Hearing Impairment Induces Frequency-Specific Adjustments in Auditory Spatial Tuning in the Optic Tectum of Young Owls

JOSHUA I. GOLD AND ERIC I. KNUDSEN
Department of Neurobiology, Stanford University, Stanford, California 94305-5125

Gold, Joshua I. and Eric I. Knudsen. Hearing impairment induces frequency-specific adjustments in auditory spatial tuning in the optic tectum of young owls. J. Neurophysiol. 82: 2197–2209, 1999. Bilateral auditory-visual neurons in the optic tectum of the barn owl are sharply tuned for sound source location. The auditory receptive fields (RFs) of these neurons are restricted in space primarily as a consequence of their tuning for interaural time differences and interaural level differences across broad ranges of frequencies. In this study, we examined the extent to which frequency-specific features of early auditory experience shape the auditory spatial tuning of these neurons. We manipulated auditory experience by implanting in one ear canal an acoustic filtering device that altered the timing and level of sound reaching the eardrum in a frequency-dependent fashion. We assessed the auditory spatial tuning at individual tectal sites in normal owls and in owls raised with the filtering device. At each site, we measured a family of auditory RFs using broadband sound and narrowband sounds with different center frequencies both with and without the device in place. In normal owls, the narrowband RFs for a given site all included a common region of space that corresponded with the broadband RF and aligned with the site’s visual RF. Acute insertion of the filtering device in normal owls shifted the locations of the narrowband RFs away from the visual RF, the magnitude and direction of the shifts depending on the frequency of the stimulus. In contrast, in owls that were raised wearing the device, narrowband and broadband RFs were aligned with visual RFs so long as the device was in the ear but not after it was removed, indicating that auditory spatial tuning had been adaptively altered by experience with the device. The frequency tuning of tectal neurons in device-reared owls was also altered from normal. The results demonstrate that experience during development adaptively modifies the representation of auditory space in the barn owl’s optic tectum in a frequency-dependent manner.

INTRODUCTION

The nervous system infers the location of a sound source in space from cues that arise from frequency-dependent interactions between the sound and the physical characteristics of the listener. In humans, for example, incident sound waves interact with the head, torso, and external ears, resulting in transformations of the sound’s spectrum that create interaural timing differences (ITDs) and level differences (ILDs) used for horizontal localization as well as spectral cues that are used for vertical localization and front/back discrimination (see Blauert 1983, for a review). These cues have also been shown to provide essential spatial information in numerous other species, including ferrets (Carlile and King 1994), guinea pigs (Middlebrooks 1987; Middlebrooks and Knudsen 1987; Musicians et al. 1990; Rice et al. 1992), and barn owls (Moiseff and Konishi 1981; Olsen et al. 1989). To help compensate for individual variability in the physical features that give rise to these cues, neurons that process auditory spatial information are calibrated by experience (ferrets: King et al. 1988; barn owls: Knudsen 1985; guinea pigs: Withington-Wray et al. 1990a,b). In this study, we investigated whether this calibration process takes into account the high degree of frequency dependence of auditory localization cues.

For barn owls, ITDs vary systematically with sound source azimuth. ILDs also vary systematically with sound source azimuth for frequencies below ~4 kHz but, due to an asymmetry in the owl’s external ears, vary systematically with sound source elevation for higher frequencies (Brainard et al. 1992; Keller et al. 1998). Neurons in the barn owl’s optic tectum (homologue of the mammalian superior colliculus) are tuned to combinations of ITD and ILD values over a broad range of frequencies. As a consequence of this tuning, a given tectal neuron has an auditory receptive field (RF) for broadband stimuli that is restricted to a single region of space (Brainard et al. 1992; Olsen et al. 1989). Moreover, tectal neurons are systematically organized with respect to their auditory RF locations to form a physiological map of auditory space (Knudsen 1982).

Auditory experience has been shown to shape the auditory spatial tuning of tectal neurons. Monaural occlusion with a dense foam plug, for example, affects the timing, level, and spectral content of sounds reaching the occluded ear. In owls raised with a chronic monaural occlusion, the topography of the tectal auditory space map, when tested with broadband noise stimuli, is abnormal with both ears open but normal with the earplug in place, indicating that adaptive changes have occurred in response to the effects of the earplug (Knudsen 1985). Similarly, raising owls with a modification of the external ears that alters the spatial patterns but not the ranges of sound localization cues results in adaptive changes in tectal unit tuning to ITD and ILD for broadband stimuli (Knudsen et al. 1994).

