

Representation of sound localization cues in the auditory thalamus of the barn owl

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ABSTRACT Barn owls can localize a sound source using either the map of auditory space contained in the optic tectum or the auditory forebrain. The auditory thalamus, nucleus ovoidalis (N.Ov), is situated between these two auditory areas, and its inactivation precludes the use of the auditory forebrain for sound localization. We examined the sources of inputs to the N.Ov as well as their patterns of termination within the nucleus. We also examined the response of single neurons within the N.Ov to tonal stimuli and sound localization cues. Afferents to the N.Ov originated with a diffuse population of neurons located bilaterally within the lateral shell, core, and medial shell subdivisions of the central nucleus of the inferior colliculus. Additional afferent input originated from the ipsilateral ventral nucleus of the lateral lemniscus. No afferent input was provided to the N.Ov from the external nucleus of the inferior colliculus or the optic tectum. The N.Ov was tonotopically organized with high frequencies represented dorsally and low frequencies ventrally. Although neurons in the N.Ov responded to localization cues, there was no apparent topographic mapping of these cues within the nucleus, in contrast to the tectal pathway. However, nearly all possible types of binaural response to sound localization cues were represented. These findings suggest that in the thalamo-telencephalic auditory pathway, sound localization is subserved by a nontopographic representation of auditory space.

The processing of sound localization cues leading to the formation of a map of auditory space in the midbrain of the barn owl has been studied extensively (1–10). Less well known is how these acoustic cues are processed beyond the midbrain auditory areas. Anatomical evidence suggests that in birds, the auditory thalamus—nucleus ovoidalis (N.Ov)—is the gateway for auditory transmission to the forebrain (11, 12). Behavioral experiments in barn owls with restricted lesions indicated that this pathway carries information concerning the location of a sound source. Knudsen *et al.* (13) found that owls that had the auditory space map in the optic tectum ablated or inactivated had a diminished capacity for sound localization, rather than a complete loss of localizing ability, whereas those in which both the optic tectum and the N.Ov were inactivated were unable to localize sound sources. Further evidence that the thalamo-telencephalic auditory pathway is capable of subserving at least some sound localization ability comes from experiments in which barn owls had restricted lesions placed in the auditory space map in the external nucleus of the inferior colliculus (ICx). These birds had deficits in head-orienting behavior that disappeared within hours (14).

We have examined the source of afferent input to the N.Ov of barn owls with retrograde tracers to better understand the anatomical basis for sound localization in the auditory thalamus and forebrain. We have also systematically recorded the

responses of neurons throughout the N.Ov to binaural sound localization cues to determine what, if any, transformations occur in the representation of auditory information.

METHODS

Adult barn owls (*Tyto alba*), while under ketamine/diazepam anesthesia (Ketaset, Aveco, Chicago; 25 mg/kg diazepam; 1 mg/kg intramuscular injection), were placed in a stereotaxic device that held the head tilted downward at an angle of 30° from the horizontal plane. A stainless steel plate was attached to the rostral cranium with dental cement, and a reference pin was glued to the cranium on the midline in the plane between the two ears. A craniotomy was performed over the diencephalon, and mineral oil was applied to the exposed dura. Body temperature was maintained between 38° and 39°C with a circulating-water heating pad throughout the time the animal was under anesthesia. All procedures were performed in accordance with Caltech Office of Laboratory Animal Resources veterinary animal care guidelines and National Institutes of Health animal welfare guidelines.

