Neural Maps of Interaural Time and Intensity Differences in the Optic Tectum of the Barn Owl

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This report describes the binaural basis of the auditory space map in the optic tectum of the barn owl (*Tyto alba*). Single units were recorded extracellularly in ketamine-anesthetized birds. Unit tuning for interaural differences in timing and intensity of wideband noise was measured using digitally synthesized sound presented through earphones. Spatial receptive fields of the same units were measured with a free field sound source.

Auditory units in the optic tectum are sharply tuned for both the azimuth and the elevation of a free field sound source. To determine the binaural cues that could be responsible for this spatial tuning, we measured in the ear canals the amplitude and phase spectra produced by a free field noise source and calculated from these measurements the interaural differences in time and intensity associated with each of 178 locations throughout the frontal hemisphere. For all frequencies, interaural time differences (ITDs) varied systematically and most strongly with source azimuth. The pattern of variation of interaural intensity differences (IIDs) depended on frequency. For low frequencies (below 4 kHz) IID varied primarily with source azimuth, whereas for high frequencies (above 5 kHz) IID varied primarily with source elevation.

Tectal units were tuned for interaural differences in both time *and* intensity of dichotic stimuli. Changing either parameter away from the best value for the unit decreased the unit's response. The tuning of units to either parameter was sharp: the width of ITD tuning curves, measured at 50% of the maximum response with IID held constant (50% tuning width), ranged from 18 to 82 μsec. The 50% tuning widths of IID tuning curves, measured with ITD held constant, ranged from 8 to 37 dB. For most units, tuning for ITD was largely independent of IID, and *vice versa*. A few units exhibited systematic shifts of the best ITD with changes in IID (or shifts of the best IID with changes in ITD); for these units, a change in the value of one parameter to favor one ear shifted the best value of the other parameter in favor of the same ear, i.e., in the direction opposite to that expected from "time–intensity trading." Overall sound intensity had little or no effect on ITD tuning, but did increase the best IIDs of units tuned to nonzero IIDs.

The tuning of units for ITD and IID changed systematically along different dimensions of the optic tectum to create coextensive, independent neurophysiological maps of ITD and IID. In the right tectum, the best ITD for driving units changed from left ear leading by 200 μsec in the caudal tectum to right ear leading by 25 μsec in the rostral tectum. For the same population of units, the best IID for driving units changed from right ear louder by 17 dB in the dorsal tectum to left ear louder by 19 dB in the ventral tectum. The best ITD and best IID of most units corresponded closely with the acoustically measured values of interaural time and intensity differences that resulted from a sound source in the center of each unit's spatial field. We conclude that the tuning of tectal units for ITD and IID is primarily responsible for their tuning for source location and that the maps of ITD and IID determine, in large part, the auditory map of space in the owl's optic tectum.

Auditory space is represented topographically in the optic tectum of several vertebrate species (Knudsen, 1982; King and Palmer, 1983; Middlebrooks and Knudsen, 1984; Wong, 1984; King and Hutchings, 1987). The auditory map is unique among sensory space maps in that it must be created by variations in the tuning of units for cues, such as interaural time differences (ITDs) and interaural intensity differences (IIDs), that are related only indirectly to the location of the stimulus. The correspondence of these cues with stimulus location arises from the physical properties of the head and ears: Interaural differences in the timing of sound are produced when the path lengths from the source to each ear are different; interaural differences in intensity result from acoustic shadows and reflections produced by the interaction of sound with the head and external ears. In nonmammalian vertebrates, ITDs and IIDs can also be produced by sound transmission through the head via an interaural canal (Chung et al., 1978; Hill et al., 1980; Feng and Shofner, 1981). Regardless of the mechanism that generates these cues, the values of ITD and of IID change in different and often irregular patterns with sound source location across space. Therefore, the existence of a physiological map of space in the optic tectum (or any other neural structure) predicts that the topography of representation of these cues is cue-specific and similarly irregular.
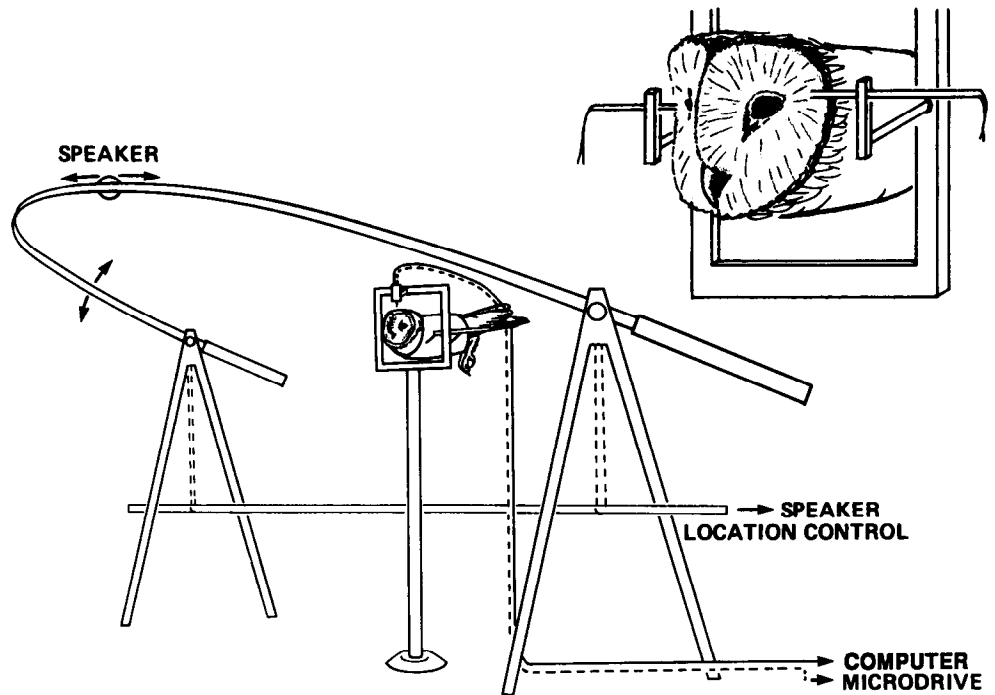
The binaural basis of the auditory space map has been partially explored in cats and in barn owls by testing units with sound stimuli presented through earphones (i.e., dichotically). Wise and Irvine (1985) demonstrated that, in cats, the tuning

Figure 1. Free field and dichotic presentation of sound. The owl was positioned at the center of the axis of rotation of a semicircular hoop which carried a loudspeaker. For free field presentation, the position of the speaker along the hoop's circumference and the elevation of the hoop (*double arrows*) was controlled and monitored remotely. For dichotic stimulation, miniature earphones were positioned in the ear canals (inset). The earphones were removed for free field stimulation.

of units for IID changes systematically from the rostral to the caudal end of the optic tectum (superior colliculus). Units located rostrally respond best when sound at the 2 ears is equal in intensity; units located more caudally respond best when sound is of greater intensity in the contralateral ear. Although the gradient of unit tuning for IID is consistent with the map of contralateral space that has been shown using free field stimuli (Middlebrooks and Knudsen, 1984), the correspondence of IID values to sound source locations was not measured. Moreover, the contribution of unit sensitivity to ITD to the auditory map of space has not been examined in cats.

For the barn owl as well, our current understanding of the acoustic basis of the tectal space map is incomplete. In the external nucleus of the inferior colliculus (ICx), which is the source of the auditory space map in the owl's optic tectum (Knudsen and Knudsen, 1983), units are tuned sharply for ITD and IID (Moiseff and Konishi, 1981). The tuning of units for ITD varies systematically across the nucleus and correlates with the progression in azimuth of unit receptive fields. Moreover, the tuning of units for ITD approximately matches the interaural delay (measured with microphones in the ear canals) resulting from a sound source centered in the units' receptive fields. Thus, azimuthal tuning and the map of source azimuth in the ICx are consistent with unit tuning for ITD. However, the contribution of IID tuning to the space map has not previously been determined.

In this study, we investigated the contribution of unit tuning for ITD and for IID to the auditory map of space in the owl's optic tectum. The correspondence of these binaural cues with locations in space was determined by presenting sounds from many different locations in the free field and measuring the consequent acoustic cues in the ear canals. Then we measured the tuning of tectal units for the location of the sound source in the free field and their tuning for ITDs and IIDs of sound presented directly to the ear canals. The results demonstrate that the tuning of tectal units for sound source location is largely the

result of their tuning for ITD and IID and that these binaural parameters are mapped along different dimensions of the optic tectum to create an auditory map of space.

Materials and Methods

Preparation. Data were collected from 5 barn owls (*Tyto alba*). During surgery, each owl was anesthetized with halothane and nitrous oxide. Immediately prior to a recording session, the owl was anesthetized with ketamine hydrochloride (20 mg/kg body weight) and tranquilized with diazepam (5 mg/kg). Anesthesia was maintained throughout the experiment with a continuous intramuscular infusion of ketamine hydrochloride (15 mg/kg/hr). A stainless-steel well was implanted in the skull over the right optic tectum to enable repeated recordings from the optic tectum over periods of weeks or months (Knudsen, 1984). The anesthetized owl was wrapped in a leather harness and suspended in a prone position inside a sound-isolation chamber equipped with earphones for dichotic stimulation and a movable loudspeaker for free field stimulation (Fig. 1).

Free field stimulation. The speaker movement system allowed the position of the speaker to be controlled remotely. The speaker moved on an imaginary sphere centered on the owl's head and at a distance of 92 cm (Fig. 1). The owl's head was positioned using retinal landmarks (the eyes of the barn owl are essentially stationary in the head) so that the median sagittal and visual planes were aligned with 0° azimuth and 0° elevation of the speaker movement system, respectively. The locations of auditory and visual stimuli are given in degrees to the left or right of the median sagittal plane (azimuth) and in degrees above or below the visual plane (elevation), measured at the center of the head. The properties of this double pole coordinate system have been described by Knudsen (1982).

Free field acoustic stimuli consisted of tone and noise bursts, 50 msec in duration, with rise/fall times of 5 and 0 msec, respectively. All stimulus waveforms were generated by a computer (sampling rate = 40 kHz) and a 12-bit digital-to-analog converter. Tones were generated by stepping through a sine look-up table. Broadband noise was generated from a pseudorandom noise function such that the amplitude of each sample was random and the distribution of sample amplitudes was uniform. The same noise waveform was used for all measurements.

The frequency response of the free field speaker, measured with a Bruel and Kjaer ½" condenser microphone (4165) located at the center of the chamber and a spectrum analyzer (Nicolet 660A), was flat to within ±4dB from 3 to 10 kHz. For tonal stimuli, the amplitude of

the input to the speaker was adjusted by the computer to produce the same sound pressure level across frequency.

Dichotic stimulation. Dichotic stimuli consisted of computer-generated broadband noise (see above) which was transduced by Knowles subminiature earphones (1914) coupled to damping assemblies (BF-1743). The amplitude of the signal in each channel was controlled with a programmable attenuator. Time delays between the channels were produced by computer-calculated shifts in the waveform of the signal: a fast Fourier transform of the signal followed by a phase shift (linear with frequency) and an inverse fast Fourier transform was used to generate look-up tables for 0, 5, 10, 15, and 20 μsec delays. Any specified delay with a 5-μsec step size could then be generated by shifting the waveform from one of the look-up tables by an integer number of samples (sampling period = 25 μsec).

