

Auditory system



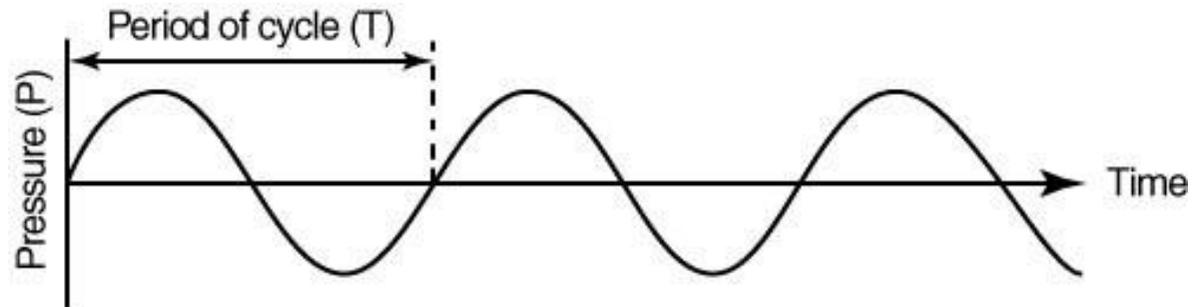
Nachum Ulanovsky

Systems Neuroscience course – 10/12/2018

The auditory system in numbers

- Frequency range:
 - ~ 20 Hz – 16 kHz (humans)
 - ~ 5 kHz – 100 kHz (small mammals: mouse, echolocating bats)
 - Frequency resolution (humans): 0.5 %
 - Temporal resolution:
 - 10 μ s (interaural time difference in humans)
 - < 400 ns (range resolution in bats)
 - Dynamic range (humans): 120 dB – from 0 dB SPL (20 μ Pa) to 120 dB SPL
 - Number of peripheral receptors in the human cochlea: 3,500 inner hair cells (very small number compared to the ~ 1 million photoreceptors in the retina)
- Good frequency resolution *and* good temporal resolution \rightarrow the auditory system is *not* a simple Fourier analyzer

Properties of sound: Power ; Frequency (1/Period)



$$f = 1/T$$

f: Frequency in Hz

T: Period in seconds

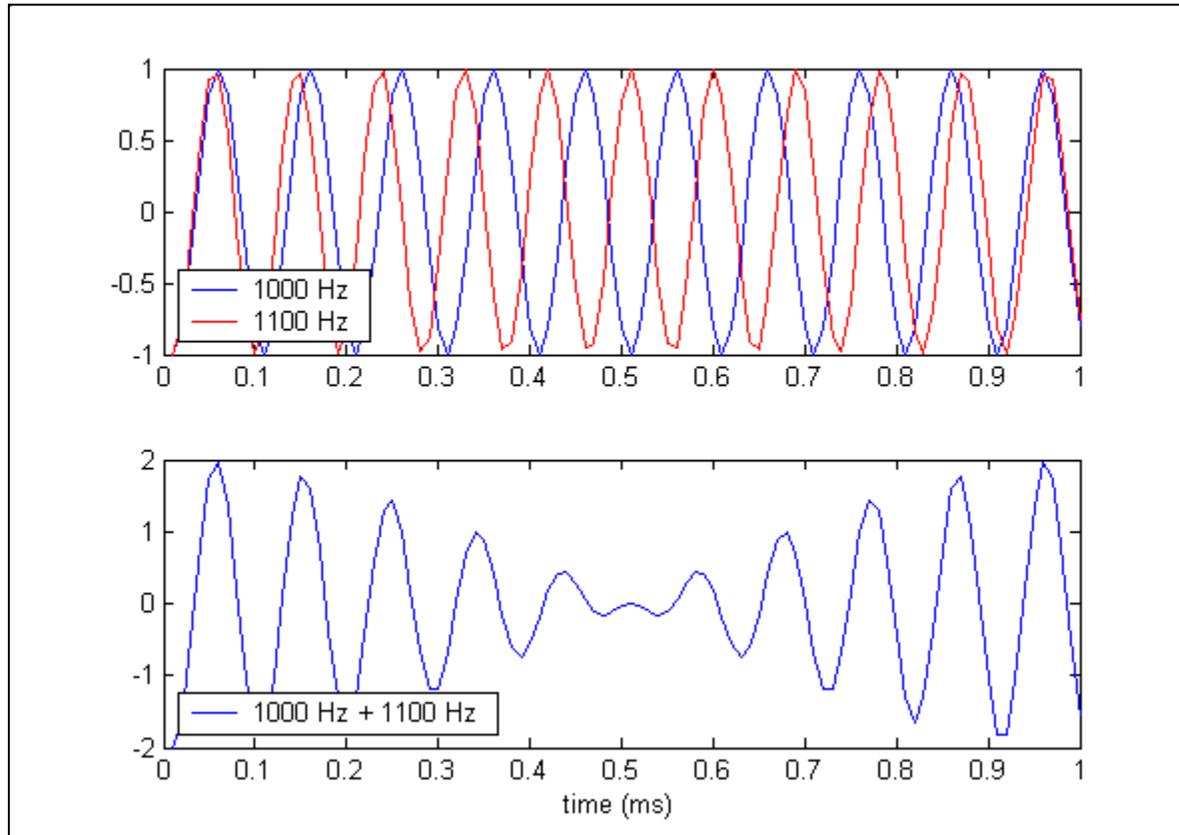
$$\text{SPL} = 20 \log(P/P_{\text{ref}})$$

SPL : Sound pressure level

P : Pressure in μPa

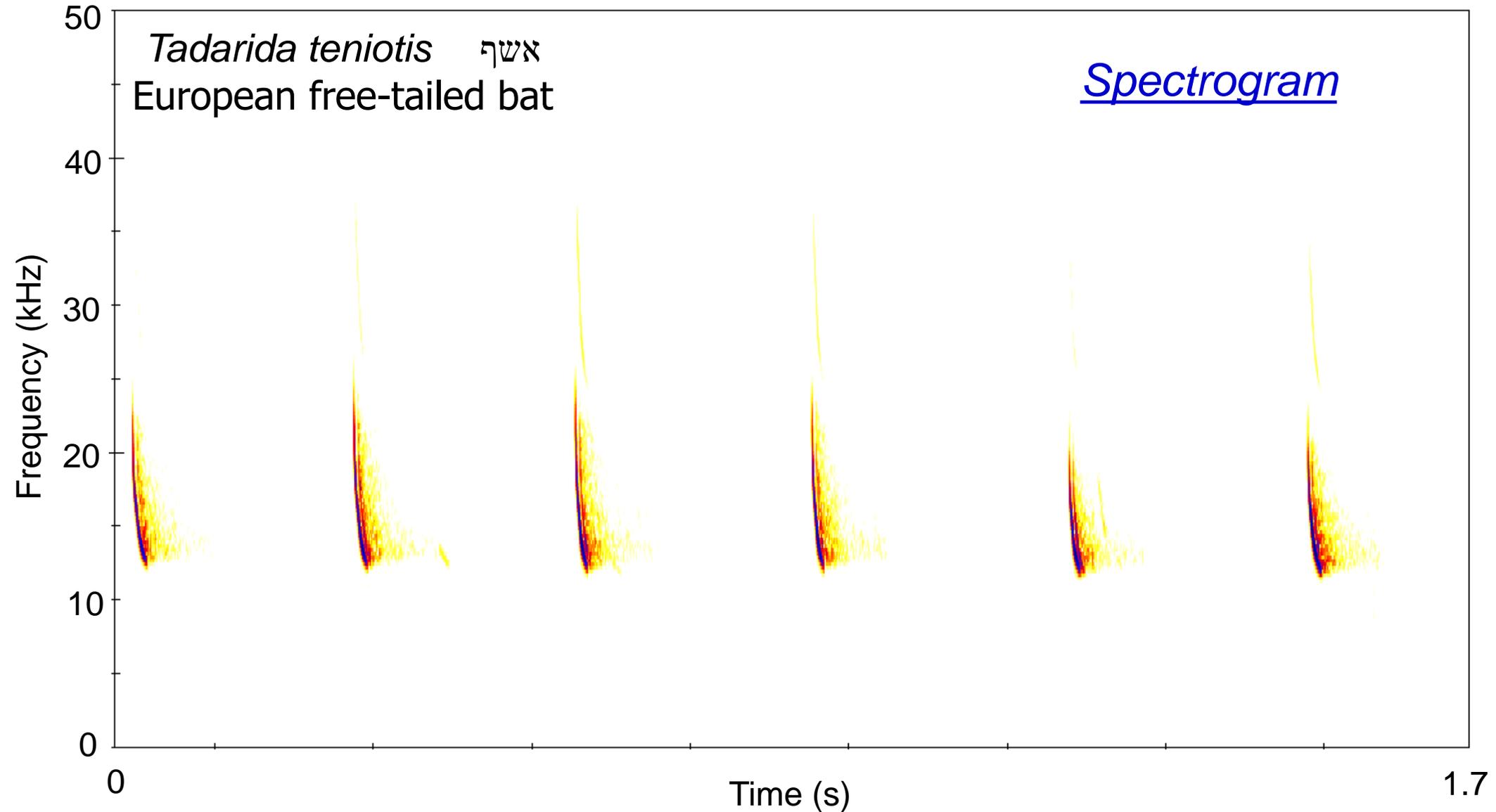
P_{ref} : 20 μPa

Properties of sound: Phase ; Amplitude modulation (AM)

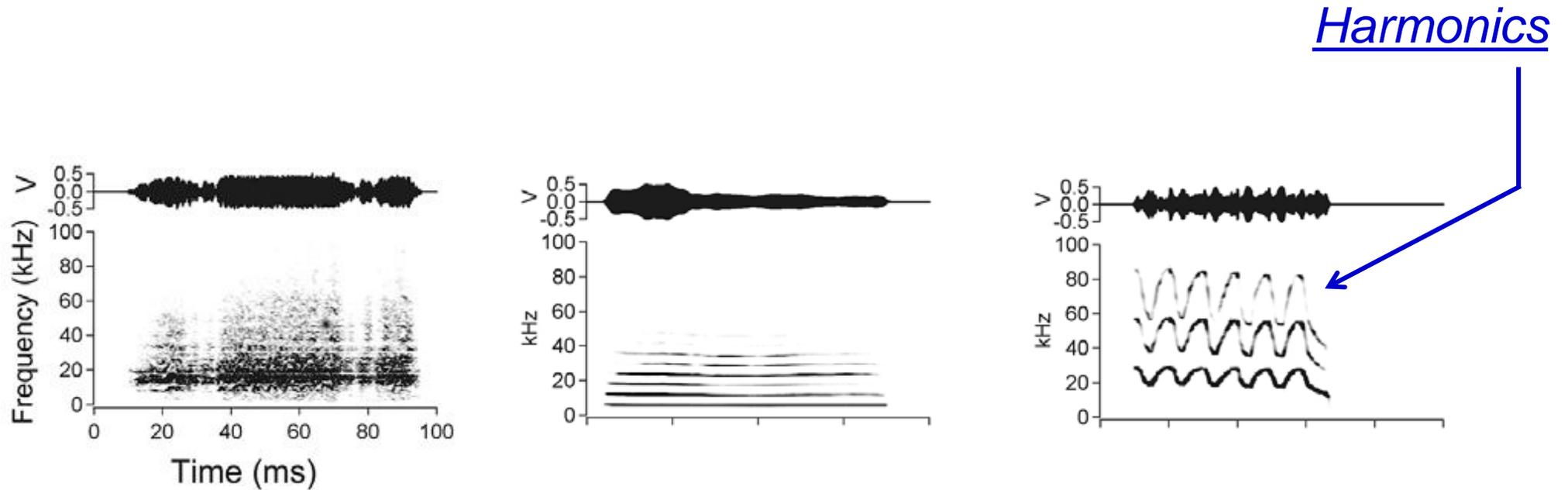


Amplitude modulation can arise from the “beats” of pure tones that are going in and out of phase with each other

Properties of sound: Frequency modulation (FM)



Properties of sound: Spectrograms of complex sounds



Examples of mustached bat communication calls (Kanwal & Rauschecker 2007)

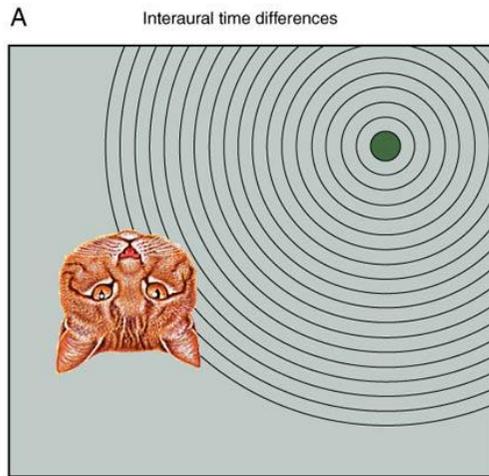
What information does the auditory system extract from sounds?

