Representation of Binaural Spatial Cues in Field L of the Barn Owl Forebrain

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Cohen, Yale E. and Eric I. Knudsen. Representation of binaural spatial cues in Field L of the barn owl forebrain. *J. Neurophysiol.* 79: 879–890, 1998. This study examined the representation of spatial information in Field L, the first telencephalic processing stage of the classical auditory pathway. Field L units were recorded extracellularly, and their responses to dichotically presented interaural time differences (ITD) and interaural level differences (ILD) were tested. We observed a variety of tuning profiles in Field L. Some sites were not sensitive to ITD or ILD. Other sites, especially those in the high-frequency region, were highly selective for values of ITD and ILD. These sites had multipeaked (commonly called “phase ambiguous”) ITD tuning profiles and were tuned for a single value of ILD. The tuning properties of these sites are similar to those seen in the lateral shell of the central nucleus of the inferior colliculus. Although the tuning properties of Field L sites were similar to those observed in the inferior colliculus, the functional organization of this spatial information was fundamentally different. Whereas in the inferior colliculus spatial information is organized into global topographies maps, in Field L spatial information is organized into local clusters, with sites having similar binaural tuning properties grouped together. The representation of binaural cues in Field L suggests that it is involved in auditory space processing but at a lower level of information processing than the auditory archistriatum, a forebrain area that is specialized for processing spatial information, and that the levels of information processing in the forebrain space processing pathway are remarkably similar to those in the well-known midbrain space processing pathway.

**METHODS**

A total of 10 barn owls (*Tyto alba*) were used in this study; 8 of the owls were used also in our examination of the tonotopic organization of Field L (Cohen and Knudsen 1996). The techniques and methodologies used in this study have been described previously (Cohen and Knudsen 1995; Knudsen 1985; Olsen et al. 1989).

**Preparation**

Barn owls were prepared for repeated experiments. Owls were anesthetized with halothane (1%) and nitrous oxide (O₂:NO₂ = 55:45) while a headpiece was cemented to the skull and a craniotomy was made over Field L. After opening the cranium, chloramphenicol (0.5%) ointment and Gelfoam (Upjohn) were applied to the brain surface. The craniotomy was then sealed with dental acrylic, and the incisions were infused with lidocaine HCl. After recovery from the anesthesia, the animal was returned to its home cage.

On the day of an experiment, the owl was anesthetized with ketamine hydrochloride (20 mg/kg body wt) and tranquilized with diazepam (1 mg/kg). Anesthesia was maintained throughout the experiment with supplemental injections of both ketamine and diazepam. The owl was wrapped in a leather harness, suspended in a prone position inside a sound-attenuated chamber, and secured to a stereotaxic device by its headpiece. The head was positioned using retinal landmarks (the eyes are essentially stationary in the head) so that the visual axes were in the horizontal plane. The dental acrylic then was removed from the craniotomy and electrophysiological recordings began. At the conclusion of an experiment, chloramphenicol ointment and Gelfoam were reapplied to the brain, the craniotomy was sealed with dental acrylic, and a
intramuscular injection of a 2.5% dextrose saline solution was administered. On recovery from anesthesia, the owl was returned to its home cage.

**Dichotic stimulation**

Dichotic stimuli consisted of 50-ms bursts of noise (0-ms rise/fall times) or tones (5-ms rise/fall times). The noise bursts were filtered digitally for a passband of 1.0–12.0 kHz. Acoustic stimuli were transduced by Knowles earphones (model 1914) coupled to damping assemblies (BF-1743). The frequency response of the earphones was measured under free-field conditions with a Briel and Kjaer 12.5 mm condenser microphone and a spectrum analyzer. The frequency response of each earphone was flattened (+2 dB between 1.0 and 12.0 kHz) by compensatory adjustments in the computer-generated waveforms. The output of the earphones was linear to within 0.2 dB over a 45-dB range of input amplitudes.

Each earphone was aligned parallel to the long axis of the ear canal, centered within it, and placed at a fixed distance from the tympanic membrane. Time delays between the two stimulus waveforms were produced by computer-calculated shifts of 5- to 50-μs increments (Olsen et al. 1989). The sound levels produced by the earphones were controlled by programmable attenuators. Frequency-specific differences in timing and level between the earphones ranged ±3 μs and 2 dB, respectively.

