

# Chapter 11

## Spectral and Intensity Coding in the Auditory Midbrain

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### 1. INTRODUCTION

This overview emphasizes general properties of spectral and intensity processing in the inferior colliculus (IC) common to mammals such as the cat, mouse, rat, guinea pig, Mongolian gerbil, chinchilla, rhesus monkey, and various species of bats. Considerable data are available for the domestic cat (*Felis catus*) and mice (*Mus musculus*, laboratory strains) so that these species can serve as representative unless specified otherwise (for special spectral processing regimens in bats see Chapters 14 and 17). Functional distinctions exist among IC subdivisions (Aitkin 1986). Accordingly, we employ a basic anatomical framework of three major divisions: the central nucleus (ICC), the external nucleus (EN), and the dorsal cortex (DC). In this framework, the ICC contains layer IV of the DC as defined in Golgi studies of the cat (Morest and Oliver 1984) and mouse (Meininger et al. 1986).

#### 1.1. PRINCIPLES OF SPECTRAL ANALYSIS AND CODING

A defining step for the organization of the entire auditory system is the spectral decomposition of the acoustic waveform in the cochlea (Patuzzi 1996). All subsequent operations directly reflect this peripheral process or are a consequence of specific central auditory filtering and transformations acting on the residue of this initial process. The orderly frequency representation along the basilar membrane, the tonotopy, is the basis of the concomitant order for characteristic frequency (CF) found in many nuclei and centers of the auditory pathways, including the ICC and extending to the primary auditory cortex. Thus, the cochlear tonotopy is the first and most general principle of spectral analysis and coding. Although the cochlear transformation of the signal is not identical to a Fourier analysis, the parallels between them are sufficiently compelling to warrant analysis of the resulting transmission channels as a bank of parallel spectral filters. Therefore, many characterizations of auditory neuronal elements are cast in the language of frequency filtering, using metrics such as center frequency,

frequency selectivity or filter bandwidth, and response magnitude. The response timing of the individual frequency channels—reflected in phase-locking of action potentials to individual cycles of a frequency—also affects auditory processing, but is confined to relatively low frequencies, and is not considered further. Here, we deal with properties of frequency filtering of IC neurons. A profile of the spectral receptive field (SRF) is a first analytic step in characterizing a neuron type or a nucleus.

## 1.2. PRINCIPLES OF INTENSITY ANALYSIS AND CODING

Relative and absolute stimulus magnitudes are two parameters in the spectral analysis of sounds with profound influence on auditory processing and perception. Mean sound pressure level (SPL) may influence neural responses in three ways: it can change spectral filter width, alter neural response strength in terms of firing rate, and modify temporal response parameters such as latency and precision of action potential timing relative to the stimulus waveform. Intensity effects on filter bandwidth are closely related to spectral receptive-field shape. Response magnitude effects are commonly discussed in terms of rate-level functions (RLs), that is, the total number of spikes/stimulus plotted against mean stimulus level. From RLs, measures of response threshold, intensity selectivity, and dynamic range can be derived.

Another aspect of stimulus magnitude is the amplitude distribution across the sound spectrum. The relative intensity of spectral minima and maxima, or the “contrast” with regard to their mean amplitudes, and the time course of these amplitude changes across the spectrum, must be encoded and represented. It is evident that amplitude coding in a complex spectral environment, the most natural listening condition, is inseparable from coding in the spectral domain.

## 2. SPECTRAL RECEPTIVE-FIELD PROPERTIES

### 2.1. EXCITATORY/INHIBITORY/FACILITATORY AREAS

Traditionally, spectrally simple sounds that are readily parameterized and manipulated are used for the exploration of receptive-field (RF) characteristics. Pure tones of various frequency and intensity combinations can demonstrate the excitatory SRF (eSRF) by identifying the parameter combinations that elevate firing rate above the spontaneous activity. The border of the eSRF represents the excitatory frequency tuning curve (eFTC) (Fig. 11.1A) and its shape is assessed by several measures:

- Characteristic frequency (CF): frequency producing a response at the lowest sound pressure levels (SPL)
- Best frequency (BF): frequency evoking the most spikes at a given SPL (CF and BF are not always identical)
- Minimum threshold (MT): SPL at CF

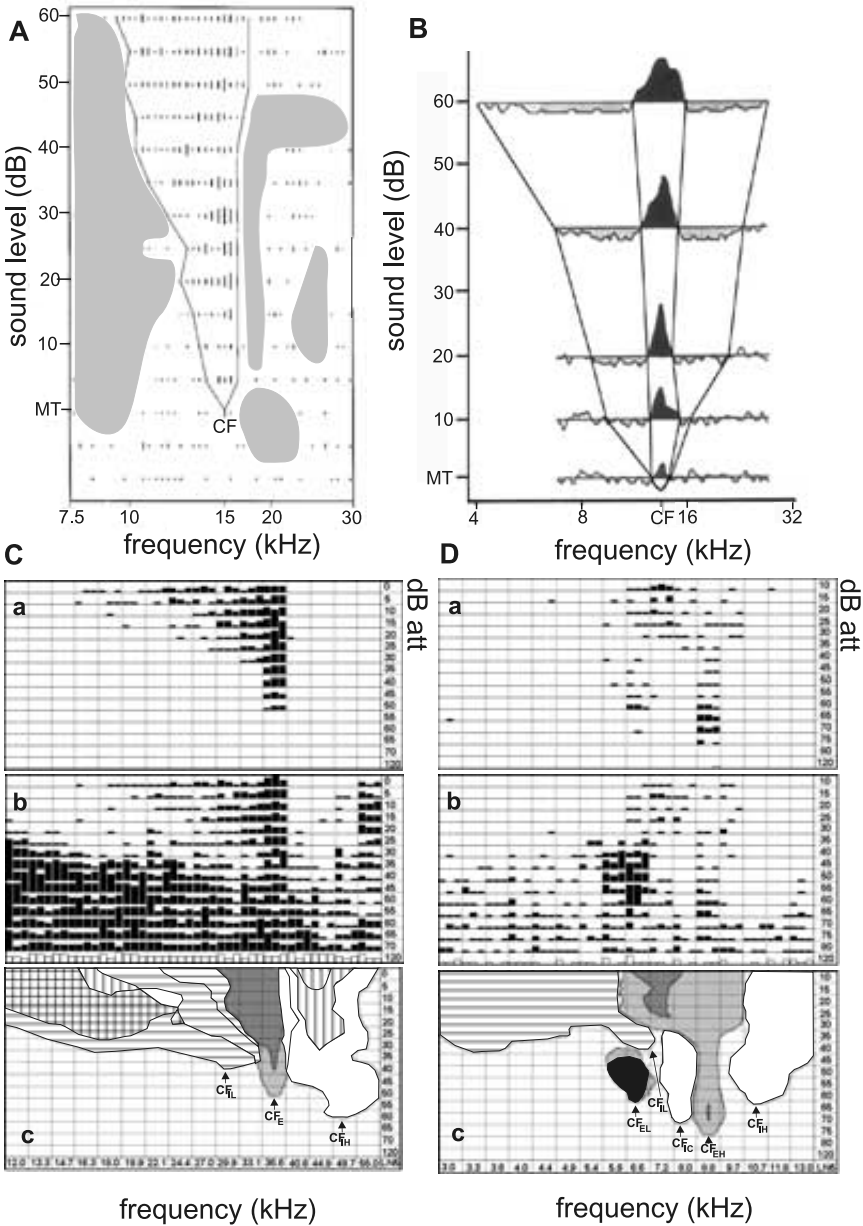


Figure 11.1. Spectral receptive fields (*SRFs*) of neurons in the central nucleus of the inferior colliculus (ICC). (A) Map of the SRF of a mouse neuron. Spike rates are shown as short vertical bars. The excitatory frequency tuning curve (*eFTC*) borders an area of increased responsiveness (above the spontaneous activity), the excitatory SRF (*eSRF*). Shaded gray areas: inhibitory SRFs (*iSRF*; suppressed spontaneous activity). (M.A. Ego-

- Bandwidth (BW): frequency width of FTC at various levels above MT
- Quality factor ( $Q$ ): the relative sharpness of tuning CF/BW at a fixed stimulus level (e.g.,  $Q/10\text{dB}$  is based on BW 10 dB above MT)
- The slopes of the low- and the high-frequency sides of the eFTC (expressed in dB/octave); also related to sharpness of tuning

A tone at a frequency and/or level outside the eSRF may have no effect on response rate or decrease it below spontaneous activity. The latter effect is called “one-tone inhibition” and reveals inhibitory areas surrounding the eSRF (Fig. 11.1A, B) if the spontaneous activity is sufficient to reliably detect an activity decrease (Suga 1964; Willott and Urban 1978; Wang et al. 1996; Ramachandran et al. 1999).

A more comprehensive approach uses a “two-tone paradigm” (e.g., Egorova et al. 2001): one tone excites the neuron at its CF (10 to 20 dB above threshold) while a second tone of variable frequency and level is presented simultaneously, with or shortly before the CF tone. This second tone can increase excitation to the constant CF tone (summation or facilitation of excitation; Fig. 11.1D), decrease or suppress the response to the CF tone (inhibition; Fig. 11.1C, D), or it can have no visible effect. Thus, the two-tone paradigm can identify the superposition of inhibitory and facilitatory receptive fields (iSRFs, fSRFs, respectively) with the eSRF. Inhibitory areas outside the eFTC are called “inhibitory side bands.” The shapes of iSRFs and fSRFs are quantified by similar measures as eSRFs and eFTCs.

