Functional Topography of Cat Primary Auditory Cortex: Distribution of Integrated Excitation

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SUMMARY AND CONCLUSIONS

1. Neuronal responses to tones and transient stimuli were mapped with multielectrode arrays in the primary auditory cortex (AI) of barbiturate anesthetized cats. Most of the dorsoventral extent of AI was mapped with multiple-unit recordings in the high-frequency domain (between 5.8 and 26.3 kHz) of all six studied cases. The spatial distributions of 1) sharpness of tuning measured with pure tones and 2) response magnitudes to a broadband transient were determined in each of three intensively studied cases.

2. The sharpness of tuning of integrated cluster responses was defined 10 dB above threshold (Q10 dB, integrated excitatory bandwidth). The spatial reconstructions revealed a frequency-independent maximum located near the center of the dorsoventral extent of AI. The sharpness of tuning gradually decreased toward the dorsal and ventral border of AI in all three cases.

3. The sharpness of tuning 40 dB above response threshold was also analyzed (Q40 dB). The Q40 dB values were less than one-half of the corresponding Q10 dB value. The spatial distribution showed a maximum in the center of AI, similar to the Q10 dB distribution. In two out of three cases, restricted additional maxima were recorded dorsal to the main maximum. Overall, Q10 dB and Q40 dB were only moderately correlated, indicating that the integrated excitatory bandwidth at higher stimulus levels can be influenced by additional mechanisms that are not active at lower levels.

4. The magnitude of excitatory responses to a broadband transient (frequency-step response) was determined. The normalized response magnitude varied between <1% and up to 100% relative to a characteristic frequency (CF) tone response. The step-response magnitude showed a systematic spatial distribution. An area dorsal to the Q10 dB maximum consistently showed the largest response magnitude surrounded by areas of lower responsivity. A second spatially more restricted maximum was recorded in the ventral-third of each map. Areas with high-transient responsiveness coincided with areas of broad integrated excitatory bandwidth at comparable stimulus levels.

5. The distribution of excitation produced by narrowband and broadband signals suggests that there exists a clear functional organization in the isofrequency domain of AI that is orthogonal to the main cochleotopic organization of the AI. Systematic spatial variations of the integrated excitatory bandwidth reflect underlying cortical processing capacities that may contribute to a parallel analysis of spectral complexity, e.g., spectral shape and contrast, at any given frequency.

6. Similarities and consistencies in the spatial distribution of responses to narrowband and broadband signals indicate that the integrated excitatory bandwidth, as determined with the multiple-unit technique, is a useful tool to explore global functional properties of AI. It is suggestive that systematic changes in 1) the convergence of the projections to the cortical locations and 2) the extent of inhibitory influences are mainly responsible for the functional organization described along the isofrequency domain.

INTRODUCTION

One of the fundamental organizational principles in the mammalian forebrain is the topographic representation of the sensory epithelium. Such a topographic organization has been demonstrated for a number of auditory cortical fields, including the primary auditory field (AI) (Knight 1977; Merzenich et al. 1975; Reale and Imig 1980; Woolsey and Walzl 1942). Although the sensory epithelium of the auditory system is one-dimensional, a row of receptor cells along the basilar membrane in the cochlea, the topographic representation of the receptor surface, occupies two spatial dimensions in AI in addition to the cortical depth. Extensive multiple-unit mapping studies of AI in the cat (Merzenich et al. 1975; Reale and Imig 1980) have shown a strict cochleotopic representation along its caudal/rostral dimension. This organization is expressed as an increase in the characteristic frequency (CF) of neuronal frequency tuning curves (ITCs) from low CFs in the caudal aspect of AI to progressively higher CFs toward the rostral border of AI. In the spatial dimension orthogonal to the cochleotopic frequency gradient of AI, i.e., in its dorsoventral extent, no clearly expressed gradient of CF has been observed. It was concluded that cortical neurons with similar CFs are arranged along “isofrequency contours” oriented along the dorsal-to-ventral extent of AI.

The first evidence for a spatial segregation of functional parameters along the “isofrequency domain” came from the discovery of “binaural interaction bands” that transect isofrequency contours in AI (Imig and Adrian 1977; Middlebrooks et al. 1980). The isofrequency domain of AI then consists of alternating patches of neurons that differ in their binaural integration of excitatory or inhibitory inputs and in their thalamic and cortical sources of input (Imig and Brugge 1978; Imig and Reale 1981; Middlebrooks and Zook 1983). The spatial distributions of other functionally significant response characteristics of neurons in the isofrequency domain of AI have not been extensively studied. However, a multiple-unit study of the secondary auditory field (AII) that included ventral aspects of AI (Schreiner and Cynader 1984) indicated a systematic spatial variation of another important functional parameter in ventral AI—the sharpness of tuning.

More extensive analyses of isofrequency-domain representations have been conducted in the auditory cortex of echolocating bats. Several topographic representations of functionally significant parameters relating to biosonar orientation sounds have been demonstrated (e.g., Suga 1965, 1984; Suga and Manabe 1982). By contrast, no clear func-
tionally identified specialization of auditory cortical fields has been described in other mammalian species. To address the issue of cortical-field organization and specificity in signal processing, an important question in auditory neurobiology is what functional parameters are represented in the extended “isofrequency dimension” of auditory cortical areas.

The goal of this study was to examine, in more detail, the spatial distribution of some response features of potential functional significance in the isofrequency domain of the high-frequency region in the AI of anesthetized cats. In this initial report the spatial distribution of excitatory neuronal activity in response to pure tones and broadband transients is presented. Cortical maps for sharpness of tuning are illustrated and compared. Reports will follow that address stimulus-intensity effects and responses to frequency sweeps in the same animals.

METHODS

Surgical preparation

Results presented in this report were obtained in the right hemispheres of adult cats. Anesthesia was induced with an intramuscular injection of ketamine hydrochloride (10 mg/kg) and acepromazine maleate (0.10 mg/kg). After venous cannulation, an initial dose of pentobarbital sodium (30 mg/kg) was administered. Animals were maintained at a surgical level of anesthesia with a continuous infusion of pentobarbital sodium (2 mg·kg⁻¹·h⁻¹) in lactated Ringer solution (infusion volume, 3.5 ml/h) and, if necessary, with supplementary intravenous injections of pentobarbital sodium. The cats were also given dexamethasone sodium phosphate (0.14 mg/kg im) to prevent brain edema and atropine (1 mg im) to reduce salivation. The temperature of the animals was monitored with a rectal probe and maintained at 37.5°C by means of a heated water blanket with feedback control.

The head was fixed, leaving the external meati unobstructed. The temporal muscle on the right hemisphere was then retracted and the lateral cortex exposed by a craniotomy. The dura overlying the middle ectosylvian gyrus was removed, the exposed cortex covered with silicone oil, and a photograph of the surface vasculature was taken to record the electrode penetration sites.

