Spatial Interaction Between Spectral Integration and Frequency Gradient in Primary Auditory Cortex

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Imaizumi K, Schreiner CE. Spatial interaction between spectral integration and frequency gradient in primary auditory cortex. J Neurophysiol 98: 2933–2942, 2007. First published September 12, 2007; doi:10.1152/jn.00511.2007. Primary sensory cortical areas are characterized by orderly and largely independent representations of several receptive field properties. This is expressed in multiple, spatially overlaying parameter distributions, such as orientation preference, spatial frequency, and ocular dominance maps in the primary visual cortex. In the auditory cortex, two main and presumably independent representational parameters are the center frequency and the frequency extent of spectral tuning curves. Here we demonstrate interactions between cortical tonotopic gradient and spectral bandwidth modules in cat primary auditory cortex (AI). First, the spatial representation of spectral integration is not equally expressed across the whole frequency range in AI. Narrow-bandwidth modules are found only in the mid-frequency region (5–20 kHz). Thus spectral integration properties delineate three frequency regions (<5, 5–20, and >20 kHz) in cat AI. Second, the extent of spectral integration covaries with the local tonotopic gradient in the low- and mid-frequency ranges. Regions with a shallow frequency gradient tend to have narrower spectral integration than those with a steep gradient. These relationships between spectral selectivity and frequency gradient constrain forebrain models of thalamo- and corticocortical convergence and connectivity and may reflect the processing of behaviorally relevant stimulus constellations.

INTRODUCTION

Sensory perception involves neural processing and representation of stimulus features in primary sensory cortex (Bushnell et al. 1999; Inouye 2000; Middlebrooks et al. 2002). In vision, the identity of an object is often invariant to spatial translation and retinal location. This may explain why receptive field (RF) features, such as orientation preference or ocular dominance, are expressed across large spans of the retinotopic extent of the primary visual cortex (Bosking et al. 2002; Hubel and Wiesel 1977; Hübener et al. 1997; Issa et al. 2000; Swindale et al. 2000). By contrast, the auditory system processes behaviorally relevant events that are often linked to specific frequency regions and thus segments along the cochlear receptor surface (Reser et al. 2000; Suga 1988). Many RF properties of primary auditory cortex (AI) neurons such as binaural interaction and intensity tuning form spatial clusters embedded in the global tonotopic organization (Eggermont 2001; Imig and Adrián 1977; Nelken 2002; Phillips et al. 1994). Some of them, such as binaural interaction classes, are frequency dependent, and their distributions can differ along the cortical tonotopic axis (Kelly and Sally 1988; Razak and Fuzessery 2002; Reser et al. 2000). Further segregation of functional AI properties exists for frequency selectivity or spectral integration (Cheung et al. 2001; Merzenich et al. 1975; Read et al. 2001; Recanzone et al. 1999; Schreiner and Mendelson 1990; Schreiner et al. 2000). Narrow-band regions contain neurons that are sharply tuned to frequency, and neighboring neurons have similar frequency preference. Broad-band regions contain broadly tuned neurons, and/or nearby cells have significant scatter in their preferred frequencies (Schreiner and Sutter 1992; Schreiner et al. 2000). The aim of this study was to determine whether frequency decomposition, expressed in the cortical tonotopic gradient, systematically interacts with spectral integration. We found that the local variation in spectral integration capacity in cat AI is frequency specific and that distinct spectral bandwidth modules are most strongly expressed in neurons with characteristic frequencies (CFs) between 5 and 20 kHz. Moreover, the magnitude of the cortical frequency gradient covaries with the local spectral bandwidth distribution. Together, these observations establish interactions and local constraints on the cortical expression of two basic auditory processing parameters.

