Structure and Measurement of the brain lecture notes

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Based on slides from Flavia Filimon, 2008

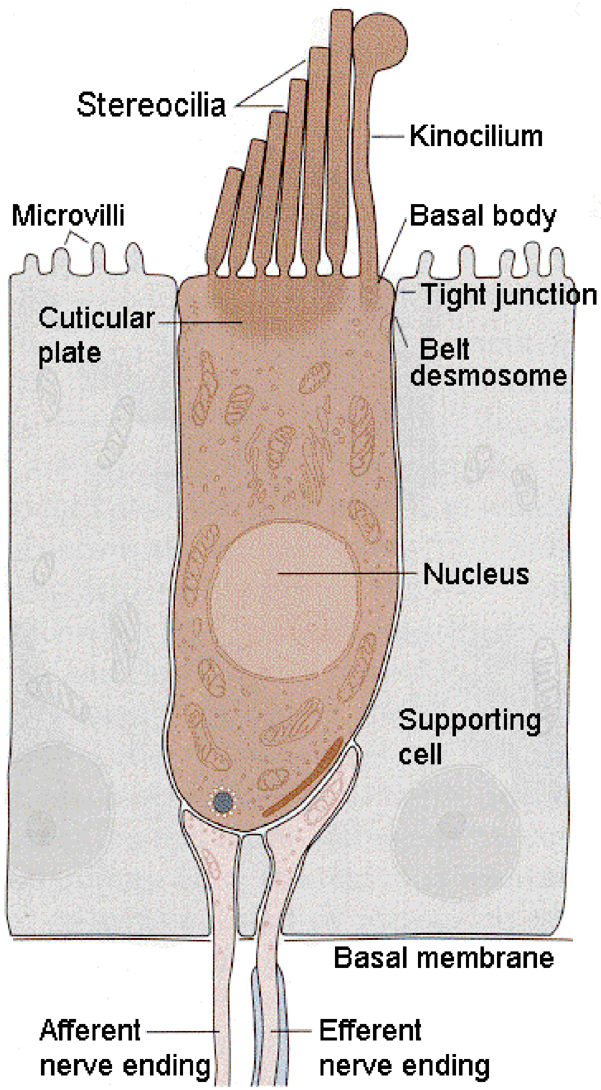
Auditory system

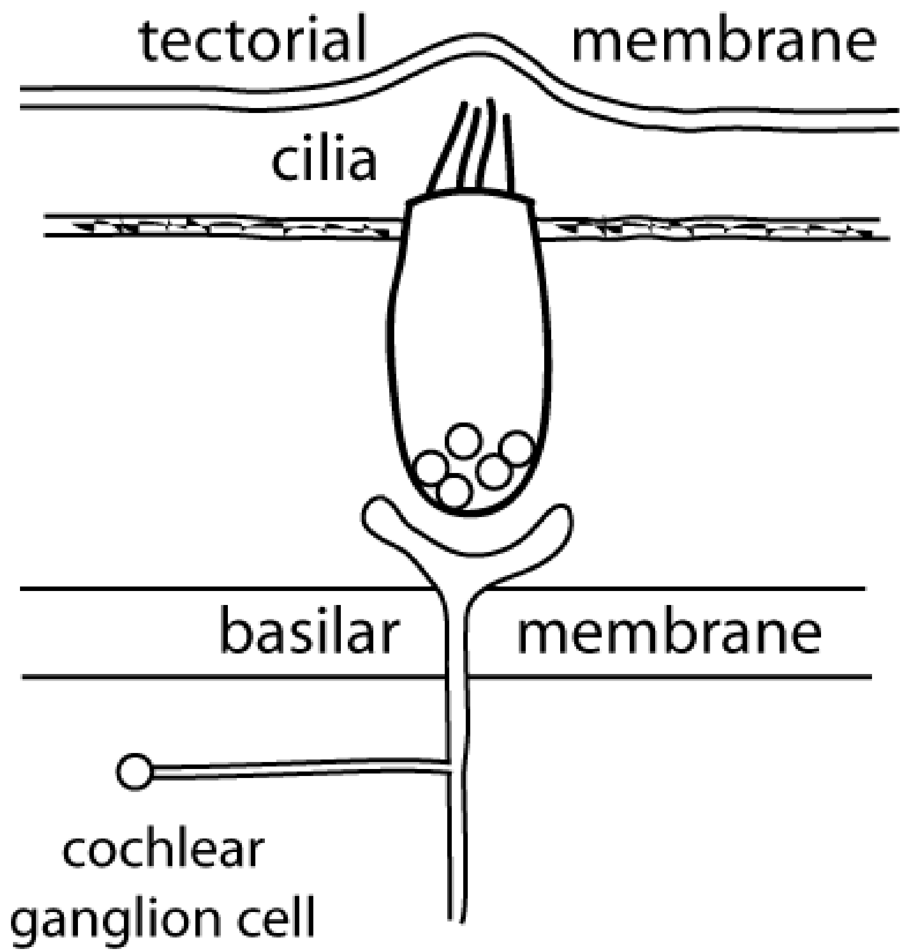
Lecture 4

Topics

- Auditory transduction and hair cell receptors
- Auditory brain stem
- Sound localization (owl)
- Echolocation (bats)
- Vowel sound processing

Auditory receptors are mechanoreceptors: hair cells



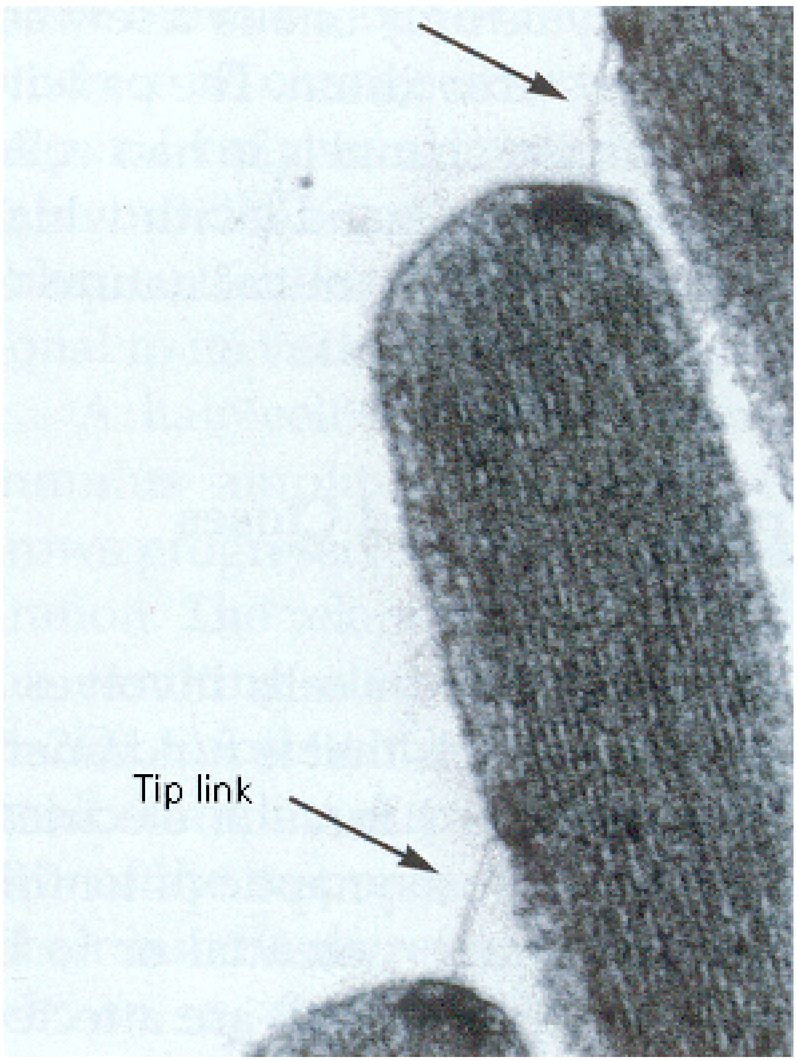


spiral ganglion

Sound makes basilar membrane vibrate up and down

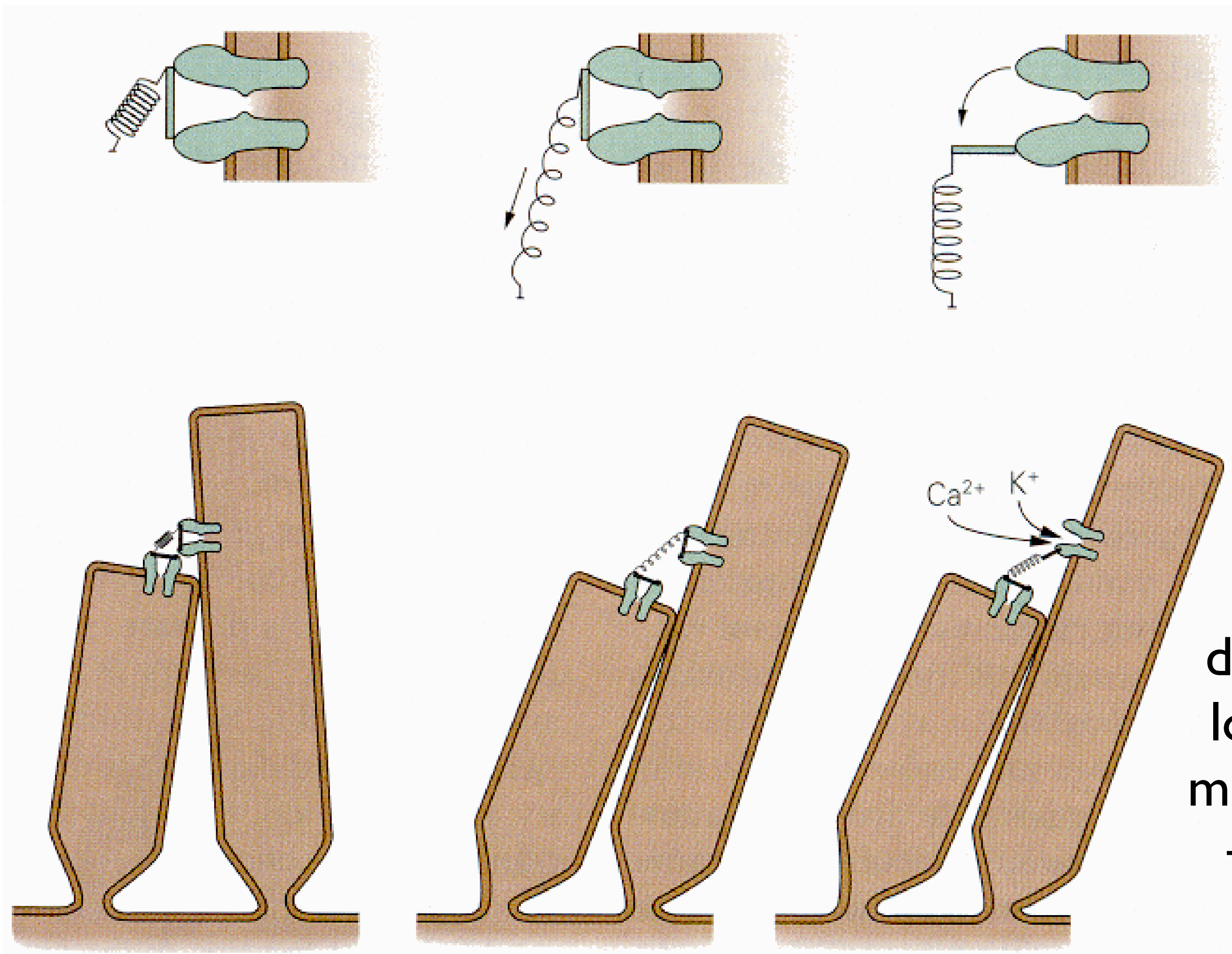
- as a result, stereocilia at the top are mechanically deflected / pushed against tectorial membrane → release of neurotransmitter