Stimulus generation and delivery

Experiments were conducted in a sound-shielded room (IAC). Auditory stimuli were presented via calibrated headphones (STAX 54) enclosed in small chambers that were connected to sound-delivery tubes sealed into the acoustic meati (Sokolich, US Patent 4,251,686; 1981). The sound-delivery system was calibrated with a sound-level meter (Bruel & Kjaer 2209) and a waveform analyzer (General Radio 1521-B). The frequency response of the system was essentially flat up to 12 kHz and did not have major resonances deviating more than 6 dB from the average level. Above 15 kHz, the output rolled off at a rate of 10 dB/octave.

Tones were generated by a microprocessor (TMS32010; 16-bit D/A converter at 120 kHz; low-pass filtered at 35 kHz). The processor-related useful dynamic range of these stimuli was <8 dB, allowing a 3-bit amplitude resolution at the lowest-applied stimulus level. Additional attenuation was provided by a pair of passive attenuators (IIP). The duration of the tone bursts was 50 ms including 3 ms rise-fall time. The interstimulus interval was 500–1,000 ms.

For each recording site responses were recorded to at least 675 different tone bursts. Tone bursts were presented in a pseudorandom sequence of different frequency-level combinations selected from 15 level values and 45 frequency values. From the responses to all stimuli, frequency-response areas (FRAs) were reconstructed. The minimum step between stimulus levels was 5 dB, resulting in a dynamic range of 75 dB for the FRA. The frequency range covered by the 45 frequency steps was geometrically centered around the estimated CF of the recording site and covered between 2 and 4 octaves, depending on the estimated width of the FRA. Stimulus frequencies were equidistant on a logarithmic frequency scale.

A frequency step generated with a Wavetek 185 was used to produce a broadband transient signal. The frequency changed from 250 Hz to 64 kHz, or vice versa, within <20 μs. The electric input and acoustic output spectra of the speaker system for the frequency step are shown in Fig. 1.

Recording procedure

Parylene-insulated tungsten microelectrodes with impedances of 0.8–1.3 MΩ were introduced into the auditory cortex with a hydraulic microdrive (KOPF) remotely controlled by a stepping motor. All penetrations were roughly orthogonal to the brain surface. The recordings reported here were derived at an intracortical depth ranging from 600 to 1,000 μm, as determined by the microdrive setting, roughly corresponding to cortical layers III and IV. Neuronal activity of single units or small groups of neurons (2–6 units) were amplified, band-pass filtered (1–10 kHz 12 dB/octave), and monitored on an oscilloscope and an audio-monitor. Spike activity was isolated from the background noise with a window discriminator (BAK DIS-1). The discriminator level was set to exclude evoked potentials and to accept events that resembled action potentials of an amplitude at least 50% above the background signal. The number of events per presentation and the arrival time of the first event after the onset of the tone bursts were recorded and stored in a computer (DEC 11/73). The recording window had a duration of 50 ms, corresponding to the stimulus duration. Poststimulus time histograms (PSTHs) were constructed for action potentials evoked by the frequency-step stimulus. Binwidth was 0.8 ms.

Data analysis

From the responses to 675 different frequency-level combinations, an objectively determined FRA was constructed for every recording site. Figure 2 shows three typical examples of reconstructed FRAs obtained in the auditory cortex. Each line corre-

![Amplitude spectrum of the transient occurring at a frequency step from 250 Hz to 64 kHz. Spectrum is the average for different phase conditions at the time of the frequency step. However, the influence of the actual phase configuration of 2 sine waves at the time of transition is small.](image)
Fig. 2. Examples of typical cortical frequency-response areas. Each line represents the averaged number of spikes produced by stimuli of different frequencies (45) and a fixed level. Fifteen different levels were used. Average spike count was derived by calculating the weighted sum of spike counts for a given frequency-level combination and its 4 nearest neighbors followed by division by 3. Central point was assigned a weight of 1; other points had a weight of 0.5. At borders of the parameter area, only 4 or 3 appropriately weighted points were used for the averaging. Dashed line corresponds to a threshold tuning curve, delineating a joint area with a stimulus-evoked activity of at least 25% above spontaneous-background activity. Open triangles mark the bandwidth used for the determination of $Q_{10\text{ dB}}$. Closed triangles indicate the same for $Q_{40\text{ dB}}$.

From the pseudo-three-dimensional representation of the FRA, several response parameters were extracted.

1) CF, the stimulus frequency with the lowest sound-pressure level necessary to evoke neuronal activity.

2) FRA threshold, lowest level evoking activity in the FRA. For a given frequency-level combination of the stimulus, the presence of evoked activity was assumed when a 100% increase in spike count above the average spontaneous activity was observed for the stimulus configuration under consideration as well as for two or more of the possible eight nearest frequency-intensity neighbors in the FRA.

3) $Q_{10\text{ dB}}$, the CF divided by the bandwidth of the FRA 10 dB above FRA threshold. Because the recordings were made from small clusters of neurons, the obtained extent or sharpness of the response area represents the spatial integration of the response bandwidth of several neurons. The resulting "integrated excitatory bandwidth" underlying the estimate of the quality factor $Q$ is indicated by open arrows in Figure 2.

4) $Q_{40\text{ dB}}$, the CF divided by the bandwidth 40 dB above FRA threshold. The integrated excitatory bandwidth is indicated by filled arrows in Figure 2.

5) Transition rate, firing rate at a point in the rate-level function that marks the transition from a fast growing, low level portion to a less-fast-growing, saturating or decreasing portion of the rate-level function. Rate-level profiles were constructed by summing for each signal level the spike counts produced by the CF and the two frequencies nearest CF, i.e., responses from 45 signal presentations were utilized. In virtually all cases a monotonic, fast-growing portion can be distinguished that rises from the response threshold (see Fig. 13, open arrows) to a transition point (see Fig. 13, filled arrow), i.e., to a clear transition to a less-fast-growing portion of the rate-level profile, a saturation, or to a decline of firing rate. The transition point is marked by a large second derivative of the rate-level profile. The transition rate is a useful measure of responsivity because it can be determined for nearly all units regardless of their high-level characteristics. Therefore it was utilized to normalize the response magnitude of a cortical location to a broadband transient signal.

In addition to the FRA a frequency-step response was determined at each sampled cortical location. A frequency step is defined as a broadband transient signal generated by a rapid frequency-step response threshold (see Fig. 13, open arrows) to a transition point (see Fig. 13, filled arrow), i.e., to a clear transition to a less-fast-growing portion of the rate-level profile, a saturation, or to a decline of firing rate. The transition point is marked by a large second derivative of the rate-level profile. The transition rate is a useful measure of responsivity because it can be determined for nearly all units regardless of their high-level characteristics. Therefore it was utilized to normalize the response magnitude of a cortical location to a broadband transient signal.

