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# Functional Organization of the Pallid Bat Auditory Cortex: Emphasis on Binaural Organization

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**Razak, Khaleel A. and Zoltan M. Fuzessery.** Functional organization of the pallid bat auditory cortex: emphasis on binaural organization. *J Neurophysiol* 87: 72–86, 2002; 10.1152/jn.00226.2001. This report maps the organization of the primary auditory cortex of the pallid bat in terms of frequency tuning, selectivity for behaviorally relevant sounds, and interaural intensity difference (IID) sensitivity. The pallid bat is unusual in that it localizes terrestrial prey by passively listening to prey-generated noise transients (1–20 kHz), while reserving high-frequency (<30 kHz) echolocation for obstacle avoidance. The functional organization of its auditory cortex reflects the need for specializations in echolocation and passive sound localization. Best frequencies were arranged tonotopically with a general increase in the caudolateral to rostromedial direction. Frequencies between 24 and 32 kHz were under-represented, resulting in hypertrophy of frequencies relevant for prey localization and echolocation. Most neurons (83%) tuned <30 kHz responded preferentially to broadband or band-pass noise over single tones. Most neurons (62%) tuned >30 kHz responded selectively or exclusively to the 60- to 30-kHz downward frequency-modulated (FM) sweep used for echolocation. Within the low-frequency region, neurons were placed in two groups that occurred in two separate clusters: those selective for low- or high-frequency band-pass noise and suppressed by broadband noise, and neurons that showed no preference for band-pass noise over broadband noise. Neurons were organized in homogeneous clusters with respect to their binaural response properties. The distribution of binaural properties differed in the noise- and FM sweep-preferring regions, suggesting task-dependent differences in binaural processing. The low-frequency region was dominated by a large cluster of binaurally inhibited neurons with a smaller cluster of neurons with mixed binaural interactions. The FM sweep-selective region was dominated by neurons with mixed binaural interactions or monaural neurons. Finally, this report describes a cortical substrate for systematic representation of a spatial cue, IIDs, in the low-frequency region. This substrate may underlie a population code for sound localization based on a systematic shift in the distribution of activity across the cortex with sound source location.

## INTRODUCTION

A systematic representation of frequency is present in the primary auditory cortices of all mammals studied, suggesting that it provides a fundamental organizing substrate on which other attributes of sound are mapped. Of these secondary attributes, the representation of sound location has received the greatest attention, and it is a major focus of the present study. Spatial representation has been examined both in terms of the distribution of binaural response properties and spatial sensitivity. The organization of binaural response properties varies

across species, but a consistent finding is that cortical neurons with similar binaural response properties occur in clusters (cat: Imig and Adrian 1977; Middlebrooks et al. 1980; Reale and Kettner 1986; rat: Kelly and Sally 1988; ferret: Kelly and Judge 1994; mustached bat: Liu and Suga 1997; big brown bat: Shen et al. 1997; owl monkey: Recanzone et al. 1999; guinea pig: Rutkowski et al. 2000). This clustering is more than the simple consequence of the frequency-specific binaural cues used in sound localization, i.e., high-frequency isofrequency bands that process interaural intensity differences (IIDs) also exhibit clusters of different binaural types. In cats and ferrets, clusters of neurons with similar binaural properties have been reported to be organized orthogonal to isofrequency bands (Imig and Adrian 1977; Kelly and Judge 1994; Middlebrooks et al. 1980), potentially endowing each frequency with a full complement of binaural machinery for spatial analysis. In other species, such as the owl monkey, this orthogonal relationship with frequency is less obvious (Recanzone et al. 1999). The cortices of echolocating bats differ in that there does not appear to be an even distribution of binaural types across frequency domains. In the mustached and big brown bats (Liu and Suga 1997; Shen et al. 1997), binaurally excited (EE) neurons are restricted to a single cluster within a limited range of high frequencies used for echolocation, while binaurally inhibited (EI) neurons have a widespread distribution.

The clustered organization of binaural types may contribute to a cortical representation of auditory space, but the nature of this representation is unclear. No clear topographic representations of space or binaural disparities have been reported within or across these clusters (e.g., Brugge et al. 1994; Clarey et al. 1994; Imig et al. 1990; Middlebrooks and Pettigrew 1981; Rajan et al. 1990). There are reports that small regions of cortical fields outside of primary auditory cortex do show systematic shifts in azimuthal tuning (e.g., Kujirai and Suga 1983; Middlebrooks et al. 1998), suggesting the presence of local topographies that may serve spatial processing. However, the caveat commonly applied to such representations is that they are apparent only near threshold and that spatial tuning deteriorates as sound intensity increases. This is in contrast to the more robust topographic representations of space reported in the superior colliculus (King and Hutchings 1987; Palmer and King 1982; Wise and Irvine 1985). This contrast has led to hypotheses that the mammalian auditory cortex may encode

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space through population codes that do not require a topographically organized substrate (e.g., Eggermont and Mossop 1998; Middlebrooks et al. 1994, 1998; review, Cohen and Knudsen 1999).

The present study provides the first survey of the primary auditory cortex of a bat that relies heavily on both echolocation and passive sound localization and seeks to offer insights into the organizational features present in both echolocators and passive listeners. It maps the cortex of the pallid bat (*Antrozous pallidus*) in the dimensions of frequency representation, selectivity for behaviorally relevant sounds, and binaural response properties and describes a systematic organization of sensitivity to IIDs that may provide a substrate for passive sound localization. The pallid bat is a “gleaner” that uses high-frequency echolocation for general orientation and attends to low-frequency, prey-generated noise transients to detect and locate terrestrial prey (Bell 1982; Fuzessery et al. 1993). These two distinct sounds, the downward FM sweep of the echolocation pulse and noise transients, serve as physiological probes to identify regions that serve echolocation and passive sound localization. They have been used to demonstrate that a high degree of selectivity for these sounds is present at the level of the inferior colliculus (IC) and that these sounds are processed through two anatomically and functionally segregated regions of the IC (Fuzessery 1994; Fuzessery and Hall 1996).

As will be described in this report, these two pathways project on adjacent regions of the auditory cortex. With regard to binaural response properties, the present study provides three main findings. First, as in other species studied, neurons of the same binaural type are organized in homogeneous clusters. Second, there is an asymmetrical distribution of binaural types across the two regions serving echolocation and passive listening, suggesting that different binaural mechanisms may serve these behaviors. Third, within the low-frequency, noise-preferring region that serves passive sound localization, neurons are systematically organized with respect to their sensitivity to IIDs, and this IID sensitivity remains stable with changes in intensity level. This finding suggests the presence of a topographically organized representation of a spatial cue in the mammalian auditory cortex.

## METHODS

Pallid bats were collected in Arizona and New Mexico and held in captivity in a  $16 \times 11$  ft<sup>2</sup> room, where they were given the freedom to fly and hunt crickets. The room was maintained at a reversed 12:12 light cycle. A few days prior to surgery, the bats were fed mealworms to increase body weight. All procedures followed the animal welfare guidelines required by the National Institutes of Health and Institutional Animal Care and Use Committee.

