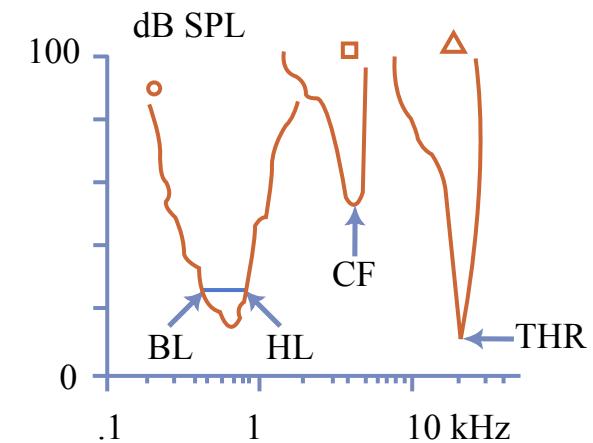


# Tuning properties of auditory nerve fibers

## Rate threshold tuning curves

Tuning Curves



Tone Burst



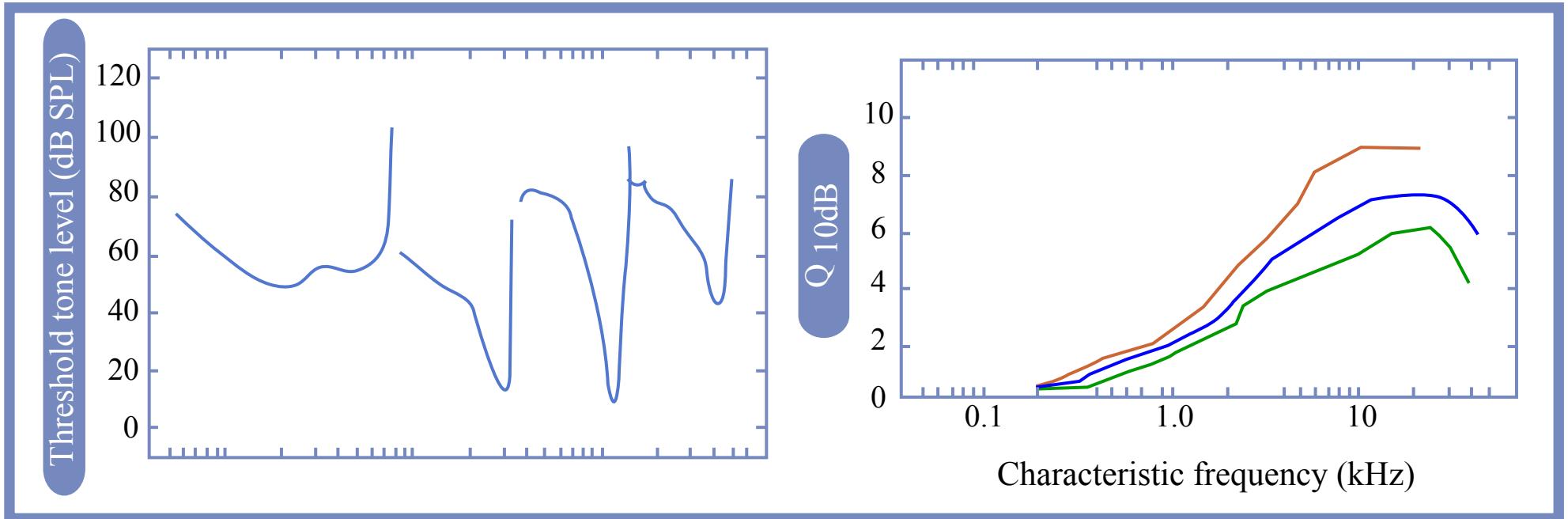
Spontaneous Activity



Continuous Tone



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



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

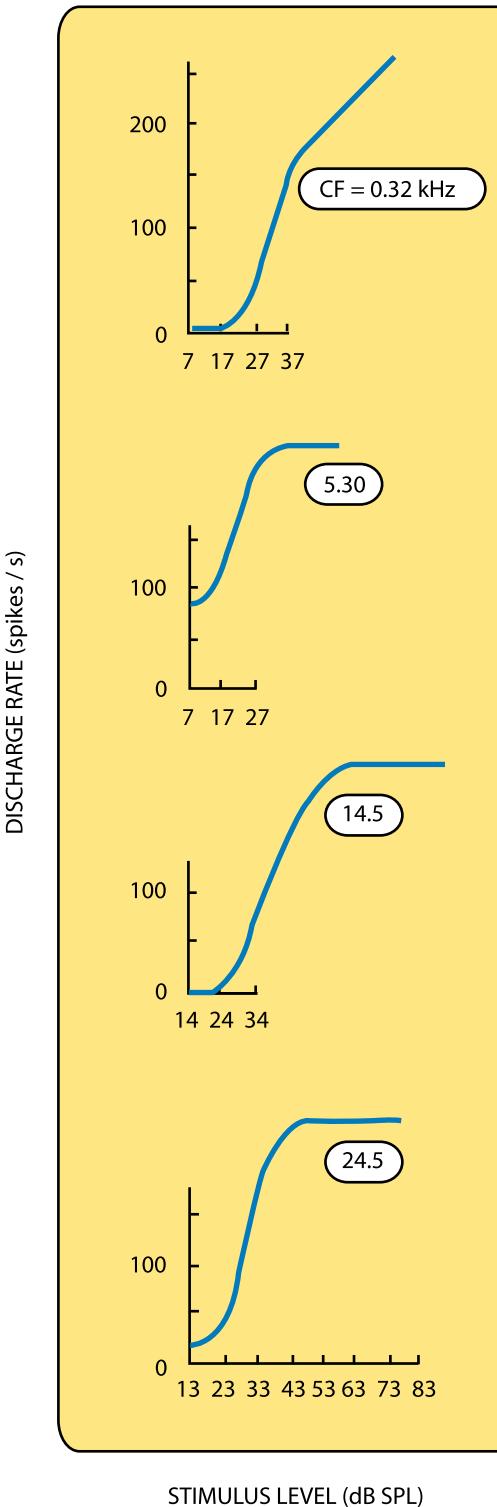
Floor and ceiling effects  
Saturation

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)