Facilitatory SRFs have rarely been studied (Fuzessery and Feng 1983; Ehret and Merzenich 1988a; Egorova et al. 2001; Jen et al. 2002) except in the highly specialized mustached bat IC (Mittman and Wenstrup 1995; Wenstrup et al. 1999; Portfors and Wenstrup 2002) (see Chapter 17). Few cells show spectral facilitation (about 11% in the mouse, 18% in the big brown bat). In the mouse, facilitation is often found within about 1 octave of CF (Egorova et al. 2001).

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Figure 11.1. *Continued*

rova and G. Ehret, unpublished observations). **(B)** Response rates to tone bursts relative to spontaneous activity (horizontal lines at five sound levels) at various frequency-level combinations indicate a narrow excitatory area (*black*) around the characteristic frequency (*CF*) bordered by inhibitory areas (*gray*) of a cat type I neuron. Lines demarcate the borders of the eSRF and the two iSRFs. (Modified from Ramachandran et al. 1999.) **(C, D)** Spike rates (*black bars*) of two mouse neurons in response to *(a)* tone bursts of various frequency-level combinations, *(b)* combinations of two tones, one at the CF and 10 dB above minimum threshold, the other at various frequency-level combinations. (Modified from Egorova et al. 2001.) *(c)* eSRFs are marked in various gray levels (proportional to response rate); iSRFs are marked with different hatching reflecting grades of inhibitory strength. The *black area* in **(C)** indicates a facilitatory SRF (fSRF).  $CF_E$ , Excitatory CF;  $CF_{IL}$ ,  $CF_{IH}$ , inhibitory CFs below and above the  $CF_E$ , respectively. The neuron in **(D)** has two excitatory CFs,  $CF_{EH}$  and  $CF_{EL}$ , both separated by a central inhibitory area with a  $CF_{IC}$ . *dB att*, Attenuation steps in dB; *MT*, minimum threshold.

Facilitation in the IC indicates that spectrally related tones can enhance responses.

## 2.2. SHAPES OF EXCITATORY AND INHIBITORY RECEPTIVE FIELDS

Basic differences have been found between IC subdivisions with regard to SRF and FTC shapes. In the DC and especially the EN, the frequency selectivity is low, with broad eFTCs, low  $Q$ -values, and irregularly shaped eFTCs (Fig. 11.2) (Aitkin et al. 1975, 1978; Willott and Urban 1978; Binns et al. 1992; Syka et al. 2000). Studies specifying iSRFs and iFTCs for DC and EN neurons remain to be done.

In the ICC, eSRFs have been studied extensively (Rose et al. 1963; Suga 1969; Gersuni et al. 1971; Ehret and Moffat 1985a; Casseday and Covey 1992; Wang et al. 1996; Ramachandran et al. 1999; Egorova et al. 2001; Le Beau et al. 2001). iSRFs measured in a two-tone paradigm have been investigated in comparatively few studies (Suga 1969; Ehret and Merzenich 1988a; Vater et al. 1992; Fuzessery 1994; Egorova et al. 2001; Lu and Jen 2001). eSRFs and iSRFs have varied shapes (Figs. 11.1, 11.3, and 11.6A) that sometimes reflect differences in stimulus presentation (monaural vs. binaural, short vs. long durations or rise times, simultaneous vs. asynchronous two-tone presentation) and data evaluation (different criteria for thresholds of excitatory and inhibitory thresholds). However, the rather uniform eFTC shapes of auditory nerve fibers (Kiang et al. 1965; Liberman 1978; Fig. 11.3A) are transformed into ICC FTCs that deviate substantially from the peripheral frequency filtering (Figs. 11.3 and

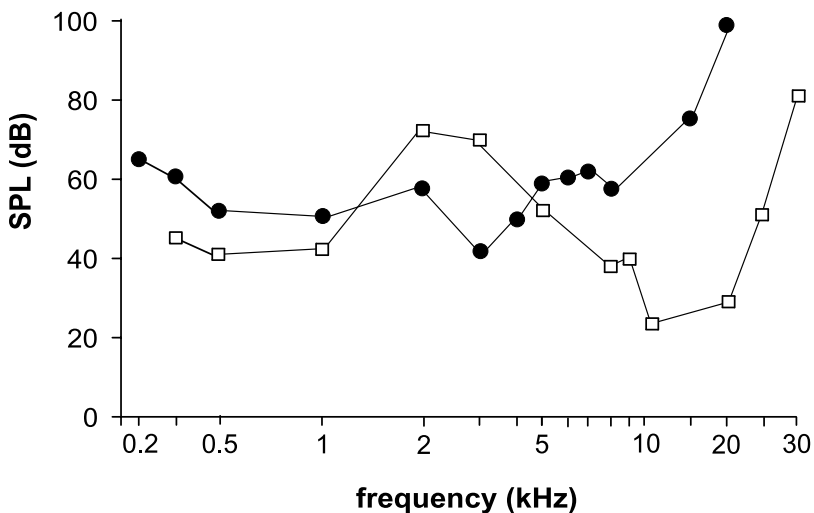


Figure 11.2. Excitatory frequency tuning curves from the external nucleus of the cat inferior colliculus. (Modified from Aitkin et al. 1975.)

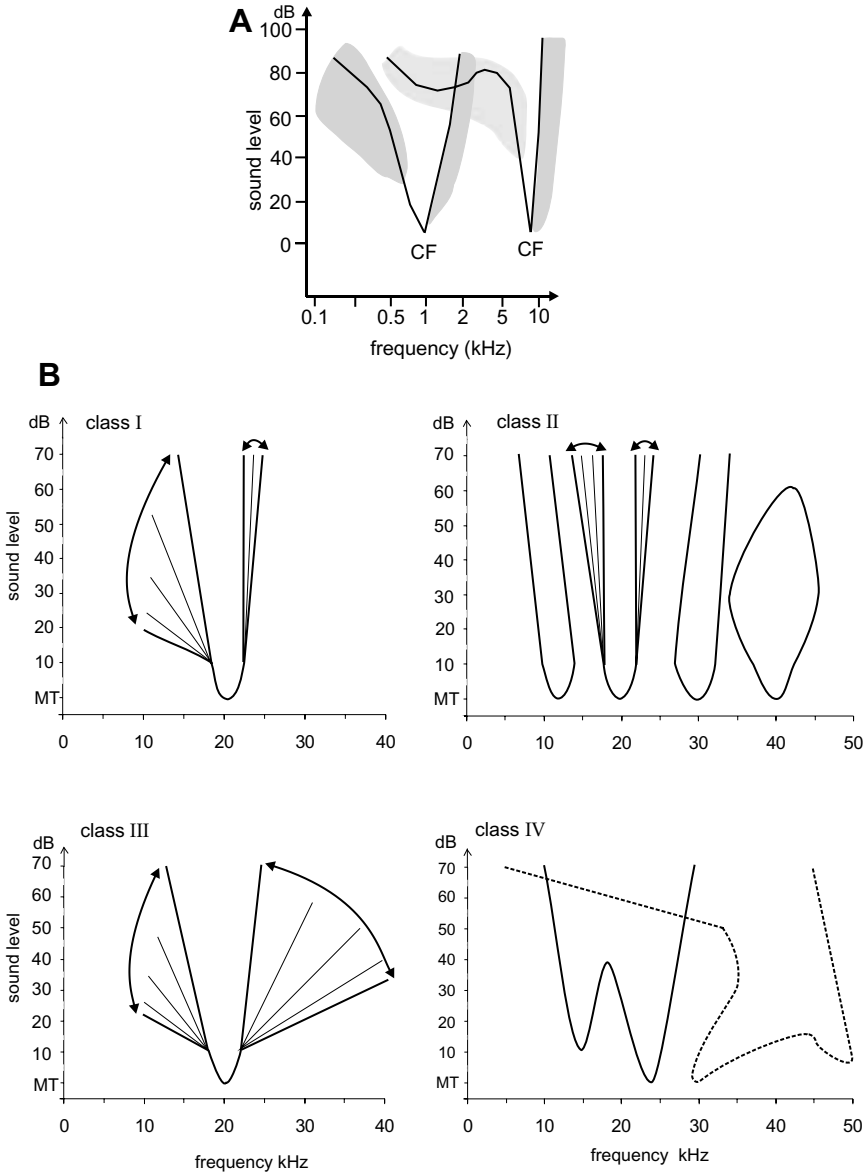


Figure 11.3. **(A)** Examples of excitatory tuning curves of auditory nerve fibers with a low and a high characteristic frequency (*CF*). Areas of lateral suppression are shaded. (Modified from Ehret 1996.) **(B)** Classification (classes I to IV) of ICC neurons according to the shapes of their excitatory frequency tuning curves (*eFTCs*). Some variability of the tuning-curve slopes and shapes within each class is indicated. (Modified from Ego-rova et al. 2001.)