### Surgical procedures

Recordings were obtained from bats that were lightly anesthetized with Metofane (methoxyflurane) inhalation, followed by an intraperitoneal injection of pentobarbital sodium (30  $\mu$ g/g body wt) and acepromazine (2  $\mu$ g/g body wt). To expose the auditory cortex (Fig. 1), the head was held in a bite bar, a midline incision was made in the scalp, and the muscles over the dorsal surface of the skull were reflected to the sides. The front of the skull was scraped clean and a layer of glass microbeads applied, followed by a layer of dental cement. The bat was then placed in a Plexiglas restraining device. A cylindrical aluminum head pin was inserted through a cross bar over

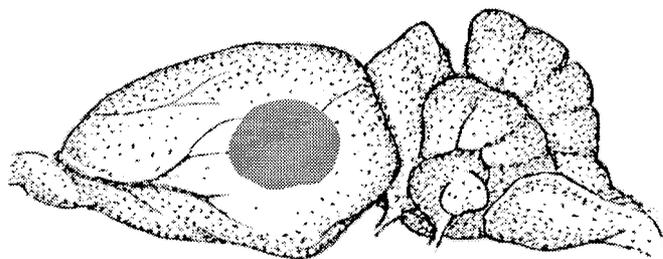


FIG. 1. The brain and the auditory cortex of the pallid bat. The shaded area in posterior neocortex shows the location of the auditory cortex from which recordings were obtained.

the bat's head and cemented to the previously prepared region of the skull. This pin served to hold the bat's head secure during the recording session. The location of the auditory cortex was determined relative to the rostrocaudal extent of the midsagittal sinus, the distance laterally from the midsagittal sinus, and the location of a prominent lateral blood vessel that travels parallel to the midsagittal sinus. The size of the exposure was usually  $\sim 2 \times 2$  mm<sup>2</sup>. Exposed muscle was covered with petroleum jelly (Vaseline), and exposed brain surface was covered with paraffin oil to prevent desiccation.

### Recording procedures

Experiments were conducted in a heated (85–90°F), sound-proofed chamber lined with anechoic foam. Bats were kept lightly anesthetized throughout the course of the experiments with sedation maintained by inhalation of Metofane and additional pentobarbital sodium (one-third of presurgical dose) injections. Stimuli were generated using Modular Instruments and Tucker Davis Technologies digital hardware, and custom-written software (Fuzessery et al. 1991). The waveforms were amplified with a stereo amplifier and presented as closed-field stimuli through Infinity emit-K ribbon tweeters fitted with funnels that were inserted into the pinnae and sealed with petroleum jelly. This procedure attenuated speaker intensity level at the opposite ear by  $\geq 30$  dB and permitted presentation of the  $\pm 25$  dB IIDs that the bat normally experiences (Fuzessery 1996) without significant acoustic interactions between speaker outputs. The speaker-funnel frequency response curve showed a gradual increase of 20 dB from 6 to 70 kHz, as measured with a Bruel and Kjaer 1/8-in microphone placed at the tip of the funnel. Bandpass filtering of noise stimuli was performed using a Krohn-Hite (model 3550) filter (24 dB/octave attenuation slope).

Using glass microelectrodes (1 M NaCl, 3–10 M $\Omega$  impedance), recordings were obtained at depths between 200 and 700  $\mu$ m. Penetrations were made orthogonal to the surface of the cortex. Electrode penetrations were placed as uniformly as possible, at increments of 50–100  $\mu$ m. Response magnitudes and poststimulus time histograms were acquired and stored with the use of Modular Instruments high-speed clock controlled by custom software. Responses were quantified as the total number of spikes elicited over 30 stimulus presentations.

Results are based on both single- and multiunit cluster recordings. The response properties of the majority of cortical sites were quantified with multiunit cluster recording due to the need to rapidly survey as many sites as possible. In these cases, measures of selectivity for relevant complex sounds are therefore influenced by the least selective neurons in the cluster. Nonetheless, the degree of selectivity was similar in both the single- and multiunit populations, suggesting that neurons in close anatomical proximity had similar response properties. For each cortical penetration, response properties were measured at two electrode depths separated by  $\geq 200$   $\mu$ m at depths associated with cortical layers 3–5. In the great majority of cases, there was little difference in the response properties measured at the two depths of penetration.

### Data acquisition

Frequency representation was studied in 34 cortices from 22 bats. Pure tones (5–75 kHz, 5- to 10-ms duration, 1-ms rise/fall times, 1-Hz repetition rate) were used to determine best frequency (BF) and frequency tuning. BF was defined as the frequency that elicited a response to at least five successive stimulus repetitions at the lowest intensity. The intensity was then increased in 5-dB steps to record tuning characteristics.

Selectivity for behaviorally relevant, complex sounds and binaural response properties were mapped in 27 cortices from 19 bats. Choice of test stimuli were based on a knowledge of the bat's auditory behavior and previous studies of the selectivity present in the bat's IC. The pallid bat attends to noise transients to detect and locate prey. Its echolocation pulse is a short, 2- to 6-ms duration, 60 to 30 kHz downward FM sweep (Brown 1976; Fuzessery et al. 1993). Two regions of the IC are known to exhibit specializations suited to processing these sounds (Fuzessery 1994, 1997; Fuzessery and Hall 1996, 1999). A low-frequency, noise-selective region contains a large percentage of neurons that respond maximally or exclusively to short-duration (<10 ms) noise bursts. A high-frequency region contains a large percentage of neurons that respond selectively or exclusively to the spectrum, duration, and direction of the downward FM sweep of the echolocation pulse.

Similar forms of selectivity were expected in the auditory cortex. Therefore the following short-duration ( $\leq 10$  ms) sounds were used as probes to test for functional specialization: pure tones at BF, band-pass noise (1–100 kHz), band-pass noise, and upward and downward FM sweeps of identical duration (5 ms) and spectrum (30–50 or 30–60 kHz).

Two forms of selectivity that will be emphasized are for the downward FM sweep of the echolocation pulse and for noise. FM sweep-selective neurons met the following criteria: they responded preferentially to the downward sweep direction over spectrally and temporally identical upward FM sweeps (indicating selectivity for sweep direction), over individual tones within the sweep (indicating an FM sweep was required) and to broadband noise and 30- to 60-kHz band-pass filtered noise that contained the same frequencies as the downward FM sweep (indicating an appropriate sequence of frequencies, and not a simultaneous presentation of the same frequency band, was required).

Neurons termed noise selective responded preferentially to noise relative to individual tones. Neurons termed band-pass noise-selective responded preferentially to band-pass filtered noise relative to broadband noise and individual tones within the excitatory band. To determine the excitatory and inhibitory bandwidths of band-pass noise-selective neurons, the minimum bandwidth that evoked a maximum response was first determined. The bandwidth was then expanded to determine whether or not the response was suppressed by inclusion of additional frequencies. Analog filtering of a broadband noise was used to create band-pass noise so the spectral energy in the band was the same in both signals; i.e., the band-pass signal was not amplified to produce the same overall intensity level as the broadband signal.

Neurons were classified as either selective or specialists for the preceding test stimuli. Selective neurons responded to more than one test stimulus but had thresholds for one stimulus that were 10 dB lower or elicited responses that were  $\geq 30\%$  greater. Neurons termed specialists responded strongly to only one test stimulus; responses to other sounds were  $\leq 10\%$  of the maximum response.

Binaural response type was determined with the best stimulus fixed at at least three different contralateral intensities, from 10 to 40 dB above threshold, while the intensity at the ipsilateral ear was varied from 30 dB below to 30 dB above contralateral (CL) intensity, in 5 dB steps. Neurons were considered binaurally inhibited if the response to binaural stimulation at any IID within the test range was  $\leq 30\%$  of the response to contralateral stimulation alone. Conversely, a neuron was considered binaurally facilitated if the response was  $\geq 30\%$  of the

response to contralateral stimulation. IID sensitivity was quantified in 19 cortices by measuring the inhibitory threshold, defined as the IID at which a neuron was maximally inhibited. IID functions were determined at more than one CL intensity and averaged to provide an inhibitory threshold value for each site.

### RESULTS

This section contains illustrations of the functional organization of the pallid bat auditory cortex, mapped in multiple dimensions (frequency representation, selectivity for noise or downward FM sweeps, binaural response properties, and IID sensitivity) to establish their anatomical relationships. These dimensions will be dealt with in the preceding sequential order. Therefore we will refer back to some of these maps as these topics are addressed. We focus on the organization of two specialized regions that lie along the most orderly tonotopic axis of the primary auditory cortex. A description of the full extent of the auditory cortex and its subdivisions is beyond the scope of this report.