Fig. 3. Demonstration of the gridding and smoothing process used in the pseudo-three-dimensional reconstruction procedure. Twenty-seven $Q_{10\text{ dB}}$ values are plotted as a function of the dorsoventral location in AI (dots, case 387-318). CFs of all locations were within the range from 7.4 to 8 kHz. Thick solid line indicates the result of the gridding process that projects actual data points onto 35 grid points with the use of a weighted distance-squared interpolation algorithm. Thin line reflects an additional smoothing with a weight of 0.8.
those responses. The maximum firing rate to a CF tone was not
able bias arising from varying numbers of neurons contributing to
evoked activity was necessary to be able to compare multiple-unit
This normalization to a uniformly defined and identifiable tone-
evoked activity was necessary to be able to compare multiple-unit
of the transition rate obtained for CF stimulation (see above).
were used for further analysis. Action potentials were counted
within a 10-ms window centered at the maximum response and
the average spike count per presentation expressed as percentage
of the transition rate obtained for CF stimulation (see above).
that showed the strongest response to the transient
was used for further analysis. Action potentials were counted
within a 10-ms window centered at the maximum response and
the average spike count per presentation expressed as percentage
of the transition rate obtained for CF stimulation (see above).

**Data representation**

Pseudo-three-dimensional projections and contour plots were
utilized to represent the spatial distribution of response parame-
ters across the cortical surface (topography software from Golden
Software). The actual spatial locations of the recording sites (accu-
rate within ±50 µm) were used to generate a two-dimensional grid
of the represented area by projecting the actual sites to the nearest
grid point. The grid size for the three-dimensional projection was
200 or 230 µm, i.e., each recording location was within 140-160
µm of the next grid point. Elevation of the gridded surface corre-
sponds to the spatially averaged magnitude of a functional para-
meter at a given site. The gridding program employs a weighted,
inverse-distance, squared algorithm for the interpolation of all
grid points. The gridding operation reduces the extreme values in
the z domain and brings them closer to the average z value,
resulting in a proportional compression. In some of the maps the
distance between recording sites was not uniform, i.e., sites were
closely spaced along an isofrequency contour and more widely
spaced between the studied isofrequency contours (see Fig. 4).
The spatial constant or search radius necessary to achieve a
smooth interpolation between more widely spaced locations re-
sulted in a spatial averaging of the values of more closely spaced
locations. To moderately emphasize general trends, an additional
smoothing operation was occasionally invoked with smoothing
factors >0.8. A smoothing factor of 1 would result in no addi-
tional smoothing of the grid surface, whereas a smoothing factor
of 0 would result in a flat map corresponding to the average z
value. Figure 3 gives a two-dimensional example of the transfor-
mation of raw data (Q10 ab, dots, n = 27, case #87-518) to a
gridded representation (thick line, 35-grid points) and to an addi-
tionally smoothed representation (thin line, smoothing factor
0.8). The result of the transformations provide a faithful, although
amplitude-compressed, version of the original information.

Because the pseudo-three-dimensional projection of the maps
always results in some perspective distortions, an undistorted
view of the spatial distribution is provided by presenting contour
plots of one of the three cases. Contours are line segments that
connect interpolated locations with equal surface elevation or z
values. Contour plots are rotated so as to allow a direct compari-
son with the pseudo-three-dimensional projections of the data. To

FIG. 4. Location of mapped areas on cortical surface and position of
recording sites. For 1 case (#87-007) observed CF values are plotted at the
approximate cortical recording location. In other plots individual record-
ings sites are marked by filled squares for each case. Estimated locations
connect locations with the same characteristic frequency (CF). Contour
lines were derived from interpolated elevations of a pseudo-three-dimen-
sional projection of actual CF values.
TABLE 1. Specifications of mapped areas in the high-frequency domain of AI

<table>
<thead>
<tr>
<th>Case</th>
<th>Dimensions, mm × mm</th>
<th>Area, mm²</th>
<th>Number of Sites</th>
<th>Average Nearest Distance, mm</th>
<th>Frequency Range of AI, kHz</th>
</tr>
</thead>
<tbody>
<tr>
<td>#87-001</td>
<td>2.0 × 4.4</td>
<td>8.8</td>
<td>95</td>
<td>302</td>
<td>10.3–26.3</td>
</tr>
<tr>
<td>#87-518</td>
<td>1.32 × 5.63</td>
<td>7.48</td>
<td>82</td>
<td>302</td>
<td>7–11</td>
</tr>
<tr>
<td>#87-706</td>
<td>3.25 × 5.57</td>
<td>18.08</td>
<td>86</td>
<td>459</td>
<td>5.8–17.3</td>
</tr>
</tbody>
</table>

AI, primary auditory cortex.

judge the correspondence of the data values with their three-dimensional representation, the value and spatial location of each data point is provided for one exemplary case.

RESULTS

In six animals functional maps of AI were objectively derived with multiple-unit recordings. One animal was excluded from the analysis because of progressive increases in response threshold during the experiment. In three intensively studied animals, maps for each of 12 different response parameters were obtained. Results of the parameters reported here (\(Q_{10\ dB}\), \(Q_{40\ dB}\), frequency-step response) are restricted to those three cases to enhance comparability with other functional properties to be presented in subsequent reports. Comparison with partial maps of the same response parameters obtained in the other animals indicates that the results of the three presented cases are representative.

All three cortical maps were located on the crest of the right ectosylvian gyrus. A total of 263 recording sites were studied. Figure 4 illustrates the location of the three mapped areas and the individual recording sites within each map. Superimposed on the recording sites are estimates of isofrequency contours indicating the approximate distributions of CFs found in these maps. For one case (#87-001), the actual CF values are indicated. Not all contour lines are bracketed by data points because the gridding is always extrapolated to rectangular boundaries of the region. The parallel arrangement of the majority of the isofrequency contours indicates that most of the mapped areas were confined to AI. In areas that were only sparsely sampled, deviation of the isofrequency contours from straight lines near the map boundaries are, to a large extent, a consequence of the gridding process and do not necessarily reflect true deviations from strict tonotopic organization. In two of the extensively studied animals, the long axis of the mapped areas was approximately aligned with the orientation of the isofrequency contours. In one case (#87-001) the orientation of the mapped area was tilted 24° relative to the isofrequency orientation, resulting in an approximate alignment of the 18- to 20-kHz contours with one of the diagonals of the mapped area, i.e., from its ventroposterior to dorsoanterior corner. Table 1 contains some basic descriptive data of the three maps. The average nearest distance of recording sites was between 300 and 450 μm for the three cases. The spatial error in determining the cortical location was approximately ±50 μm.

Within the range of cortical depth sampled in this study, 600–1,000 μm, response properties were similar, i.e., no

TABLE 2. Mean values of \(Q_{10\ dB}\) and \(Q_{40\ dB}\)

<table>
<thead>
<tr>
<th>Case</th>
<th>(Q_{10\ dB})</th>
<th>(Q_{40\ dB})</th>
</tr>
</thead>
<tbody>
<tr>
<td>#87-001</td>
<td>5.39 ± 2.98</td>
<td>1.94 ± 0.97</td>
</tr>
<tr>
<td>#87-518</td>
<td>5.41 ± 3.29</td>
<td>2.52 ± 1.81</td>
</tr>
<tr>
<td>#87-706</td>
<td>4.28 ± 2.40</td>
<td>1.92 ± 1.31</td>
</tr>
</tbody>
</table>

Values are means ± SD; number of cortical locations given in parentheses. \(Q_{10\ dB}\), the characteristic frequency divided by the bandwidth of the frequency-response area 10 dB above frequency-response–area threshold; \(Q_{40\ dB}\), the characteristic frequency divided by the bandwidth 40 dB above frequency-response–area threshold.
clear deviation from a columnar organization was observed.