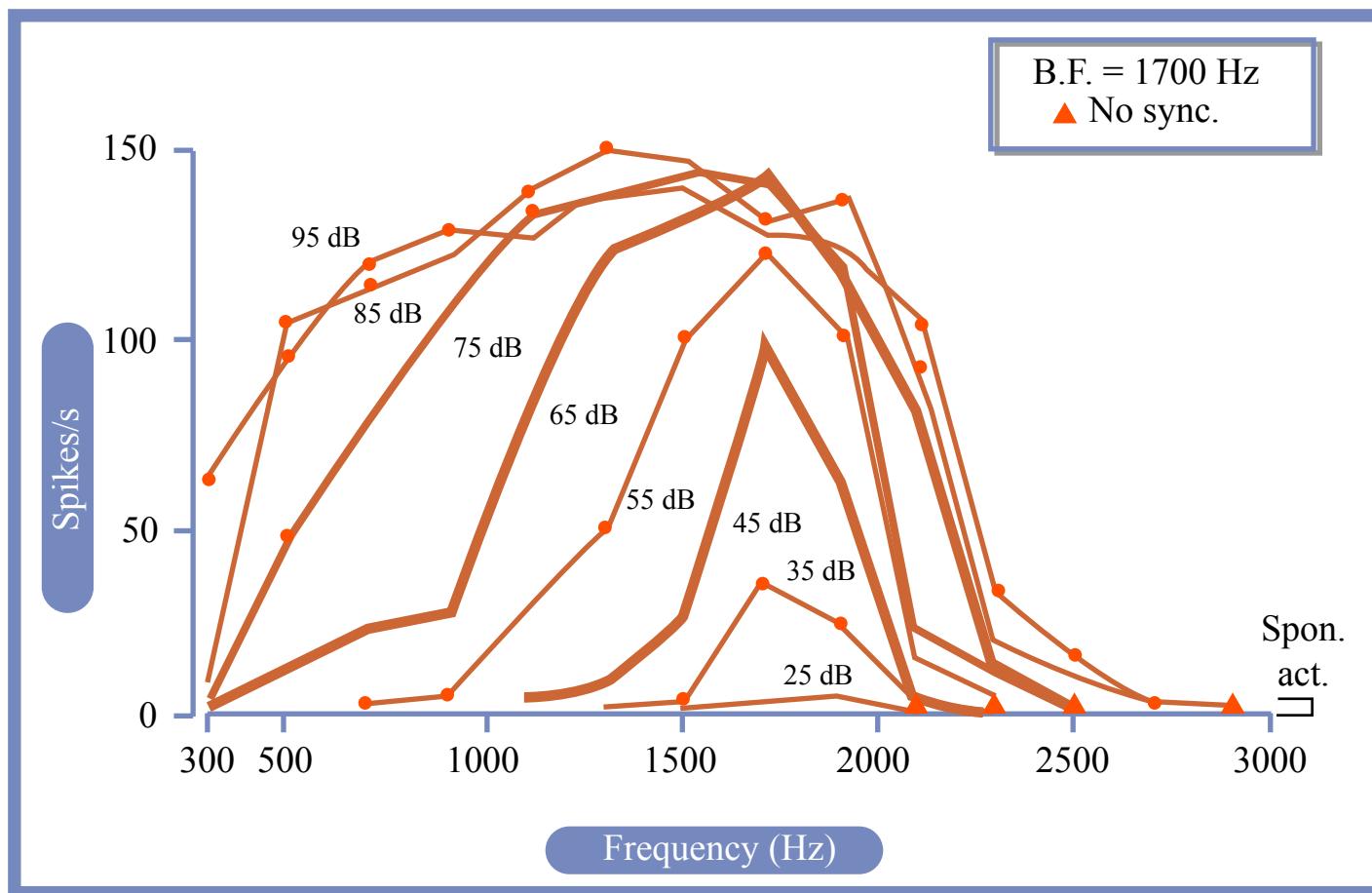


## Responses to tones, keeping SPL constant

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**

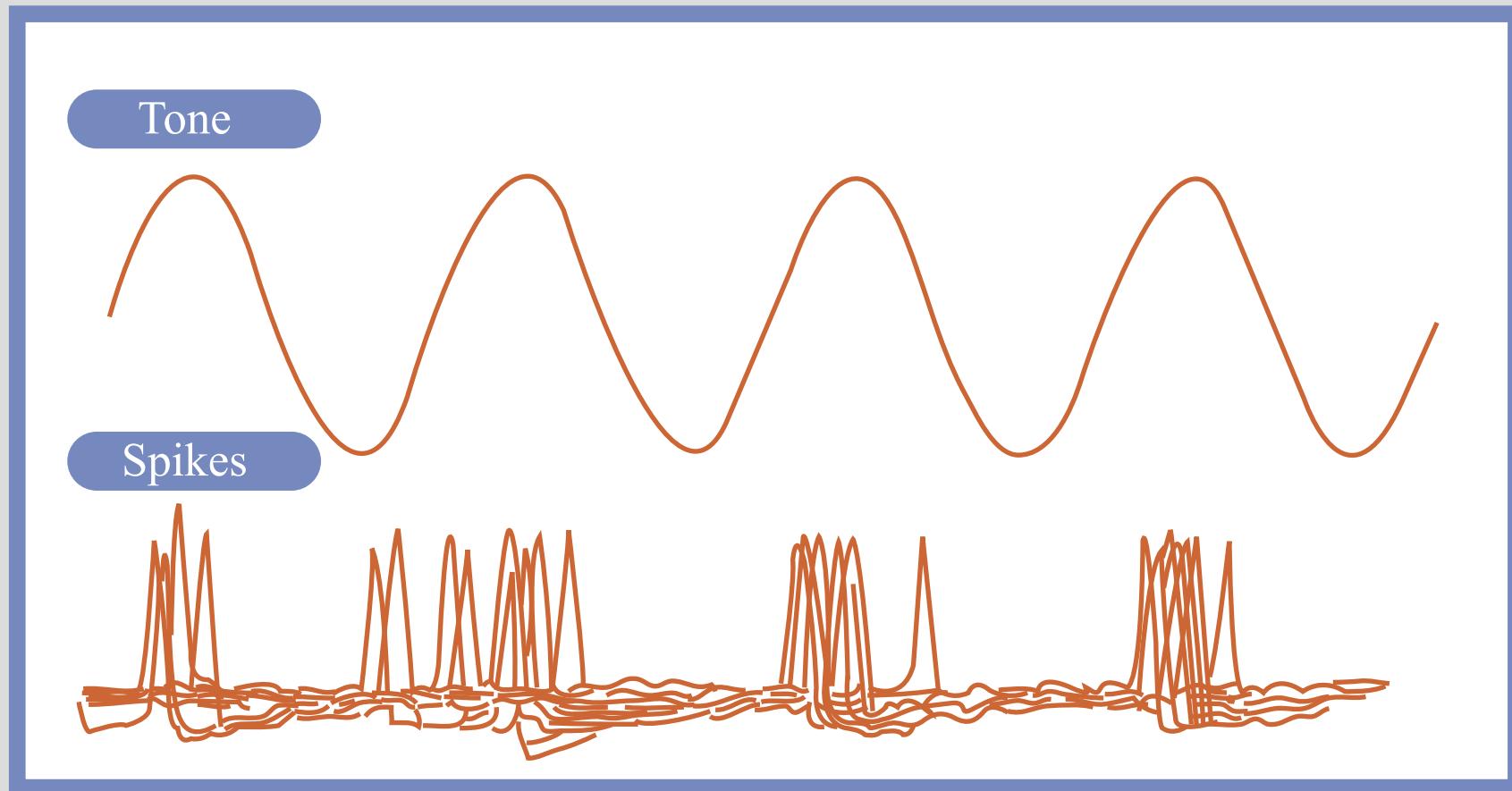
**The temporal microstructure of the tone (not the CF) determines the temporal patterning of response for frequencies below 4-5 kHz  
(This limit is somewhat species dependent)**