#### Tonotopy

All cortices mapped showed a general increase in frequency tuning along the caudolateral to rostromedial axis (Figs. 2A, 3A, 4A, and 5A). In cortices that were mapped to their most rostral extents (Fig. 2A), there was an abrupt change in BFs from  $>40$  to  $<12$  kHz at the rostral end of the acoustically responsive region of cortex, with no representation of intermediate frequencies. This is therefore considered a discontinuity in frequency representation rather than a reversal of tonotopy.

Frequency representation was variable across individuals and also between the left and right cortices of individuals. Variability arose from both differences in anatomical locations of isofrequency regions and the amount of representation of certain frequency bands. However, the common trend observed in all cortices was that the 24- to 32-kHz band was consistently under-represented, while the higher and lower frequency bands of 10–22 and 34–44 kHz were over-represented. A summary of the best frequencies from all recording sites (Fig. 6) shows this roughly bimodal distribution of best frequencies. The two over-represented frequency bands of 10–22 and 34–44 kHz will be referred to as the low- and high-frequency bands, respectively. The most orderly change in frequency representation occurred along the rostrocaudal axis. A more abrupt transition from the low- to high-frequency representation occurred along the lateromedial axis (e.g., Figs. 3A and 4A), indicating that the region of high-frequency representation extended caudally and medially over low-frequency representation.

#### Selectivity for behaviorally relevant sounds

The low- and high-frequency domains correspond, respectively, to centers of the spectral bands used in passive sound localization and echolocation. Selectivity for the downward FM sweep of the echolocation pulse was confined largely to the high-frequency region, while a preference for noise over single tones occurred primarily in the low-frequency region. However, there was overlap; noise-selective neurons were also found in the high-frequency region.

Representative examples of selectivity for downward FM







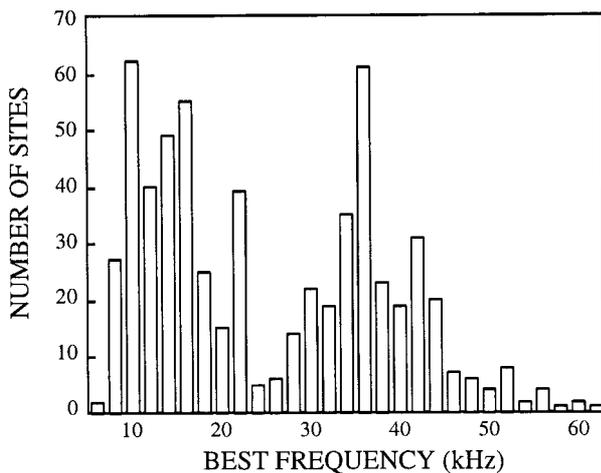


FIG. 6. Distribution of BFs in the pallid bat auditory cortex. BFs had an approximately bimodal distribution with peaks between 10–16 and 34–45 kHz ( $n = 680$ ). Each bin in the histogram encompasses a 2-kHz range of BF.

For example, the cortical maps in Fig. 8 show two clusters of band-pass-selective neurons located caudomedial and caudolateral to a large cluster of neurons that responded maximally to broadband noise.

#### Binaural response properties

The binaural response properties of neurons in the pallid bat auditory cortex have been previously described (Lohuis and Fuzessery 2000); a brief recapitulation is provided here (Fig. 9). Binaural response properties were categorized in terms of relative responses to monaural and binaural stimulation and by the shapes of their IID functions. Seven binaural types and four IID function configurations were observed. The two metrics showed consistent relationships. The convention used to classify aural type is response to contralateral and ipsilateral monaural stimulation (E, excitatory; O, no effect) and response to binaural stimulation (O, no effect; F, facilitation; I, inhibition). For example, a monaural neuron excited by contralateral stimulation, and with no effect from binaural stimulation, is represented as EO/O. Because they are monaural, their IID functions were flat (Fig. 9E). Binaurally inhibited neurons (EO/I) were excited by contralateral stimulation and inhibited by ipsilateral stimulation (Fig. 9A). Their IID functions were stepped, exhibiting a relatively constant maximum response at IIDs favoring the contralateral sound field that then typically showed a complete inhibition as relative ipsilateral intensity increased. Neurons with mixed binaural interactions (EO/FI; Fig. 9, B and D) were excited by contralateral stimulation, but their responses were increased (facilitated) by binaural stimulation over a limited IID range, typically between IIDs of  $\pm 10$  dB. EO/FI neurons had step-peaked IID functions, responding submaximally to IIDs favoring the contralateral ear, rising to a maximum response near 0 dB IID ( $\geq 30\%$  of monaural response) and then typically being completely inhibited as relative ipsilateral intensity was increased. OO/FI neurons responded only to binaural stimulation (monaural stimulation evoked  $\leq 10\%$  of maximum response, Fig. 9C). OO/FI neurons had peaked IID functions with a maximum response occurring at IIDs near 0 dB. These two binaural types (EO/FI and OO/FI) were grouped together because their IID functions sometimes

changed from one form to the other as a function of absolute intensity (Fig. 9D). Binaurally facilitated neurons (EO/F) responded to contralateral stimulation but increased their response by  $\geq 30\%$  with binaural stimulation (Fig. 9F). The shapes of their IID functions were variable; the example shown was facilitated at IIDs favoring the ipsilateral ear. Binaurally excited neurons (EE/O and EE/F) were excited by monaural stimulation of either ear; the latter group elicited a greater response ( $\geq 30\%$ ) to binaural stimulation.

A striking feature of the pallid bat auditory cortex was a consistent association between frequency tuning, response selectivity, and binaural response properties (Figs. 2C, 3C, 4C, and 5C). This relationship is summarized for 642 multiunit recordings in Fig. 10A, and 93 single-unit recordings in Fig. 10B. The low-frequency region was dominated by EO/I and EO/FI neurons. Seventy percent of all neurons tuned  $< 20$  kHz were EO/I. A large homogenous cluster of EO/I neurons was found in all cortices, and most had a smaller cluster of EO/FI neurons located rostralateral to the EO/I cluster. Monaural neurons were rarely encountered in the low-frequency region, and EO/F neurons were not found at all.

The high-frequency region had a more diverse array of binaural types: EO/O, EO/FI, EO/F, and EO/I (Figs. 2C, 3C, 4C, and 5C). More than 75% of sites tuned  $> 40$  kHz were monaural or had mixed binaural interactions. A consistent feature in all cortices was a cluster of EO/O neurons located at the caudal boundary of the high-frequency region, so as one progressed from the low-frequency to the high-frequency regions, there was an abrupt change in binaural type (from EO/I to EO/O) that attended changes in frequency representation and response selectivity. EO/F and EO/FI neurons were typically located lateral and rostral of the cluster of monaural neurons, while EO/I neurons were typically encountered only in the extreme rostromedial aspect of the high-frequency region.

A curious feature of the pallid bat auditory cortex is the almost complete absence of EE-type neurons excited by monaural stimulation of either ear. Only three such neurons were recorded; all were located in the high-frequency region.

#### Intrinsic organization of binaural clusters in the low-frequency region

The binaural response properties of the large low-frequency region were examined in greater detail to determine whether any features of their sensitivity to binaural disparities varied topographically. We focused on the sensitivity to IIDs within the clusters of EO/I and EO/FI neurons. Both binaural types responded maximally to IIDs favoring the contralateral excitatory ear. As the intensity level increased at the ipsilateral ear, the great majority of neurons were completely inhibited. IID sensitivity was quantified in terms of a neuron's inhibitory threshold, defined as the least negative IID value at which a neuron is maximally inhibited. Positive inhibitory threshold values indicate IIDs that favor the contralateral ear; negative values favor the ipsilateral ear.

