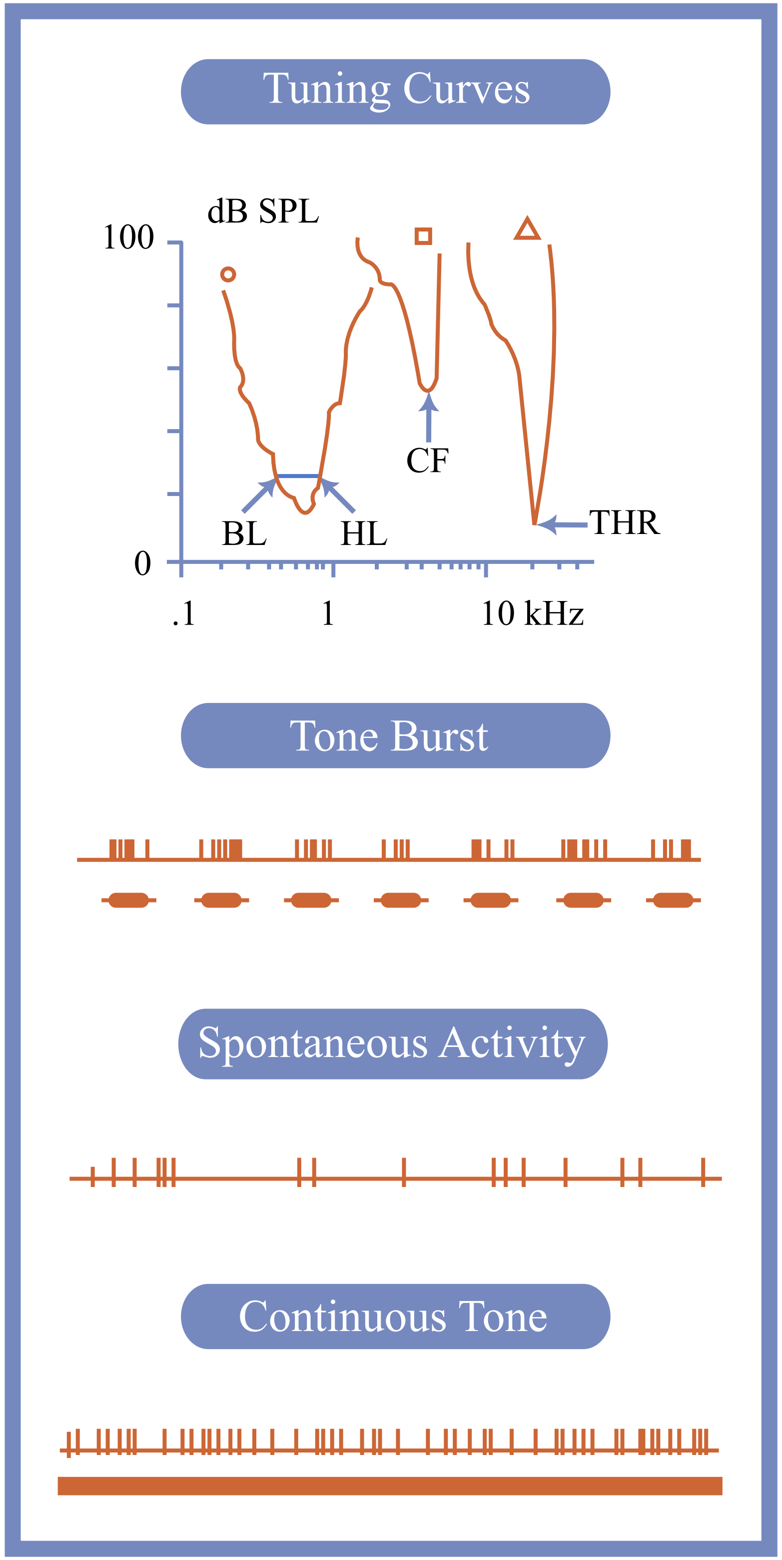
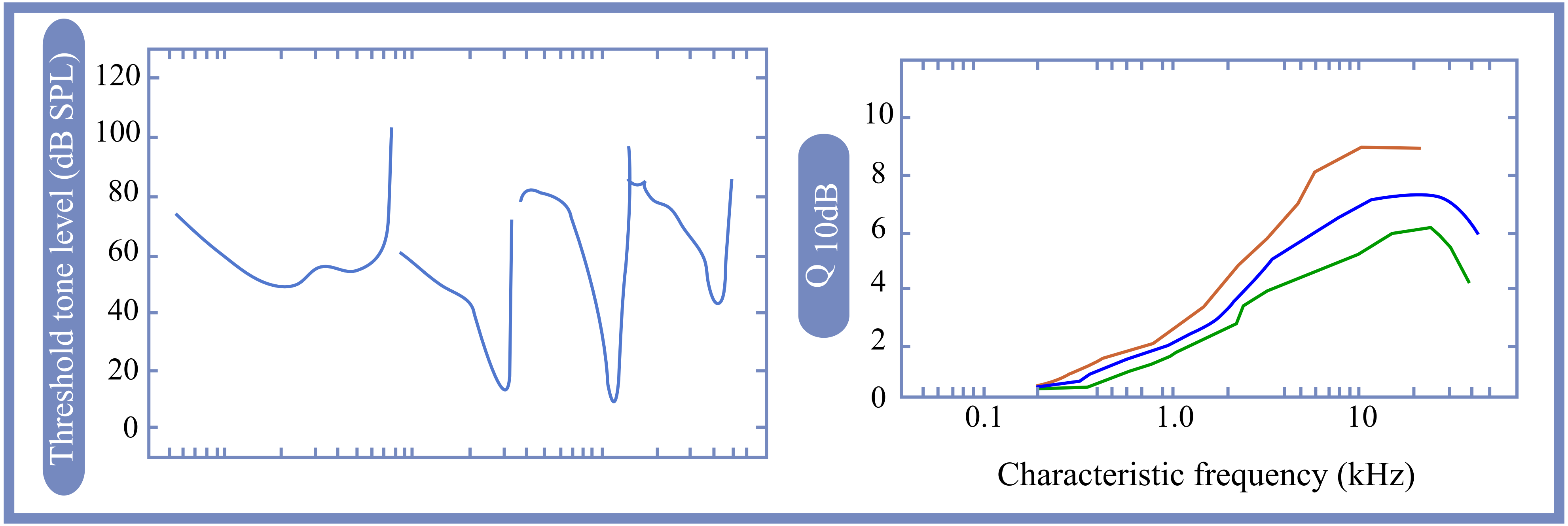
Tuning properties of auditory nerve fibers

Rate threshold tuning curves



Place principle: neural tuning as a function of cochlear "place" (CF)



Rate-level functions of auditory nerve fibers to pure tones at CF

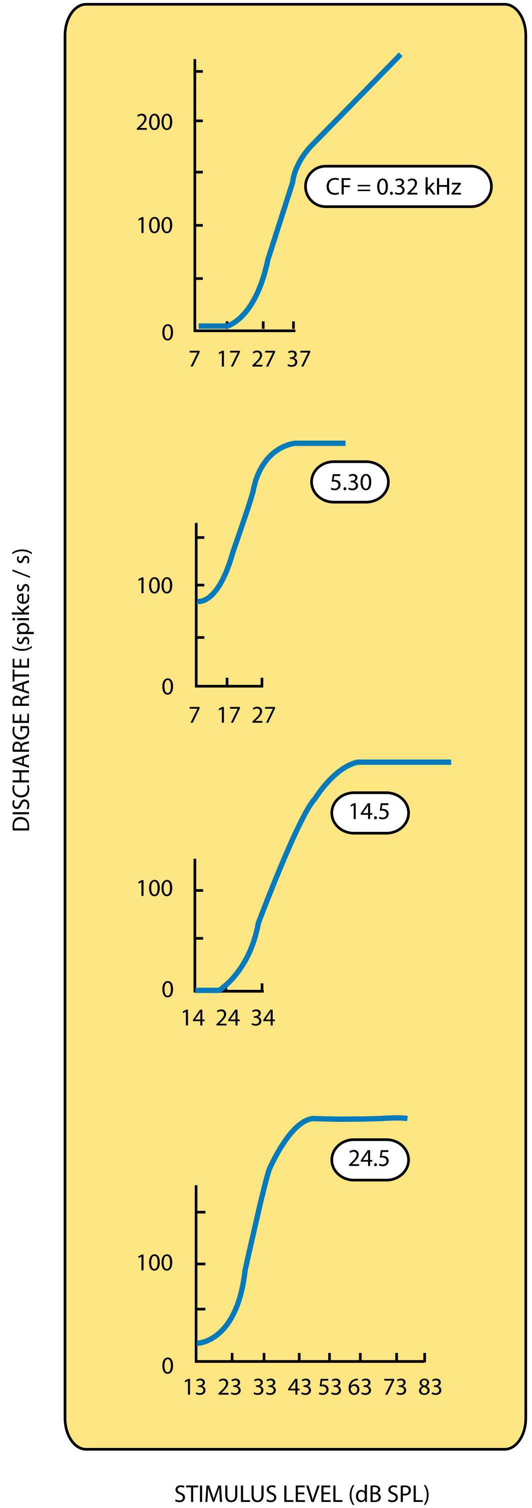
Floor and ceiling effects
Saturation

Dynamic range is relatively restricted (20-30 dB)