METHODS

Surgery and animal preparation

Experiments were conducted on four right hemispheres from one male and three adult female cats. All protocols were approved by the University of California San Francisco Committee on Animal Research in accordance with federal guidelines for care and use of animals in research. Animals were sedated by intramuscular injections of a mixture of ketamine (22 mg/kg) and acepromazine (0.11 mg/kg). After venous cannulation, sodium pentobarbital (15–30 mg/kg) was administered and supplemented as required throughout the surgical procedure. After tracheotomy, a craniotomy exposed the ectosylvian gyrus. The dura mater was partially removed, and the cortical surface was covered with thick silicone oil. Before commencing the electrophysiological recordings, sodium pentobarbital anesthesia was replaced with a continuous intravenous infusion of a mixture of ketamine (2–10 mg/kg/h) and diazepam (0.05–0.2 ml/kg/h) in lactated Ringer (1–3 ml/kg/h). To prevent edema and mucus secretion, dexamethasone (1.2 mg/kg sc) and atropine sulfate (0.04 mg/kg sc) were injected at regular intervals. Body temperature was monitored and maintained by a water heating pad at 37 ± 1°C. Electrocardiogram and respiration were monitored continuously during the surgery and recording procedures. Because recordings lasted for 3–4 days, cefalosporin (11 mg/kg iv) was administered to prevent wound infection.
Acoustic stimulus

Experiments were conducted in a double-walled, anechoic chamber (Industrial Acoustic, Bronx, NY). Pseudorandomized tone bursts (675) at different frequencies (45 different frequencies in 3–6 octaves) and sound level (70-dB range in 5-dB steps) were presented to the left ear sealed by a STAX speaker. The system frequency transfer function was nearly flat (±6 dB) for frequencies ≤14 kHz and attenuated 10 dB/octave >14 kHz. As a consequence, CFs > ~28 kHz tend to be underestimated (see following text). Sound stimuli of 50-ms duration including 3-ms linear rise and fall time were generated at an interval of 400–750 ms by a microprocessor (TMS32010, 16 bit resolution and 120 kHz D/A sampling rate). Pure tone or white noise bursts were used as search stimuli.

Brain mapping

A video picture of the auditory cortex (AC) surface was captured and digitized with a CCD digital camera (Cohu, San Diego, CA). A parylene-coated tungsten microelectrode (0.5–1.5 MΩ, Micro Probe, Gaithersburg, MD) was advanced perpendicular to the AC surface with a hydraulic microdrive (David Kopf Instruments, Tujunga, CA). Recordings of single- and multiunit activity were performed at depths of 750–1,050 μm (corresponding to layers IIIb and IV) (Huang and Winer 2000). Each penetration was marked on the digitized picture using Canvas software (Deneva, Miami, FL). The marked sites were used to reconstruct tessellation maps of the recording area.

The anterior border of AI was determined by CF-gradient reversal for all four cases (Imaizumi et al. 2004; Knight 1977). The dorsal and ventral extent of AI was estimated from the occurrence of multipeaked tuning curves (Sutter and Schreiner 1991), long onset latencies (He and Hashikawa 1998), increased response thresholds, and loss of strict tuning curves (Sutter and Schreiner 1991), long onset latencies (He and Hashikawa 1998), increased response thresholds, and loss of strict tuning curves (Sutter and Schreiner 1991) over as broad a frequency range as experimentally possible. Q10 and Q40 values reflect spectral bandwidth (or excitatory RF size) near and away from response threshold, respectively, and, thus, reveal different contributions to spectral integration related to thalamocortical input and local cortical transformations (Suga 1995; Sutter et al. 1999).

Spectral integration analysis

Cochleotopic representation is a conspicuous physiological feature in AI (Merzenich et al. 1975), and is expressed as a smooth gradient of the CF. Tessellation maps (Fig. 1, A and B) capture an undistorted view of the spatial organization of AI with a postero-anterior tonotopic gradient from low to high frequencies (red to purple colors). The spatial pattern of the Q10 and Q40 values (Fig. 1, C–F) reveals a nonuniform distribution of spectral integration along the frequency gradient as well as within the isofrequency domain. Blue and red polygons correspond, respectively, to recording sites with broad and narrow spectral bandwidths. The spatial distribution of the Q10 values differs from that of the Q40 values. Large high-Q10 clusters appear in the mid to high-frequency range and rarely in the lower-frequency region (Fig. 1, C and D). By contrast, high Q40 clusters are spatially more confined and are limited to the mid-frequency region (Fig. 1, E and F). There, high Q40 clusters are flanked dorsally and ventrally by low Q40 clusters, resulting in a systematic modular organization of spectral bandwidth along these isofrequency contours (Read et al. 2001; Schreiner et al. 2000). In the lower- and higher-frequency regions, however, Q40 values appear more homogeneously distributed (Fig. 1, E and F).