- What *(lion roar)*
- Where *(a lion roared on the left – and nearby. Oh my god !)*
- Details *(Ah, I am a lion expert, so I can tell this lion is not hungry)*

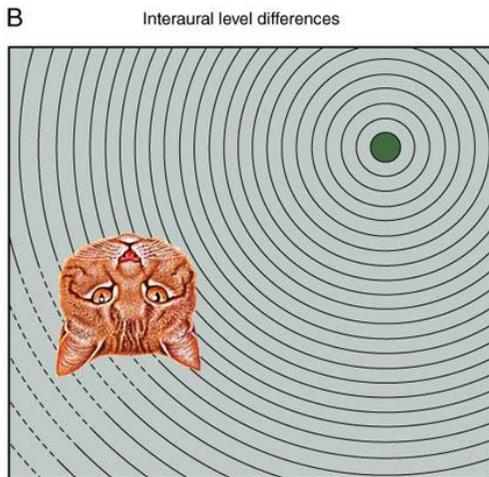
Let's start with WHERE – Auditory localization – the best understood auditory function.

** Note that the sound location has to be computed – since it is not encoded in the peripheral receptors (unlike in the somatosensory or visual systems). Thus, a map of auditory space is a computational map.*

Auditory localization: What cues are available to the animal ?



Interaural Time Difference (ITD)

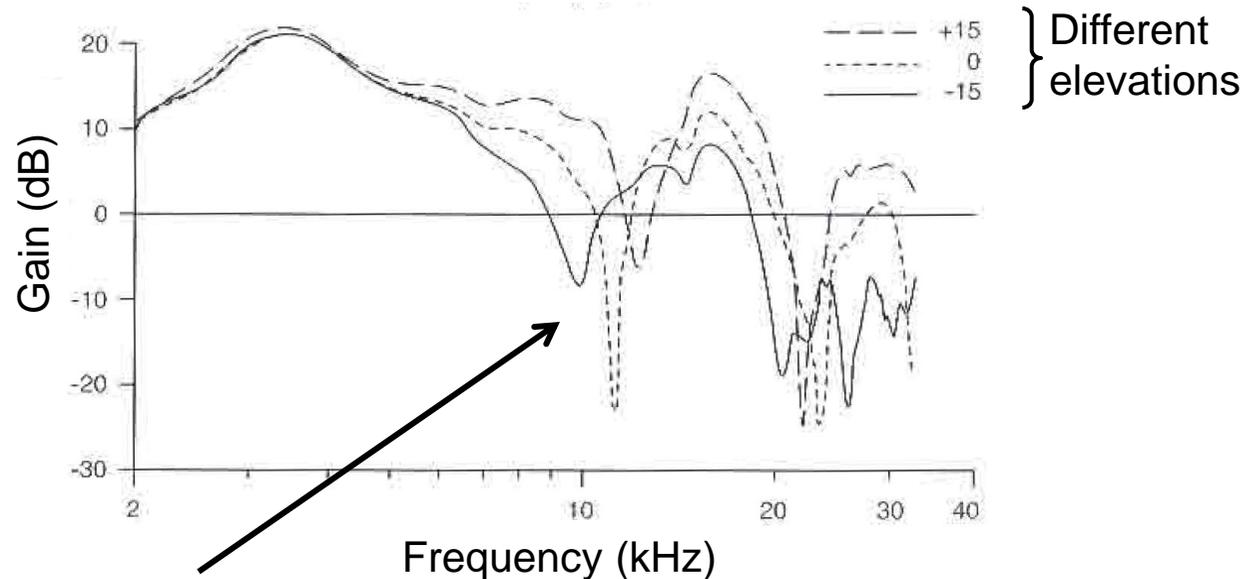


Interaural Level Difference (ILD)

ITD and ILD provide information about the azimuth of the sound, but not its elevation (“cone of confusion”) – unless the two ears are asymmetric in elevation, as in the barn owl.

Auditory localization: What cues are available to the animal ?

Filtering properties of the ears and head – “Head Related Transfer Function” (HRTF) – Provide information about sound-source elevation



Note the prominent spectral notch whose frequency shifts systematically with elevation

Sound localization in elevation + general power gain: This is what pinnae do for animals.



Auditory localization: Neural processing of spectral notches

Neurons sensitive to notches are found in several subcortical stations in the ascending auditory pathway – most notably in the cochlear nucleus. These neurons are sensitive to notches at differing frequencies, so they may encode the elevation of the sound source (HRTF spectral cues).

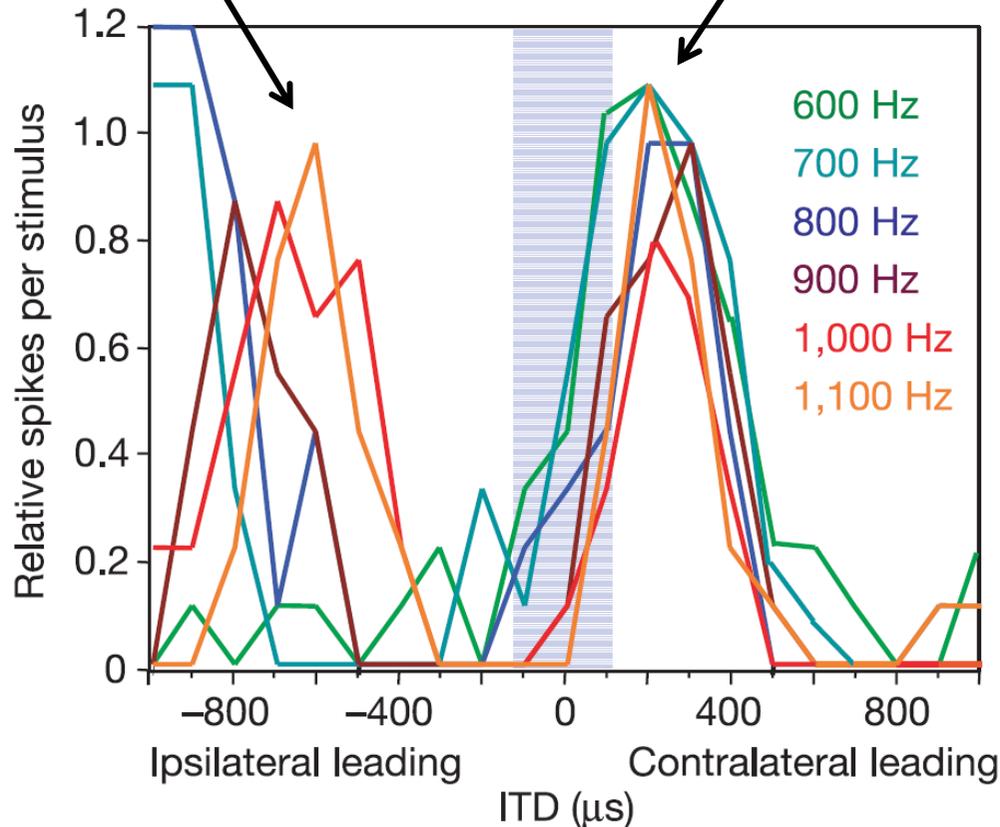
Auditory localization: Neural processing of ITD

ITD-tuned neurons are found in the medial superior olive (MSO).

Secondary peak due to the cyclicity (ambiguity) of the tone's sine wave

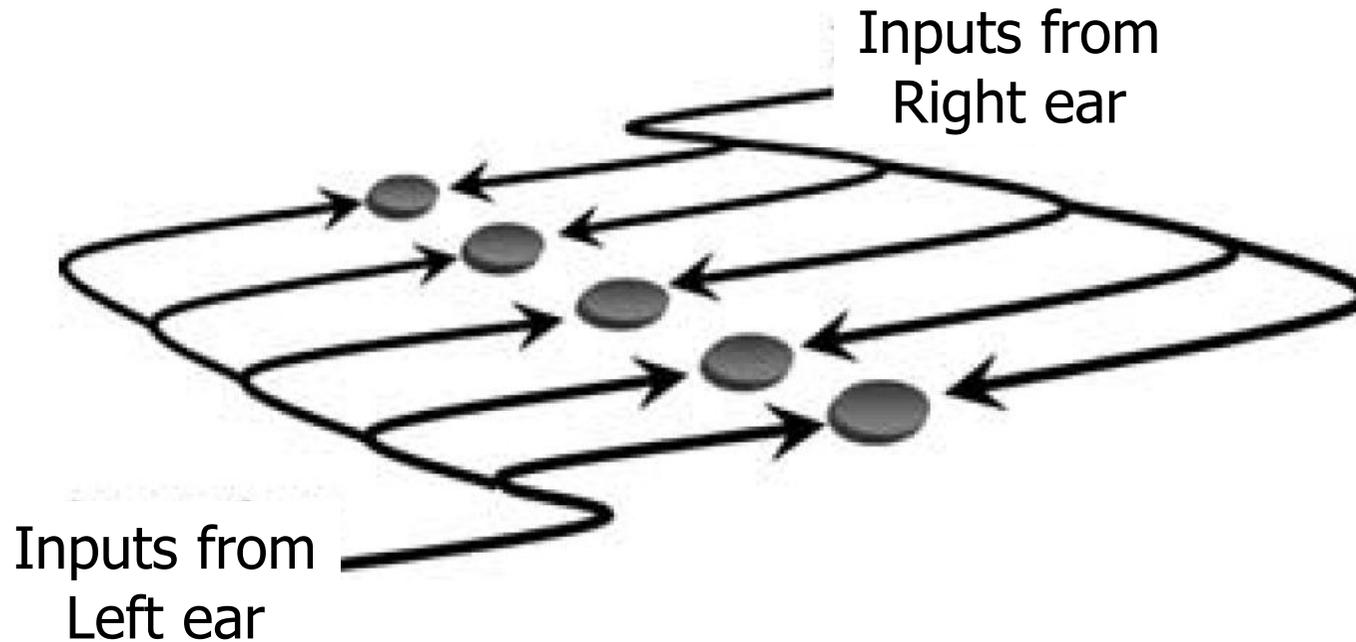
The "Best ITD" is independent of frequency

ITD tuning curve from a single MSO neuron of a gerbil:



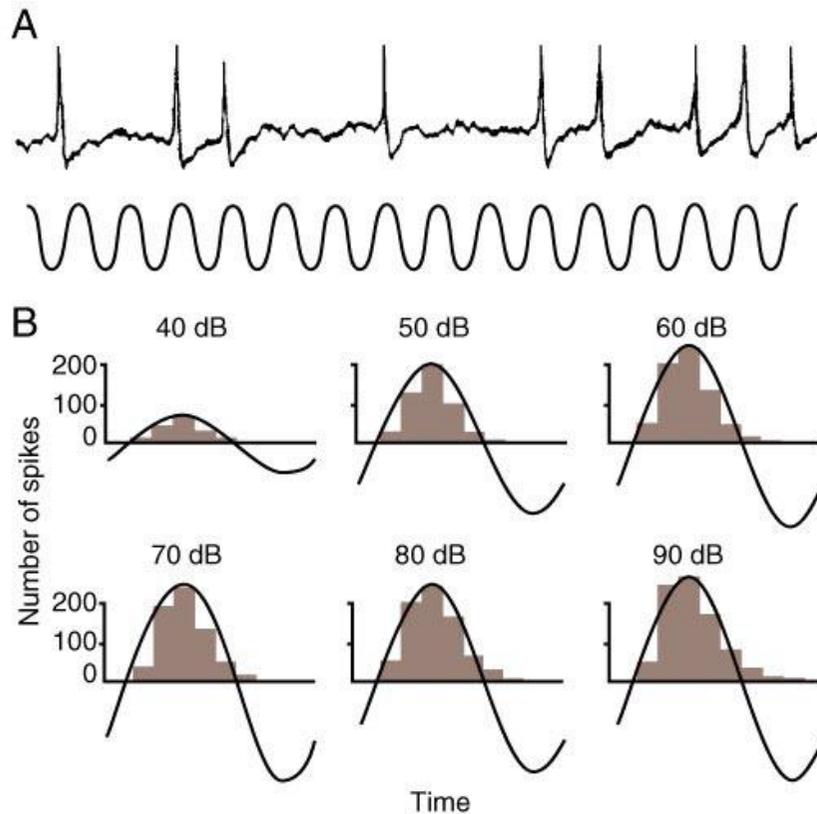
NOTE: "Best ITD" is outside the physiological range of hearing (gray). Here the *maximal-slope* is the most relevant. → Example of why a "best parameter" is not always relevant biologically...

Auditory localization: The Jeffress model for processing ITD



Auditory localization: What are the necessary ingredients for a “neural recipe” that implements the Jeffress model ?

