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D. P. Phillips · M. N. Semple · M. B. Calford
L. M. Kitzes

Level-dependent representation of stimulus frequency in cat primary auditory cortex

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Abstract The tonotopicity of the cat's primary auditory cortex (AI) is thought to provide the framework for frequency-specific processing in that field. This study was designed to assess this postulate by examining the spatial distribution of neurons within AI that are activated by a single tonal frequency delivered to the contralateral ear. Distributions obtained at each of several stimulus evels were then compared to assess the influence of stimulus amplitude on the spatial representation of a given stimulus frequency in AI. Data were obtained from 308 single units in AI of four adult, barbiturate-anesthetized cats, using extracellular recording methods. Stimuli were 40-ms tone pulses presented through calibrated, sealed stimulating systems. In each animal, he CF (stimulus frequency to which the unit is most ensitive), threshold at CF, response/level function at CF, and binaural interactions were determined for isoated neurons (usually one per track) in 60–90 electrode racks. For each unit, regardless of its CF, responses to 40 repetitions of contralateral tones of a single frequency, presented at each of four or five sound pressure levels SPLs) in the range from 10 to 80 dB were obtained. Different test frequencies were used in each of four cats 1.6, 8.0, 11.0, and 16.0 kHz). For tones of each SPL, we generated maps of the response rates across the cortical urface. These maps were then superimposed on the more traditional maps of threshold CF. All units whose CF was equal to the test frequency could be driven at ome SPL, given an appropriate monaural or binaural onfiguration of the stimulus. There was a clear spatial segregation of neurons according to the shapes of their CF tone response/level functions. Patches of cortex, often occupying more than 2 mm^2, seemed to contain only monotonic or only nonmonotonic units. In three cortices, a patch of nonmonotonic cells was bounded ventrally by a patch of monotonic cells, and in one of these cases, a second patch of monotonic cells was found dorsal to the nonmonotonic patch. Contralateral tones of any given SPL evoked excitatory responses in discontinuous cortical territories. At low SPLs (10, 20 dB), small foci of activity occurred along the isofrequency line representing the test frequency. Many of these cells had nonmonotonic response/level functions. At mid- and high SPLs, the CFs of neurons activated by a pure tone varied across 3 octaves. At the highest SPL used (80 dB), most of the neurons with nonmonotonic response/level functions were inactive, or responded poorly; the active neurons were widely spread across the cortex, and the distribution of activity had a pattern bearing little relationship to the threshold CF contour map. These data indicate that only isolated patches of units within the relevant isofrequency contour are activated by a given suprathreshold contralateral tone. At suprathreshold stimulus levels, the region of cortex containing active patches extends widely beyond the threshold isofrequency contour region corresponding to the test stimulus frequency. The spatial representation of a stimulus delivered to the contralateral ear appears, therefore, to be highly level dependent and discontinuous. These observations suggest that in the cat's AI, tonotopicity and isofrequency contours are abstractions which bear little resemblance to the spatial representation of tonal signals.

Key words Primary auditory cortex · Frequency representation · Intensity representation · Single neuron · Cortical topography · Cat

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D. P. Phillips[1] (✉) · M. N. Semple · M. B. Calford[2]
M. Kitzes
Department of Psychology, Dalhousie University,
Halifax, NS, Canada B3H 4J1;
FAX no: (902) 494–6585, e-mail: ears@ac.dal.ca

On leave from: Departments of Psychology
and Otolaryngology, Dalhousie University,
ax, NS, Canada B3H 4J1
On leave from: Vision, Touch and Hearing Research Center,
Department of Physiology and Pharmacology,
he University of Queensland, Brisbane, Qld, Australia 4072

Introduction

A central issue in sensory physiology concerns the way in which stimuli are "represented" in the activity of neurons at successive levels of the neuraxis. There are at least two related levels at which one can understand a stimulus to be represented in spike activity: in the discharges of individual neurons, since spike rate or timing may vary systematically with parametric changes in one or more stimulus dimensions, and in pattern of spike activity distributed across a neural population, ideally in an individual animal. In the auditory system, experiments on the cochlear nerve have shown that the spectral identity of a given sound can be represented in the timing of spike discharges across the nerve fiber array, at least for frequencies below about 4 kHz, and that this code is relatively level-tolerant (e.g., Kim and Molnar 1979; Kim et al. 1990; Rose et al. 1967; Sachs and Young 1979; Young and Sachs 1979). A second code is based on spike rates, irrespective of their timing. At threshold levels of stimulation, the number of nerve fibers excited by a tonal signal is small and the discharging cells are restricted to those innervating the cochlear place most responsive to the test frequency. At only slightly higher signal levels however, there is considerable longitudinal spread of excitation along the cochlear partition, with the result that very large sectors of the auditory nerve array are excited to comparable, high response rates (Evans 1975; Kim and Molnar 1979; Pfeiffer and Kim 1975). Accounts of how the population response rate profile might indicate the test frequency have often alluded to the "edges" of the activated fiber arrays rather than to foci of maximal activity (cf. Kim and Parham 1991; Kim et al. 1990; Moore 1989).

The general experimental paradigm of studying the responses of a large population of single neurons in individual animals with a small set of stimulus conditions has not been applied to the primary auditory cortex (AI). In AI, the traditional *single-unit* approach has sought to describe quantitatively the encoding of a stimulus parameter in the discharges of individual AI neurons, and to explore the mechanisms shaping the code (e.g., Eggermont 1991; Imig et al. 1990; Phillips 1988, 1990, 1993a,b; Phillips and Hall 1990; Reale and Brugge 1990; Semple and Kitzes 1993a,b). The single-unit studies have revealed that while most AI neurons, like cochlear nerve fibers, have a single characteristic frequency (CF, the tone-pulse frequency to which a neuron is most sensitive), there are other factors that determine whether a tone at the contralateral ear will evoke spike discharges. First, for many cortical neurons, the excitatory range of tone frequency-intensity conjunctions (excitatory "response area") is often flanked by inhibitory ones (Phillips 1988; Phillips and Hall 1992; Phillips et al. 1985; Shamma and Symmes 1985; Calford et al., unpublished work). These cells often have completely circumscribed excitatory response areas, i.e., excitatory responses are elicited by tones within only a narrow window in frequency-intensity space. Unlike any cochlear nerve fiber, these cells have a nonmonotonic relation between spike count and stimulus level ("response/level function") for CF tones. This property would be expe ed to constrain any spread of excitation in comparis with that seen in a population of neurons whose response areas more closely resemble those of cochlear neurons. Second, the vast majority of AI neurons are influenced by the presence of stimuli at both ears (Brugge et al. 1969; Imig and Adrian 1977; Kitzes et al. 1980; Phillips and Irvine 1983). Third, the temporal code for low-tone frequencies (phase-locking to individual stimulus cycles) is not available in the cortex (see Phillips 1993a for review). The strict single-unit approach has thus offered reasons for believing that the factors influencing the spread of excitation across neurons of adjacent CF may be very different in the cochlea and the cortex. On the other hand, it has offered relatively little insight into the spatial organization of activity in AI. In part, this may have been because the pragmatic constraint of the time required to characterize any given neuron quantitatively precluded, in any individual cortex, study of the scores of sites required for even a partial map.

A second physiological approach used to study the cortex utilizes the *mapping* strategy. Using this method, parametric data on single units are not typically obtained. Rather, the data collected are observations of the responses of small clusters of units, often simply audiovisual inspections of the electrode signal. Such observations can be gathered quickly and have permitted large numbers of cortical loci to be studied in sin animals. This approach was the first to provide compelling evidence for tonotopic organization of the primary (Merzenich et al. 1975) and other (Knight 1977; Reale and Imig 1980) cortical auditory fields. Using tones of each neuron's preferred ear, in these experiments, the threshold CFs of neural elements are charted across the cortical surface, and "isofrequency lines" (lines of cells with similar CFs, after Merzenich et al. 1975) are interpolated between points on the spatial map. The same general strategy has recently been used to reveal gradients of frequency tuning bandwidth (Schreiner and Cynader 1984; Schreiner and Mendelson 1990) and monotonicity (Schreiner et al. 1992) within isofrequency lines. The mapping strategy has also revealed a form of binaural organization in the primary field (e.g., Imig and Adrian 1977; Middlebrooks et al. 1980; Reale and Kettner 1986).

Insofar as understanding stimulus representation in AI is concerned, interpretation of the data provided by the mapping studies have several constraints. A methodological concern is the ambiguity of the measured responses, since there is potentially great heterogeneity in the physiological properties, distance from the electrode, and pre- or postsynaptic identity among the neural elements contributing to the cluster response (Phillips and Irvine 1979, 1983). Second, what these studies have generally "mapped" across the corti mantle has been a response property (e.g., C threshold, tuning curve bandwidth), which is not the same thing as a response to the stimulus. In the case of notopic maps, the CF determination is made without specifying absolute stimulus level, or which ear is stimulated. It follows from this that knowledge of the CF map may provide very little information about which neurons will be activated by any specified tonal signal at the ear(s). Moreover, the kinds of observations on response parameters provided by the mapping studies do not permit statements to be made about absolute response magnitudes in general, or about their distribution within active cortical territories.

It follows from this discussion that data from neither the traditional single-unit, nor the more recent mapping experiments, have provided a satisfactory answer to the apparently simple question of which AI neurons are activated by a given signal, even a pure tone. The single-unit observations have revealed classes of neurons distinguished by the shapes of their response areas, but have indicated little about the distribution of these cell types within and across isofrequency lines. On the other hand, while the mapping experiments have provided evidence on the spatial distribution of multiple-neuron CFs and other response parameters, they have not provided direct information about the spatial pattern of cortical activation evoked by any given stimulus.