**Neurophysiological recordings**

An insulated tungsten microelectrode (1–3 MΩ at 1.0 kHz) was used to record extracellularly. Single- and multunit clusters consisting of two to three single units were differentiated from background activity with a level discriminator. The electrode was aligned perpendicular to the horizontal plane, positioned stereotaxically, and advanced into Field L with a microdrive while neural activity was monitored on an audio monitor and an oscilloscope.

Sequential dorsoventral penetrations were spaced at intervals of 0.25–1.0 mm. Sites along an electrode penetration were separated by ≥150 μm. In some experiments, we recorded from many different frequency regions of Field L and sampled only a few units per electrode penetration. In other experiments, we focused exclusively on the high-frequency (≥4 kHz) region of Field L, and sampled from as many units as could be isolated in an electrode penetration. We focused on the high-frequency region because it represents those frequencies that are most important for sound localization (Brainard et al. 1992; Knudsen and Konishi 1979; Knudsen et al. 1979; Konishi 1973; Konishi et al. 1988; Olsen et al. 1989).

**Response profile analysis**

Tuning curves were generated by presenting series of binaural stimuli consisting of either noise (1.0–12.0 kHz) bursts with random sequences of ILDs or ITDs or of tone bursts with random sequences of frequencies. For each tuning curve, ≥10 repetitions of each binaural stimuli were presented. The response to a dichotic stimulus was quantified by subtracting the number of spikes occurring during a 100-ms period before stimulus onset (baseline activity) from the number of spikes evoked during the 100 ms after stimulus onset. When ITD response profiles were obtained, ILD was held constant at the site’s best value. Similarly, when ILD response profiles were obtained, ITD was held constant at the site’s best value. Frequency response profiles were obtained with ITD and ILD held at their respective best values based on responses to noise burst stimulation. The sensitivity of a site to ITD and ILD was examined over the entire physiological range (ITD: 200 μs left-ear leading to 200 μs right-ear leading; ILD: 20 dB left-ear greater to 20 dB right-ear greater) (Brainard et al. 1992; Knudsen et al. 1991, 1994; Olsen et al. 1989) using the dichotic noise stimulus.

Field L sites were categorized as being either “insensitive” or “sensitive” to ITDs (Fig. 1). Sites that had ITD insensitive response profiles (Fig. 1A) did not show any systematic modulation in the magnitude of their response to different values of ITD. Those sites that were sensitive to ITD were classified further as having single-peaked, multipeaked, contralateral-ear (contra-ear) leading, ipsilateral-ear (ipsi-ear) leading, or notch ITD response profiles.

Sites with single-peaked ITD response profiles (Fig. 1B) responded best to one ITD value. Sites with multi-peaked ITD response profiles (Fig. 1C) responded nearly equally to multiple values of ITD (see RESULTS). Typically, at these sites, one peak was the largest and is referred to as the primary peak, whereas the smaller peaks are referred to as secondary peaks. Sites with contra-ear leading ITD response profiles (Fig. 1D) responded preferentially to contra-ear leading values of ITD, whereas sites with ipsi-ear leading ITD response profiles (Fig. 1E) responded preferentially to ipsi-ear leading values of ITD. Sites with notch ITD response profiles (Fig. 1F) responded strongly to both contra-ear leading and ipsi-ear leading values of ITD but responded minimally or not at all to small values of ITD.

The ITD selectivity of sites with single- or multi-peaked ITD response profiles was characterized using two indexes: ITD response modulation and ITD tuning width. ITD response modulation was the difference between a site’s largest and smallest response, expressed as a percentage of the largest response. The maximum attainable value of ITD response modulation was limited by a site’s level of baseline activity: the responses at sites with high levels of baseline activity could be modulated by >100%, whereas responses without any baseline activity were limited to a maximum response modulation value of 100%. To eliminate the effect of differences in baseline activity on response modulation, response modulations that were >100% were assigned a value of 100%. ITD tuning width was the continuous range of ITD values that elicited >50% of the largest response. The center of this range was a site’s “best ITD.”

At sites with multi-peaked ITD response profiles, selectivity for a specific value of ITD was quantified by calculating the size of the largest secondary peak relative to the size of the primary peak, an index referred to as the relative size of the secondary peak.