Inhibitory thresholds were found to be organized in a graded fashion in all cortices studied. Figures 4D and 5D show the distribution of inhibitory thresholds within the context of frequency representation, response selectivity and binaural types. Figure 11 shows the distribution of inhibitory thresholds within

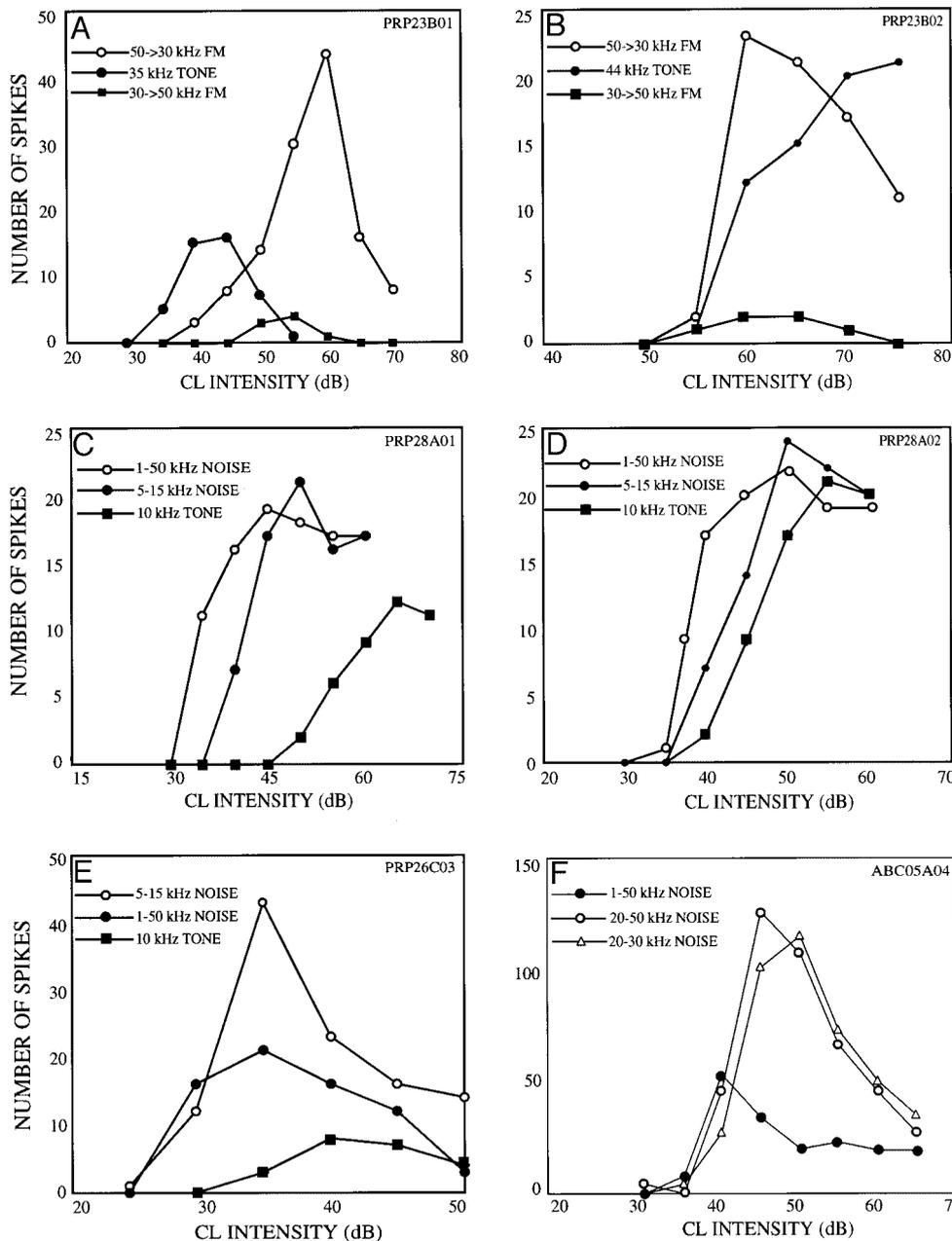


FIG. 7. Response selectivity of neurons in the pallid bat auditory cortex. *A*: a downward FM sweep-selective site. This neuron did not respond to equal duration (6 ms) tones, noise (not shown), or upward sweep. *B*: a site that responded equally well to BF tone and downward FM sweep but not to an equal-duration (5 ms) upward sweep or noise. *C*: a site categorized as noise-selective based on differences in thresholds. This neuron responded equally well to both broadband and narrowband noise, but threshold for BF tone was 15 dB higher than for noise. *D*: this neuron responded equally well to noise and BF pure tone. *E*: a site categorized as low-frequency, band-pass selective based on response magnitudes. *F*: a high-frequency band-pass selective site.

the noise-selective region of four other cortices. In each of these maps, a small cluster of neurons with positive inhibitory thresholds was at least partially surrounded by neurons with more negative inhibitory thresholds. The result was a roughly radial organization in which, as one moved further from the small cluster of neurons with positive inhibitory thresholds, a progressively louder intensity at the ipsilateral ear was required to maximally inhibit the neurons. The range of inhibitory thresholds and their topographic distributions varied considerably across individuals, but the graded nature of the shifts in inhibitory thresholds was present in all individuals.

The inhibitory threshold of a neuron will determine the medial border of its spatial receptive field (Fuzessery et al. 1985; Wenstrup et al. 1988a,b) because it will stop responding at azimuthal locations where maximally inhibitory IID values occur in the sound field. However, inhibitory thresholds must

remain constant with changes in absolute intensity level for the receptive field borders to remain stable. To test the stability of inhibitory thresholds, binaural functions were obtained over a range of fixed contralateral intensities. A metric derived by Irvine and Gago (1990) was used to obtain the ratio of changes in inhibitory threshold relative to changes in absolute intensity level. For example, if the inhibitory thresholds of a neuron were 3, 6, and 7 dB at contralateral intensities of 30, 40, and 50 dB, respectively, then the inhibitory threshold/contralateral intensity range ratio is 0.2 [i.e.,  $(7 - 3)/(50 - 30) = 4/20 = 0.2$ ]. The distribution of this ratio (Fig. 12) shows that >50% of the low-frequency, noise-selective neurons sampled had a ratio <0.2, and >80% of these neurons had a ratio <0.4. These results suggest that the inhibitory thresholds of the majority of neurons in the low-frequency, noise-selective region would remain quite stable with changes in absolute intensity level,