The purpose of the present study was to determine the distribution of cortical excitation evoked by tone pulse stimulation at the contralateral ear. Our general rategy was to use the best features of both the single- it and mapping studies, viz., to restrict observations to quantitative measures of single units identified by their CF, threshold, rate-level function, and binaural class, and to do so for a large number (60–90) of cortical sites in individual animals. Further, rather than study each cortical neuron only with tones of its CF, we studied each cortical site with a fixed set of stimuli: this enabled us to map out the distribution of neurons activated by a limited set of test stimuli across the cortical mantle, and in particular, across the traditional threshold-CF map. This design also permits a comparison of our cortical data with those previously presented for the cochlear nerve. The question that characterizes this study, then, is: "given the stimulus, who's listening?", rather than the converse question addressed by both of the earlier approaches to the cortex: "given the neuron, what is it listening to?"

Materials and methods

Animal preparation

This report describes in detail studies of four adult cats shown by preliminary otoscopic examination to be free from outer and middle ear disease. Surgical anesthesia was induced by intraperitoneal administration of pentobarbital sodium (30 mg/kg), and was maintained by supplemental doses administered intravenously ubital vein, as required to maintain a state of areflexia: approx- ately 1–2 mg/kg per hour). Each cat was given doses of atropine sulfate (0.03 mg/kg i.m.) and dexamethasone sodium phosphate (0.12 mg/kg i.m.), at the beginning of the experiment and at 24-h intervals subsequently, as prophylactics against respiratory secretions and cerebral edema, respectively. The animal was placed on an intravenous drip of 5% dextrose in lactated Ringers solution for the duration of the recording session. The animal's core temperature was maintained at 37.5°C using a thermostatically controlled heating pad.

Following induction of anesthesia, the cat's trachea was cannulated, and the dorsal skull was cleared. A head-holder was cemented to the skull in a fashion that left the ears unobstructed. The pinnae were resected, and the external auditory meatuses were transected to permit insertion of the stimulus delivery systems (see below). A craniotomy was performed over the left middle ectosylvian gyrus; the dura mater was cut and reflected, and the cortex was bathed in a shallow well of warmed (37.5°C) dimethylpolysiloxane oil. The cortical surface was digitally imaged, and electrode penetration sites were marked in relation to cerebrovascular landmarks.

Stimulating and recording systems

Tonal stimuli were generated and shaped digitally by a custom system incorporating modified Hewlett-Packard (8904A) digital synthesizers (Semple and Kitzes 1993a). Tone pulses were 40 ms in duration, including 2.5-ms (cat 02L001) or 5.0-ms (all other experiments) rise-decay times. Interstimulus intervals were 700 ms. Stimuli were transduced by Stax earphones in shielded housings, that were connected directly to acoustic couplers whose speculae were, in turn, inserted into the transected ear canals. The acoustic couplers incorporated calibrated probe-microphone assemblies for in situ measurement of stimulus sound pressure levels (SPL: decibels re 20 μPa) close to the tympanic membranes. Prior to the recording session, each ear was calibrated from 100 Hz to 40 kHz; the maximum outputs were stored as a look-up table for on-line adjustment of stimulus levels to experimenter-set SPLs.

The responses of single neurons were recorded with platinum- and gold-plated, Parylene-insulated tungsten microelectrodes. The electrode signal was filtered, amplified, monitored on an audio amplifier, and displayed on a digital oscilloscope whose sweep was triggered at stimulus onset. A second oscilloscope was used for continuous monitoring of spike waveform and for providing trigger pulses to a custom-built unit event timer (1 μs resolution). Unit activity was continuously displayed as both peri-stimulus time histograms (PSTHs) and dot rasters.

Data collection protocol

Search stimuli were tone pulses whose frequency, amplitude and binaural configuration were systematically varied. When a single unit was isolated, its CF and CF threshold were determined using the optimal binaural stimulus configuration (usually contralateral stimulation alone, ipsilateral stimulation alone, or simultaneous, equally intense stimulation of the two ears). Response thresholds were determined by the activity indicated in the on-line dot rasters. Using CF tones of the cell's optimal binaural configuration, the shape of the cell's response/level function was determined by comparing response rates for tones 10–20 dB and 50–60 dB above CF threshold (after Phillips et al. 1985; Phillips and Hall 1992). If spike counts evoked at the higher stimulus level were less than 50% of those evoked at the lower stimulus level, then the neuron was classified as nonmonotonic. All other cells were classified as monotonic. The binaural classification of neurons is not considered for this report and will be described in detail in a later paper.

The foregoing procedures were used to characterize every neuron in our sample. Occasionally, complete response area data were also collected. This entailed accumulating responses to 40 repetitions of tone pulses whose frequency-amplitude conjunctions spanned the effective range for that neuron. The purpose of collecting these data was simply to confirm that the physiological types of neurons examined in this study were comparable with those described in other studies (Brugge et al. 1969; Phillips et al. 1985).

The first electrode penetration was typically made in the center of the craniotomy, and the CF at that recording site was usually the one selected as the test frequency for that animal. For that recording site, and for all others in that animal, the quantitative data collected were the responses to 40 repetitions of the test frequency tone, presented at each of five SPLs (10, 20, 40, 60, and 80 dB) monaurally to the contralateral ear. The test frequencies used were 1.6 kHz (experiment 02L001), 11.0 kHz (experiment 02L002), 8.0 kHz (experiment 02L003), and both 16.0 and 7.0 kHz in experiment 02L005. In general, data were collected at only one depth in each penetration. The short latencies of the responses studied suggested that most of the recordings were made in the middle cortical layers. Data were also collected for test tones presented to the ipsilateral ear and to both ears simultaneously with various interaural level differences. The results obtained with those signals will be the subject of a later report.

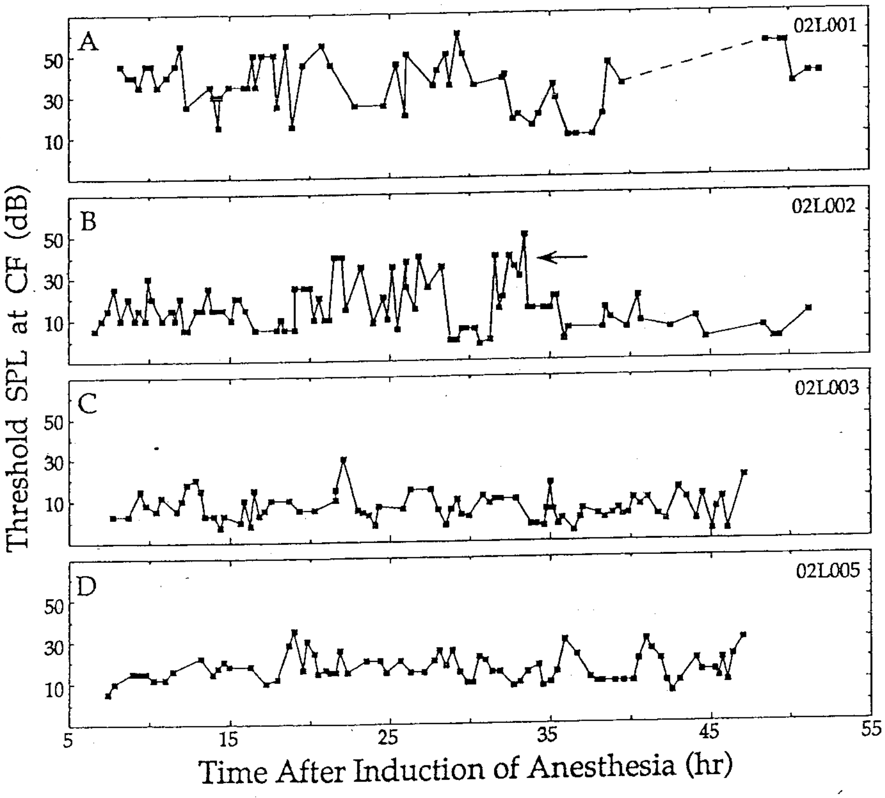
The experiments varied between 47 and 52 h in duration. At the end of the experiment, the cat was killed with an overdose of anesthetic (pentobarbital sodium i.v.).

Results

General observations

Quantitative data on the responses to monaural contralateral stimulation with the test stimuli were obtained from 308 single neurons in the four animals. Studied with CF tones, most neurons in the sample had peak firing rates between 1 and 3 spikes/trial. In each animal, units were sampled with CFs that varied between 1.0 and 1.5 octaves above and below the test frequency. Because the recording sessions were long and particularly since a principal goal of the study entailed topographic mapping, it was important to monitor t animal's physiological state over time. One relatively sensitive measure of the animal's condition is threshold SPL at CF, since this measure is sensitive to the state of both the brain and the cochlea. In Fig. 1 the CF thresholds of all units studied in each animal are plotted as a function of time following the induction of general anesthesia. These thresholds were determined using tones of each cell's optimal binaural stimulus configuration. In no case was there evidence of a progressive deterioration of unit thresholds during the recording ses-

Fig. 1A–D Variation in CF threshold (stimulus frequency to which the unit is most sensitive), plotted as a function of time during the recording session. **A–D** indicate, for each of the four animals separately, CF threshold of a single neuron studied with tones of the cell's optimal binaural stimulus configuration. Note that although there are considerable local variations in CF threshold, there was no evidence of a progressive lowering or elevation of CF threshold across the recording session. *Arrow* in **B** indicates a small aggregation of high-threshold neurons, TWIN cells, displaying a preference for relatively high sound pressure levels (SPLs) at the two ears. CF thresholds in **A** are systematically higher than those in the other animals. This reflects the fact that the cortical territory sampled was resticted to the low-frequency representation, i.e., a frequency range where the animal's behavioral sensitivity is also relatively poorer. Absence of data points between 40 and 48 h in **A** (*dashed line*) reflects time spent collecting quantitative data on neurons in the second auditory field (AII), which are not germane to this study