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

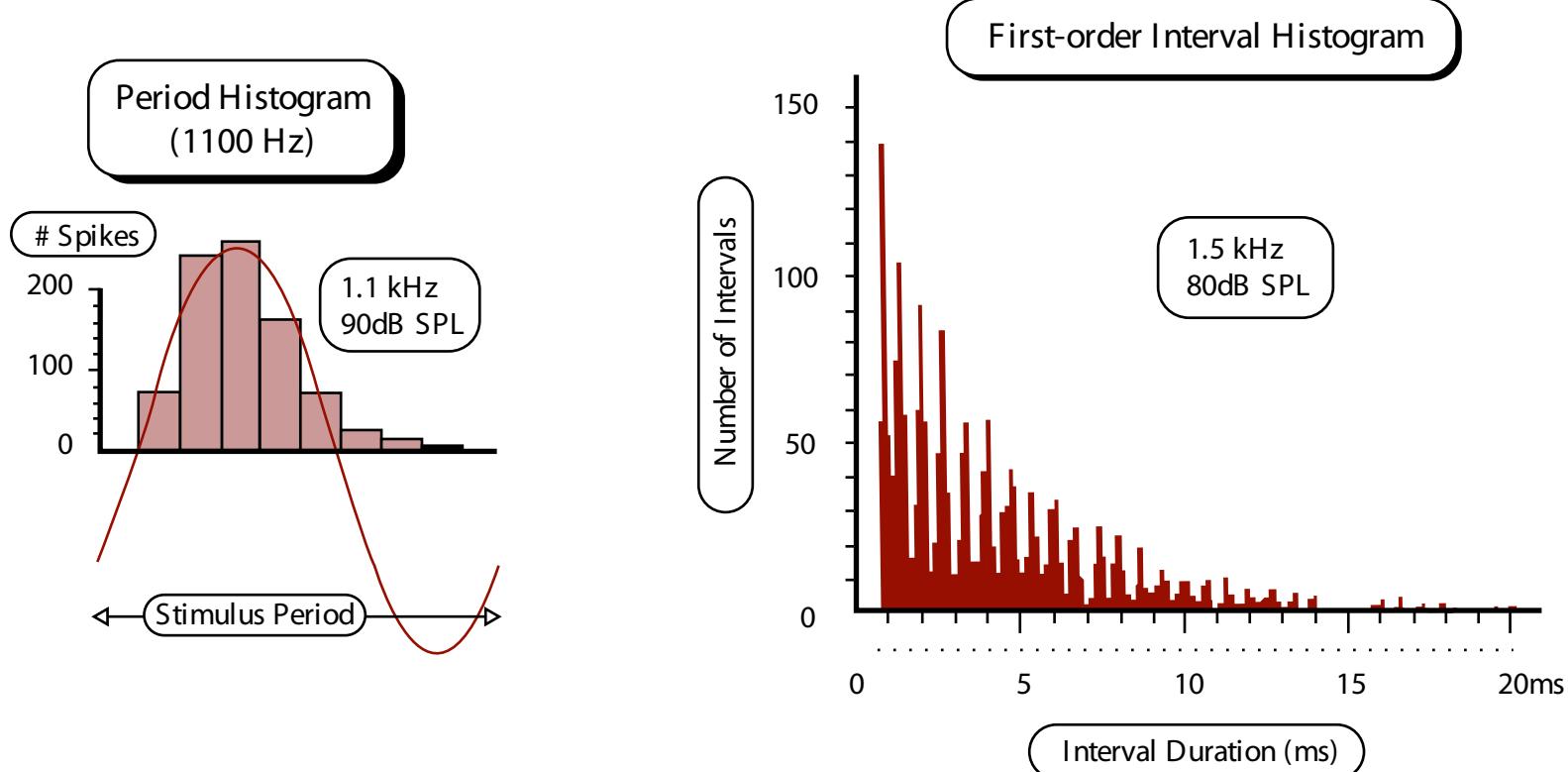
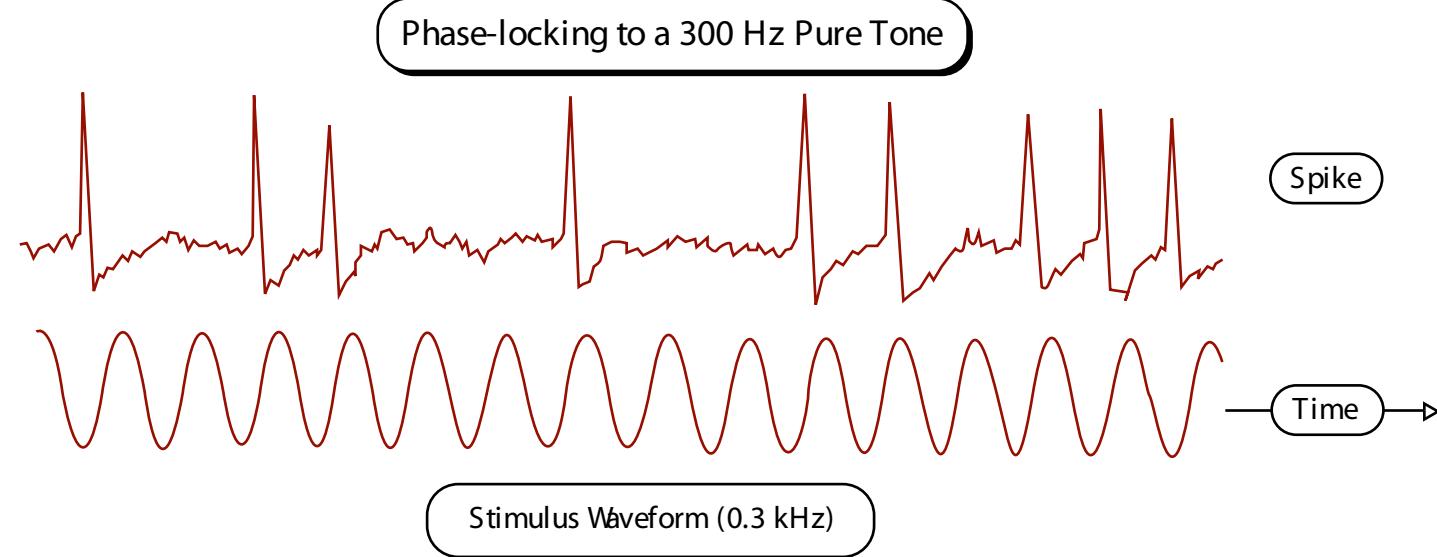
Please see Irvine, D. R. F. *The Auditory Brainstem : A Review of the Structure and Function of Auditory Brainstem Processing Mechanisms*. Berlin, New York : Springer-Verlag, 1986. ISBN : 3540162992.

**Rate-adaptation at onsets of sounds**

# 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)

Low CFs

0.14

0.35

0.44

0.58

0.70

1.00

1.20

1.48

1.67

1.80

2.08

2.32

2.55

2.95

3.64

4.12

7.52

F1

F2

F3

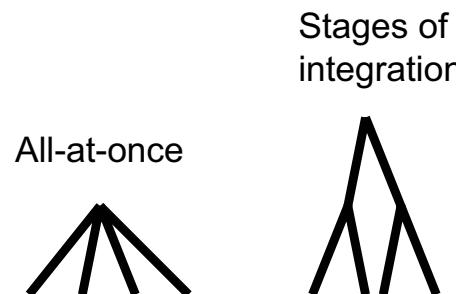
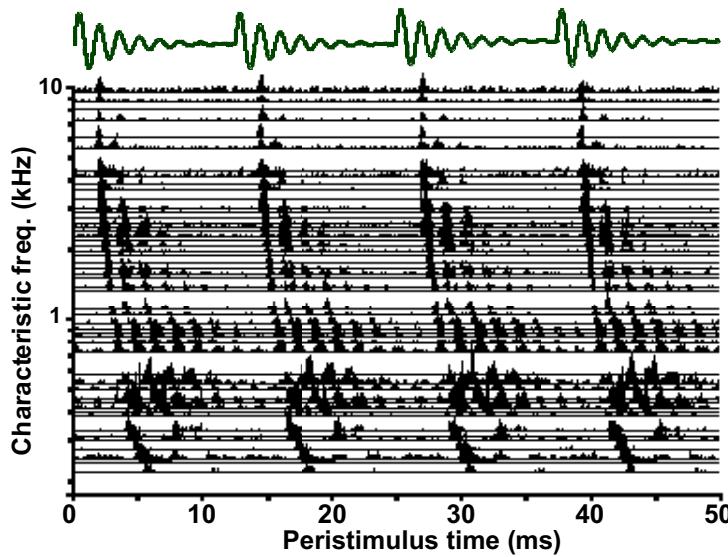
10

Peristimulus time (ms)

30

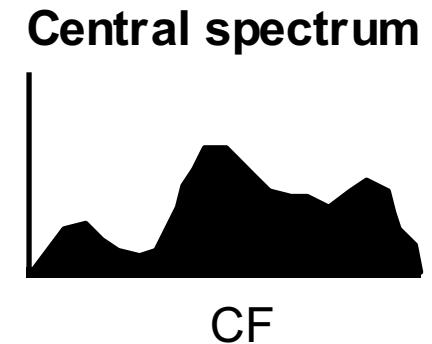
High CFs

# Some possible auditory representations



Local  
Rate-place →

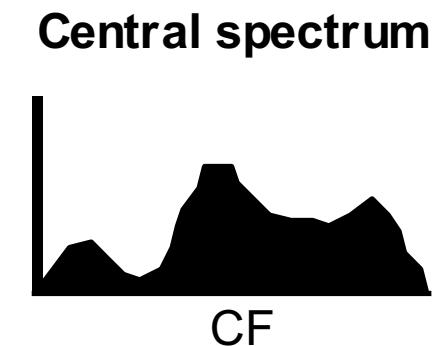
Masking phenomena  
Loudness



Synchrony-place

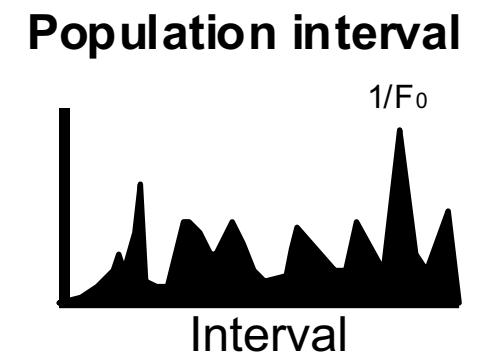
Interval-place

Pure tone pitch JNDs



Population-interval →  
Complex tone pitch

Global



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.