ILD response profiles were obtained using two different methods. In the first method, the average binaural level (ABL) constant method, the sound level in the contralateral and ipsilateral ears was varied symmetrically around a specific ABL (20 dB above threshold); ABL is the sum of the sound levels (in dB) at the two ears divided by two. In the second method, the contralateral-ear constant method, the sound level at the contralateral ear was held constant at 20 dB above threshold while the level was varied in the ipsilateral ear.

Field L sites also were categorized as being either insensitive or sensitive to ILDs (Fig. 2). Sites with ILD insensitive response profiles (Fig. 2A) did not show any systematic modulation in the magnitude of their response to different values of ILD. Sites that were sensitive to ILD were classified further as having tuned, contra-ear greater, ipsi-ear greater, or notch ILD response profiles. Sites with tuned ILD response profiles (Fig. 2B) had a single response peak and responded best to one value of ILD. Sites with contra-ear greater ILD response profiles (Fig. 2C) responded preferentially to contra-ear greater values of ILD; sites with ipsi-ear greater ILD response profiles (Fig. 2D) responded preferentially to ipsi-ear greater values of ILD. Sites tuned for large values of ILD (e.g., 17 dB ILD) were differentiated from those sites with contra-ear or ipsi-ear greater ILD response profiles by expanding the range of ILD values that we normally used (±20 dB ILD) to ±35 dB ILD and determining whether the response was tuned for a large value of ILD or was contra- or ipsi-ear sensitive. Sites with
FIG. 1. Types of interaural time differences (ITD) response profiles observed in Field L. A: ITD-insensitive; B: single peaked; C: multipeaked; D: contralateral-ear leading; E: ipsilateral-ear leading; and F: ITD notch. Error bars indicate 1 SD from the mean.

FIG. 2. Types of interaural level differences (ILD) response profiles observed in Field L. A: ILD-insensitive; B: single peaked; C: contralateral-ear greater; D: ipsilateral-ear greater; and E: ILD notch. Error bars indicate 1 SD from the mean.
notch ILD response profiles (Fig. 2E) responded strongly to large contra-ear greater and ipsi-ear greater values of ILD but poorly to values of ILD near 0 dB ILD.

At sites with tuned ILD response profiles, selectivity for a specific value of ILD was quantified using two indexes: ILD response modulation and ILD tuning width. ILD response modulation was the difference between a site’s largest and smallest response, expressed as a percentage of the largest response. ILD tuning width was defined as the continuous range of ILD values that evoked >50% of the largest response. The center of this range was a site’s best ILD.

Finally, we measured the frequency response profile at each site. As in our earlier study (Cohen and Knudsen 1996), sites were categorized as either unresponsive or responsive to tonal stimulation (cf. Muller and Leppelsack 1985). Sites that were responsive to tones were categorized further as having tuned (responding maximally to a single continuous range of frequencies) or multipeaked (responding strongly to more than one range of frequencies) response profiles. If a site was tuned for frequency, we quantified its frequency tuning width and best frequency. Frequency tuning width was the continuous range of frequencies that elicited >50% of the maximum response. The center of this range was the site’s best frequency.

**Analyses of functional organization**

We performed cluster analyses on data only from electrode penetrations made in the high-frequency (≥4 kHz) region of Field L. The low-frequency (<4 kHz) region of Field L was not sampled adequately for these analyses.

**Organization of binaural tuning type.** We used a Monte Carlo analysis, similar to that described by Rajan et al. (1990), to examine whether, along an electrode penetration, sites with similar types of response profiles were clustered together. Data were analyzed from all penetrations in which measurements were made at two or more sites. From these penetrations, we counted the number of sequential sites (separation ≥150 μm) exhibiting similar response profiles. We will refer to this number as the same-type sequence length. By including sequences that contained large separations, the chances of finding a clustered organization of response profile type decreases. Thus this analysis is a conservative estimate of clustering (see Rajan et al. 1990).

Next, a distribution of same-type sequence length and tuning type that would occur in a random distribution of tuning types was calculated from 2,000 Monte Carlo simulations. In each simulation, we counted the number of sequential “sites” with similar response profiles that occurred in a simulated penetration. The number of sites in this simulated penetration and the ITD tuning type associated with each site were selected randomly from distributions that were identical to the empirically observed distributions. From these simulations, a probability distribution of same-type sequence length and tuning type was created. The simulated distribution of different same-type sequences lengths was calculated by multiplying this probability distribution by the total number of electrode penetrations with two or more sites. A χ² test determined whether the empirically measured and simulated frequency of same-type sequences differed at a significance level of 0.05. This same procedure was used to determine the organization of ILD tuning type.