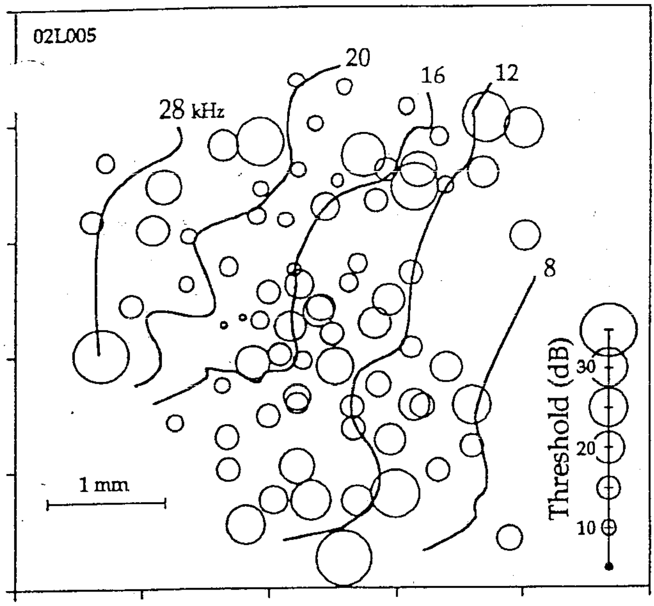


Fig. 2 Spatial distribution of CF tone thresholds in experiment 02L005. *Thick lines* are isofrequency contours, derived in the usual ashion; *circles* indicate the CF threshold of a neuron at that site, ccording to the legend at *lower right*

sion. Certainly, each of the graphs shows local variations in CF threshold across time, but these typically reflected sampling of different portions of the frequency resentation in AI (and thus the absolute sensitivity of animal) or sampling of local regions of neurons with nusual binaural tuning. Thus, for the group of neurons ndicated by the arrow in Fig. 1B, optimal stimuli were elatively high, and not necessarily identical SPLs at the wo ears (TWIN cells, after Semple and Kitzes 1987, 993b), and this was reflected in their CF thresholds.

Interestingly, there was a modest tendency for neuons with the highest CF thresholds to be preferentially ocated toward the dorsal and ventral edges of the napped regions of the isofrequency lines studied in each nimal. Figure 2 illustrates this point for the case of cat 2L005. This diagram is a schematic of the surface of his animal's cortex, with the thick lines representing sofrequency contours, i.e., interpolated lines linking ells with similar CFs, specified in kilohertz. The circles pecify the CF thresholds of neurons at those points, ccording to the legend. In this animal, the range of hresholds seen in cells of comparable CF was close to 0 dB, which was only modest in comparison with the ther animals in the study (cf. Fig. 1). Nevertheless, note hat while cells with low to medium CF thresholds were cattered across much of the mapped territory, the cells ith the highest CF thresholds tended to be found at the orsal and ventral edges of that region.

Figure 3 shows response area data from six neurons. he density shading plots depict spike counts plotted ntly as a function of tone frequency (abscissa) and (ordinate). The four levels of shading correspond to pike counts that were 20–39, 40–59, 60–79 and 80–100% of maximum for that neuron, with solid black shading indicating the stimulus domains associated with the highest spike counts (after Phillips et al. 1985). These six neurons were selected to illustrate the range of response area organizations seen in this study. To facilitate comparison, each response area has been plotted on an abscissa exactly one decade wide. Each neuron showed clear tuning to its respective CF and some modest tuning to tone amplitude at CF. In the cases illustrated in Fig. 3A–C, response/level functions at CF (i.e., a vertical slice through the response area at CF) were only modestly nonmonotonic, since even at the highest tone levels tested, spike counts were still greater than 60% of maximum. In contrast, the response areas of the units presented in Fig. 3D–F were more completely circumscribed, reflecting the fact that spike counts were strongly nonmonotonic functions of tone frequency and tone amplitude. The further point to be gleaned from Fig. 3 is that, by and large, the general shape of the response/level function (i.e., monotonic or nonmonotonic) for off-CF tones was the same as that for CF tones.

Analysis by CF

In the auditory periphery, increasing the amplitude of a stimulating tone causes a longitudinal spread of excitation along the cochlear partition, resulting in the excitation of auditory nerve fibers whose CFs differ increasingly from the stimulating frequency (see Evans 1975; Phillips 1987 for review). To examine the expression of this phenomenon in cat AI, we plotted spike counts evoked by the test tone as a function of unit CF, separately for test tones of different amplitudes (up to 5 SPLs in each animal). The complete data set is shown in Fig. 4. The columns are data for the different test frequencies (one per animal), and the rows represent responses for the specified test tone amplitude. The vertical dashed line in each plot indicates the test stimulus frequency.

At very low stimulus amplitudes, only a small proportion of the sampled neurons discharged significant numbers of spikes, and these neurons had CFs very close to the stimulating frequency (Fig. 4C,I,N,R). In the plots of Fig. 4, this is expressed as a narrow, peaked distribution of data points centered at CFs close to the frequency specified for each column. Increases in the amplitude of the stimulating tone modestly increased the proportion of excited units, and this increase was expressed in two ways. First, the CFs of the excited elements spanned increasingly broad ranges (e.g., Fig. 4J–N). Thus, tested with 80-dB test tones, the CFs of activated neurons spanned 2–3 octaves in three of the cats (Fig. 4E,J,O), and closer to 4 octaves in another (Fig. 4A). Interestingly, the spread of excitation, expressed in octaves, was greatest in the animal studied with the lowest-frequency test tone (1.6 kHz; Fig. 4A–D). Second, the proportion of excited units with CFs near the stimulating frequency also modestly increased.

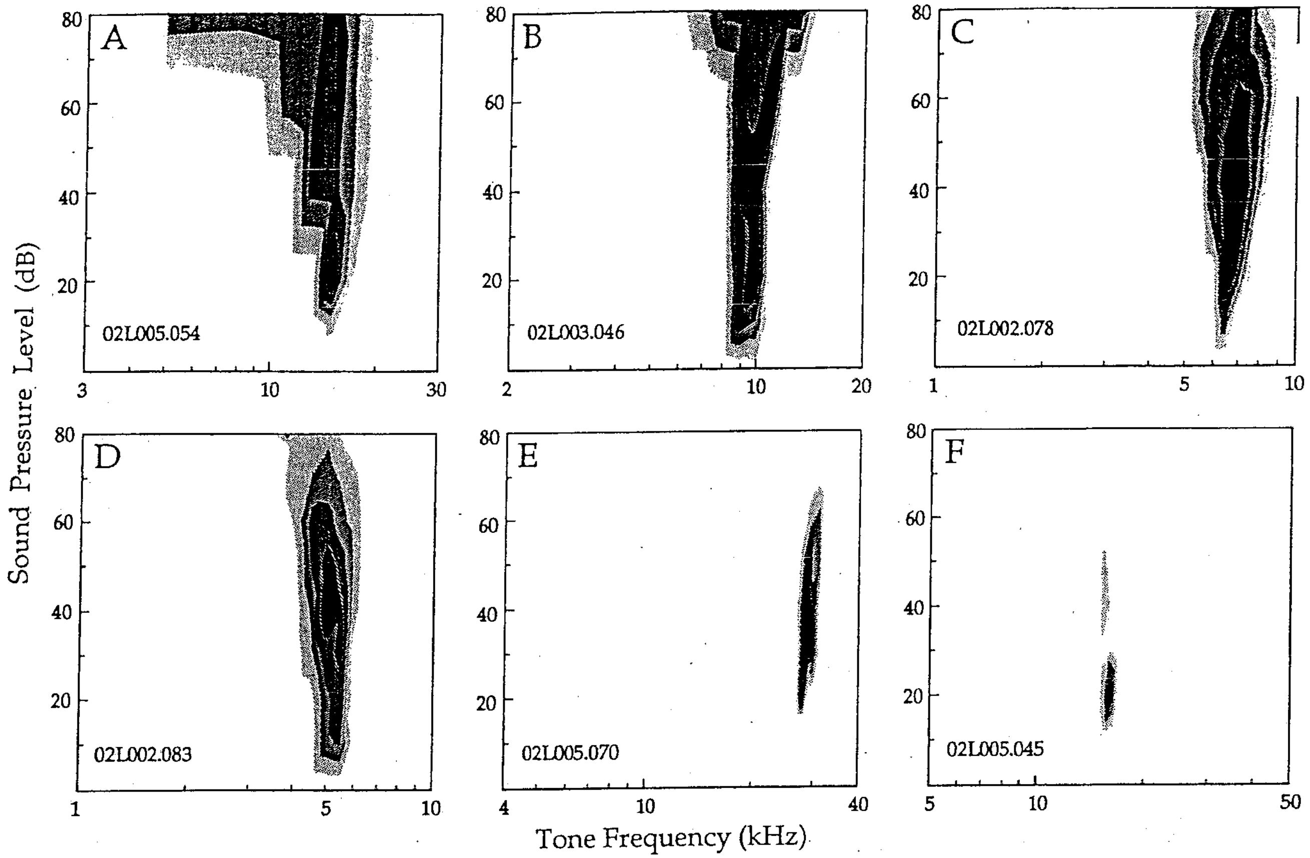


Fig. 3A–F Response area data on six neurons. *Areas of shading* indicate spike count ranges associated with stimulus parameters specified by abscissa and ordinate. *Levels of shading* indicate normalized pentile ranges (i.e., 20–39%, 40–59%, 60–79% and 80–100% of maximum response for that neuron) with *black area* depicting highest spike counts. In A–C, spike counts for CF tones 50 dB above CF threshold were greater than 50% of maximum for those neurons, and the cells were therefore labeled monotonic. In D–F, spike counts at high stimulus levels were less than 50% of maximum, and the neurons were classified as nonmonotonic

There are two further and related features of the data in Fig. 4 that warrant special mention. One is that irrespective of the test frequency or the amplitude of the test stimulus, the spike counts of the activated neurons were broadly and continuously distributed. That is, even cells whose CFs were close to the stimulating frequency were not equivalently activated by test tones of any specified amplitude (e.g., Fig. 4O–R). The related point is that, irrespective of the test frequency or the amplitude of the test tone, the proportion of activated units was typically small.