An earplug or a modification of the external ear has different effects on different frequencies of sound. Consequently, a complete adjustment in spatial tuning requires different adjustments for cues at different frequencies. Nevertheless, the effects of these manipulations have to date been tested only with broadband stimuli. It is not known, therefore, the extent to which the auditory spatial tuning of tectal neurons adjusts to frequency-dependent variations in spatial cues. In the present...
study, we used narrowband stimuli presented through a free-field speaker to characterize the spatial tuning of neurons in the optic tectum of normal owls and owls raised with abnormal auditory experience. The results demonstrate that auditory experience does indeed adjust the spatial tuning of tectal neurons in a frequency-specific and adaptive manner.

**Methods**

We collected data from two normal barn owls (Tyto alba) and five barn owls raised with an acoustic filtering device in one ear. One owl wore an early prototype of the device and the four others wore a standard version of the device.

**Acoustic filtering device**

Figure 1 shows the acoustic filtering device that was used to alter auditory experience. The device was a custom-designed chamber made from acetal delrin (Plastics SRT) that was sutured into the owl’s right ear canal (the owl’s ear canals are asymmetrically positioned on the head, and the left ear canal opens at an angle relative to the facial ruff feathers that makes it difficult to place the device on the left side). A small, circular flange fit tightly to the inner walls of the ear canal, and the rest of the device was located just behind the preaural flap and in front of the facial ruff feathers. We designed the device to increase the path length of sound reaching the affected ear and to change the resonance properties of the ear canal while still providing a low-impedance pathway to the tympanic membrane. One owl was raised with an early version of the filtering device that had a shorter and smaller diameter chamber; the acoustic properties of this device were not measured. Electrophysiological data from this owl are presented separately.

Owls raised with an acoustic filtering device were first binaurally occluded with dense foam rubber earplugs (E.A.R. Cabot) to limit auditory experience from 25 to 35 days of age, corresponding to the time that their ear canals were open but too narrow to accommodate the device. At ~35 days of age, the binaural foam plugs were removed, and the filtering device was sutured into the right ear canal. The earplugs and the device were sutured into place while the owls were anesthetized with halothane (1%) in a mixture of oxygen and nitrous oxide (5:4).

All owls were raised initially in brooding boxes with their siblings. After insertion of the device, each owl was placed in an individual cage next to a large flight cage that housed numerous adult owls, providing a rich auditory and visual environment. When the owls could fly (at ~60 days of age), they were placed in the large flight cage. Owls were at least 95 days of age when electrophysiological recordings began.

The device was removed at the beginning of each experiment, at which time the canal, eardrum, and device were inspected for damage and accumulation of earwax. The device was sutured back into place at the end of each experiment.

The owls were provided for in accordance with the National Institutes of Health Guide for the Care and Use of Laboratory Animals and the guidelines of the Stanford University Institutional Animal Care and Use Committee.

**Acoustic measurements**

The effects of the device on the level and timing of sounds reaching the affected ear were determined using bilateral cochlear microphonic (CM) measurements. In five owls, CM electrodes were implanted and recordings made after all other electrophysiological measurements had been completed. With the owl anesthetized with halothane and nitrous oxide, a small hole was made at the base of the skull over each middle ear cavity. Two silver wire electrodes were inserted through each hole, one placed against the edge of the round window and the other in the perilymph. The electrodes were anchored to the skull with cyanoacrylate glue and the holes sealed with dental cement.

CM measurements were made while the owl was suspended prone with its head bolted in place in a sound-attenuating chamber (IAC 404A) lined with acoustic foam to suppress echoes. Retinal landmarks were used to align the head relative to a free-field speaker apparatus (a barn owl’s eyes are essentially fixed in the head). The loudspeaker had a frequency response that was flat to within ±4 dB from 2 to 10 kHz, as measured with a Brul and Kjær 1/2-in. condenser microphone. The loudspeaker was placed directly in front of the owl or, for a single owl, at fixed intervals along the horizontal plane, at a distance of 92 cm from the owl. CM measurements were made with continuous tones stepped at 0.5- or 1-kHz intervals from 2 to 10 kHz. The delay (or advance) in the timing of sounds reaching the affected ear was determined by measuring the induced shift in phase between the CMs from the two ears. Time shifts were computed from the phase shifts by calculating the time difference closest to 0 μs that corresponded to the given phase difference. Note that a given phase difference corresponds to more than one ITD, a phenomenon that results from the periodic nature of interaural phase. The attenuation caused by the device was measured by the amount of amplification required to bring the CM amplitude up to a criterion level that was set with both ears open. The criterion amplitude was within the nonsaturating portion of the CM’s range.