Spontaneous rates range from near 0 to 200 spikes/sec

Generally, the higher the spontaneous rate, the lower the rate threshold

Conventionally, rate thresholds are defined as a difference of 20 sp/s (1 extra spike in 50 ms)

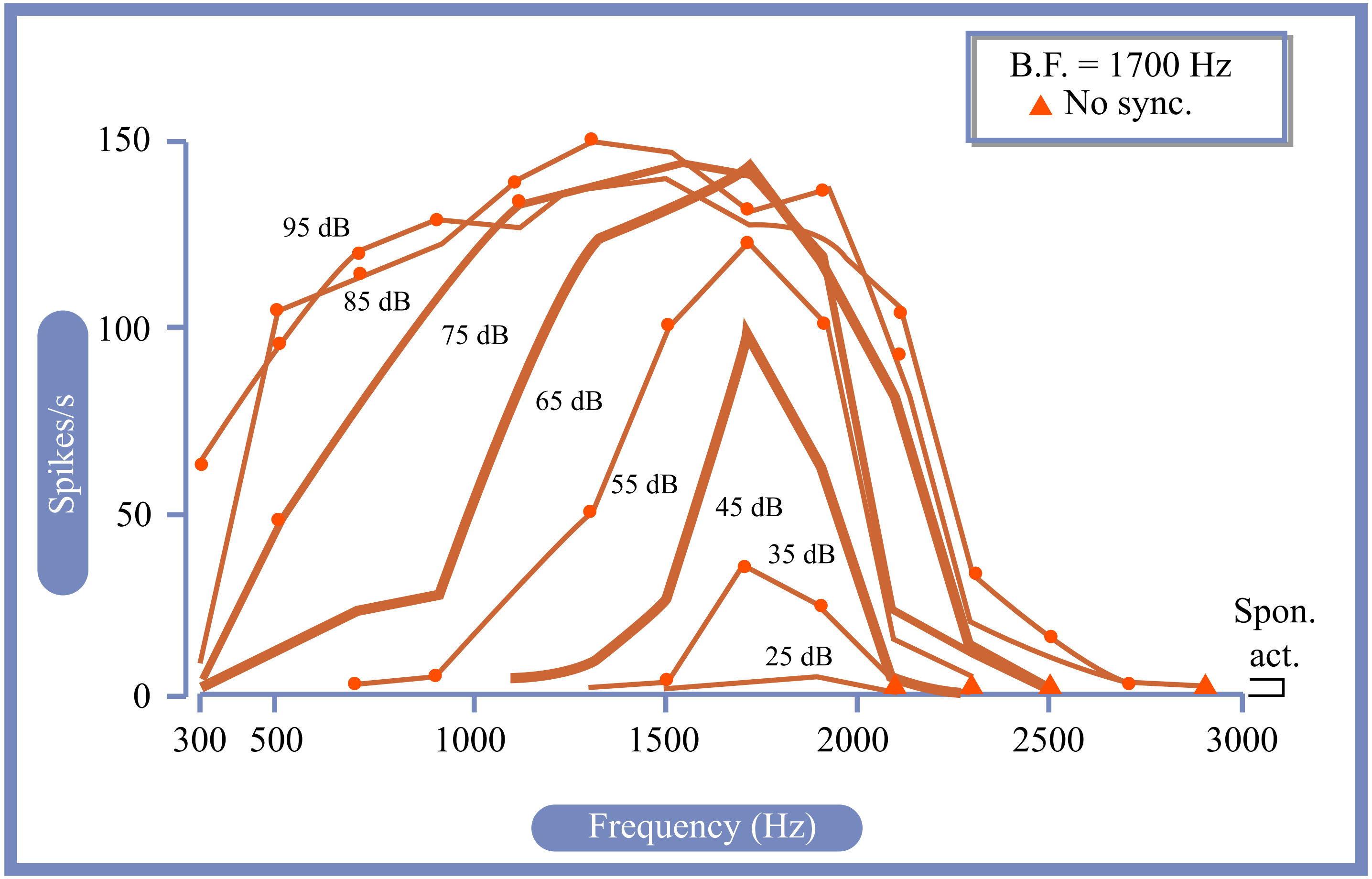


Responses to tones, keeping SPL constant

Please see figure 60 and 61 in Wolf, D. Keidel, S. Kallert, and M. Korth. *The Physiological Basis of Hearing*: *A Review*. Special editor, Larry Humes. New York: Thieme-Stratton; Stuttgart; New York: Georg Thieme Verlag, 1983. ISBN: 0865770727.

Broad tuning and rate saturation at moderate levels in low-CF auditory nerve fibers confounds rate-based resolution of harmonics.

Low SR auditory nerve fiber



Responses of ANFs to tones

CF determines the frequencies of tones to which the fiber will respond at the lowest SPLs

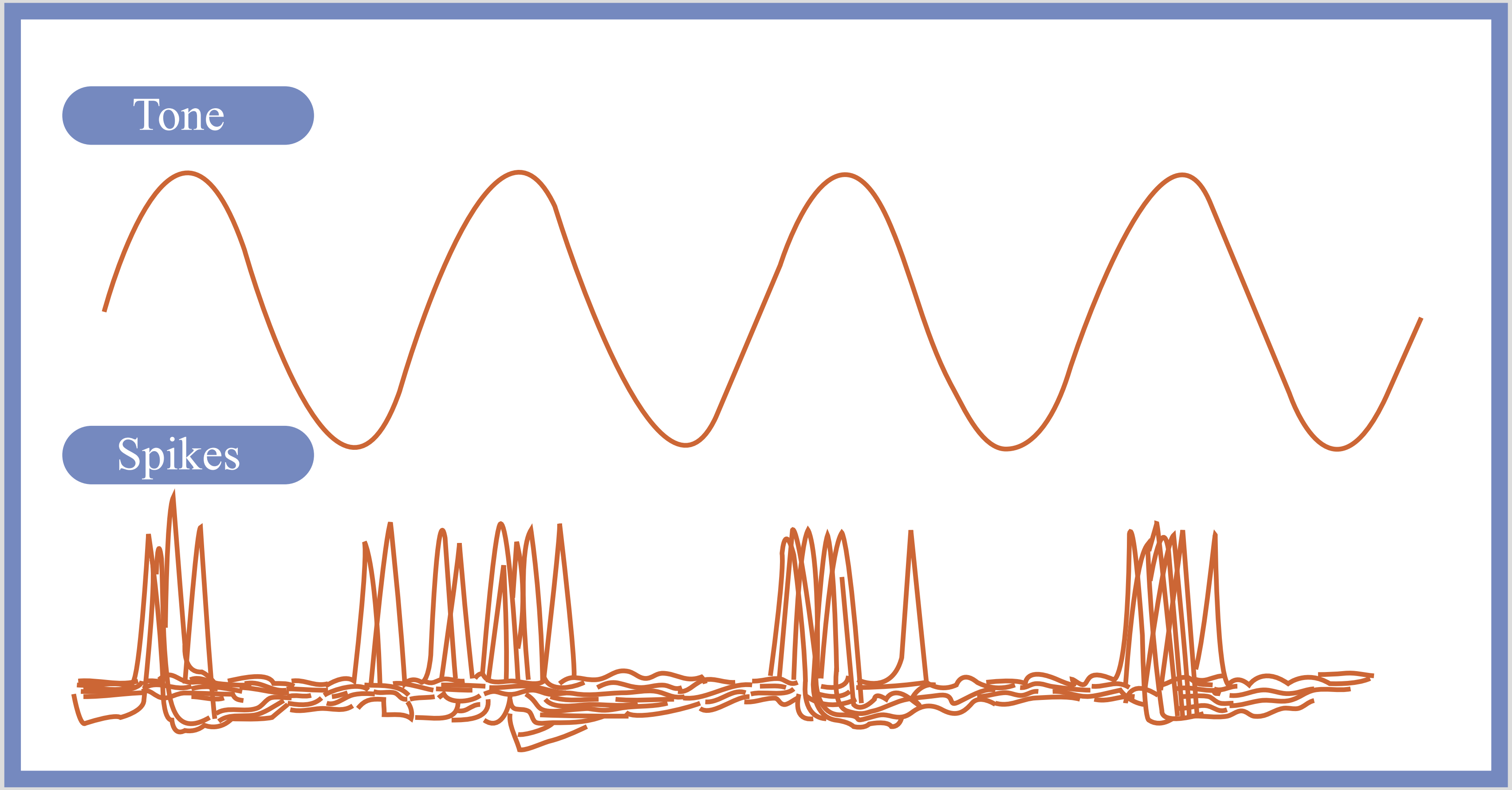
The temporal microstructure of the tone (not the CF) determines the temporal patterning of response for frequencies below 4-5 kHz (This limit is somewhat species dependent)