Our frequency mapping spanned more than five octaves in three cases and four in the other (Table 1). Q values pooled from the four cases showed a similar distribution as individual tessellation maps (Fig. 2, A and B). Q10 and Q40 values <5 kHz are low and are homogeneously distributed, whereas Q values in the mid-frequency range have a wide distribution including low and high values. Q40 values in the high-frequency range are more confined and, with some exceptions, have more homogeneous distribution than in the mid-frequency range (Fig. 2B; note difference in scales). The mean Q10 and Q40 values in 1/2-octave bands as a function of CF reveal the global frequency dependence of AC spectral integration (Fig. 2, C and D). Statistically, the highest mean Q values lay between ~9 and 33 kHz for Q10 and between 9 and 21 kHz for Q40 (central white region in Fig. 2, C and D).

**Table 1.** Receptive field parameter ranges in each case

<table>
<thead>
<tr>
<th>Case</th>
<th>Site</th>
<th>CF, kHz</th>
<th>Threshold, db SPL</th>
<th>Q10</th>
<th>Q40</th>
</tr>
</thead>
<tbody>
<tr>
<td>AWD3</td>
<td>202</td>
<td>1.2–40.1</td>
<td>2.5–57.5</td>
<td>0.5–20.7</td>
<td>0.1–7.3</td>
</tr>
<tr>
<td>AMC6</td>
<td>206</td>
<td>0.8–34.0</td>
<td>2.5–37.5</td>
<td>0.3–23.9</td>
<td>0.2–3.1</td>
</tr>
<tr>
<td>ADF4</td>
<td>161</td>
<td>1.4–44.2</td>
<td>12.5–42.5</td>
<td>0.1–13.1</td>
<td>0.1–4.3</td>
</tr>
<tr>
<td>046R</td>
<td>162</td>
<td>2.0–33.3</td>
<td>7.5–52.5</td>
<td>0.5–12.9</td>
<td>0.2–7.5</td>
</tr>
</tbody>
</table>

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FIG. 1. Tessellation maps for characteristic frequency (CF) and Q10 and Q40 values (cases AWD3 and AMC6). Polygon maps are reconstructed by Voronoi-Dirichlet tessellation. Three sulcus patterns are illustrated by thick black lines. sss, suprasylvian sulcus; pes, posterior ectosylvian sulcus; aes, anterior ectosylvian sulcus. White and black dashed lines represent 5-and 20-kHz isofrequency contours for references. A and B: CF organization. Values are smoothed by a 2nd-order weighted least-square linear regression model. C and D: Q10 maps. Red and blue colors represent high (narrow band) and low (broad band) Q10 values. E and F: Q40 maps. A, anterior; D, dorsal. Scales: 1 mm.

FIG. 2. Population distribution of Q values. A and B: distribution of Q10 and Q40 values across 4 cases. C and D: mean Q values (±SE) in 1/2-octave bins calculated for CF increments of 1/4 octave. Comparison between nonoverlapping bins revealed statistically significant differences (ANOVA adjusted by the sequential Bonferroni correction) between low and high Q ranges (white background). Bins in transition ranges (gray background) did not differ from bins in either low- or high-Q value regions.
Significantly lower Q10 values were found <3.8 kHz (F test adjusted by the sequential Bonferroni correction). Gray background in Fig. 2, C and D, indicates transition ranges, i.e., these CF ranges showed no statistically significant differences to either low or high Q regions (white areas).

The range of Q values in different frequency bands is not uniform. Figure 3, A and B illustrates the distribution of Q40 values from individual cases (○). Shown are fitted models of the CF dependence by a second-order nonparametric, local regression (—) to illustrate the mean Q40 distribution. The individual cases indicate a frequency dependence of mean and variance in the Q40 distribution. Because a modular organization of spectral bandwidths appears most prominently expressed for Q40 (Fig. 1), we further quantified this distribution in two ways. First, we determined the range of Q40 values as a function of CF. This was computed as Q40 residuals by a second-order nonparametric, local regression fit to the Q40 distribution. The range of Q values in different frequency bands is not quantified in contiguous 4-kHz bands across the mapped frequency range (Fig. 4). Figure 4B depicts the population of Q40 MI values. ANOVA reveals a significant difference (P = 0.002, F = 5.4) in the expression of bandwidth modularity between different frequency regions. Specifically, CFs between 5 and 21 kHz show a significantly larger strength of spatial organization than the 1- to 5- and 25- to 29-kHz ranges (P < 0.01; Fisher’s protected least significant difference test). This suggests that spectral bandwidth modularity is heterogeneously expressed across different CF ranges. Between CFs of 5 and 21 kHz, Q40 values are spatially organized along isofrequency contours (Fig. 4B). By contrast, no consistent spatial modulation of Q40 values is discernable <5 and >~20 kHz along the dorso-ventral axis. As a consequence of the wider range of Q40 values and the spatial Q40 organization along mid-frequency isofrequency contours, the local Q gradient is substantially shallower in the low- and high-frequency regions.