11.6A). With the simultaneous two-tone paradigm, grades of inhibition and heterogeneous iSRF shapes are seen in almost all ICC neurons. Owing to the glycinergic and  $\gamma$ -aminobutyric acid-positive (GABAergic) projections to the ICC (see Chapters 2, 4, and 9) and the intrinsic network with many GABAergic neurons (see Chapters 2, 5, and 9), inhibition is a prominent feature (Oliver et al. 1994; Winer et al. 1995; Le Beau et al. 1996, 2001).

The eSRFs and iSRFs of mouse ICC neurons have properties that define four classes of cells (Egorova et al. 2001) (Figs. 11.3B and 11.6A). All may have fSRFs.

Class I neurons closely resemble the excitatory and lateral suppression areas of auditory nerve fibers (Sachs and Kiang 1968). Their essential properties are: (1) strongly asymmetric eFTCs with steep high-frequency slopes and shallow low-frequency slopes; (2) inhibitory areas below and above CF that are asymmetric with higher inhibitory thresholds below the CF; (3) inhibitory areas that can overlap eSRFs only partially.

Class II neurons are dominated by inhibition. Their main features are: (1) inhibitory areas that are nearly symmetrical, with similar inhibitory thresholds below and above CF and that always invade eSRFs, often completely overlapping them; (2) the eFTCs have either steep slopes on both sides, are skewed toward the low- or high-frequency side at high levels, or are closed (with an upper response threshold); (3) inhibitory and excitatory thresholds and CFs are in close register.

Class III neurons have weak inhibition. Their other attributes are: (1) symmetric and shallow eFTC slopes; (2) inhibitory areas are small, inhibition is weak, and inhibitory areas are often only on one side of the eSRF; (3) excitatory and inhibitory thresholds are unrelated.

Class IV neurons have complex eSRFs and iSRFs, always with several eSRFs or multiple CFs.

iSRFs have not been determined in most ICC studies. Profiles of sound processing in the spectral domain are, however, incomplete without such measures and considerations of the graded influence of inhibition implicit in any RF classification. The gradient of eFTC slopes is an estimate of the extent and strength of inhibition, without direct measurement of iSRFs (Egorova et al. 2001). Most (93%) class I to III neurons can be classified by the slope criterion alone. Class I cells have low-frequency slopes  $<150$  dB/octave and high-frequency slopes  $>250$  dB/octave. Class II neuron low-frequency slopes are  $>150$  dB/octave and high-frequency slopes  $>250$  dB/octave. Class III neurons have low-frequency slopes  $<150$  dB/octave and high-frequency slopes of  $<250$  dB/octave. The critical slope values for classifying neurons may be species-specific. It is encouraging that the assignment of ICC neurons into four classes extends to other ICC studies for comparative purposes, and for functional considerations such as amount and extent of inhibition. Inhibition-dominated class II neurons have similar proportions in mice (27% to 28%; Egorova et al. 2001; Ehret et al. 2003), cats (27%; Ehret and Merzenich 1988a), and guinea pigs (26%; Le Beau et al. 2001). This suggests comparable inhibitory innervation patterns and functions. Class IV neurons are sparse in mice (6% to 10%; Egorova et al. 2001;

Ehret et al. 2003), guinea pigs (2%; Le Beau et al. 2001), and big brown bats (3%; Lu and Jen 2001), and high (40%) in the mustached bat (Portfors and Wenstrup 2002). Combinations of the harmonics of biosonar calls play a decisive role in echolocation, and selective adaptations may create combination-sensitive neurons and irregular FTCs (Mittmann and Wenstrup 1995; Leroy and Wenstrup 2000).

In the decerebrate cat, a related tuning curve classification (Ramachandran et al. 1999) is based on excitatory FTCs and inhibition of spontaneous activity (one-tone inhibition). Type “I” neurons combine a narrowly tuned I-shaped excitatory SRF with flanking inhibitory regions (Fig. 11.1B), like some class II neurons defined previously. Type “V” neurons show more broadly tuned, V-shaped excitatory areas with no inhibition of spontaneous activity (much like some class I/III neurons). Type “O” units have frequency response maps dominated by inhibition except for a circumscribed (O-shaped) island of excitation near CF and MT, also resembling some class II cells. The distribution of these classes seems to be method-specific: type O neurons comprise some 70% of ICC neurons in decerebrate cats (Ramachandran et al. 1999) but only 5% in nondecerebrated and anesthetized cats (Ehret and Merzenich 1988a) and 8% in nondecerebrated and anesthetized mice (Egorova et al. 2001). Differences between the two classification schemes will likely resolve when similar methodologies are applied across species.

Detailed descriptions of RFs in DC and EN are sparse, especially for inhibitory properties. Excitatory SRFs are broadly V-shaped or irregular (cat: Aitkin et al. 1975; guinea pig: Syka et al. 2000), suggesting many class III and IV neurons. Because class IV receptive fields are rare in the dorsal cochlear nucleus (Rhode and Smith 1986; Spirou and Young 1991) and superior olivary complex (Guinan et al. 1972) and ICC, they are likely the result of interactions between ascending (and descending) inputs.

### 3. FREQUENCY ORGANIZATION

#### 3.1. *THE CENTRAL NUCLEUS*

Virtually all ICC neurons are frequency tuned, although tuning sharpness differs from auditory nerve fibers. The one-dimensional cochlear frequency map is transformed into a three-dimensional map in the ICC (Fig. 11.4A). ICC tonotopy consists of two frequency gradients. The first is steep with stepwise changes from low frequencies (dorsal and dorsolateral ICC) to high frequencies (ventromedial ICC; Fig. 11.4B). This gradient, typical for most mammals, is orthogonal to the cellular laminae (see Chapter 2) and their input projections (see Chapters 3 to 5) and has been demonstrated with electrophysiologic measurements of single- or multiunit CFs (Merzenich and Reid 1974; Fitzpatrick 1975; Roth et al. 1978; Semple and Aitkin 1979; Stiebler and Ehret 1985; Poon et al. 1990; Romand and Ehret 1990; Casseday and Covey 1992; Brückner and Rübsamen 1995; Schreiner and Langner 1997), with activity-dependent glucose labeling



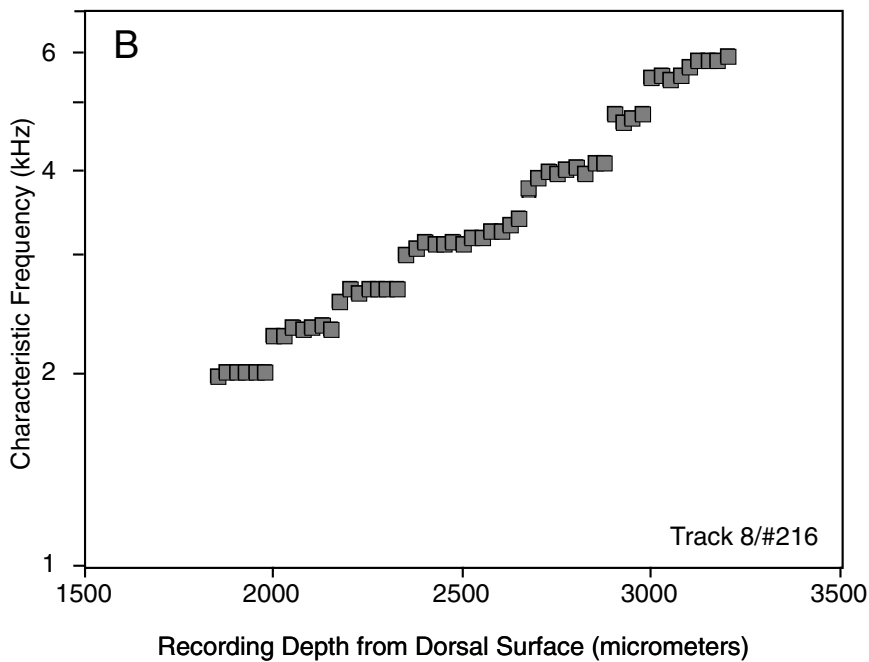
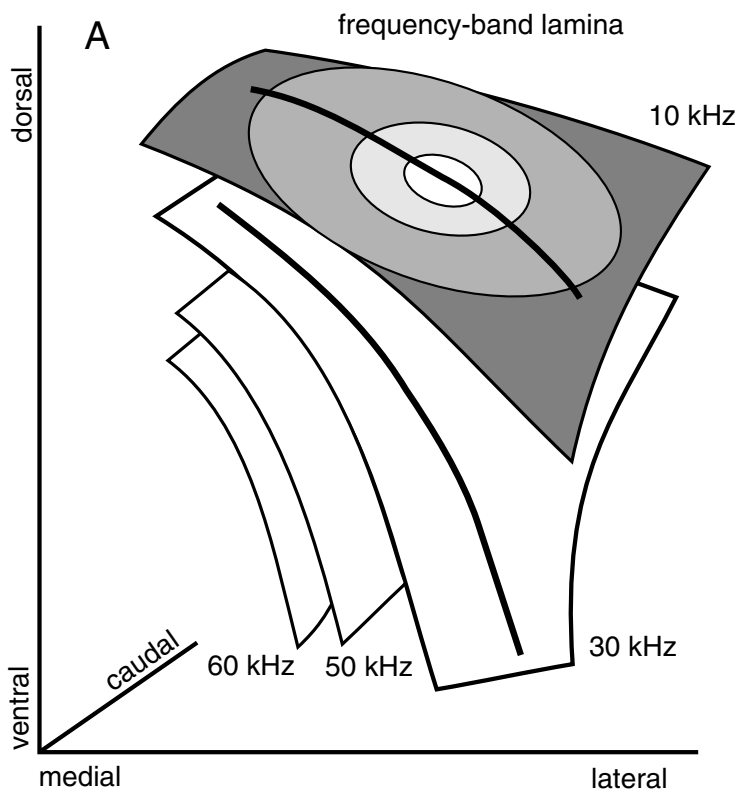
by [ $^{14}\text{C}$ ]2-deoxyglucose autoradiography (Servièrè et al. 1984; Webster et al. 1984; Huang and Fex 1986; Martin et al. 1988; Ehret and Romand 1994; Brown et al. 1997), and with immediate-early gene activation using c-Fos immunocytochemistry (Ehret and Fischer 1991; Friauf 1992; Reimer 1993). This tonotopic organization forms a stack of “isofrequency sheets” of variable sizes and shapes covering the frequency spectrum of hearing (Fig. 11.4A). Isofrequency sheets parallel the ascending projections to the ICC (see Chapter 2). Cochlear CF space is often distorted in the ICC with frequency ranges important in communication or echolocation overrepresented (bat: Casseday and Covey 1992; mouse: Stiebler and Ehret 1985).