Only for aperiodic broadband stimuli (clicks, noise) does one see temporal response patterns dominated by CF-related factors (ringing of filters)

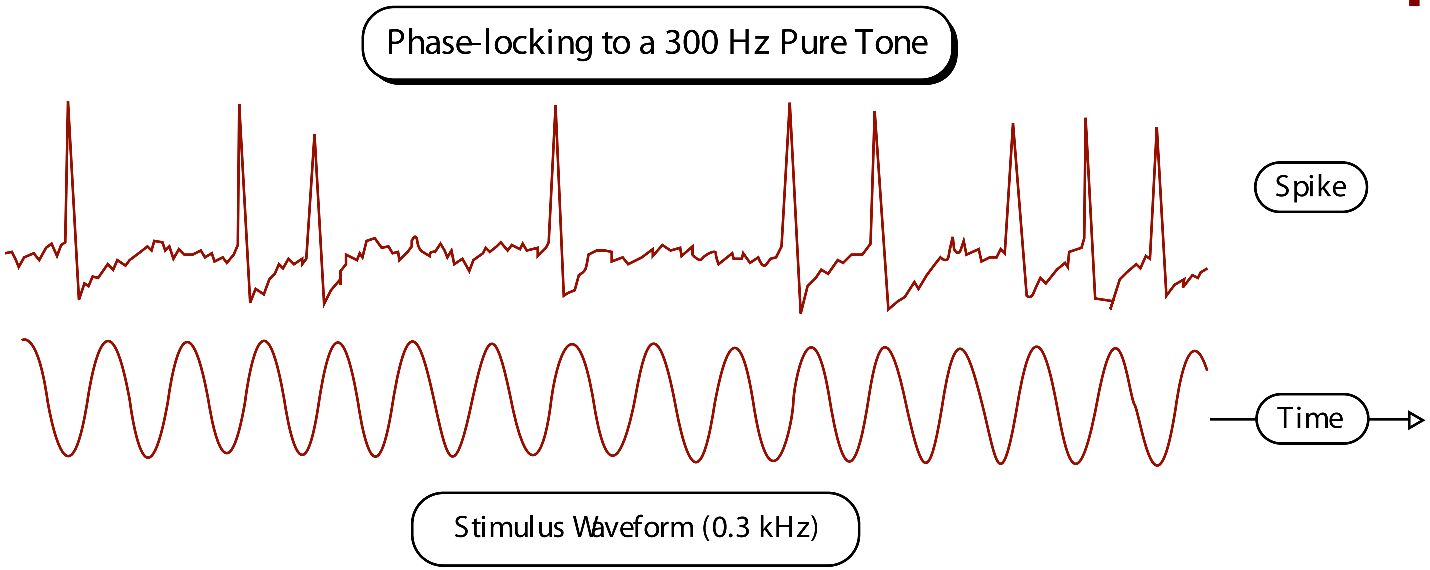
Rate-adaptation at onsets of sounds

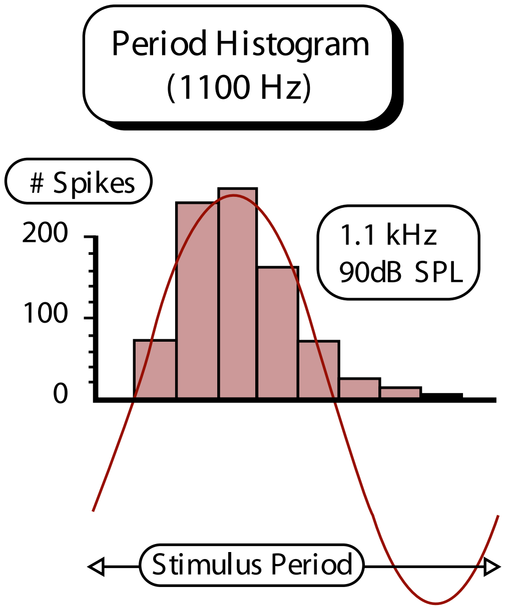
Please see Irvine, D. R. F. *The Auditory Brainstem : A Review of the Structure and Function of Auditory Brainstem Processing Mechanisms*. Berlin, New York : Springer-Verlag, 1986. ISBN : 3540162992.

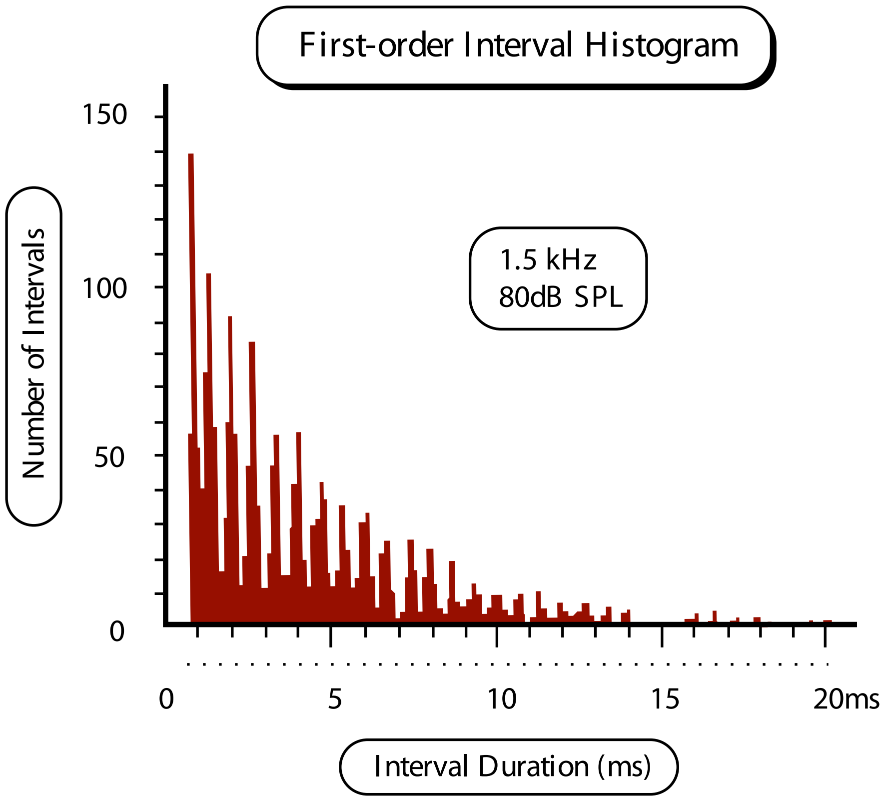
Phase-locking in auditory nerve fibers



Phase-locking







Temporal discharge patterns 40-90 dB SPL

Please see Rose, Hind, Anderson, Brugge J. *Neurophysiology* 34 (1971) : 685-99; reprinted in Keidel, Kallert & Korth (1983).