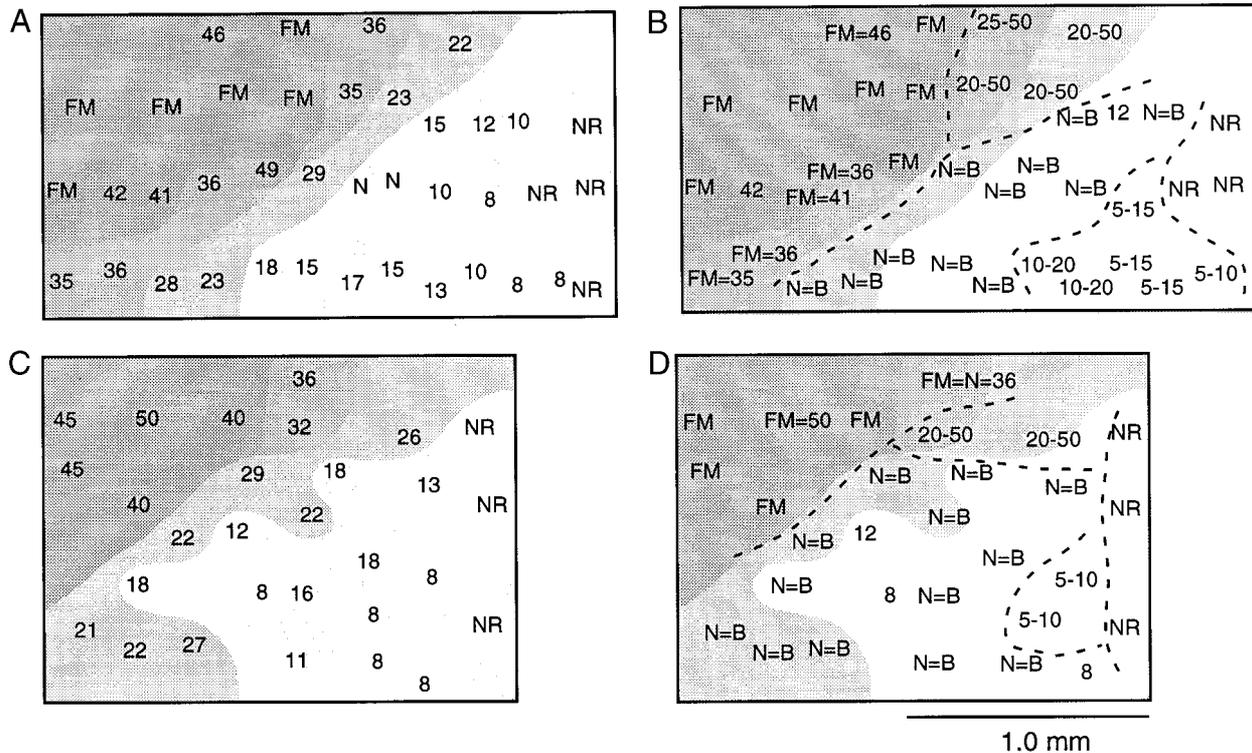


FIG. 8. Topographical distribution of band-pass selectivity within the noise-selective region. BF distribution (A and C) and band-pass selectivity (B and D) in 2 cortices of the pallid bat show that neurons that preferred a narrow band of noise around BF were located separately from neurons that responded equally well to band-pass noise and broadband noise. ---, separate neurons with various ranges of band-pass selectivity. Sites denoted as "N = B" did not prefer narrowband noise over broadband noise. Sites shown with a range of frequencies responded best for that narrowband of frequencies. Neurons that preferred low-frequency band-pass noise (5 to 20 kHz range) were located in the caudolateral portion of noise-selective region, while neurons that preferred high-frequency band-pass noise (20 to 50 kHz range) were located in the caudomedial portion. NR, no response for the search stimuli used. Sites indicated as a single frequency responded best to the BF tone.

and could provide consistent information about the azimuthal location of a sound source.

#### DISCUSSION

At least one orderly cortical representation of frequency has been found in all species studied (review, Merzenich and Schreiner 1991). The auditory cortex of the pallid bat is no exception; tonotopy progresses from low to high frequencies along the caudolateral to rostromedial axis. In bats, functionally significant frequency bands associated with echolocation are over-represented (e.g., Dear et al. 1993; Suga 1984). The present study provides the first description of the auditory cortex of a "gleaner" that relies on low-frequency passive sound localization as well as echolocation. The tonotopy of its auditory cortex reflects these dual specializations. Both the peak spectral energy in its echolocation pulse (35–45 kHz), and lower frequencies (10–20 kHz) used in the passive sound localization of prey, are over-represented. Intermediate frequencies between 24 and 32 kHz are under-represented. The result is an abrupt transition in frequency representation at the boundary between regions serving passive sound localization and echolocation. These two cortical regions contain a high percentage of neurons that respond preferentially to either the downward FM sweep of the echolocation pulse or low-frequency noise used in the passive sound localization of prey, a finding that lends weight to the supposition that these regions indeed subserve these functions.

A selectivity for behaviorally relevant sounds in the auditory cortex at least partially reflects what is already present at the level of the IC, where two functionally distinct regions exhibit similar frequency representation and selectivity (Fuzessery 1994). The central nucleus of the IC (ICC) of the pallid bat contains a hypertrophied region of low-frequency representation that extends along the lateral wall. This lateral extension represents frequencies from 5 to 40 kHz with an overrepresentation of 10–25 kHz and contains a significant percentage of neurons (23%) that respond selectively or exclusively to noise transients used in passive sound localization. The region of high-frequency representation in the pallid bat ICC contains a large percentage of neurons that are remarkably selective, even among bat species, for the downward FM sweep of the echolocation pulse, with a third of the neurons responding exclusively to the downward FM sweep.

These exaggerated expressions of selectivity in the pallid bat IC may serve to functionally isolate two parallel pathways dedicated to echolocation and passive listening (Fuzessery 1994). Because the pallid bat must attend to both streams of acoustic information while hunting, these functionally distinct pathways may act as filters that facilitate the pallid bat's ability to segregate these streams. Present results suggest that these two ascending pathways project on adjacent regions of auditory cortex along the main tonotopic axis. With its overrepresentation of low and high frequencies and underrepresentation of intermediate frequencies, the tonotopic axis of the