The latter point is illustrated in Fig. 5, which shows the proportion of neurons whose response rates equalled or exceeded 20 spikes/40 trials, plotted as a function of the SPL of the test signal. These data are presented separately for the four animals (i.e., separately for the four test frequencies). Inspection of the four curves in Fig. 5 reveals that at no stimulus level did the proportion of significantly activated neurons exceed 40%, and in only one case did it exceed 30%. Moreov it is perhaps unlikely that further elevations in the lev of the stimulus would have significantly increased the proportion of excited neurons, since half of the curves in Fig. 5 had either saturated or tended towards saturation by 80 dB. The data in Fig. 5 were combined across CF, and it might therefore be argued that one would not expect a high proportion of the sampled units to be driven by a test tone of any (single) specified frequency or amplitude, since many of the sampled neurons had CFs off the test frequency. A careful scrutiny of the data in Fig. 4, however, reveals that the trends seen in Fig. 5 for the total samples are also seen in the data for cells with CFs very close to the test frequency. Thus, in every plot in Fig. 4, and particularly those for the 8.0-, 11.0- and 16.0-kHz test tones, there are a significant number of data points at zero, or near-zero, spike count, even at CF ranges near the stimulating frequency. The data in Fig. 4 depict responses to monaural contralateral tones: we emphasize that every neuron in the sample with a CF near the stimulating frequency *did* respond to the test signal if the stimulus had the appropriate combination of SPLs at the *two* ears.

Analysis by response/level function shape

The analysis in Fig. 5 revealed that only a minority sampled neurons responded on any given trial wi spike probabilities in excess of 0.5, irrespective of the

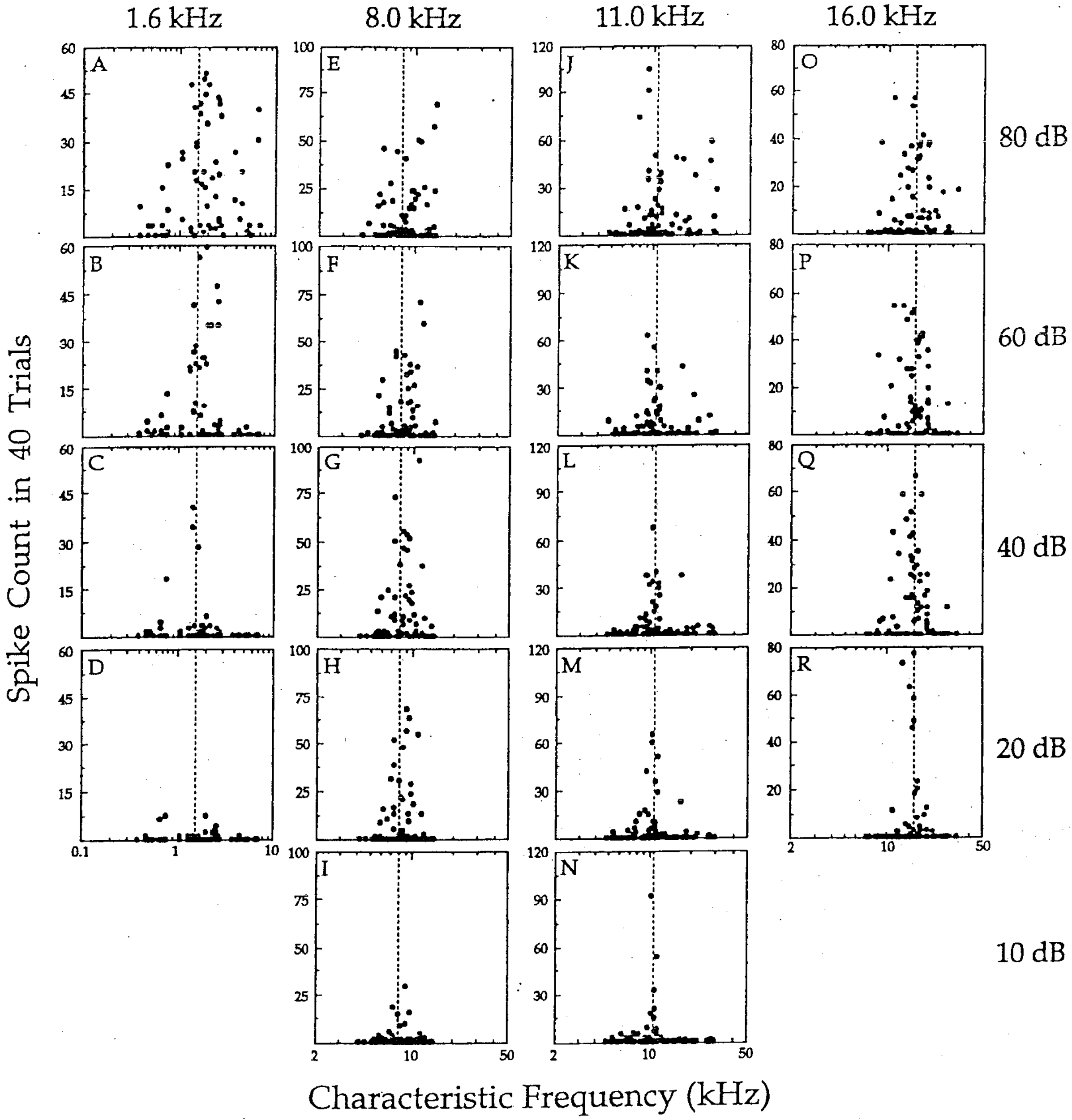


Fig. 4A–R Distribution of spike counts evoked by 40 repetitions of tones specified by column (frequency) and row sound pressure level (SPL). Each *column* presents data for one animal. Each *panel* shows spike count plotted as a function of unit CF. *Dashed vertical line* in each panel indicates test frequency. At low SPLs, activated neurons had CFs very close to the stimulating frequency. At higher SPLs, there was a spread of excitation to neurons with CFs lower and higher than the test frequency. Note, however, that in every panel there was a proportion of neurons with CFs close to the test frequency but with zero, or near-zero, spike counts

stimulus condition, and that this proportion was sometimes relatively constant across SPLs. This need not imply, however, that in any given animal the same subset neurons responded to the test signal at each SPL. Indeed, it is likely that changes in the stimulus SPL result in shifts in the population of activated neurons. The purpose of Fig. 6 is to illustrate this point in the case of experiment 02L005.

Figure 6 presents spike count data for the animal studied with the 16.0-kHz test tone, and the general form of the plots is the same as that for Fig. 4. The data have been presented separately for neurons classified as monotonic (Fig. 6A–D), and nonmonotonic (Fig. 6E–H). Inspection of the data for the monotonic neurons reveals that, with increases in the amplitude of the stimulus tone, the proportion of responding neurons increased rapidly between 20 and 40 dB, and more modestly thereafter. Note that, at the intermediate and high stimulus levels, there is some spread of excitation to neurons with CFs above and below the stimulating frequency. At 80 dB (Fig. 6D), most of the monotonic neurons with CFs close to the stimulus frequency had nonzero spike counts. The population of nonmonotonic

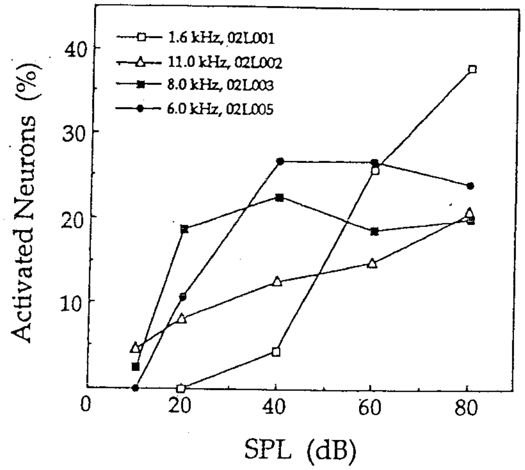


Fig. 5 Proportion of neurons activated, plotted as a function of test stimulus SPL, separately for each animal. Ordinate defined as the proportion of neurons whose spike rates exceeded 20 spikes/ 40 stimulus trials. Data include observations collapsed across CF (about a 3-octave range in each animal). Note that the proportion of active neurons rarely reached even 30% at any SPL