In addition, the acoustic properties of the device alone were measured using a Brul and Kjær artificial ear. The effects of device insertion into the artificial ear were measured using a Brul and Kjær 1/2-in. condenser microphone attached to a 0.3 × 15 mm probe tube. The loudspeaker was positioned in front of, and 60° to either side of, the device at a distance of 92 cm.

**Electrophysiology**

Each owl was prepared for electrophysiological measurements in a single surgical session. The owl was anesthetized with halothane and nitrous oxide, and a stainless steel plate was cemented to the base of the skull. In addition, small craniotomies were made above the left and right optic tecta. At the end of the surgery, the craniotomies were filled with dental acrylic, and the tissues surrounding all incisions were infused with lidocaine, treated with betadine, and closed.

At the beginning of each recording session, the owl was anesthetized with halothane and nitrous oxide, given 3 ml of 2.5% dextrose in 0.45% sterile saline (administered intramuscularly), and wrapped in a soft leather jacket. The owl was positioned in the sound chamber as described above for CM measurements. A tungsten microelectrode was stereotaxically positioned and advanced through the telencepha-
ion until a characteristic pattern of bursting activity signaled entry into the superficial layers of the optic tectum (Knudsen 1982), where multunit recordings were made. A level discriminator was used to isolate the action potentials of a small number of neurons at each site. A response to a sound burst was measured as the number of action potentials that occurred in the 100 ms immediately following stimulus onset (poststimulus response) minus the number of action potentials in the 100 ms immediately preceding stimulus onset (baseline activity), typically averaged over 20 repetitions.

The owl was anesthetized during the initial 20 min of setup with the halothane/nitrous mixture and normally remained calm and motionless during the course of the experiment. Occasionally, however, brief doses of halothane and nitrous oxide or nitrous oxide alone were administered if the owl became active.

At the end of each recording session, the craniotomy was bathed in chloramphenicol (0.5%) and resealed with dental acrylic. The owl was kept warm with a heat lamp until it had fully recovered (usually 1–2 h), and then it was returned to its home flight cage.

**Auditory measurements**

Auditory RFs of tectal neurons were mapped using the same loudspeaker that was used for the CM measurements, described above. Using a remotely controlled positioning system, the loudspeaker was moved on an imaginary sphere, 92 cm in radius and centered on the owl’s head. Speaker position is reported in a double-pole coordinate system (see Knudsen 1982), in which azimuth (az) and elevation (el) refer to degrees to the left (L) or right (R) of the median sagittal plane and degrees above (+) or below (−) the visual (horizontal) plane, respectively.

Free-field acoustic stimuli consisted of computer-generated tone and noise bursts, 50 ms in duration. Tone bursts, used to determine frequency tuning, had 5-ms rise/fall times. Narrowband noise bursts had a 1 kHz-wide passband centered on the given frequency and 5-ms rise/fall times; these were used instead of tones to map frequency-specific RF locations because tones often did not elicit a consistent response. Broadband noise bursts had a passband of 3–10 kHz and 0-ms rise/fall times.

At every site, auditory RFs were measured for both narrowband and broadband stimuli, with and without the device in the ear canal. For each condition, RF location was initially estimated, and the response threshold was determined from a level-response function measured with the speaker positioned at the center of the estimated RF. The RF was then determined using a sound level that was 20–40 dB above the threshold measured for that stimulus and its response is reported as the speaker positions that elicited a response >50% of the maximum response. Response threshold was defined as the lowest sound level that evoked a response that was at least 25% of the maximum response elicited. Levels were calibrated using A-weighted signals from a Brüel & Kjær ¼-in. condenser microphone positioned where the center of the owl’s head would be in the sound chamber. Narrowband response thresholds were measured in dB relative to 4-kHz thresholds.

Frequency-response functions were measured with both ears open in normal and device-reared owls. These measurements were made using a sound level that was 20 dB above threshold and with the speaker positioned at the center of the estimated RF for the given stimulus.

Location-response functions were determined by making transects through the center of each auditory RF and, in some cases, at additional locations. A transect consisted of measurements of tectal responses to fixed speaker positions at 10° intervals, stepping the speaker in one direction, and a second set of measurements, offset by 5°, stepping the speaker back in the opposite direction. This procedure was performed twice. For a given transect, best location was defined as the midpoint of the region over which responses were >50% of the maximum response. For sites that responded strongly to sounds from multiple, discrete regions of space, the best location was defined as the midpoint of the response peak located nearest to the site’s visual RF.