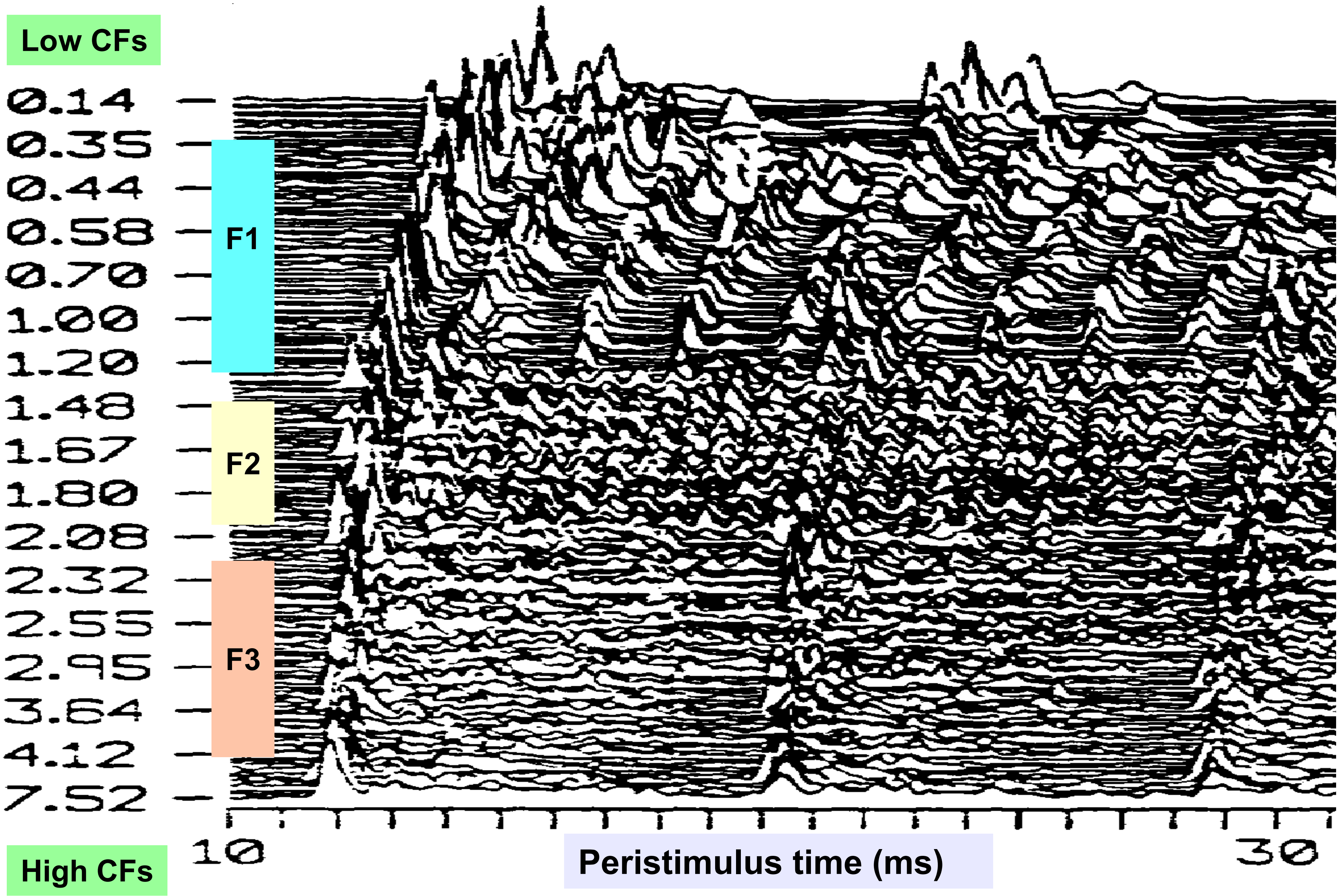
Interspike interval (ISI) distributions
(times between spikes)

Reflect temporal microstructure of the low-frequency partials that are most effective in driving the fiber (i.e. nearest the fiber's characteristic frequency)

Please see Rose, Brugge, Anderson, & Hind, 1967.

Cochlear Territories

Time domain analysis of auditory-nerve fiber firing rates.
Hugh Secker-Walker & Campbell Searle, J. Acoust. Soc. 88(3), 1990
Neural responses to /da/ @ 69 dB SPL from Miller and Sachs (1983)

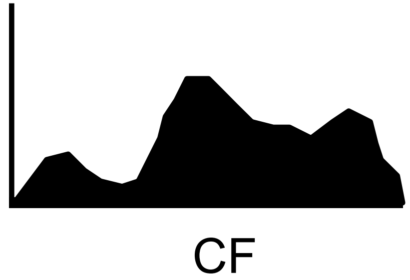


Some possible auditory representations

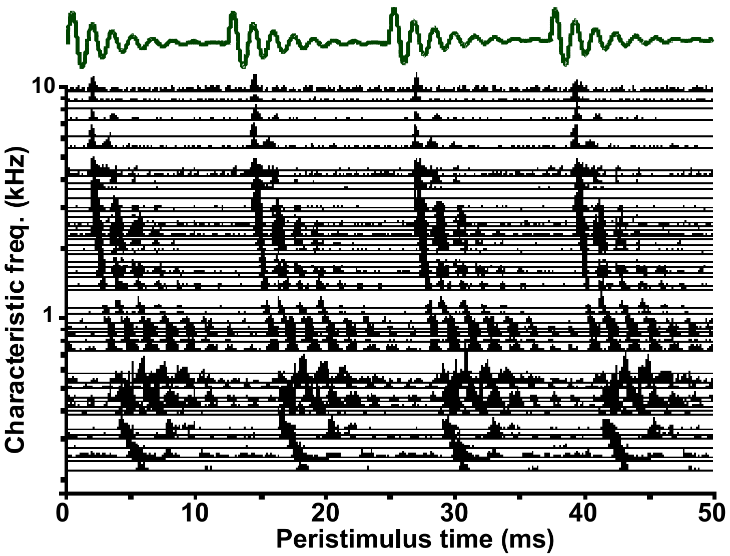
Local

Rate-place →

Central spectrum

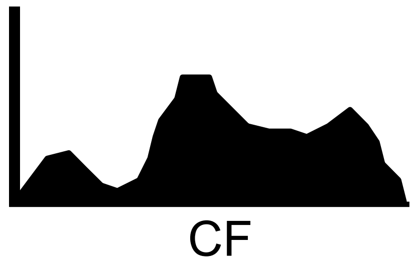


Masking phenomena
Loudness



Synchrony-place

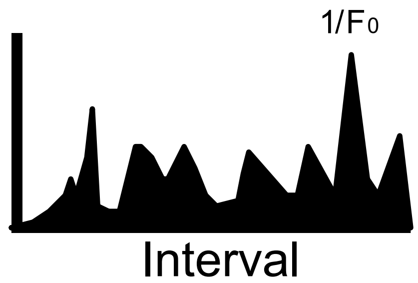
Central spectrum



Interval-place

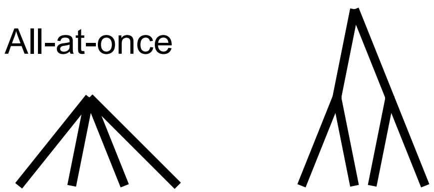
Pure tone pitch JNDs

Population interval



All-at-once

Stages of integration



Population-interval →

Complex tone pitch

Global

(Reprinted with permission from Secker-Walker HE, Searle CL. 1990. Time-domain analysis of auditory-nerve-fiber firing rates. J. Acoust. Soc. Am. 88 (3): 1427-36. Copyright 1990, Acoustical Society of America.)

Rate-place profiles:

Level-invariant character of high frequency activity profiles;

Level-dependent character of low frequency activity profiles; (Runs opposite to perception)

Please see figure 4, by Alan Palmer, in Moore B. C. J. *An Introduction to the Psychology of Hearing*. Fifth ed. San Diego: Academic Press. 2003.

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Interactions of tones

Although the auditory nerve itself has no inhibitory inputs, addition of a second pure tone at another frequency can suppress firing rates and synchrony to the first tone:

"two-tone rate suppression"

"two-tone synchrony suppression"

These interactions depend on relative level, frequency separation between the tones, and fiber CF.