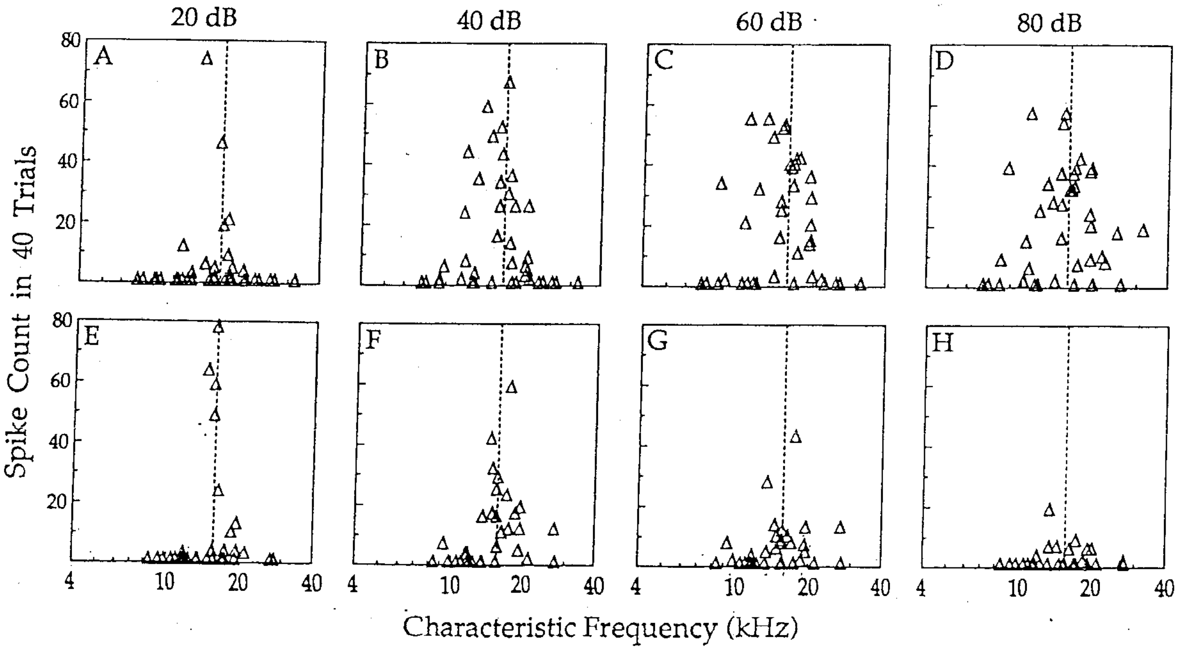
neurons behaved rather differently. Of those nonmonotonic cells which responded to the test tone, most did so only at the lower stimulus SPLs (Fig. 6E,F). In contrast to the case for the monotonic cells (Fig. 6D), the majority of nonmonotonic cells had spike counts close to zero at 80 dB SPL (Fig. 6H). These data indicate that changes in the SPL of a stimulating tone result in changes to both the number and the identities of the discharging neurons making up the active population.

Comparable data from a second case, experiment 02L003, are presented in Fig. 7. In this cat, the test tone was 8.0 kHz. The behavior of the population of monotonic neurons (upper panels) followed the pattern seen for the case illustrated in Fig. 6: increases in the amplitude of the stimulating tone resulted in increases in the proportion of neurons responding. In this instance, much of this increase in the proportion of ac vated neurons was due to a spread of excitation to ce whose CFs were off the stimulating frequency. For the nonmonotonic cells (lower panels), those with CFs at the stimulating frequency were most strongly excited by the low-amplitude tones (Fig. 7F–H). However, even at 80 dB, some nonmonotonic neurons were still responding to the test tone, although these neurons typically had CFs off the stimulating frequency and were relatively few in number (Fig. 7J).

Analysis by cortical place

The preceding section revealed that, at any given SPL, contralateral tonal stimuli excited only a portion of the AI neurons whose CFs were within about an octave of the stimulus frequency, and that changes in the test-tone SPL resulted in shifts in the identities of the neurons contributing to the population response. In particular, nonmonotonic cells tuned to the stimulating frequency were most strongly excited by low-stimulus amplitudes, while monotonic and nonmonotonic cells with CFs off the test frequency were silent at low-stimulus levels, but active at high ones.

Fig. 6A–H Data from experiment 02L005, in which the test f quency was 16.0 kHz. *Upper and lower panels* present data monotonic and nonmonotonic neurons, respectively. Each panel shows spike count plotted as a function of unit CF. Data are shown separately for each stimulus SPL. *Dashed vertical lines* represent stimulus frequency. In **A–D**, note that increases in SPL resulted in an increase in number of excited neurons with CFs near, and off, the stimulus frequency. In **E–H**, note that cells that were active at low SPLs were inactive at 80 dB



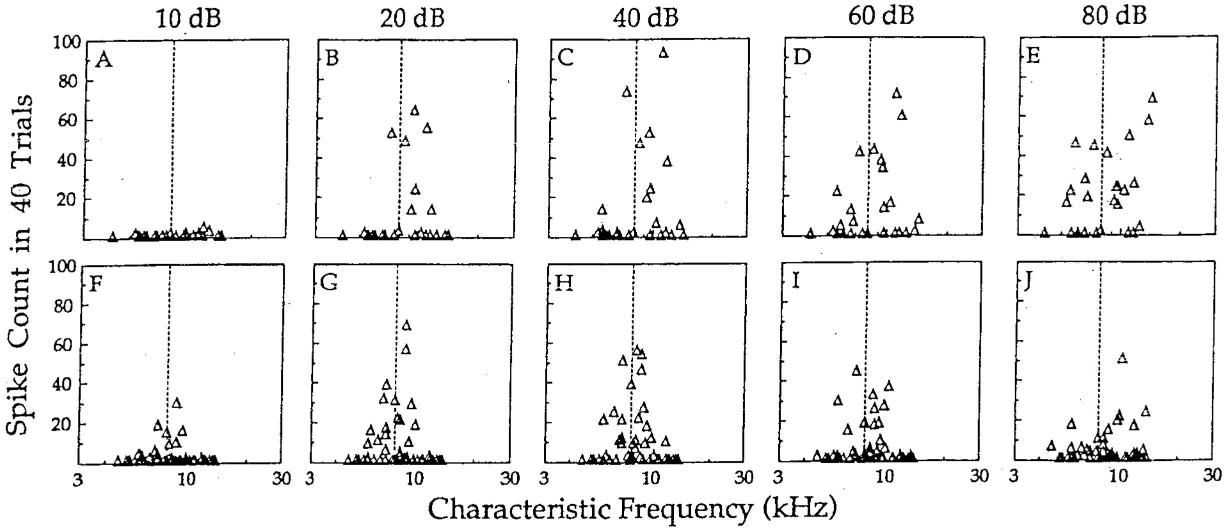


Fig. 7A–J Data from experiment 02L003, in which the test frequency was 8.0 kHz. Other details as for Fig. 6

These observations raise the further question of whether monotonic and nonmonotonic neurons have different spatial distributions within the cortical territory representing the frequency of the test tone. In each of the four cats, we encountered substantial numbers of both cells types in the mapped territories. The proportions of neurons judged to be nonmonotonic in each experiment were: 31% (experiment 02L001), 45% (02L005), 49% (02L002), and 66% (02L003). Figure 8 presents the spatial distribution of the two cell types, shown in relation to the threshold-CF map, separately for the four animals. The isofrequency lines in these maps were computer generated interpolations from the distribution of threshold CFs. Open and solid symbols, respectively, indicate that the neurons studied at those locations had monotonic or nonmonotonic response/level functions for CF tones.

In each animal, the two cell types were nonrandomly distributed within the mapped territory. This is perhaps most marked in the case of experiment 02L002 (Fig. 8B), in which the dorsal half of the explored territory contained exclusively nonmonotonic cells, while the ventral portion of the mapped region was dominated by monotonic neurons. In each of the animals, there was some mingling of the two neuron types, but this mingling occurred between cortical regions occupied overwhelmingly by one or other cell type. Note that some of these territories extended over several square millimeters of the cortical surface. Interestingly, in three of the animals (Fig. 8A,B,D), the patch of nonmonotonic neurons is bounded ventrally by a patch of monotonic cells. In one of these cases (Fig. 8D), the patch of nonmonotonic cells is bounded dorsally by a second patch of monotonic neurons.

It remains to examine the spatial distribution of response rates aroused by the test tones across the cortical mantle. Figures 9 and 10 present spatial plots that depict the distribution of neurons according to the spike counts evoked by 40 presentations of the test tone. Data from two cats are presented in each illustration, and each panel presents data for one specified test-tone amplitude. The lines in each panel represent interpolated isofrequency contours (specified in kilohertz). The shaded areas cover the regions between interpolated discharge rate contours. The different levels of shading indicate response rates (in spike count/40 trials) as specified in the legends at the sides of the illustration. At the edge of the mapped territory, or where the spatial resolution of the sampling is low, the interpolation may result in arbitrary contour shapes. To allow the reader to interpret whether the shape of a particular contour is important, the location of every recording site (i.e., the spatial grain of the sampling) is indicated by a dot in each panel. In any event, we place no special credence on the shapes of the contours: in what follows, we are concerned largely with the continuity of the cortical territories containing neurons excited by the test stimulus.

In each animal, and at each test SPL, the cortical regions containing the neurons with the highest spike counts had a discontinuous, patchy distribution across the mapped region. At the lowest effective SPLs, focal patches of active neurons were scattered in idiosyncratic patterns along the isofrequency contour (Figs. 9B,E, 10A,E). Note that the foci of highly activated neurons are, in every case, separated from each other by one or more cortical locations in which response rates were very low. The discontinuous nature of the distributions is thus not an artifact of the interpolation procedure.

Increases in the SPL of the stimulating tone resulted in shifts in the spatial locations of the most active neurons. These shifts seemed to follow a pattern that was reproduced in at least three of the animals. In experiment 02L005 (Fig. 10E–H), the 20-dB test tone evoked activity in four places along the 16-kHz isofrequency contour, and these neurons were separated by recording sites which were effectively silent under this stimulating condition. A comparison of Figs. 10E and 8D (which