Distribution of $Q_{10\, \text{dB}}$

Pure tones are commonly used to determine the spectral range that produces an excitatory response of neurons. The extent of the excitatory receptive field or the sharpness of the excitatory FTC of neurons is then assessed by obtaining the $Q$ factor near response threshold. In multiple-unit recording, a similar measure can be applied to the sum of all units in a cluster, resulting in the integrated $Q_{10\, \text{dB}}$. The value range for sharpness of tuning expressed as $Q_{10\, \text{dB}}$ is...
shown in Fig. 5 for the three cortices. For sufficiently sampled CFs, a range of $Q_{10\,\text{dB}}$ values was observed that approximately corresponded to a factor of 10. The mean values and standard deviations of $Q_{10\,\text{dB}}$ for the three cases are shown in Table 2.

The spatial distribution of the observed $Q_{10\,\text{dB}}$ values is shown in Fig. 6 for all three cases as pseudo-three-dimensional maps. For cases #87-518 and #87-001, the accompanying contour plot or the actual $Q_{10\,\text{dB}}$ values are shown. A common global feature of all three maps was the presence of an area of relatively high-$Q_{10\,\text{dB}}$ values in the center of the maps bordered by areas of relatively low-$Q$ values on the ventral and dorsal side. The $Q$ values in the center of the map were not uniformly high, with relative low values being encountered in close proximity of some high-$Q$ values. Despite this local fluctuation of $Q$ values, a fairly gradual transition from a central area of largely narrow integrated excitatory bandwidths to surrounding areas with broader integrated excitatory bandwidths and lower-$Q$ values was apparent. Both of the $Q$ gradients, the ventral as well as the dorsal, appear to occur at map sectors that are well within the tonotopically organized part of the mapped area, i.e., within AI, as judged from the systematic CF distribution (see Fig. 4). Although a few of the most ventral recording sites may already belong to AII, a clear and distinct boundary between AI and AII was not apparent based on $Q_{10\,\text{dB}}$ alone (for discussion see Schreiner and Cynader 1984). Similarly, some of the most-dorsal recording sites may already be part of the dorsal fringe area bordering AI (Middlebrooks and Zook 1983). However, a clear dorsal boundary of AI based solely on CF and $Q_{10\,\text{dB}}$ estimates was not discernible.

In the region of AI that contained the $Q_{10\,\text{dB}}$ maximum, a posterior-to-anterior gradient of $Q_{10\,\text{dB}}$ was apparent in all three maps, reflecting an increase of sharpness in tuning with an increase in CF. This trend was absent or obscured by the scatter of $Q$ values for the more broadly tuned areas of AI.

In summary, the integrated excitatory bandwidth 10 dB above threshold was not uniformly distributed along the isofrequency domain in the high-frequency region of AI. It showed a systematic, although noisy, spatial distribution with a bandwidth minimum or $Q$ maximum near the center of the dorsal-ventral extent of AI and somewhat gradual increases of the bandwidth toward the ventral and dorsal boundaries of AI. In the center region of AI, a $Q$ gradient as a function of CF was observed.

**Distribution of $Q_{40\,\text{dB}}$**

For cortical neurons an estimate of the sharpness of tuning or the extent of the excitatory receptive field based on $Q_{10\,\text{dB}}$ is often insufficient for extrapolating the spectral characteristic of tuning curves at higher stimulus levels (e.g., Suga and Tsuzuki 1985). To estimate the extent of the excitatory receptive field at higher stimulus intensities, the $Q$ factor 40 dB above response threshold, $Q_{40\,\text{dB}}$, was assessed (see Fig. 2). The value range for sharpness of tuning expressed as $Q_{40\,\text{dB}}$ is shown in Fig. 7 for three individual cases. Similar to the observed $Q_{10\,\text{dB}}$ values, $Q_{40\,\text{dB}}$ values varied over about one order of magnitude. $Q_{40\,\text{dB}}$ values were usually less than one-half of the corresponding $Q_{10\,\text{dB}}$ at the same cortical site. The mean values and standard deviations of $Q_{40\,\text{dB}}$ are given in Table 2.

The spatial distribution of the observed $Q_{40\,\text{dB}}$ values is shown in Fig. 8 for all three cases as pseudo-three-dimensional maps. For case #87-518 a contour plot is shown, and the actual $Q_{40\,\text{dB}}$ values are shown. A common global feature of all three maps was the presence of an area of relatively high-$Q_{40\,\text{dB}}$ values in the center of the maps bordered by areas of relatively low-$Q$ values on the ventral and dorsal side. Despite some scatter in the distribution, a fairly gradual transition of $Q$ values from the central area (high-$Q$ values) to the ventral area (lower-$Q$ values) is apparent. A similar decrease of $Q_{40\,\text{dB}}$ was also apparent toward the dorsal end of the map. However, in case #87-706 and to a certain extent also in case #87-706, the decline of $Q_{40\,\text{dB}}$ values dorsal to the main-$Q$ peak was reversed in the most dorsal-third of the mapped areas. The $Q_{40\,\text{dB}}$ values asso-
associated with this secondary, dorsal maximum were slightly smaller and were more scattered compared with the main peak in the spatial-$Q$ distribution. The slope of the ventral-$Q$ gradient was less steep than the slope on the dorsal side of the main-$Q$ peak.

In summary, the integrated excitatory bandwidth 40 dB above response threshold showed a systematic distribution in the isofrequency domain of AI. A region in the center of AI revealed narrow excitatory bandwidths, ventrally and dorsally bordered by areas with broader bandwidths, i.e., lower-$Q$ values. Most portions of the two main-$Q$ gradients were located in AI as indicated by its relation to the cochleotopic organization. The spatial gradient of $Q_{40 \, \text{dB}}$ appeared to be more shallow on the ventral side of the center peak then on the dorsal side. Evidence for a second, smaller maximum of $Q_{40 \, \text{dB}}$ in the dorsal portion of the mapped areas was obtained in two of the three cases.