Earphones were mounted on the ends of 15-cm lengths of stainless-steel tubing (2 mm diameter) which fit into guides on the stereotaxic frame (Fig. 1). Each earphone was oriented parallel to the long axis of the ear canal and was centered in the ear canal. The depth of insertion, as measured from the tip of the earphone assembly to the ruff–skin junction near the opening of the ear canal, was 5 mm; the distance from the tip of the earphone assembly to the lateral edge of the eardrum was approximately 10 mm. The dimensions of the earphone in cross section (2 mm × 3 mm) were small relative to the diameter of the ear canal (10 mm), which was not sealed.

The response characteristics of the earphones were measured under free field conditions using the ½″ condenser microphone and the spectrum analyzer. The frequency response of each earphone was flat to within ±2 dB from 4 to 10 kHz. Below 3 kHz, the acoustic output of the earphones decreased by 16 dB per octave. Interearphone differences in the timing and intensity of the transduced signal were less than 3 μsec and 2 dB between 4 and 12 kHz. The dynamic response of the earphones was linear to within 0.2 dB over a 45 dB range of input amplitudes, including the highest input amplitudes used in this study.

Interaural differences in time and intensity produced by the earphones in the ear canals were determined from bilateral cochlear microphonic (CM) recordings. We used CM recordings rather than probe tube measurements because the CMs can show the effect of sound transmission through the interaural canal and because the presence of both probe tubes and earphones in the ear canals affected ear canal resonances. CM potentials were recorded from the round windows with silver ball electrodes. The shank of each electrode was secured to the skull, and the bullae were sealed with cyanoacrylate glue and dental cement. Left and right CMs were calibrated by delivering continuous tones at frequencies from 2 to 12 kHz (in 1 kHz steps) separately to each ear through the earphones. For each ear, the attenuator settings required to reach a standard, nonsaturated CM response at each frequency were recorded. The results indicated that for frequencies between 4 and 12 kHz the gain of the right ear was 3 dB greater than that of the left ear. The calibration was confirmed by a comparison of CM and probe tube measurements of the IID spectrum produced by a free field stimulus (see below).

With the earphones in the standard position, continuous broadband noise was delivered dichotically with nominal ITD = 0 μsec and nominal IID = 0 dB. ITDs were calculated from phase difference spectra. The CM data show that actual ITDs corresponded closely with their nominal values between 4 and 10 kHz: between 4.2 and 10 kHz, actual ITDs remained within ±10 μsec of their nominal values (Fig. 2A).

IIDs produced by the same dichotic stimulus were measured from bilateral CM recordings, calibrated as described above. Between 4 and 10 kHz, actual IIDs changed gradually over a 6 dB range, exceeding their nominal values by 0–6 dB in favor of the right ear (Fig. 2B). Between 5.5 and 7.5 kHz, a range that includes the best frequencies of 75% of tectal units, nominal 0 dB IID corresponded to right ear louder by approximately 3 dB.

To assess the error produced by variability in the placement of the earphones, time and intensity difference spectra were measured from bilateral CM recordings for 2 different positions of the earphones. After the difference spectra were measured with the earphones in their normal position, the right earphone was withdrawn 1.0 mm (a noticeable misalignment) and the measurements were repeated. Moving the right earphone out caused a 3 μsec delay and a 0–2 dB decrease in the amplitude of the right ear CM for frequencies between 4 and 10 kHz. In practice, the earphones could be withdrawn and replaced with an error of less than ±0.5 mm. Thus, errors in ITD and IID produced by earphone placement are less than 3 μsec and 2 dB, respectively.
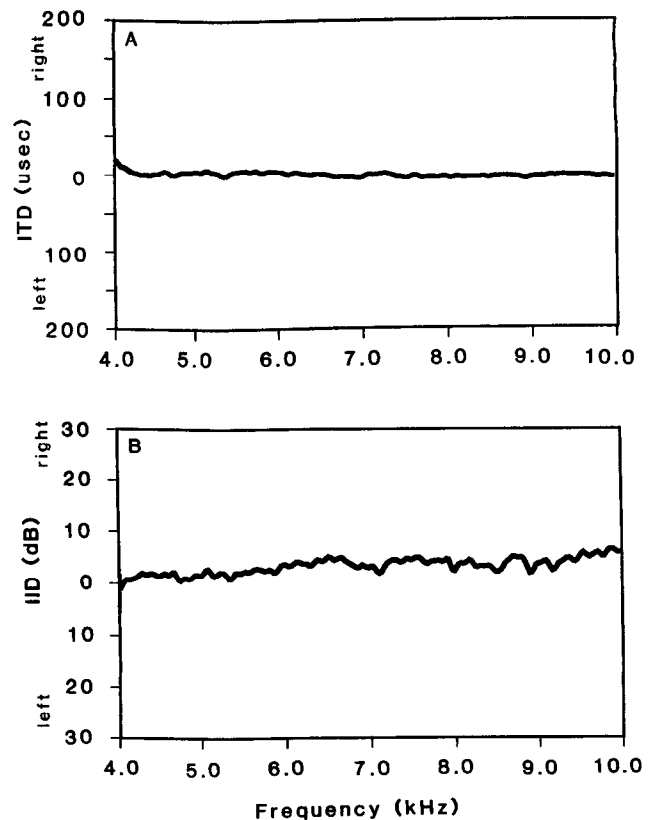
Figure 2. Interaural differences in time (*A*) and intensity (*B*) as a function of frequency produced by a dichotic stimulus with nominal ITD = 0 μsec and nominal IID = 0 dB. The data are based on bilateral recordings of the CM. Time differences between the CM responses on the left and right sides were calculated from the phase difference spectrum. IIDs were calculated by subtracting the amplitude spectrum of the left CM from that of the right CM. CM amplitude was calibrated as described in Materials and Methods. "Left" and "right" designate the ear for which sound is leading (*A*) or louder (*B*). Data for frequencies below 4 kHz are not presented since sound transmission through the interaural canal at these low frequencies (Fig. 3; Hill et al., 1980; Rosowski and Saunders, 1980; Calford, 1988) causes actual ITDs and IIDs of dichotic noise to deviate substantially from their nominal values.

Unilateral recordings of the cochlear microphonic responses were used to determine the acoustic separation of the ears during dichotic stimulation. Acoustic separation sets limits on the maximum IIDs that can be delivered dichotically. With the earphones in position, continuous tones at frequencies from 2 to 10 kHz were delivered to each ear in turn. We recorded the amplitude of each tone necessary to produce a standard, nonsaturated CM response. To calculate the acoustic separation at each frequency, the sound amplitude in dB SPL needed to produce the standard CM response from stimulation of the ipsilateral ear was subtracted from that for the contralateral ear. Acoustic separation was frequency dependent (Fig. 3). At low frequencies, sound propagates readily from the earphone to the opposite ear. The maximum acoustic separation was 34 dB and occurred for frequencies between 6 and 10 kHz.

Ear directionality. Interaural differences in time and intensity produced by free field noise were measured to determine the range of binaural cue values normally available to the owl and the dependence of these values on the location of the source. The noise broadcast from the speaker was recorded in each ear canal with probe tubes (length = 35 mm, internal diameter = 0.5 mm), fitted to ½″ Bruel and Kjaer microphones. The probe tubes were inserted into the ear canals and fixed at the usual positions of the earphones as described above. Difference spectra for interaural phase and interaural intensity were calculated using the spectrum analyzer and were corrected for differences
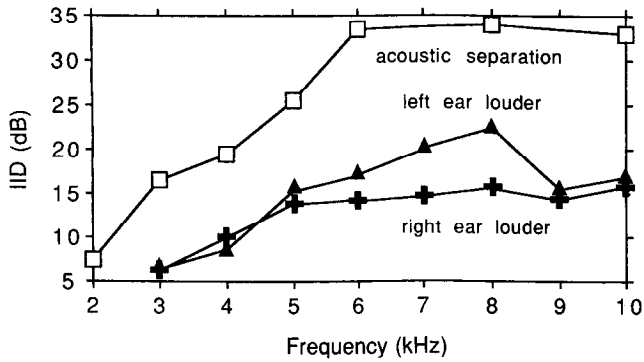
Figure 3. Maximum IIDs produced by sound presented under dichotic (*open squares*) and free field (*filled triangles, crosses*) conditions as a function of frequency. The acoustic separation of the ears (*squares*) during dichotic stimulation was determined from unilateral recordings of CM responses to tones delivered through the earphones (see text). IID spectra produced by a free field noise at each of 129 sound source locations were measured using probe tubes in the ear canals. The source locations used formed a regular array across the region of space represented in the right optic tectum (from L80° to R20° of azimuth and from −80° to +80° of elevation, in 10° steps). For each IID spectrum, IID values were averaged over ⅓ octave bands for center frequencies from 3 to 10 kHz. For each center frequency, the maximum IID for sound louder in the left ear (*filled triangles*) and for sound louder in the right ear (*crosses*) was defined as the largest ⅓ octave IID value of all 123 sound source positions.

between the probe tubes. Difference spectra were taken for 178 speaker positions in the frontal hemifield (L80° to R80° azimuth, −80° to +90° elevation, in 10° steps).

To allow a comparison of ITDs and IIDs produced by dichotic stimulation (measured with the calibrated CMs) with ITDs and IIDs produced by free field stimulation (measured with the probe tubes), the IID spectrum produced by a free field noise source at 0° azimuth, 0° elevation was measured with the CMs and with the probe tubes. ITD and IID spectra measured with both methods had a similar shape (frequency dependence), and differed by less than 10 μsec and 2 dB, respectively, between 4 and 10 kHz.

Visual stimulation. Visual stimuli consisted of slits of light from an ophthalmoscope that were projected onto a portable translucent hemisphere (radius = 57 cm) placed in front of the owl. Borders of visual receptive fields were defined by the stimulus locations where the visual stimulus produced an increase in the unit's discharge rate. Receptive field borders were recorded on the hemisphere, which was aligned with the speaker coordinate system and marked in degrees of azimuth and elevation. The hemisphere was removed for acoustic measurements.

Recording and analysis of unit data. To record from the optic tectum, electrodes were positioned stereotaxically and advanced through the forebrain. Because of the curvature of the tectal surface, the vertical penetrations used in this study usually passed through the tectal layers obliquely and intersected each tectal layer twice (see Fig. 13B). A characteristic bursting pattern of spontaneous activity signaled the entry of the electrode into the superficial cell layers of the tectum. In deeper layers, these "bursty" units were replaced by units that had sustained or transient responses, as described by Knudsen (1982, 1984). The stimulus used to search for each successive unit in a penetration was a free field noise at the optimal location for the previously recorded unit.

Action potentials from single units or clusters of 2–3 units were recorded extracellularly with insulated tungsten wire microelectrodes or with glass micropipettes filled with 3 M NaCl. Action potentials in the filtered signal were converted into uniform pulses by a level discriminator. The computer recorded the number and timing of action potentials for the 100 msec preceding and the 100 msec following the onset of a stimulus and constructed pre- and poststimulus time histograms for 10–15 repetitions of each stimulus condition (see below). Unit responses to each stimulus condition were quantified by subtracting the total spikes in the prestimulus periods from the total in the poststimulus periods.