The second frequency gradient, described in cat ICC, is a shallow continuum within the isofrequency sheets (Schreiner and Langner 1997). Low CFs are dorsomedial and higher CFs lateral and ventrolateral (Fig. 11.4A: arrows). The frequency range covered within an isofrequency sheet is about one critical band (Schreiner and Langner 1997; see below). Thus, the sheets of the classic dorsoventral tonotopic gradient constitute “frequency-band laminae” (Merzenich and Reid 1974; Schreiner and Langner 1997). They are larger than synaptic domains, the microarchitectonic compartments of ICC laminae (see Chapter 2).

### 3.2. THE DORSAL CORTEX AND EXTERNAL NUCLEUS

The frequency representations in DC and EN have not been studied in the same detail as in the ICC. Historical differences in the definition of the DC have confounded a clear picture of its CF organization. Some studies show a frequency gradient from high (dorsal) to low (ventral at the border to the ICC) (Merzenich and Reid 1974; Servièrè et al. 1984), whereas others indicate that the ICC frequency-band laminae encroach dorsomedially into the DC, thus creating a continuous tonotopic organization for both subnuclei, at least in DC layers III and IV (Stiebler and Ehret 1985; Schreiner and Langner 1988; Romand and Ehret 1990). This physiologic ambiguity has a parallel anatomical component, with inputs from the lateral superior olive and other medullary structures (Oliver 1987) encroaching far beyond the architectonically recognized border of ICC (Morest and Oliver 1984; Oliver and Morest 1984) into layer IV of

Figure 11.4. (A) Three-dimensional plot of frequency-band laminae (10, 30, 50, 60 kHz) of the left-side ICC of the mouse. (Modified from Stiebler and Ehret 1985.) The *long thick lines* on the 10- and 30-kHz lamina indicate the direction of the shallow gradient of frequency increase (mainly from medial to lateral) within a lamina, as found in the cat (Schreiner and Langner 1997.) The concentric increase in the darkness of shading (10-kHz lamina) relates to the increase of the minimum threshold (*MT*) of neurons on a lamina (Stiebler 1986). (B) Electrode penetration from dorsal to ventral through the ICC of the cat showing a stepwise increase of the neuronal characteristic frequency (*CF*). The CF plateaus comprise frequency-band laminae. (Modified from Schreiner and Langner 1997 and unpublished data.)



the DC and perhaps beyond. In small mammals such as the mouse, a clear CF-based distinction between the DC and the ICC may not have been seen because of the thin DC (only layers I to III) (Meininger et al. 1986). Consequently, the ICC itself may not contain a representation of the lowest CF range because this area may be regarded as DC on the basis of anatomical criteria. Further study is necessary.

In the EN, a frequency gradient runs from high (lateral) to low (medial) in the cat (Rose et al. 1963; Roth et al. 1978) and in the mouse from low (lateral and dorsal) to high (medial and ventral) (Stiebler and Ehret 1985). Despite species differences there is agreement from studies in the possum (Aitkin et al. 1978), rat (Clopton and Winfield 1973), and gerbil (Kitzes 1984) that EN tonotopy is separate from that of ICC. Moreover, the CF ranges of DC and EN neurons are incomplete, with the high-frequency part absent or underrepresented. In the mouse EN, for example, CFs  $>35$  kHz have not been found while in the ICC CFs extend to  $>60$  kHz (Stiebler and Ehret 1985; Romand and Ehret 1990).

## 4. SPECTRAL RESOLUTION AND INTEGRATION

A basic principle of auditory processing is the decomposition of complex sounds into perceptually distinct frequency components or narrow frequency bands such as formants (Fletcher 1940; Scharf 1970; Patterson 1974). Each cochlear hair cell and most central auditory neurons respond only to a limited part of the spectrum, the RF bandwidth, and can distinguish or “resolve” these frequencies from those outside its range. Frequency components within an RF cannot be distinguished, and their acoustic energy is summed for further processing, a process defined as spectral integration. Much of the ascending auditory pathway can thus be interpreted as a bank of band-pass filters. At any given CF, the bandwidths of auditory nerve fibers are uniform, although intensity dependent (Rhode and Smith 1985). In view of the various excitatory, facilitatory, and inhibitory shapes of IC receptive fields, the uniformity of the peripheral band-pass filters and thus a common mechanism of spectral resolution, is either lost in the IC or transformed. The choice of experimental stimuli and of analytic methods influences the picture of spectral integration. We discuss three approaches: responses to pure tones, to tones in noise, and to various spectral envelopes of broadband signals.

### 4.1. SHARPNESS OF PURE-TONE TUNING CURVES

A common metric of the neuronal frequency resolution is the quality factor  $Q$ . Small  $Q$ -values reflect broad tuning or low frequency resolution, and large values narrow tuning and high resolution. The range of  $Q_{10\text{dB}}$ -values in IC neurons is enormous, from  $<0.05$  to  $>43$  (cat: Aitkin et al. 1994; rat: Kelly et al. 1991; guinea pig: Syka et al. 2000; mouse: Egorova et al. 2001). A portion of the

large variability (Fig. 11.5A) stems from the frequency dependence of  $Q$ -values established in the cochlear filtering.

Frequency resolution differs between subdivisions. The median  $Q_{10\text{dB}}$  in the ICC for cat is 4 (Aitkin et al. 1994), for guinea pig 2.5 (Syka et al. 2000) and for the big brown bat 4.4 (Jen et al. 2002), which is higher than in the EN of these species (cat: 2; guinea pig: 1.1; big brown bat: 2.2).

The categories of ICC tuning curve shapes (see Section 2) also reflect differences in frequency resolution (Egorova et al. 2001). Class II neurons have high (5 to 10)  $Q$ -values that are largely intensity independent (Fig. 11.5A).  $Q$ -values of class I neurons resemble those of class II neurons at 10 dB above threshold, but decrease at 80 dB. Class III  $Q$ -values decrease from about 6.5 to 0.5 (Fig. 11.5A) with increasing sound intensity. Similarly, sharply tuned cat ICC type I neurons have  $Q_{10\text{dB}}$ -values from 2 to 8 and  $Q_{40\text{dB}}$ -values from 1 to 7 with little

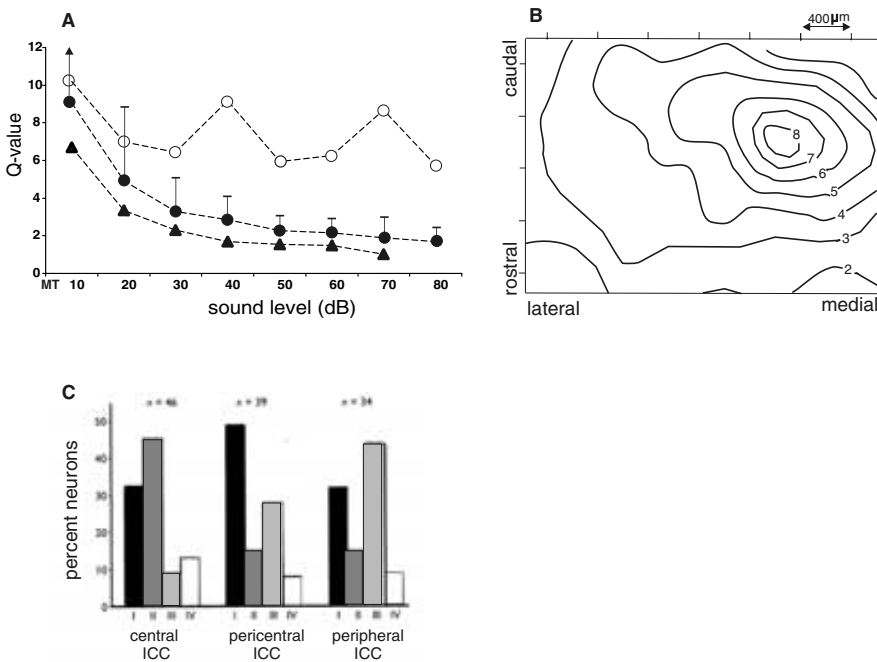


Figure 11.5. Sharpness of frequency tuning. (A) Average  $Q$ -values (see Section 2.1) as a function of the sound level for class I (filled circles), class II (open circles), and class III neurons (triangles) in the mouse ICC. (Modified from Egorova et al. 2001.) (B) View on the horizontal projection of a frequency-band lamina of the cat ICC. The lines are iso- $Q_{10\text{dB}}$  contours. The average  $Q_{10\text{dB}}$  decreases from about 8 near the center to around 2 near the peripheral margin of the lamina. (Modified from Schreiner and Langner 1988.) (C) Distribution of neurons of the tuning-curve classes I to IV as a function of their location in the central, pericentral, or peripheral area of frequency-band laminae of the mouse ICC. (Modified from Ehret et al. 2003.)