$Q_{10 \, \text{dB}}$ versus $Q_{40 \, \text{dB}}$

Comparison of the spatial distribution of two measures of integrated excitatory bandwidth, $Q_{10 \, \text{dB}}$ and $Q_{40 \, \text{dB}}$, revealed that the main maximum in the $Q_{10 \, \text{dB}}$ distribution largely overlapped with the main maximum in the $Q_{40 \, \text{dB}}$ distribution.
Two cases exhibit dorsal islands of high-Q dB values tilted to the left. Overlapping areas of high-Q values appear crosshatched. (87-001), 2.5 (87-518), and 2.25 (87-706) are shown with hatching tilted to the right. Areas with Qdo dB values above 2.25 dB values above 6.0 (87-001), 6.25 (87-518), and 6.0 (87-706) are excitatory tuning curves. The highest correlation was seen tones are less influenced (Phillips 1988; Phillips and Cyn- differences in functional properties expressed by the Q the excitatory cortical response to a broadband signal, the

The results of a linear regression analysis for Qlo dB and Qdo dB are given in Table 3. Two cases showed statistically significant correlation between the two Q factors of the excitatory tuning curves. The highest correlation was seen for the case that did not show a second, dorsal maximum in the Qdo dB distribution, indicating the possibility of spatial differences in functional properties expressed by the Q measures. To explore further whether the lower correlation in the remaining two cases was due to scatter in the data or to systematic spatial differences between the two Q measures, the standardized residuals of the linear regression analysis, expressed in units of standard deviations, were plotted as a function of cortical location (Fig. 10). As expected from its relatively high correlation coefficient, case #87-001 (Fig. 10C) showed only relatively small residual values. The residuals were approximately evenly distributed across the entire map with a slight elevation in the anterior center of the map corresponding to the main peak of both Q distributions. The residual values for the other two cases were substantially higher and, more important, they showed some circumscribed spatial clustering. Some clustering of higher residuals in the dorsal area of the two maps (Fig. 10, A and B) was to be expected due to the second maximum in the Qdo dB distribution that was absent in the Qlo dB distribution. A more pronounced maximum of residuals is apparent in the ventral-third of these maps, indicating the presence of different quantitative relationship between the two Q measures in this area compared with the rest of the mapped region. Figure 11 overlays regions containing relatively large residuals with regions of high-Qlo dB values. From this presentation it becomes apparent that the large residuals were mostly confined to the center and ventral slope of the maximum in the Qlo dB distribution.

Figure 12A shows a scatter plot of Qdo dB versus Qlo dB values with the linear regression curve for case #87-518 y = 0.17x + 1.48; r² = 0.2; P = 0.001; n = 76). In Fig. 12B data points are marked (C) that correspond to locations with large residuals confined to the main maximum seen in the residual plot (Fig. 10A) and, therefore, corresponding to the ventral slope of the Qlo dB distribution. Exclusion of those regionally confined outliers from the regression analysis resulted in a substantially better description of the Qlo dB-Qdo dB relationship for the rest of the map (y = 0.34x + 0.66; r² = 0.55; P = 0.0001; n = 68). The observation that six out of a total of eight outliers showed Qdo dB values that were substantially smaller than predicted by the linear regression may indicate a larger than proportional growth of integrative bandwidth with level in that area.

It is concluded that the integrated excitatory bandwidth at different stimulus levels strongly covaried for the majority of cortical locations. In certain areas, i.e., the dorsal portion of AI and the ventral slope of the Qlo dB maximum, however, additional factors determined the extent of the integrated excitatory bandwidth at higher levels.

**Frequency-step response**

Estimation of the integrated excitatory bandwidth through mapping of FRAs with pure tones may not reflect the excitatory behavior of a cortical location or neuron to stimulation with broadband signals. At higher stimulus levels inhibitory mechanisms decisively shape the neural response to broadband signals, whereas responses to pure tones are less influenced (Phillips 1988; Phillips and Cynader 1985; Phillips and Hall 1986). To explore the relationship between the integrated excitatory bandwidth and the excitatory cortical response to a broadband signal, the activity produced by a large and rapid frequency step (see METHODS) was obtained for the majority of locations tested with pure tones.

Figure 13 illustrates five examples of responses to frequency steps in combination with the corresponding FTCs and spike count-level functions at CF. PSTHs for the step

<table>
<thead>
<tr>
<th>Case</th>
<th>Qlo dB vs. Qdo dB</th>
<th>Step vs. Qlo dB</th>
<th>Step vs. Qdo dB</th>
</tr>
</thead>
<tbody>
<tr>
<td>#87-001</td>
<td>0.646</td>
<td>0.0001</td>
<td>-0.11</td>
</tr>
<tr>
<td>#87-518</td>
<td>0.45</td>
<td>0.001</td>
<td>-0.19</td>
</tr>
<tr>
<td>#87-706</td>
<td>0.163</td>
<td>0.14</td>
<td>0.18</td>
</tr>
</tbody>
</table>

See Table 2 for abbreviations. Linear regression, r = correlation coefficient, P = level of significance.
response show the number of spikes after 40 presentations of the stimulus. The time of occurrence of the frequency steps is indicated by the left side of the calibration bar of the time axis. For each spike count-level function, three response characteristics are indicated: response threshold (open, horizontal arrow), transition point from rapid to slow growth rate of the spike count-level function (filled, vertical arrow), and the relative step response rate (star) expressed as spikes per presentation of the frequency step and marked 40 dB above threshold. This level corresponds to the stimulus level of the frequencies preceding and following the frequency step. The percentage magnitude of the step response given in Fig. 13 represents the number of spikes per transient relative to the firing rate at the transition point of the spike count-level function (see METHODS).

The examples in Fig. 13 suggest that locations with broader excitatory bandwidth may be more responsive to a transient broadband signal than locations with narrower bandwidth and/or non-monotonic rate-level functions.

Figure 14 shows the distribution of step-response magnitudes for the three studied cases. All three cases show a wide range of response magnitudes that are approximately evenly distributed along a logarithmic magnitude scale. The magnitude of the transient response never exceeded the firing rate at the CF transition point.

The spatial distributions of the obtained frequency-step responses is illustrated in Fig. 15. All three cases show a clear clustering of locations with either small or large step-response magnitudes. Cases #87-518 (Fig. 15A) and #87-706 (Fig. 15B) show two maxima. One maximum was approximately located at the border between the dorsal and central-thirds of the mapped areas. A second, less-well-defined region with high-response magnitudes to the transient signal was located in the ventral-third of the mapped areas. The third case deviates somewhat from this
In summary, there was a clearly expressed coincidence of areas with low-\(Q_{10 \text{ dB}}\) values and large magnitudes of the frequency-step response. The linear regression between the two parameters yielded only small values, indicating the influence of factors additional to excitatory bandwidth on the response to broadband signals.

DISCUSSION

Sharpness of frequency tuning

Single-unit studies in the AI of the cat have shown that, whereas many units are narrowly tuned, the sharpness of frequency-tuning curves can exhibit large variations, even for neurons with similar CFs (Abeles and Goldstein 1970; Goldstein et al. 1970; Phillips and Irvine 1981). Similar findings were made in the auditory cortex of bats (Suga and Tsuzuki 1985). The question arises as to whether narrowly tuned and broadly tuned neurons are spatially segregated or randomly distributed across AI.