Histology. Following physiological experiments, owls were overdosed with pentobarbital (Nembutal, Abbot, 200 mg/kg) and perfused intracardially with 0.9% NaCl. In owls in which a 2.5% solution of horseradish peroxidase was iontophoretically injected into target brain regions (7–10 μ A positive DC current, pulsed 7 sec on/7 sec off for 15–30 min), a perfusion with a cold (15°C) fixative solution of 1% paraformaldehyde and 1.25% glutaraldehyde in 0.1 M phosphate buffer (PB), pH 7.4, followed. Following fixation, the owl was perfused with a cold 10% sucrose solution and then a cold 20% sucrose solution. In owls in which 10% biotinylated dextran-amine (BDA; Molecular Probes) in 0.2 M KCl with 0.1% Triton X-100 was iontophoretically injected into identified brain regions (5–8 μ A DC current, pulsed 7 sec on/7 sec off for 30 min), the perfusing fixative consisted of 4% paraformaldehyde, 0.1 M lysine, and 0.01 M sodium-periodate in PB. In both cases, the brain was blocked, removed, and sunk in 30% sucrose in 0.025 M PB. Sections (30 μ m) were cut on a freezing microtome into fresh PB. Sections containing horseradish peroxidase were rinsed in cold acetate buffer (pH 3.3), incubated with tetramethylbenzidine (15), reacted with 0.3% H₂O₂, rinsed three times with acetate buffer, mounted, and counterstained with neutral red. Sections containing biotinylated dextran-amine (BDA) were processed with a Vectastain ABC Elite kit (Vector Laboratories) (16), incubated with a nickel/cobalt/diaminobenzidine solution, and reacted with 0.3% H₂O₂. Sections were then mounted, cleared, dehydrated, and counterstained with neutral red.

Antibodies to calcium binding protein (CaBP) stain the ICx and the core subdivision of the ICc darkly and do not stain the

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Abbreviations: N.Ov, nucleus ovoidalis; ICc, central nucleus of the inferior colliculus; ICx, external nucleus of the inferior colliculus; IID, interaural intensity difference; ITD, interaural time difference; CaBP, calcium binding protein; ABI, average binaural intensity; BDA, biotinylated dextran-amine.

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medial or lateral shell subdivisions of the ICc (17). Sections through the midbrain of the barn owl that had been stained for CaBP were used as templates to determine whether neurons retrogradely labeled from injections in the N.Ov were located within the ICx. Sections were used from different owls whose brains were blocked and sectioned in the same plane as those that received retrograde tracer injections. Camera lucida drawings of sections through the inferior colliculus (IC) containing retrogradely labeled neurons were made, then CaBP-stained sections through the midbrain were placed on the microscope and projected onto the camera lucida drawings. The CaBP section that best fit the outline of the IC drawn in camera lucida was used as the template. In every case, a CaBP section was found that matched the outline of the IC within 100 μm .

Stimulation and Recording. In a double-walled soundproof chamber (Industrial Acoustics, Bronx, NY), digitally synthesized pure-tone or pseudo-random noise bursts were delivered to the ears via a calibrated earphone assembly. Noise signals were adjusted to be flat in the frequency domain between 1 and 10 kHz. Two channels of output from a D/A converter (EF12M, Masscomp, Westford, MA) were passed through a digital reconstruction filter and sent to a pair of digital attenuators that controlled the intensity level at each earphone. The D/A conversion rate was 100 kHz, allowing for a minimum interaural time difference (ITD) of 10 μsec .

The activity of single neurons was recorded extracellularly with glass electrodes filled either with Woods Alloy metal plated with gold and platinum or 0.5 M sodium acetate containing 2% pontamine sky blue. Action potentials were amplified, filtered (300-Hz high pass, 10-kHz low pass), level-discriminated, and recorded with microsecond resolution by a custom-made event timer board (Beckman Electronics Shop) on a Masscomp 5600 computer. Custom software delivered stimuli and synchronously acquired action potential timing data in real time. Neural activity was recorded over a 300-msec period: 100 msec prior to the stimulus, 100 msec for the duration of the stimulus, and 100 msec after the stimulus was complete. Information about spontaneous activity was obtained on each repetition from the 100 msec preceding the stimulus. Stimuli were delivered approximately once per second. At each point in a tuning curve, the number of spikes was averaged over the total number of stimulus repetitions. The mean and standard error were calculated and plotted for the evoked activity, and the mean was plotted for the spontaneous activity. Broadband noise was used as a search stimulus. Electrode tracks were histologically verified, and recording sites were marked with electrolytic lesions when Woods Alloy metal electrodes were used (5 μA DC current for 10 sec), or by iontophoretic injection of pontamine sky blue when sodium acetate electrodes were used (-10 μA DC current pulsed 7 sec on/7 sec off for 5 min).