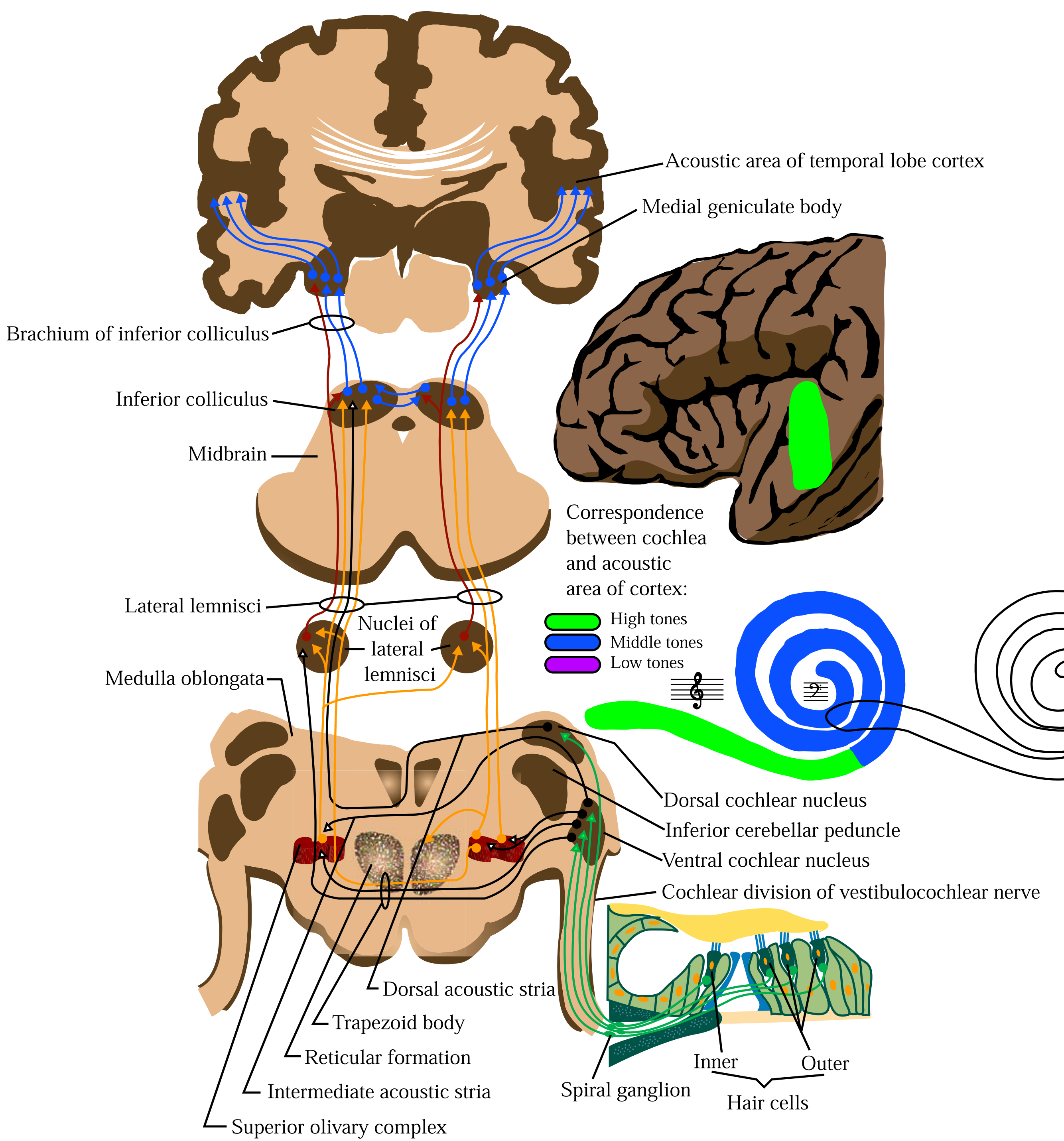
See

1] D. G. Sinex and D. C. Havey, "Neural mechanisms of tone-on-tone masking: patterns of discharge rate and discharge synchrony related to rates of spontaneous discharge in the chinchilla auditory nerve," *J Neurophysiol*, vol. 56, pp. 1763-80, 1986.

[2] B. Delgutte, "Physiological mechanisms of psychophysical masking: observations from auditory-nerve fibers," *J Acoust Soc Am*, vol. 87, pp. 791-809, 1990.

From cochlea to cortex

10,000k	**Primary auditory cortex (Auditory forebrain)**
	Auditory thalamus
500k	**Inferior colliculus (Auditory midbrain)**
	Lateral lemniscus
	Auditory brainstem
30k	**Auditory nerve (VIII)**
3k	**Cochlea**



Basic problems to be solved

- "Hyperacuity problem"
- Account for the precision of pitch discriminations given the relatively coarse tunings of auditory neurons (at all levels), especially lower-frequency ones (BFs < 2 kHz)

- "Dynamic range problem"
- Account for the ability of listeners to discriminate small fractional changes ($\Delta I/I$) in intensity over a large dynamic range, and especially at high SPLs, where the vast majority of firing rates are saturated.

- "Level-invariance problem"
- Account for the invariance (and precision) of auditory percepts over large dynamic ranges given the profound changes in neural response patterns that occur over those ranges (rate saturation, rate non-montonicities).

- Pitch equivalence
- Account for the ability to precisely match pitches of pure and complex tones (pitch equivalence, metamery) given differences in spectra and under conditions where stimulus intensities are roved 20 dB or more

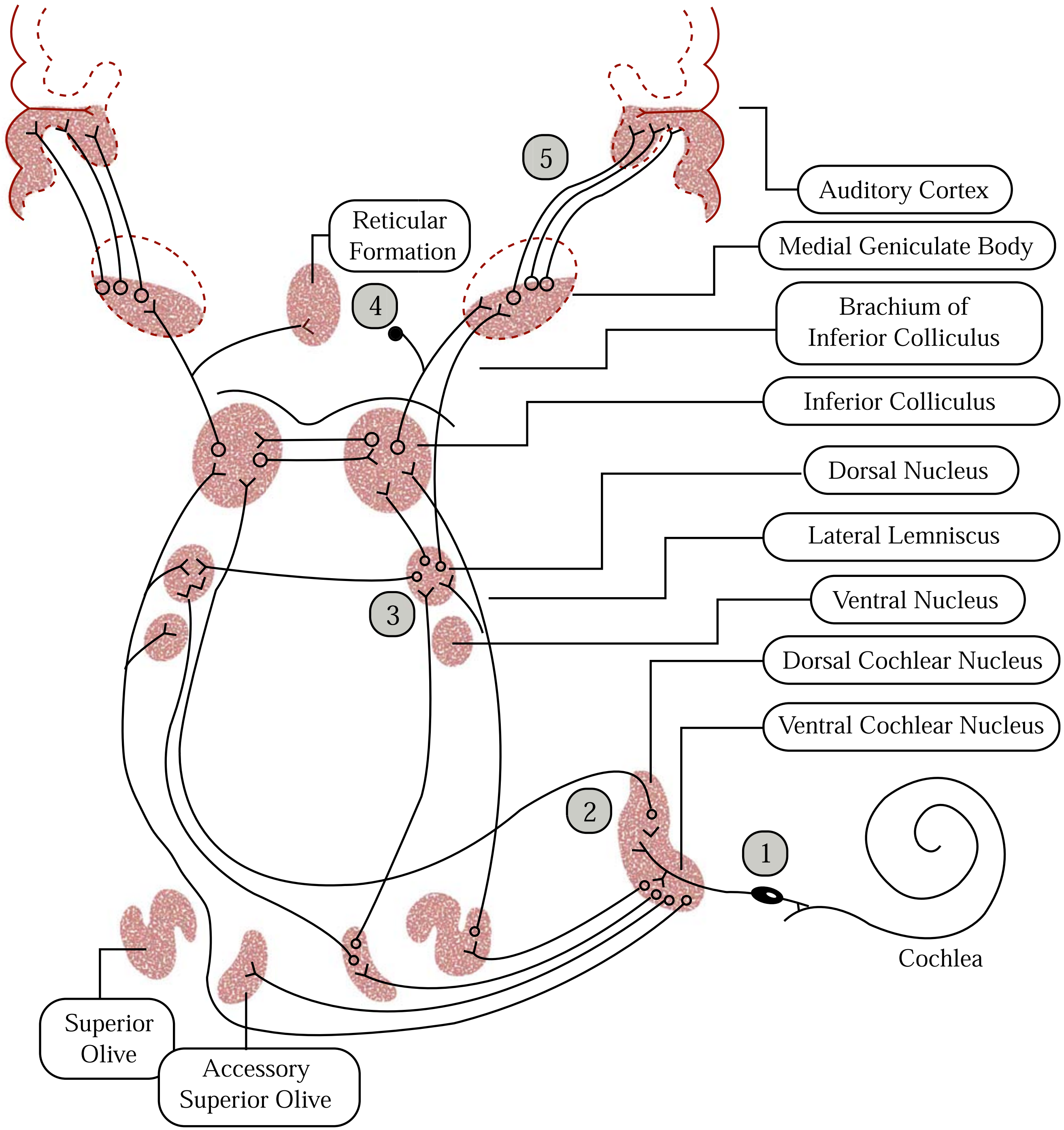
- Relative nature of pitch & transpositional invariance
- Account for the ability to precisely match pitches an octave apart (and/or to recognize patterns of pitch sequences) in the absence of an ability to identify absolute frequencies/periodicities. Account for ability to recognize transposed melodies as similar.

Some generalities about the auditory system

- Rough cochleotopy is found at all levels, but not necessarily in all neural populations
- Highly ordered tonotopic maps exist only at low tone levels, near neural thresholds
- As one ascends the afferent pathway:
- Numbers of neurons at each level increases
- Fine timing information exists in great superabundance in lower stations, but becomes successively sparser
- Firing rates (spontaneous & driven) decline
- Inhibition increases; % nonmontonic rate-level fns incr.
- Diversity and complexity of response increases
- History-dependence and contextual effects increase
- Some modulation tuning that suc. declines in periodicity

  Typical BMFs: AN: 200-300 Hz; IC: 50-100 Hz; Ctx (< 16 Hz)
- No clear "pitch detectors" (Schwarz & Tomlinson, 1991)
- No narrow (BW < 0.3 octaves) "frequency channels" for BFs < 2 kHz