intensity dependence, whereas type V neurons show much broader and intensity-dependent tuning ( $Q_{10\text{dB}} < 3$ ;  $Q_{40\text{dB}} < 1.5$ ; Ramachandran et al. 1999). This range in  $Q$  behavior suggests that frequency resolution may serve different roles in different functional tasks.

The processing of sensory information through filters of different widths, a multiresolution analysis, is a general concept in sensory processing (Graham 1989). Such a multitask filtering operation may be expressed in the spatial organization of tuning sharpness and eFTC shape in the ICC. Multiunit recordings show a continuous spatial eFTC bandwidth gradient across frequency-band laminae (Stiebler 1987; Schreiner and Langner 1988; Fig. 11.5B), with higher frequency resolution in the center and declining resolution toward the laminar periphery, suggesting processing subdomains within laminae. This bandwidth gradient likely embodies the distribution of the different eFTC classes (Ehret et al. 2003; Hage and Ehret 2003). An abundance of sharply tuned class II neurons in the laminar center decreases toward the laminar periphery, while the number of broadly tuned class III neurons increases from center to periphery (Fig. 11.5C). Frequency resolution gradients are also present in the thalamocortical system (Read et al. 2001), suggesting that they are a general feature in central auditory organization.

#### 4.2. CRITICAL BANDS: SPECTRAL RESOLUTION

Psychophysical considerations have led to the concept of a bank of auditory filters or “critical bands” that subserve many perceptual aspects such as tone discrimination in noisy environments and the summation of loudness (Fletcher 1940; Zwicker et al. 1957; Scharf 1970; Moore 1997). Critical bands determined from narrow-band masking experiments cover equal distances of about 0.7 to 1 mm of the basilar membrane (BM) (Greenwood 1961, 1990; Ehret 1983, 1988). Thus, mice whose BM is short (about 7 mm; Ehret and Frankenreiter 1977) have fewer critical bands ( $< 10$ ; Ehret 1976) and poorer spectral resolution than cats (some 22 mm BM; Schuknecht 1960; some 24 critical bands; Pickles 1975, 1979; Nienhuys and Clark 1979), and humans (around 32 mm BM; von Békésy 1960; approximately 41 critical bands; Schafer et al. 1950; Margolis and Small 1975).

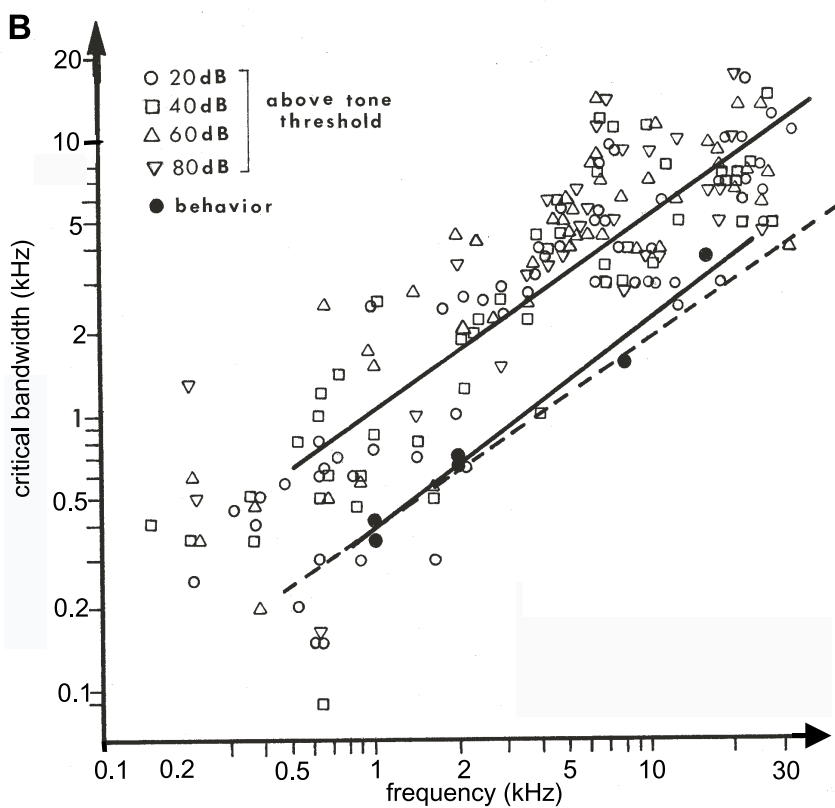
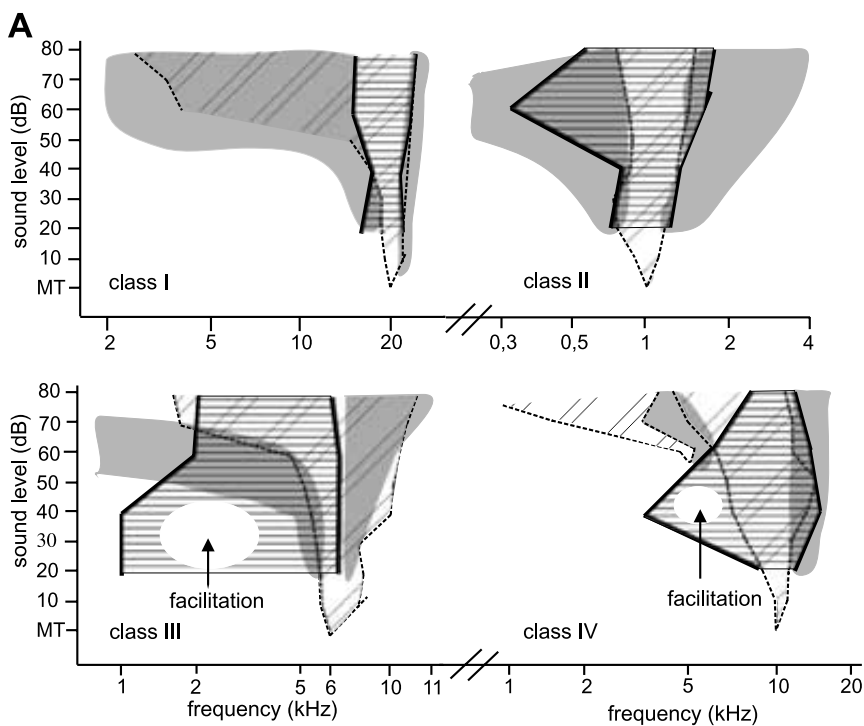
Auditory filter shape, bandwidth, and level dependence rests on the choice of test stimuli and psychophysical method. Accordingly, filter estimates in neurons must faithfully emulate psychophysical test conditions to be useful. For the ICC, two sets of data fulfill this condition (cats: Ehret and Merzenich 1985, 1988a; mice: Vartanian et al. 1999; Egorova et al. 2002). They show that ICC neural critical bandwidths follow the same rules as psychophysical critical bands (i.e., frequency dependence and level tolerance) when determined with a CF-centered tone and narrowband noise masker (Fig. 11.6A, B). Thus, critical-band related perceptual phenomena such as masking of tonal signals by noise (Fletcher 1940; Scharf 1970), the transition from consonance to dissonance evoked by shifting frequency components in a tone complex (Plomp and Levelt 1965), and changes

in the identification of vowels and animal vocalizations by shifts of frequency components (Flanagan 1972; Ehret and Haack 1982) are embedded in the spectral filter properties of ICC neurons. Perceptual critical-band properties are absent in auditory nerve fibers (Ehret 1995), and human auditory brain stem and middle-latency responses suggest that they first emerge in the IC (Zerlin 1986; Burrows and Barry 1990).