**Visual RF measurements**

Visual RF location was determined for each recording site by projecting bars and spots of light, produced by an ophthalmoscope, onto a calibrated, translucent hemisphere positioned directly in front of the owl at a distance of 57 cm. Visual RF locations are reported in double-pole coordinates as described above.

**RESULTS**

**Frequency-specific effects of the acoustic filtering device**

Insertion of the acoustic filtering device into the right ear canal altered the timing and level of sounds reaching the eardrum in a frequency-dependent manner, as determined with cochlear microphonic measurements. Figure 2, A and B, shows the effects of device insertion on CM responses for sound sources located directly in front of the owl. In five owls tested, device insertion caused frequency-dependent phase shifts that were equivalent to delays of 33–91 μs at 4 kHz, delays of 12–54 μs at 6 kHz, and changes at 8 kHz that ranged from a delay of 17 μs to an advance of 53 μs. In addition, in four owls tested, device insertion changed sound levels by between a gain of 2 dB and an attenuation of 12 dB at 4 kHz, and by attenuations of 10–23 dB at 6 kHz and 8–21 dB at 8 kHz.

The acoustic effects of the device varied as a function of sound source location (Fig. 2, C and D). Particularly striking was the reduced attenuation of high-frequency (6–9 kHz) stimuli for sources located to the right. However, the acoustic properties of the device alone did not vary with sound source location out to 60° az (probe tube measurements, not shown). This result suggests that the location-dependent effects of the device result from the interference of the device with the direction-dependent sensitivity of the external ear.

**Effects of the acoustic filtering device on spatial receptive fields**

Acute insertion of the device altered the auditory RFs of tectal neurons in a frequency-specific manner. Figure 3, A and B, illustrates, in a normal owl, the effects of acute device insertion on auditory RFs at a tectal site with a visual RF at L4° el. With both ears open, a broadband stimulus and narrowband stimuli centered on 4, 6, and 8 kHz each elicited robust, spatially tuned responses. The narrowband RFs in insertion on auditory RFs at a tectal site with a visual RF at L4° el. With both ears open, a broadband stimulus and narrowband stimuli centered on 4, 6, and 8 kHz each elicited robust, spatially tuned responses. The narrowband RFs included the region of space covered by the broadband RF and the visual RF (Fig. 3A). The 8-kHz RF included additional discrete regions. Presumably, these regions corresponded to locations that produced similar interaural phase differences (see dashed line in Fig. 2A) and ILDs (Keller et al. 1998). Insertion of the device in the owl’s right ear changed both the auditory RF locations and the range of frequencies over which responses could be elicited: the 4-kHz RF was shifted to the right of and above the visual RF; no location was found from which the 6-kHz stimulus could elicit a response for sound levels up to 50 dB above the threshold measured for the 4-kHz stimulus; the 8-kHz RF closest to the visual RF was shifted slightly to the left; and the broadband RF was shifted to the
right of and above the visual RF. The results presented in Fig. 3, A and B, were qualitatively similar to those from two additional sites with similar, frontally located visual RFs in a different normal owl (data not shown).

Chronic experience with the device during development altered the auditory spatial tuning of tectal neurons in a frequency-dependent and adaptive manner. Figure 3, C and D, shows frequency-specific RFs at a site with a visual RF located at R3° az, 15° el in an owl raised with the filtering device in its right ear. With the device removed, the broadband and narrowband RFs were not aligned with each other or with the visual RF (Fig. 3 C). The 4-kHz RF was located nearly 20° to the left of the visual RF. No responses could be elicited for a narrowband stimulus centered on 6 kHz for any loudspeaker location at any sound level (up to 50 dB above the threshold measured for the 4-kHz stimulus). The two regions of the 8-kHz RF that were located nearest to the visual RF were 5° to the right and 50° to the left of it. The broadband RF included multiple discrete regions of space, the locations of which corresponded to those of the individual narrowband RFs (in contrast, responses to broadband stimuli normally tend to be inhibited at locations corresponding to nonoverlapping regions of narrowband RFs; Brainard et al. 1992). When measured with the device in place, the RFs for the 4- and 8-kHz stimuli and for the broadband stimulus were aligned with each other and with the visual RF; there were still no responses to 6-kHz stimuli regardless of stimulus location (Fig. 3 D). The data presented in Fig. 3, C and D, were qualitatively similar to those collected at three additional sites with similar, frontally located visual RFs in two different device-reared owls (data not shown).