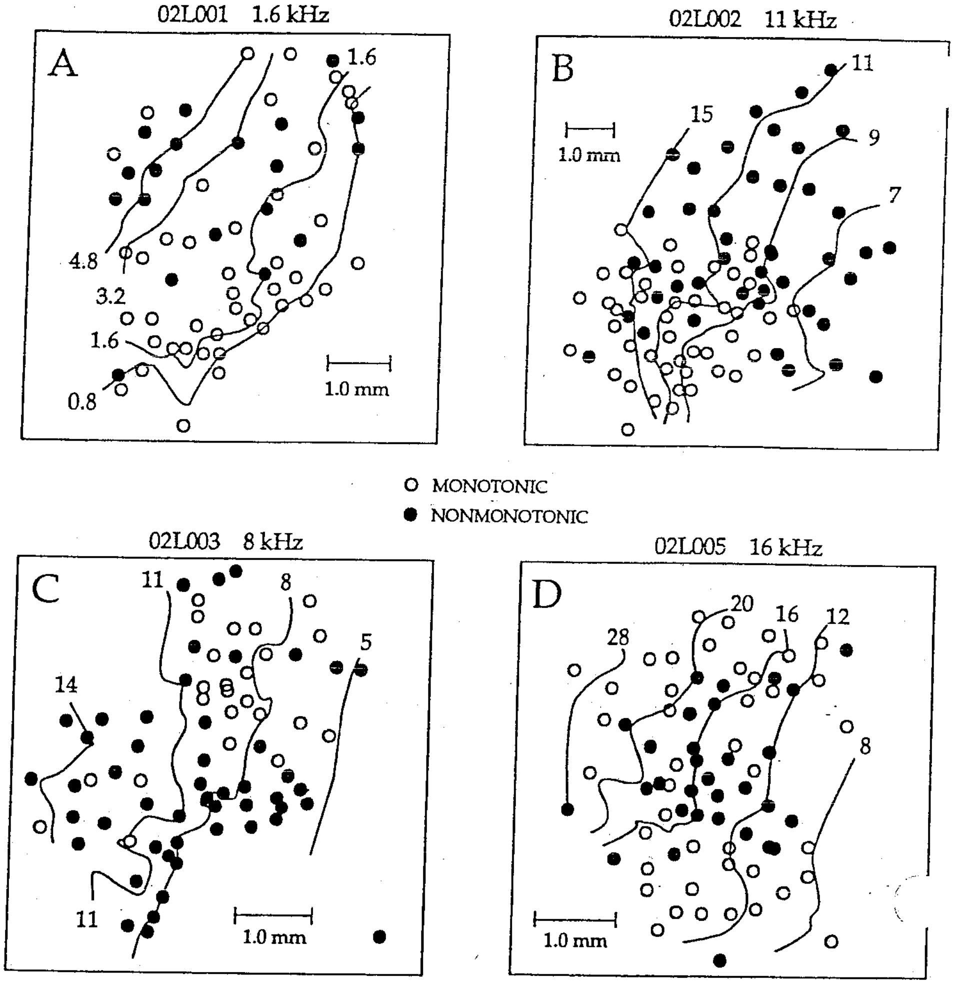


Fig. 8A–D Spatial maps obtained in the four cats. *Continuous lines* are isofrequency contours obtained by interpolation from the spatial distribution of threshold CFs. *Numbers* indicate represented tone frequency, expressed in kilohertz. *Open circles* indicate recording sites yielding monotonic neurons. *Filled symbols* indicate nonmonotonic cells. *Scale bar* indicates cortical distance in millimeters. In each panel, dorsal is *up* and anterior is *left*. Note that in each cortex the distribution of monotonic and nonmonotonic cell types was nonrandom. Sampling density was restricted primarily by cortical vasculature and by the necessity to sample broadly across the two dimensions of the cortical surface

showed the distribution of monotonic and nonmonotonic cell types in this cortex) reveals that the active neurons located in the center of the isofrequency line in Fig. 10E were nonmonotonic, while the active cells located at the ends of the isofrequency contour in Fig. 10E were monotonic cells. With increases in the level of the stimulating tone, the central patches (seen in Fig. 10E) were no longer prominent in the contour plot, whereas the outer patches either expanded, or became more numerous, across the tonotopic axis.

The same general trends are apparent in the cortex of cat 02L002 (Fig. 10A–D). At low test-tone SPLs (e.g., 20 dB) most of the active cortical territories reflected the activity of nonmonotonic cells with CFs at, or close to, the stimulating frequency (cf. Figs. 10A, 8B). Thus, most of the evoked responses at 20 dB were located dorsally along the isofrequency line, which Fig. 8B revealed to contain exclusively nonmonotonic cells. Increases in the SPL of the stimulating tone resulted in most of these patches of activity dropping out and being replaced by activity ventrally in the isofrequency contour (Fig. 10C,D), which our earlier analysis revealed to contain monotonic cells spanning a relatively broad CF range (Fig. 8B). These changes reflect a general rule: as SPL is increased, there is a declining contribution of nonmonotonic cells tuned to the test frequency, and an increasing contribution of monotonic cells with CFs off the test frequency. The patches emerge because these are segregated neural populations. In only one of the animals (02L001; Fig. 9A–D) were these trends somewhat less evident, but this was largely due to the fact that few nonmonotonic cells were encountered along the isofrequency contour representing the test frequency (Fig. 8A) in this animal. There were, therefore, no patches of nonmonotonic cells to drop out of the map at higher stimulus levels. Nevertheless, the spread of excitation seen in the upper and/or lower (monotonic) portions of the maps in the other three cats was also seen in this one, but it was more spatially generalized (Fig. 9A–D).

Discussion

Summary of major findings

In addressing the question of "who's listening?", t study has provided the first description of the distribu-

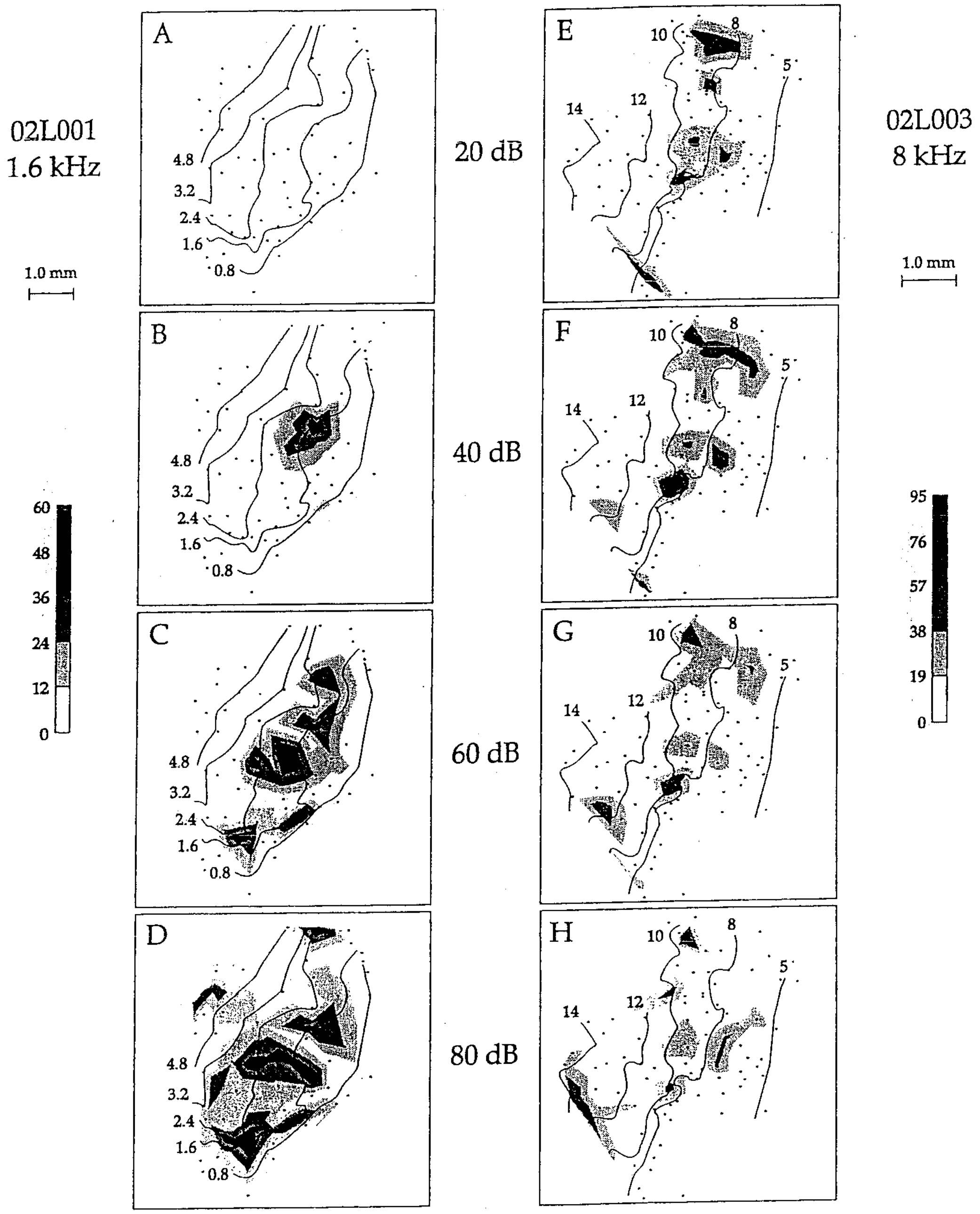


Fig. 9A–H Spatial maps showing the distribution of single-unit excitation in AI of cats 02L001 (**A–D**) and 02L003 (**E–H**), shown separately for each test SPL. *Continuous lines* are isofrequency contours, identical to those in Fig. 8; *dots* indicate recording sites. *Shaded areas* depict territories containing neurons whose spike counts fell in the ranges (specified in spikes/40 trials) indicated in the legend for each cat. Note that at each SPL, active neurons were spatially distributed in discontinuous patches separated by recording sites yielding inactive cells. Details and description in text

tion of single neurons activated by a given tonal stimulus in the AI. In a stable animal preparation (Fig. 1), we showed that neurons with monotonic and nonmonotonic response/level functions (Fig. 3) were largely segregated in any given sector of the frequency representation (Fig. 8). Thus, in each cortex studied, it was possible to delimit significant territories occupied largely or exclusively by one or the other cell type. Contralateral tones of any given SPL excited only a subset of the neurons with CFs at or near the stimulating frequency (Fig. 4). Cells with CFs near the test frequency and with nonmonotonic response/level functions were typically excited by the test tone only at low SPLs (e.g., Fig. 6). At high SPLs, nonmonotonic cells with CFs equal to the test frequency were often inactive, but the population of activated monotonic neurons expanded to include those with CFs off the test frequency (Figs. 6, 7). Analyses of the *spatial* distribution of the activated cells revealed