Several anatomical properties of the ICC are congruent with spectral integration within the frequency range of critical bands. For example, ICC frequency-band laminae cover a CF range similar to one critical bandwidth. Also, for any point within a frequency-band lamina, the CF distance to the neighboring laminae is about one critical bandwidth (Schreiner and Langner 1997; Fig. 11.4B). ICC neurons with disc-shaped or flat dendritic configurations constrain their integration to a limited part of the isofrequency domain (cf. Chapter 2) (Oliver and Morest 1984; Malmierca et al. 1993) and may process spectral components within a critical band. By contrast, multipolar or stellate cells with dendritic trees orthogonal to frequency-band laminae (Oliver and Morest 1984; Meininger et al. 1986; Wagner 1994; Reetz and Ehret 1999) may process information across frequency-band laminae (Oliver et al. 1991; Reetz and Ehret 1999), a feature perhaps essential for the analysis of spectral shape and other perceptual phenomena (Hall et al. 1984; Moore 1997; O'Connor et al. 1999). Critical band analyses of neurons in the DC and EN are not yet available.

#### 4.3. SPECTRAL ENVELOPE CODING: SPECTRAL INTEGRATION

The structural complexity of natural sounds and nonlinear mechanisms in auditory processing disbar simple stimuli alone, such as pure tones, from providing a complete characterization of spectral integration (Smolders et al. 1979; Nelken et al. 1999; Theunissen et al. 2000; Escabí and Schreiner 2002). Broadband stimuli derived from a few essential components in natural sounds can be effective for a more comprehensive characterization of spectral RF properties. Broadband sounds with sinusoidal spectral envelopes ("ripple spectra") represent a class of complex stimuli intermediate between narrow-band artificial sounds and broadband natural vocalizations (Schreiner and Calhoun 1994; Shamma et al. 1995; Kowalski et al. 1996; Escabí and Schreiner 2002). They retain white noise criteria necessary for measuring reverse correlations (Eggermont et al. 1983): these include a flat power spectrum and an impulsive autocorrelation function and can probe the responsiveness of neurons in an unbiased manner. The resulting spectrotemporal receptive field (STRF) is a profile of the spectral and temporal envelope features to which a neuron responds. The SRF or spectral component of the STRF profile can quantify neuronal responses to complex spectra (e.g., formants speech) and can reveal the RF arrangement of excitation and inhibition (Kowalski et al. 1996; Calhoun and Schreiner 1998; Versnel and Shamma 1998; Miller et al. 2002; Qiu et al. 2003). This approach allows the study of spectral integration properties to dynamic broadband sounds with a rich spectral structure and thus under more natural conditions. The ability of IC



neurons to represent specific spectrotemporal feature combinations is a relatively common property in central auditory stations in species with specialized acoustic behavior (see Chapters 14, 16, and 17). With the STRF approach, stimulus feature selectivity can be generalized and applied to acoustically less specialized species.

The spectral integration properties found with ripple spectra parallel and expand those seen with tones. In cat ICC neurons tuned to 8 to 16 kHz, SRF bandwidths varied from 0.14 to 4.8 octaves with most (93%) bandwidths below about 2.0 octaves (Qui et al. 2003). Unlike pure-tone estimates, these bandwidth estimates were not strongly level dependent (Escabí et al. 2003), recalling critical-band measurements demonstrating spectral integration to be level independent (Ehret and Merzenich 1985, 1988a). SRF bandwidth distribution was unimodal (mean 1 octave). The best ripple density, the number of spectral envelope peaks/octave that produces a maximal neural response (Schreiner and Calhoun 1994; Klein et al. 2000; Escabí and Schreiner 2002) was low (mean = 0.61 cycles/octave) for most ICC neurons, indicating a preference for broadly spaced spectral features. The wide range of best ripple-density (0.02 to 2.11 cycles/octave), also reflects a wide range of spectral integration/selectivity. It is unclear how these measures relate to psychophysical or physiologic estimates of critical bands. Comparison of spectral envelope preferences in the ICC, the ventral division of the medial geniculate body, and primary auditory cortex reveals that general spectral integration properties seem well conserved in the lemniscal pathway between the IC and the auditory cortex (Miller et al. 2001, 2002; Qiu et al. 2003).

#### 4.4. ORIGINS OF SPECTRAL TUNING AND RESOLUTION

Cochlear filtering represented in the RFs of auditory nerve fibers is the basis for spectral tuning in higher centers of the auditory pathways. Careful removal of a narrow frequency channel at the level of the spiral ganglion can result in a narrow gap at corresponding frequencies in the eFTCs of ICC neurons (Snyder et al. 2000; Snyder and Sinex 2002). Auditory nerve fibers have relatively uniform eSRFs with areas of lateral suppression (Sachs and Kiang 1968; Schmiedt

Figure 11.6. (A) Excitatory spectral receptive fields (*eSRFs*, *cross-hatched areas*) bordered by the eFTC (*thin lines*), inhibitory SRFs (*iSRFs*, *shaded areas*), critical bandwidths (horizontal hatching bordered by thick lines), and facilitation areas (*arrows*) of class I to IV neurons of the cat ICC. The critical bandwidths are nearly independent of the FTC shapes. (Modified from Ehret and Merzenich 1988a and unpublished observations.) (B) Frequency dependence of critical bandwidth from cat ICC neurons (*open symbols*, measurements at various tone levels) and from behavioral measurements (*closed symbols*; Pickles 1975, 1979). Average behavioral and neural regression lines (*thick lines*) follow virtually the same functions if the neural data are adjusted to compensate for overmasking (*dashed line*). (Modified from Ehret and Merzenich 1985.)



1982; Delgutte 1990) but no facilitation areas (Fig. 11.3A). Brain stem neurons have far more diverse eSRF (eFTC) shapes, and reflect the presence of inhibition (Guinan et al. 1972; Young et al. 1988; Rhode 1991) and facilitation (Palmer et al. 1995; Winter and Palmer 1995). These diverse eSRF, iSRF, and fSRF shapes converge onto the IC and, in some cases, may be directly inherited by IC neurons (Ramachandran et al. 1999; Egorova et al. 2001).

The SRF of a given ICC neuron may be dominated by brain stem input as well as intrinsic biophysical properties (see Chapter 10). For example, many class I (I-type) ICC neurons (Ramachandran et al. 1999; Egorova et al. 2001) may inherit eSRF properties of type I cells in the ventral cochlear nucleus (Young et al. 1988) projecting to the ICC (Romand and Avan 1997). Similarly, many closed eSRFs of ICC neurons (type O; Ramachandran et al. 1999) are derived from O-shaped eSRFs of dorsal cochlear nucleus neurons, as blocking this projection reduces the incidence of O-neurons in the ICC by nearly 80% (Davis 2002). Further, medial superior olive neurons with broader tuning (Goldberg and Brown 1969; Guinan et al. 1972) project to the lateral ICC (Aitkin and Schuck 1985; Kudo and Nakamura 1988) and may engender the many broadly tuned class III neurons there. Pharmacologic blockade of GABAergic input to ICC neurons showed that inhibitory interactions can arise from sub-collicular cells projecting to the ICC and from intrinsic ICC neurons. These inputs may affect SRFs in class I and II neurons (Yang et al. 1992; Pollak and Park 1993; Fuzessery and Hall 1996; Palombi and Caspary 1996; Lu and Jen 2001). Further, neurons with complex FTCs (class IV) likely arise from the convergence of neurons with class I and/or class II properties and somewhat different CFs (Egorova et al. 2001). Thus, SRFs of ICC neurons can be inherited from ascending projections and generated locally by excitatory–inhibitory interactions. The weight of both factors on a given neuron may depend on the location of the neuron in the three-dimensional fibrodendritic (see Chapter 2) and critical band (Schreiner and Langner 1997) space in the ICC. The origin of neural critical bandwidths with properties of psychophysical critical bands is associated with ICC neural filtering properties. Perhaps the genesis of critical-band properties reflects the shape of converging neuronal SRFs. This seems at first to be the case only for neurons with level-tolerant, sharp tuning (some class II or I-type neurons) because of the differences in shapes of FTCs and critical-band filters in class I, III, IV (and some class II) neurons (Fig. 11.6A). The steep slopes of the critical-band borders may derive from class I and class III eSRFs; however, they are shaped by inhibitory and facilitatory iSRF and fSRF influences (Ehret 1995). The suggestion that neural critical bands are sculpted from eSRFs mainly by inhibition (Ehret and Merzenich 1988a) has been supported in the mouse ICC (Egorova et al. 2002, 2003), where a strong correlation between critical-band cutoff frequencies and the CFs of inhibition (Figs. 11.1C and 11.6A, class I and II) occurs. In class II neurons, the border frequencies of the critical bands align almost perfectly with the peak frequencies of the iFTCs below and above the CF.

In summary, both spectral filtering (FTCs) and spectral resolution/integration are based on the same kind of processing in the ICC. The shapes of eFTCs can be considered a special case of “critical-band” filters for a one-tone stimulus. Whenever a multitone or complex spectrum is processed, inhibitory and facilitatory influences are activated from off-CF components that refine the neural response into a critical band. Accordingly, the properties of the composite SRF of a neuron (eSRF + iSRF + fSRF) determine its functional capabilities as spectral integrator.

## 5. INTENSITY CODING

The total dynamic range of the human ear comprises about 130 dB SPL in the frequency range of best hearing. Within this range, loudness can be matched across frequencies, and small intensity steps can be discriminated. Because loudness estimates are rather independent of the sound’s spectral composition (Zwicker and Feldtkeller 1967; Scharf 1978; Moore 1997), the neural coding of sound level and level differences seems to be largely independent of the type of sound.