The tuning of tectal units to sound location was measured by counting

spike discharges to noise bursts presented from various locations in space and at 20 dB above the unit's threshold. Unit thresholds were measured by stepping stimulus amplitude in 5 to 10 dB steps with the speaker located where the response was maximal (as determined from an audiovisual scan of the unit's responses to various speaker locations) and were later confirmed once quantitative data had been taken. Unit responses were sampled for speaker positions every 5° in azimuth and every 5–10° in elevation across the unit's auditory receptive field. The region of space from which presentation of a sound elicited greater than 50% of the maximum response was defined as the best area of the unit. A unit's best azimuth and best elevation were defined by the center of the best area.

The tuning of tectal units to stimulus frequency was measured by presenting tone bursts with the speaker at the center of the best area. The frequency of the tone burst was varied from 2 to 10 kHz in 1-kHz steps, in random order and at 20 dB SPL above the neuron's threshold to noise. The series of tone bursts was repeated 15 times, and the responses were summed to generate a frequency-spike count function. The best frequency was calculated as a weighted average (see below) of the frequency-spike count function. The bandwidth of the frequency-spike count function was determined from the frequencies at which the response dropped to (or below) the spontaneous level.

To measure the selectivity of unit responses for ITD, the timing of the waveform in one channel was delayed in steps of 10 to 50 μsec with IID held constant. Fifteen series of stimuli were presented; within each series, the order of the ITD values was randomized. To measure unit tuning to IID, IID was varied from left ear louder to right ear louder in 4, 6, or 10 dB steps, with ITD and average binaural intensity held constant. Average binaural intensity was defined as the algebraic sum of sound intensities in the left and right ears divided by 2. The series of IIDs was repeated 15 times. For most units, ITD and IID spike count functions were measured at 2 or more average binaural intensities.

Best ITDs, best IIDs, and best frequencies were calculated as weighted averages of ITD-, IID-, and frequency-spike count functions, from which spontaneous discharges had been subtracted, by the formula: Best value = $\Sigma(V_i \cdot R_i)/\Sigma(R_i)$, where V_i is the value of the stimulus parameter (μsec, dB, or kHz) and R_i is the spike count of the ith measurement. Responses less than 25% of the maximum response were not included in the calculation of weighted averages. Responses to nominal IIDs greater than 30 dB were not included in the calculation of best IIDs because of acoustic cross-talk at these large IID values (Fig. 3). The best IID was calculated at the 75% response level for the few units that continued to respond at the 25% level beyond 30 dB IID. Best IIDs were shifted 3 dB in favor of the right ear to compensate for the difference between nominal and actual IIDs (Fig. 2B).
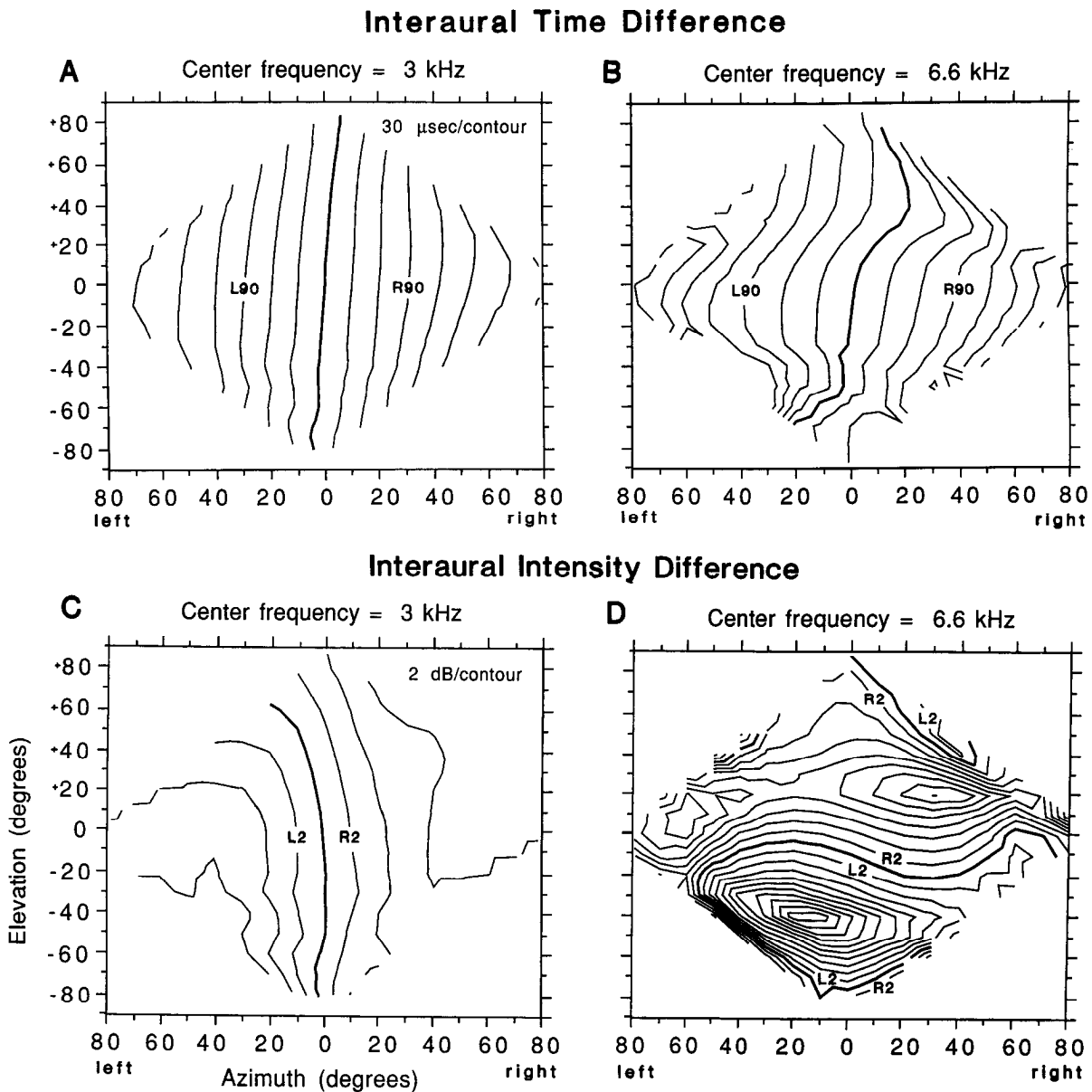
Histology. In one owl (owl 5), 2 vertical penetrations through the optic tectum were marked with small electrolytic lesions which were made by passing 10 μamps of current through a tungsten electrode for 30 sec. Two days later, the owl was deeply anesthetized with pentobarbitol sodium and perfused through the heart with fixative (10% formal-saline). The brain was blocked and sectioned in the transverse plane. The sections were stained with cresyl violet.

Results

Interaural differences in time and intensity produced by a free field noise source

Probe tube measurements of interaural differences in time and intensity that result from a free field noise source reveal the range of interaural cue values experienced by the owl and their pattern of change across space. For a given location of the sound source, ITDs and IIDs depend on the frequency of the stimulus; for a given frequency, ITDs and IIDs vary with the location of the sound source (Fig. 4). The spatial patterns of ITDs at frequencies between 2 and 10 kHz indicate a nearly linear variation of ITD with the azimuth of the sound source (Fig. 4, A, B). At frequencies below 4 kHz, ITD varies with azimuth only. At higher frequencies, ITD also varies with elevation, but this variation is smaller and less systematic than the variation of ITD with azimuth.

IIDs vary both with the azimuth and with the elevation of the source, and the spatial pattern of IIDs changes markedly

Interaural Time Difference

A Center frequency = 3 kHz **B** Center frequency = 6.6 kHz

Interaural Intensity Difference

C Center frequency = 3 kHz **D** Center frequency = 6.6 kHz

Figure 4. Interaural differences in time (*A, B*) and intensity (*C, D*), versus the position of a free field noise source. Interaural difference spectra were measured for each of 178 source directions which formed a regular array across the frontal hemifield. "Left" and "right" indicate source directions relative to the median sagittal plane; positive and negative values of elevation indicate source directions above and below the horizontal plane. Source directions are given in double pole coordinates. For this coordinate system, the sum of the coordinates of any one point is always ≤90°. Lines are iso-ITD and iso-IID contours based on averages of ITDs or IIDs over ⅓ octave bands centered on 3 kHz (*A, C*) and on 6.6 kHz (*B, D*). Bold contours indicate 0 μsec ITD (*A, B*), and 0 dB IID (*C, D*). Labeled contours in *A* and *B* represent sound leading by 90 μsec in favor of the left ear (L90) or the right ear (R90); in *C* and *D*, labeled contours represent sound louder by 2 dB in favor of the left ear (L2) or the right ear (R2).

with frequency. At 3 kHz, for example, IIDs vary primarily with source azimuth. Sound intensity is greater in the right ear when the source is located to the right of the midsagittal plane and greater in the left ear when the source is located to the left. In the region of space directly in front of the owl (within 30° of the visual axes), lines of iso-IID are oriented nearly vertically, a pattern which is typical for frequencies below 4 kHz (Fig. 4C). At higher frequencies, the locations where IID is maximal move frontally, the rate at which IID changes with source location increases, and IID becomes increasingly dependent on source elevation (Fig. 4D). In the region of space between the 2 IID maxima, iso-IID contours are nearly horizontal. Thus, over this

frontal region of space, IIDs at high frequencies change from left ear louder to right ear louder as the sound source ascends but change little with source azimuth. This dependence of IIDs at high frequencies on source elevation is a consequence of the vertical asymmetry of the owl's external ears (Payne, 1971; Knudsen and Konishi, 1978).

In this study we recorded from the right optic tectum. The range of IIDs that result from sound sources in the area of space represented in the right optic tectum, i.e., from L80° to R20° and from −80° to +80°, was determined by averaging IID values over one-third octave bands for center frequencies from 3 to 10 kHz. In general, the larger IIDs occurred at the higher frequen-