Definition of Terms. Interaural intensity difference (IID) is the sound intensity (in dB) in the right ear minus the sound intensity in the left ear. The average binaural intensity (ABI) is the mean of the sound intensity in both ears. Thus, at zero IID the sound intensity in both ears is the same and equal to the ABI. IID can be varied either by holding the ABI constant, or by holding the intensity to one ear constant while varying the intensity to the other ear. In the former case, as the intensity to one ear is increased, the intensity to the other ear is decreased by the same amount. In the latter case, the ABI varies with the IID. IID tuning curves were collected at constant ABI, whereas neurons were checked for monaural responses (response to stimulation from one ear only) with a fixed intensity in one ear and variable ABI. Neurons excited by sounds that are louder in the contralateral ear and inhibited by sounds that are louder in the ipsilateral ear have EI IID tuning. Conversely, if a neuron is inhibited by contralaterally loud sounds and excited by ipsilaterally loud sounds, it is labeled as

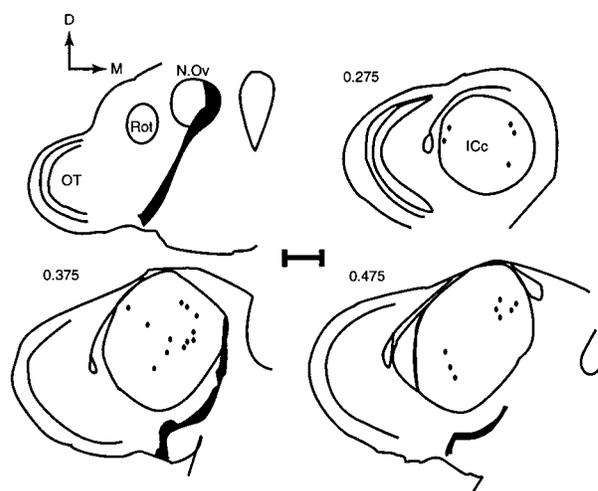


FIG. 1. Camera lucida drawings of transverse sections containing a BDA injection site in the N.Ov (*Upper Left*) and retrogradely labeled neurons in the ipsilateral inferior colliculus. The dark band of tracer running dorsoventrally in the section containing the injection site is due to stained axonal fibers in the tractus ovoidalis, the afferent fiber tract from the IC. The numbers in the upper left of the sections indicate the anterior-posterior (A-P) position of the section within the nucleus normalized to the A-P extent of the entire nucleus. Bar = 1 mm.

having IE IID tuning (18). Best frequency is defined as the tonal frequency that elicits the largest number of action potentials from a neuron when the intensity of all tone frequencies used to stimulate the neuron is held constant. ITD is the temporal offset between identical portions of the carrier waveform delivered to the two ears. In neurons that are tuned to ITD, a plot of the mean number of action potentials against ITD shows peaks and troughs separated by constant intervals. When the peaks are of the same height, the response pattern is called phase-ambiguous. When one peak is higher than the other peaks, then the ITD tuning is said to be side-peak suppressed (5).

RESULTS

Afferent Connections to the Auditory Thalamus. Retrograde tracer injections were made in different regions of the N.Ov (one tracer injection per owl), and the central auditory pathways were examined for labeled cell bodies. Both free

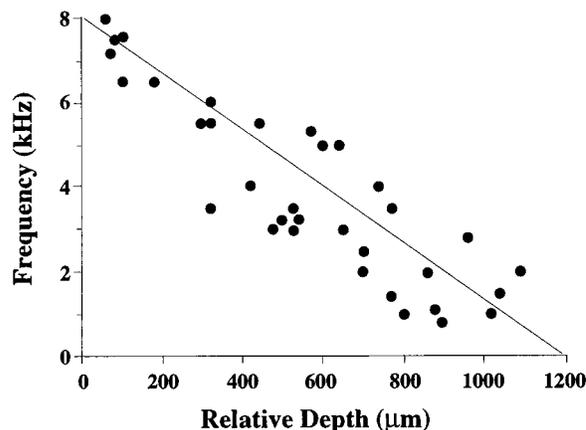


FIG. 2. Plot of neuronal best frequency vs. location along the dorsoventral axis in the N.Ov. Positions along the x-axis are relative to the dorsal border of the nucleus as determined by the location where auditory activity was first discernible.