Multiple-unit studies of the areas ventral and dorsal to AI have indicated more broadly tuned responses compared with AI (Merzenich et al. 1975; Middlebrooks and Zook 1983; Reale and Imig 1980; Schreiner and Cynader 1984). Furthermore, a multiple-unit mapping study of AI that included study of the ventral-third of AI have revealed a systematic decrease of the sharpness of tuning (\(Q_{10 \text{ dB}}\)) in AI as the border with AI1 was approached (Schreiner and Cynader 1984). This study has indicated that the distribu-

\(Q_{40 \text{ dB}}\) versus frequency-step response

The spatial relationship between \(Q_{40 \text{ dB}}\) and the activity evoked by a rapid frequency step is illustrated in Fig. 16. The hatched areas correspond to regions with high-\(Q_{40 \text{ dB}}\) values (>50% of the \(Q\) ranges plotted in Fig. 8), and the dotted areas represent regions with a strong response to the broadband transient (>75% relative response magnitude). It is apparent that there is only little overlap between the two spatial representations. In other words, regions with a narrow excitatory bandwidth showed a weak responsiveness to the broadband stimulus and vice versa. Linear regression analysis revealed only one case (#87-518) that showed a significant correlation between the two parameters (see Table 3). Figure 17 shows the spatial distribution of the standardized residuals of the linear regression analysis for that case. The relationship of the main peaks in this distribution to the step-response distribution and the \(Q_{40 \text{ dB}}\) distributions are indicated in the contour-plot representation of Fig. 17. The largest residuals coincided with the dorsal maximum of the step response (see Fig. 15) and the dorsal minimum of the \(Q_{40 \text{ dB}}\) distribution (see Fig. 8).

In summary, there was a clearly expressed coincidence of areas with low-\(Q_{10 \text{ dB}}\) values and large magnitudes of the frequency-step response. The linear regression between the two parameters yielded only small values, indicating the influence of factors additional to excitatory bandwidth on the response to broadband signals.
Fig. 13. Frequency-step responses at five physiologically characterized locations in Al. Left: five multiple-unit frequency tuning curves obtained in Al (case #87-706). CF, Q10 dB, and Q40 dB tuning curves are given (right). Middle: spike count-level functions obtained at the CF of those locations. Open arrow heads indicate estimates of the response threshold. Filled arrow heads indicate the transition point from a monotonically increasing characteristic to saturation or nonmonotonic characteristic (see METHODS). Right: PSTHs for 40 repetitions of a frequency step from 0.25 to 64 kHz. Time of occurrence is marked by the left vertical bar of the time calibration. Level of tones before and after the step corresponded to a CF tone 40 dB above threshold as indicated by the star in the middle column. Number of spikes in a 10-ms window centered at the maximum response is given in the right column. Step-response magnitude in percent relative to the firing rate of a CF tone at the transition point is indicated as "step." Average number of spikes-per-frequency step is represented as a star in the spike count-level functions. Top to bottom: note the decrease in relative step-response magnitude, the decrease of integrative bandwidth at high levels, and the nonmonotonic behavior of the lower three spike count-level functions.

A systematic distribution of the sharpness of tuning in the isofrequency domain had been described for the central nucleus of the inferior colliculus (Schreiner and Langner 1988). An orderly representation of sharpness of tuning might therefore be expected for Al...
This study, applying multiple-unit recordings and pseudo-three-dimensional spatial reconstructions, has demonstrated variations of basic response properties along the isofrequency domain of AI. Although both recording methods and spatial reconstruction methods limit the spatial and functional resolution of the observations, they were sufficient to resolve global aspects of functional cortical topography. The approximate spatial error in placing the electrodes (±50 μm) and the maximal spatial error caused by projecting the actual recording sites to grid locations (<163 μm for a grid size of 230 μm) were both significantly smaller than the average distance between recording sites. The influence of these errors on the estimation of the spatial distribution of the observed parameter is negligible. The location of all three maps was essentially restricted to AI as defined by its consistent cochleotopic gradient. An increase in CF scatter and a decrease of sharpness of tuning toward the dorsal and ventral borders of the mapped areas were taken as indication of the border regions of AI. However, no strictly defined functional or anatomic measures were applied to determine the dorsoventral extent of AI because neither has been found to provide estimates of high precision (Middlebrooks and Zook 1983; Rose 1949; Schreiner and Cynader 1984).

The current findings reveal several functional features of the isofrequency domain of AI. First, they reveal that the sharpness of tuning as obtained with the multiple-unit technique is not uniformly distributed throughout the dorsoventral extent of AI. Second, they confirm the observation of an overall gradual change of tuning sharpness from the dorsoventral center of AI toward AII. Third, they indicate a similar gradual decline of sharpness of tuning for the dorsal portion of AI. Finally, they demonstrate that these systematic changes in sharpness of tuning are not restricted to estimates close to response threshold (Q_{10 db}) but also hold, to a certain degree, for higher stimulus levels (Q_{40 db}), although some additional influences are apparent.

**Sharpness of tuning: single neuron versus multiple neurons**

Before attempting an appropriate functional interpretation of these observations, the implications of the multiple-unit-recording method for an interpretation has to be considered. For a single unit, the sharpness of tuning (extent of excitatory receptive field, excitatory bandwidth) at a given stimulus level represents a measure of the range of stimulus frequencies that provide an effective excitatory input. For multiple-unit or cluster responses, sharpness of tuning has to be interpreted in a more general way. A given small volume in AI contains a number of morphologically different cell-types with presumably different functions in the processing circuitry (Mitani et al. 1985; Winer 1984a-c). Because a multiple-unit recording samples several neurons within such a small volume, it cannot be assumed that all contributing neurons have identical response properties. However, the columnar organization of the AI (Abeles and Goldstein 1970; Merzenich et al. 1975; Phillips and Irvine 1981) combined with the smooth cochleotopic distribution in the horizontal domain are consistent with the postulate that most or even all neurons within a small volume reflect and/or contribute to local processing and local response characteristics (e.g., Mountcastle 1978). The integrated response from a small cluster of neurons, then, can provide information about the boundaries of the range of physiological parameters operative at a given location. Thus the range of stimulus frequencies that can elicit an excitatory cluster response, the integrated excitatory band-
FIG. 15. Spatial distribution of excitatory response magnitude in AI evoked by a broadband transient. A: Top depicts a pseudo-three-dimensional projection of the spatial distribution of the frequency-step magnitude in AI. Additional smoothing factor of 0.9. Bottom: undistorted contour-plot representation of same data. Contour interval is 5. For further details see Fig. 6. B: spatial distribution of frequency-step magnitude in AI (case #87-706) represented as pseudo-three-dimensional projection. C: spatial distribution of frequency-step magnitude in AI (case #87-001) represented as pseudo-three-dimensional projection. Bottom: obtained response magnitudes (in percent rounded to the nearest integer) at their approximate cortical location (see Fig. 4).

width, can be used to characterize the extent of the spectral input available to the neuronal circuitry at a given cortical location. This range of frequencies may not be a direct reflection of the actual physiological output, or true neural integration, of the cortex, because the direct contribution from thalamocortical axons to the response cannot be excluded. The similarity of the latencies of cortical neuron and cluster responses and the dissimilarity in the temporal response characteristics of thalamic and cortical neurons (Creutzfeldt et al. 1980) makes it unlikely that the contribution from thalamocortical fibers to the cortical-cluster response is significant. However, the interpretation of the integrated excitatory response has to include this possibility and therefore is considered to represent the neural activity that contributes to the shaping of the cortical output.
Another factor that might contribute to systematic variations of spike counts from cluster responses is the temporal relationship among the contributing spikes. In a cluster response, two or more simultaneously occurring spikes may result in a superposition of action potentials producing only one crossing of the window-discriminator threshold level. Desynchronization of those spikes could increase the number of accepted events without an actual increase of action potentials in the cluster response. This effect may indeed contribute to some variations in response strength; however, nothing definite is known about the local synchronization of cortical responses to estimate the magnitude of potential desynchronization effects. It is highly probable that the large range of step-response magnitudes (0-100%) as well as the estimates of the $Q$ values are not significantly influenced by this effect.