**Organization of best ITDs and best ILDs.** We used a Monte Carlo analysis to determine whether values of best ITD or best ILD exhibited clustered distributions along the dorsoventral axis of the high-frequency regions of Field L. Data were analyzed from all electrode penetrations in which measurements were made at three or more sites. For each pair of adjacent sites in a given electrode penetration, the absolute difference between best ITD values was determined, and the average difference for all such pairs of sites, the experimental mean, was calculated for that penetration. Next, the distribution of average differences that would result from random combinations of best ITD values for a similar number of recording sites was calculated. This distribution was determined from 1,500 Monte Carlo simulations, which randomly selected n best ITD values from the pool of best ITD values measured in that animal, where n equals the number of sites in the penetration being tested. The average value from this distribution was the simulation mean. The experimental mean then was compared with the simulation mean. Those penetrations with experimental means that were smaller than the simulation mean were termed clustered, and those with experimental means that were larger were termed not clustered. A sign-test then was applied to determine whether the proportion of electrode penetrations with clustered best ITDs occurred more frequently than expected by chance. The same procedure was followed to determine whether best ILDs were clustered along the dorsoventral axis.

**Spatial extent of clustered distributions.** We examined the spatial extent of clustering using a Monte Carlo simulation similar to that described by LeVay and Voigt (1988). Data were analyzed from all electrode penetrations in which measurements were made at three or more sites. First, for all pairs of sites in a penetration, the difference between best ITD values and the dorsoventral separation between the sites were calculated. Differences between best ITDs then were binned as a function of dorsoventral separation and the mean best ITD difference (experimental mean difference) was determined for each bin. Next, the distribution of mean best ITD differences that would occur randomly was calculated using a Monte Carlo simulation. In each simulation, we selected randomly two best ITD values and calculated their difference. These best ITD values were chosen from the pool of best ITD values that were used to determine the experimental mean difference. From 1,000 such simulations, a random distribution of best ITD differences was created. The random mean difference was the average value of this distribution. The random mean difference then was compared with each of the binned experimental mean differences. A Mann-Whitney U test determined whether the experimental mean differences and the random mean difference differed significantly at a criterion level of P < 0.05. This same procedure was used to determine the spatial extent of ILD clustering.

**Histology**

Injections of anatomic tracers (either 10% biotinylated dextran amine, Fluoro-Gold, Fluorochrome, or rhodamine-coupled latex beads) (see Cohen et al. 1998) or the placement of electrolytic lesions into selected locations of Field L served as fiducial markers so that recording sites could be reconstructed with a camera lucida.

Following survival times ranging from 4 days (electrolytic lesions) to 1 mo (Fluoro-Gold and rhodamine-coupled latex beads), owls were anesthetized deeply with pentobarbital sodium and perfused intracardially with 4% paraformaldehyde and 5% sucrose in 0.1 M phosphate buffer. The brains were cryoprotected, blocked in the plane parallel to the plane of the electrode penetrations (the transverse plane), and cut on a freezing microtome in 40-μm sections. These sections then were mounted on glass slides. Sections containing either latex beads or Fluoro-Gold were cleared and examined under a fluorescence microscope. The dextran amine was visualized with an avidin-biotinylated horseradish peroxidase (ABC) procedure followed by a standard diaminobenzidine reaction. Alternate sections were stained with cresyl violet or with a myelin (modified Gallyas) stain. Recording sites were reconstructed with a camera lucida.
RESULTS

Dichotic tuning properties

Responses to dichotic noise were assessed at 439 single- or multiunit sites from both hemispheres of 10 barn owls. Because single- and multiunit activity at the same site showed comparable tuning properties, single- and multiunit data are presented together. Differences in the sample sizes for the different analyses occurred because units were occasionally lost before a complete set of tuning curves could be obtained.

ITD response profiles

GENERAL OBSERVATIONS. As seen in Fig. 1, Field L sites exhibited a diversity of ITD response profiles. Except for ipsi-ear leading ITD and single-peaked ITD response profiles, all of the different types of ITD response profiles were found throughout Field L (Table 1). Ipsi-ear leading ITD and single-peaked ITD response profiles were, in general, limited to the low-frequency (<4 kHz) region of Field L. In addition, all of these ITD response profiles were found both at single- and multiunit sites.