ITD: 60 IID: 0 ABI: 50

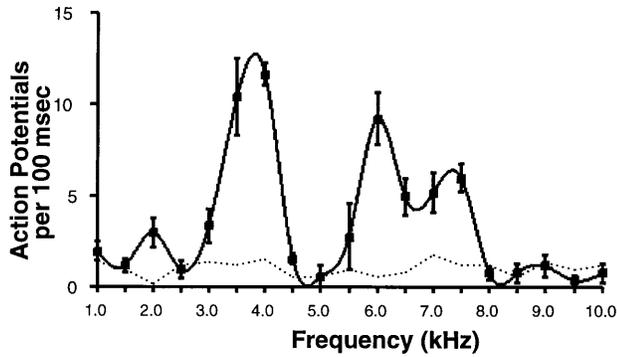


FIG. 3. Example neuron with a best-frequency tuning curve that contained more than one peak. Data points indicate the mean response; error bars indicate standard error. The solid line is the cubic spline interpolation between data points; the dashed line is the mean of the spontaneous activity level.

horseradish peroxidase and BDA were used as tracers to control for possible differences in the efficacy of retrograde transport. Localized injections of either tracer were confined to the rostral, caudal, medial, lateral, or central aspect of the N.Ov. Regardless of the site of the injection, we observed retrogradely labeled somata that were sparsely distributed across the dorsoventral and mediolateral extent of the ICc (Fig. 1). There was no clustering of labeled cell bodies or pattern of retrogradely labeled neurons that was specific for the location of the injection site within the N.Ov. Tracer injections into the medial N.Ov resulted in slightly more labeled neurons in the medial aspect of the ICc than on the lateral aspect, and injections into the lateral N.Ov caused slightly more neurons to be labeled on the lateral aspect of the ICc than on the medial aspect. Neurons were retrogradely labeled bilaterally in the ICc with the same sparse distribution, but with far fewer neurons labeled in the ICc contralateral to the injection site (approximately 1/10 the number labeled ipsilaterally). Retrogradely labeled neurons were found in the ventral nucleus of the lateral lemniscus ipsilateral to the injection site only. There were no retrogradely labeled cell bodies in the optic tectum on either side of the injection site. Based on the cytoarchitecture of the nucleus in counterstained sections, there were no retrogradely labeled cell bodies that could be unequivocally located in the ICx on either hemisphere relative to the injection site. Using the CaBP section template method, we found no labeled cell bodies within the ICx.

Tone Responses in the Auditory Thalamus. The N.Ov contained neurons that were tonotopically organized; neurons with high best frequencies were located dorsally, whereas those with lower best frequencies were located progressively more ventral (Fig. 2). This frequency representation consisted of isofrequency regions that extended mediolaterally and rostrocaudally, lying roughly perpendicular to the dorsoventral plane of electrode penetration. All frequencies tested (0.5–9 kHz) were represented by approximately equal areas of the nucleus.

Fourteen out of 153 isolated single neurons were recorded within the N.Ov that had frequency-tuning curves with multiple distinct peaks (Fig. 3). The frequencies at which these peaks occurred varied between neurons, with one peak cor-

responding to the frequency tonotopically represented in that portion of the nucleus. The frequency difference between peaks was as small as 1 kHz and as large as 3.5 kHz. In two cases the peaks were separated by a frequency region in which tone inhibited the neuron below spontaneous discharge rates.

Three neurons responded to particular pure-tone frequencies with inhibition below spontaneous activity levels and had no response above spontaneous levels to stimulation with tones other than those that resulted in inhibition. Though inhibited or insensitive to pure tone stimuli, these neurons nonetheless responded well to broadband noise. Two additional neurons had no significant response above background activity levels when stimulated with tones between 0.5 and 9 kHz and yet had robust excitatory responses to broadband noise stimulation.