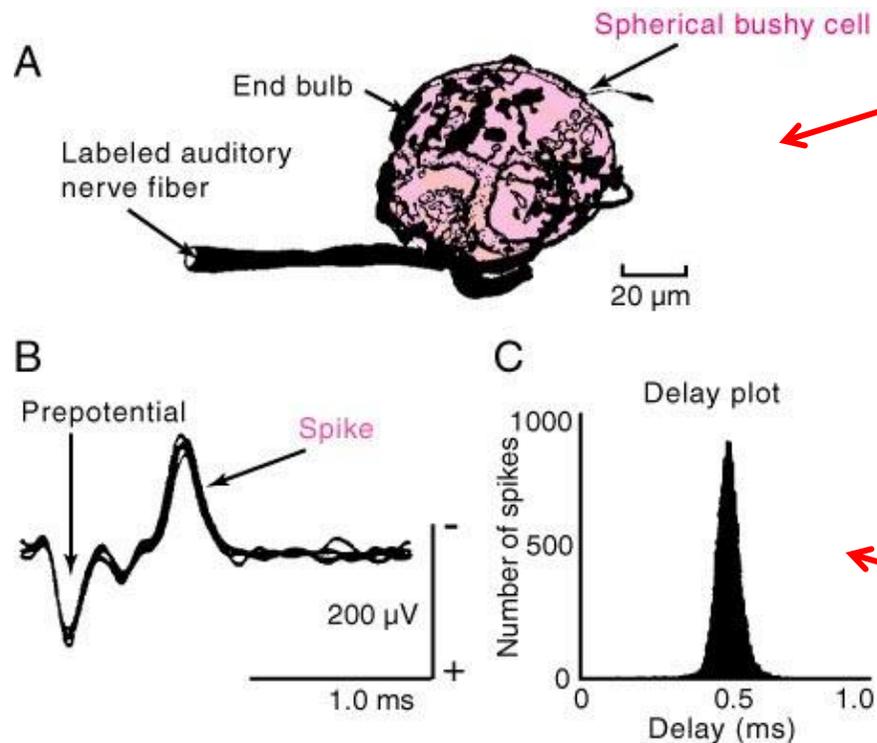
1. Phase locking of neurons in the auditory nerve (for sounds $< \sim 3\text{kHz}$)



Example of
'temporal coding' in
the auditory system

Auditory localization: What are the necessary ingredients for a “neural recipe” that implements the Jeffress model ?

2. High-fidelity (1:1) synaptic transmission between Left and Right

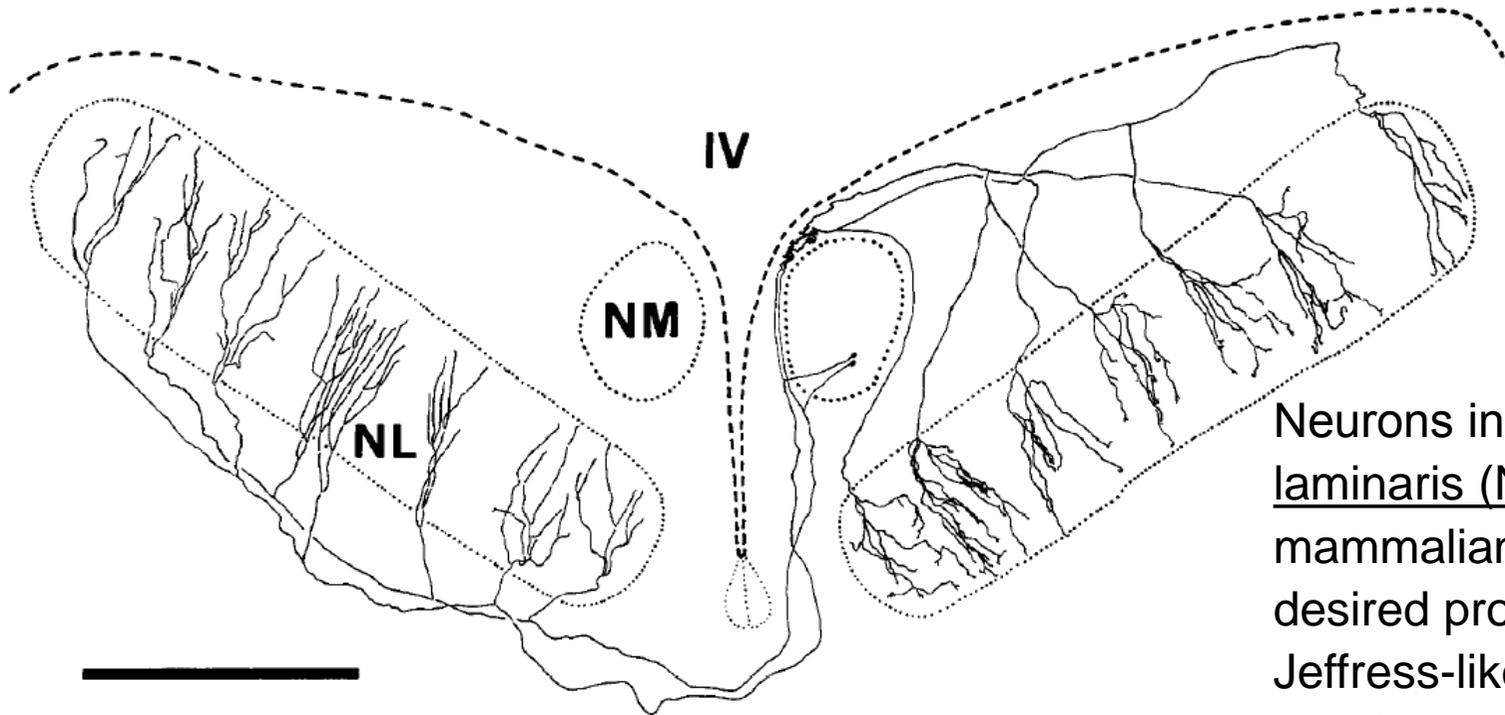


The End bulb of Held, the synapse between the auditory nerve → spherical bushy cells in the cochlear nuclei, provides such 1:1 transmission, and is crucial for ITD processing. *(Together with the Calyx of Held, between auditory nerves → MNTB's, these are the two largest synapses in the brain).*

* Notice the low temporal jitter between the postsynaptic spike and the prepotential (*prepotential = End-bulb's synaptic potential that is so huge that it looks like a spike in these extracellular recordings*).

Auditory localization: What are the necessary ingredients for a “neural recipe” that implements the Jeffress model ?

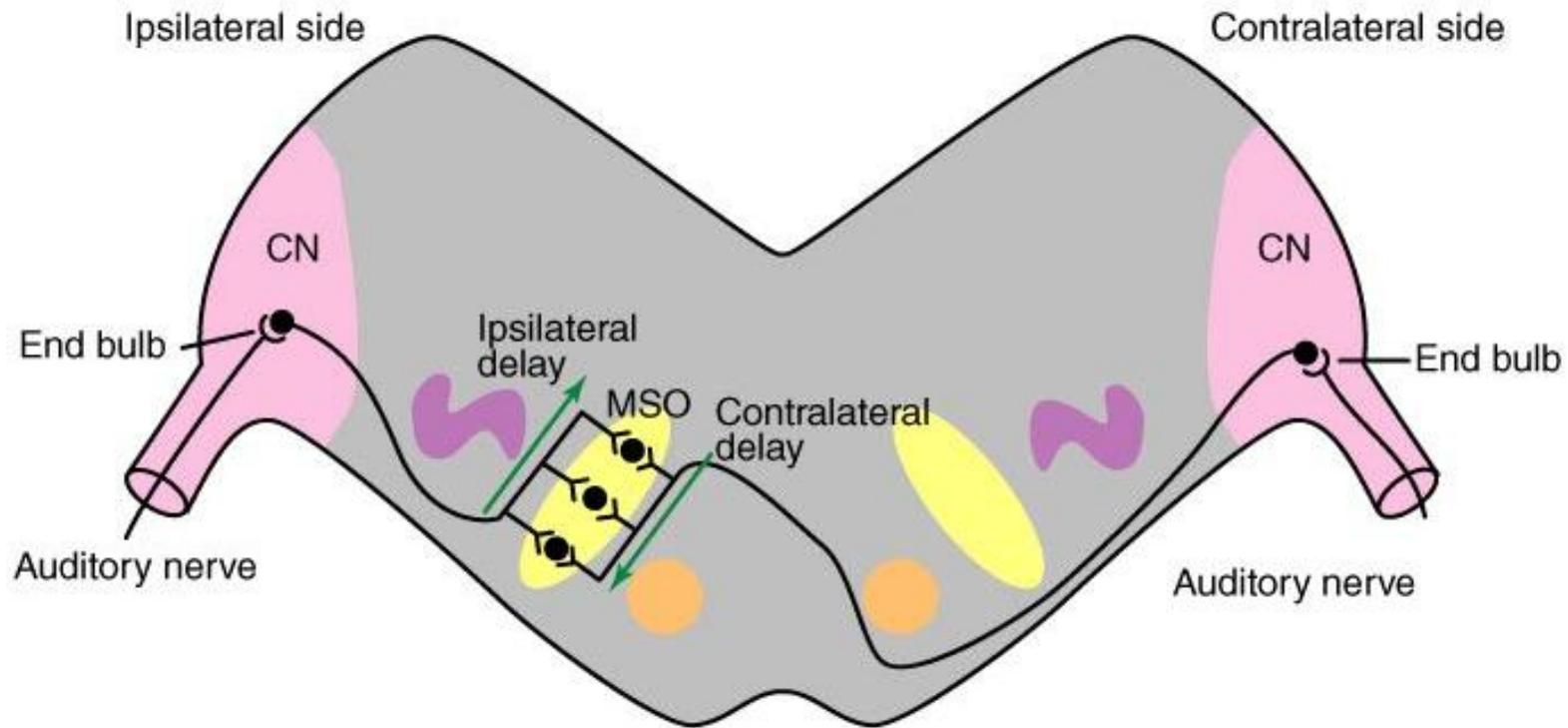
3. Anatomy that subserves delay lines & coincidence detectors



From *Carr and Konishi (1990)* – shown are the projections of two stained neurons from nucleus magnocellularis (NM, the bird’s analog of the cochlear nucleus) to nucleus laminaris (NL).

Neurons in the barn owl’s nucleus laminaris (NL), the bird analog of the mammalian MSO, show exactly the desired properties – including a Jeffress-like anatomical structure, and physiological recordings showing topographically-ordered “best ITD” values within the NL.

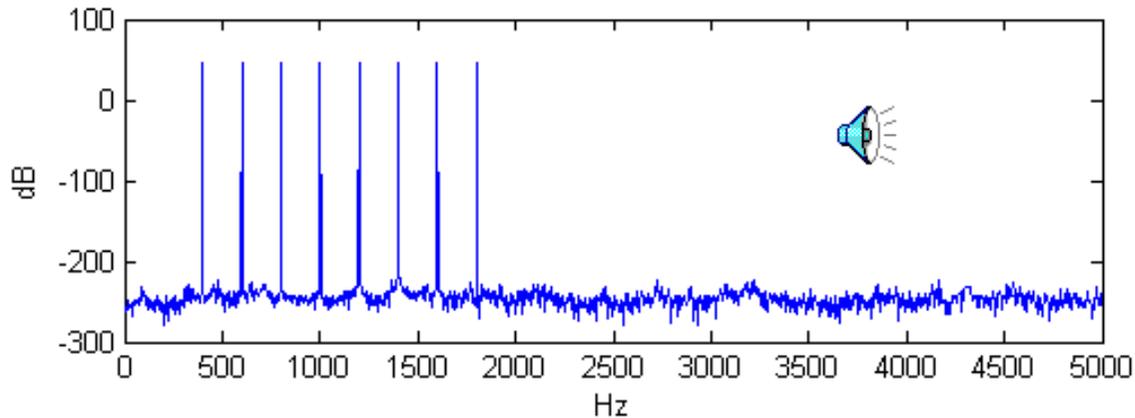
Auditory localization: What are the necessary ingredients for a “neural recipe” that implements the Jeffress model ?



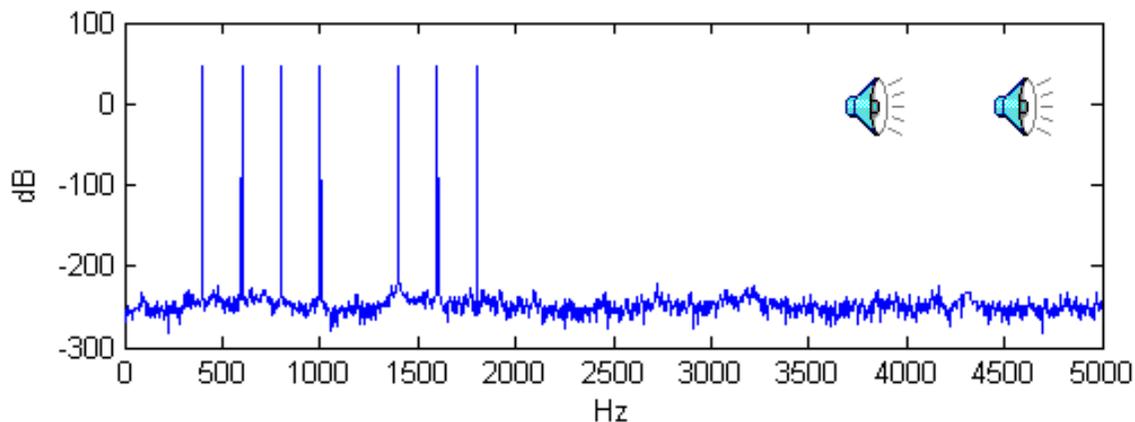
Auditory localization: What are the necessary ingredients for a “neural recipe” that implements the Jeffress model ?