Sites with multipeaked ITD response profiles responded strongly to ITDs that were separated by integral numbers of periods of their best frequency (Fig. 3). The relationship between response peak separation and best frequency suggests that these sites were tuned to a particular interaural phase difference (IPD). Such sites have been referred to as phase ambiguous in previous reports (see Brainard et al. 1992; Carr and Konishi 1988; Fujita and Konishi 1991; Konishi et al. 1988). There was no systematic relationship between best frequency and ITD response peak separation for sites with notch ITD response profiles.

ITD SELECTIVITY. ITD selectivity was quantified using the three indexes described in Fig. 4A. For sites with multipeaked response profiles, the median size of the secondary peak was 81% (Fig. 4B) of the primary peak. For sites with single- or multipeaked ITD response profiles, ITD response modulation ranged from 44 to 100% with a median value of 93% (Fig. 4C). At 60% of the sites, ITD response modulation was <100%, indicating that these sites responded, to some degree, to any ITD within the physiological range (±200 μs). ITD tuning width averaged 85 ± 37.2 (SD) μs (range = 22.2–181 μs; Fig. 4D).

BEST ITDS. Best ITDs were calculated for 173 sites (Fig. 5) that had multi- or single-peaked ITD response profiles. Although the range of best ITDs (contralateral 205 μs to ipsilateral 204 μs) covered the entire physiological range, a substantial proportion (68%; 117/173) of sites had values that were <50 μs ITD (Fig. 5), corresponding to sound sources located within the frontal 40° of space (Cohen and Knudsen 1995; Knudsen et al. 1991; Olsen et al. 1989).

Within each iso-frequency region between 4 and 7 kHz (1-kHz bandwidth), we found no statistical difference in the distribution of best ITDs (df = 3; F = 1.7, P > 0.05). In this analysis, we did not include multipeaked ITD sites with primary and secondary response peaks that were of equal magnitude (i.e., the relative size of the secondary peak = 100%).

TABLE 1. Distribution of binaural response profile type

<table>
<thead>
<tr>
<th>ILD Response Profile Type</th>
<th>ITD Response Profile Type</th>
</tr>
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<tbody>
<tr>
<td>I</td>
<td>MP</td>
</tr>
<tr>
<td>---</td>
<td>---</td>
</tr>
<tr>
<td>Low-frequency region*</td>
<td></td>
</tr>
<tr>
<td>I</td>
<td>8</td>
</tr>
<tr>
<td>T</td>
<td>22</td>
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<tr>
<td>CG</td>
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<td>N</td>
<td>3</td>
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<td>3</td>
</tr>
<tr>
<td>N</td>
<td>0</td>
</tr>
<tr>
<td>Total</td>
<td>69</td>
</tr>
</tbody>
</table>

1, insensitive; MP, multipeaked; SP, single peaked; CL, contra-ear leading; IL, ipsi-ear leading; N, notch; T, tuned; CG, contralateral-ear greater; IG, ipsilateral-ear greater. * n = 142, BF <4 kHz. † n = 297, BF ≥4 kHz.
GENERAL OBSERVATIONS. As seen in Fig. 2, Field L sites exhibited a diversity of ILD response profiles. Sites that were insensitive to ILD responded well to any value of ILD throughout the physiological range (Fig. 2A). Sites that were most selective for ILD responded strongly to only one value of ILD (tuned; Fig. 2B). Other sites were less selective and responded only to contra-ear greater ILDs (Fig. 2C), ipsi-ear greater ILDs (Fig. 2D), or large values of ILD (notch; Fig. 2E). All of the different identified types of ILD response profiles were found in all frequency regions of Field L except for notch ILD response profiles that were found only in the low-frequency (<4 kHz) region (Table 1). In addition, all of these ILD response profiles were found both at single- and multiunit sites.

ILD SENSITIVITY AT SITES TUNED TO FREQUENCIES <4 kHz. In the low-frequency (<4 kHz) region of Field L, many sites were sensitive to dichotically presented ILDs. However, the acoustic basis of this sensitivity is unclear, because at low frequencies (<3 kHz), the barn owl’s ears are not acoustically isolated from each other (interaural attenuation <10 dB) (Moiseff and Konishi 1981b). Consequently, the sounds produced by the two earphones interact in a complex manner so that the stimuli transduced by the tympanic membrane may differ substantially from the original stimuli generated by the earphones. As these interactions are not well understood, it is difficult to interpret the observed sensitivity to nominal ILD changes for low-frequency sounds. Therefore, we did not include data from sites with frequency tuning <4 kHz in our quantitative analysis of ILD selectivity.