Brainstem stations involved in localization of sounds



Three cochlear nuclei :
AVCN
PVCN
DCN

Bifurcation of auditory nerve

Innervation of 3 major cochleotopically-organized regions

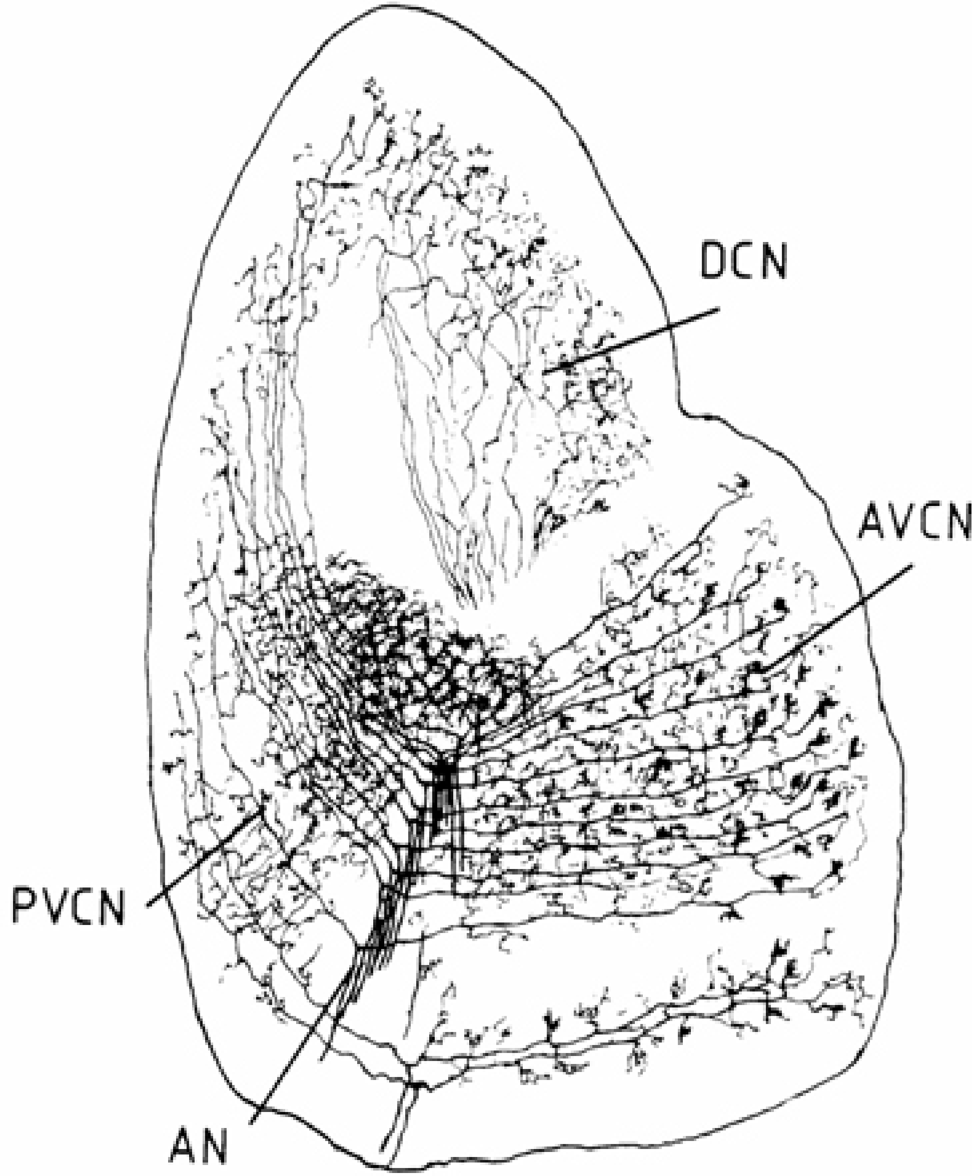


FIG. 2. Parasagittal section through cochlear nucleus of 4-day-old cat stained by Golgi method. Auditory nerve fibers, AN, bifurcate to yield ascending branch to AVCN and descending branch to PVCN and DCN. Ascending branch terminates in AVCN with large end bulbs of Held. [From Lorente de Nó (279).]

Cochlear nuclei : first station in the auditory CNS

Please see figure 13 and 14, by D. R. F. Irvine. *The Auditory Brainstem: A Review of the Structure and Function of Auditory Brainstem Processing Mechanisms*. Berlin: New York: Springer-Verlag, 1986. ISBN: 3540162992.

Cochlear nuclei : 3 major divisions (AVCN, PVCN, DCN)

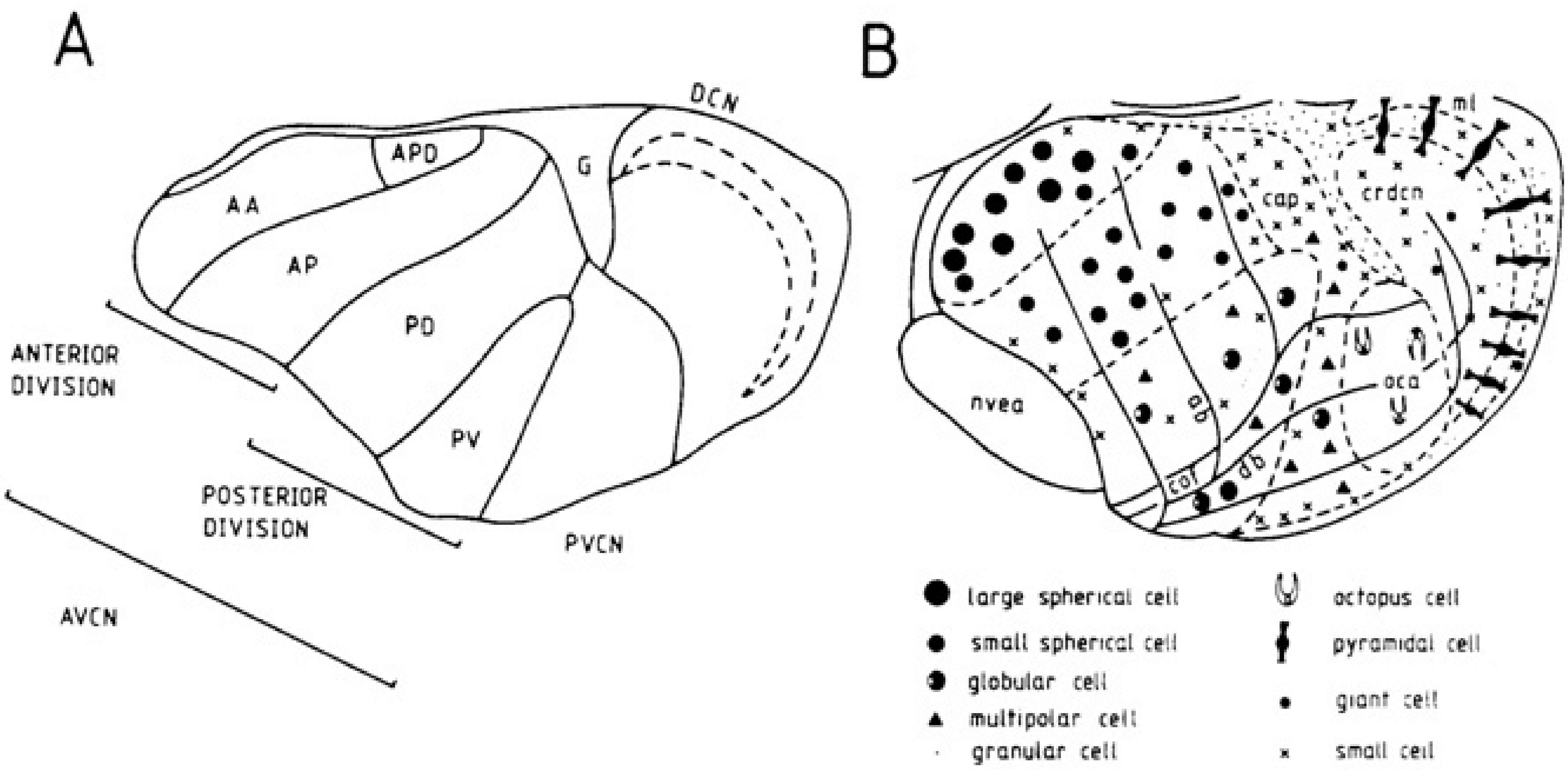


FIG. 4. Schematic drawings of sagittal sections comparing *A*: divisions of cochlear nucleus identified by Brawer et al. (59), and *B*: divisions of cochlear nucleus of Osen (343). In *A*: AVCN, anterior ventral cochlear nucleus, which is divided into anterior division comprising AA, anterior; AP, posterior; and APD, dorsal parts; and a posterior division comprising PD, dorsal; and PV, ventral parts; PVCN, posterior ventral cochlear nucleus; G, granule cell layer; DCN, dorsal cochlear nucleus; *dotted line* represents position of fusiform (pyramidal) cell layer. In *B*: nvea, vestibular nerve; oca, octopus cell area; cap, small cell cap; crdcn, central region of dorsal cochlear nucleus; ab, ascending cochlear branch; cof, cochlear nerve fiber; db, descending cochlear branch; ml, molecular layer.