Responses to Sound Localization Cues. There was no apparent topographic organization of neurons sensitive to sound localization cues either alone or in combination in the dorsoventral, rostrocaudal, or mediolateral planes. Furthermore, there was no clustering or grouping of neurons with similar responses to sound localization cues in the N.Ov. In the dorsoventral plane, single neurons were typically isolated approximately every 40 μm , and the response types to sound localization cues varied widely over sequentially isolated neurons. All electrode penetrations were made in the dorsoventral orientation so that mapping of the N.Ov in the rostrocaudal and mediolateral planes required sequential electrode penetrations, which were made at approximately 100- μm intervals. Neuronal responses between electrode penetrations were compared at the same depth within the nucleus and the same best frequency. A grid of fiducial marks (lesions or pontamine sky-blue stains) was placed within the nucleus to allow the response types to be mapped to their relative location in the N.Ov. Because all sections were cut in the coronal plane, fiducial marks in the rostrocaudal plane had to be compared across sections. In all cases fiducial marks were located within 150 μm of each other.

All neurons recorded within the N.Ov responded in a tuned manner to at least one sound localization cue. Most neurons (62%) responded in a tuned manner to both ITD and IID, but a large number (36.6%) were unresponsive to ITD (Table 1). Four neurons (2.6%) were tuned to ITD but not IID. These four neurons were excited by stimulation applied to either ear (EE). No exclusively monaural (E0 or 0E) neurons were observed.

Every possible combination of IID tuning (EI, IE, peaked) and ITD tuning (side-peak suppressed, phase-ambiguous), with one exception, was observed (Tables 2 and 3). The one response-type combination not found was IE IID tuning with side-peak-suppressed ITD tuning. Of the neurons that were tuned to IID, nearly half (49.7%) had a tuning curve that was specific for a particular IID (peaked IID tuning curves). Slightly more than half of the neurons that were tuned to IID had monotonic, sigmoid-type response functions when stimulated with noise. Of the neurons that had peaked IID tuning curves, 69.3% had ITD tuning curves with multiple peaks of similar size when stimulated with broadband noise (phase-ambiguous ITD tuning curves), and 17.3% had ITD tuning curves with a prominent central peak and suppressed side peaks. Finally, 13.3% of neurons with peaked IID tuning curves were insensitive to changes in ITD.

Neurons that had monotonic, sigmoid-type IID tuning curves were either EI (56.6%) or IE (43.4%) neurons. Of the

Table 1. Characterization of neurons in the N.Ov according to their response to sound localization cues (153 neurons were completely characterized)

IID-responsive: 149			ITD responsive: 97		
IID only	54	EI 43	ITD only	4	Phase-ambiguous 83
IID and ITD	95	IE 33	ITD and IID	93	Side-peak-suppressed 14
		Peaked 73			

Table 2. Number of neurons in the N.Ov that respond to IID, categorized according to IID response type

Response type	Peaked	EI	IE
IID only	10	20	24
IID and ITD	63	23	9

EI neurons, 51.2% had ITD tuning curves with multiple peaks in response to broadband noise, whereas 48.8% were not sensitive to ITD variations. Conversely, 75.8% of the IE neurons displayed no ITD tuning, whereas 21.2% had ITD curves with multiple peaks.

Of the neurons that responded to ITD, 85.6% did so with multiple peaks in the ITD tuning curve, whereas the remainder (14.4%) were classified as having side-peak suppression. Of the 83 isolated neurons that responded to ITD variations in a phase-ambiguous manner, 51 had the trough of the ITD curve well above the spontaneous activity level. In the remaining 32 neurons, troughs were at or below the spontaneous activity level.