A

B
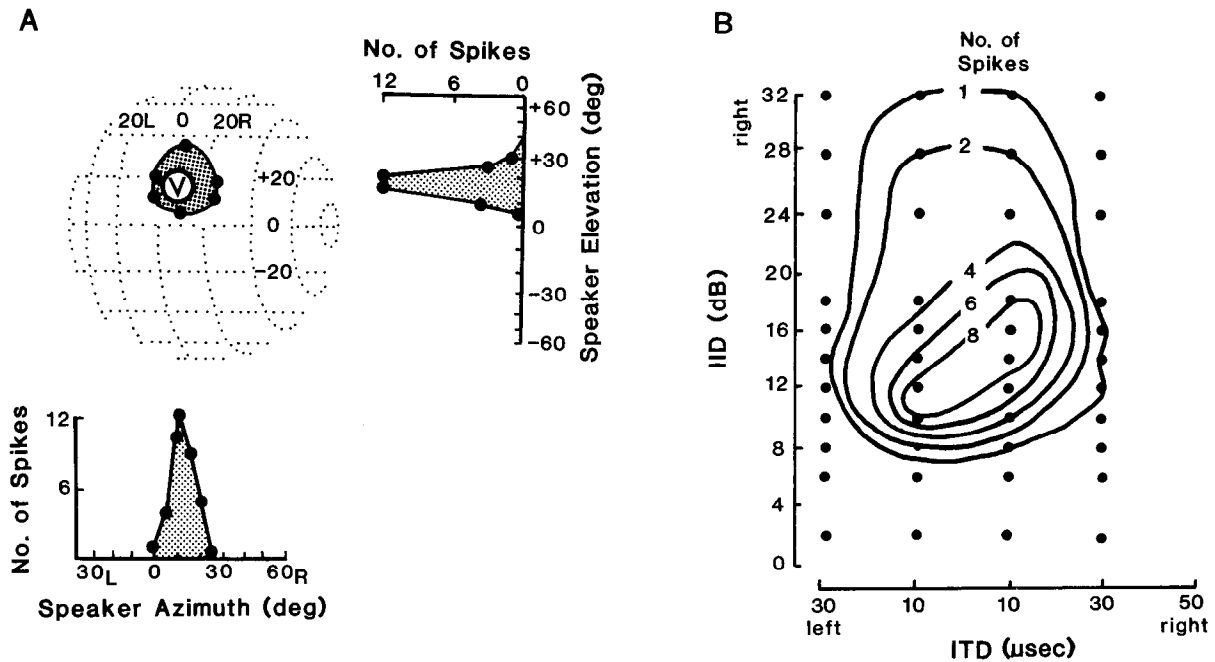
Figure 5. Free field (*A*) and dichotic (*B*) tuning of a tectal unit. *A*, Unit's visual (*V*) and auditory (*stippled*) receptive fields are shown on a globe which represents stimulus locations measured relative to the center of the owl's head. The globe is marked with lines of azimuth and elevation separated by 20° intervals. Visual stimuli consisted of bars of light rear-projected onto a curved screen. Auditory stimuli consisted of bursts of broadband noise presented from a free field speaker. The effect of varying source azimuth and source elevation on the unit's response is shown below and to the right, respectively. Unit tuning to source azimuth was measured with the source at the unit's best elevation (+18°); tuning to source elevation was measured with source at the unit's best azimuth (R13°). Spike counts are summed responses to 10 repetitions of the stimulus. *B*, Response of the same tectal unit to dichotic stimulation as ITD and IID was varied. *Lines* are iso-response contours based on the total number of spikes produced by 10 repetitions of the dichotic noise for each of 44 combinations (*points*) of ITDs and IIDs. The best ITD of the unit was 0 μsec; the best IID was 15 dB right ear louder.

cies (Fig. 3). The maximum IIDs for this region of space were 22 dB left ear louder for a center frequency of 8 kHz, with the source located at L30°, −30°, and 17 dB right ear louder for a center frequency of 8 kHz with the source located at L40°, +10°.

Spatial tuning

When stimulated with free field noise bursts, tectal units responded best when the speaker was located within a particular area of space (Fig. 5*A*). Best areas were measured at 20 dB above threshold for 35 single units and for 79 clusters of 2 or 3 units. The average best area for the single unit data was 18.3 ± 4.6° wide (mean ± SD) and 31.7 ± 11.8° high.

Most tectal units (81 of 91 sites tested) responded both to visual and to auditory stimuli. Visual receptive fields were much smaller than auditory best areas (Fig. 5*A*). Visual receptive fields and auditory best areas always overlapped, and their centers were approximately aligned. The alignment of visual receptive fields and auditory best areas was most precise for units that had visual receptive fields within 10° of the visual axes (straight ahead).
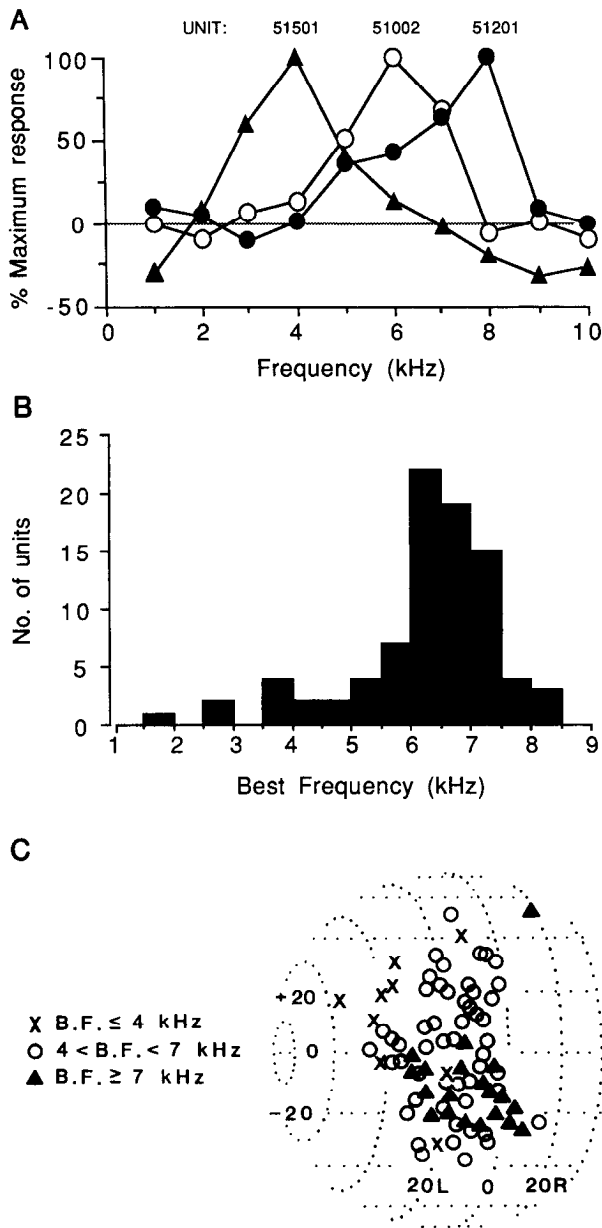
Frequency tuning

The frequency tuning of units at 85 sites was measured by presenting tone bursts from the free field speaker at the center of each unit's best area. We assume that, with free field stimulation, ITD and IID at each frequency were close to the optimal values for the unit. Units were broadly tuned to stimulus frequency (Fig. 6*A*). Quality factors, calculated by dividing the widths of frequency-spike count functions (see Materials and Methods)

by the best frequency, ranged from 0.3 to 5.3 (1.4 ± 0.6). Best frequencies of tectal units ranged from 1.5 to 8.5 kHz (median = 6.4 kHz); 75% had best frequencies between 5.5 and 7.5 kHz (Fig. 6*B*). With one exception, units that had the highest best frequencies had best area centers that were located out to 35° of azimuth, between +5° and −25° of elevation (Fig. 6*C*). Units with the lowest best frequencies had best area centers located peripherally. These data confirm previous studies that show that the best frequency of tectal units varies topographically (Knudsen, 1984).

Dichotic tuning

Once a unit's best area had been determined, the earphones were placed in the ear canals and broadband noise was presented dichotically. Auditory units at all but 6 of 125 recording sites responded to the dichotic stimulus. Of the units that responded, all but 2 were tuned for ITD (the response was a nonmonotonic function of the stimulus parameter), and all but 3 were tuned for IID. Thus, nearly all tectal units were tuned for *both* ITD and IID, as shown by the unit in Figure 5*B*.

Interaural time and interaural intensity differences were varied independently until the largest response was obtained. The values of ITD and IID that produced the largest response, as determined from the weighted average of the response at a particular average binaural intensity (see Materials and Methods), are called the best ITD and the best IID, respectively. The best ITD and the best IID varied from unit to unit. In the right optic tectum, best ITDs and best IIDs measured at 20 dB above the

A

B

C

X B.F. ≤ 4 kHz
O 4 < B.F. < 7 kHz
▲ B.F. ≥ 7 kHz

Figure 6. Frequency tuning of tectal units. *A*, Frequency-spike count functions for 3 representative single units. The best frequencies of these single units were 3.8, 6.2, and 7.7 kHz, respectively. Negative values indicate responses that were less than the spontaneous rate. *B*, Distribution of best frequencies of tectal units at 82 recording sites. *C*, Distribution of unit best frequencies as a function of unit best area center, plotted in double pole coordinates. Each symbol represents unit properties at one recording site. For the purpose of this illustration, units were divided into 3 groups according to their best frequency, as shown in the key.

unit's threshold, ranged from L200 to R25 μsec and from L19 to R17 dB, respectively.

Tectal units responded strongly to the dichotic stimulus. For 34 single units, the response to dichotic noise at the best ITD and the best IID was compared to the response to free field noise presented at the center of the best area. For both dichotic and free field stimuli, the intensity was fixed at 20 dB above the unit's threshold. For all but one of these units, the response

A

B
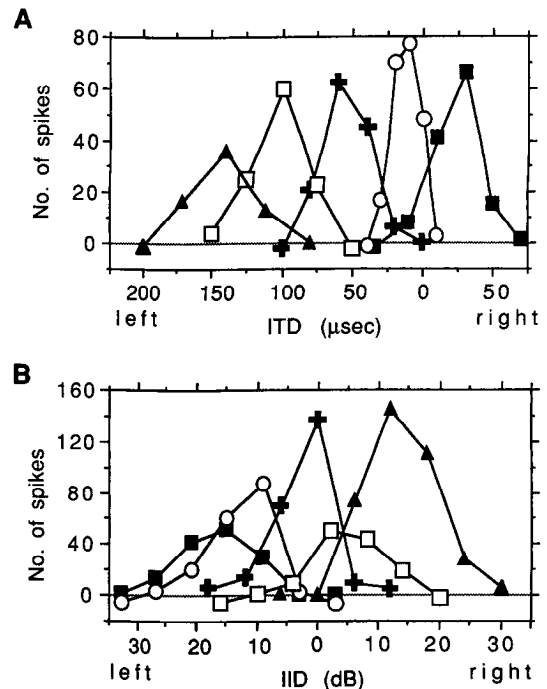
Figure 7. Tuning of 5 representative units to ITD (*A*) and to IID (*B*). The total number of spike discharges to 15 repetitions of each stimulus condition is shown. ITD-spike count functions were measured at the unit's best IID; IID-spike count functions were measured at the unit's best ITD.

magnitude to dichotic and to free field stimuli differed by less than 10%.

Tectal units responded to dichotic noise only when ITD and IID were within particular ranges (Figs. 5*B*; 7; 8, *A*, *B*). Of 34 single units stimulated with dichotic noise at 20 dB above threshold, 22 (65%) responded only when ITD was within ±40 μsec of the best ITD and when IID was within ±15 dB of the best IID. For these 34 units, the tuning widths of ITD tuning curves, measured at 50% of the maximum response (50% tuning width), ranged from 18 to 82 μsec (40.1 ± 16.1 μsec; Fig. 8*C*); 50% tuning widths of IID tuning curves ranged from 8 to 37 dB (15.4 ± 6.6 dB; Fig. 8*D*).