In contrast, at frequencies ≥4 kHz, the two ears are relatively well isolated from each other (interaural attenuation >25 dB) (Moiseff and Konishi 1981b). Consequently, the acoustic stimuli transduced by the tympanic membranes are the same as the dichotically presented stimuli and measured ILD sensitivity is an accurate reflection of level difference processing.

ILD SELECTIVITY. For sites with best frequencies ≥4 kHz (n = 239), selectivity was assessed using the two indexes defined in Fig. 7A (see METHODS). ILD response modulation...
FIG. 6. A and B: ILD response profiles obtained from 2 sites using the average binaural level (ABL)-constant method (●) and the contralateral-ear–constant method (○). Error bars indicate 1 SD from the mean.

ranged from 23 to 100% with a median value of 99% (Fig. 7B). Approximately half of the sites had ILD response modulation values of <100%, indicating that these sites responded, to some degree, to any ILD within the physiological range (±20 dB). ILD tuning width averaged 24 ± 9 (SD) dB (range = 2–55 dB; Fig. 7C).

BEST ILDS. For sites with tuned ILD response profiles and best frequencies ≈4 kHz, best ILDs ranged from 17 dB contra-ear greater to 18 dB ipsi-ear greater (Fig. 8); this corresponds well with the range of ILD values that the owl’s auditory system normally experiences (±20 dB ILD) (see Brainard et al. 1992; Knudsen et al. 1994). The vast majority of sites (93%) were tuned to ILD values of <10 dB ILD. Within each iso-frequency region between 5 and 7 kHz (1-kHz bandwidth), we found no statistical difference in the distribution of best ILDs (df = 2; F = 2.4, P > 0.05). The average best ILD in the 3- and 4-kHz regions, however,

FIG. 7. ILD selectivity. A: schematized ILD tuning curve illustrating the indexes used to quantify ILD selectivity. ILD response modulation was the difference between a site’s largest (e) and smallest (f) response to an ILD value and was expressed as a percentage of the largest response: (e − f)/e*100. ILD tuning width was the range of ILD values that elicited >50% of the largest response (g). Best ILD was the center of this range. B: distribution of ILD response modulation. C: distribution of ILD tuning width.
quency region of Field L could contain clusters of sites with different types of response profiles (Fig. 9). Finally, this clustering was organized on a relatively small spatial scale (Fig. 9): penetrations through clusters of sites with multipeaked ITD response profiles and penetrations through clusters of sites with ITD-insensitive response profiles could be separated as little as 250 µm.

We did not find any statistical evidence ($P > 0.05$) for a clustered organization of ILD tuning in the high-frequency ($\geq 4$ kHz) region of Field L. The lack of a clustered organization of sites with tuned ILD response profiles could be attributed to the fact that most Field L sites (239/287) had tuned ILD response profiles. Hence, the occurrence of sequential sites having tuned ILD response profiles was likely due to chance.

**Organization of Binaural Localization Cue Values.** We found no evidence of an organization, based on binaural tuning, that would be consistent with the existence of a single, continuous map of auditory space in Field L: best ITDs and best ILDs did not change systematically along any dimension of Field L.

We did find evidence, however, for a clustering of best ITDs in the high-frequency ($\geq 4$ kHz) region of Field L. Best ITDs either changed smoothly and gradually or remained constant along dorsoventral penetrations. Examples of data from dorsoventral electrode penetrations, together with their Monte Carlo analyses for clustering (see Methods), are shown in Fig. 10. The data shown in Fig. 10A are from a penetration in which best ITDs remained essentially constant. In this example, the average nearest-neighbor difference was 2.5 µs, which was in the third percentile of the Monte Carlo distribution, indicating more clustering of best ITDs than would be expected by chance. In the penetration shown in Fig. 10B, best ITDs progressed smoothly along the penetration. The average nearest-neighbor difference for this penetration was 11.4 µs, which was in the 10th percentile of the Monte Carlo distribution, which again indicates more clustering than would be expected from a random distribution. Of the 28 penetrations in which we were able to measure best ITDs at three or more sites, 20 (71%) exhibited clustering of best ITDs. This is a significantly greater number of penetrations exhibiting a clustered organization than would have been expected by chance ($Z = 2.27, P < 0.01$).