DISCUSSION

The distribution of neurons that were retrogradely labeled in the inferior colliculus following tracer injections into the N.Ov suggests that a scattered set of neurons in the ICc provide input to the N.Ov. The labeled neurons were distributed sparsely across the mediolateral, rostrocaudal, and dorsoventral planes of the ICc. Because the ICc is tonotopically organized in the dorsoventral plane (3), neurons labeled at various locations across this plane suggest that frequency information converges within the region of the tracer-injection site in the N.Ov. Furthermore, because the ICc is subdivided in the mediolateral plane according to sound localization cue response (10, 19–21), the distribution of retrogradely labeled neurons suggests that neurons tuned to different sound localization cues converge in the N.Ov within the area of the tracer injection. No retrogradely labeled neurons were located in the central or lateral portion of the ICx or in the most anterior sections of the inferior colliculus where ICx is the widest. It is quite clear that neither the auditory space map in the ICx as a whole nor a large portion of it projects to the auditory thalamus. The afferent pattern of connections described here is consistent with the results of Karten (22), who demonstrated that in the pigeon the N.Ov receives its input from the mesencephalicus lateralis pars dorsalis (MLd), which is called ICc in the barn owl, and of Wild (23), who showed that the lateral lemniscus projects directly to the N.Ov in the pigeon.

The tonotopic organization of the N.Ov is inverted from the map of frequency found in the inferior colliculus (3, 6). The tonotopic organization we observed in the N.Ov has also been described in the N.Ov of the zebra finch (24) and the starling (25). Auditory nuclei in the brainstem and midbrain of the owl have a tonotopic organization that is best fit by regression lines of different slope, with frequencies between 4 and 8 kHz being overrepresented and frequencies less than about 3 kHz being relegated to narrow regions of the nucleus (3, 4). The N.Ov, however, did not contain an overrepresentation of those frequencies that are used by the barn owl for sound localization (26, 27). In contrast to all other auditory areas described in the barn owl, the N.Ov contained neurons that had multiple peaks

Table 3. Number of neurons in the N.Ov that respond to ITD, categorized according to ITD response type

Response type	Phase-ambiguous	Side-peak-suppressed
ITD only	4	0
ITD and IID	79	14

in their best frequency-tuning curve. It is unlikely that the multiple peaks that were observed in the frequency-tuning curves were due to harmonic distortion in the sound delivery system, because at all frequencies at which pure tones were used, the frequency spectrum of the output of the earphones was examined for extraneous frequencies. No such frequencies were observed for the stimulus levels used in this study. Furthermore, the results of the retrograde tracer experiments demonstrating that afferents from different frequency regions of the ICc converge within a region of the N.Ov provide an anatomical basis for this type of frequency tuning. Biederman-Thorson (28) described neurons in the N.Ov of the Ring dove that had “w-shaped” frequency-tuning curves, and Banks and Margoliash (29) mentioned finding neurons that had frequency-tuning curves with multiple peaks in the N.Ov of the zebra finch. Bigalke-Kunze *et al.* (25), however, did not find any neurons with more than a single excitatory frequency band in the starling.

Although all ovoidalis neurons responded to at least one sound localization cue, there was no systematic mapping of sound localization parameters in the nucleus. This finding is consistent with the anatomical results mentioned above. In contrast to the ICx, where space is mapped but frequency is not (30), it appears that in the N.Ov, frequency is mapped but space is not. Interestingly, some topographic organization of ITD tuning reappears in the forebrain (31). In contrast to the organization of the ICc, neurons with similar response types to sound localization cues were not segregated in distinct portions of the N.Ov. Furthermore, in all binaural auditory nuclei downstream from the N.Ov that have been studied to date, either space or a combination of frequency and a dichotic cue is topographically arranged (2–4, 8, 30). This trend apparently is broken in the auditory thalamus, though the possibility of slanted or curled maps of sound localization cues that cross frequency laminae in the N.Ov has not been ruled out.

The nucleus ovoidalis appears to be unique among the auditory nuclei of the barn owl. It takes its input from multiple subdivisions of the inferior colliculus and the lateral lemniscus, representing different stages in the processing of sound localization cues, and combines those inputs while maintaining tonotopy without preserving any obvious form of localization cue topography. Whatever ability the auditory forebrain has for supporting sound localization does not arise from an auditory map of space in the N.Ov. If anything, the processing of sound localization cues by the auditory thalamus appears less refined and much less organized than in the midbrain. In the barn owl, sound localization behavior appears to be subserved by both topographic and nontopographic representations of auditory space.

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