How stereocilia transduce sound into current



- Tips of individual stereocilia are linked
- deflections to one side depolarize; to the other: hyperpolarize

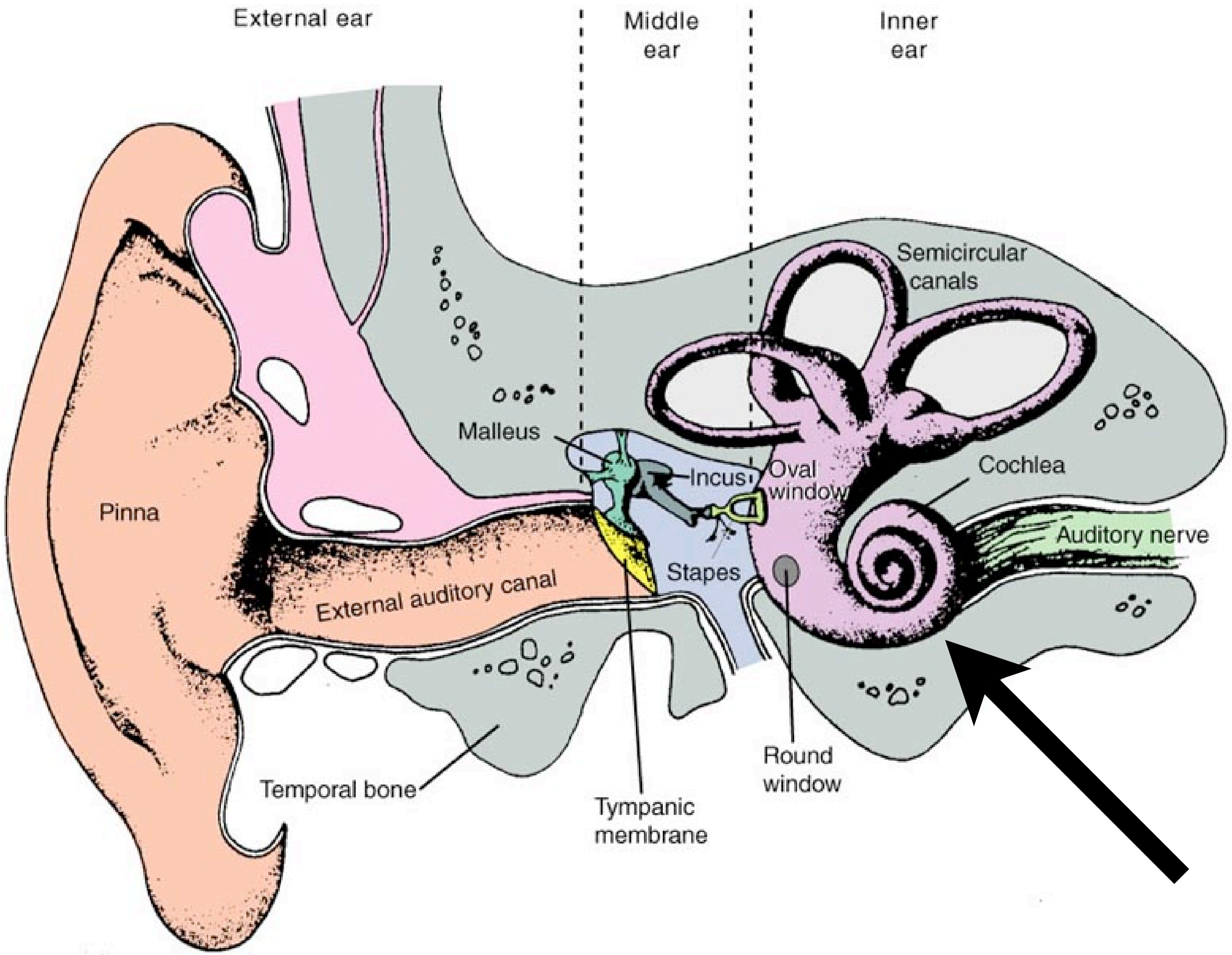
How stereocilia transduce sound into current



mechanically-gated ion channels

deflection towards longest stereocilia: more channels open → depolarization → response to sound

The cochlea is the sensory endorgan for the auditory system

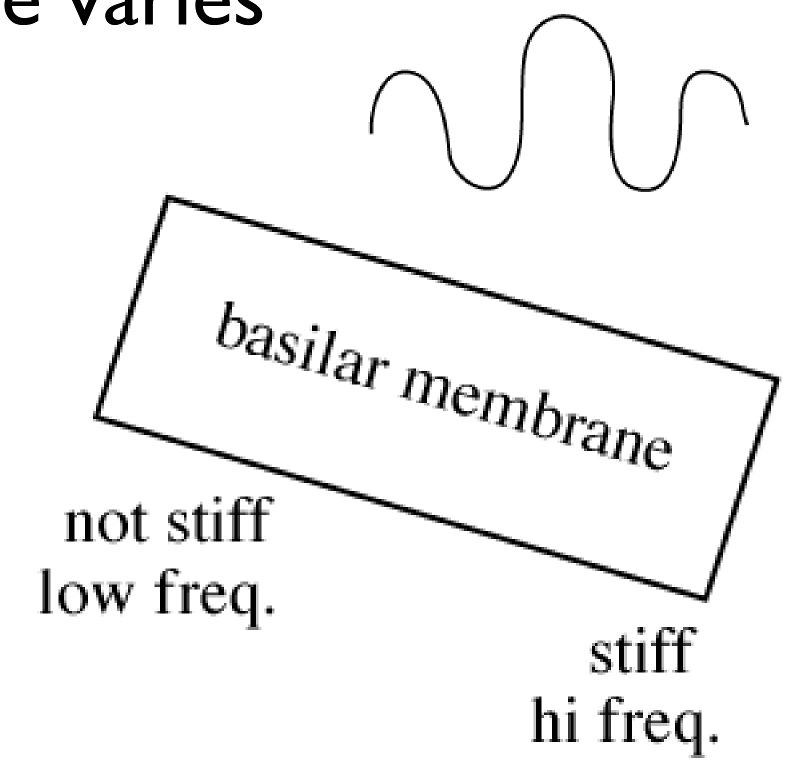


Basilar membrane stiffness

- stiffness of basilar membrane varies
- tonotopic organization:

  - hair cells are arranged by frequency (from low to high)

  → <u>frequency tuning</u>



Two types of frequency tuning (mechanisms for frequency selectivity in hair cells)

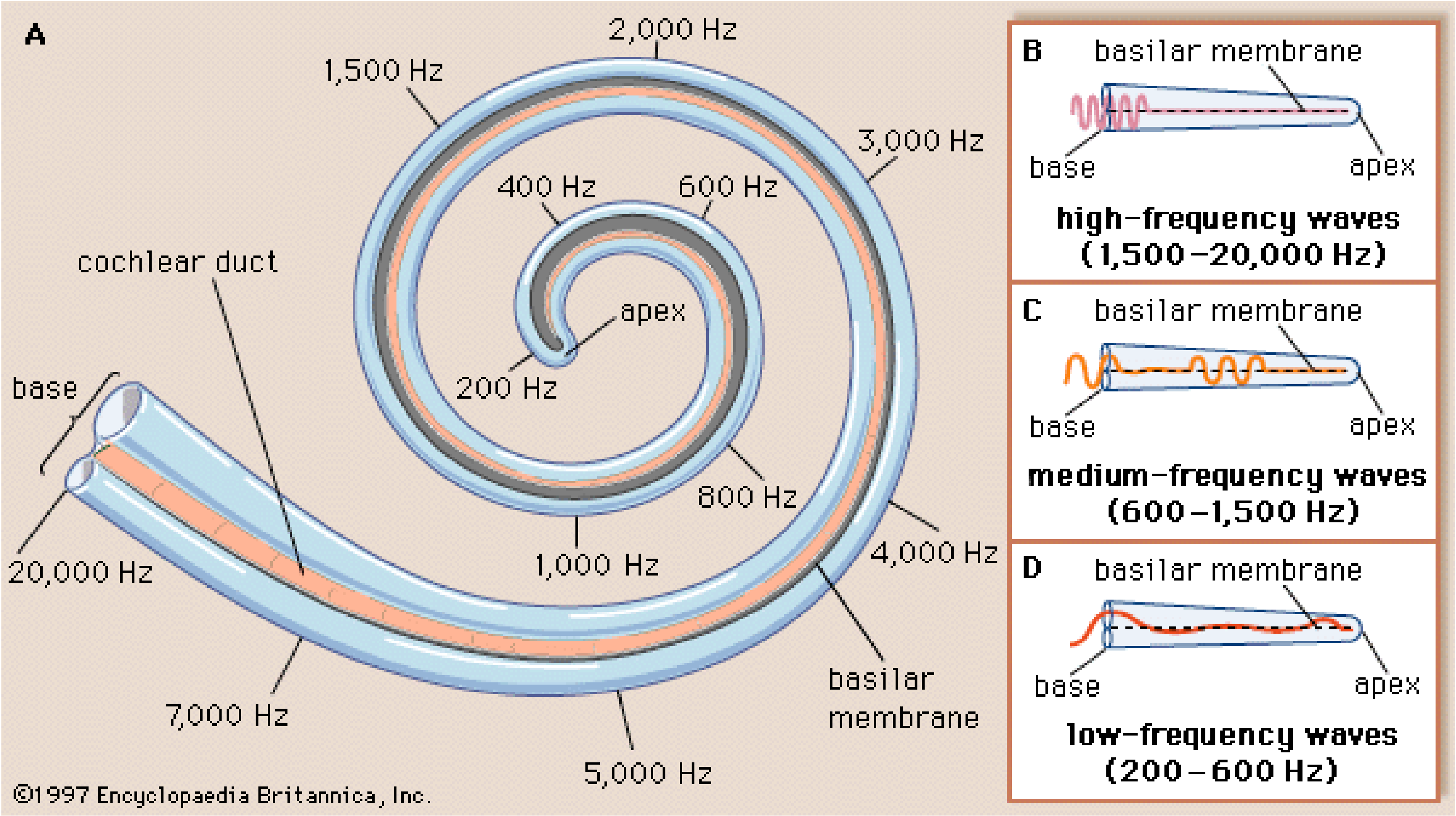
- mechanical: due to <u>stiffness in basilar membrane</u>

  (in lower vertebrates: height of stereocilia varies: longer toward the low-freq. end)

- electrical: due to <u>kinetics of K+ channels</u> in hair cell
  →conductance of ionic current differs among hair cells

- E.g. recording from single turtle hair cell: depolarization will lead to "ringing" of membrane potential at **characteristic frequency** of that cell (< 500 Hz).