Mutual independence of ITD and IID tuning

To determine the effect of changing one dichotic parameter on unit tuning to the other, IID tuning curves for 11 single units were measured at 2 or more values of ITD (separated by 20–160 μsec), and ITD tuning curves for 8 single units were measured at 2 or more values of IID (separated by 4–23 dB). The direction in which the best IID shifted (for all units that showed a shift) depended on the direction in which ITD was changed; changing ITD in favor of one ear shifted the peak of the IID tuning curve in favor of the same ear (Fig. 9*A*), i.e., in the direction opposite to that expected for time–intensity trading (David et al., 1959; Hall, 1965). The same direction of shift was found for the complementary experiment in which shifts in best ITDs were measured (Fig. 9*B*). The dependence of IID tuning on ITD (and of ITD tuning on IID), however, was limited by the narrow ranges of ITDs and IIDs to which the neuron would respond (Fig. 5*B*): shifts in best IID with a change in ITD equal to the 50% tuning width of the unit's ITD tuning curve ranged from 0 to 8 dB (3.7 ± 2.6 dB). Shifts in best ITD with a change
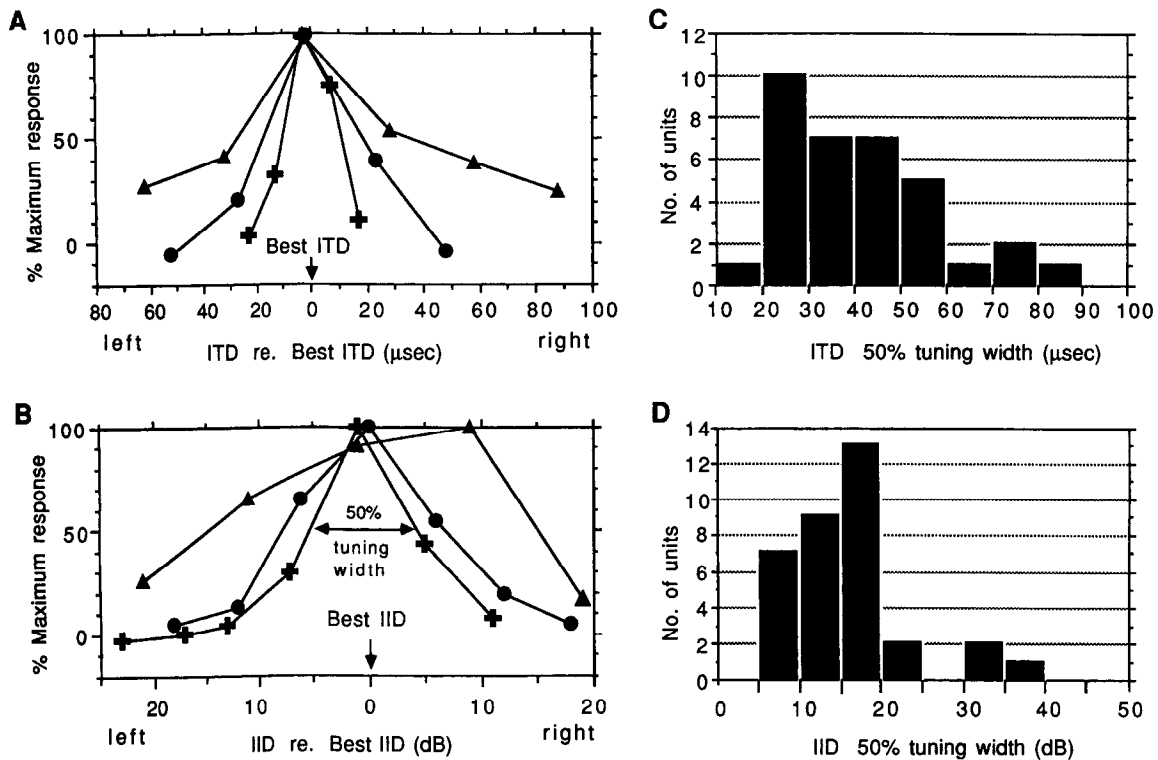
Figure 8. Sharpness of tuning of tectal units to ITD (*A, C*) and to IID (*B, D*). *A*, ITD-spike count functions for 3 single units selected from among the median 10% (*circles*), the broadest 10% (*triangles*), and the narrowest 10% (*crosses*). *B*, IID-spike count functions for 3 representative single units chosen as described above. All spike count functions are normalized to the maximum response and are aligned according to the unit's best ITD or best IID. The distributions of 50% tuning widths of ITD- and IID-spike count functions for 34 single units, measured as indicated by the *double arrow* in *B*, are shown in *C* and *D*, respectively.

in IID equal to the 50% width of the unit's IID tuning curve ranged from 0 to 27 μsec (7.9 ± 8.0 μsec). For most units, these shifts were relatively small compared to unit 50% tuning widths: the shifts in best IID or best ITD were, on the average, 22% of the 50% tuning widths of IID and ITD tuning curves; 13 of the 19 units showed shifts of 20% or less, whereas 6 units showed shifts greater than 20%.

Influence of average binaural intensity on neural tuning to ITD and IID

To determine the effect of increasing the average binaural intensity on the width of dichotic tuning curves, the 50% tuning widths of ITD and IID tuning curves were measured at 20 and at 40 dB above threshold for 31 single units. Increasing the average binaural intensity from 20 to 40 dB above threshold had a small but significant effect on the sharpness of tuning to ITD and IID (Fig. 10, *A–D*): on the average, the 50% tuning width for ITD decreased 3.7 μsec ($p = 0.01$; two-tailed, paired *t* test; Fig. 10*A*), whereas the 50% tuning width for IID increased 3.6 dB ($p = 0.0003$; Fig. 10, *B–D*).

Best IIDs of some units were affected by changes in average binaural intensity (Figs. 10, *C, D*; 11*B*), whereas best ITDs generally were not (Figs. 10*A*, 11*A*). Increases in average binaural intensity shifted the best IID towards the favored ear. For units that were tuned to IIDs smaller than 5 dB, however, the shift in best IID was small (0–3 dB; Figs. 10*B*, 11*B*). For 10 of the 26 single units that showed a shift, the shifts in best IID were caused primarily by a translation of the curve along the IID axis (Fig. 10*C*). For most ($n = 16$) units, however, the

shift in best IID was caused primarily by an asymmetric broadening of the IID tuning curve (Fig. 10*D*) such that the cutoff at large IIDs shifted to larger values and the cutoff closer to 0 dB IIDs was relatively unaffected.

Covariation of dichotic and free field tuning

The tuning of neurons to dichotic stimulus parameters was compared to their tuning to free field sound (Fig. 12). The data show that best ITD correlates strongly and positively with best azimuth (Fig. 12*A*) but correlates only weakly with best elevation (Fig. 12*C*). Conversely, best IID is a function of best elevation (Fig. 12*D*) but correlates weakly with best azimuth (Fig. 12*B*).

The relationship between best ITD and best azimuth is linear over the sampled range of best azimuths (L55° to R18°). Although the correlation of best ITD with best azimuth holds for all of the sampled space, the correlation is stronger when units with best elevations within a limited range are considered, owing to the weak correlation of best ITD with best elevation (Fig. 12*A*). The data set was divided into 2 complementary subsets: the first contained data from units that had best elevations above +10°, and the second contained data from units that had best elevations at or below +10°. The slope of the regression line for one subset was not significantly different from that of the other ($p > 0.1$). However, best ITDs of units tuned to low elevations were shifted towards right ear leading relative to best ITDs of units tuned to high best elevations. The weak dependence of best ITD on best elevation is also apparent from the negative slope of the data in Figure 12*C*. These data indicate that the tectal axis representing iso-best ITDs is oblique to the axis rep-

resenting iso-best azimuths, as predicted from the orientation of iso-ITD contours across space (Fig. 4B).

The relationship between best elevation and best IID is monotonic only between −25° and +20° of best elevation, which is consistent with the spatial pattern of IIDs for high frequencies (Fig. 4D). The plateaus of best IIDs for high and low best areas indicate that best area locations of units that have high or low best areas are not uniquely specified by their tuning to IIDs, as supplied by the broadband dichotic noise (Fig. 12D).

Map of auditory space

Best area locations changed systematically with the position of the recording site in the tectum, confirming the map of auditory space reported previously (Knudsen, 1982; Fig. 13, A–C): As the electrode traversed the tectum from dorsal to ventral, the best elevations of units progressed systematically from high to low (Fig. 13C), whereas the best azimuths remained relatively constant. Penetrations placed rostrally within the tectum encountered units with best azimuths located frontally, whereas penetrations placed more caudally encountered units with best azimuths located further contralaterally (Fig. 13, A, C). Our sample of the auditory space map consisted of recordings from 35 single units and 85 clusters of 2 or 3 units. Best azimuths ranged from 55° contralateral to 18° ipsilateral, and best elevations ranged from +56° up to −65° down.

Maps of binaural parameters

Maps of best ITD and best IID in the optic tectum were derived by positioning the best ITD or best IID for each unit on a flattened representation of the tectal surface according to the location of the unit's visual or auditory receptive field (Fig. 14, A, B) using the tectal maps of visual and auditory space (Knudsen, 1982). Wherever possible, visual rather than auditory receptive fields were used, since visual receptive fields are more precise indicators of recording site location within the tectum (Knudsen, 1982). The accuracy of this method was verified by electrode tract reconstructions (Fig. 13B). Best ITDs and best IIDs varied systematically across independent axes of the optic tectum: best ITDs varied primarily along the rostrocaudal axis, whereas best IIDs varied primarily along the dorsoventral axis (Fig. 13D). Contour lines of iso-best ITD are oriented dorsoventrally, almost parallel to lines of iso-best azimuth (Fig. 14A). The relative orientations of the lines of iso-best ITD and of iso-best azimuth are reflected in the relationship between ITD and source azimuth at high frequencies (Fig. 4B). Contour lines of iso-best IID are oriented rostrocaudally, in general (Fig. 14B). The topography of best IID representation in the tectum is strikingly similar to the pattern of IID variation across space for high frequencies (Fig. 4D).

Discussion

The auditory space map in the optic tectum, or superior colliculus, consists of units tuned for sound source location organized systematically according to the locations of their best areas (Knudsen, 1982; King and Palmer, 1983; Middlebrooks and Knudsen, 1984; Wong, 1984; King and Hutchings, 1987). We have shown that in the owl the spatial tuning of these units is consistent with their sensitivity to interaural differences in time and intensity, and that the map of space can be explained by the systematic representation of these binaural parameters across the tectal surface. This is an example of a coextensive mapping of different categories of binaural cues.
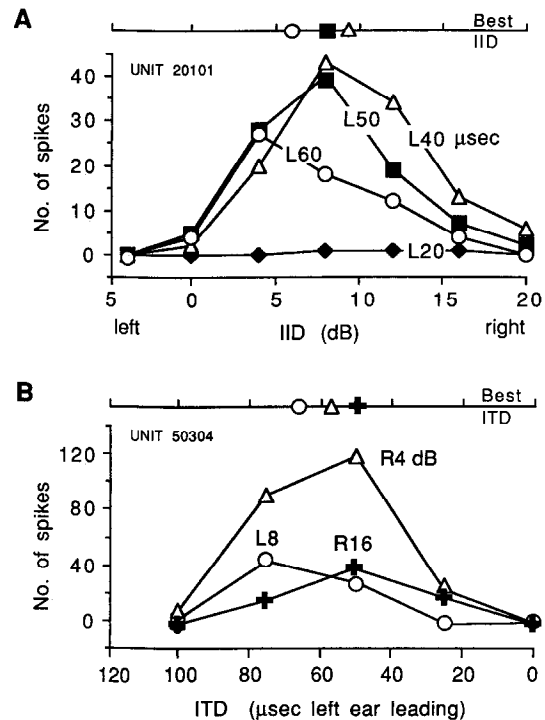

Figure 9. Interdependence of IID and ITD tuning for 2 tectal units (units 20101 and 50304). The symbols above the graphs indicate "best" IID (A) and "best" ITD (B) calculated for each curve. A, Effect of changing ITD on the tuning of a single unit to IID. When the lead of sound to the left ear was increased, the peak response shifted towards left ear louder, as shown. The unit's tuning to IID was measured at the best ITD (L40 μsec) and at 3 other values of ITD (L20, L50, and L60 μsec). The maximum response was attained only at the best ITD, regardless of the IID. B, Effect of changing IID on tuning to ITD for another single unit. The unit's tuning to ITD was measured at 3 different values of IID as indicated, including the best IID (R4 dB). When the IID was changed to favor the left ear, the peak response shifted towards larger left ear leads. The direction of the shift in the peak response to one parameter with changes in the other parameter was the same for all units that showed an interdependence of ITD and IID tuning (see text). However, for all units, the maximum response occurred for only one combination of ITD and IID.