Cochlear nuclei : 3 major divisions (AVCN, PVCN, DCN)

Please see Otolaryngol, Acta. "The Intrinsic Organization of the Cochlear Nuclei." Osen KK 67, no. 2 (Feb-Mar, 1969): 352-9.

Cochlear nuclei :

Types of responses seen

(to tone bursts at CF):

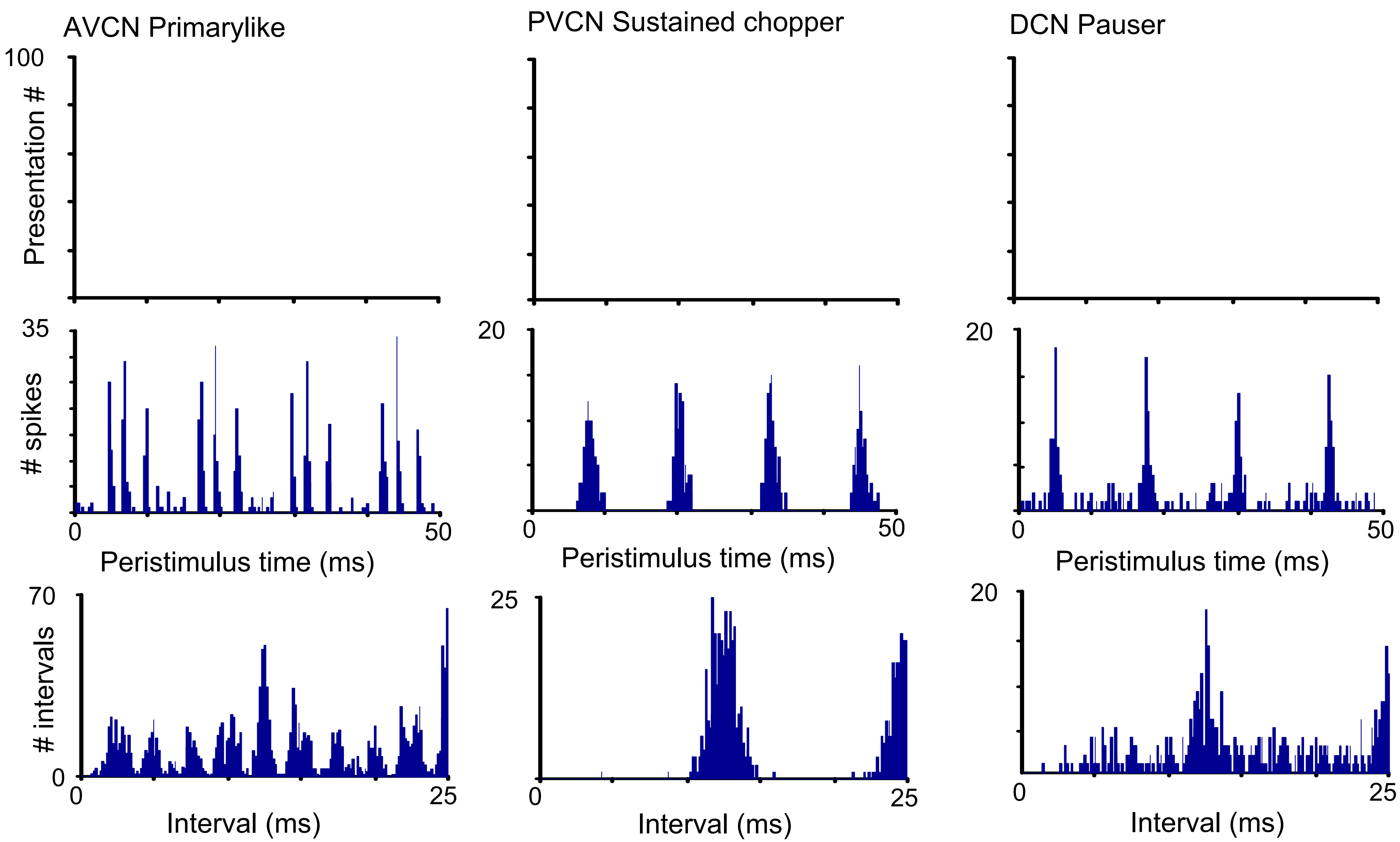
Primary-like (AVCN)
Primary-like w. notch (AVCN)
Phase-locked (PVCN)
Chopper (PVCN)
Pauser (DCN)
Build-up (DCN)
Onset (PVCN)

Most are linked to a particular neuronal morphological type

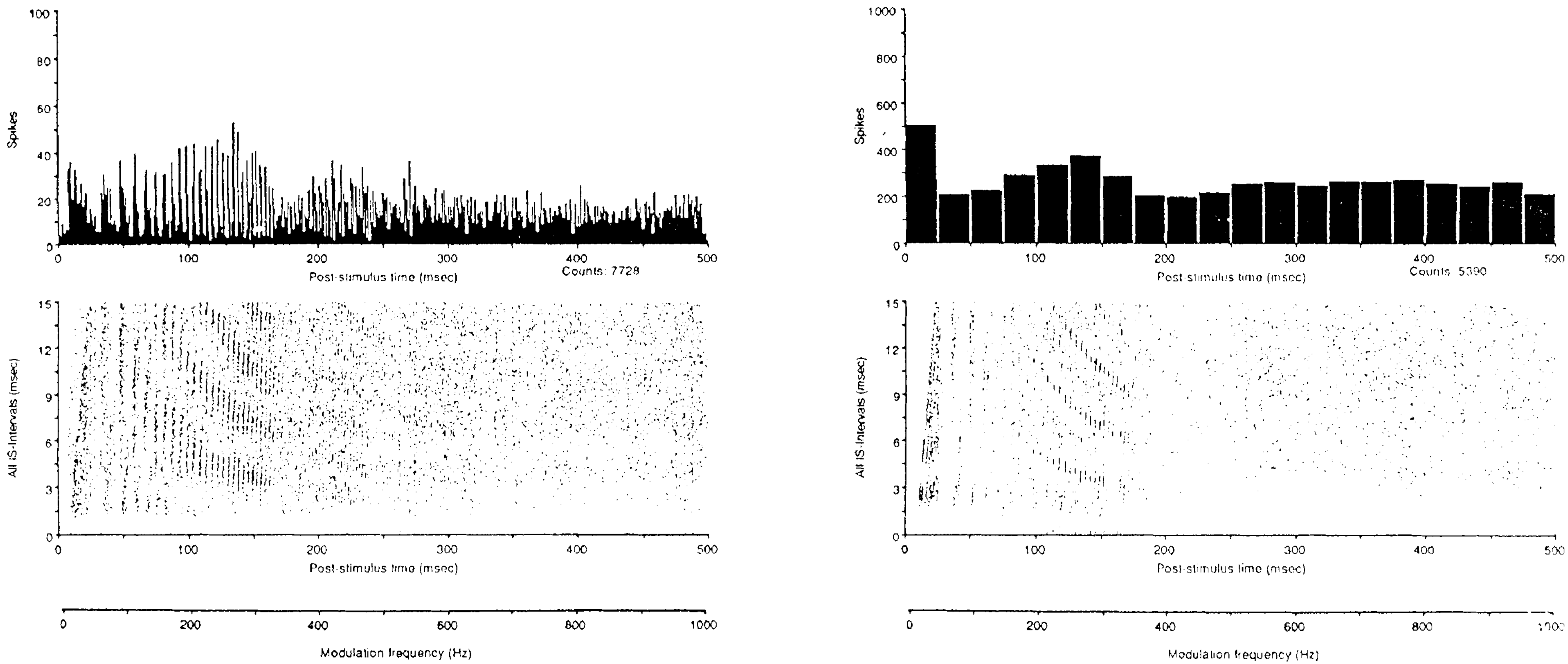
(-) indicate main regions where responses are seen

Please see Irvine D. R. F. *The Auditory Brainstem : A Review of the Structure and function of auditory Brainstem Processing Mechanisms*. Berlin, New York: Springer-Verlag, 1986. ISBN: 3540162992.