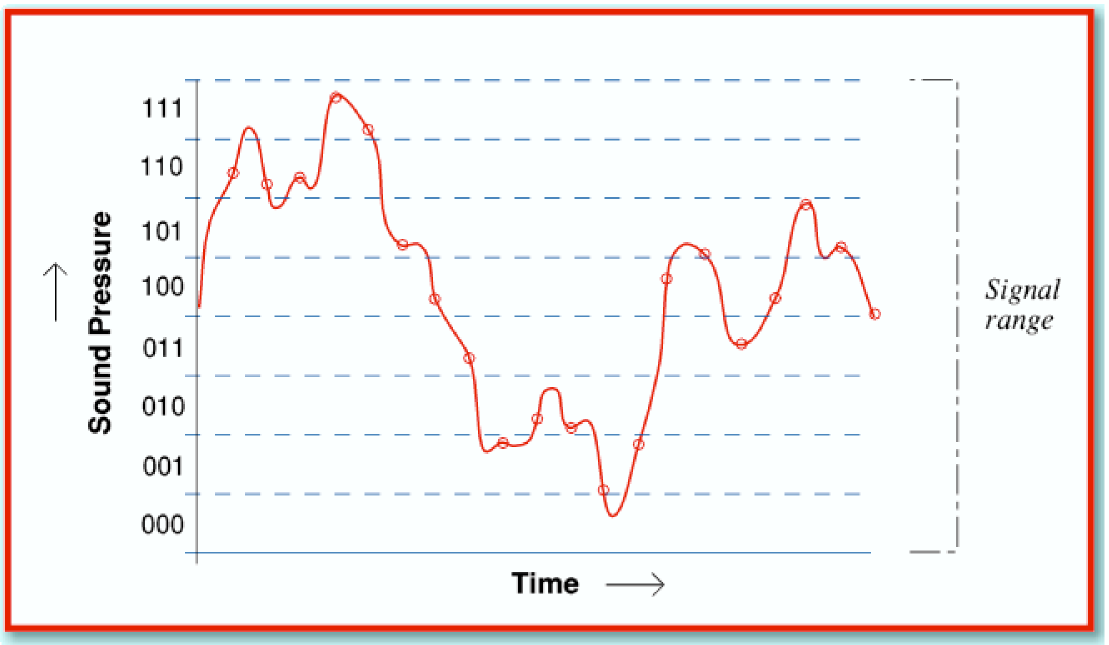
Basilar membrane: frequency mapping (tonotopy)

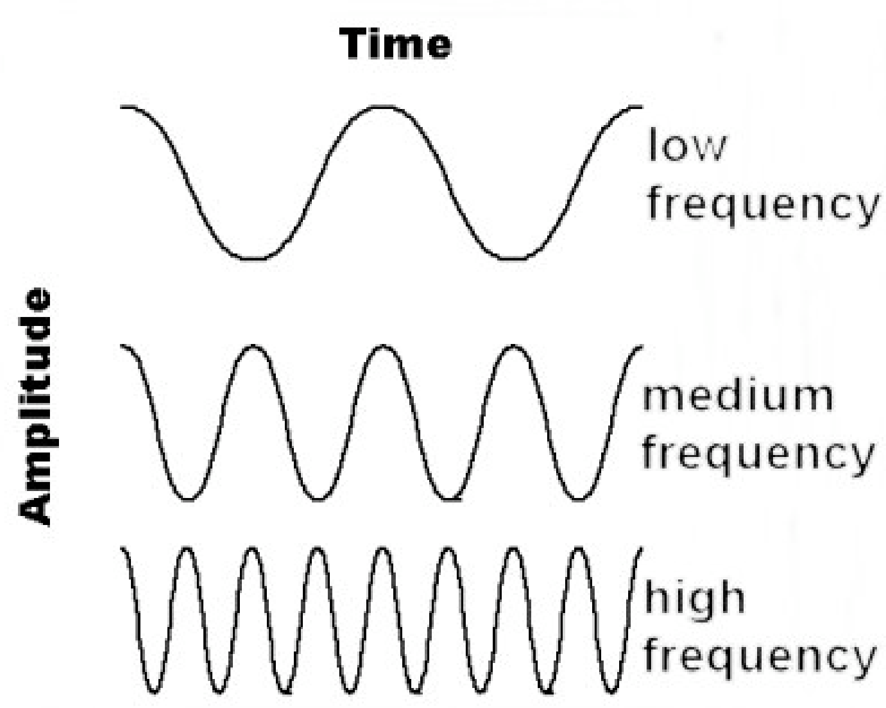


Cochlea breaks incoming sound into individual frequencies

- = Fourier Transform

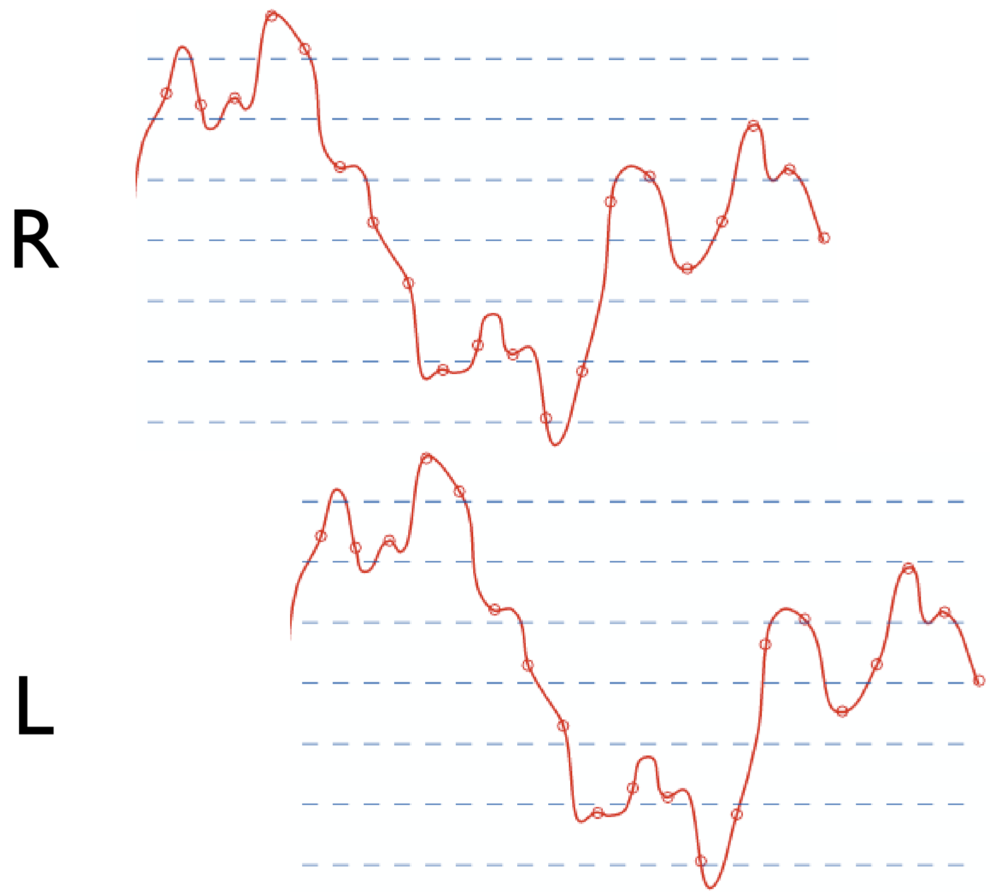
What is the Fourier Transform?





Decompose sound waveform into component frequencies (sine waves)

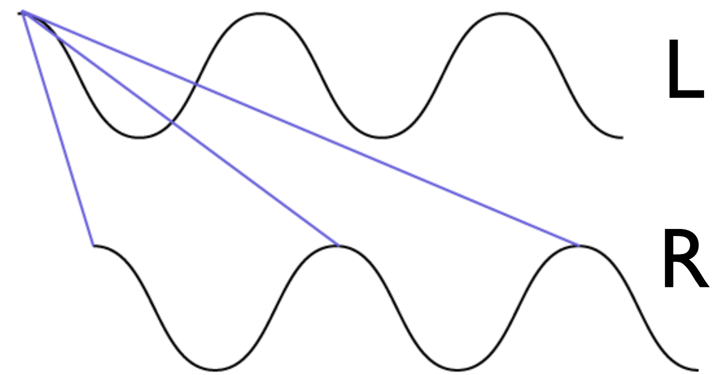
ITD - interaural time delay



- how to localize sound - need to know which ear heard it first - compare L w/ R
- if one ear delayed relative to the other → sound coming from first ear's direction

Aperture Problem for Sound Localization

- frequency filtering poses a problem for sound localization - a pure sound wave cannot be localized in space.
- Aperture Problem: each receptor only sees a tiny part of the picture - one frequency
- How does the auditory system solve this problem?

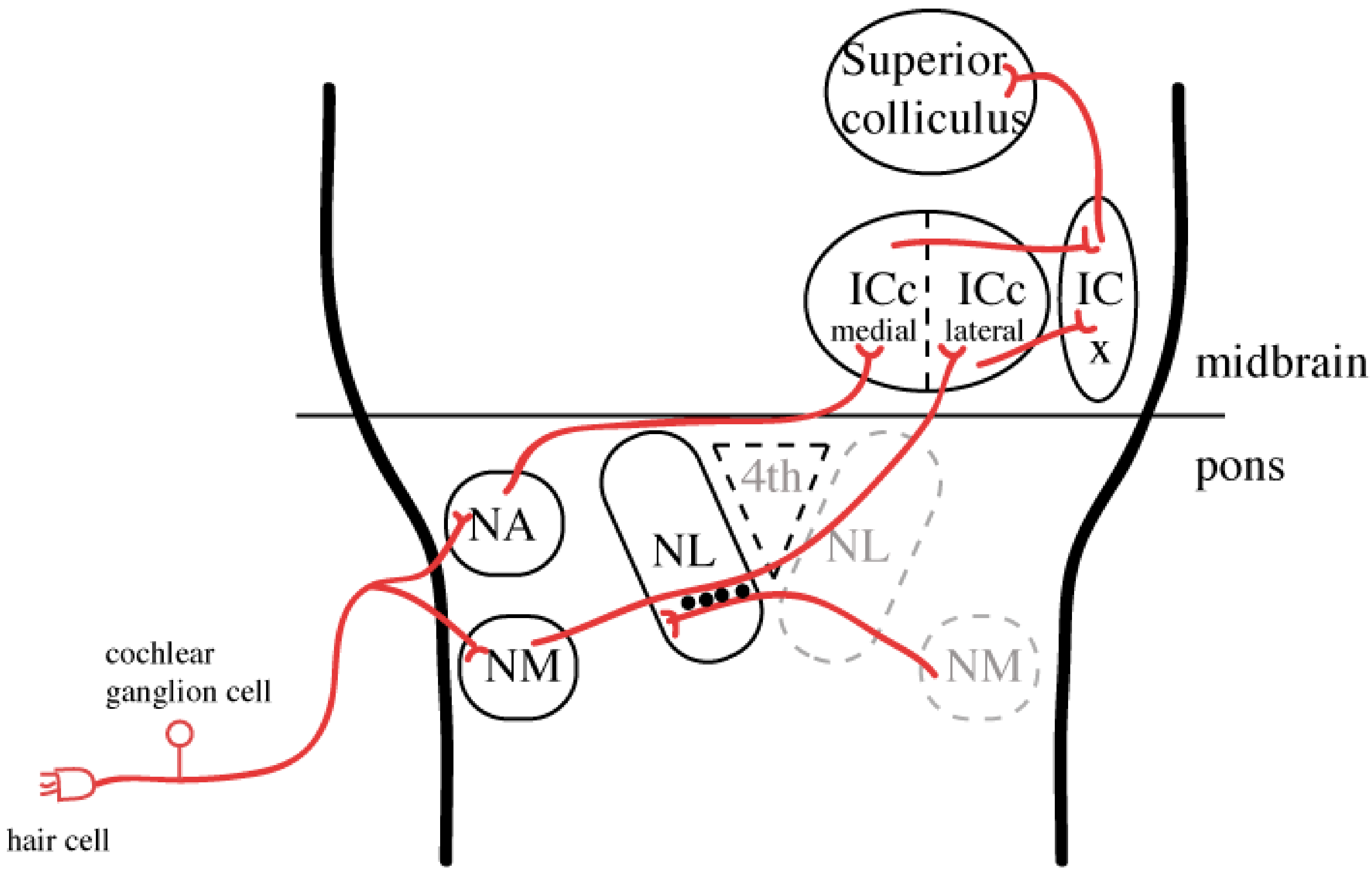


can’t tell which peak matches up with which (i.e. which came first - L or R?)