Cues for auditory spatial analysis

Potential cues for sound localization include those available at each ear (monaural cues) as well as those that require binaural comparison. Monaural cues arise because ear directionality varies with frequency, and as a result the monaural spectrum (the pattern of intensity variation across frequency) will vary with the location of a sound source. The monaural spectrum is used by the human auditory system to localize sources in elevation (Gardner and Gardner, 1973; Hebrank and Wright, 1974; Humanski and Butler, 1988). The sensitivity of tectal units to this cue has not yet been tested.

Binaural cues are more reliable than monaural cues. The accurate interpretation of monaural cues requires assumptions about the free field amplitude spectrum of the stimulus—i.e., requires that the sound and the acoustic environment be familiar. Binaural cues, however, are based on interaural differences, and therefore their interpretation requires only that the auditory system be calibrated to the acoustic properties of the head and ears. This is perhaps the reason why binaural cues are the principal basis of the auditory space map in the tectum.

Figure 10. Dichotic tuning curves for 4 single units (*A–D*) measured at 2 different average binaural intensities as indicated in *D. A*, Tuning of this unit to ITD, like that of most units, was largely insensitive to changes in average binaural intensity. *B*, For this unit, increasing the average binaural intensity from 20 to 40 dB above threshold broadened the IID tuning curve slightly but had no effect on the best IID, as was typical of units tuned to IIDs near 0 dB. *C, D*, For these 2 units, increasing average binaural intensity broadened the IID tuning curve and shifted the best IID towards larger values (in favor of the dominant ear). For some units, as illustrated in *C*, the intensity-dependent increase in the best IID was due to a translation of the curve along the IID axis. However, for most units, as exemplified by the unit in *D*, increasing the average binaural intensity led to an asymmetric broadening of the IID tuning curve such that the unit's sensitivity to large IID values increased, whereas the unit's sensitivity to small IID values remained relatively unaffected.
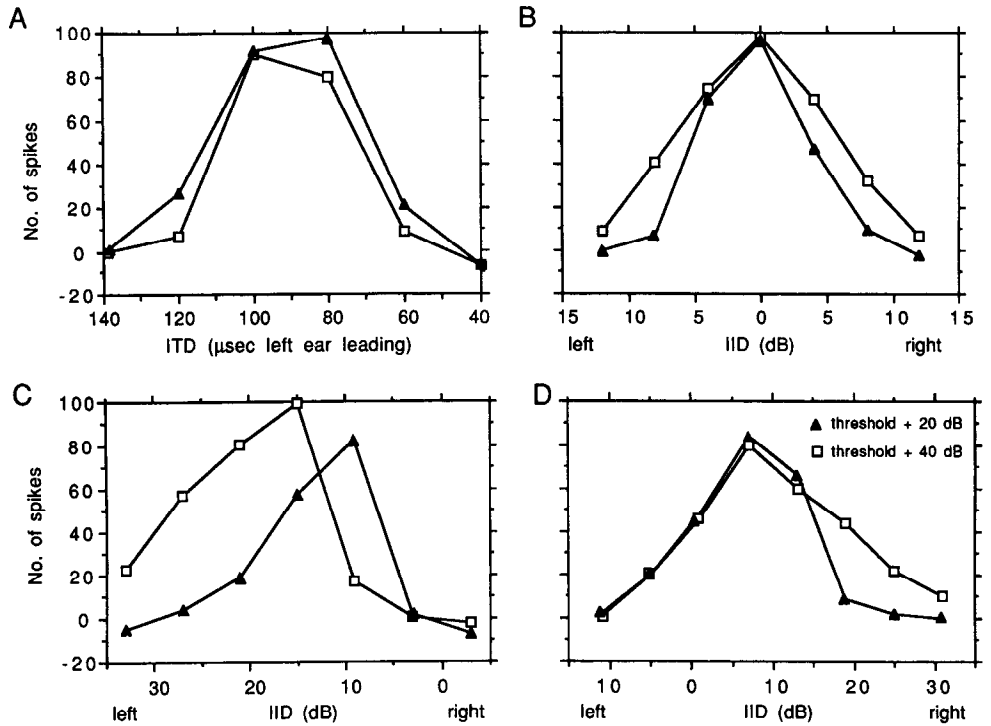

Importance of frequency-specific spatial cues

Acoustic measurements of the time and intensity difference spectra in the 2 ears show that the correspondence of ITD and IID with source location varies with frequency. In the owl, as in other species (Shaw, 1974; Phillips et al., 1982; Fuzessery and Pollak, 1984; Palmer and King, 1985; Middlebrooks and Knudsen, 1987), the acoustic axes of the ears change with frequency. At low frequencies, IID changes gradually over a narrow range and peaks at either side of the head; at high frequencies IID changes rapidly over a large range and peaks more frontally. Thus, across the frontal hemifield, IID is a monotonic function of source location for low frequencies and a nonmonotonic function of source location for high frequencies. Neither in barn owls nor in species with symmetrical ears does IID vary simply as a function of azimuth or elevation (Phillips et al., 1982; Fuzessery and Pollak, 1984; Middlebrooks and Knudsen, 1987). The con-

spicuous difference in the patterns of IID variation between owls and other species is that, because of the physical asymmetry of the barn owl's external ears, IIDs at high frequencies vary primarily with the elevation rather than with the azimuth of the source. Nevertheless, the requirement that the auditory system associate values of IID with locations in space in a frequency-specific manner holds for all species.

The correspondence of dichotic tuning with binaural cues and free field tuning

The interaural differences in timing and intensity that result from free field stimuli vary with frequency (Figs. 4, 15). The dichotic stimulus used in this study did not incorporate this natural frequency dependence of ITD and IID: the values of each dichotic parameter were nearly constant across frequency and were not varied as a function of frequency (Fig. 2). The neurophysiological data suggest that at least some of the units

Figure 11. The effect of average binaural intensity on the best ITDs (*A*) and the best IIDs (*B*) of tectal units. Each point represents data from a single unit. The lines in *A* and *B* are *y = x. A*, Best ITDs measured at 2 different binaural intensities (20 dB above threshold and 40 dB above threshold) are plotted. The data show little change in unit best ITDs with changes in average binaural intensity over this range. *B*, Best IIDs at 20 dB above threshold are plotted versus best IIDs at 40 dB above threshold. Increasing the average binaural intensity caused the best IIDs of tectal units to increase. This increase was most apparent for units tuned to IIDs greater than 5 dB.
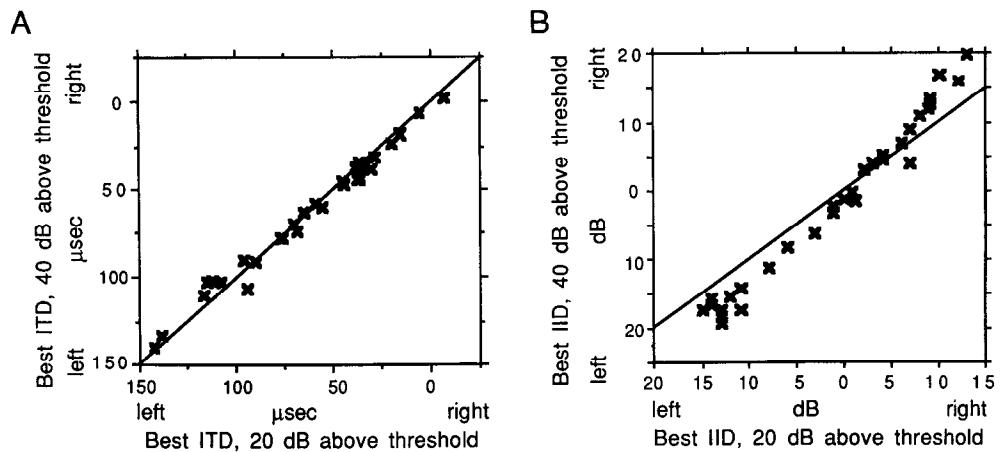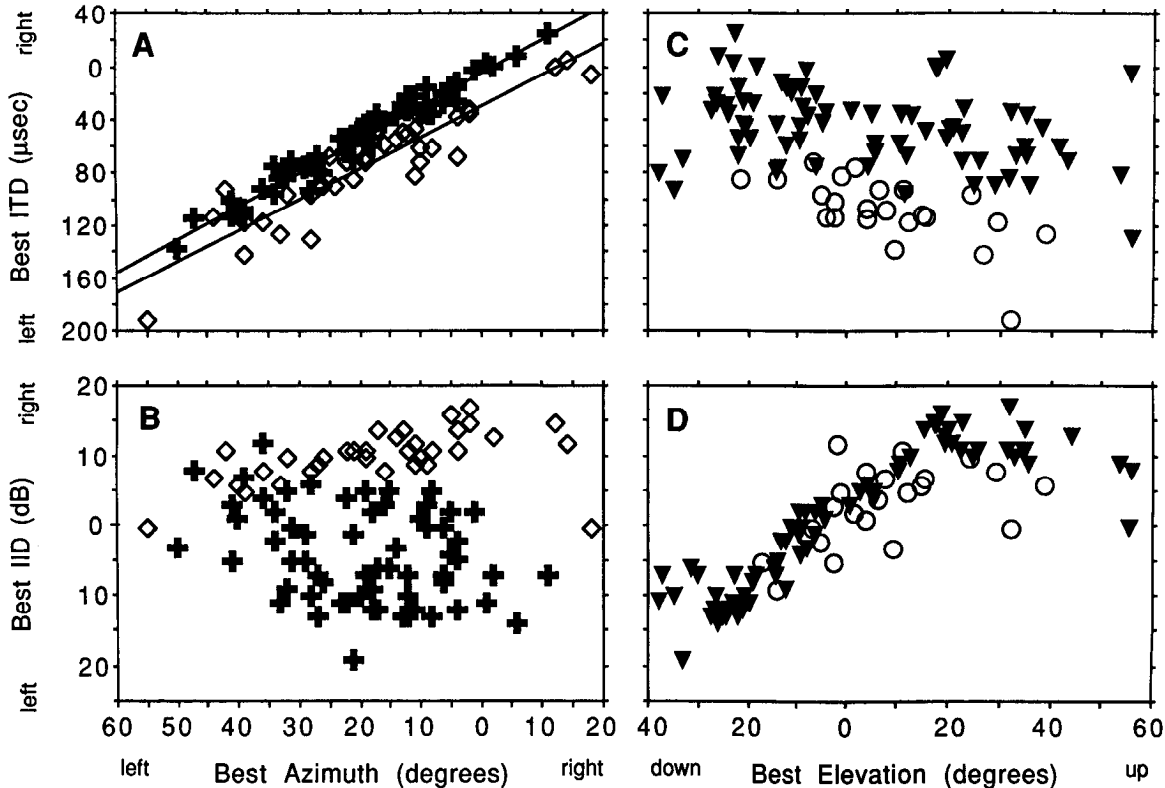
Figure 12. Comparison of spatial tuning and dichotic tuning of units recorded at 105 sites in the right optic tecta of 5 owls. (The data are from paired measurements of best ITDs and best IIDs of 87 units, plus 9 units for which only the best ITD was measured, and an additional 9 units for which only the best IID was measured.) All measurements were made at 20 dB above threshold. *A, B,* Auditory best azimuths are plotted versus best ITDs (*A*) and best IIDs (*B*). The data are divided according to unit best elevation: *diamonds* indicate units that had best elevations above +10° (*n* = 39); *crosses* indicate units that had best elevations at +10° or below (*n* = 57). *A,* Unit best azimuths and unit best ITD are strongly and positively correlated (r^2 = 0.833, *p* = 0.0001, diamonds; r^2 = 0.959, *p* = 0.0001, crosses). For the units with high best elevations (*diamonds*), the equation of the regression line (*lower line* in the figure) is best ITD = 2.31•best azimuth − 30.1; for the units with low best elevations (*crosses*), best ITD = 2.52•best azimuth − 4.3. The slopes of the 2 regression lines are not significantly different (*p* > 0.1). However, the true means of best ITDs for the 2 populations are significantly different (*p* < 0.05). These data indicate a strong dependence of best ITD on best azimuth and a relatively weak dependence of best ITD on best elevation, which is also evident in *C. B,* Unit best azimuth is very weakly correlated with unit best IID (r^2 = 0.221, *p* = 0.005, *diamonds*; r^2 = 0.095, *p* = 0.015, *crosses*). *C, D,* Auditory best elevations are plotted versus best ITDs (*C*) and best IIDs (*D*) for the same units as in *A* and *B*. The data are divided according to best azimuth: *circles* indicate units that had best azimuths to the left of L30° (*n* = 23); *triangles* indicate units that had best azimuths at or to the right of L30° (*n* = 73). *C,* Unit best elevation is correlated with unit best ITD, but only weakly (r^2 = 0.128, *p* = 0.002, *circles*; r^2 = 0.426, *p* = 0.001, *triangles*). *D,* Best IIDs vary systematically with best elevations, although this relationship is nonlinear.