Several single-unit-response properties other than sharpness of tuning may influence and contribute to the integrated excitatory bandwidth of a local group of neurons. Among them are the distribution of CFs, unit thresholds, shape of rate-level functions, and inhibitory properties within the cluster. Although the specific contribution of single neurons to the cluster response can only be determined by identification of individual spike waveforms, some general assertions about the contributing units can be made. Clusters with a narrow integrated excitatory bandwidth likely contain single units that are also narrowly tuned and have similar CFs (see Fig. 6 in Robertson and Irvine 1989). By contrast, broad integrated excitatory bandwidths may contain either broadly tuned units with similar CFs and/or a number of narrowly tuned units with some scatter in their CFs. The latter point of view is supported by recent studies of pairs of units that were encountered at the same recording location. Recordings in the medial geniculate body (Morel et al. 1987; Rouiller and de Ribauipierre 1989) and the auditory cortex of cats (Hui et al. 1989) and guinea pigs (Redies, personal communication) revealed that the CFs of two neurons that were recorded at the same electrode location often differed by up to one-half of an octave. This implies that strict single-unit mapping could result in a large random scatter in the spatial distribution of basic properties, including CF, as long as the morphological cell-type and any possible functional differences are not taken into consideration for the reconstruction of maps.

The fact that multiple-unit recordings in this study did reveal a significant variation of the integrated excitatory bandwidth along the isofrequency domain of AI indicates that the functional content of the sampled neuron clusters varied as a function of location in an isofrequency contour. Although the precise nature of the spatial functional changes is not known, it can be inferred that the excitatory spectral content available for processing at a cortical site varies from a narrow pass band in the dorsoventral center of AI to increasingly broader bands toward the dorsal and ventral borders of AI. It can be hypothesized, then, that a given spectral component is simultaneously pro-

**FIG. 16.** Comparison of areas with high frequency-step responses and high $Q_{40\,\text{dB}}$. Areas with step-response values above 25% are stippled. Areas with $Q_{40\,\text{dB}}$ values above 2.25 (#87-001), 2.5 (#87-518), and 2.25 (#87-706) are shown with hatching tilted to the left. Note 2 cases with dorsal islands of high-$Q_{40\,\text{dB}}$ values.

**FIG. 17.** Spatial distribution of normalized residuals in AI after linear regression analysis of frequency-step response and $Q_{40\,\text{dB}}$. After applying linear regression to the step response vs. $Q_{40\,\text{dB}}$ distribution, residuals were calculated and expressed in units of standard deviation. Sign of residuals was ignored. Top: pseudo-three-dimensional projection of the spatial distribution of the normalized step response vs. $Q_{40\,\text{dB}}$ residuals in AI. Additional smoothing factor of 0.9. Bottom: undistorted contour-plot representation of the data. Contour intervals are 0.2. Stippled areas in the contour plot represent locations with frequency-step responses above 25% of CF-tone response.
cessed in AI utilizing a variety of analyzing bands centered around that component. This analysis results in a spatially distinct representation of information within the isofrequency domain differentially weighted by the local and global spectral energy distribution of the signal. Such a distributed “multiple-bandwidth spectral analyzer” could be of special value in the evaluation and extraction of spectral shape in complex sounds.

Sharpness of tuning: $Q_{10\,\text{dB}}$ versus $Q_{40\,\text{dB}}$

The overall spatial distribution of the sharpness of tuning 10 and 40 dB above response threshold was quite similar. In particular, the location of the maximum in the $Q_{10\,\text{dB}}$ distribution and the main (ventral) maximum in the $Q_{40\,\text{dB}}$ distribution were closely aligned in all three cases. Inspection of the $Q_{40\,\text{dB}}$ distribution and the results of a cross-correlation analysis, however, revealed two differences in the respective spatial distributions. First, two of the three cases showed a second, spatially restricted maximum in the dorsal aspect of the $Q_{40\,\text{dB}}$ map, unlike the $Q_{10\,\text{dB}}$ distribution. This is indicative of 1) a larger variability in the functional organization of the dorsal aspects of AI and 2) the presence of an additional spectral-sharpening mechanism in that area that is most effective at higher intensities. Second, two of three cases showed only a weak correlation between $Q_{10\,\text{dB}}$ and $Q_{40\,\text{dB}}$ in a rostrocaudal strip extending 1–1.5 mm on the ventral side of the $Q_{10\,\text{dB}}$ maximum. The reason for the apparent functional independence of $Q_{10\,\text{dB}}$ and $Q_{40\,\text{dB}}$ in restricted areas may be related to additional functional mechanisms that only operate at higher intensities. It is likely that the mechanisms responsible for the sharpness of tuning include strong inhibitory contributions, e.g., through sideband inhibition (Suga and Tsuzuki 1985). These inhibitory properties are likely to be more powerful at higher stimulus levels, and the $Q_{40\,\text{dB}}$ distributions would reflect more of its influence than the $Q_{10\,\text{dB}}$ maps. Corroborating evidence was derived from the study of the response distribution to large frequency steps, a transient broadband stimulus.

Strength of excitation: broadband stimuli

Several studies have reported classes of cortical neurons that may differ dramatically in their response strength to noise and click stimuli (Phillips and Cynader 1985; Phillips et al. 1985; de Ribaupierre et al. 1972). Although the broadband stimulus used in this study was generated differently than the usually applied signals, a comparable wide range of strength of excitation was observed. The encountered range of relative response strength to a transient broadband signal, a rapid frequency step, was fairly evenly distributed over the full response range as determined with a CF tone. Additionally, the excitatory activity in response to a large frequency step showed a clear and systematic spatial distribution in the isofrequency domain of AI. Segregated clusters of locations with large or small step responses relative to a CF response were observed. Larger responses were seen approximately between the middle- and dorsal-third of the maps and, to a lesser degree, in the ventral-third of the mapped area near the transition into AI.

It is likely that inhibitory mechanisms, e.g., sideband inhibition strongly invoked by broadband stimuli, were largely responsible for the reduction in response strength to frequency steps (Phillips 1988; Phillips and Cynader 1985; Phillips et al. 1985). The fairly gradual transition from areas with large responses to areas with small responses may be accounted for by two effects: 1) a gradual change in strength of inhibition operating evenly on all units in a cluster, and/or 2) a constant amount of inhibition operating on a systematically changing proportion of cells in a cluster. The extremes of the distribution of excitatory strength, i.e., areas of maximal or minimal responses to the frequency step, suggest that the presence or absence of inhibition applies uniformly to all members of a cluster. This can be interpreted as indication of at least some functional homogeneity of clusters for this functional property and at selected cortical locations.