BUT: recent findings from gerbil MSO (starting with *Brand et al., Nature 2002*) – a structure that is notoriously difficult to record from in mammals – suggest that the ITD-tuning mechanism in mammals is different than in birds: ITD tuning in mammals seems to rely on excitatory inputs from both ears and on *temporally precise inhibition* from the contralateral ear.

Processing of “WHAT”: Perceptually, sounds are often grouped into *Auditory Objects* (e.g., a lion roar)



Simple Example (from Jan Schnupp): Harmonically related frequency components are often perceived as a single sound.



Properties that often (but not always) bind sounds together into a single “auditory object”:

- Harmonic relations
- Common onset
- Common amplitude modulation
- Common spatial source
- ...

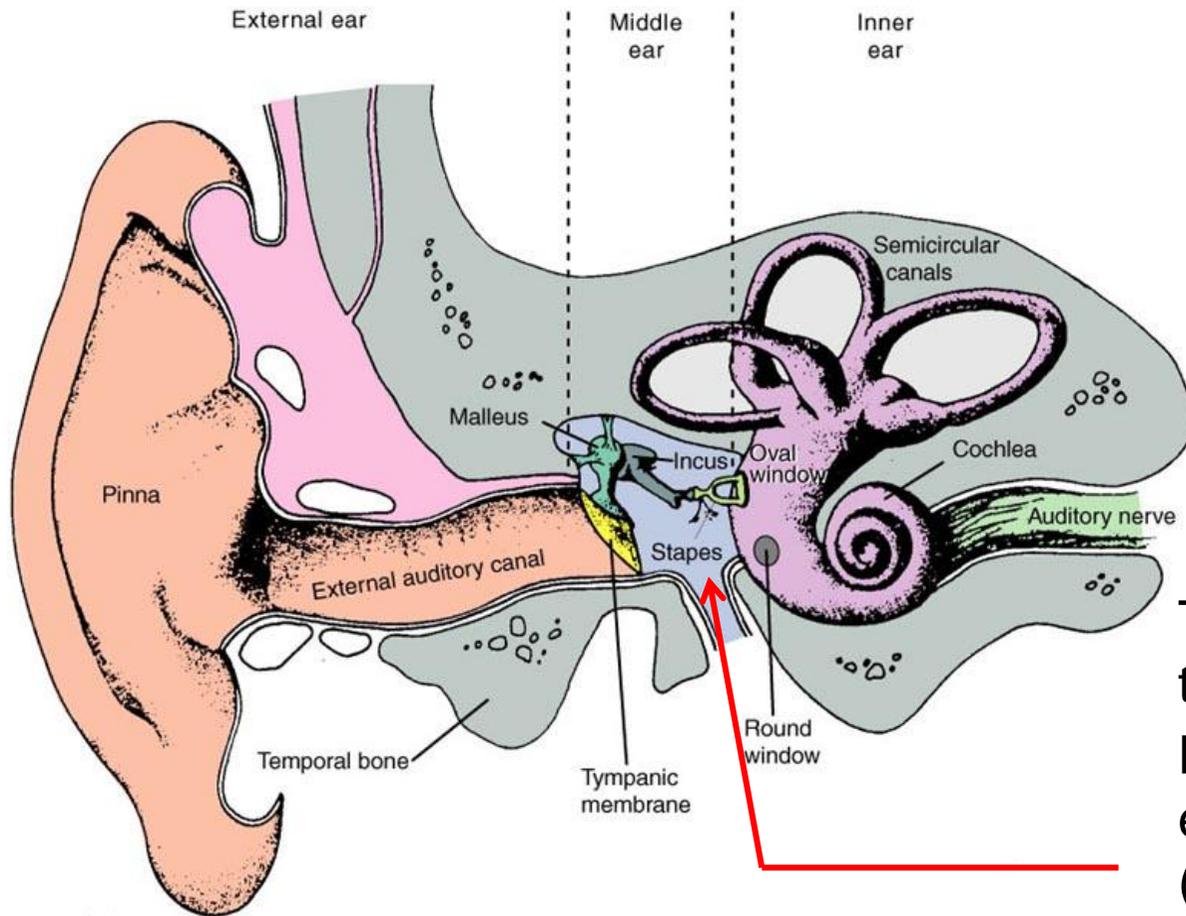
→ The bottom example is perceived as: (harmonic stack) – (pure tone)

... However, at the neural level, auditory research has classically focused on simple sounds (pure tones, white noise, FM and AM sounds...) – so we are still far from understanding how complex sounds like lion roars are processed by the auditory system

Let's go now through some classical findings on the neural organization and responses in the ascending auditory pathway – using simple sounds.

(We will *not* talk today about the *descending* projections, that go all the way down to the cochlea, and mediate top-down modulation of auditory processing.)

Ascending auditory pathway: 1. Tonotopic (frequency) organization that is inherited from the cochlea



The middle ear bones act as a *lever* to amplify sound.

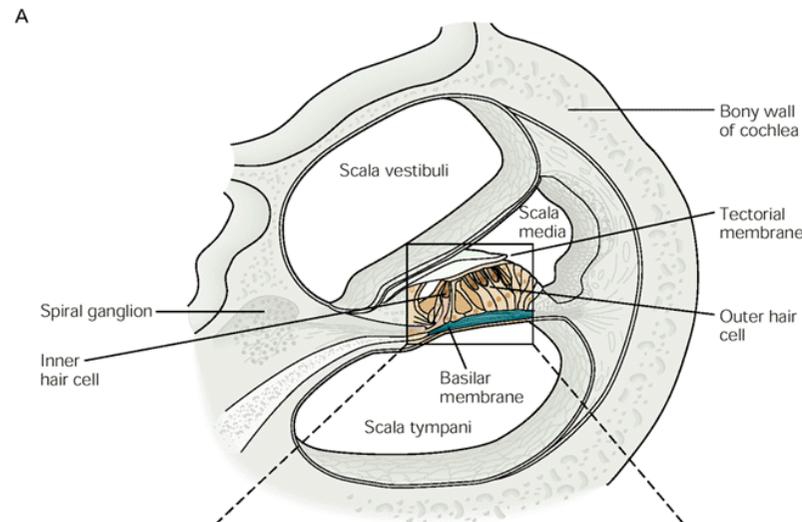
During sound *production*, the middle ear bones are partially disconnected (in humans) or almost totally disconnected (in bats), to avoid self-deafening when vocalizing.

Ascending auditory pathway: 1. Tonotopic (frequency) organization that is inherited from the cochlea



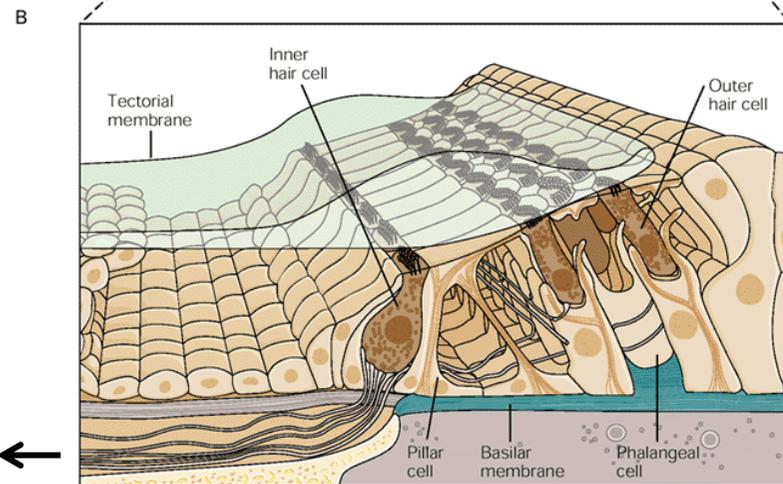
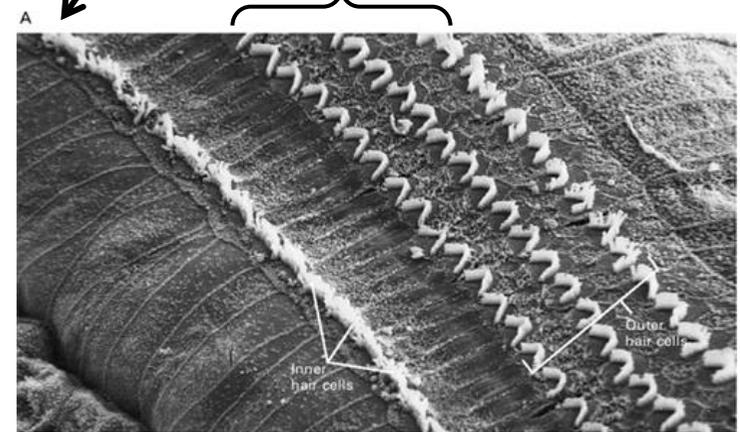
Cochlea – the movie (James Hudspeth)

Ascending auditory pathway: 1. Tonotopic (frequency) organization that is inherited from the cochlea

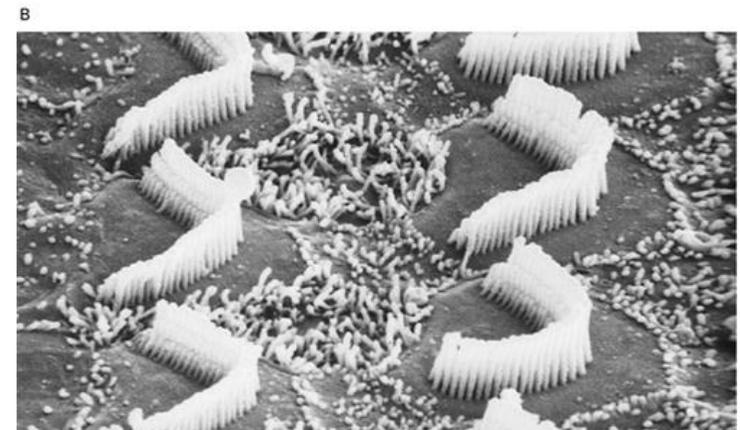


Inner hair cells (IHC's), 1 row

Outer hair cells (OHC's), 3 rows

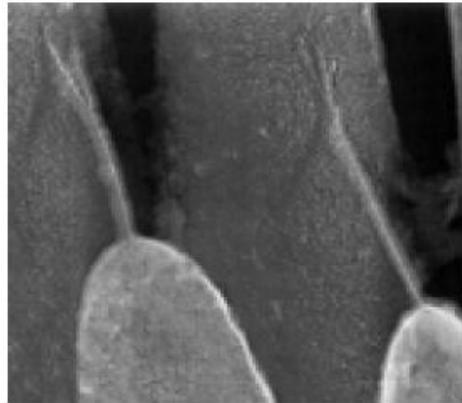
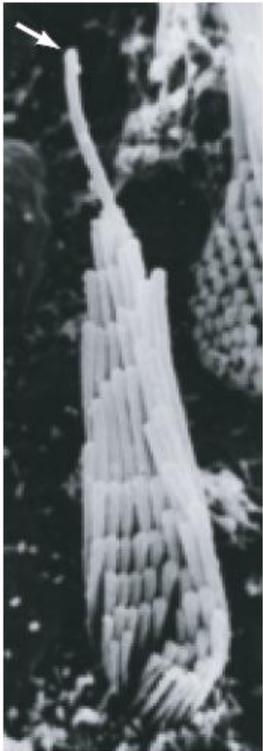