The majority of these recordings were made in the mid-frequency regions due to the geometry of sulci and large exposure of this region on the cortical surface (Fig. 1). Figure 5A illustrates the distribution of sampling in the different CF ranges for the whole population. About 63% of the recordings originated in the mid-frequency range (5–20 kHz), whereas ~11 and ~25% of the recordings were made in either the low- or high-frequency range, respectively. Given the prevalence of high Q40 values in the mid-frequency range, the sampling difference between the three frequency regions may create a bias in the statistical evaluation. Monte Carlo analysis was performed to assess whether estimates of the mean Q40 values were influenced by these sampling differences. Eighty Q40 values corresponding to the number of recorded low-frequency units (Fig. 5A) were randomly chosen 10,000 times from the mid-frequency range dataset (463 units). The resulting distribution of mean Q40 values was compared with the actual mean values obtained for the low- and high-frequency regions (Fig. 5C and D). The spatial bandwidth organization was further quantified by assessing bandwidth modularity strength within isofrequency contours. Spatial modulation of Q40 values along the dorso-ventral (isofrequency) dimension was quantified as Q40 MI (see METHODS) in contiguous 4-kHz bands across the mapped frequency range (Fig. 4A). Along many isofrequency contours, two discrete maxima of Q40 values correspond to two narrow-bandwidth modules embedded in regions of broader bandwidth (Fig. 1E for case AWD3).
5B). As shown in Fig. 5B, the mean Q40 values for the low- and high-frequency ranges (▼) were significantly (P < 0.0001 for low-frequency range and P = 0.0011 for high-frequency range) below the distribution of those for the randomized mid-frequency samples. Therefore higher mean Q40 values in the mid-frequency range are not influenced by oversampling. Rather they accurately reflect the nature of sound frequency magnitude, reflecting the local variations in isofrequency contours spacing (Figs. 6C and 7, A, C, and E). Overlaying the Q40 distribution onto the CF gradient map illustrates that high Q40 values are concentrated in the mid-frequency region with a shallow CF gradient (Figs. 6D and 7, B, D, and F) and the high Q40 regions are surrounded by patches of particularly steep frequency gradients (with the exception of the high-frequency side; see following text).

The frequency dependence of the local CF gradient is seen individually (2 examples in Fig. 8A) and for the population mean (Fig. 8B). The correlation coefficients of a logarithmic fit of the individual cases (F-test, P < 0.001) ranged from r = −0.37 (AMC6) to r = −0.46 (ADX4 illustrated in red line in Fig. 8A). Comparison with the CF gradient predicted from the cochlear frequency map (Fig. 8B, blue line; adjusted for the extent of cat AI) (Greenwood 1990) reveals that the cortical gradient is substantially steeper <~5 kHz, indicating a smaller than expected cortical magnification factor. The CF gradient between 9 and 20 kHz matches the cochlear gradient adjusted to the extent of AI. For high CFs, the gradient is the shallowest. However, estimation of CFs >~28 kHz was influenced by the sensitivity roll-off in the loudspeaker transfer function (see METHODS) possibly leading to underestimation of the actual CF and, thus, underestimate the slope of the CF gradient (super-

Frequency gradient analysis

Inspection of Fig. 1, A and B, suggests that the tonotopic gradient across Ai is not uniform. Replotting the CF map as an interpolated but true-value representation (Fig. 6A) with overlaying isofrequency contours (1/3-octave intervals) confirms that the interval between neighboring isofrequency contours is not uniform across Ai. In other words, the CF gradient is variable. Overlaying the isofrequency contours onto the Q40 distribution (Fig. 6B) suggests a wider frequency contour spacing in high Q40 regions (red regions) than in broadly tuned (blue) regions. Plotting the local slope of the tonotopic map (in octaves/mm; the inverse of the cortical frequency magnification factor) reveals distinct regions of high and low gradient