Owl auditory system

- barn owls are nocturnal
- very good at sound localization
- feathers guide sound towards ears ('radar dish'); special facial muscles

From cochlea to brain stem, midbrain



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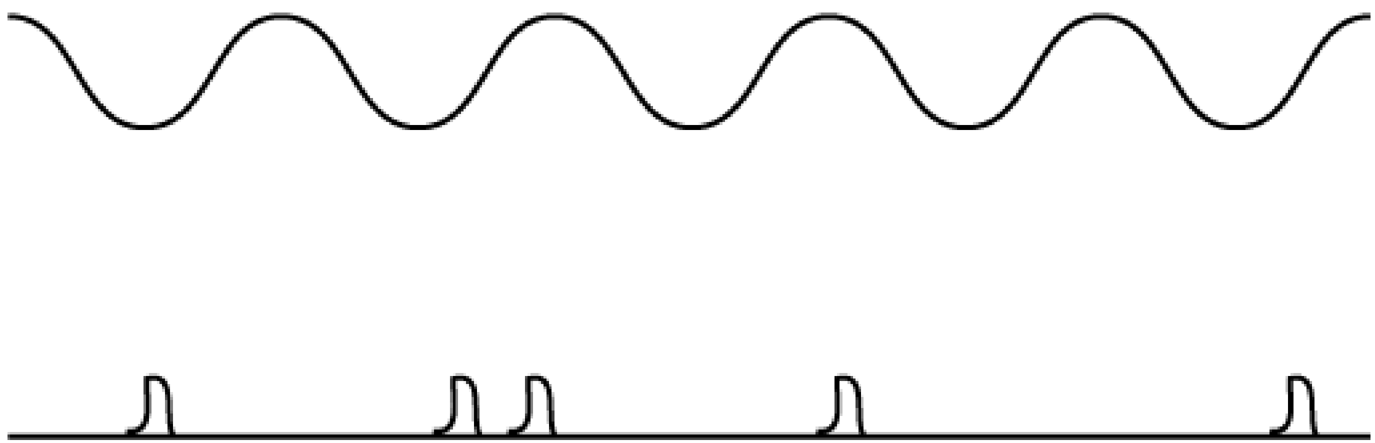
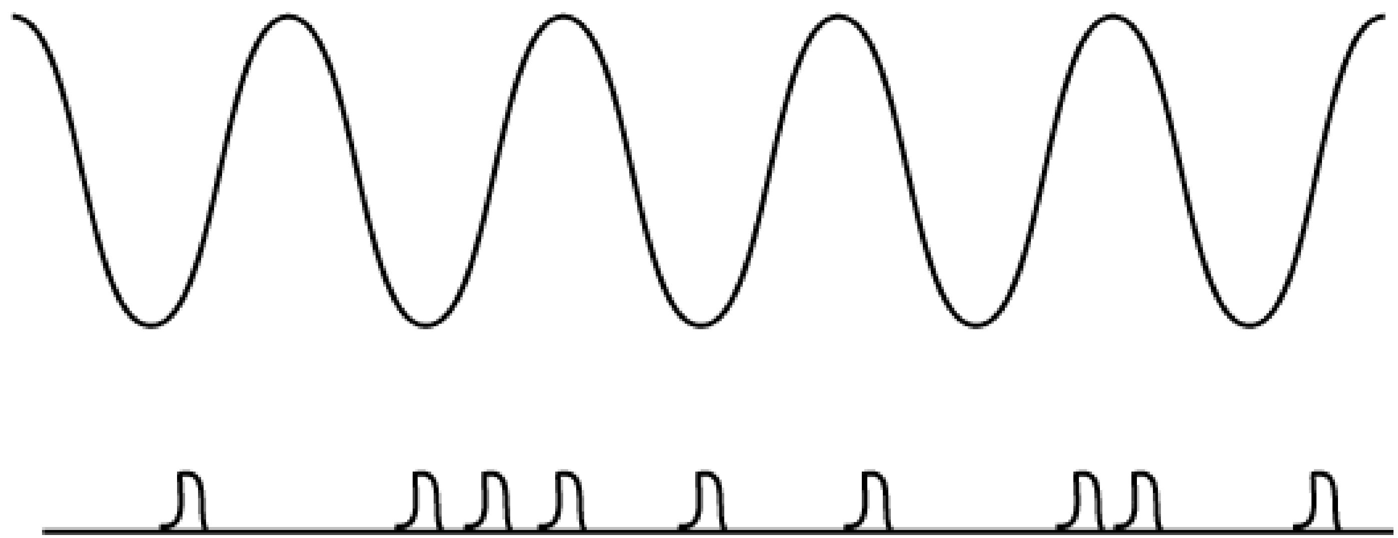
- NA = nucleus angularis (amplitude pathway) (PVCN)
- NM = nucleus magnocellularis (frequency/timing pathway) (AVCN = anterior ventral cochlear nucleus)
- NL = nucleus laminaris (binaural; coincidence detector) (MSO = superior olive in humans)
- IC = inferior colliculus
- ICc lat = central inferior colliculus, lateral part; ICc med; ICx = IC external part
- ICx has a complete space map of both horizontal and vertical location in space; projects to SC (superior colliculus)

Nucleus Angularis response properties



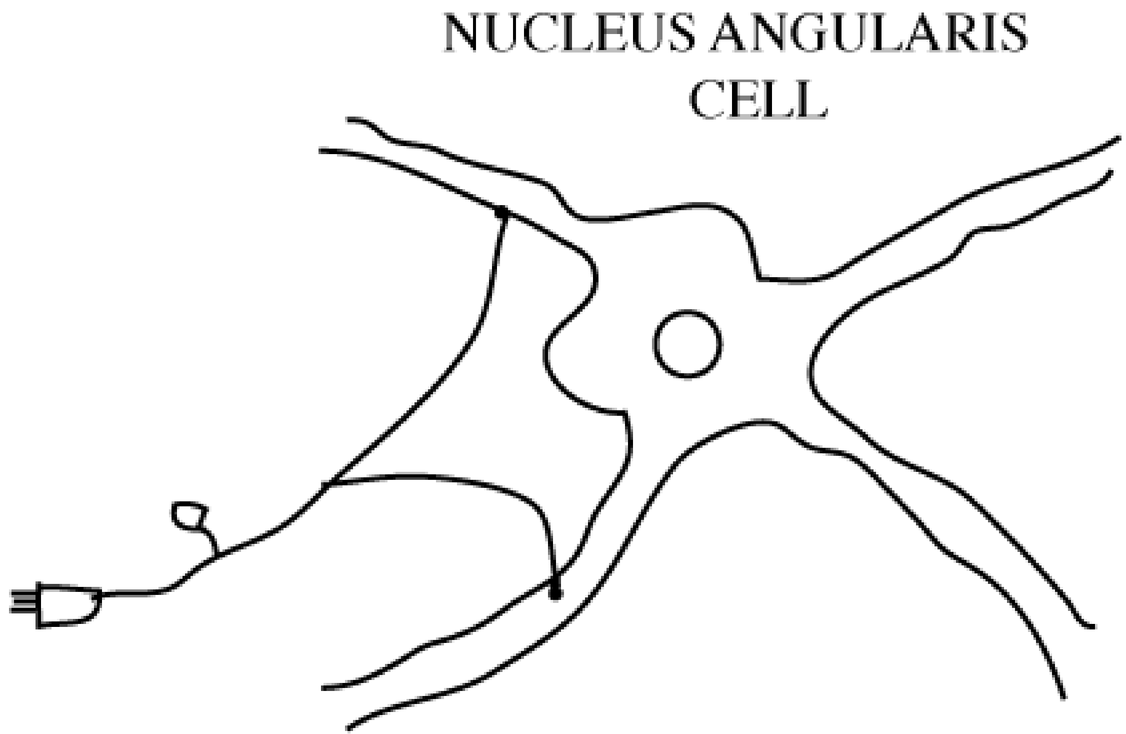
- NA codes for AMPLITUDE (loudness) of sounds
- NA is tonotopic: each neuron codes for 1 frequency
- monaural
- response is not phase-locked to wave

Nucleus Angularis response properties:



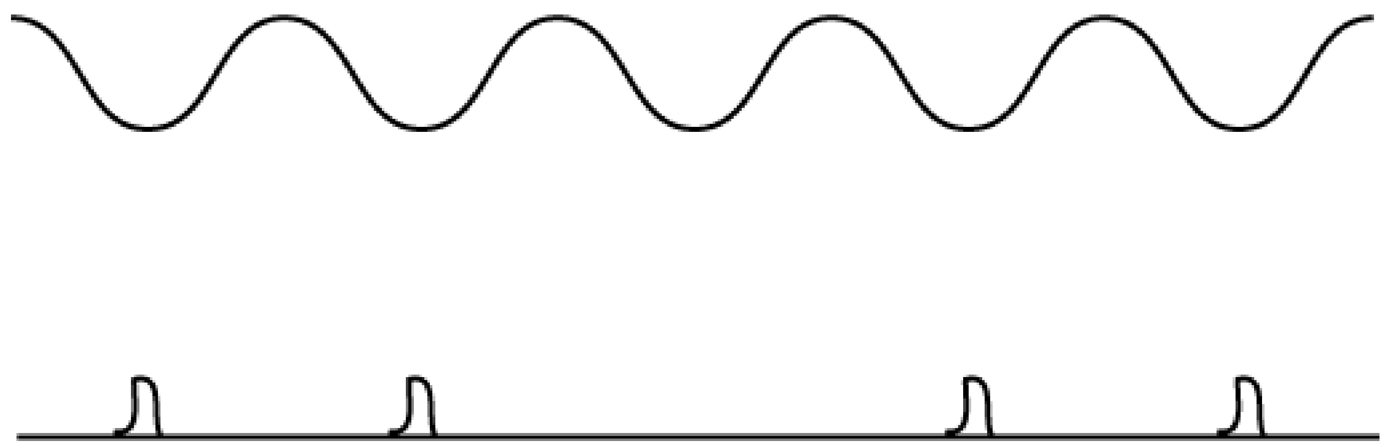
- if you have a louder sound: more spikes.

Reason for NA's non-time-locked response:



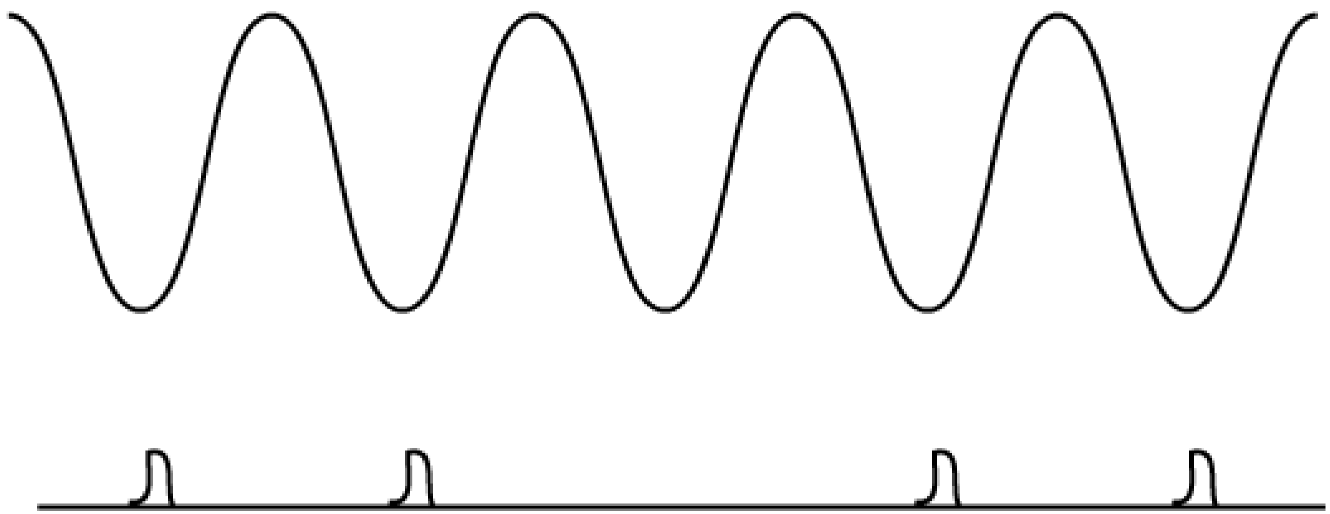
- big dendrites smear out the temporal signal; capacitance of membrane delays signal integration.