Auditory nerve ←

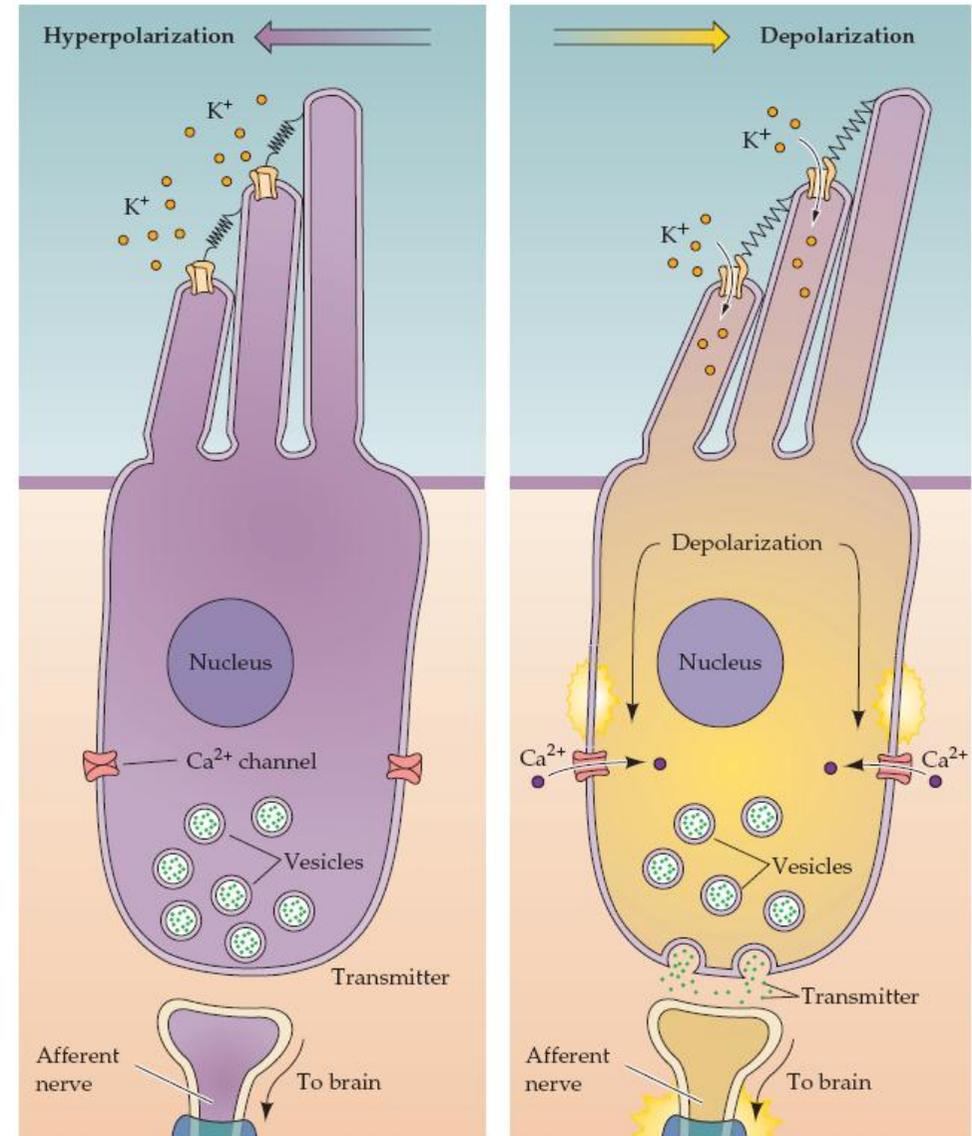


Ascending auditory pathway: 1. Tonotopic (frequency) organization that is inherited from the cochlea

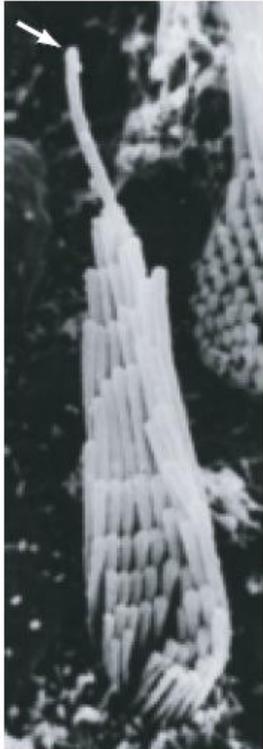
A vestibular hair cell. Note gradient in the length of individual hair calls (stereocilia).



Stereocilia are connected to each other by structures known as *tip links*. These tip links are thought to underlie the mechano-electrical transduction by hair cells.



Intermezzo: Vestibular system

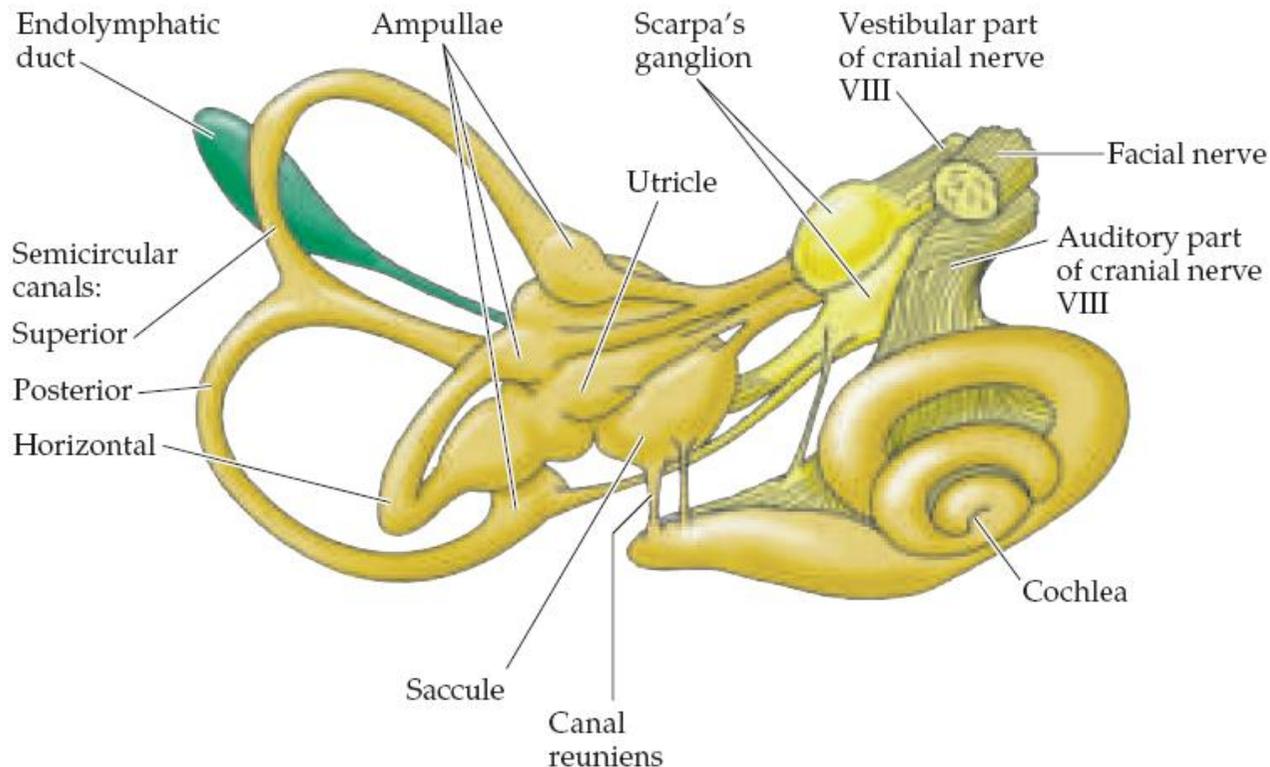


Vestibular hair cells are similar to auditory hair cells, except the long kinocilium (arrow) which they have and auditory hair cells don't. Vestibular hair cells are easier to access (are not surrounded by the hardest bone in the body like the cochlea is), hence much of what we know about hair cells comes in fact from the vestibular system.

Intermezzo: Vestibular system

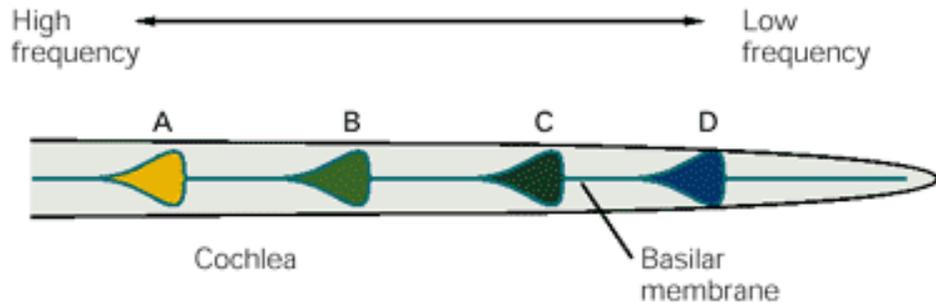
Each inner ear contains in fact 6 sensory organs, 5 of which carry out vestibular processing:

- 1 cochlea (*hearing*)
- 3 semicircular canals (*angular acceleration*) – sense motion of liquid elicited by head rotation
- Otolith organs: 1 utricle + 1 saccule (*linear acceleration, e.g. gravity*) – contain a gelatinous structure with embedded “ear stones” (*otolith* in Greek) which deform the gelatin upon motion-related acceleration, or due to gravity, and the hair cells sense these deformations

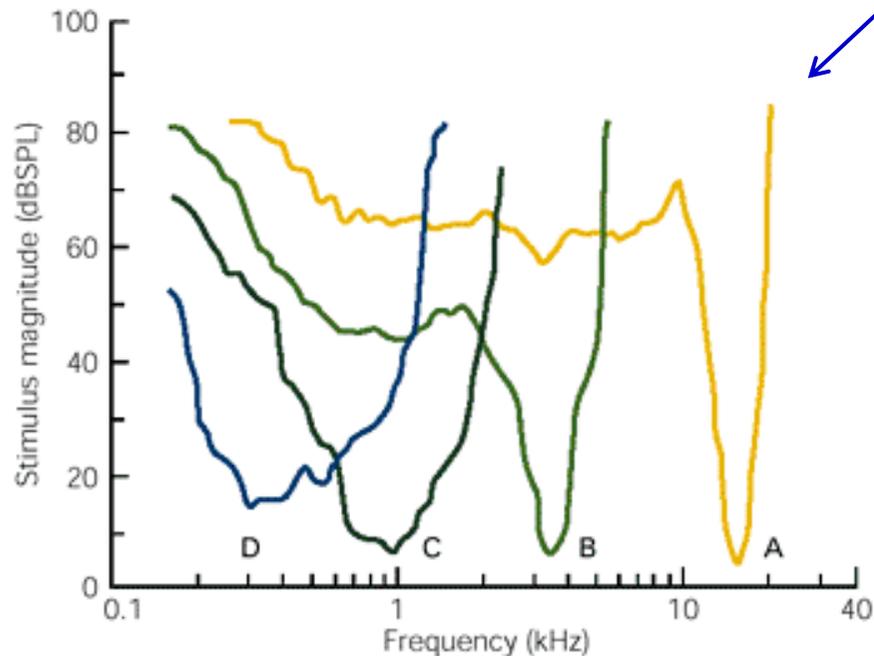


More details on the Vestibular System are found in the book chapter posted on the course website.

Ascending auditory pathway: 1. Tonotopic (frequency) organization that is inherited from the cochlea



Tuning curves of inner hair cells have a broad component (mechanically related: von Békésy) **BUT** also a very narrow component.



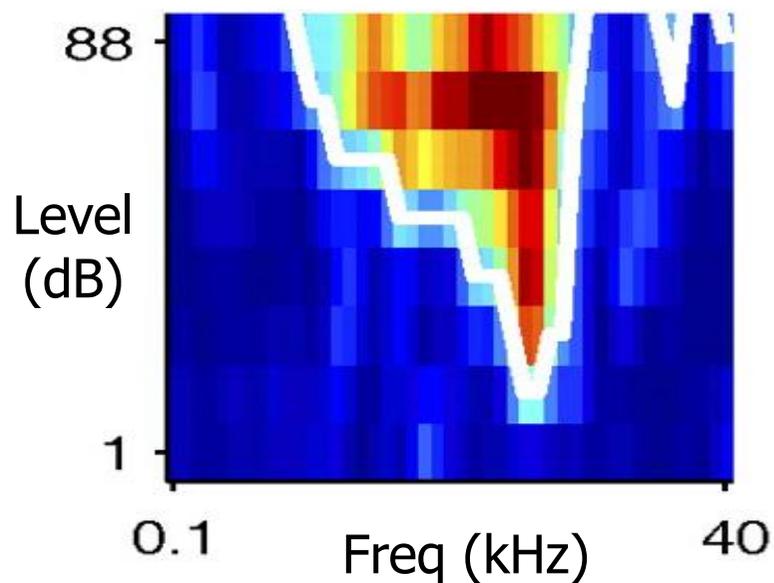
How is the narrow tuning achieved?

The outer hair cells contain a 'piezoelectric' protein (prestin) that is thought to convert electrical potentials to mechanical motion – the "cochlear amplifier" positive feedback mechanism – which serves to narrow the tuning curves of the inner hair cells.

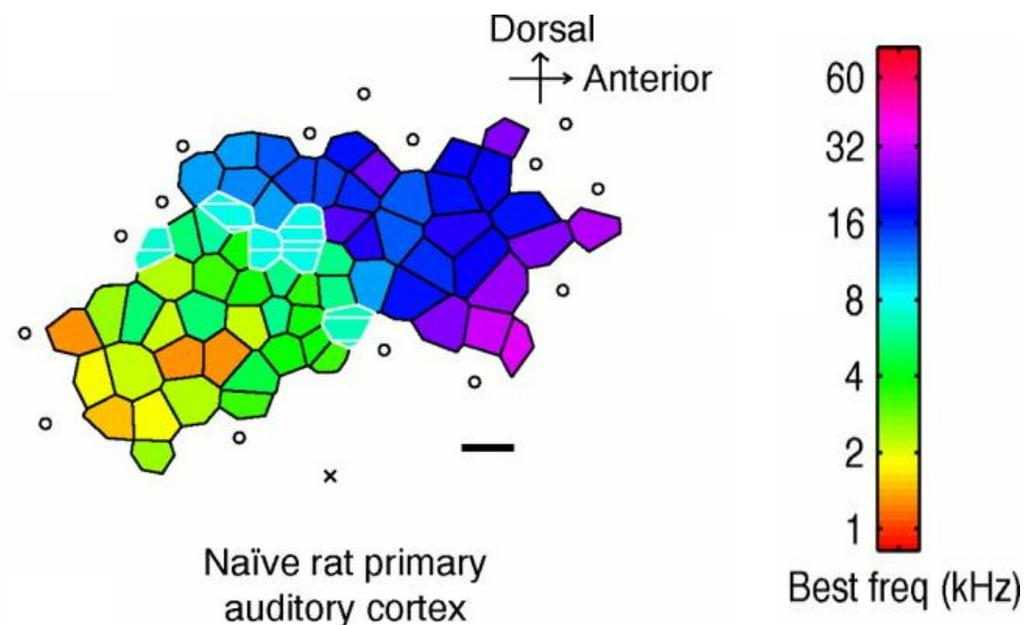
[An alternative theory is that the cochlear amplifier is mediated by a positive feedback on the ion channels, not via prestin.]