![Image A](http://example.com/imageA.png)

![Image B](http://example.com/imageB.png)

**FIG. 5.** A: distribution of recorded sites in the 3 different frequency ranges. The proportion of recording sites were ~11% for low (1–5 kHz)-, ~63% for mid (5–20 kHz)-, and ~25% for high (>20 kHz)-frequency ranges. B: Monte Carlo analysis of mean Q40 values in the mid-frequency range. The distribution of mean Q40 values was computed 10,000 times for 80 randomly chosen sites in the mid-frequency range. ▼, mean Q40 values in the low- and high-frequency ranges. They were significantly different (P < 0.0001 for low-frequency range and P = 0.0011 for high-frequency range) from the random sample distribution in the mid-frequency range.
threshold Q values, especially Q40, are less affected by the roll-off. The transition between steep and shallow gradient ranges (Fig. 8B, gray area; no statistical difference with either high- or low-CF gradient regions) is centered around ~7 kHz. This corresponds well to the transition ranges between high and low Q10 (midpoint of transition range: ~6 kHz) and Q40 (~6.5 kHz) values (see Fig. 2, C and D).

The relationship between CF gradient and spectral integration can be assessed by plotting the inverse of Q40 (bandwidth/CF) against the CF gradient (Fig. 9, A and B). Three of four cases showed significant linear regressions (F-test, \( P < 0.001 \)) with correlation coefficients for 1/Q40 versus CF gradient ranging from \( r = 0.32 \) (case 046R) to \( r = 0.51 \) (case ADX3). In one case (AMC6), the linear regression was not significant (see Discussion). Averaged over all cases, the first-order relationship between cortical spectral integration and the local CF gradient reveals an increase (broadening) in receptive field bandwidth with increasing (steeper) CF gradient (Fig. 9B).

**Discussion**

**Spatial organization of bandwidth modules**

Many response features in primary sensory cortex have an orderly periodic, uniform distribution (Bosking et al. 2002; Hubel and Wiesel 1977; Hübener et al. 1997; Issa et al. 2000; Swindale et al. 2000). Examples include orientation selectivity, spatial frequency, and ocular dominance in the primary visual cortex. We find that this principle does not extend to the spectral bandwidth organization in cat AI. Previously, spectral bandwidth organization in cat AI had only been assessed in a part of the mid-frequency range (Read et al. 2001; Schreiner and Mendelson 1990). The current findings suggest that cat AI comprises three frequency regions (<5, 5–20, and >20 kHz) distinguished by the range of Q40 values and the expression of spatial organization of spectral bandwidths.

The heterogeneity of spectral integration properties across AI is in contrast to psychophysically determined spectral integration that is relatively constant at a “critical bandwidth” of ~1/3 octave throughout the cat hearing range (Ehret and Schreiner 1997; Nienhuys and Clark 1979; Pickles 1975). Differences in the spatial distribution between Q10 and Q40 values suggest differences in the neural mechanisms underlying the neural cluster responses that are related to peripheral representation and thalamocortical projections as well as to the RF construction in AC (Miller et al. 2001; Suga 1995; Sutter et al. 1999). Spectral bandwidth is already influenced by cochlear tuning properties (Liberman 1978; Narayan et al. 1998) and is reflected in subsequent processing stations. However, the spectral integration differences described here for three frequency regions likely include higher-order processing principles, presumably related to specific behavioral tasks (e.g., Razak and Fuzessery 2006; Suga 1988) and reflecting neuroanatomical connectivity principles (Prieto et al. 1994; Read et al. 2001).