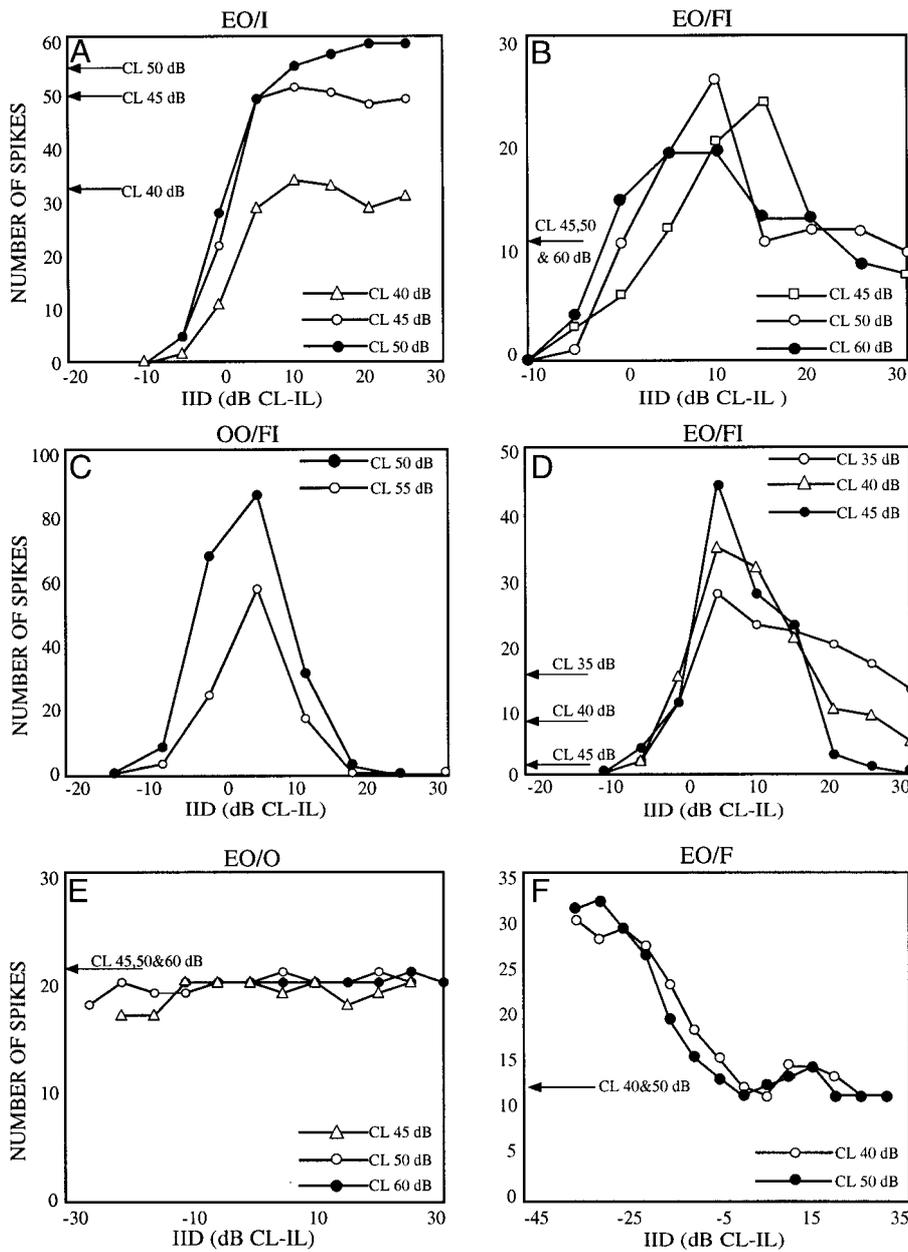


FIG. 9. Classification of binaural types. The convention used to classify aural type is response to contralateral and ipsilateral monaural stimulation (E, excitatory; O, no effect; F, facilitation; I, inhibition). A: binaurally inhibited neuron (EO/I). Monaural and binaural responses were tested with 1 to 50 kHz noise (BF = 16 kHz). B: neuron with mixed binaural interactions (peaked function). Response tested with a 50 to 30 kHz downward sweep (BF = 41 kHz). C: neuron with mixed binaural interactions (stepped-peak function). Response tested with 1 to 50 kHz noise (BF = 22 kHz). D: neuron for which binaural property changes from OO/FI to EO/FI with CL intensities. Response tested with 50 to 30 kHz downward FM sweep (BF = 42 kHz). E: monaural neuron (EO). Response tested with 50 to 30 kHz downward FM sweep (BF = 39 kHz). F: binaurally facilitated neuron (EO/F). Response tested with 60 to 30 kHz downward FM sweep (BF = 49 kHz). The stimulus used to test binaural properties of each of these neurons was the most excitatory stimulus. ←, response to stimulus presented monaurally to the CL ear.

pallid bat auditory cortex appears to be organized more to segregate two forms of information processing than to simply re-represent the cochlear partition.

The only other gleaner bat in which frequency representation has been studied is *Megaderma lyra* (Rubsamen et al. 1988). Like the pallid bat, the IC of *Megaderma* also exhibits an over-representation of low frequencies used in passive sound localization, and this also occurs in a lateral hypertrophy of what is presumably the ICC. Many neurons in this low-frequency region also showed preferential or exclusive responses to noise. It appears that two phylogenetically distant species of bats that have converged on the use of low-frequency, prey-generated noise for hunting show similar neural specializations at the level of the IC.

Finally, a peculiar feature of frequency representation in the pallid bat auditory cortex is an abrupt change in frequency representation, from 30–40 to 8–10 kHz, at the extreme rostral

end of the tonotopic axis. We mention this because a similar discontinuity in tonotopy has also been reported in the same location in two other bat species (Dear et al. 1993; Jen et al. 1989; Radtke-Schuller and Schuller 1995). The functional significance of this abrupt change to low-frequency representation is not clear.

#### Distribution of binaural response properties

After sound frequency, the stimulus dimension that has received the most attention in terms of cortical representation is binaural response type. A common feature in all species studied is a clustering of neurons according to aural type (e.g., Kelly and Sally 1988; Reale and Kettner 1986; Recanzone et al. 1999; Rutkowski et al. 2000). In the cat (Imig and Adrian 1977; Middlebrooks et al. 1980) and ferret (Kelly and Judge 1994), these clusters appear as binaural bands that run orthog-

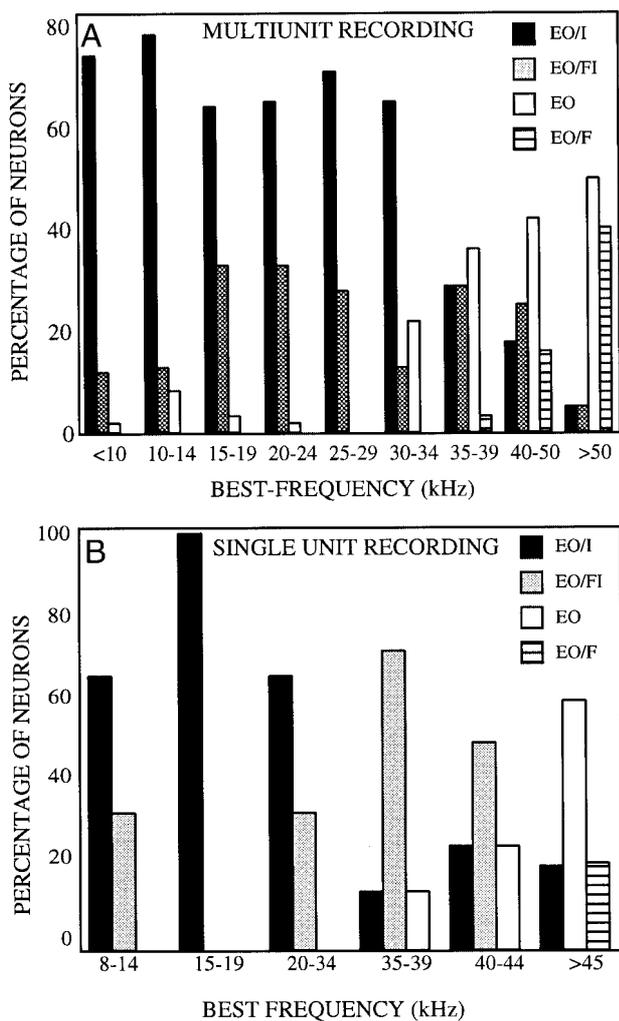


FIG. 10. Frequency-dependent distribution of binaural types in the pallid bat auditory cortex. *A*: summary of multiunit cluster data. *B*: summary of single unit data. Most low-frequency sites were binaurally inhibited (EO/I), while a smaller number of sites had mixed binaural interactions (EO/FI). With increasing frequencies, the number of binaurally inhibited sites decreased and the number of monaural (EO) and binaurally facilitated (EOF) sites increased.

onal to isofrequency contours, suggesting that each isofrequency band has access to different binaural types.

The auditory cortices of echolocating bats also show clustered organization but not all isofrequency domains contain all aural types. In the mustached bat auditory cortex, for example, the hypertrophied 60-kHz isofrequency region [the Doppler-shift constant frequency (DSCF) region] has binaurally inhibited neurons in its dorsal aspect, while binaurally excited neurons dominate the ventral aspect. Binaurally inhibited neurons are present throughout the remainder of the tonotopic axis, but binaurally excited neurons are restricted to the DSCF region (Liu and Suga 1997). Similarly, in the big brown bat, a single cluster of binaurally excited neurons is limited to neurons tuned >30 kHz (Shen et al. 1997). Binaural types are thus asymmetrically distributed across frequency, perhaps in a task-dependent manner. In the mustached bat 60-kHz region, the binaurally excited neurons, with their broader spatial receptive fields, may serve detection, while binaurally inhibited neurons may serve localization (Suga 1984).

The pallid bat auditory cortex also has an asymmetrical

distribution of aural types across the low- and high-frequency regions. The most distinctive feature of the low-frequency region was a large, homogeneous cluster of binaurally inhibited (EO/I) neurons. In contrast, the high-frequency region contained a cluster of monaural (EO/O) neurons that were not found in the low-frequency region. This monaural cluster invariably occurred along the boundary between the two regions, resulting in abrupt changes in frequency tuning, response selectivity, and binaural type. Other aspects of binaural representation did not show this contrast between the two cortical regions. Along the lateral aspect of the boundary between the low- and high-frequency regions, the cluster of neurons with mixed binaural interactions (EO/FI) lay astride the boundary and, in some individual cortices, was shared by the two regions. Both the low- and high-frequency regions contained a cluster of EO/I neurons, but these clusters were discontinuous.