## 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)**

500k

**Auditory thalamus**

**Inferior colliculus  
(Auditory midbrain)**

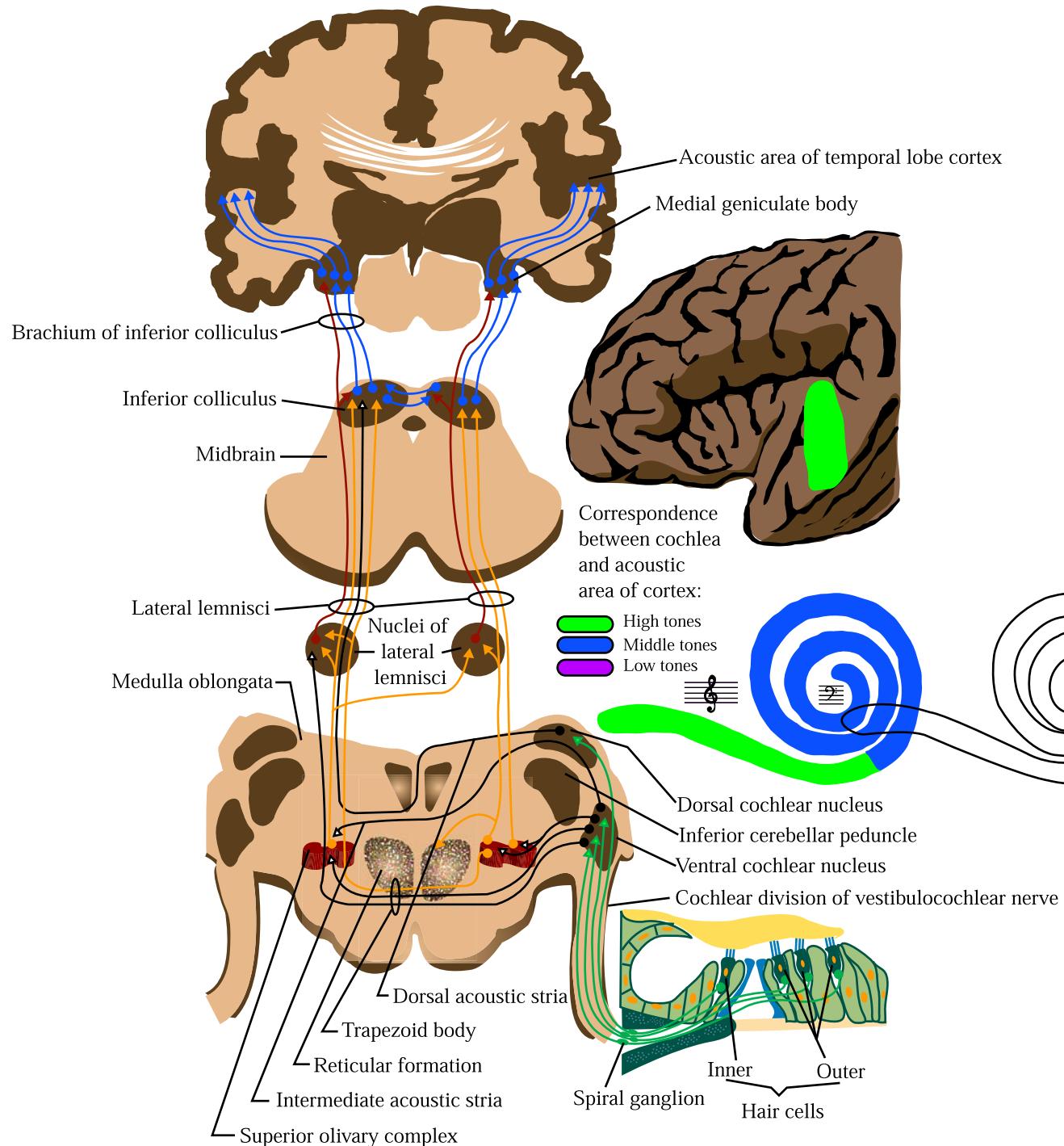
30k

**Auditory brainstem**

3k

**Cochlea**

## Afferent Auditory Pathways



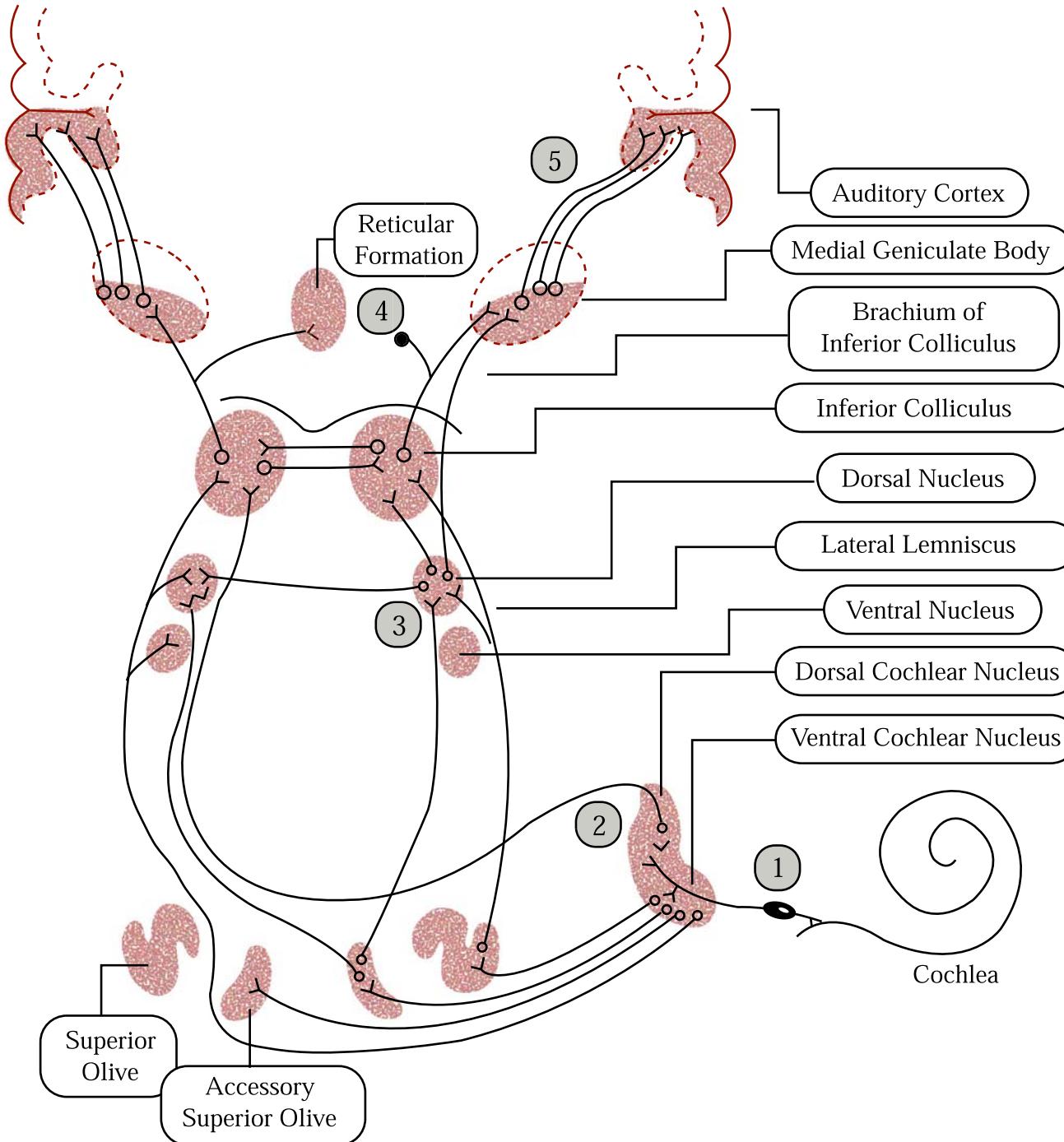
# Basic problems to be solved

- "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-monotonicities).
- 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; % nonmonotonic 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**

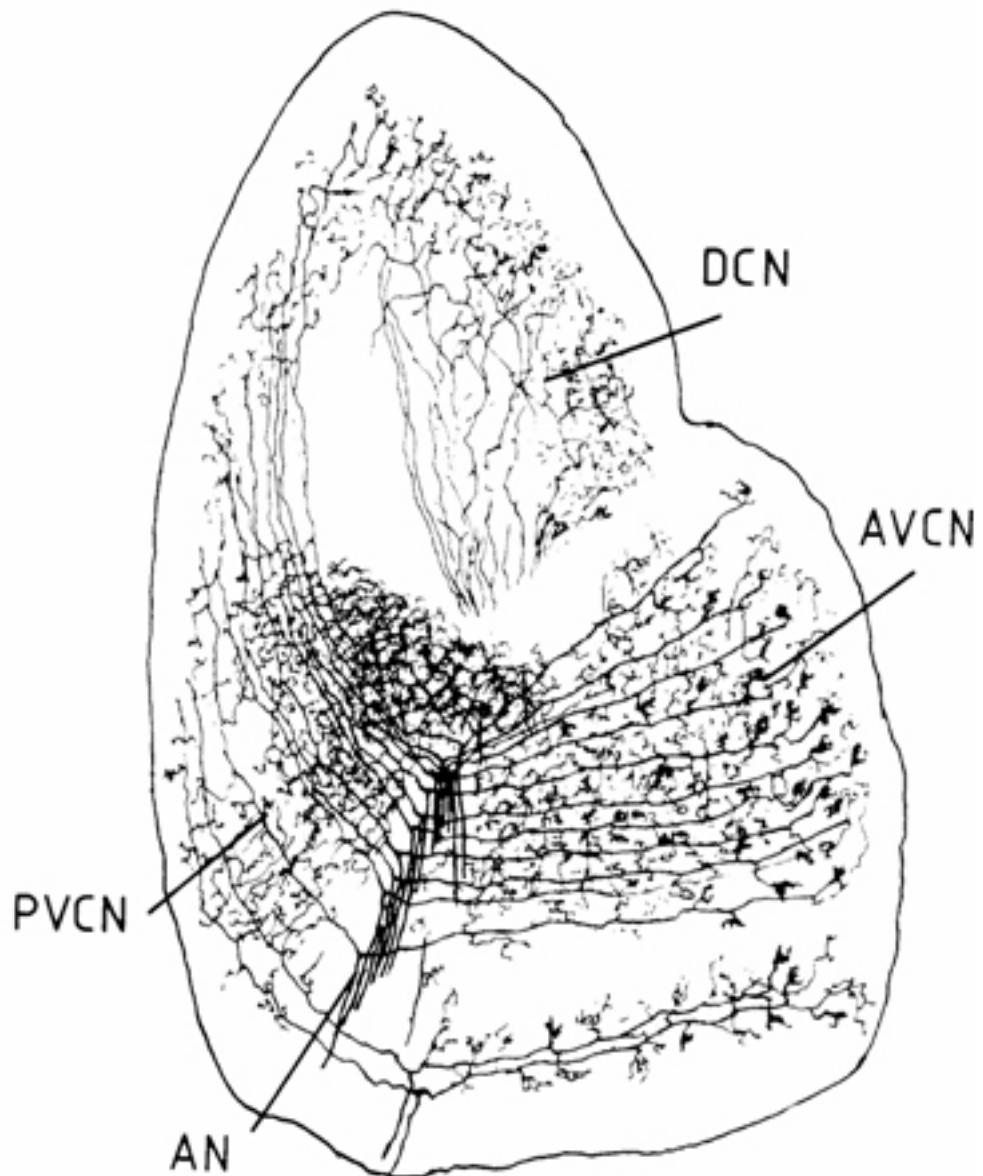


FIG. 2. Parasagittal section through cochlear nucleus of 4-day-old cat stained by Golgi method. Auditory nerve fibers, AN, bifurcate to yield ascending branch to AVCN and descending branch to PVCN and DCN. Ascending branch terminates in AVCN with large end bulbs of Held. [From Lorente de Nò (279).]