Nonuniform distributions of spectral integration properties may be seen in other species such as the ferret (Shamma et al. 1993), owl monkey (Recanzone et al. 1999), squirrel monkey (Cheung et al. 2001), and marmoset (Philibert et al. 2005). However, the expression of spectral integration properties in these species varied from case to case and revealed no clear frequency dependence. A modular organization of spectral bandwidth in cat anterior auditory field (AAF), the other primary field, is highly idiosyncratic and frequency-independent as well (Imaizumi et al. 2004). Functional segmentation of the tonotopic domain is also found in the moustached bat AI: a primary area for object velocity and angle detection (DSCF area) occupies a narrow frequency range (CF = 61–63 kHz) devoted to processing of a dominant frequency in the bat’s biosonar signal (Suga 1988). Thus three different frequency regions in the moustached bat AI are related to specific auditory tasks. By analogy, the three distinct frequency regions in cat AI may reflect specific functional tasks. An anatomical study in guinea pig AI also suggested functional distinctions between low- and high-frequency regions based on differences.
in their projections (Wallace et al. 2002). A prospective candidate task for the mid-frequency range may be the processing of spectral sound localization cues. Monaural cues to locate sound sources in the form of spectral notches are created by filtering properties of the head and pinnae (Yin and May 2005; Young and Davis 2002). The first spectral notch in the cat head-related transfer functions occurs predominantly at frequencies between $5$ and $20$ kHz depending on the sound source direction (Yin and May 2005; Young and Davis 2002). The frequency range closely matches that for the occurrence of high and low Q40 modules. However, unlike the dorsal cochlear nucleus (Young and Davis 2002), no clear evidence yet links cortical function to notch processing. Binaural summation and suppression bands also appear to be more strongly expressed in the mid- to high-frequency ranges, whereas low-frequency regions are dominated by summation interactions (Imig and Adrián 1977; Imig and Brugge 1978), suggesting the potential link between spectral shape processing and binaural interactions. However, preliminary data from an AI mapping study revealed no systematic relationship between spectral bandwidth and binaural interaction (Teng et al. 2006). A recent study in cat AI has shown that prolonged sound exposure of juvenile cats to the mid-frequency range of 5- to 20-kHz shapes the functional organization (Noreña et al. 2006), thus indicating a particular susceptibility of this region for environmental and behavioral influences.

The functional interpretation of these findings is confounded by systematic variations of other RF parameters with frequency and within the isofrequency domain. In this scenario, the combinations of different RF properties present in each neuron, such as spectral bandwidth, response threshold, monotonicity, etc., will affect the response strength and disclose important principles of population activity and consequences of multidimensional influences on stimulus representation. The current
The current findings suggest that the spatial variations in frequency gradient are related to variations in spectral integration across AI. The spectral integration properties of AI neurons are shaped by many factors that affect the excitatory and inhibitory components of cell inputs and the subsequent determination of action potential generation. An unresolved question about the generation of cortical spectral RFs is whether there is a match, or at least proportionality, between a cortical neuron’s output bandwidth and the converging thalamic and cortical frequency information. Intracellular studies find that the bandwidths of excitatory and inhibitory inputs are well

![Figure 8](http://jn.physiology.org/)

**FIG. 8.** CF gradient distribution as a function of CF in AI: A: frequency-dependence of the CF gradient for 2 cases. Straight lines are linear regression (over log CF) for AWD3 (black line; \( r = 0.43; P < 0.01 \)) and for ADX4 (red line; \( r = 0.46; P < 0.01 \)). B: mean (±SE) for 4 cases in 1/2-octave bins spaced at 1/4 octaves. Comparison between nonoverlapping bins revealed statistically significant differences (\( F \)-test adjusted by the sequential Bonferroni correction, \( P < 0.01 \)) between high and low gradient ranges (white background). Bins in transition ranges (gray background) did not differ from high- or low-gradient regions. The blue line is the cat cochlear CF gradient (Greenwood 1990) adjusted for the length of the cortical frequency axis.

study focuses on simple RF properties that, in themselves, do not provide a very satisfactory answer to the question of how a given stimulus is represented. However, it allows a first assessment whether regional functional differentiations exist and how that topography may be related to other functional topographies and spatial patterns of thalamocortical projections.