were sensitive to the natural frequency dependence of IID variation. First, some tectal units that responded to the free field stimulus could not be driven by any combination of ITD and IID of the dichotic stimulus. Apparently these units were tuned for cue values not contained in the dichotic stimulus—either monaural cues or frequency-specific variations of the binaural cues. Second, as shown in Figure 12*D*, the tuning of units to high or low source elevations cannot be accounted for by changes in tuning for IID of the dichotic stimulus. Finally, preliminary experiments using narrowband dichotic noise indicate that the IID tuning of tectal units is indeed frequency dependent and can be predicted by the shape of the intensity difference spectrum associated with the direction in space for which the unit is tuned (Esterly and Knudsen, 1987).

Figure 15 compares acoustic measurements of interaural differences in time and intensity (at 4, 7, and 9 kHz) to unit best ITDs and best IIDs, respectively. All of the data are from one owl. Acoustic measurements at 4 and 9 kHz were chosen for the comparison since these frequencies approximate the range

over which most units responded to tones at 20 dB above threshold. Frequencies between 4 and 9 kHz and best IIDs vary monotonically with source elevation and best elevation, respectively, between −25° and +20°. This range of source elevations and best elevations is the same as that for which the correlation between best IID and best elevation is strongest (Fig. 12*D*). These relationships suggest that a unit's best IID, as measured with dichotic noise, probably represents an average across frequency of the IIDs to which a unit is tuned. Consequently, our measurements of best IIDs correlate well with best elevations as measured with free field noise (Fig. 12*D*) despite the absence of natural, frequency-dependent variations of IID in the dichotic stimulus. The same argument holds for the match between best ITDs and best azimuths.

Overall, there is a close match between a unit's best ITD and the ITDs at 4–9 kHz produced by a free field sound at the spatial location to which the neuron is tuned (Fig. 15*A*). Similarly, there is good agreement between best IIDs and IIDs at frequencies of 7 kHz or greater (Fig. 15*B*). Seven kiloHertz is close to the
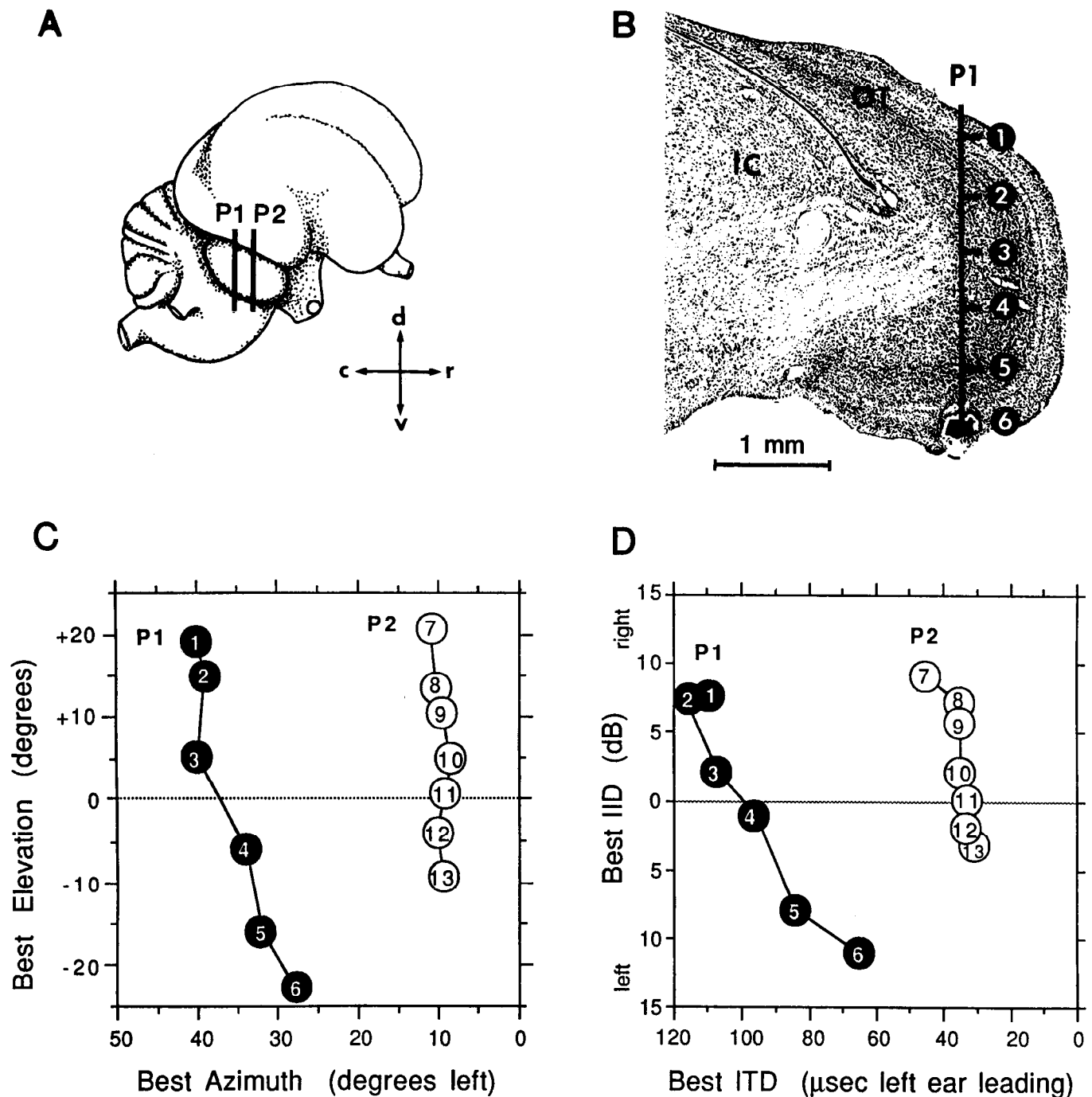
Figure 13. Reconstruction of recording sites from vertical penetrations through the optic tectum (*A, B*) and unit tuning for free field (*C*) and dichotic (*D*) stimulus parameters. *A,* Sketch of the right side of the owl's brain on which the positions of 2 electrode penetrations (P1 and P2) are indicated. *B,* Photomicrograph of the section containing the caudal penetration (P1), stained with cresyl violet, on which the recording sites of the 6 units (1–6) recorded in this penetration are indicated. The lesion, visible at the bottom of the photograph, marks the last recording site in P1. For both P1 and P2, the first unit was located within 200 μm of the dorsal surface of the tectum. For P1 the electrode was advanced 500 μm between unit recordings, whereas for P2 the electrode was advanced 300–400 μm between unit recordings. *C,* Auditory best azimuths are plotted versus auditory best elevations for the units recorded in P1 (units 1–6) and P2 (units 7–13). The data indicate that unit best elevations depend most strongly on the dorsoventral position of the recording site, whereas unit best azimuths depend most strongly on the rostrocaudal position of the recording site. *D,* Unit best ITDs are plotted versus unit best IIDs for the same 2 penetrations. A comparison of free field tuning (*C*) with dichotic tuning (*D*) reveals that best ITDs and best IIDs covary strongly with best azimuths and best elevations, respectively. Abbreviations: *IC,* inferior colliculus; *OT,* optic tectum.

average best frequency of these units, which probably accounts for the good fit between the neural data and the acoustic data at this frequency. It should be noted that the range of frequencies that excites a particular unit is not necessarily the same as the range that contributes to its spatial tuning. For example, bin-

aural cues at high frequencies may, through inhibition, contribute to the spatial tuning of units that are apparently tuned to low frequencies. The data predict that this is indeed the case, since units that respond to low frequencies, for which IID varies little with elevation, are nevertheless tuned for source elevation.