The asymmetrical distribution of aural types across the low- and high-frequency regions may be related to their roles in echolocation and passive sound localization. The sharp directionality of the pallid bat external ears at high frequencies for sounds near the center of the sound field (Fuzessery 1996) predicts that both monaural neurons and EO/FI neurons with IID functions that peak between  $\pm 10$  dB IID will be most sensitive to echoes returning along the bat's flight path. In contrast, ear directionality is broad over the 10- to 20-kHz band used for passive sound localization, and the spatial sensitivity of low-frequency neurons would presumably require sharpening through binaural inhibition to provide adequate spatial information. The large cluster of binaurally inhibited neurons in the low-frequency region may be needed to extract the spatial information required for passive sound localization of terrestrial prey.

One unexpected feature of the pallid bat cortex is the almost complete absence of neurons excited by monaural stimulation of either ear (EE), particularly since this binaural type is common in most species that have been examined (cat: Reale and Kettner 1986; rat: Kelly and Sally 1988; ferret: Kelly and Judge 1994; guinea pig: Rutkowski et al. 2000; big brown bat: Shen et al. 1997).

#### *Intrinsic organization of the low-frequency region*

The nature of spatial representation in the mammalian auditory cortex has proven a difficult issue. The clustering of aural types in several species, and their relationship to frequency representation, suggests a modular organization, with one function being the extraction of spatial information. Free-field stimulation studies have reported that neurons are also clustered with respect to spatial sensitivity (Clarey et al. 1994; Imig et al. 1990; Rajan et al. 1990). However, unlike the superior colliculus, no topographic organization of binaural cues or spatial sensitivity that might provide an ordered representation of space has been found in the mammalian auditory cortex (review, Cohen and Knudsen 1999). Large receptive fields and effects of intensity level, which tend to degrade spatial tuning observed near intensity thresholds, have led to suggestions that auditory space may be represented in the cortex through nontopographically organized population codes, using such information as the temporal pattern of neural spikes, mean spike latencies, or coordinated firing among multiple neurons. For example, using artificial neural network

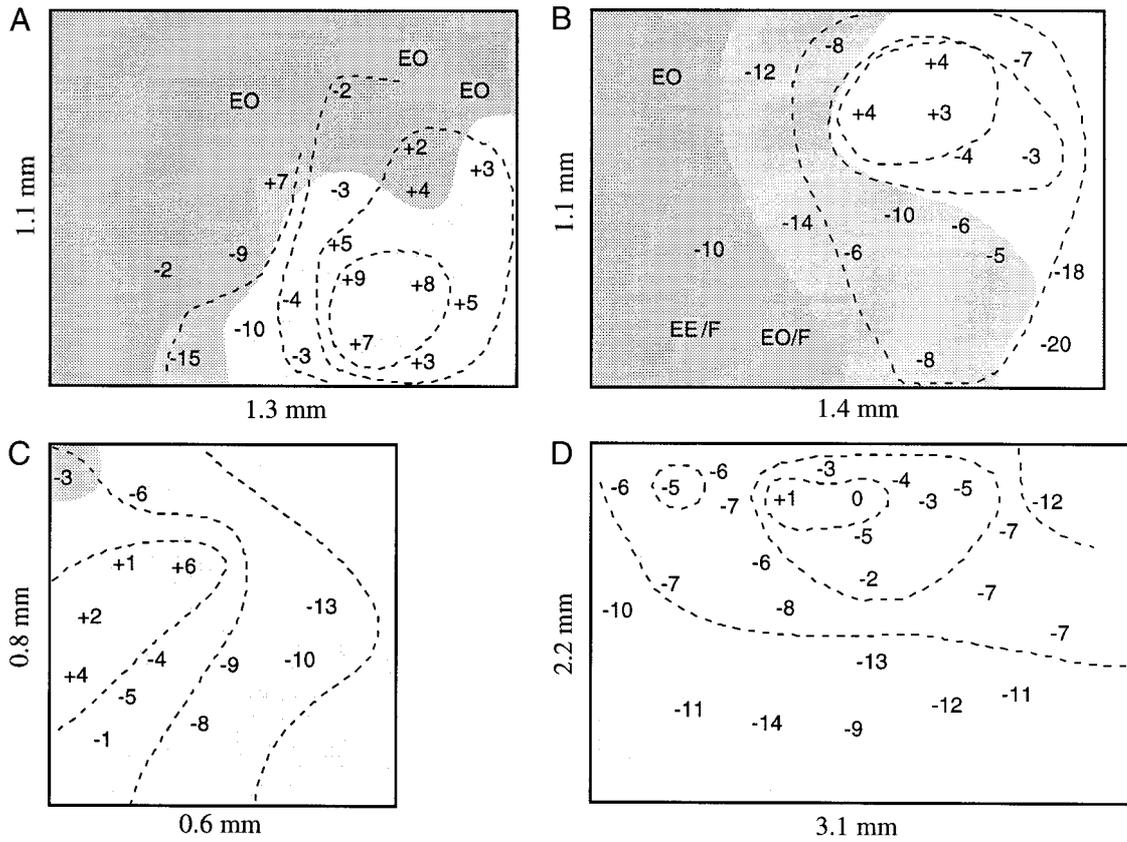


FIG. 11. Maps of inhibitory thresholds within the noise-selective region. Inhibitory thresholds were arranged systematically within the low-frequency region such that a positive cluster was partially surrounded by increasingly more negative values. These neurons had BF between 8 and 30 kHz and were either EO/I or EO/FI. The iso-BF contour shading scheme is similar to Fig. 3.

modeling based on cat cortical data, the temporal spike patterns of single neurons were found to carry more spatial information than spike counts (Middlebrooks et al. 1994, 1998). Most of these neurons appeared to encode sound locations over a wide range of azimuths, suggesting a code based on information extracted by a distributed population of neurons. Other modeling data suggest that relative spike counts across a population of neurons may also contribute to sound localization (Fu-

rukawa et al. 2000). The common theme underlying these proposed codes is a representation of space that does not require a systematic anatomical spatial correlate. An exception is a spatial representation based on tonotopy, suggested in the big brown bat (Jen et al. 1989). Frequency-dependent changes in ear directionality could provide an orderly topographic shift in the spatial sensitivity of cortical neurons along the tonotopic axis. However, without additional constraints on receptive field size, this mechanism is likely to be effective only at threshold intensity levels.

The low-frequency region of the pallid bat auditory cortex offers evidence of a topographic organization of binaural sensitivity. Neurons in the EO/I and EO/FI clusters that dominate this region are topographically organized with respect to the IID at which they are maximally inhibited, i.e., its inhibitory threshold. In individual cortices with the most orderly expressions, this organization takes a concentric or semiconcentric form in which a small cluster of neurons with the most positive inhibitory thresholds (inhibited at IIDs favoring the contralateral ear) are surrounded by neurons with inhibitory thresholds that become more negative as one moves away from this central cluster.