We found no statistical evidence for a clustered organization of best ILDs. Of the 42 penetrations, in which best ILDs were measured at three or more sites, only 23 (55%) exhibited clustering, which was not more than would have been expected by chance ($P > 0.05$).

In addition, cluster analyses, similar to those described above, did not reveal any statistical evidence ($P > 0.05$) for a systematic organization of any other binaural parameter or selectivity index along any dimension of Field L, including across the different zones, or layers (L1, L2, and L3), of Field L (cf. Cohen et al. 1998; Scheich 1990).

**Spatial Extent of Clustered Distributions.** We examined the spatial extent of the clusters of best ITD values. The data shown in Fig. 11 illustrates the relationship between mean best ITD differences and the distance between sites (see Methods). In our data set, mean best ITD differences were significantly less ($P < 0.05$) than the random mean.
difference (51 μs; gray line in Fig. 11) at distances of <950 μm but were not significantly different from the random mean difference at distances ≥950 μm. Thus, on average, sites separated by <950 μm had clustered best ITD distributions. However, because we do not know the exact orientation or shape of the ITD clusters, 950 μm represents an upper bound on the size of the ITD clusters.

**Discussion**

We have characterized the representation of binaural information in the barn owl Field L. Field L sites varied substantially in their sensitivity to binaural cues. A large population of sites, particularly those in the high-frequency region, responded preferentially to certain binaural cue values. Others responded to virtually any values. Sites with similar binaural tuning were found to be clustered within Field L. In the discussion that follows, we compare levels of auditory spatial information processing in the auditory forebrain with those in the auditory midbrain, we examine the transformation of spatial information between Field L and the AAr, and we speculate as to why spatial information is organized locally in the auditory forebrain.

**Similarities between levels of information processing in the forebrain and midbrain**

The different stages of the space processing pathway in the avian auditory forebrain have been described recently (Cohen et al. 1998). In brief, spatial information enters the forebrain at the level of the auditory thalamus (nucleus ovoidalis) via ipsilateral input from all areas of the central nucleus of the inferior colliculus (ICC). From the auditory thalamus, information is relayed to Field L and then, from Field L, to the AAr.

The levels of spatial information processing observed at different stages of this forebrain pathway closely mirror the well-known levels of information processing seen in the auditory midbrain of the barn owl. Equivalent levels of spatial information processing in the forebrain and midbrain are Field L and the lateral shell of the central nucleus of the inferior colliculus (ICC LS), respectively. Both areas are organized tonotopically and contain sites that are tuned narrowly for frequency, tuned for both IPD and ILD (Cohen and Knudsen 1996; Konishi et al. 1988; Mazer 1995; Takahashi and Konishi 1986; Wagner et al. 1987; current paper). The next level of information processing is represented by the response properties of units in the AAr and the external nucleus of the inferior colliculus (ICX), respectively (Knudsen and Knudsen 1983; Cohen et al. 1998). By integrating IPD and ILD information across frequency, units in these areas eliminate much of the spatial ambiguity that is associated with any single, frequency-specific cue (Brainard et al. 1992; Takahashi and Konishi 1986; see Cohen and Knudsen 1995). Consequently, these units are tuned for ITDs and ILDs across a broad frequency range and, therefore, have spatially
TABLE 2. Clustering of ITD tuning type in the high-frequency region of Field L

<table>
<thead>
<tr>
<th>Tuning Type</th>
<th>Value</th>
<th>Number of Sequential Sites With the Same Tuning Type</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td>2</td>
</tr>
<tr>
<td>Multipeaked</td>
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<td>119</td>
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<tr>
<td></td>
<td>E</td>
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<td></td>
<td>$\chi^2$</td>
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<tr>
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<td></td>
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<tr>
<td></td>
<td>$\chi^2$</td>
<td>0†</td>
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<td>Notch</td>
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<td></td>
<td>$\chi^2$</td>
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<tr>
<td>Insensitive</td>
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<td></td>
<td>$\chi^2$</td>
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<tr>
<td>Ipsilateral</td>
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<tr>
<td>Single peaked</td>
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</tr>
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<td></td>
<td>E</td>
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O, observed; E, expected based on Monte Carlo simulation. * $P < 0.005$.
† Not significant, df = 1. § $P < 0.05$.