The coding of sound level in the auditory nerve rests on three mechanisms: (1) there is an approximately 60-dB range of response threshold across AN fibers with similar CFs (Liberman 1978); increasing sound level recruits more auditory nerve fibers with similar CFs. (2) AN fiber RLs vary in shape and dynamic range between 20 and 70 dB for CF tones (Sachs and Abbas 1974; Jackson and Relkin 1998). Dynamic ranges for tones above CF can exceed 70 dB. Thus, some AN fibers vary their response rate to tones over many levels. (3) With increasing amplitude, excitation spreads along the basilar membrane, especially toward the high-frequency end so that louder sounds recruit more AN fibers of increasing CFs (Zwicker and Feldtkeller 1967).

For the first two mechanisms, sound level at a given cochlear position (or CF) is coded over the 130-dB dynamic range by jointly considering the number of activated fibers and their activity levels. The code for AN sound intensity could equal the integrated activity of a small neural ensemble of similar CF. The third mechanism may enhance this population code at higher levels (Chatterjee and Zwislocki 1998) and may underlie the just-noticeable-intensity differences in psychoacoustical tests, which decrease with growing sound level (Maiwald 1967; Ehret 1989). Can the distribution of response thresholds and shapes of RLs illuminate how sound intensity is coded in the IC?

### 5.1. RESPONSE SENSITIVITY (THRESHOLDS)

The stimulus with the lowest SPL to evoke a neural response characterizes neural sensitivity (minimum threshold, MT) to sound pressure level. The behavior of response thresholds in psychophysics and for onset-responses, from auditory

nerve fibers to cortical neurons, is well described by the temporally integrated pressure envelope of a stimulus, in particular its onset envelope (Heil and Neubauer 2001, 2003). The site of this integration process is postulated to be at the inner hair cells and auditory nerve fiber's synapse (Heil and Neubauer 2003). Usually, neuronal responses are expressed as a function of the steady-state SPL although a metric that emphasizes dynamic stimulus aspects may be more appropriate (Heil 1997).

IC minimum thresholds for CF tones range over 60 to 80 dB in the cat (Aitkin 1991) and 35 to 45 dB in mice (Ehret and Moffat 1985a; Stiebler 1986). Because MTs may vary with the physiological state and anesthesia (Ehret and Moffat 1985b; Zurita et al. 1994), a large threshold range at a given CF may embody the animal's status rather than the actual MT range in a behaving animal. MTs are frequency dependent and typically follow the behavioral detection thresholds (Ehret and Moffat 1985a; Kelly et al. 1991; Egorova et al. 2001). The lowest contralateral values are  $-10$  and  $+10$  dB SPL for most species, and ipsilateral thresholds are about 10 to 20 dB higher (Aitkin 1991). Neurons of different spectral response types can also be characterized by MT differences: cat type V neurons have MTs 8 to 10 dB above that of type I and type O cells (Ramachandran et al. 1999). Mouse class III neurons have MTs 10 to 15 dB higher than cells of other classes (Egorova et al. 2001). The median MTs in the DC and the EN are 4 to 7 dB above ICC values (Palombi and Caspary 1996; Syka et al. 2000). Considering the spectral integration within critical bands, MTs for complex sounds such as noises are much lower than pure-tone MTs, if expressed as spectrum level (level/Hz) (Ehret and Moffat 1985a).

Tone MTs of cells in a frequency-band lamina vary systematically in mouse ICC, with lowest MTs in the center and progressively higher values peripherally (Stiebler and Ehret 1985; Stiebler 1986; Fig. 11.4A). Analogous topographic variations occur in the auditory cortex (Sutter and Schreiner 1995). Systematic spatial variations of intensity parameters may contribute a central (cortical) place-code component for loudness representation (Heil et al. 1994).

## 5.2. INTENSITY SELECTIVITY

The shape of RLs for superthreshold tones reveals several characteristics to increasing stimulus amplitude (Fig. 11.7). A segment of monotonic increase of firing rate with intensity shows a near-linear relationship between rate and SPL in all ICC neurons. However, few neurons maintain such growth at higher stimulus levels (Fig. 11.7A; Table 11.1). Most saturate at a certain intensity (plateau RLs, Fig. 11.7B), decline in rate (nonmonotonic RLs, Fig. 11.7C), or show variable behavior (complex RLs, Fig. 11.7D). Nonmonotonic RLs are intensity tuned, as the maximum rates are limited to a narrow range of stimulus levels. In most studies, these represent the preponderant tonal RL type in ICC (Table 11.1). Each type of RL to tones (Fig. 11.7) is found in varying proportions in the DC and EN (Table 11.1).

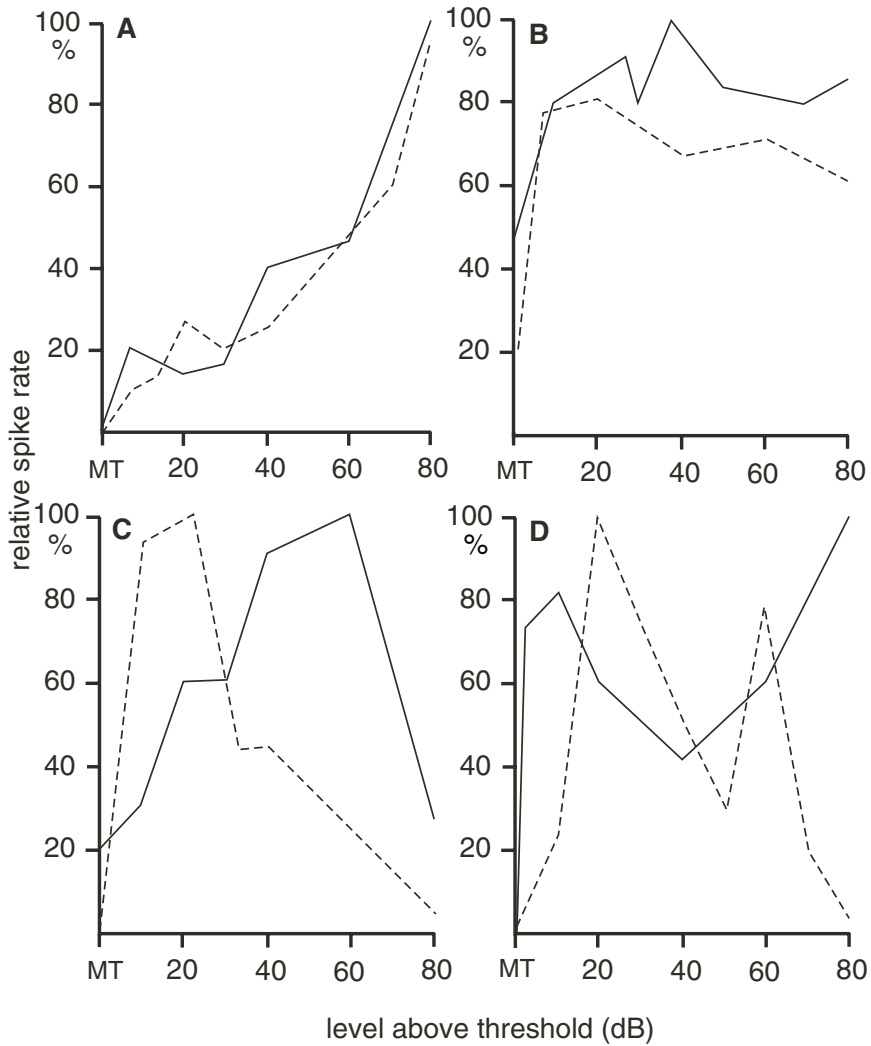


Figure 11.7. Examples of rate-level functions (RLs) in response to tone bursts from the cat ICC showing monotonic (**A**), plateau (**B**), nonmonotonic (**C**), and complex (**D**) shapes. *MT*, Minimum threshold. (Modified from Ehret and Merzenich 1988b and unpublished data.)

Table 11.1. Ranges of percentages for pure-tone rate-level functions of four basic types in IC subdivisions in cats (Ehret and Merzenich 1988b; Aitkin 1991; Aitkin et al. 1994), mice (Ehret and Moffat 1985a), rats (Palombi and Caspary 1996), and guinea pigs (Rees and Palmer 1988; Syka et al. 2000).

	Monotonic	Nonmonotonic	Plateau	Complex
ICC	6–28	15–66	5–35	7–26
EN	32–43	24–32	24–30	11–16
DC	6–39	21–59	4–58	0–31

The level eliciting maximal discharge is the “best” level. Best levels of non-monotonic neurons occur at any superthreshold level in the cat (Ehret and Merzenich 1988b; Irvine and Gago 1990; Aitkin 1991) and have a range 10 to 40 dB above MT in rat and guinea pig (Rees and Palmer 1988; Palombi and Caspary 1996). Dynamic range is the extent of superthreshold sound levels over which an increased response rate occurs (Fig. 11.7). Dynamic ranges of monotonic neurons can exceed 80 dB (Ehret and Merzenich 1988b; Irvine and Gago 1990), while those of other RL types fall within about 50 dB (Aitkin 1991).