## 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)

680

HANDBOOK OF PHYSIOLOGY - THE NERVOUS SYSTEM III

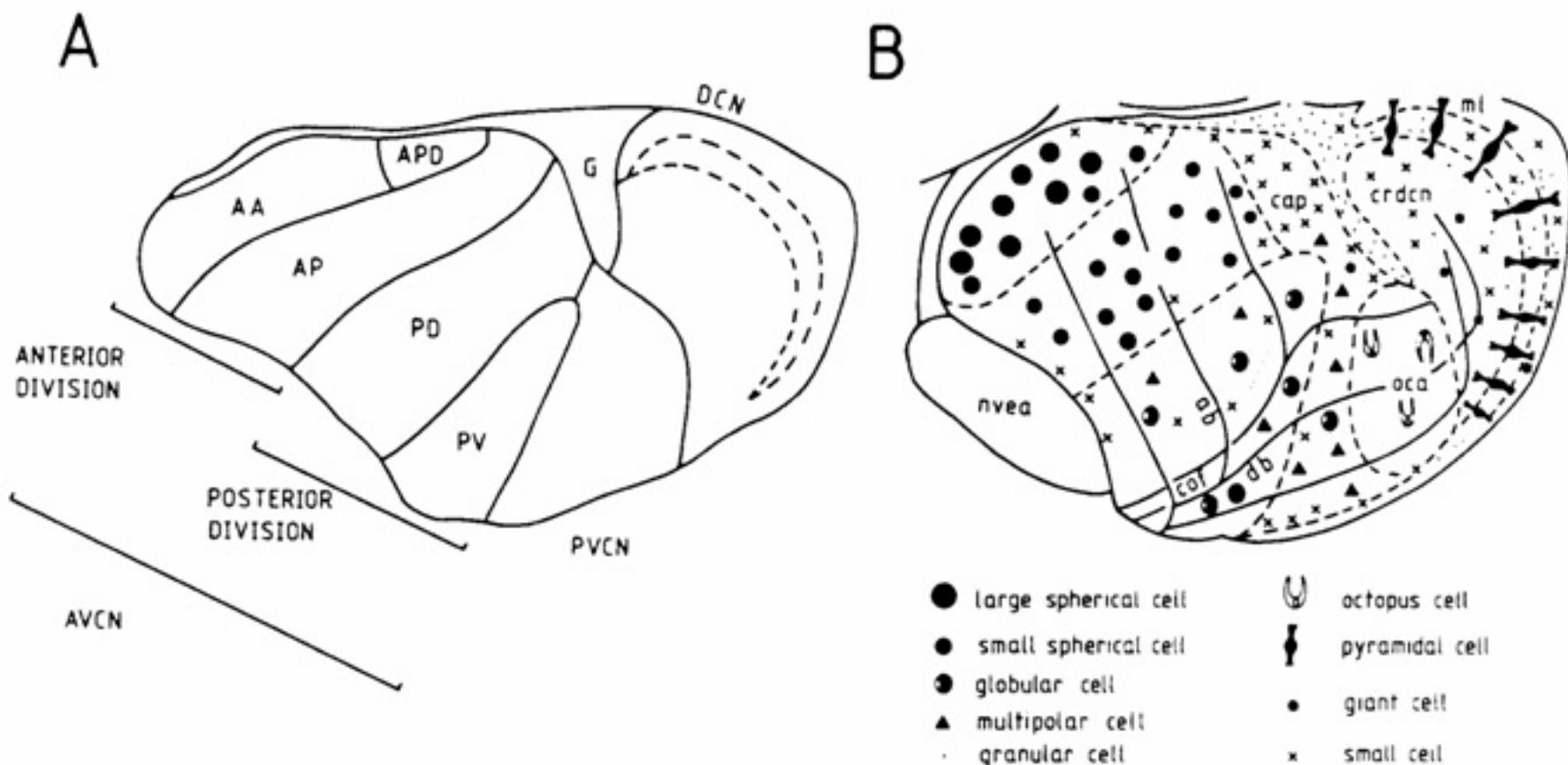


FIG. 4. Schematic drawings of sagittal sections comparing A: divisions of cochlear nucleus identified by Brewer et al. (59), and B: divisions of cochlear nucleus of Osen (343). In A: AVCN, anterior ventral cochlear nucleus, which is divided into anterior division comprising AA, anterior; AP, posterior; 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)**

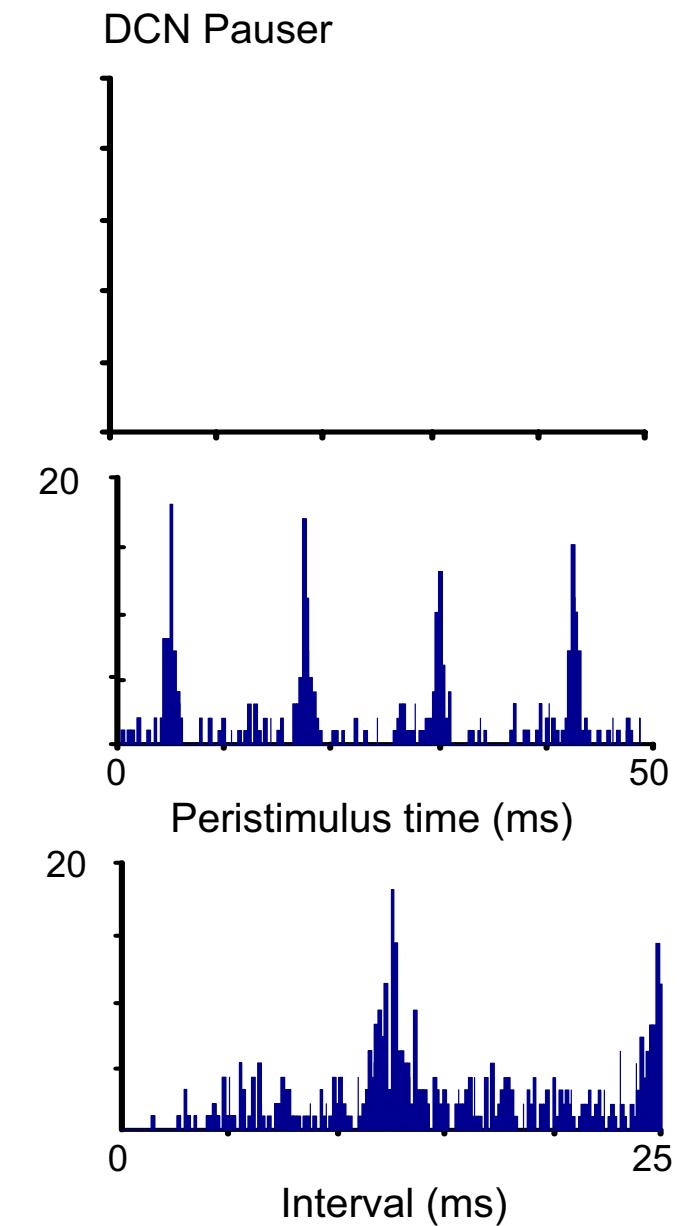
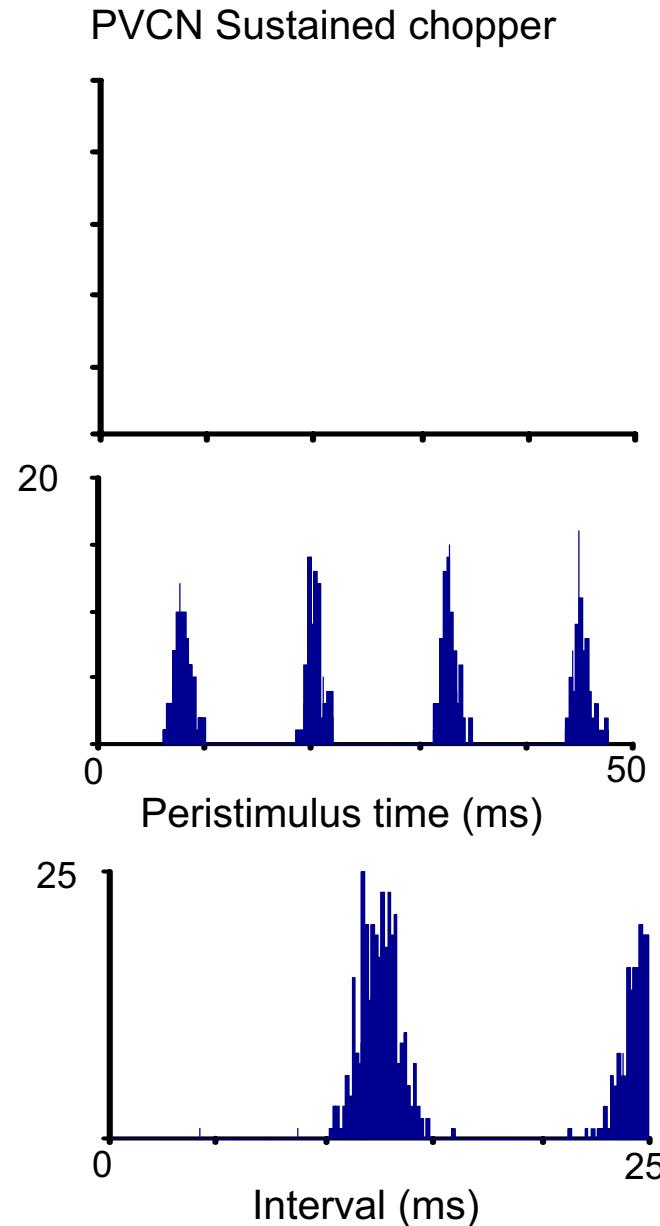
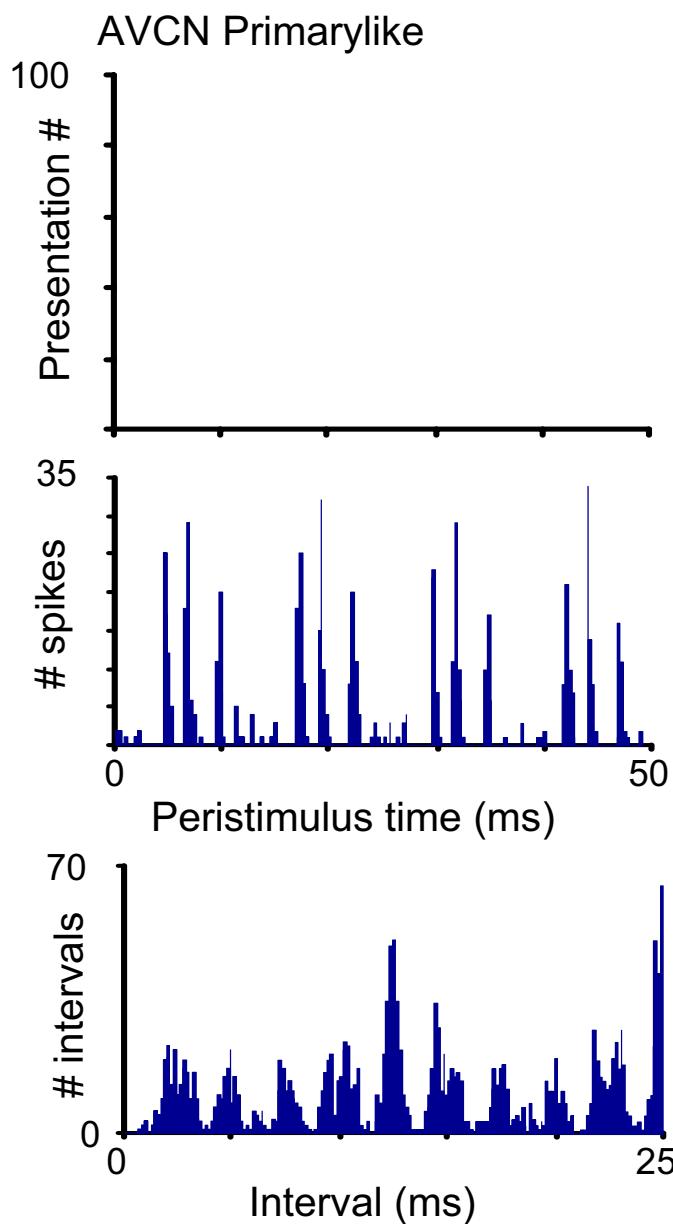
**Onset (PVCN)**