Transformation of information between Field L and the AAr

The degree to which spatial information is transformed between Field L and the AAr can be quantified by comparing the selectivity of Field L and AAr units for particular binaural cue values. For example, the degree to which a site is selective for a particular ITD value is indicated by the relative size of its secondary peaks. Field L sites have multipeaked (IPD-tuned) response profiles with secondary peaks that are nearly as large as the primary peak (relative median size = 81%; Figs. 1C and 4B). In contrast, AAr sites preferentially respond to one single value of ITD and have significantly smaller secondary peaks than Field L (relative median size = 55%; $Z = -8.31$, $P < 0.0001$) (Cohen and Knudsen 1995). Other selectivity indexes indicate also that AAr sites are more selective for binaural cue values than Field L sites: ILD and ITD tuning widths are significantly sharper (ILD: $df = 256$, $t = 4.66$; $P < 0.0001$; ILD: $df = 358$, $t = 3.35$; $P < 0.001$), and ITD response modulation is significantly higher ($Z = 3.01$, $P < 0.0027$) in AAr sites than in Field L sites. Although it has not been examined directly, the transformation of spatial information between Field L and the AAr appears to be qualitatively, if not quantitatively, similar to the transformation of information between the ICC$_{LS}$ and the ICX (Mazer 1995; Takahashi and Konishi 1986; M. S. Brainard, personal communication).

Clustered representation of spatial information in the forebrain

Although unit response properties are similar at comparable levels of integration in the forebrain and midbrain, the functional organization of spatial information is fundamentally different. In the ICC$_{LS}$, there is a single, continuous representation of ITD along the rostrocaudal axis (Wagner et al. 1987); the organization of ILD information in the ICC$_{LS}$ is unknown. At the next higher level of information
processing, the ICX, there is a single, continuous representation of both ITD and ILD and, hence, of auditory space (Knudsen and Konishi 1978; Mogdans and Knudsen 1993; Moiseff and Konishi 1981a). Similar maps of auditory spatial information have been found in the mammalian ICC (cf. Irvine and Gago 1990; Wenstrup et al. 1986) and ICX (Binns et al. 1992).

In contrast, in the barn owl Field L and at higher levels of processing, such as the AAR and the paleostriatum augmentum, the avian analogue of the striatum (Cohen and Knudsen 1994, 1995), auditory spatial information is organized into clusters of units tuned to similar binaural cue values. Because binaural tuning is an accurate indicator of spatial tuning (Cohen and Knudsen 1995; Olsen et al. 1989), unit tuning for sound source location also must be clustered in these structures. Similarly, in the mammalian AI, there seems to be no global topographic space map but, instead, cells with similar spatial tuning are clustered together within iso-frequency contours (cf. Clarey et al. 1994; Middlebrooks et al. 1980; Rajan et al. 1990). These similarities in the functional organization of Field L and the AI suggest that the clustering of sites with similar properties may be an intrinsic organizational feature of the auditory forebrain in a wide variety of species (see also Scheich 1990).

The clustered representation of auditory information in the forebrain can be interpreted in different contexts. First, a clustered organization can be interpreted in the context of a self-organizing system that processes many different parameters of a stimulus (Kohonen 1989; Schreiner 1995). In such a system, clustered representations of a stimulus parameter develop naturally when a network processes independent stimulus parameters simultaneously. Indeed, in both Field L and the AI, unit sensitivity to parameters of the auditory scene other than sound source location have clustered organizations (for a review, see Scheich 1990; Schreiner 1995). A second, nonexclusive possibility is that a clustered organization is the optimal organization for those computations needed to mediate behaviors different from the midbrain’s control of gaze to stimuli currently present in the environment (Cohen and Knudsen 1994, 1995; Knudsen et al. 1993; see also, Bower and Kassel 1990; Nelson and Bower 1990; Sanes et al. 1995). For example, the forebrain is essential probably for detailed analysis of content, for the selection of particular auditory stimuli for attention, and for the mediation of behavioral responses based on auditory spatial memory (Knudsen and Konishi 1996b). The computations that contribute to these complex functions require the integration of auditory spatial information with information about body position and with information from memory stores and limbic structures. It is possible that to accomplish such complex tasks a clustered organization, rather than a global auditory space map, is the optimal representational scheme.

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