Effects of the acoustic filtering device on frequency-response functions

The frequency-response functions of tectal units representing frontal space were abnormal in owls raised with the acoustic device. Specifically, device rearing substantially reduced normally robust responses to stimuli near 6 kHz. Figure 4A shows level-response functions for seven sites with frontally located visual RFs (between L6° and R3° az and 0° and 17° el) in normal owls. At these sites, thresholds were lower for narrowband stimuli near 6 kHz than for stimuli near 4 or 8 kHz, with median values and interquartile ranges of 0 and 13 dB at 4 kHz, 22 and 47 dB at 6 kHz, and 25 and 25 dB at 8 kHz. Responses to super-threshold stimuli increased with increasing sound level and typically plateaued at a maximum spike rate. At six of the seven sites, the maximum response rate was highest for stimuli near 6 kHz; at one site, the maximum response rate was highest for the 8-kHz stimulus.

Figure 4B shows level-response functions for five sites with frontally located visual RFs (between L6° and R3° az and 0° and 7° el) in normal owls. At these sites, thresholds were lower for narrowband stimuli near 6 kHz than for stimuli near 4 or 8 kHz, with median values and interquartile ranges of 0 and 13 dB at 4 kHz, −24 and 47 dB at 6 kHz, and −5 and 25 dB at 8 kHz. Responses to super-threshold stimuli increased with increasing sound level and typically plateaued at a maximum spike rate. At six of the seven sites, the maximum response rates were highest for stimuli near 6 kHz; at one site, the maximum response rate was highest for the 8-kHz stimulus.

FIG. 2. Acoustic properties of the device. A: cochlear microphonic (CM) measurements of the difference in the timing of sounds reaching the eardrum before vs. after device insertion in the right ear canal for 5 owls. Data from the individual owls are shown as thin, solid lines, and the median values of these measurements are indicated by the thick, solid line. The thick, dashed line represents phase offsets of 360° from the median values. B: CM measurements from 4 owls of the attenuation caused by device insertion, measured by determining the amount of amplification required following device insertion to restore the CM response amplitude to the value measured without the device in place. The 5th owl died before these measurements could be completed. The sound source was located at 0° az, 0° el for all measurements in A and B, C and D. C: CM measurements from a single owl of the difference in the timing (C) and level (D) of sounds reaching the eardrum before vs. after device insertion, plotted as a function of stimulus frequency for different speaker azimuths (see legend in C). Bold lines indicate data measured using a sound source located at 0° az, as in A and B. Speaker elevation was 0° for all measurements.
maximum response for any speaker location was weak (<25% of the maximum response to 4 kHz) at four of these sites, so thresholds were not determined. Indeed, responses plateaued at spike rates that were substantially lower for stimuli near 6 kHz than for stimuli near 4 or 8 kHz, even for sound levels up to 48 dB above the threshold measured at 4 kHz.

Frequency-response functions were measured with narrowband stimuli at sites with visual RFs in similar regions of space in normal owls and in device-reared owls with the device removed (Fig. 5). These functions, measured with the sound source centered in the estimated RF and presented at 20 dB above threshold for the given stimulus, reflected not only the spectral selectivity of tectal neurons but the spectral filtering imposed by the owl’s head and external ears, as well. However, because the spectral filtering by the head and ears was similar for all owls tested, differences between these functions indicated changes in neuronal spectral selectivity caused by experience with the device. For example, at a site representing frontal space in a normal owl (Fig. 5A), stimuli near 6 and 7 kHz elicited the strongest responses. In contrast, at a matched site in a device-reared owl tested with the device removed (Fig. 5B), stimuli near 8 kHz elicited the strongest responses, stimuli near 4 kHz elicited weaker responses, and stimuli near 6 kHz, presented at 30 dB above the 4-kHz threshold, elicited almost no responses.

This device-induced reduction of responses to stimuli near 6 kHz was evident at most sites with visual RFs in frontal space. In normal owls (Fig. 5C), tectal neurons with visual RFs between L13° and R3° az and 0° and 113° el responded most strongly to narrowband stimuli near 6 kHz, slightly less to stimuli near 8 kHz and even less to stimuli near 4 kHz, which is consistent with previously published reports (Knudsen 1984; Olsen et al. 1989). In contrast, in device-reared owls tested with the device removed (Fig. 5D), tectal neurons with visual RFs at similar locations (between L15° and R6° az and 0° and +12° el) responded significantly less strongly to narrowband stimuli near 6 kHz than to stimuli near either 4 or 8 kHz (paired t-tests; P < 0.05).