Nucleus Magnocellularis Response Properties



- NM has phase-locked responses
- NM is also tonotopic: each cell represents one frequency
- monaural
- don’t need to respond to each wavefront - but always with the same delay

Nucleus Magnocellularis Response Properties

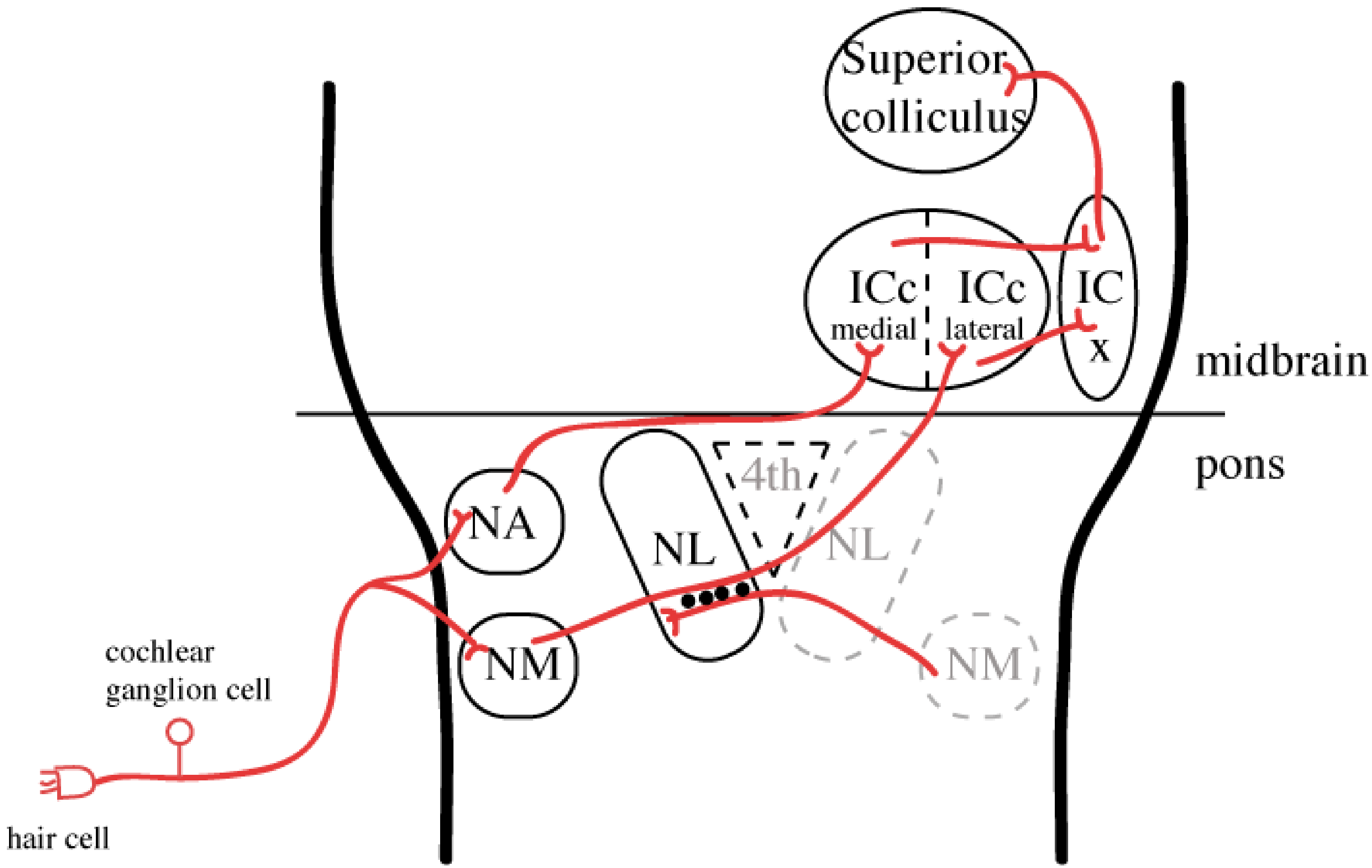


- amplitude does not affect time-locked response

Reason for NM's phase-locked response:

- cochlear ganglion synapses tightly directly onto cell body of NM neurons
- no dendrites; no delay

Ipsilateral and contralateral NM project to Ipsilateral Nucleus Laminaris



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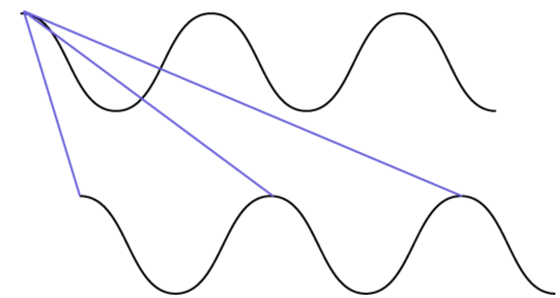
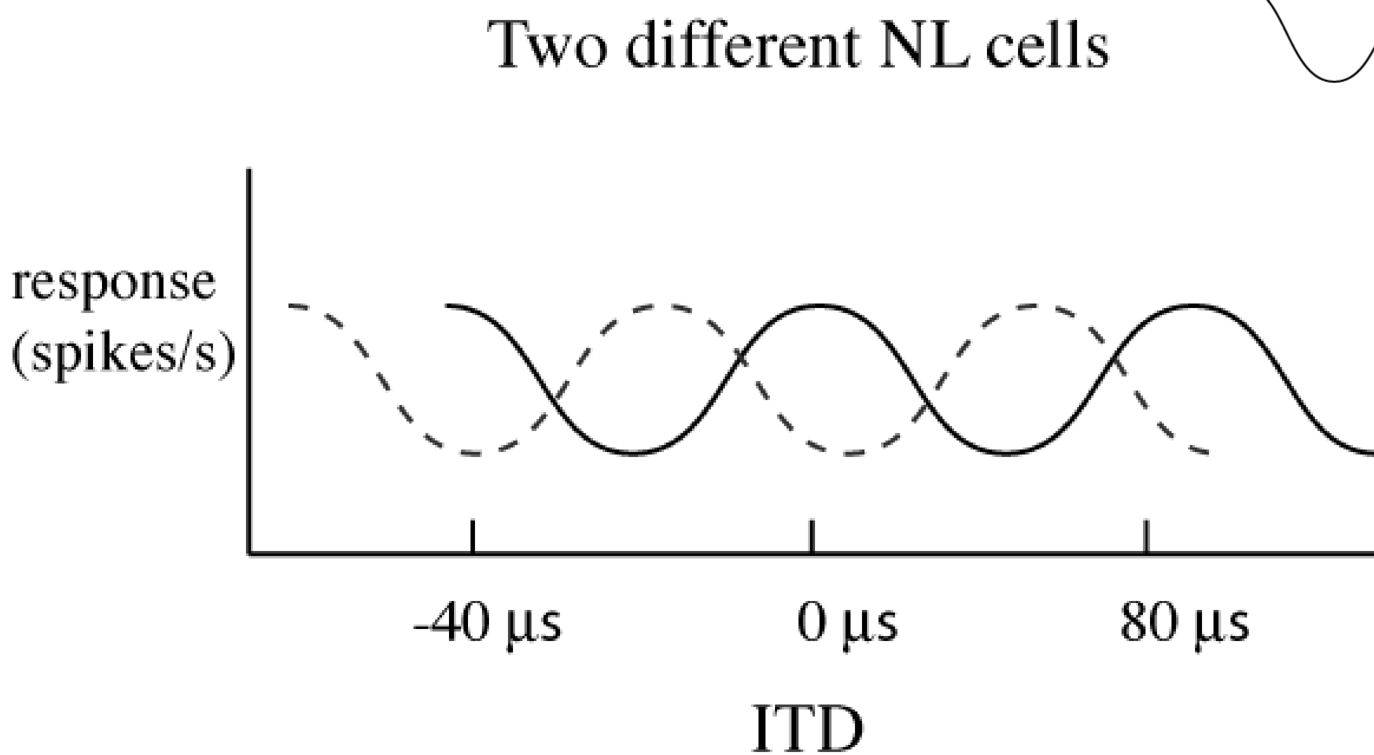
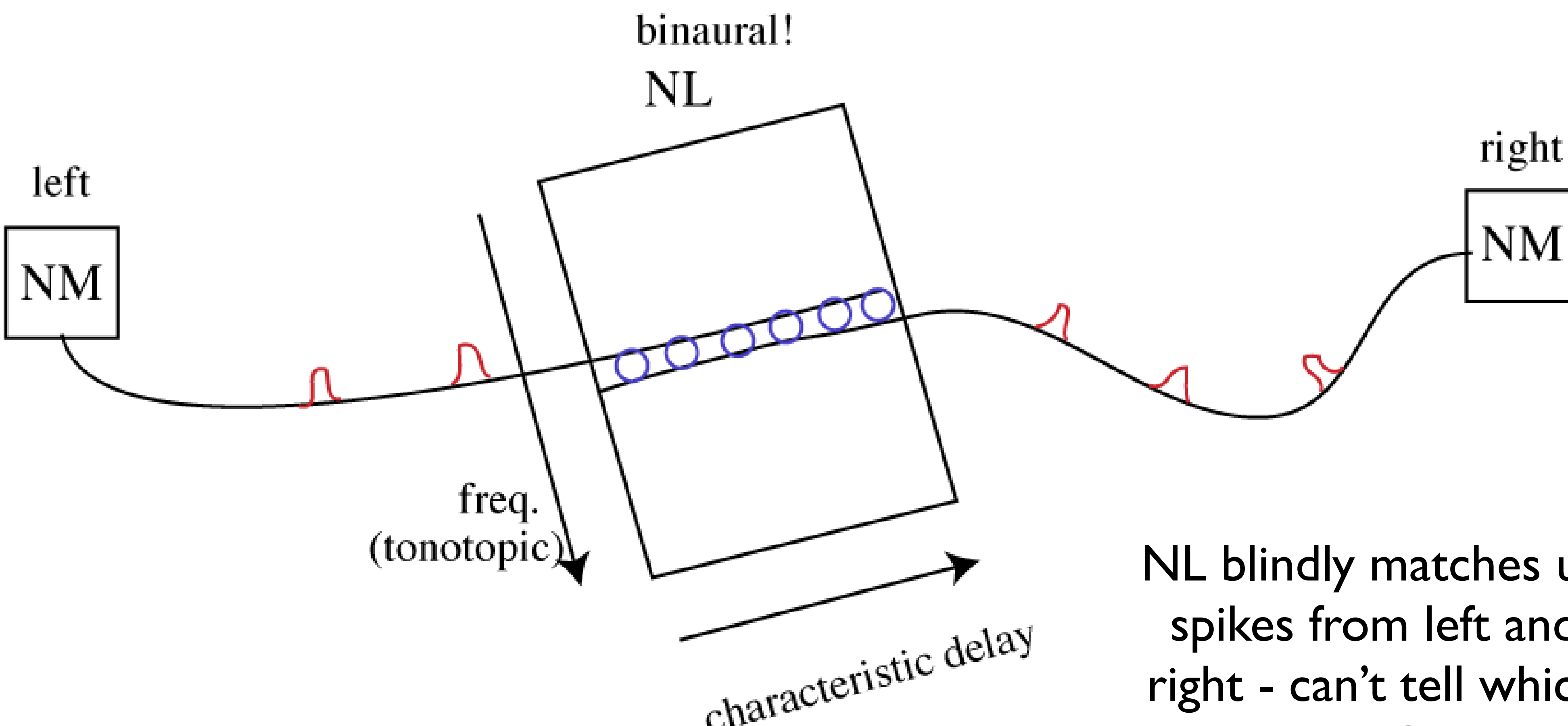
NL can’t figure out true true ITD