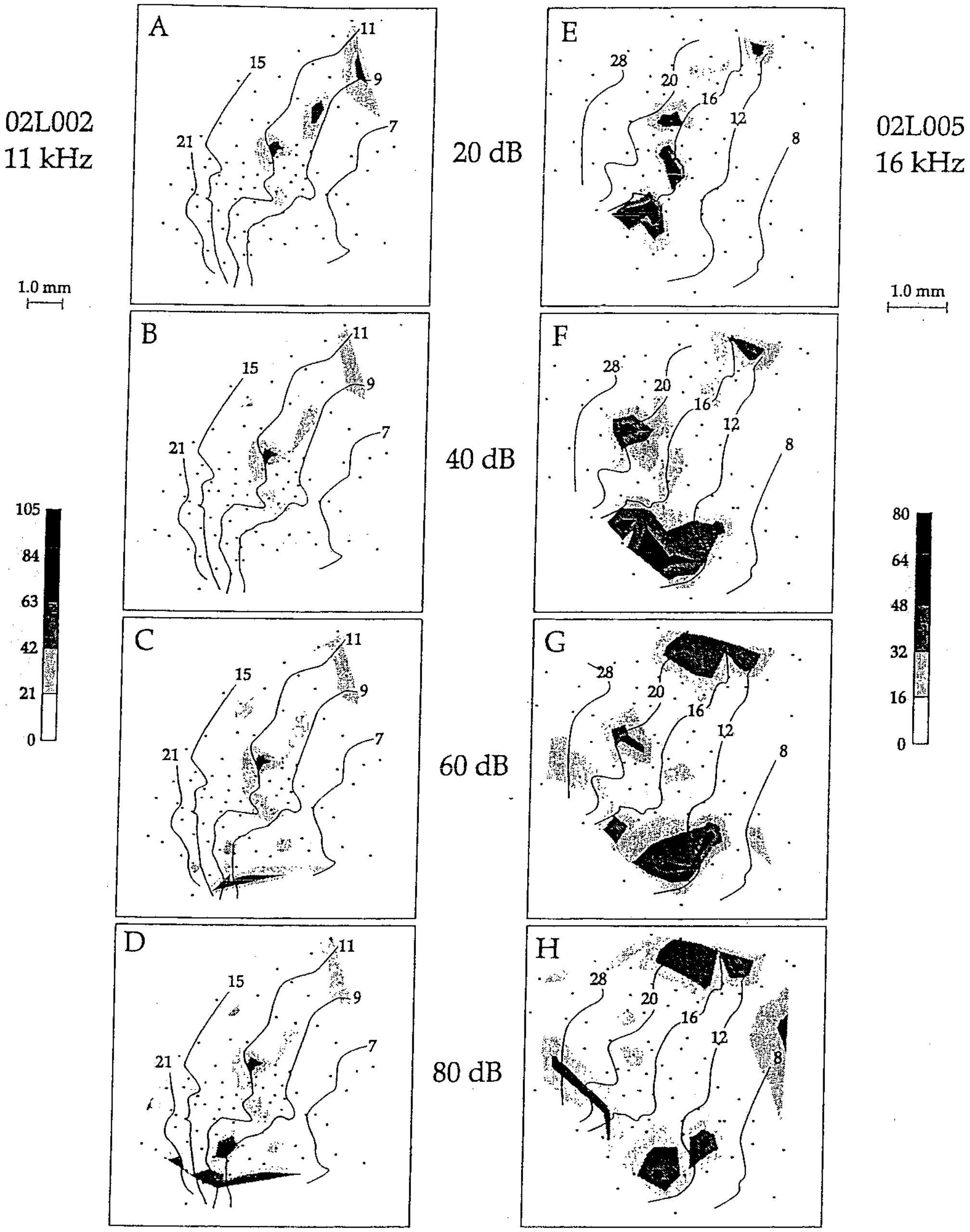


Fig. 10A–H Spatial maps showing the distribution of single-unit excitation in AI of cats 02L002 (**A–D**) and 02L005 (**E–H**), shown separately for each test SPL. Details as for Fig. 9

that at low SPLs there were discontinuous, circumscribed foci of active, nonmonotonic cells distributed along the isofrequency contour representing the stimulus frequency (e.g., Fig. 10). At higher SPLs, these patches of nonmonotonic cells were typically inactive, but there were larger territories of active, monotonic, and some nonmonotonic cells that spread quite widely across the tonotopic axis (Figs. 9, 10).

Because we typically studied only one neuron in each electrode penetration, the possibility that the apparent horizontal segregation of monotonic and nonmonotonic cell types in Fig. 8 might reflect a sampling artifact needs to be addressed. Based on electrode penetration distances (micrometer readings), almost all of our recordings were probably from the middle cortical depths; this is supported by the fact that response latencies to CF tones were very short, and it is in the middle cortical layers of cat AI that reuronal latencies are shortest (Phillips and Irvine 1981). Now, if monotonic and nonmonotonic cell types were in fact mingled within the middle layers, then it is inescapable that their horizontal spatial distributions must also be mingled, and this was not the case. Another possibility is that two cell types are in fact segregated vertically. However, given that our recordings were made only in the middle rtical depths, the only way in which such a vertical segregation could have given rise to the present observations would be through systematic differences in the cortical layers in which recordings were made across the cortex, as might occur close to cerebral sulci. Since the maps presented in Fig. 8 are based on recordings across the crown of the ectosylvian gyrus, this hypothesis is highly unlikely. Notwithstanding these points, note that because we usually obtained data for only a single cortical depth at each site in the map, the present evidence does not bear on the question of the existence of cortical columns defined by neuronal response/level function shape. Our data indicate only that the two cell types are segregated horizontally within the middle cortical layers. The extent to which this spatial segregation reflects properties of the thalamic input, rather than local processing within the thalamocortical recipient layers, remains to be determined.

Tonotopic organization, isofrequency lines, and frequency-specific processing channels

There is agreement that the primary auditory cortex is tonotopically organized in cats (Merzenich et al. 1975; Reale and Imig 1980), primates (Aitkin et al. 1986; Imig et al. 1977; Merzenich and Brugge 1973), and other species (Kelly et al. 1986; Merzenich et al. 1976; Redies et al. 1989; Sally and Kelly 1988). In all of these studies, the threshold CFs of units or unit clusters obtained using tones of the preferred ear have been plotted across the cortical surface. Interpolations between the actual data points reveal that, orthogonal to the high-to-low tonotopic gradient, there are lines or bands of cells with similar threshold CFs (isofrequency lines, after Merzenich et al. 1975). This was no less true in the present study (Figs. 8–10) than in the earlier studies of cat AI.

Three broad lines of evidence can be adduced to suggest that isofrequency lines (and thus, tonotopic organization) in some way form a structural framework within which the representation or "processing" of other stimulus dimensions (e.g., amplitude, bandwidth, or spatial location) occurs. First, traditional single-unit and mapping studies have revealed that any isofrequency strip (with the possible exception of those devoted to very low frequencies, since this portion of AI has not received detailed study), is likely to consist of elements that exhibit all binaural interactions and degrees of bandwidth tuning (e.g., Imig and Adrian 1977; Middlebrooks et al. 1980; Phillips et al. 1985; Schreiner and Cynader 1984; Schreiner and Mendelson 1990). Second, the thalamic (Andersen et al. 1980; Brandner and Redies 1990; Morel and Imig 1987), callosal (Imig and Brugge 1978), and orticocortical connections of AI (Imig and Reale 1981; Rouiller et al. 1991) interconnect tonotopically homotypic loci. Third, the behavior-lesion study of Jenkins and Merzenich (1984) revealed that cats deprived of local isofrequency sectors in AI were unable to localize only those stimulus frequencies that were deprived of cortical representation.

A good argument, then, can be made for the view that AI represents or processes acoustic information on a frequency-specific basis. It remains the case, however, that the strictly physiological demonstration of AI's tonotopic organization (and presumably, therefore, of the neural substrate of the processing channels) has been based wholly on the spatial distribution of *threshold* responses. Plotting the spatial distribution of threshold CFs is, in practice, a kind of *normalization*, since it focusses on frequency while ignoring stimulus level and laterality. Thus, isofrequency contours alone provide no information about the variation in the absolute thresholds of the neurons comprising them, and this variation may be as great as 20 dB (Fig. 2). The present study is apparently the first in which the cortical distribution of suprathreshold responses to single tones has been mapped. In each animal, while analysis of threshold CFs of a set of neurons revealed the familiar threshold-CF maps (Fig. 8), analysis of the suprathreshold responses of the same units revealed discontinuous territories of active units (Figs. 9, 10). At low SPLs, there were typically focal patches of activated neurons, usually located on, or close to, the relevant isofrequency line. At higher SPLs, the excitation seen along an isofrequency line for low-SPL tones was often lost, and was replaced by activity distributed at new sites along and outside the isofrequency contour. At the highest SPLs, it is difficult to specify any isofrequency contour on the basis of the distribution of active neurons. In describing Figs. 6, 7, 9, and 10, we argued that increases in the amplitude of a stimulating tone brought about shifts in the elements composing the active population: principally from a population which included nonmonotonic cells tuned to the test tone, to a population which included monotonic and some nonmonotonic cells whose CFs were off the test frequency. This spread of excitation to cells with CFs off the test frequency was less marked among nonmonotonic cells, presumably because these neurons typically have very narrow frequency tuning (e.g., Fig. 3). Nevertheless, one source of the discontinuities in the territories activated by tonal stimuli is thus the response/level function shape of the neurons responsive to the test frequency. A second source of the discontinuities is probably the pattern of binaural input to the neurons, since there are some cortical neurons that do not discharge spikes in response to monaural contralateral stimuli (Kitzes et al. 1980; Phillips and Irvine 1983; Semple and Kitzes 1993b).