**Most are linked to a particular  
neuronal morphological type**

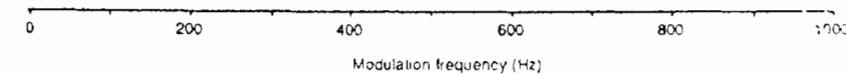
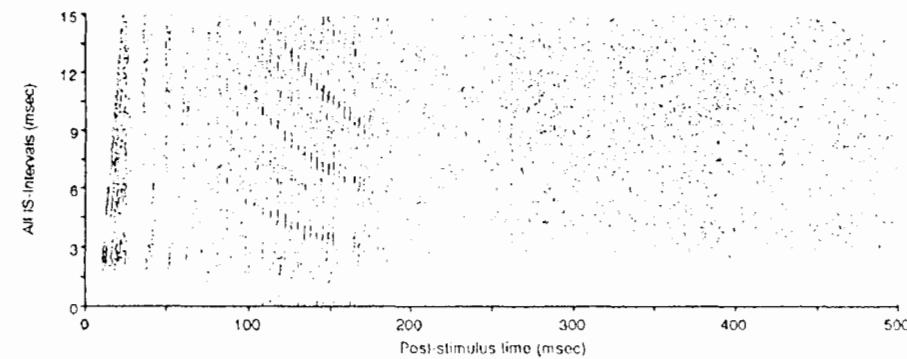
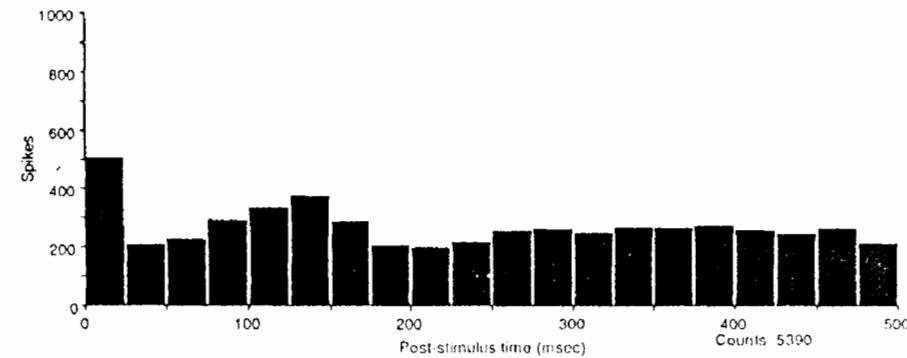
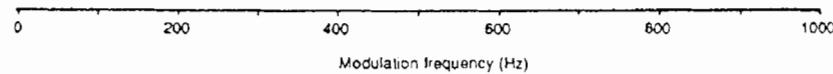
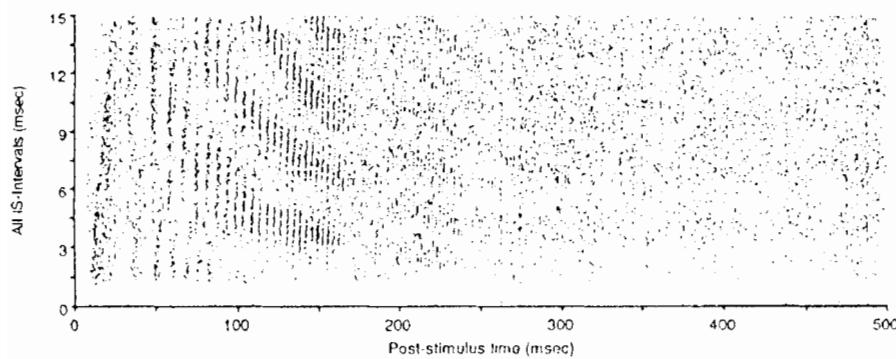
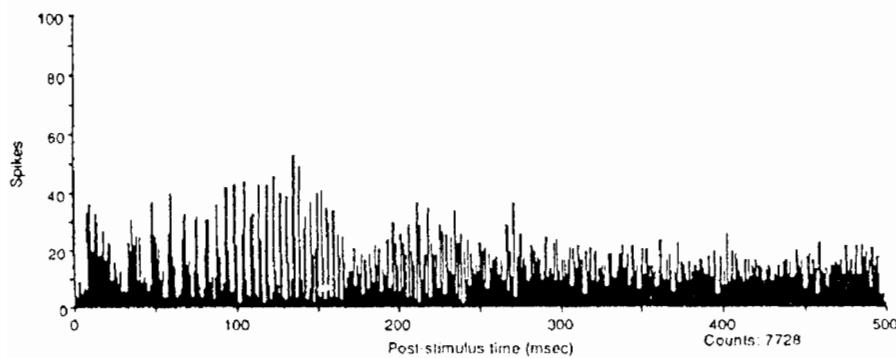
**(-) indicate main regions  
where responses are seen**