**Cortical spectral integration and frequency gradient**

Fine-grain cortical frequency mapping showed a nonuniform CF gradient in AI. The gradient distribution has two features. First, the mean gradient changes as a function of CF with the steepest gradient <5 kHz. This corresponds to a smaller magnification factor and a relative underrepresentation of those frequencies. A previous study (Merzenich et al. 1975) had also noted a nonuniform frequency representation and interpreted it as a potential overrepresentation of the mid-frequency range. A comparison between the cortical and cochlear frequency gradients (Fig. 8B) suggests that the cortical mid-frequency magnification matches that of the cochlea. As explained in the preceding text, the shallow cortical gradient observed in the high-frequency range is likely influenced by the speaker system. A second aspect of the CF-gradient distribution is that most frequency bands exhibit a wide range of gradients (Fig. 8). For the mid-frequency range, this reflects steeper gradients at the dorsal and ventral poles of iso-frequency contours and less ordered CF organization near the borders of the other auditory fields (Fig. 6). However, the AI tonotopic gradient is smooth relative to the other primary field, AAF, that has gross local distortions and even omissions in its CF representation (Imaizumi et al. 2004). The functional interpretation of the observed differences between cortical and estimated cochlear frequency gradients remains difficult. The issue of an under- or overrepresentation of certain frequency regions in AC (Merzenich et al. 1975) depends on a precise estimate of the AC extent, which is hampered by the sulci. Furthermore, the observation of different frequency gradients along the iso-frequency domain suggests that a functional interpretation of cortical frequency gradient requires experimental approaches that are more task- and region-specific than provided by a simple RF analysis.

The current findings suggest that the spatial variations in frequency gradient are related to variations in spectral integration across AI. The spectral integration properties of AI neurons are shaped by many factors that affect the excitatory and inhibitory components of cell inputs and the subsequent determination of action potential generation. An unresolved question about the generation of cortical spectral RFs is whether there is a match, or at least proportionality, between a cortical neuron’s output bandwidth and the converging thalamic and cortical frequency information. Intracellular studies find that the bandwidths of excitatory and inhibitory inputs are well

![Figure 9](http://jn.physiology.org/)

**FIG. 9.** CF gradient and spectral bandwidth. A: 1/Q40 (bandwidth/CF) is plotted as a function of the CF gradient for 2 cases. Straight lines are regression lines for ADX4 (red) \( r = 0.51 \) and for 046R (blue) \( r = 0.46 \). B: 1/Q40 population means (4 cases) for CF gradient bins of 0.5 octave/mm above 1 octave/mm and for bins of 0.25 octave/mm below 1 octave/mm. Dashed gray line, linear regression.
matched (Tan et al. 2004; Wehr and Zador 2003) and are usually wider than the RF derived from action potentials. The inhibitory contributions are all of cortical origin and predominantly from local interneurons (Prieto et al. 1994). It is reasonable to predict that local excitatory cortical contributions will match the spectral extent of the inhibitory inputs. However, it is not clear how thalamic and cortical spectral bandwidths map onto the cortical output. Cross-correlation studies of spiking activity indicate that the excitatory portions of connected thalamocortical neuron pairs either closely match in CF and bandwidth or only partially overlap, i.e., they can differ in CF (by up to an 1/3 octave) and bandwidth (Miller et al. 2001). The former case suggests cortical inheritance of thalamic spectral tuning, and the latter case supports new RF construction and, thus, a change in spectral integration.

A parsimonious scenario is that the spectral extent of the thalamic and cortical contributions covary: narrow-band neurons link narrow and frequency-matched thalamic and cortical inputs; broad-band neurons join either broadly tuned thalamic and cortical inputs and/or narrowly tuned inputs that are remote in CF. This does not imply, however, that the spectral convergence from thalamic and cortical sources must be identical. It has been proposed that the core-region of cortical RFs may be predominantly supplied by thalamic inputs, whereas flanks may be dominated by cortical input (Metherate et al. 2005).

The critical parameters for spectral convergence, in any case, are the CF range and the individual neuronal bandwidth of the thalamic and cortical neurons that contribute to the creation of either narrow- or broad-band cortical modules.

Concluding remarks

We find two interactions between the CF organization and spectral bandwidth modules in cat AI: the spectral integration range and the expression of distinct bandwidth modules are frequency dependent and the tonotopic gradient, at least as a first approximation, covaries with the spectral integration range. These findings allow more refined models of thalamocortical and corticocortical spectral convergence and integration to be developed and tested. This is of specific significance for the question whether AI receives and/or is the source of distinct functional channels and how these might contribute to signal processing in other cortical fields. These findings also suggest modality-specific organizational principles that may help us to delineate general cortical processing features.

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