as mapped with 10-dB noise from the roving speaker and 10-dB noise from the driving speaker, is projected onto spherical coordinates of space as in Fig. 1. The inhibitory area under these conditions is stippled. In the graphs surrounding the receptive field projection, the responses of the unit to ten tone bursts from the roving speaker are plotted as a function of tone frequency for five different locations of the roving speaker (large arrows). The unit was simultaneously being driven by 10-dB noise bursts from the driving speaker. The unit's control response level to noise from the driving speaker alone is designated by the dashed lines in each graph. The inhibitory effect of the tone bursts is graphically represented by the area marked by diagonal lines. The tone intensity was kept constant at 25 dB sound pressure level for all frequencies.

These results support the contention that the space-mapped region of the MLD is functionally specialized for spatial analysis of auditory signals. The center-surround nature of L-F receptive fields and their spatiotopic distribution are properties that are strikingly similar to aspects of functional organization in visual, somatosensory, and lateral-line centers of the brain (10), in which spatial analysis is of primary importance. As in these other sensory modalities, center-surround fields in the auditory system may maintain spatial contrast sensitivity despite changes in the absolute intensity of the stimulus.

What distinguishes auditory center-surround fields from those found in other sensory modalities is the underlying neuronal circuitry. Since space projects directly onto the retina and the body surface, center-surround fields can be based simply on lateral inhibition of neighboring receptors. By contrast, space does

not project onto the cochlear partition. The auditory system must, instead, extract spatial information from the relative patterns of auditory nerve input arriving from the ears. Thus, auditory center-surround fields require not only that units respond to a unique configuration of auditory input, but that they also are inhibited by all others. The fact that the auditory system has created center-surround receptive fields based on functional properties of the input and independent of the topography of the sensory surface argues strongly for the importance of center-surround organization in spatial analysis of sensory input.

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#### References and Notes

1. E. I. Knudsen and M. Konishi, *Science* **200**, 795 (1978).
2. ———, *J. Neurophysiol.* **41**, 870 (1978).
3. Single units were recorded extracellularly with glass-insulated tungsten electrodes. Electrode penetrations were made dorsoventrally in the transverse plane.
4. The experiments were conducted in a 5 by 3 by 3 m anechoic chamber (Industrial Acoustics). The cut-off frequency of the chamber was rated at 300 Hz; our own calibration showed that sound attenuation at different points along the length of the chamber followed the inverse-square law for frequencies down to at least 500 Hz.
5. The roving speaker was a 5-cm speaker with a flat frequency response ( $\pm 2$  dB) from 3.5 to 10 kHz. The driving speaker was a 7.5-cm speaker with a flat frequency response from 1 to 5 kHz and an attenuation of 10 dB per octave for frequencies above 5 kHz.
6. Anesthesia was induced with an intramuscular injection of ketamine hydrochloride (4 mg per kilogram of body weight) and was maintained at a light level with repeated injections as necessary. The owl was restrained with a soft leather jacket which was fastened to a post in the center of the speaker sphere. The owl's head was bolted to a specially designed head holder that permitted accurate adjustment of the owl's head position while avoiding distortion of the sound field.
7. Positioning of the owl's head was accomplished ophthalmoscopically by exploiting retinal landmarks that bear specific relationships to the owl's visual and median planes (2).
8. Sound stimuli included noise and tone bursts. Electrical noise, supplied by a noise generator (Grason-Stadler), was band-filtered at 800 Hz and 12,000 Hz with graphic spectrum equalizer (B & K Instruments). Sine waves were generated by a function generator (Wavetek model 111). Sine wave and noise bursts were shaped with an electronic switch (Grason-Stadler). The bursts were 100 msec in duration with 2.5-msec rise and decay times, repeated every 1 to 1.25 seconds.
9. R. S. Payne, *J. Exp. Biol.* **54**, 535 (1971).
10. S. W. Kuffler, *J. Neurophysiol.* **16**, 37 (1953); D. H. Hubel and T. N. Wiesel, *J. Physiol. (London)* **155**, 385 (1961); V. B. Mountcastle and T. P. S. Powell, *Bull. Johns Hopkins Hosp.* **105**, 201 (1959); J. Bastian, *J. Neurophysiol.* **38**, 285 (1975).
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