- NL is BINAURAL. Can it solve the problem? - No:
- each neuron has its own preferred “ITD”
- ambiguity





NL - nucleus laminaris: coincidence detector



NL blindly matches up spikes from left and right - can't tell which came first

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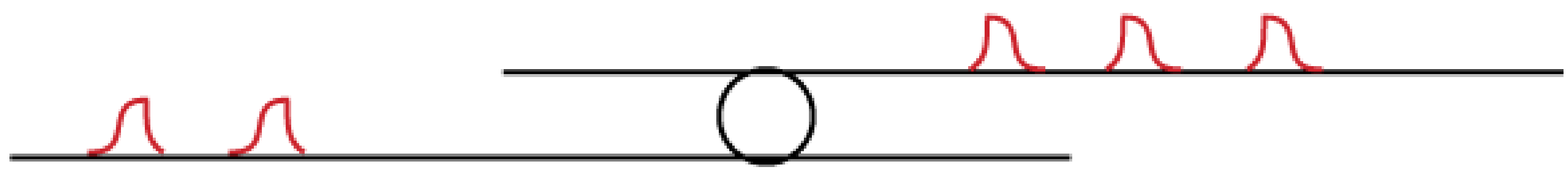
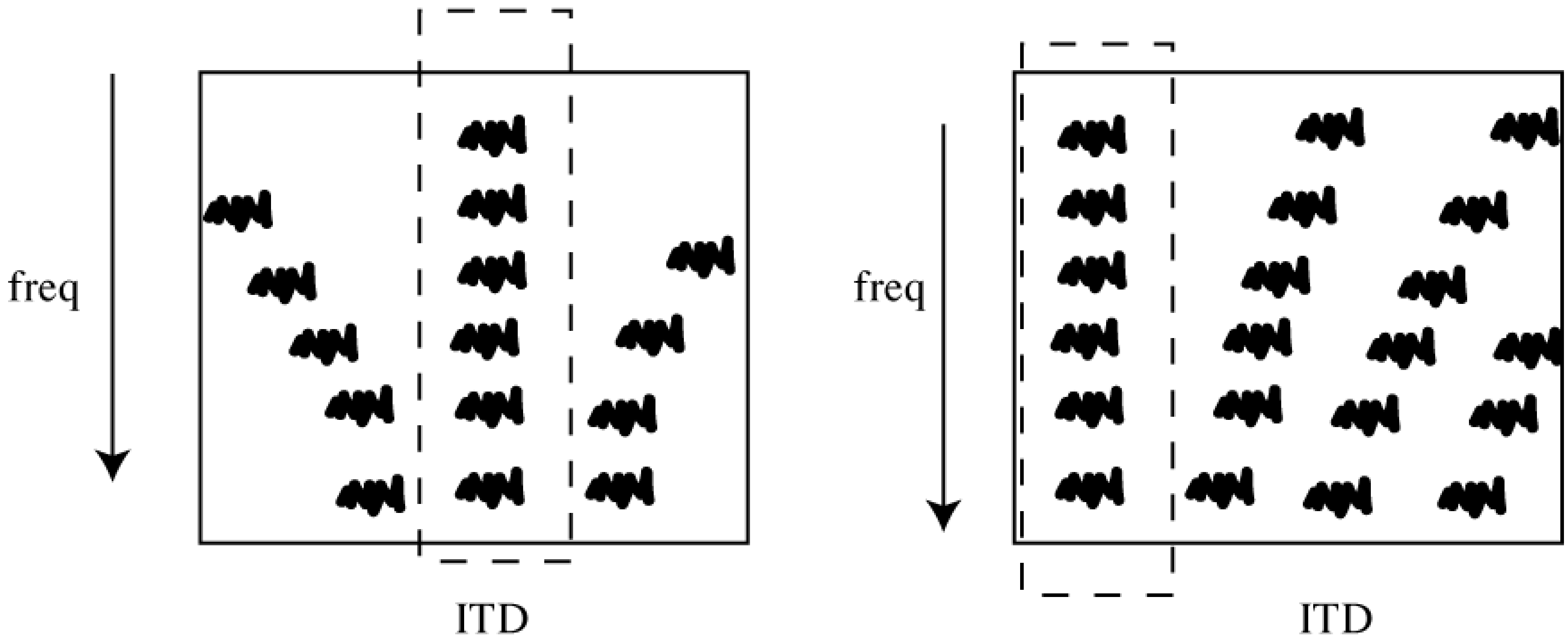
Each NL neuron only spikes when spikes coming from left and right NM coincide



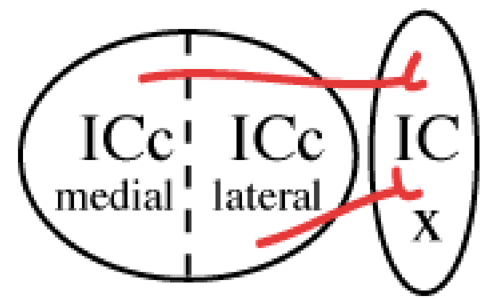
- how many times would this coincidence detector spike?

from NL to ICc_lateral: solution



- greatest activation (in column of ICc_lat cells) reflects true interaural time delay; bands of activated neurons

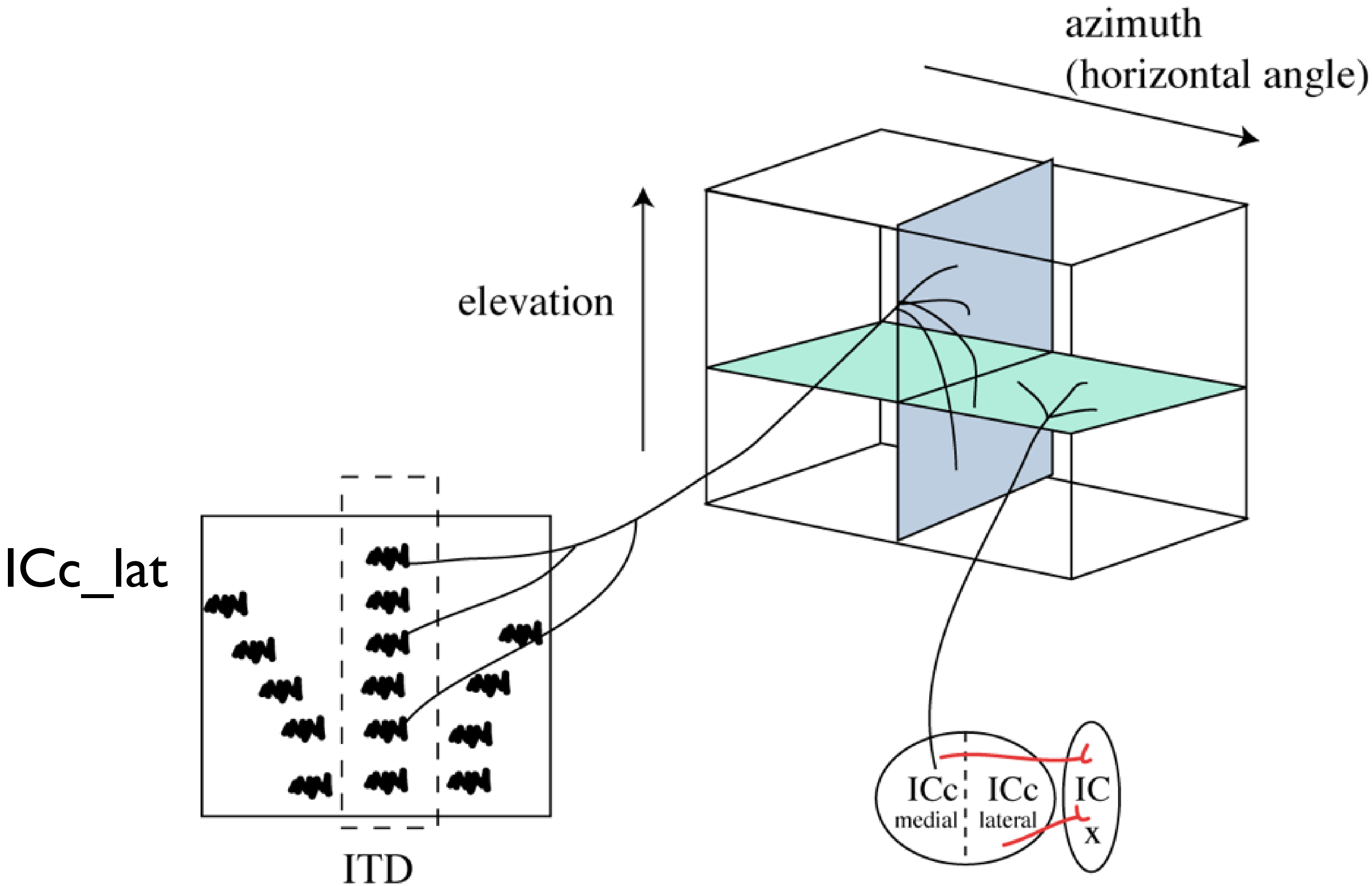
ICc_medial does similar thing in the amplitude pathway



- interaural intensity difference (IID)

- vertical location perceived b/c owl ears are asymmetrical - R ear closest to the ground, noises from below are **louder**

Projections from ICClat & ICCmed to ICx

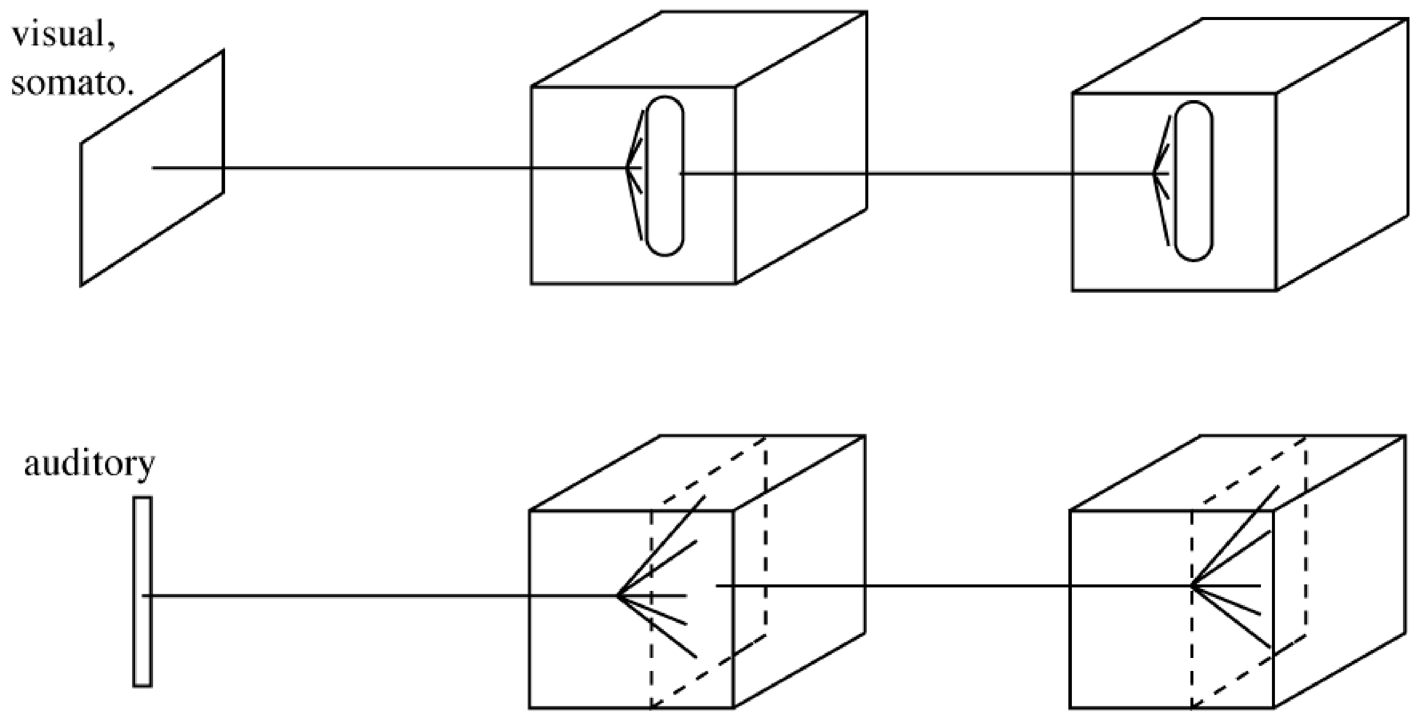


- ICx contains complete spatial map (vertical and horizontal)