Device rearing did not appear to affect frequency-response functions for sites representing peripheral space. Normally, the frequency responses of tectal neurons vary systematically with visual RF azimuth, such that neurons representing frontal space respond best to stimuli near 6 or 7 kHz, whereas those representing peripheral space respond best to lower frequencies.
(Knudsen 1984; Olsen et al. 1989). Accordingly, tectal sites with visual RF azimuths between 25 and 38° to the left or right of center in normal owls responded strongest to stimuli near 3 or 4 kHz, with steadily decreasing responses to stimuli with center frequencies increasing to 8 kHz (Fig. 5E). In device-reared owls, tectal sites with similarly peripheral visual RFs (azimuths between 35 and 41° to the left or right of center) showed a similar pattern of frequency responses (Fig. 5F).

Effects of the acoustic filtering device on location-response functions

Device rearing caused frequency-dependent changes in unit tuning to sound source azimuth and elevation. We assessed these changes quantitatively by measuring location-response functions at 12 sites in 2 normal owls and at 13 sites in 4 device-reared owls. Figure 6 shows azimuth-response func-
In contrast, in the device-reared owl without the device in place, the elevation-response functions were frequency dependent, with a peak at +23° for the 4-kHz stimulus, a peak at −2° for the 8-kHz stimulus, and a broad curve for the broadband noise stimulus with peaks that corresponded to each of the narrowband peaks. When the device was replaced in the ear, however, narrowband and broadband response functions became mutually aligned at about +20°.

Because neurons representing peripheral space were tuned to lower frequencies than were those representing frontal space (Fig. 5), we measured location-response functions at peripheral sites using a lower range of frequencies: narrowband stimuli centered on 3, 5, and 7 kHz. Figure 8, A and B, shows the effects of acute insertion of the device in a normal owl at a site with a visual RF at R34° az, +7° el. At this site, device insertion caused slight shifts in azimuth-response functions for both the narrowband stimuli and the broadband stimulus, and responses to all frequencies up to ~7 kHz remained strong. The effects of device insertion on the azimuth-response functions at a corresponding site (visual RF at R40° az, +9° el) in a device-reared owl are shown in Fig. 8, C and D. At this site, tested without the device, the narrowband and broadband azimuth-response functions were slightly displaced to the left of the visual RF (arrow in Fig. 8C) but became aligned with the visual RF when the device was reinserted.

At a site representing space to the far left (visual RF at L25° az, +9° el), acute insertion of the device in a normal owl caused azimuth-response functions to shift by ~30° to the right.
A broadband stimulus (Fig. 9, for narrowband stimuli centered on 3, 5, and 7 kHz and for a broadband stimulus (Fig. 9, A and B). Robust responses to all frequencies up to 7 kHz remained. At a similar site in a device-reared owl (visual RF at L41° az, +9° el), azimuth-response functions for the same stimuli were displaced by ~30° to the left of the visual RF (arrow in Fig. 9C) when tested without the device in place. When tested with the device in place, the azimuth-response functions for the narrowband and broadband stimuli became more closely aligned with the visual RF (Fig. 9D).

The frequency-dependent shifts in tectal unit location-response functions that were induced by device rearing depended on the specifics of the acoustic manipulation. A single owl was raised with an early version of the acoustic device that affected sound in a different manner than did the standard device. Accordingly, location-response functions in this owl were shifted differently than were those in the other device-reared owls (Fig. 10). As in the other device-reared owls, however, these shifts appeared to compensate for the acoustic effects of the device.

The adaptive nature of the frequency-dependent shifts in location-response functions that were induced by device rearing is summarized in Fig. 11. In normal owls (C; 12 sites with visual RFs between L25° and R38° az and 0° and +13° el), location-response functions aligned with visual RF location to within 15° in azimuth and 30° in elevation, at nearly all sites and frequencies tested. In device-reared owls with the device in place (● and ◆; 13 sites with visual RFs between L41° and R40° az and 0° and +12° el), azimuth-response functions were similarly aligned with visual RFs. Elevation-response functions were aligned less precisely in both normal and device-reared owls, with some sites exhibiting auditory RFs that were unbounded either upward or downward for various frequencies.