A Best ITD (μsec)

B Best IID (dB)
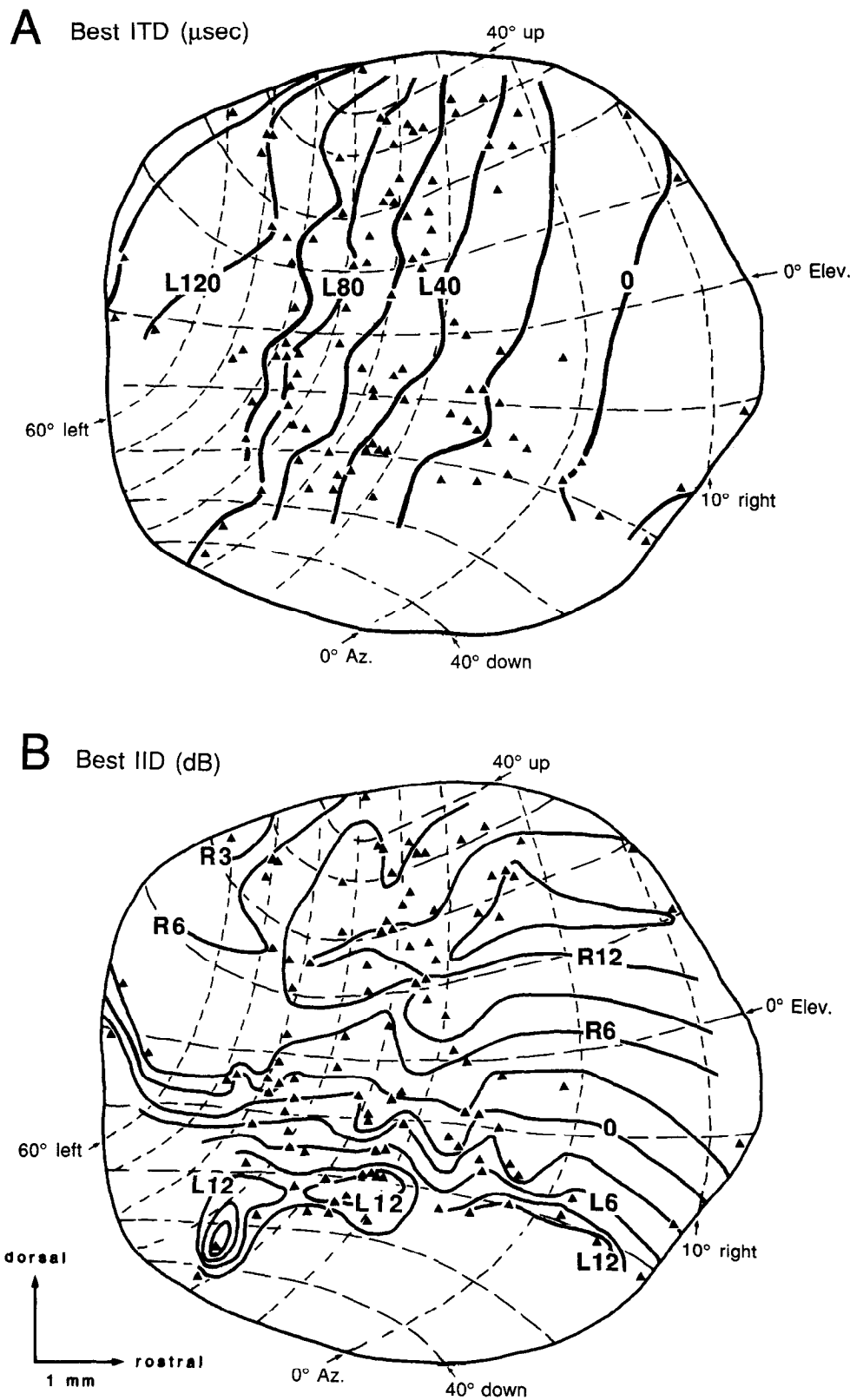
Figure 14. Maps of best ITD (*A*) and best IID (*B*) in the optic tectum. Both maps are shown on flattened representations of the tectal surface on which the neural map of visual space is drawn in lines of azimuth (*dashed lines*) and elevation (*broadly dashed lines*) (Knudsen, 1982). Most recording sites (*triangles*) were placed on the maps according to the locations of the units' visual receptive fields. (Auditory receptive fields and the corresponding map of auditory space were used for units for which no visual receptive field was available.) *A,* Unit best ITDs were measured at the indicated recording sites. *Bold lines* are iso-best ITD contours, showing the representation of best ITD in 20-μsec intervals. *B,* Unit best IIDs were measured at the indicated recording sites. Iso-best IID contours (*bold lines*) are drawn to indicate the representation of best IID in 3-dB intervals. All measurements of best ITD and best IID were made at 20 dB above threshold. Iso-best ITD and iso-best IID contours were drawn by hand, using linear interpolation between data points.

Average binaural intensity has little effect on the IID tuning of most units that have best IIDs of less than 5 dB (Figs. 10*B*, 11*B*). In contrast, units tuned to larger IIDs exhibit an increase in best IID with increasing average binaural intensity: for most of these units, the increase in best IID is due primarily to an increase in the unit's response to intensity differences that are

unnaturally large, whereas the unit's response to small intensity differences remains relatively unaffected (Fig. 10*D*). For these units, the contribution of IID selectivity to spatial tuning is determined entirely by the unit's selectivity for small intensity differences (since the large intensity differences never occur with free field stimuli). Thus, the observed variation in IID tuning
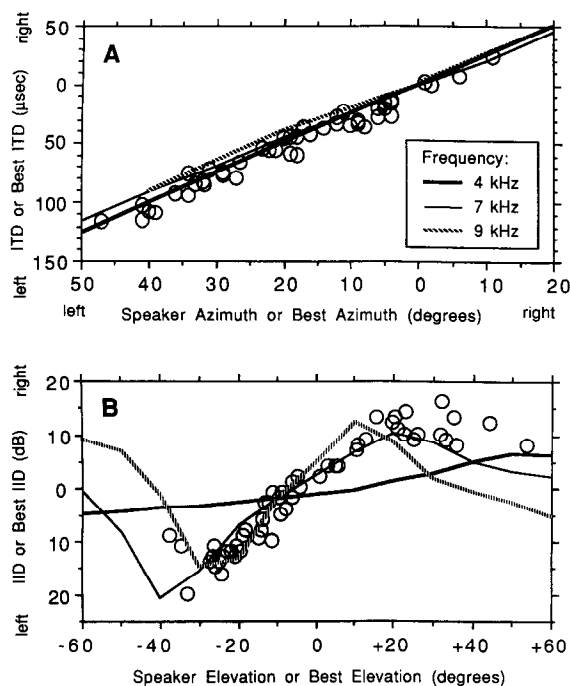
Figure 15. Free field and dichotic tuning of tectal units (*circles*) compared to acoustic measurements of ITDs (*A*) and IIDs (*B*) produced by a free field noise source (*lines*). All data are from one owl. Acoustic data are ⅓ octave averages of ITDs (*A*) and IIDs (*B*) for center frequencies at 4 kHz, 7 kHz, and 9 kHz, as shown in the key. For clarity, only the lines connecting the acoustic data points are shown. *A,* Best azimuths are plotted versus best ITDs (*circles*); these data are restricted to units that had best elevations between −30° and +10°, inclusive (*n* = 45). Acoustic measurements of ITD were taken at source locations from L50° to R20° of azimuth, in 10° steps, with source elevation held constant at −10°. (An ITD value for 9 kHz at L50° could not be measured because of poor coherence.) *B,* Best elevations are plotted versus best IIDs for units that had best azimuths between L30° and R10°, inclusive (*n* = 55). IIDs were measured for source locations from −60° to +60° of elevation, in 10° steps, with source azimuth held constant at L10°.

with average binaural intensity will have little, if any, effect on the position of the spatial receptive fields of these units. The absence of regulation of the responsiveness of tectal units to unnaturally large IIDs reflects the fact that the auditory system does not normally encounter them.

The cause of the intensity dependence of IID tuning is unknown. This intensity dependence is not unique to tectal neurons in the barn owl, but is a property common to IID-sensitive neurons in other species and in other neural structures (Brugge et al., 1969; Geisler et al., 1969; Goldberg and Brown, 1969; Brugge et al., 1970; Hirsch et al., 1985; Wise and Irvine, 1985; Wenstrup et al., 1986; Manley et al., 1988). For the barn owl, Moiseff and Konishi (1981) have reported that space-specific units in the ICx are not sensitive to average binaural intensity. In their study, however, the effect of increasing average binaural intensity was shown only for a neuron that was tuned to an IID of approximately 0 dB. As shown here for the optic tectum, only those units tuned to large IIDs consistently show intensity dependence of IID tuning. More recently, Manley et al. (1988) have demonstrated intensity dependence for IID-sensitive cells in the owl's lower brain stem (nucleus VLVp; see below).

Comparison of the neurons in the optic tectum with other binaurally sensitive neurons in the barn owl

In the barn owl, the brain stem nucleus *ventralis lemnisci lateralis pars posterior* (VLVp) is the first site of binaural convergence in the intensity difference processing pathway (Moiseff and Konishi, 1983; Manley et al., 1988). Neurons in VLVp are sensitive to interaural differences in intensity, but insensitive to interaural differences in time. In contrast to the responses of neurons in the ICx and optic tectum, IID-spike count functions of VLVp neurons are monotonic and saturating, similar to the responses of units in the lateral superior olive of mammals (Boudreau and Tsuchitani, 1968; Tsuchitani, 1988). Thus, tectal neurons are tuned to particular IID values, whereas VLVp neurons are not. These data suggest that VLVp neurons sensitive to different ranges of IIDs interact to produce the IID tuning found in the midbrain.

The tuning of neurons in the optic tectum of the barn owl to free field and dichotic stimulus parameters is similar to that of the space-specific neurons in the ICx. The neurons of the ICx are sensitive to both interaural time and interaural intensity differences, and are arranged systematically to represent ITDs (Moiseff and Konishi, 1981). A map of IIDs remains to be demonstrated, however. The space-specific neurons in the optic tectum and in the ICx are virtually identical in the sharpness of their tuning to ITD. Because the space-specific neurons in the optic tectum are more sharply tuned to source elevation than are their counterparts in the ICx (Knudsen, 1982), the neurons of the optic tectum are likely to be more sharply tuned to IID. The data available on the widths of IID tuning curves of ICx neurons, however, are not sufficient to verify this inference.

Properties common to spatially tuned neurons

In the optic tectum of the owl (Knudsen, 1982) and the cat (Middlebrooks and Knudsen, 1984), neurons are tuned to the azimuth and the elevation of a free field sound source. Tectal neurons in both species are relatively broadly tuned to frequency and respond better to broadband stimuli than they do to tones. The tectal neurons in the cat, however, are sensitive to IID and are apparently insensitive to ongoing ITD (Hirsch et al., 1985). Thus, in the cat, IID tuning is apparently adequate to produce restricted auditory receptive fields.

The tectal neurons of the barn owl are most similar to the "OO/F" neurons of the cat's superior colliculus (Wise and Irvine, 1985); OO/F neurons are unresponsive to monaural stimulation, are facilitated by binaural stimulation, and show nonmonotonic tuning to IID. In the cat's superior colliculus, these neurons are the most sharply tuned to IID. However, the median 50% tuning width of cat OO/F neurons (25 dB; Wise and Irvine, 1985) is approximately twice as broad as that of tectal neurons in the barn owl.

Development of the auditory space map

The interaural differences in time and intensity to which tectal neurons are tuned fall within the ranges of these parameters generated by the head and ears. This relationship implies that the auditory system matches its range of ITD and IID analysis to the range of values that the animal experiences. Behavioral experiments indicate that this scaling is shaped and modified by early sensory experience (Knudsen and Knudsen, 1986).

To correctly associate binaural cues with locations in space,

the owl's auditory system must be calibrated to the acoustics of the head and ears. In this study we have shown that in the adult owl the maps of dichotic stimulus parameters and of sound source locations coincide, as predicted from the dependence of interaural time and interaural intensity differences on the location of the sound source in space. The size and shape of the head and external ears (facial ruff) change as the owl matures, and therefore the binaural cues that correspond to a particular source location must also change (Knudsen et al., 1984). Experiments in which owls were raised with monaural earplugs have demonstrated that the auditory space map in the optic tectum can be modified during development in response to altered binaural cues (Knudsen, 1985). We are pursuing this issue by raising owls in which the facial ruff feathers have been altered. We plan to measure the effect of ruff alteration on binaural cues and the effect of altered cues on the tuning of tectal neurons for these cues. From a comparison of dichotic tuning in the ruff-altered owls with the data presented here, we hope to determine the degree to which the owl's auditory system is modified by experience.

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