Ascending auditory pathway: 1. Tonotopic (frequency) organization that is inherited from the cochlea

... and tuning curves and tonotopic frequency organization are found all the way up to the auditory cortex



Neuron in primary auditory cortex (A1) of cat (Moshitch et al. 2006)

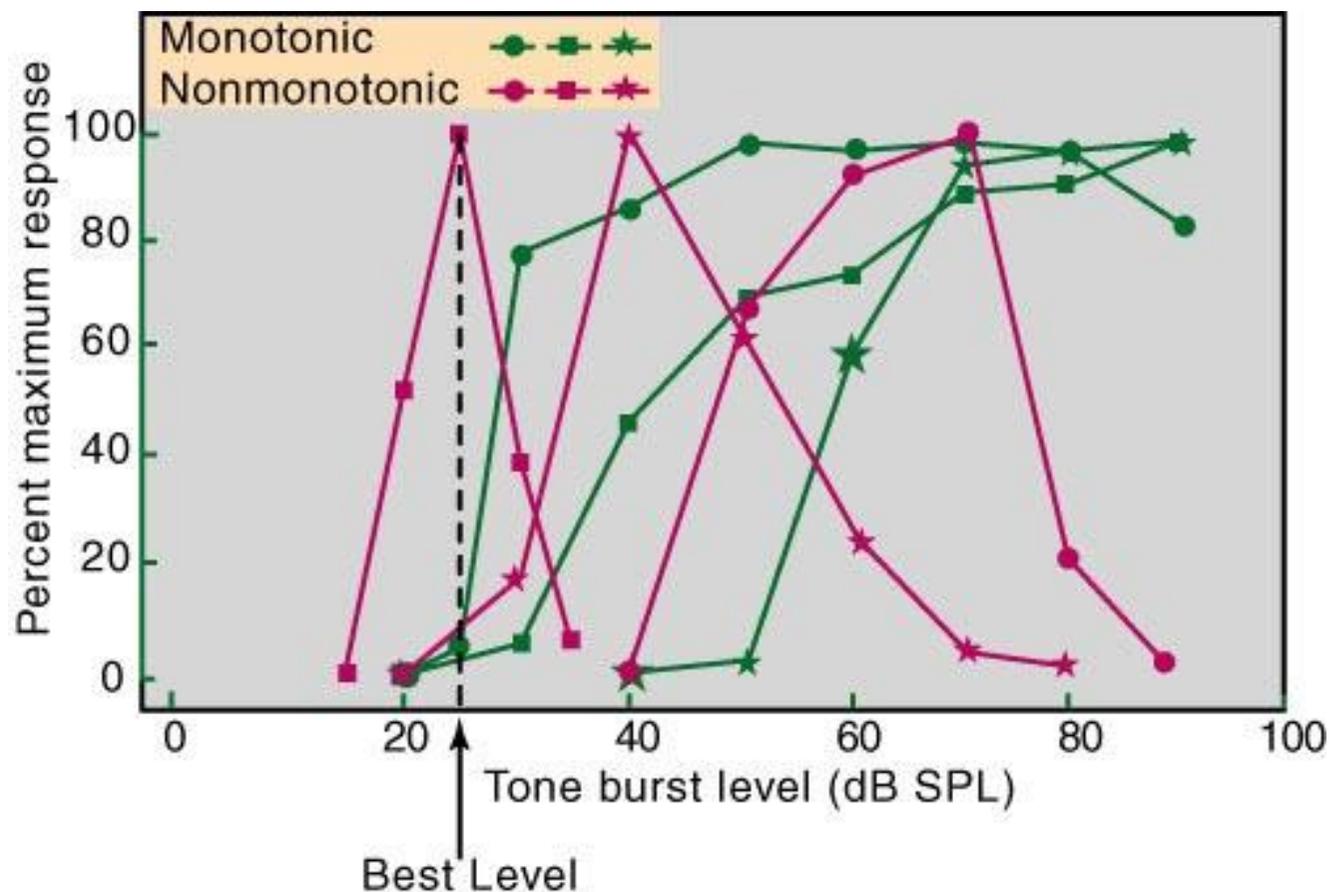


(Kilgard and Merzenich 1997)

Ascending auditory pathway: 2. Coding of stimulus intensity

Examples of six neurons in cat primary auditory cortex (A1)

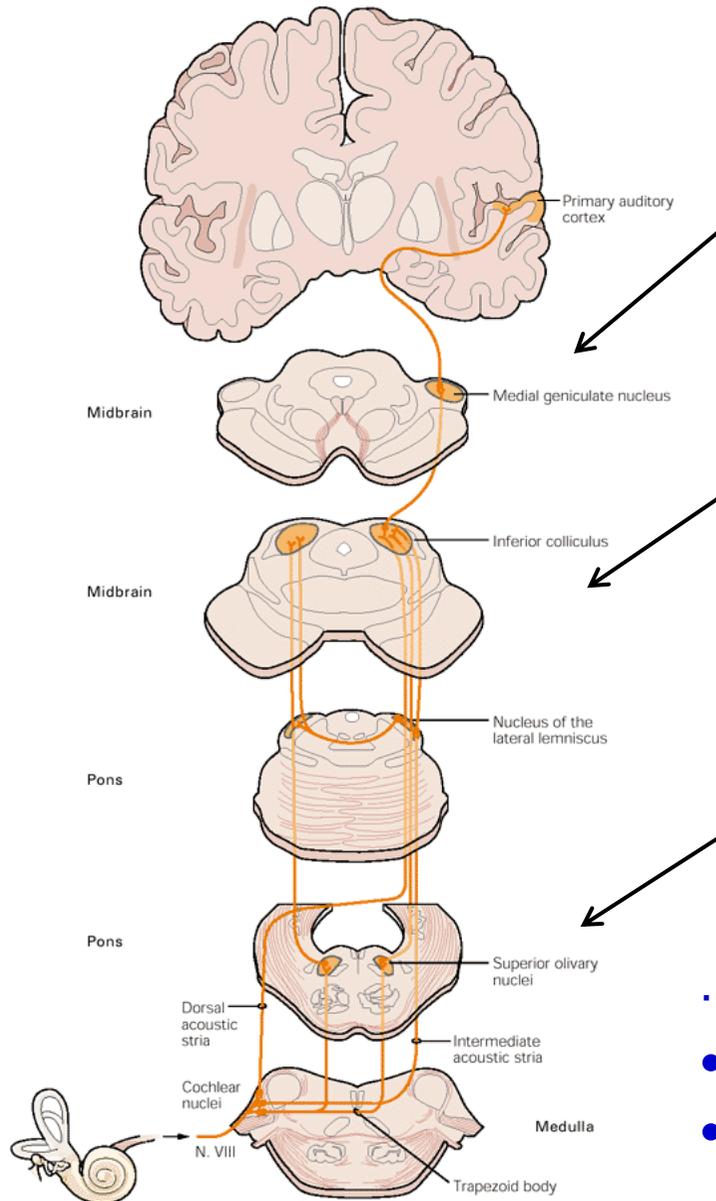
Neuron's firing rate is related to stimulus intensity ('rate coding')



Ascending auditory pathway: 3. Lateral inhibition

Two-tone suppression in the auditory nerve (suppression of the response to one frequency by the presentation of another frequency) acts similarly to lateral inhibition in the visual system. It serves to further sharpen the frequency tuning.

Ascending auditory pathway: 4. Rich subcortical processing



MGN (MGB) = auditory thalamus: Neurons selective for *species-specific vocalizations*; involvement in *fear conditioning* (projections to amygdala).

Inferior colliculus (IC): First obligatory convergent station for the ~15 parallel ascending subcortical pathways. *Spatial tuning in IC*: is based on the combination of ITD, ILD and spectral cues (HRTF).

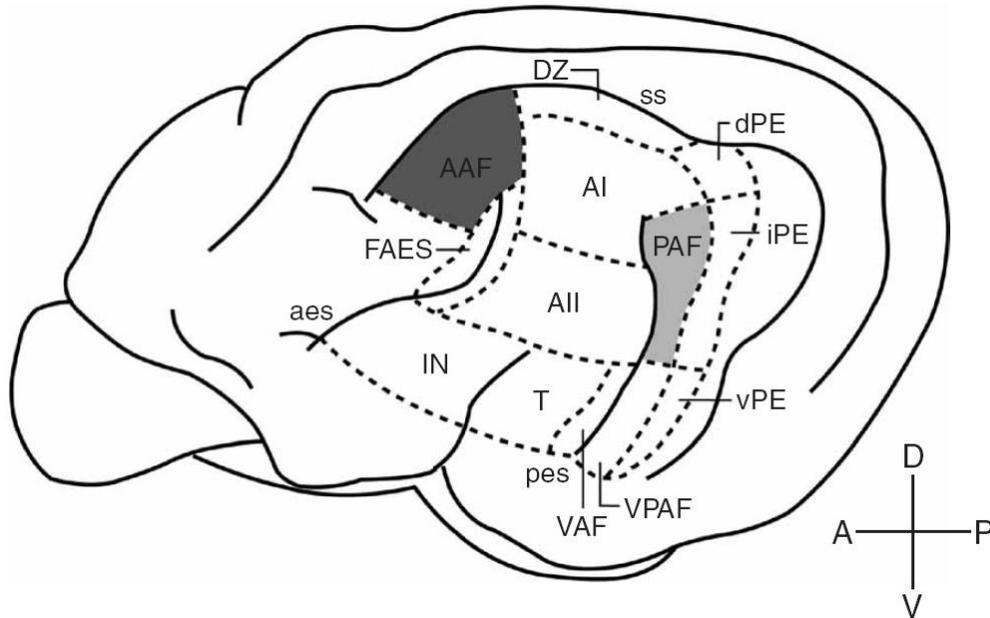
Medial superior olive (MSO) – *ITD*
Lateral superior olive (LSO) – *ILD*

...

- A lot of processing is taking place before the cortex.
- Multiple decussations (cross-overs) for sound localization.

Ascending auditory pathway: 5. Multiple fields in auditory ctx

Most cortical research is done in the primary auditory cortex, A1 (denoted also AI). The specific roles of the different cortical fields in cat / rat / primate is *not* well understood.



Cat auditory cortical fields

[A study in cats (Lomber and Malhotra, *Nat. Neurosci.* 2008) used a reversible cooling technique to show behaviorally a double dissociation between field PAF that was crucial for sound localization (“Where”) and field AAF that was crucial for pattern discrimination (“What”). Supports the notion of separate “What” and “Where” streams in auditory cortex? (Similar to the visual cortex.)]

But the roles of the different cortical fields are much better understood in the mustached bat – much better than in other mammals.

The auditory system of echolocating bats

Moreover, we generally have a rather poor understanding of how the auditory cortex of cats / rats / primates processes complex natural sounds like communication calls.

... so let's turn now to an animal where the processing of complex sounds is much better understood, and where we have a fair understanding of what the auditory system is 'trying to do' – the echolocating bat.

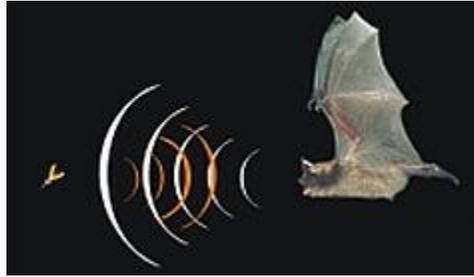
(there are also other organisms where we “know what the auditory system is trying to do” – e.g. insects, that process primarily the communication sounds of conspecifics + the sounds of predators such as bats – and there is a fair amount of research on insect auditory neurophysiology – but we will not talk about it today. We'll briefly discuss the echolocating bat as an example of a top-down approach to studying the auditory system.)

Bats comprise ~23% of mammalian species (~1,300 species)



Photos: Merlin Tuttle

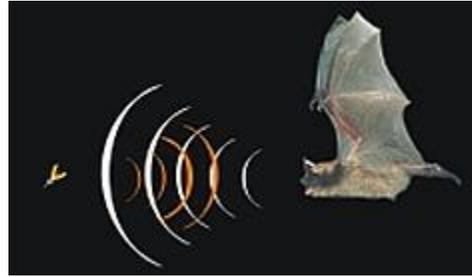
The basics of echolocation (also known as 'biological sonar')



Echolocation is an active-sensing system, similar to most of the sensory systems in nature (somatosensory, visual, olfactory, electrolocation) – but different from passive hearing.

- Insect-eating bats detect and localize small insects via the returning echoes.
- Fish-eating bats use the echoes returning from the concentric water-ripples that are created by the fish on the water surface.
- Flower bats use the highly specific echoes returning from their favorite flowers to compute the best direction from which to access the flower nectar.