**Comparison of shifts in unit tuning with device acoustics**

The alterations in location-response functions that resulted from experience with the device were, to some extent, predictable from the acoustic effects of the device. Figure 12 shows the acoustic effects of the device on sound timing or level for a sound source located directly in front (○, △, and □, replotted from Fig. 2) alongside the device-induced shifts in unit ITD or ILD tuning that were inferred from the observed changes in location-response functions for seven sites with visual RFs located in frontal space (●, ▲, and ■). The inferred shifts in ITD and ILD tuning were derived, as described in Fig. 12, from the difference between the cue values corresponding to the measured best location for each frequency following device removal and the values corresponding to the visual RF location (predicted normal values). For example, the visual RF at the site illustrated in Fig. 3C was centered at R3° az, +5° el, which, according to the average head-related transfer function, corresponds to an ITD of +8 μs at 4 kHz. However, the auditory RF for the 4 kHz stimulus measured with the device removed was centered at L17° az, +21° el, which corresponds...
to an ITD of $-61\,\mu s$. Thus at 4 kHz, this site had an inferred ITD shift of $-69\,\mu s$, which is similar to the 80-$\mu s$ delay imposed by the device in this owl (bold squares, Fig. 12A).

The inferred shifts in unit ITD tuning were similar to the acoustic effects of the device on sound timing (compare $\bigcirc$, $\triangle$, and $\square$ with $\bullet$, $\Delta$, and $\blacksquare$ in Fig. 12A). At 4 kHz, the device delayed sound to the right ear by 33–80 $\mu s$, and the shifts in location-response functions predict shifts in unit ITD tuning of 48–70 $\mu s$ toward right-ear delayed. At 8 kHz, the device caused between a 6-$\mu s$ delay and a 53-$\mu s$ advance in sound timing, compared with inferred shifts in unit ITD tuning of between 15 $\mu s$ toward right-ear delayed to 21 $\mu s$ toward right-ear leading. In contrast, the inferred shifts in unit ILD tuning did not follow closely the acoustic effects of the device on sound level (Fig. 12B). Although the direction of the inferred shifts in ILD tuning was consistent with the acoustic effects of the device, the magnitude of these shifts was usually less than that predicted by the acoustic measurements.

**DISCUSSION**

This study demonstrates that the auditory spatial tuning of neurons in the barn owl’s optic tectum adjusts adaptively to the frequency-dependent effects of an acoustic filtering device worn chronically in one ear during early life. The results attest to the precision with which the neural representation of auditory space in the optic tectum is shaped to reflect the experience of the individual. In the discussion that follows, we first summarize the properties of the acoustic filtering device, emphasizing those properties that distinguish it from other auditory manipulations. We then review device-induced changes in frequency-specific auditory RFs and in the ranges of frequencies to which neurons respond. Finally, we discuss the implications of these results on possible sites of auditory experience-dependent plasticity in the barn owl’s sound localization pathway.

**Properties of the auditory manipulation**

The acoustic effects of the device were similar in some ways to the effects of more familiar auditory manipulations such as monaural occlusion with an earplug (King et al. 1988; Knudsen 1985) and modifications of the external ears, including removal of the pinna and concha in mammals (Carlile and King 1994) and of the ruff feathers and external ears in owls (Knudsen et al. 1994). Each of these manipulations causes frequency-dependent changes in the correspondence between level and timing cue values and spatial locations. The effects of the device and of earplugs are more severe than those of external ear Modifications, however, because they shift the ranges of ITDs and ILDs to abnormal ranges, whereas external ear modifications tend to decrease these ranges, especially of ILDs. Therefore device and earplug rearing test more thoroughly the capacity of tectal units to adjust their tuning to binaural cues.

The acoustic attenuation caused by the device was substantially less than that caused by earplugging, however. Earplug effects have been shown to be variable but may attenuate sound by up to 60 dB (Knudsen et al. 1984). In
contrast, the device attenuated sound by a maximum of ~20–25 dB at 6 kHz, less for other frequencies. Even when the device was inserted acutely in a normal owl, speaker positions could usually be found that elicited responses from binaurally tuned neurons in the tectum. Thus as a hollow chamber that provided a low-impedance pathway through which sound could travel to reach the eardrum, the device had less of a deprivation effect on neuronal response properties than earplugging.

**Frequency-specific changes in auditory RFs**

The present results demonstrate that early auditory experience shapes the auditory RF locations of neurons in the optic tectum in a frequency-dependent and adaptive manner. In normal owls, different frequency-specific RFs of a given tectal neuron are aligned with each other and with the visual RF (Brainard et al. 1992). In device-reared owls tested with the device removed, frequency-specific RFs in the optic tectum were shifted from their normal locations in a direction and by a magnitude that depended on stimulus frequency (e.g., Fig. 3C). Such shifts in auditory RF location are adaptive to the extent that they compensate for the acoustic effects of the device and restore alignment between auditory and visual RFs. Indeed, tectal auditory and visual RFs were aligned in azimuth and, to a lesser extent, in elevation in device-reared owls tested with the device in place (Fig. 11, ● and ◆).