This study suggests that inhibitory effects are systematically distributed along the isofrequency axis of AI. Single- and multiple-unit studies (Shamma and Fleshman 1990; Sutter and Schreiner 1990) of the cortical distribution of inhibitory properties have provided preliminary evidence that the location and strength of the upper- and lower-inhibitory sidebands systematically change across the dorsoventral extent of AI. Supporting evidence for a systematic representation of inhibition in AI, although indirect, was previously provided by a study that categorized rate-level functions with regard to monotonic and nonmonotonic growth behavior (Phillips et al. 1985).

Strength of excitation: narrowband versus broadband stimuli

Comparison of the distributions of $Q_{40\,\text{dB}}$ values and frequency-step responses show a complementary spatial pattern. Areas in AI with high-$Q_{40\,\text{dB}}$ values were usually associated with small-step responses, and areas with low-$Q_{40\,\text{dB}}$ values were associated with high-step responses. This close correspondence in the spatial distribution of these two parameters would suggest that both methods estimate similar functional properties. Cross-correlation analysis of these parameters, however, revealed only a relatively small correlation coefficient. Besides the inherent scatter in the data, this is likely due to differences between the magnitude of frequency-step values in the two main maxima and the corresponding values in the $Q_{40\,\text{dB}}$ minima. The dorsal maximum of the step response had higher values than the ventral maximum in two out of three cases. Although the $Q_{40\,\text{dB}}$ values were small at both corresponding areas, the $Q$ values in the ventral minimum were, on the average, smaller than in the dorsal minimum. By contrast, the dorsal $Q$ minimum should have smaller values than the ventral region if step response and $Q_{40\,\text{dB}}$ values were linearly related. This deviation from a simple linear relationship between step response and $Q_{40\,\text{dB}}$ across the total dorsoventral extent of AI then suggests that there are additional regional differences that have to be taken into account for the prediction of responses to stimuli as different as pure tones and broadband transients.

Nevertheless, the overall similarity of the $Q_{40\,\text{dB}}$ and frequency-step distributions indicate that use of narrowband and broadband signals may result in closely related esti-
mates of some aspects of the functional organization of AI, including combined effects of excitatory and inhibitory mechanisms. In a series of studies, Phillips and colleagues (Phillips and Cynader 1985; Phillips and Hall 1986; Phillips et al. 1985) explored the relationship of rate-level functions with the response to tones and wide-spectrum stimuli. They postulated that the excitatory response characteristics of cortical neurons may be shaped by multiple, incompletely overlapping inputs of varying sensitivities, i.e., reflecting the influence of neurons with a range of CFs and thresholds. This study suggests that the extent of convergence of effective overlapping excitatory inputs may systematically vary along the isofrequency domain.

**Relationship to binaural interaction bands and anatomic studies**

Almost all response parameters in this study were derived from monaural, contralateral stimulation. The main orientational axis of the described functional organization, e.g., minimal integrated excitatory bandwidth or maximum response to transients, ran parallel to the rostrocaudal axis of the high-frequency portion of AI. This orientation is similar to the orientation of binaural interaction bands found in AI (Imig and Adrian 1977; Middlebrooks et al. 1980). Although the functional and spatial relationship between the properties observed in this study and binaural interaction bands will be reported in a subsequent paper, it is sufficient to state here that there appears to be only a weak relationship between the spatial organization of basic binaural aspects and the global spatial distribution of spectral-processing properties demonstrated in this paper for AI. However, slight modulations of the basic spectral distribution because of properties of individual binaural bands are conceivable and may relate to some aspect of the fine-structure-scatter of the spatial organization as suggested in an unsmoothed representation (Fig. 3). The spatial frequency of the binaural distribution (~4–6 distinct binaural bands across AI) appears to be higher than the spatial frequency of the excitatory bandwidths.

There is evidence obtained in cats (Andersen et al. 1980; Brandner and Redies 1990; Merzenich et al. 1982; Middlebrooks and Zook 1983; Morel and Imig 1987) and guinea pigs (Redies et al. 1989) that the thalamic projections to the isofrequency domain of AI are topographically organized. Although the exact nature of these projection is still debated, recent retrograde-transport studies (Brandner and Redies 1990) have suggested that, independent from binaural properties, cortical neurons located dorsally in an isofrequency band receive projections predominantly from the rostral part of the ventral nucleus of the medial geniculate body, whereas cortical neurons located more ventrally receive projections from the caudal portion of the nucleus. The implications of such a projectional gradient for the functional gradients in the isofrequency domain as reported here are intriguing; however, further and more detailed projectional studies are required.

**Concluding remarks**

Although there exist a clear interindividual variability in the mapped cortices, most aspects described here for the central high-frequency AI, including narrow integrated bandwidth and low-transient response, tend to run continuously along the tonotopic gradient for higher frequencies and, therefore, may be considered to be largely frequency independent. In the dorsal and ventral areas of AI, however, areas with high Q_{00} or large-transient responses appear to be more variable from animal to animal and are distributed in a more patchy fashion. The significance of these spatially more restricted and therefore frequency-dependent functional properties and their relationship to other anatomic or functional properties, e.g., patchy intracortical connections (Matsubara and Phillips 1988), remains an open question.

The spatial distribution of excitatory and inhibitory properties, as reflected in the integrated excitatory bandwidth and the integrated frequency-step response, suggests an orderly functional organization of the isofrequency domain of AI. This organization is mainly orthogonal to the basic cochleotopic layout. The functional interpretation of the spatial distribution of frequency-step responses strengthens the conclusions about the functional implications of such an organization as derived from the distributions of the integrated excitatory bandwidths, namely, that signals with different bandwidths produce different activation patterns along the isofrequency axis of AI. The observed functional organization of AI may contribute to a parallel analysis of several aspects of complex signals within each frequency band. The distinction of natural sounds based on their spectral complexity as expressed in the spectral shape, tilt, and contrast may be one of the functional benefits. What types of sound might preferentially excite units in sharply tuned versus broadly tuned areas of AI remains to be seen. The use of frequency sweeps of different speeds and directions, however, indicated response preferences that closely correlated with the spatial distributions described here (Mendelson et al. 1988). Recent evidence of a systematic distribution of the properties of inhibitory sidebands along the isofrequency axis of AI (Shamma and Fleshman 1990; Sutter and Schreiner 1990) and of an accumulation of neurons with multipeaked excitatory tuning curves in the dorsal-third of AI (Sutter and Schreiner 1989) are suggestive of the neuronal properties underlying the observed global-functional characteristics.

The results of this study provide evidence for functional organizations of primary auditory cortex beyond tonotopy and binaural organization principles. The findings provide an additional functional frame of reference for more detailed studies of the spatial distribution of functional organization orthogonal to the cochleotopic gradient. The findings also support the notion that the functional transition from AI into the ventrally and dorsally bordering cortical areas are rather gradual (Middlebrooks and Zook 1983; Schreiner and Cynader 1984).

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REFERENCES