The basics of echolocation (also known as 'biological sonar')



Basic sonar equations:

$$\text{Target range : } R = c T / 2$$

$$\text{Doppler shift : } f_r = f_e (1 + 2v/c)$$

The factors $\frac{1}{2}$ and 2 in these equations are due to the two-way travel of sound

Where:

R = target range

c = speed of sound in air ~ 340 m/s

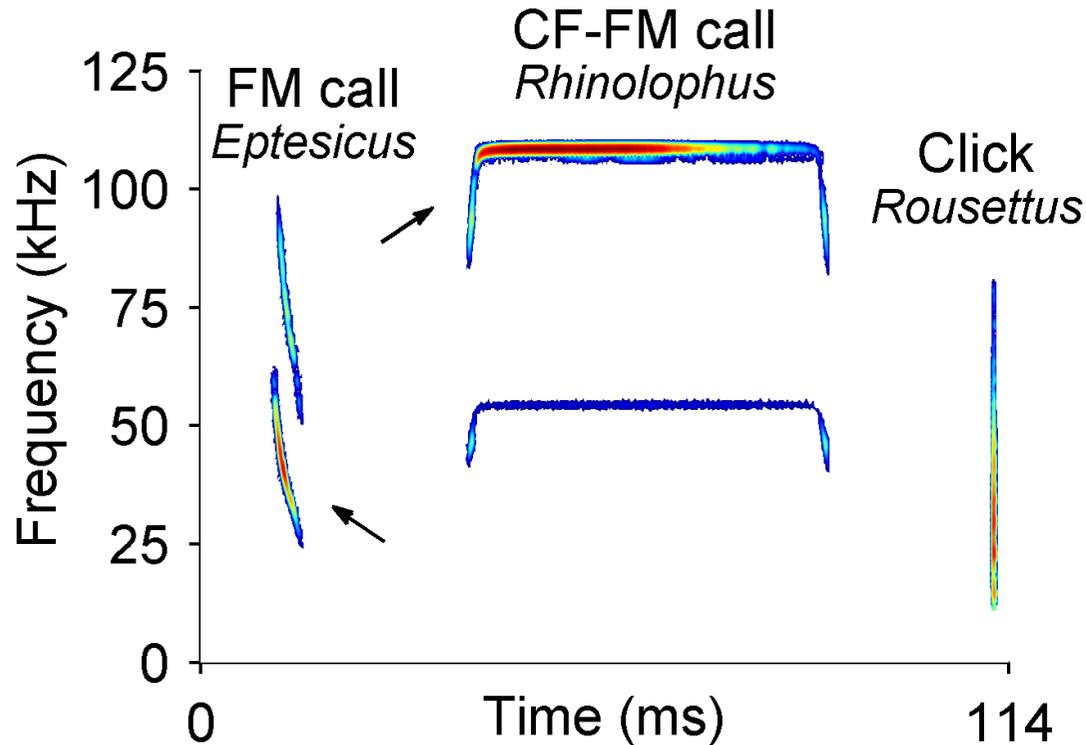
T = pulse-echo delay

f_r = frequency as received in the bat's ears

f_e = frequency emitted from bat's mouth (or bat's nose)

v = bat's flight speed

Basic types of echolocation calls



(Ulanovsky & Moss, *PNAS* 2008)

The most-studied bats are:

FM bats, that use frequency modulated (FM) calls

and

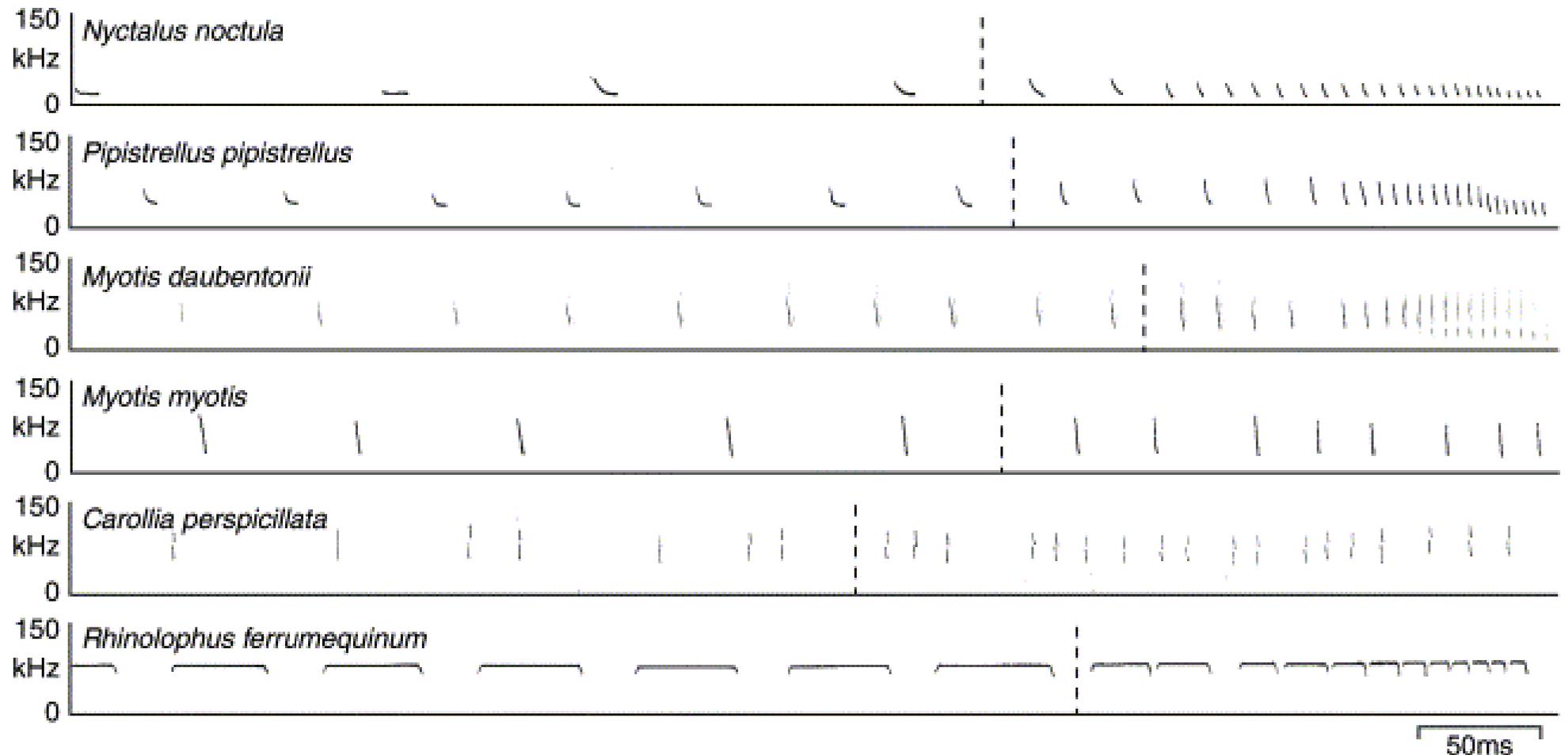
CF-FM bats, that have a long constant frequency (CF) component together with an FM chirp at the beginning and/or end of the call

Basic types of echolocation calls

FM bats are able to discriminate jitter in target range down to < 400 ns (less than 0.1 mm). This extraordinary temporal resolution (together with the $10 \mu\text{s}$ behavioral resolution in ITD-based sound localization) is far below the rise-time of action potentials !

CF–FM bats can compute the Doppler shift (target velocity). They can also detect Doppler modulations caused by the insect's wing flutter – and these bats can even tell apart different insect species based on their different flutter rate.

Aerial insectivores have a typical insect-catching echolocation behavior, with phase transitions: *Search* → *Approach* → *Buzz*



Aerial insectivores have a typical insect-catching echolocation behavior, with phase transitions: *Search* → *Approach* → *Buzz*



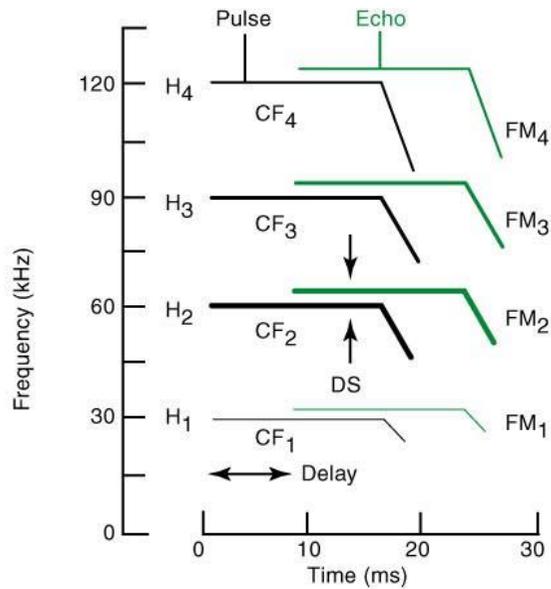
Bat chasing an insect – the movie (K. Ghose & C. Moss)

Aerial insectivores have a typical insect-catching echolocation behavior, with phase transitions: *Search* → *Approach* → *Buzz*

Changes in echolocation calls during the closing-in on the insect:

- Larger bandwidth = gives better accuracy in estimating the target range (proof: mathematical theory of sonar)
- Higher rate of calls = higher update rate, allows better tracking of the moving target.
- Shorter call duration = smaller overlap between outgoing call and incoming echo, allows tracking insects at closer ranges (this is needed because the bat cannot hear echoes while he is emitting a call – due to the disconnection of the middle-ear bones).

The auditory cortex of the mustached bat (CF–FM bat)

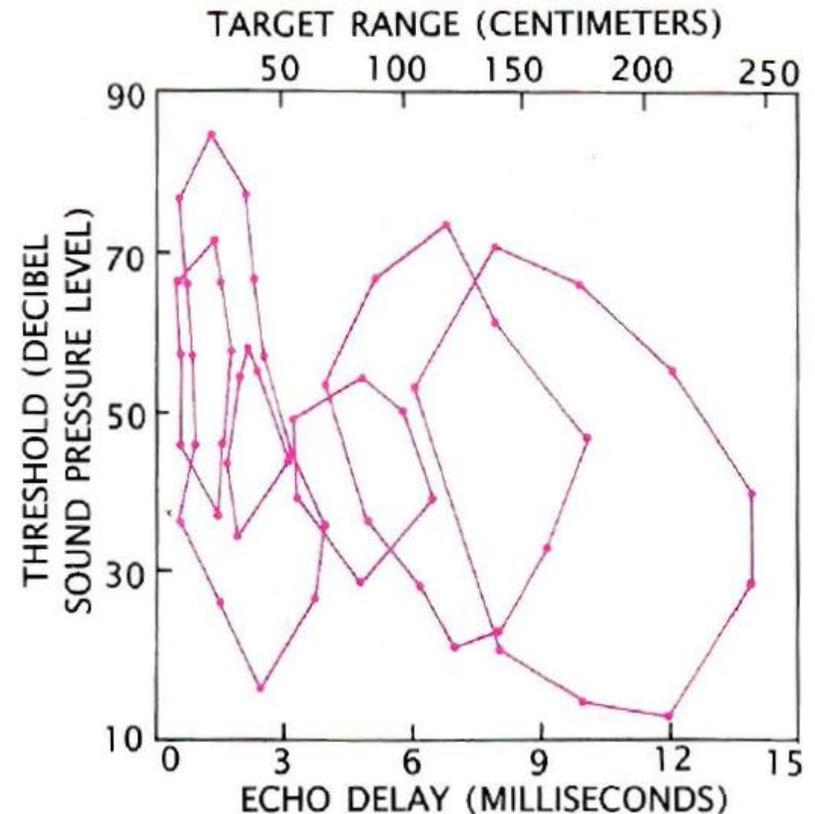
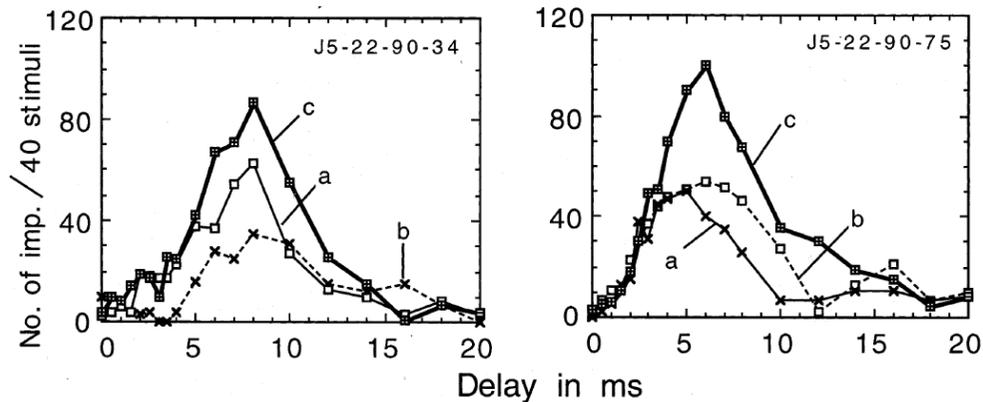