This topographic organization may extract spatial information in the following manner. Combined closed- and free-field studies have demonstrated that the IID sensitivity of a binaurally inhibited neuron determines the medial border of its spatial receptive field (e.g., Fuzessery and Pollak 1985; Wenstrup et al. 1988a,b). Therefore knowledge of the IID at which

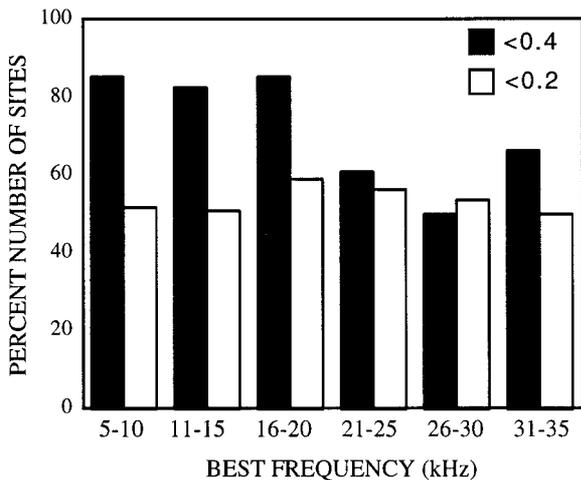


FIG. 12. Effect of absolute intensity on IID sensitivity. The inhibitory threshold/CL ratio was  $< 0.4$  for  $> 80\%$  of low-frequency, noise-selective neurons. It was  $< 0.2$  for  $> 50\%$  of these neurons. This suggests that the values of inhibitory thresholds are relatively stable across intensity.

a neuron is inhibited, and the distribution of IIDs in the sound field, can be used to predict its spatial receptive field. Because the inhibitory thresholds of neurons in the low-frequency region vary systematically with anatomical location, the medial borders of spatial receptive fields will also vary with location. Consequently, activity levels across the cortex can be expected to vary systematically with horizontal sound location. The accuracy of this spatial information is dependent on the stability of the inhibitory thresholds with changes in absolute intensity; present results indicate that inhibitory thresholds remained stable at least over a range of 15–20 dB above threshold.

A population code that could represent horizontal location in the pallid bat cortex is the same suggested to operate in the IC of the mustached bat (Fuzessery et al. 1985; Wenstrup et al. 1986). In this species, the hypertrophied 60-kHz region contains a population of binaurally inhibited neurons whose inhibitory thresholds vary systematically along the vertical axis of the IC. The proposed population code is based on both the percentage of active neurons within the population, and the anatomical locations of these neurons. A sound deep in the excitatory, contralateral field will excite all neurons. As the sound moves toward the ipsilateral field, an increasingly greater percentage of the population will stop firing as their inhibitory thresholds are encountered. Because the population is anatomically ordered with respect to inhibitory thresholds, changes in activity levels across the population will also be ordered. In the pallid bat auditory cortex, this population code would take the form of radial shifts in activity levels around the region of positive inhibitory thresholds (for further information, see Razak and Fuzessery 2000).

Whether an ordered representation of sensitivity to binaural disparity values is a common feature of the mammalian auditory cortex is unclear. If it is present, it may be found within the intrinsic organization of binaural clusters. However, this intrinsic organization may be obvious only in species like the pallid bat, in which considerable cortical tissue has been devoted to the hypertrophied binaural clusters tuned to a limited, low-frequency band used in accurate passive sound localization. Other mammalian species may spread spatial representation across multiple isofrequency domains of primary auditory cortex to extract the required spectral cues, or may dedicate specific nonprimary cortical fields to this task (e.g., Imig and Samson 2000; Rauschecker and Tian 2000).

We should emphasize that we are not proposing that the low-frequency region provides a point-to-point representation of space as seen, for example, in the optic tectum of the barn owl (Knudsen 1982), and it is unlikely that a free-field stimulation analysis of spatial tuning across this cortical region would reveal such a map. The auditory cortex is responsible for identifying sounds as well as localizing them. The construction of a “space map” might interfere with cortical representations of other stimulus features. Moreover, these other features would have to be re-represented across the map to permit identification because only a limited portion of the population in a point-to-point space map would be active for a given sound location. The representation of a binaural cue, as described in the preceding text, does not have this limitation. Because the majority of the EO/I and EO/FI neurons in the population have negative inhibitory thresholds and would be suppressed only at IIDs that strongly favor the inhibitory, ipsilateral sound field, most of the neuronal population will remain active with

changes in sound location, allowing other stimulus dimensions to be represented within the same population.

#### *Band-pass noise selectivity and sharpened spatial tuning*

The population code for spatial representation described in the preceding text is an oversimplification in that it deals only with the IID sensitivity of neurons in the low-frequency region. This region represents frequencies ranging from 8 to 40 kHz. The directionality of the pallid bat ear, and consequently the spatial distribution of IIDs, changes dramatically from 10 to 30 kHz (Fuzessery 1996). Thus there are potent monaural and binaural spectral cues available within this spectral band that could be used to enhance the accuracy of horizontal and vertical passive sound localization. The noise-preferring neurons in this region integrate information over broad spectral ranges. Some of those that respond maximally only to limited spectral bands receive differentially tuned excitatory and inhibitory inputs. Combined with available spectral cues, this broadband integration may serve to sharpen their spatial receptive fields.

Numerous behavioral studies have demonstrated that broadband sounds are localized with greater accuracy than tones because they permit evaluation of monaural and binaural spectral cues (e.g., Butler 1986; Martin and Webster 1987; Middlebrooks 1992; Musicant and Butler 1984). Characteristic head-related transfer functions derived from noise can be associated with particular points in space (e.g., Butler and Musicant 1993; Rice et al. 1992). The band-pass noise-selective neurons in the low-frequency region of the pallid bat auditory cortex would seem to be effective in extracting this spectral information as their response properties suggest that they receive differentially tuned converging excitatory and inhibitory inputs that allow them to integrate spatial information across a broad spectrum, a feature that may sharpen the spatial tuning of these neurons. Neural correlates of a sharpened spatial selectivity for noise over tones have been reported in the IC and auditory cortex of the cat (Aitkin and Martin 1987; Clarey et al. 1995). In auditory cortex, Clarey et al. (1995) reported that the greatest sharpening of azimuthal tuning seemed to be based on monaural spectral cues. Using free-field stimulation, they found dramatic differences in azimuthal sensitivity when neurons were tested with noise and tones. A sharpening of azimuthal tuning with noise occurred in both monaural and binaurally inhibited neurons even when the ipsilateral ear was plugged and binaural interactions precluded. Their interpretation was that noise stimulation recruited differentially tuned inputs, some of which are inhibitory, and it is the inhibitory input that sharpens azimuthal tuning. It is likely that similar mechanisms occur within the cluster of binaurally inhibited neurons in the pallid bat cortex and serve to enhance spatial sensitivity.

#### *Concluding comments on overall cortical organization*

Echolocating bats, with their highly specialized auditory behaviors, have provided some of the clearest examples of structure/function relationships in the auditory cortex. In the mustached bat, which has the most highly structured cortical organization, there appears to be a division of labor in which various cortical regions are specialized to extract different features of biosonar signals (e.g., target distance, velocity)

(Suga 1984). Previous studies of bat cortices have dealt with species that rely primarily, if not entirely, on echolocation to acquire information about their prey and immediate environment. In contrast, the pallid bat uses echolocation primarily for general orientation and relies on passive listening to detect and locate prey. The organization of its auditory cortex appears to reflect a need to concurrently acquire information from what can be considered two auditory submodalities. A hunting pallid bat emits echolocation pulses at a rate of  $\geq 5$  pulses/s to maintain an acoustic image of its immediate environment, while passively listening for sounds generated by potential prey. It likely encounters situations in which these streams of information overlap in time. To what extent the pallid bat can attend to both streams of information is unclear in light of auditory scene analysis studies indicating that humans are able to fully attend to only one stream at a time (e.g., Bregman 1990). We can, however, rapidly shift attention between two streams, proportionate to the extent that they are distinct and coherent in spectrum, temporal features, and spatial origin.

This may be the strategy employed by the pallid bat. Its auditory cortex seems to enhance contrast in multiple stimulus dimensions along at least part of the boundary between these two regions. Not only are there abrupt changes in frequency tuning and response selectivity but in binaural processing as well. One way in which this organization of binaural processing can be interpreted in light of the need for dual-stream processing is that regions serving echolocation and passive listening have substrates for independent spatial representation. These independent substrates may further enhance the coherence of these streams, facilitate concurrent processing of echolocation and passive listening, and establish independent cortical representations of information acquired from these streams.

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