These observations raise intriguing questions about the physiological instantiation of a cortical frequency-specific processing channel. The present data (Figs. 6, 7, 9, 10) indicate that, depending on the level of the stimulus tone, the cortical territory activated by that tone may span up to 3 octaves of the CF distribution centered on that representing the test frequency. Remarkably, in at least one instance (Fig. 10H), a high-amplitude tone evoked very little activity along the relevant isofrequency line, but considerable activity outside it. Clearly then, an isofrequency line, narrowly defined as the line of cells with the same CFs, is not the functional unit that represents or processes the frequency of a tonal stimulus. Two recent lines of evidence support this view. One is the demonstration by Uno et al. (1993): using a voltage-sensitive dye and optical recording, they showed that wide sectors of the guinea pig's auditory cortex were activated by suprathreshold tonal stimuli. While those authors did not obtain independent tonotopic maps in the same animals, the fact that their recording array spanned nearly 3 mm suggests that, at high stimulus levels, much of the primary field must have been activated. A second line of evidence comes from Eggermont (1992). Using cross-correlation analyses of the timing of spikes in simultaneously recorded pairs of cat AI neurons, he showed the existence of significant temporal correlation between spontaneous spikes of neurons separated by as much as 1.75 octaves across the CF map (a physical distance of nearly 2 mm; larger separations were not tested). Both of these lines of evidence are consistent with the present observations on the spread of excitation across the cortical mantle with suprathreshold tones.

Note that the patchiness of activity along isofrequency lines seen in this study (Figs. 9, 10) does not in itself dispute that some form of strip-like neural assembly constitutes the frequency-specific channel: the present study revealed that the *fashion* in which stimulus dimensions other than frequency are represented (or processed) might reside in *which* particular neurons of the array are most active. The frequency, the amplitude, and the laterality of a tonal stimulus jointly determine a cortical neuron's firing rate; since there is a patchy distribution of neural territories distinguished by the fashions in which these stimulus parameters influence spike rate, it follows that the representation of the frequency of a tone (of any single specified laterality and amplitude) in the firing rates of cortical cells is also patchy. The patchiness simply results from the modular (perhaps columnar) distribution of neurons with particular properties, viz., form of their response/level functions and binaural interaction pattern.

What emerges from these considerations is the appreciation that, from the standpoint of stimulus representation in the cat's AI, *tonotopicity and isofrequency contours are abstractions* that ignore the contribution of SPL and stimulus laterality as determinants of unit responsiveness. Threshold CFs are the data base for tonotopic maps: they are obtained by considering each neuron individually in a highly normalized fashion that eliminates recognition of the multiplicity of factors that determine cortical neuron responsiveness to tonal stimuli. For this reason, while the spatial location of isofrequency lines (tonotopicity) may be useful for some studies of neuroanatomical connectivity, knowledge of them offers little information about the spatial location of activity evoked by a tonal stimulus. The *representation* of any tonal stimulus lies not in the isofrequency line c responding to the test frequency, but in the spatial distribution of activity evoked by the signal. That distribution may bear little relation to the isofrequency line.

Comparison with previous studies of cat AI

The present data are compatible with previous descriptions of both AI's tontotopic organization (Merzenich et al. 1975; Reale and Imig 1980) and the response areas of its constituent neurons (Brugge et al. 1969; Phillips et al. 1985) in the anesthetized cat. The present study revealed significant patches of nonmonotonic cells in each of the four animals (Fig. 8). We mapped much of the length of isofrequency lines in each animal and found a broad patch of nonmonotonic neurons in each cortex. Our data revealed in three cases that the nonmonotonic patch was bounded ventrally by a monotonic one, and in one of these animals the nonmonotonic patch was bounded both dorsally and ventrally by monotonic cells. Previous single-unit studies have shown that nonmonotonic cells often have excitatory response areas that are exceptionally narrow in the frequency domain (present study, Fig. 3; Phillips et al. 1985). Most of these cells are unresponsive to wideband signals (Phillips 1988; Phillips and Cynader 1985; Phillips et al. 1985), suggesting that their excitatory response areas flanked by sensitive inhibitory ones. The segregation nonmonotonic and monotonic cells could, thus, also be viewed as a segregation of (relatively) sharply and broadly tuned cells. This is apparent from inspection of the spatial distribution of active neurons at high SPLs (compare Fig. 8 with Figs. 9D,H and 10D,H).

It is likely that this segregation is in accord with the findings of Schreiner and Mendelson (1990). They mapped isofrequency sectors of cat AI for the bandwidth tuning of unit cluster activity and found that the most narrowly tuned activity was in the middle of AI's dorsoventral extent. They also showed that the narrowly tuned region was the one containing the neurons least responsive to broadband signals. More recently, Schreiner et al. (1992) showed that unit clusters with nonmonotonic response/level functions were located in roughly the same territories as those containing sharply tuned neurons. In the mapping studies, tuning bandwidth or monotonicity was depicted as a continuous U-shaped gradient along AI's dorsoventral extent. The impression given by the present data (Figs. 8–10) is of discontinuous patches. This difference might simply reflect the use of single units in the present study (cf. unit clusters in the mapping ones) and the fact that the gradients depicted in the earlier mapping study were the result of a smoothing, interpolation algorithm. Nevertheless, the present demonstration that the central portion of isofrequency lines are often occupied by cells w nonmonotonic response/level functions is consistent ith the findings of the earlier mapping studies.

There is also anatomical evidence of a discontinuous, patchy organization of AI. As mentioned above, the connectivity of AI with the thalamus and with the contralateral and ipsilateral cortical auditory fields is tonotopically constrained. But it is also very patchy in the sense that neurons of only some sectors in a given portion of the frequency representation participate in any specified set of connections (Imig and Brugge 1978; Imig and Reale 1981; Middlebrooks and Zook 1983). Similarly, the intracortical connections of neurons within AI have a discontinuous, patchy distribution (Matsubara and Phillips 1988; Wallace et al. 1991). The anatomical data and the present observations, then, suggest that the functional organization of AI should be viewed as a relatively continuous tonotopic organization that is overlaid by patchy mosaics of territories defined by monotonicity of response/level relations and by binaural interactions. As argued elsewhere (Phillips et al. 1985; Phillips 1993a), the territories defined by these properties probably do not respect each other's boundaries, i.e., they are independently determined. Indeed, were this not the case, then the representation in AI of any one stimulus dimension (or range within it) would be specifically linked to the representation of another.

omparison with the auditory nerve

Kim and his colleagues (Kim and Molnar 1979; Kim and Parham 1991; Kim et al. 1990; Pfeiffer and Kim 1975) have previously presented data from studies of the population response to single tones of the cochlear nerve-fiber array. Using *low-frequency* tones,they showed that at low SPLs (e.g., 20 dB) the population of nerve fibers giving phase-locked (temporal) responses to the test tone shifted systematically with the test frequency, at least up to about 3600 Hz (Pfeiffer and Kim 1975). At higher stimulus levels (e.g., 45 dB), low-frequency tones evoked high spike rates from fibers innervating broad regions of the cochlear partition (Kim and Molnar 1979), although the spatial spread of cells giving phase-locked responses was less marked. At very high stimulus levels, even phase-locked responses to a low-frequency tone were seen in cells of widely varying CF. For *higher frequency* signals (e.g., 5 kHz, Kim and Parham 1991), a temporal code for the test frequency is not available, and the representation of tone frequency in the nerve fiber array presumably lies in the firing rates and spatial distribution of activated neurons. Interestingly, for fibers of similar CF, firing rates evoked by a tone of any specified level were generally comparable. At 70 dB SPL, the spread of CFs of activated cells spanned about 4 octaves.

In the AI, there is probably no significant population f neurons capable of phase-locking spike discharges to tones even at the frequency (1000 Hz) used by Kim and Molnar (1979). Thus, a fundamental difference between the population response of neurons in the cortex and in the cochlear nerve is the absence of a temporal code for tone frequency in the former. This means that any ambiguity with which the population of activated cortical neurons specifies a low-frequency tone cannot be resolved by periodicities in the timing of spike discharges.

Among cortical cells with CFs relatively close to any stimulating frequency, the range of discharge rates evoked by the test signal was large in comparison to the auditory nerve. Thus, whereas high-SPL signals result in saturated firing rates of comparable magnitude in auditory nerve fibers, similar signals result in a more continuous distribution of firing rates in cortical neurons. This presumably reflects the greater range of factors that influence the spike rates of cortical cells, notably stimulus laterality and sibeband inhibition. Note that, on the one hand, this means that the spike output of any single cortical neuron is (still) more ambiguous than that of a cochlear nerve fiber. On the other hand, the distribution of discharge rates across the whole AI specifies more stimulus parameters than does the the pattern of output across the auditory nerve array.

Tones of 80 dB were found to excite cortical cells with CFs spanning up to 3 octaves. This range and the envelope of the distribution of spike rates is similar to that described for the cochlear nerve (Kim and Parham 1991). These similarities are not surprising for, although many studies have emphasized the relative complexity of response at cortex, there is a subpopulation of cortical neurons characterized by good responses to contralateral stimulation, monotonic response/level functions, and lack of significant sideband inhibition (Phillips et al. 1985; Phillips 1988, 1993a). Such cells respond over an increasing frequency bandwidth with increasing stimulus level (e.g., Fig. 3A) and, thus, among these cells the spread of excitation should be just as great as in the cochlear nerve fiber array. The striking difference between the cortex and the nerve, however, lies in the fact that cortical neurons of this type are in the minority: it is for this reason that while the breadth of the spread of excitation may be comparable between the nerve and the cortex, the proportion of units so affected is small. Restated, the multiplicity of response factors that determine the excitation levels of cortical cells have the consequence that high-SPL tones of any given frequency will arouse activity in only a subset of cortical neurons tuned to the stimulus frequency. The major finding of the present study lies not simply in the demonstration of this phenomenon, but in the demonstration that these neurons are spatially segregated.

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