The fact that these adaptive modifications of the auditory spatial tuning of tectal neurons can occur on a frequency-by-frequency basis supports the idea that these neurons make optimal use of auditory spatial information. Normally, the auditory spatial tuning of tectal neurons reflects the integration of ITD and ILD cues across frequency channels (Brainard et al. 1992; Olsen et al. 1989). Previous studies have shown that both auditory and visual experience can shape the auditory spatial tuning of these neurons by altering their tuning for broadband ITD and ILD (Brainard and Knudsen 1993; Mogdans and Knudsen 1992). The present results predict that these adjustments in ITD and ILD tuning will be highly frequency dependent, as well.

In principle, similar frequency-dependent modifications could help shape the auditory spatial tuning of neurons in the mammalian superior colliculus. As in barn owls, the auditory spatial tuning of these neurons compensates for abnormal auditory experience early in life brought about by, for example, chronic monaural occlusion with a foam plug (King et al. 1988). Because mammals, like owls, use frequency-dependent information to localize sound sources, complete adaptation of the auditory spatial tuning of collicular neurons to abnormal auditory experience would take into account the frequency dependence of this information.

**Experience-induced changes in frequency-response functions**

The present results demonstrate that experience exerts a powerful shaping influence on the frequency responses of tectal neurons during development. In device-reared owls, the
loss of responsiveness to frequencies of around 6 kHz for neurons representing frontal space was particularly striking, because these frequencies consistently elicit robust responses from these neurons in normal owls (Figs. 4 and 5; Knudsen 1984). A possible explanation for this loss of responsiveness is based on the observation that following acute device insertion in normal owls, there was no location from which a 6-kHz stimulus produced robust responses from these neurons (e.g., Fig. 3B). If, during development, neurons in the optic tectum adjust their frequency tuning according to the relative strength of stimulus-driven activity in different frequency channels, then for these frontal neurons in device-reared owls, the loss of neural activity in the 6-kHz channel could have led to their selective loss of sensitivity to 6-kHz stimuli.

Device rearing did not appear to affect the frequency-response functions of neurons in regions of the optic tectum that represent peripheral space (Fig. 5, E and F). In both normal and device-reared owls, these neurons responded most strongly to frequencies below ~6 kHz and progressively more weakly to higher frequencies. The absence of device-induced changes in the frequency responses of these neurons, particularly for frequencies near 6 kHz, can be accounted for by the observation that in normal owls, when the device was inserted acutely, neurons tuned to peripheral locations could still be driven effectively by stimuli up to ~7 kHz (e.g., Figs. 8B and 9B). According to the hypothesis stated above, the maintained responsiveness of these neurons to these frequencies reflects the influence of maintained stimulus-driven activity in these frequency channels during the experience with the device.

FIG. 10. Adaptive adjustment of azimuth- (A and B) and elevation-response (C and D) functions in an owl raised with an early version of the acoustic device. Stimuli were either broadband (3–12 kHz) noise bursts or narrowband (1-kHz bandwidth) noise bursts centered on the given frequency. A and C: tested with the device removed. B and D: tested with the device reinserted. Arrows indicate visual RF location.

FIG. 11. Summary of the alignment of azimuth- (A) and elevation- (B) response functions with visual RF location in normal owls (○) and in device-reared owls with the device in place (● and ●). Diamonds represent data from the owl raised with an earlier version of the acoustic filtering device. “BBN” refers to a broadband (3–12 kHz) noise stimulus. All other stimuli were narrowband (1-kHz bandwidth) centered on the given frequency. “Open” (○) refers to location-response functions that were unbounded to the side indicated. Note that additional peaks from multi-peaked azimuth-response functions were not included.
level of the ICX. The possibility that the ICX might be a site of adaptive adjustment in response to hearing impairment is intriguing, because it has already been shown to be a site of adjustment in response to a very different sensory manipulation: raising owls with displacing prisms, which causes a shift in the auditory space map that matches the visual displacement imposed by the prisms (Brainard and Knudsen 1993; Knudsen and Brainard 1991).

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Present address and address for reprint requests: J. I. Gold, Dept. of Physiology and Biophysics, University of Washington Medical School, Box 357290, Seattle, WA 98195-7290.

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