Flavia Filimon, Systems Neuroscience 2008

- ICx has auditory map of space
- azimuth: horizontal position
- elevation: vertical position
- from ICx to SC: point-to-line projection again (auditory system connecting to visual system)

Difference between auditory system and visual & somatosensory systems



- Vis., somato.: receptors are arranged on a 2-D sheet; point-to-column projection
- Auditory: receptors are arranged in a 1-D line; point-to-sheet projection

Note:

- bat head is too small to use ITD (inter-aural time delay: delay too small, since ears are so close)

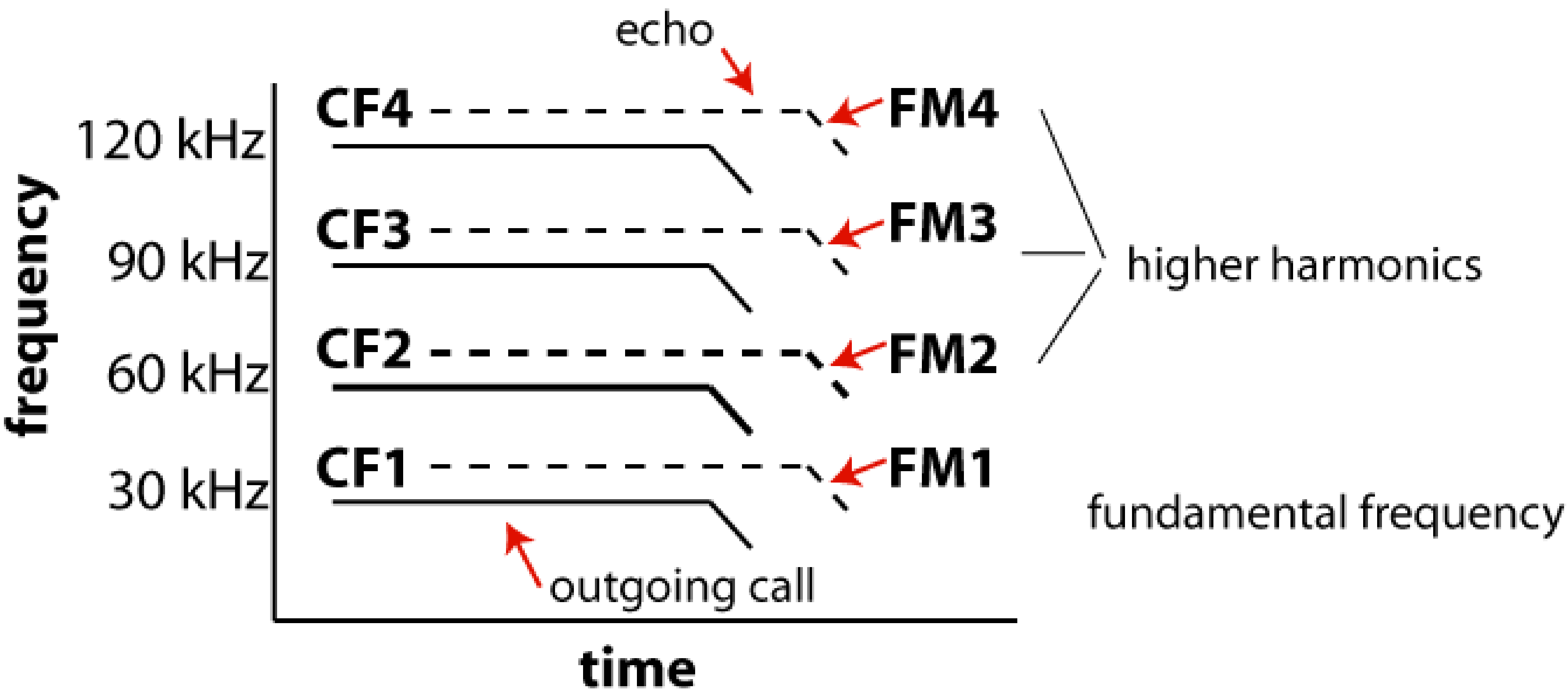
Bats navigate and find prey via echolocation

- high-frequency, very loud (120dB) sound emitted (biosonar pulse); bounces off prey (moth) and echo returns to bat:

  - Doppler-shifted (CF: constant frequency component)

  - delayed (FM: frequency-modulated component)

Bat call sonogram



- CF = constant frequency; FM = frequency modulation

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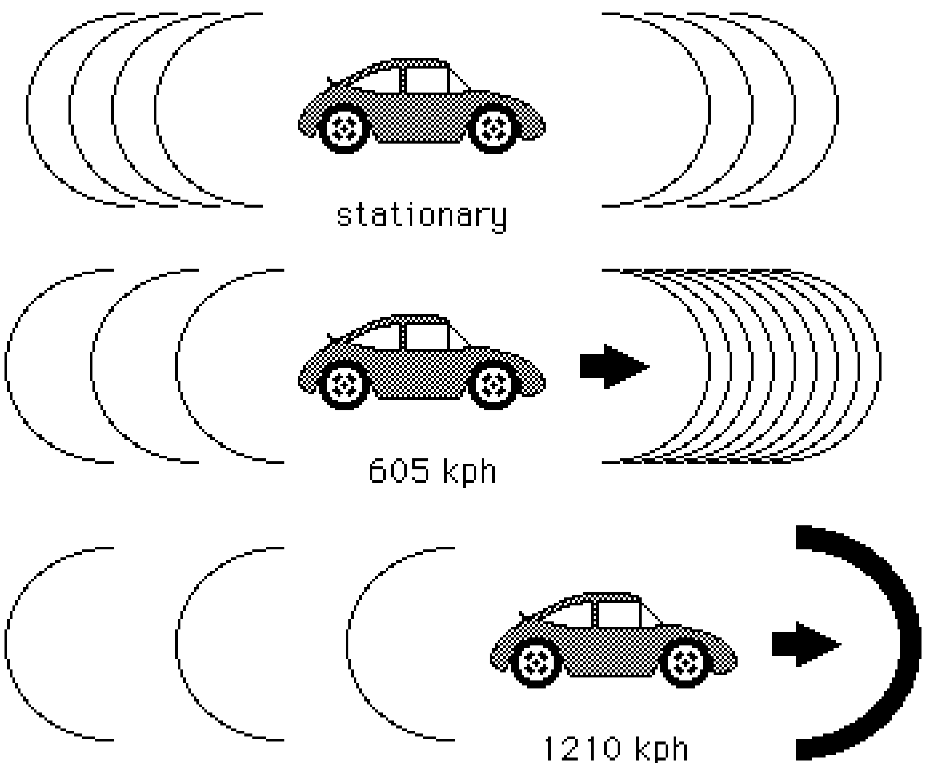
CF and FM components

- Constant Frequency: the Dopper shift of the frequency tells bat how fast the moth is flying away from it → relative velocity
- Frequency Modulated part: the delay between the FM part in the outgoing call and incoming echo signals the range or distance of the target

Doppler shift

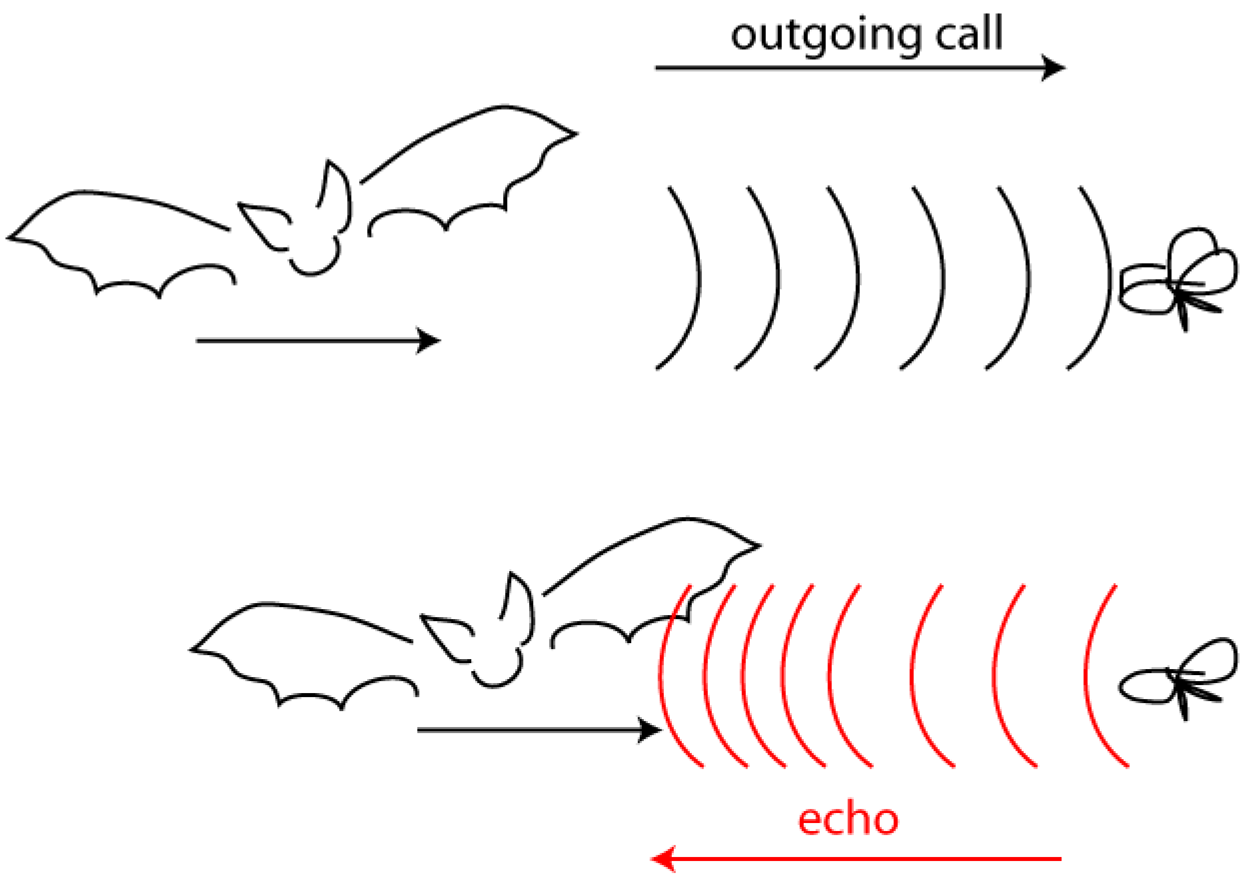


- a moving source of sound compresses sound waves in the direction of movement; → higher frequency (ambulance effect)
- sound in the wake of source: waves are more spaced out → low freq.