Responses of three units in the cochlear nucleus to 100 presentations of a single-formant vowel



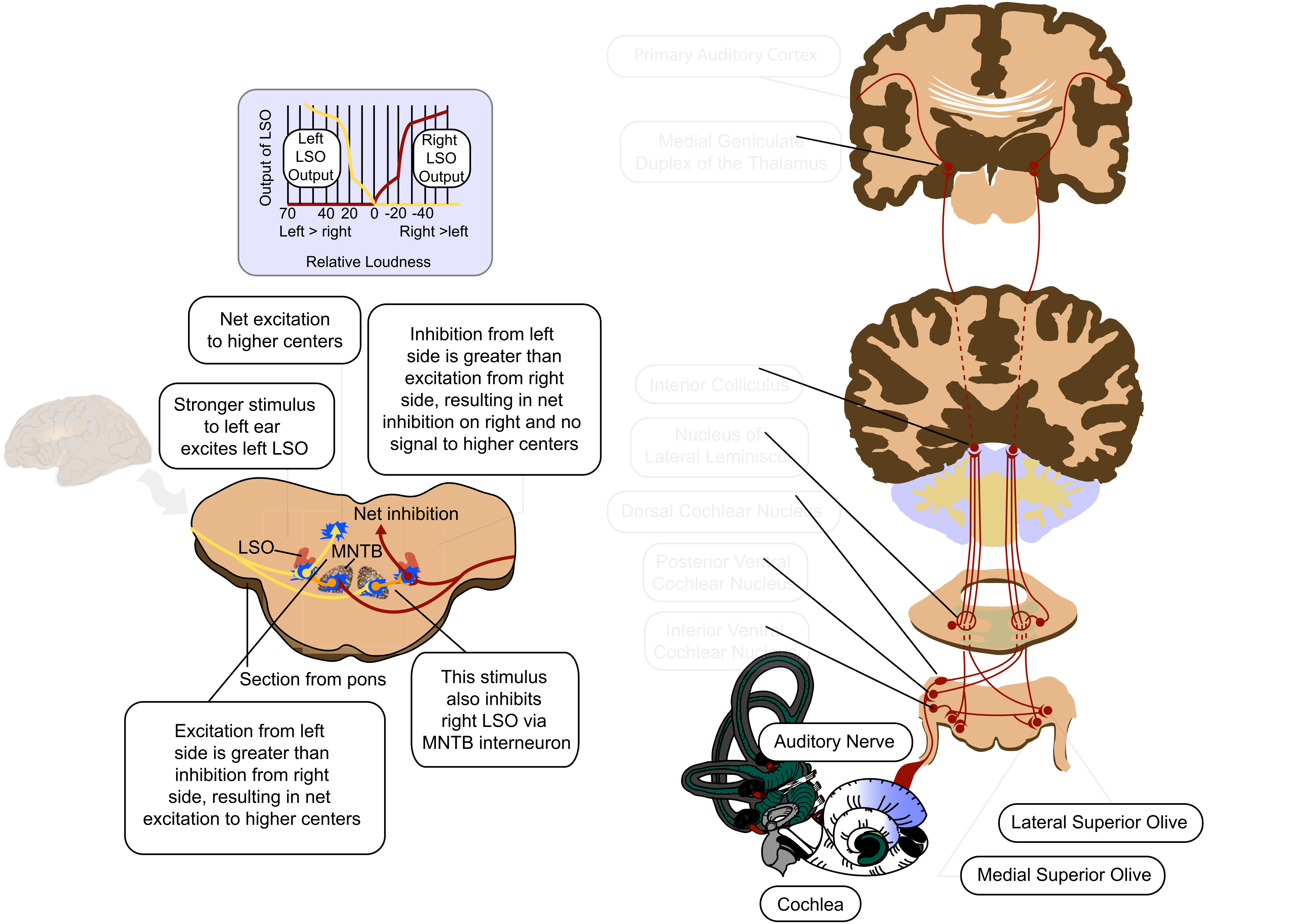
Responses of Two Posterior-Ventral Cochlear Nucleus (PVCN) Sustained Chopper (Chop-S) Units to an Amplitude Modulated Sweep at CF



Auditory central pathways: road map

Please see Irvine D. R. F. *The Auditory Brainstem : A review of the Structure and function of auditory Brainstem Processing Mechanisms*. Berlin, New York: Springer-Verlag, 1986. ISBN: 3540162992.

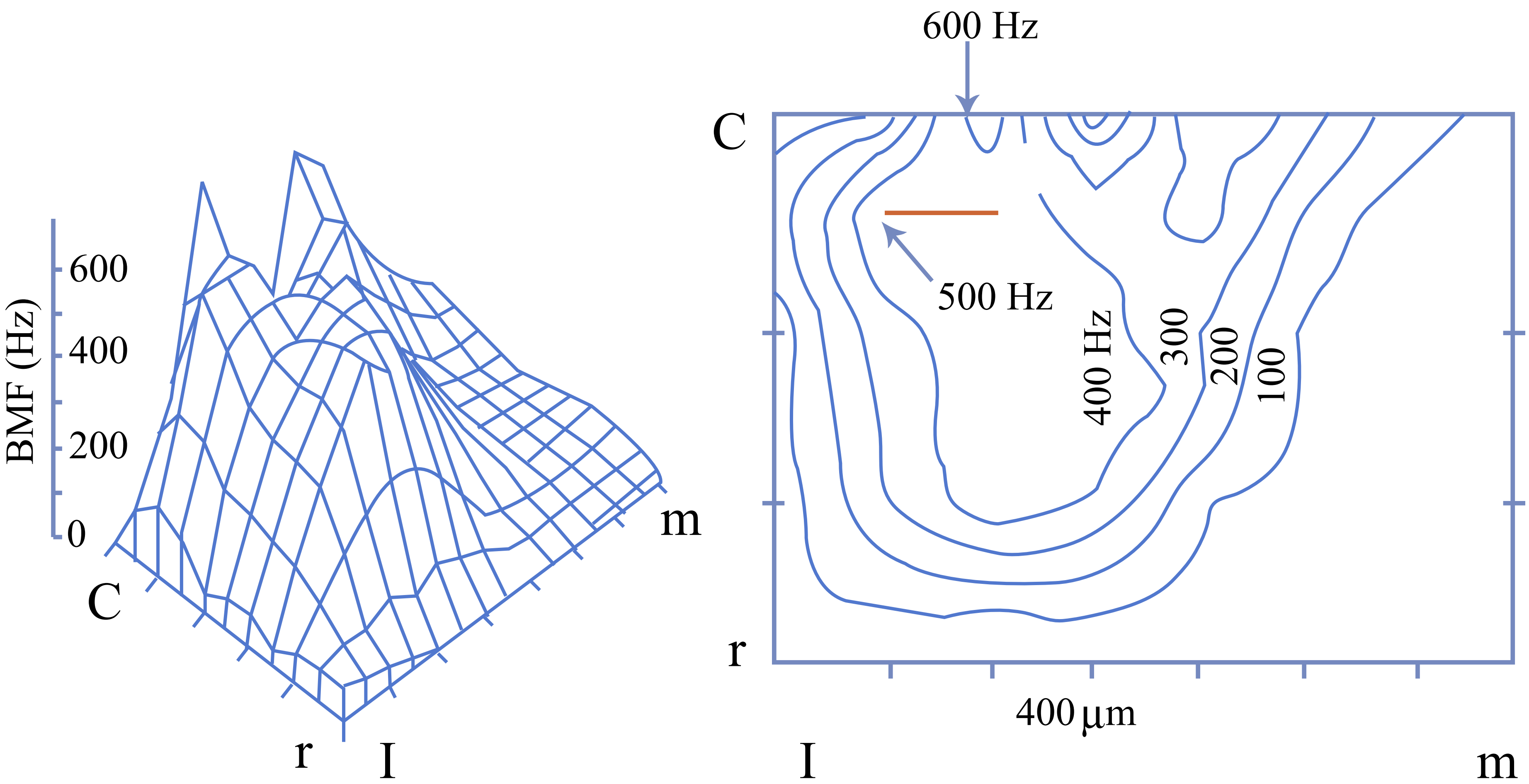
Brainstem stations involved in localization of sounds



Auditory midbrain: inferior colliculus

Please see Morest D. K., D. L. Oliver. The Neuronal Architecture of the Inferior Colliculus in the Cat: Defining the Functional Anatomy of the Auditory Midbrain. *J. Comp Neurol*. 222, no. 2 (Jan 10, 1984): 209-36.

Auditory midbrain: periodotopy?



View on the 3 kHz isofrequency plane of the inferior colliculus of a cat. Best modulation frequencies (BMF of amplitude modulation) are indicated as three-dimensional contour lines (left) and as iso-best modulation lines (right).

Modulation detectors in the midbrain

Problems:

1) MTF tuning degrades at high SPLs & in noise

2) Wrong operation. Modulation tuning does not account for pitches of resolved harmonics of inharmonic tones (pitch-shift exps)

3) Representation will degrade when multiple F0s are present (doesn't support scene analysis)

4) Does not explain pitch equivalence of pure & complex tones

5) Structural. Could be due to ratio of excitation-inhibition rather than for specific function

Sources for auditory CNS figures: Günter Ehret (1997) The auditory midbrain, a “shunting yard” of acoustical information processing. In: The Central Auditory System, Ehret, G. & Romand, R., eds. Oxford University Pres. Langner, G. and Schreiner, C.E. Periodicity coding in the inferior colliculus of the cat. I. Neuronal mechanisms. J. Neurophysiol. 60:1799-1822. See also Langner (1992) review, Periodicity coding in the auditory system. Hearing Research, 60:115-142.