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



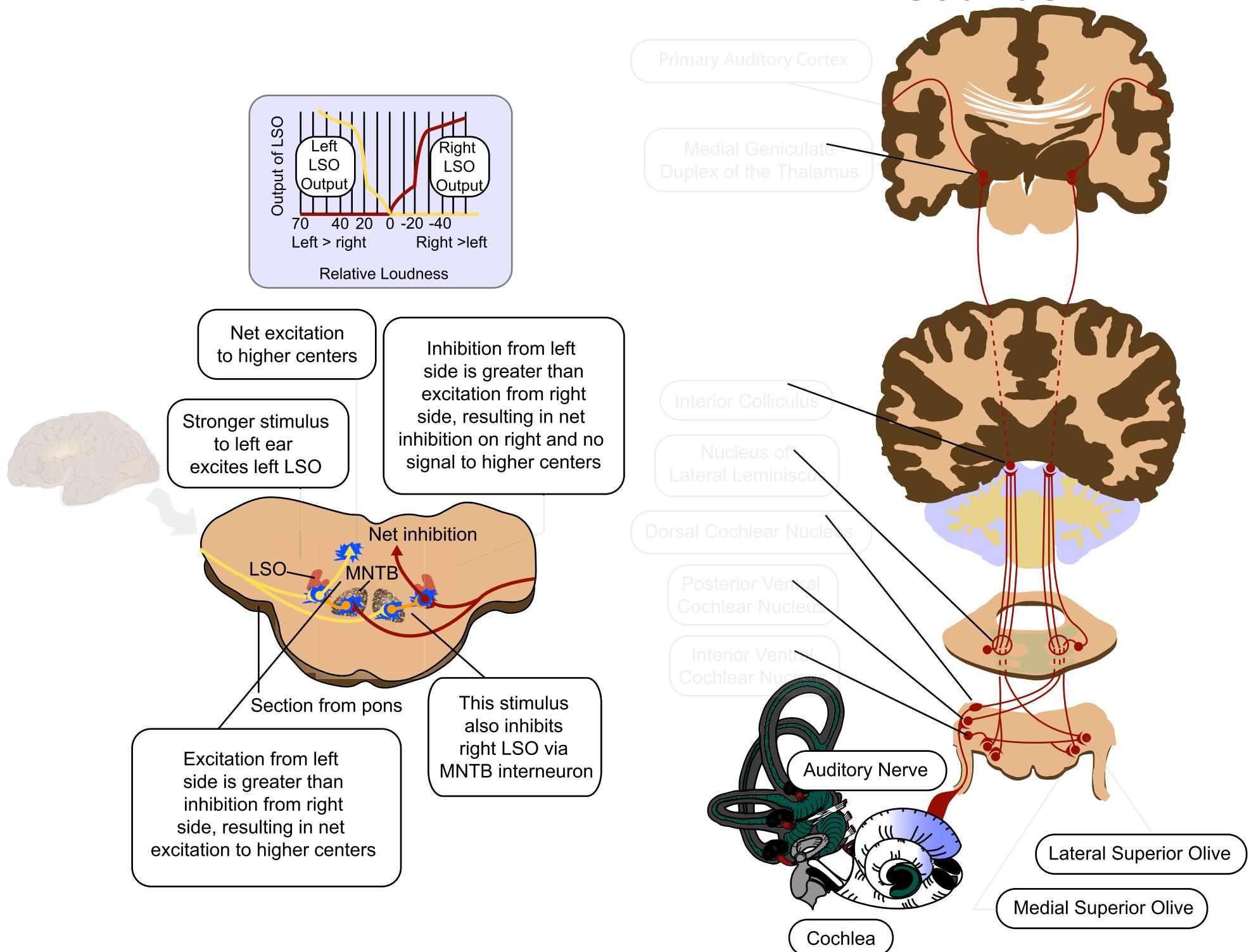
**Responses of Two Posterior-Ventral Cochlear Nucleus (PVCN) Sustained Chopper (Chop-S) Units to an Amplitude Modulated Sweep at CF**



# 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.

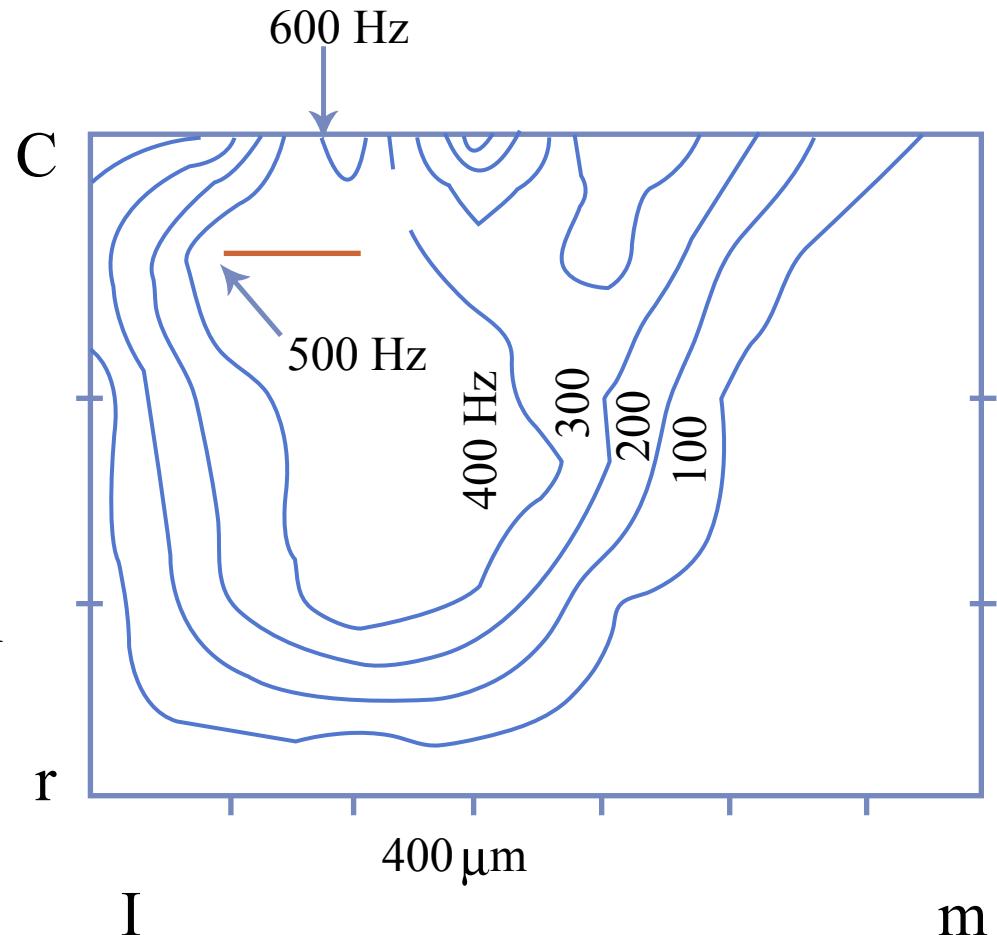
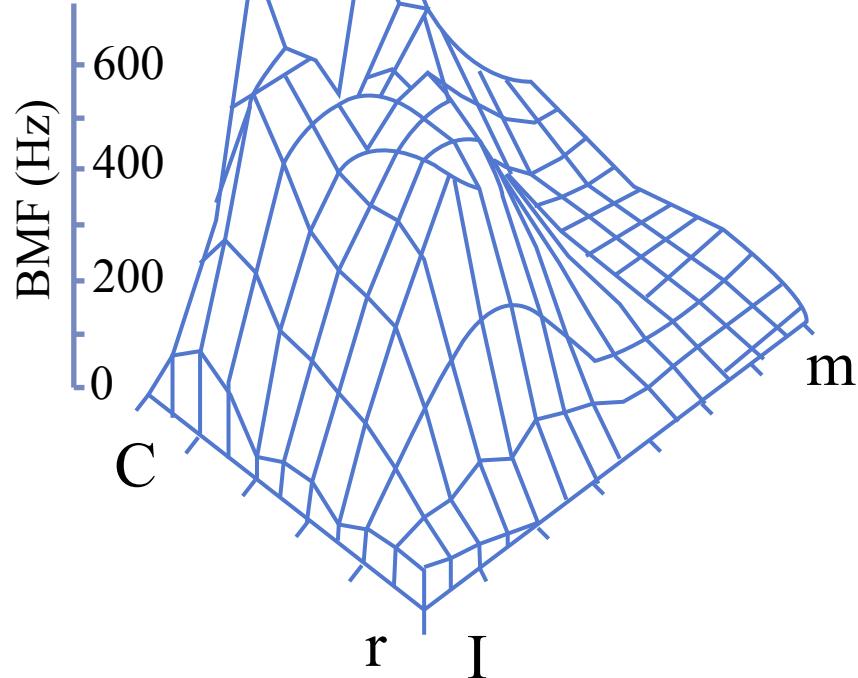
# Brainstem stations involved in localization of sounds



## 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.