Schematic of the CF–FM call of the mustached bat

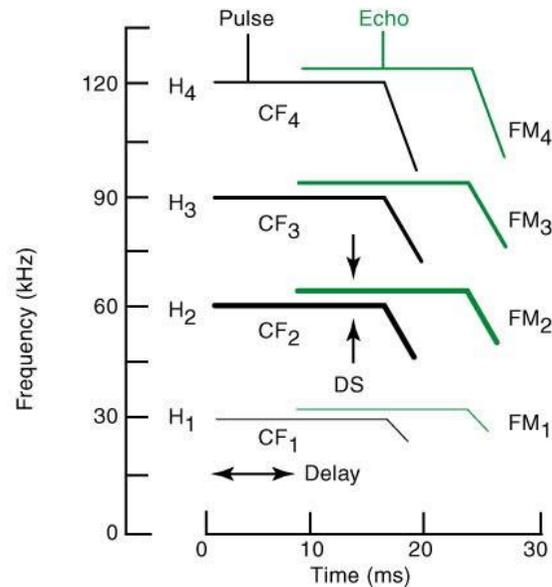
The auditory cortex of the mustached bat (CF-FM bat)

Prominent characteristics of the auditory cortex of this bat:

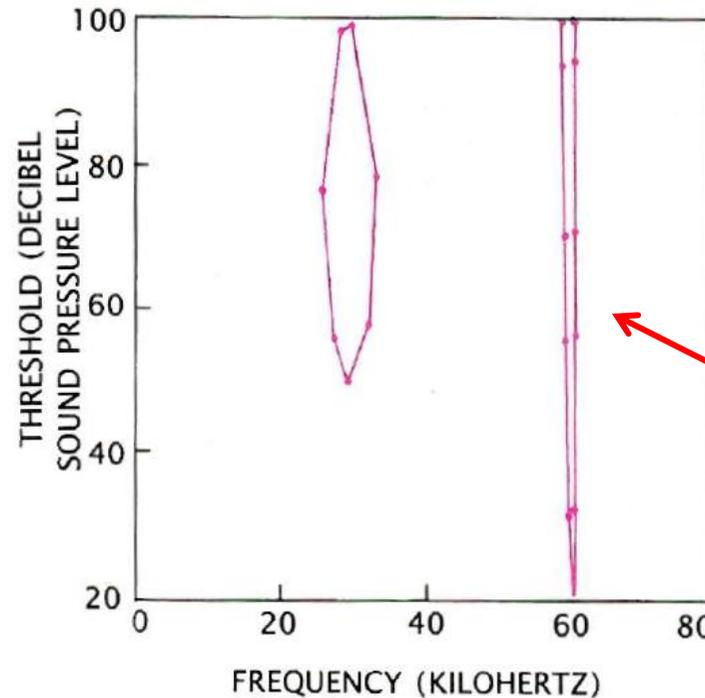
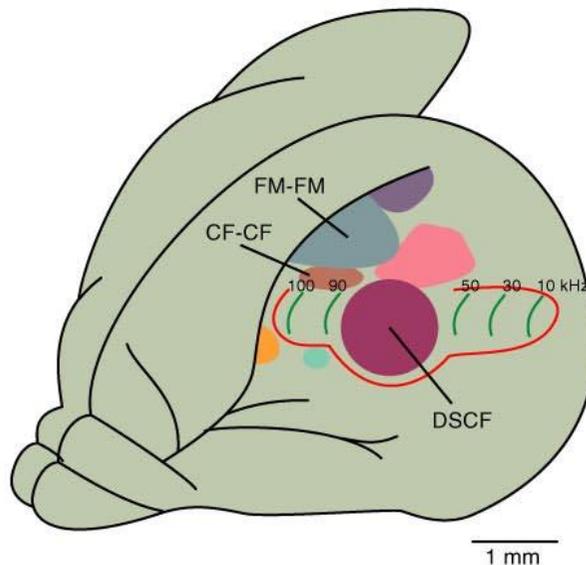
1. Delay tuned neurons (neurons sensitive to target range) – first discovered by Nobuo Suga



The auditory cortex of the mustached bat (CF-FM bat)

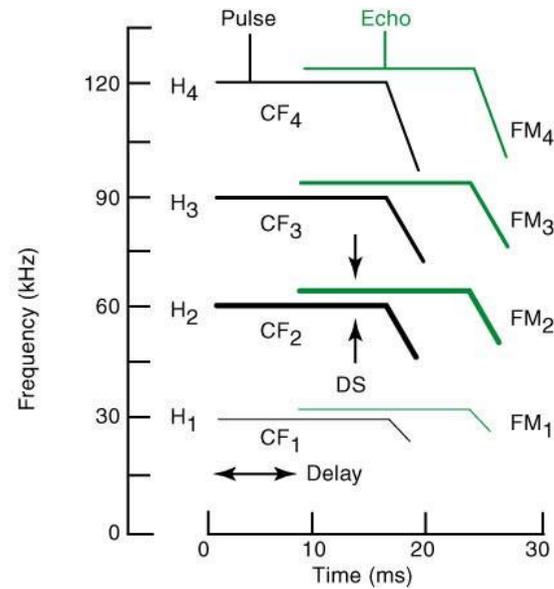


2. 'Auditory fovea' (DSCF area) contains neurons with extremely narrow frequency tuning, centered around the dominant harmonic of the bat call (CF₂, the 2nd harmonic). The narrowest frequency tuning in any animal.

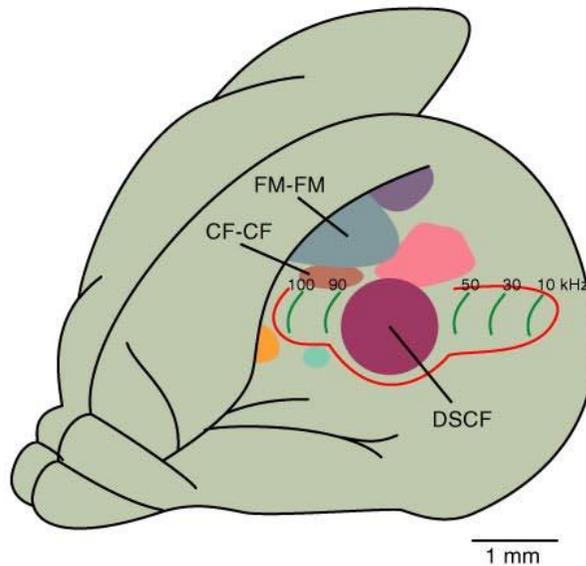


Frequency tuning of neuron from DSCF area

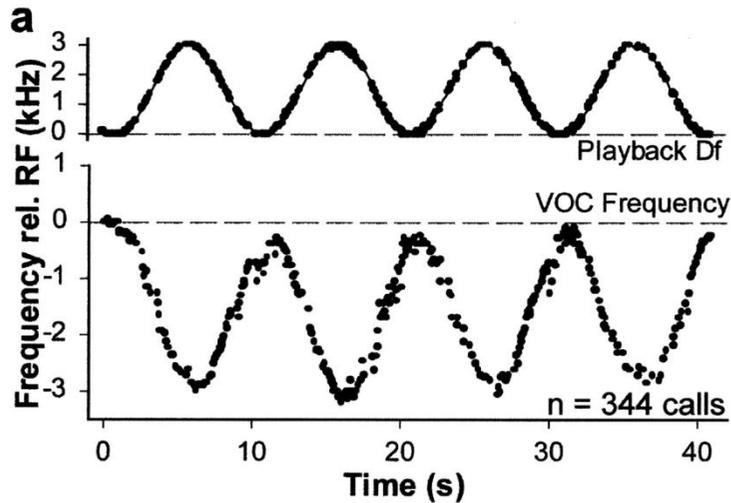
The auditory cortex of the mustached bat (CF-FM bat)



Neurons in the DSCF area specialize in detecting rapid Doppler modulations (*insect wing flutter*).



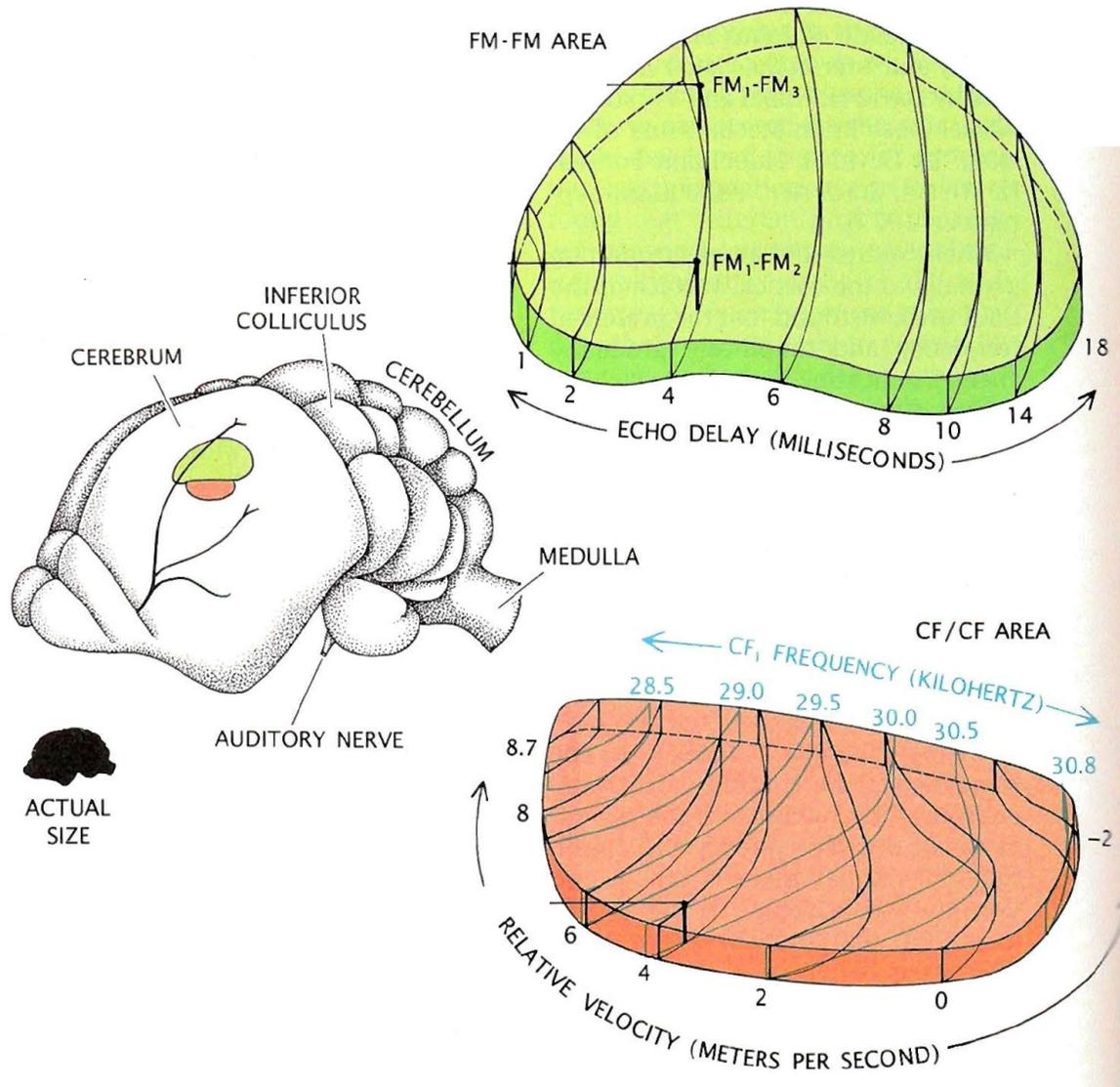
The auditory cortex of the mustached bat (CF–FM bat)



Doppler shift compensation behavior:
Mustached bat (and Horseshoe bats, other CF-FM bats) shift their frequency so as to keep the frequency of the echo inside the narrow frequency tuning of their neurons.

Doppler shift compensation in horseshoe bats
(Smotherman et al. 2003)

The auditory cortex of the mustached bat (CF-FM bat)



3. Modularity of auditory cortical fields, and computational maps:

FM-FM areas: neurons specializing in computing pulse-echo delay (*target range*). Some of these neurons even respond preferentially to sequences of pulse-echo pairs with shortening delays ("tracking neurons").

CF-CF areas: neurons specializing in computing Doppler magnitude (*target velocity*).

Summary: Comparing the Auditory System to other sensory systems

Similarities to other sensory systems:

- Coding of stimulus intensity.
- Labeled-line projections from the periphery (cochlea). *[encode sound frequency]*
- Labeled-line coding, temporal coding, rate coding.
- Modularity of cortical processing: Different cortical fields – differing functions.
- Cortical columns.

Differences from other sensory systems:

- Stimulus location is *computed*, not inherited directly from peripheral receptors as in the somatosensory or visual systems.
- Extent of subcortical processing is probably largest in the auditory system.
- The auditory system excels at temporal processing more than any other sensory system (with the possible exception of electrolocation in weakly electric fish).