The large variability of the RL type percentages (Table 11.1) has several causes, including methodologic differences between studies and possible species differences. Studies available are constrained by a limited range of sound levels (<85 dB) tested; failure to consider the tone burst repetition rate (Galazyuk et al. 2000); or the fact that RLs were not calculated separately from the onset and the sustained response of neurons, which results in different RL shapes (Rees 1992). Moreover, differential criteria for assigning neurons to different RL types have been used. RL shapes often depend on stimulus type (Ehret and Merzenich 1988b; Aitkin 1991; Syka et al. 2000; Palombi and Caspary 1996), on the sound angle incidence (Semple and Kitzes 1985; Irvine and Gago 1990), on behavioral state (Ryan and Miller 1977), and on corticofugal influences (Syka et al. 1988; Zhang and Suga 1997; Jen et al. 1998; Suga et al. 2000; Zhou and Jen 2000; Yan and Ehret 2001, 2002; see Chapter 8). Hence, the shapes of RLs in response to tones and other stimuli are diverse and reflect many variables.

RL shape may be predicted in part from the SRF shape. Class II or type O neurons with a closed eSRF or class II neurons with an eSRF skewed toward higher or lower frequencies at high sound levels (Fig. 11.3) must have non-monotonic (or complex) RLs to CF-tone bursts because, at higher SPLs, the CF may be outside the eSRF border. Thus, the RL shape embodies the same factors molding RFs (convergence of excitatory, inhibitory, and facilitatory input). Intracellular recordings and current injection of IC cells showed that monotonic, nonmonotonic, and plateau RLs may be locally produced by different ionic regimens interacting with membrane properties (Smith 1992; Wagner 1994; Reetz and Ehret 1999; Peruzzi et al. 2000; Sivaramakrishnan and Oliver 2001; Bal et al. 2002).

### 5.3. CONTRAST SENSITIVITY

The ability of the auditory system to encode amplitude differences has been studied almost exclusively in the context of intensity discrimination and loudness coding (Evans and Palmer 1980; Ehret and Merzenich 1988b; Viemeister 1988). The range of amplitude values present during a short segment of natural sounds, its contrast, can be substantial (Attias and Schreiner 1998), and varies considerably over time (e.g., during speech) and between sound environments (Escabí et al. 2003). The decibel amplitude distribution of spectrotemporal contrast in natural sounds is approximately normal (Fig. 11.8A). Perhaps the operating range of IC neurons, reflected in the RLs, is matched to the natural amplitude statistics, and thus can efficiently process sounds and thereby detect and segregate signals. ICC neurons are tuned to naturally occurring contrast distributions (Escabí et al. 2003). Moreover, mean intensity and contrast coding appear to be independent. Like RLs for stimulus level, rate-contrast functions are monotonic or nonmonotonic but are independent of the type of RL function in the cell (Fig. 11.8B). This independent response behavior for two stimulus amplitude measures (mean and variance) suggests that both are relevant features of the acoustic landscape and its neural representation. Understanding the role of contrast in

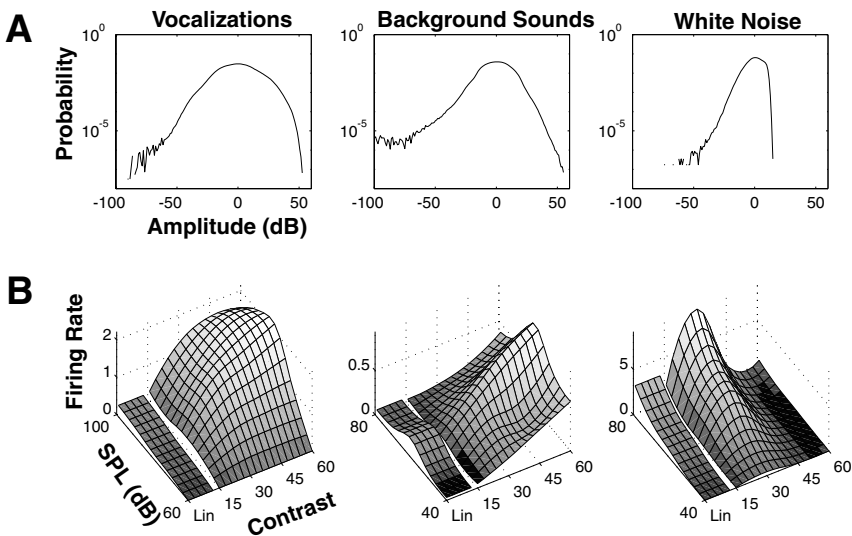


Figure 11.8. (A) Probability distributions of amplitude values in three different sound classes. The width of the distributions corresponds to the contrast of the sounds. Note the differences in width between white noise and natural signals. (B) Firing rate profiles for three different neurons in the ICC for “ripple-spectra” (broadband stimuli with noise-like spectral envelopes) that were systematically and independently varied in mean intensity and contrast. (Adapted from Escabí et al. 2003.)

auditory processing from the perspective of natural contrast distributions must receive further attention.

#### 5.4. *MODELS OF SOUND INTENSITY CODING*

The available evidence for sound intensity coding at the IC does not allow conclusive statements about how sound intensity, level or loudness, and intensity differences or contrasts are coded. At present, three fundamental ideas about intensity coding are plausible (Irvine 1992; Ehret 1997): (1) Small groups of neurons with monotonic, sound-type independent RLs over 80 dB or more code sound intensity and level variation by their integrated spike response. (2) Neurons with nonmonotonic RLs aggregate by their best levels at ICC loci in frequency-band laminae and map sound intensity by their location. A similar spatial code for sound level occurs in a specialized field of the mustached bat's auditory cortex (Suga 1977; Suga and Manabe 1982). (3) From maps of absolute response thresholds in frequency-band laminae (Stiebler 1986), a model of the transfer of cochlear sound parameters to the three-dimensional ICC space predicts a spatial code for sound intensity, that is, a shift of the maximum of the neural response from the center of a frequency-band lamina to its periphery with increasing amplitude (Herrnberger et al. 2002). Implications of this model include systematic neural arrangements with monotonic and nonmonotonic RLs in frequency-band laminae. These three propositions about midbrain intensity coding incorporate RL variability and predict that an average-rate code for sound intensity derived from a large proportion of ICC neurons is unlikely (Ehret and Merzenich 1988b). Onset and sustained responses could have unique contributions to intensity and contrast coding. The biological significance or semantic content of environmental and communication sound is often coded independently of intensity. This suggests as yet unidentified mechanisms in the auditory pathways that separate the influence of the total sound level from that of biologically significant level differences or contrasts. However, as total level can mediate arousal, emotions, and motivations, information about it must be coded, and may be transmitted, independently of semantic information, to higher brain centers.

## 6. CONCLUSIONS AND QUESTIONS FOR FUTURE RESEARCH

The coding of sound frequency and intensity are fundamental tasks of auditory processing and have been extensively studied in the IC. Despite the impressive body of studies available for RF properties, many aspects of the midbrain contribution to various sound processing tasks are unknown. The convergence of input from many sources and the several types of spectral/intensity RFs creates an interpretational dilemma. The segregation of subcollicular pathways in the

cochlear nucleus complex, superior olivary complex, and nuclei of the lateral lemniscus can be construed in terms of specialized tasks that require certain dedicated structural and functional substrates of neural organization. After the massive convergence at the midbrain level, this paradigm is simply no longer appropriate without a deeper grasp of the nature, purpose, or task-specificity of the convergence. Parallel output from an abundance of subcollicular nuclei appears compressed in the ICC onto a single tonotopic substrate, giving a new meaning to the term convergence, with no counterpart in either the visual or somatosensory systems (Ehret 1997). The challenge still is to decipher how the neurons of this substrate are specialized in their structure, physiology, and network properties to serve the many functional demands of sound processing.

We note here just a few immediate tasks directly related to matters of spectral and intensity processing:

1. What are the relationships between the morphologic and physiologic types of neurons and functional maps within ICC frequency-band laminae and those in the DC and the EN?
2. How are the composition and pattern of input projections from lower auditory centers related to the type of IC neuron (morphologic, physiologic, biophysical, functional)? Are there unique circuitries between neighboring neurons and potential laminar and subnuclear synaptic domains?
3. IC neurons are modulated by neurotransmitter-specific inputs such as the cholinergic and noradrenergic systems (Faingold et al. 1991; see Chapter 9) and by descending projections from the auditory cortex and thalamus (see Chapter 8). How do these influence sound processing under natural conditions in awake and behaving animals, and what role do they play in auditory scene analysis, hearing impairment, and neural plasticity?

## Abbreviations

BF	best frequency
CF	characteristic frequency
DC	dorsal cortex of the inferior colliculus
eFTC	excitatory frequency tuning curve
EN	external nucleus of the inferior colliculus
eSRF	excitatory spectral receptive field
fSRF	facilitatory spectral receptive field
FTC	frequency tuning curve
GABA	$\gamma$ -aminobutyric acid
IC	inferior colliculus
ICC	central nucleus of the inferior colliculus
iFTC	inhibitory frequency tuning curve
iSRF	inhibitory spectral receptive field
MT	minimum threshold
RF	receptive field



RL	rate-level function
SPL	sound pressure level
SRF	spectral receptive field
STRF	spectrotemporal receptive field

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