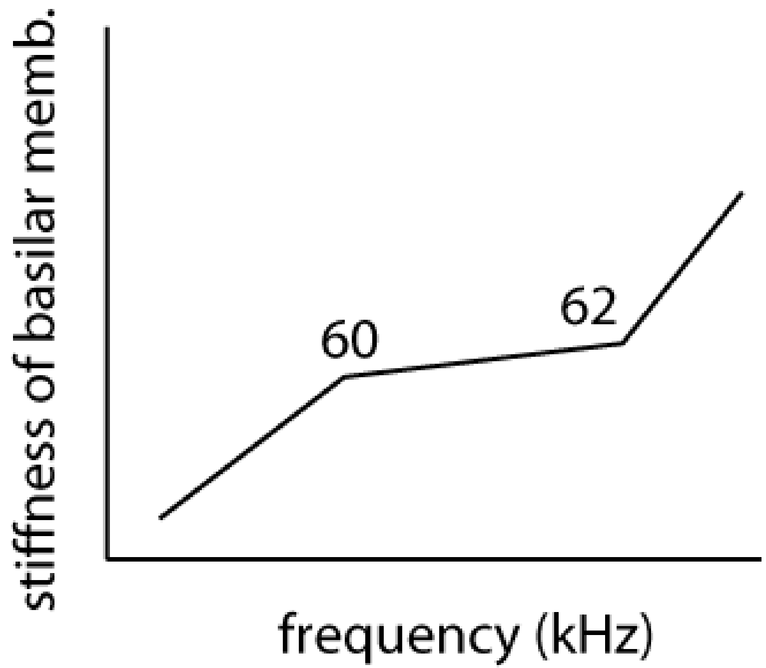
Doppler shift demo

- http://www.kettering.edu/~drussell/Demos/doppler/carhorn.wav

Doppler shift in bat call



Doppler shift compensation

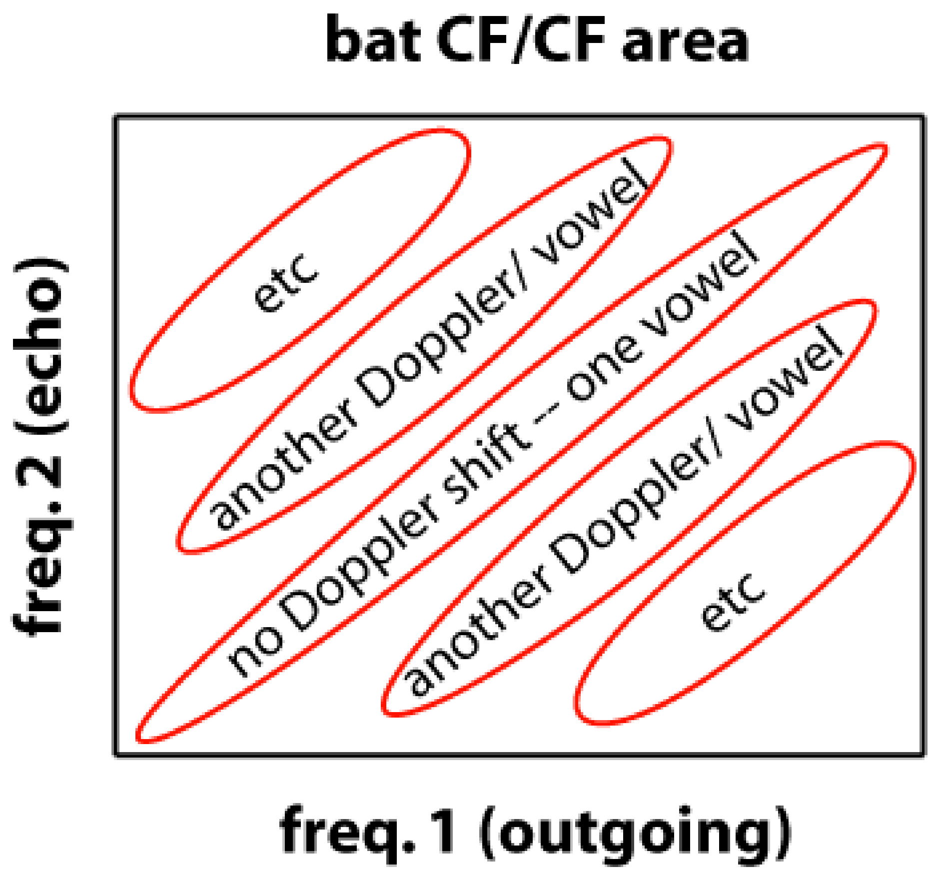


- bats adjust outgoing call so that Doppler-shifted echo is in the range of 60-62 kHz
- bats have an "auditory fovea" - more receptors devoted to this frequency range

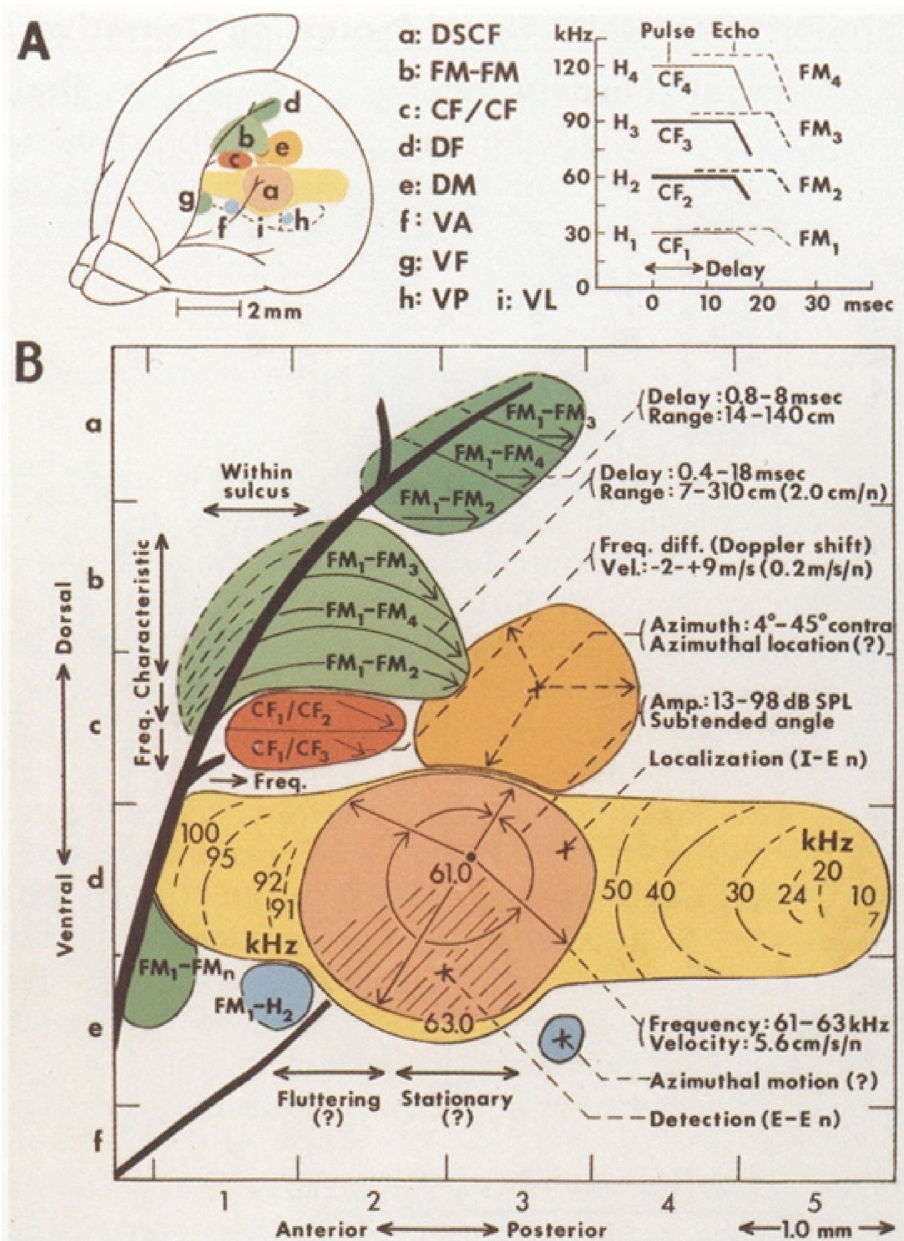
Doppler shift compensation

- If moth is flying away (distance increasing), will bat increase or decrease the frequency of its call?
- If bat is approaching moth (distance decreasing), will bat increase or decrease the frequency of its call?

Bat auditory cortex has combination-sensitive neurons: CF-CF and FM-FM



- in CF-CF region, the outgoing frequency (CF1) is compared with the incoming echo frequency (CF2)
- this makes individual neurons selective for particular moth velocities

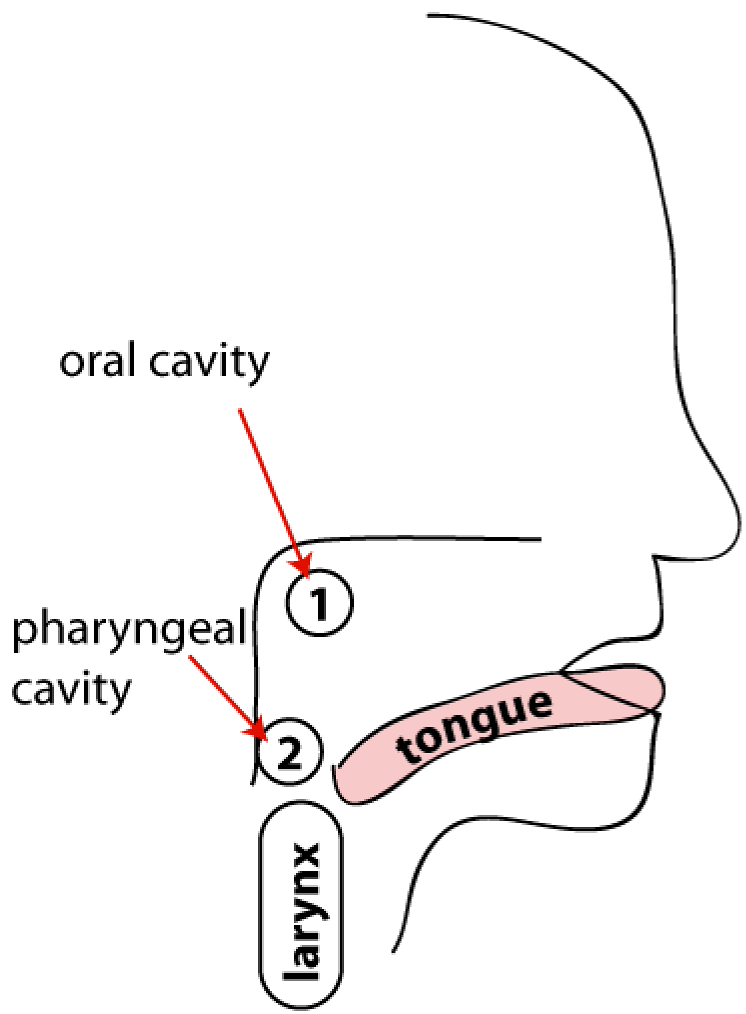


Nobuo Suga, 1988

Bat auditory cortex

- CF-CF combination-sensitive neurons: relative velocity of moth
- FM-FM combination-sensitive neurons: target range

What bat echolocation has to do with human speech processing

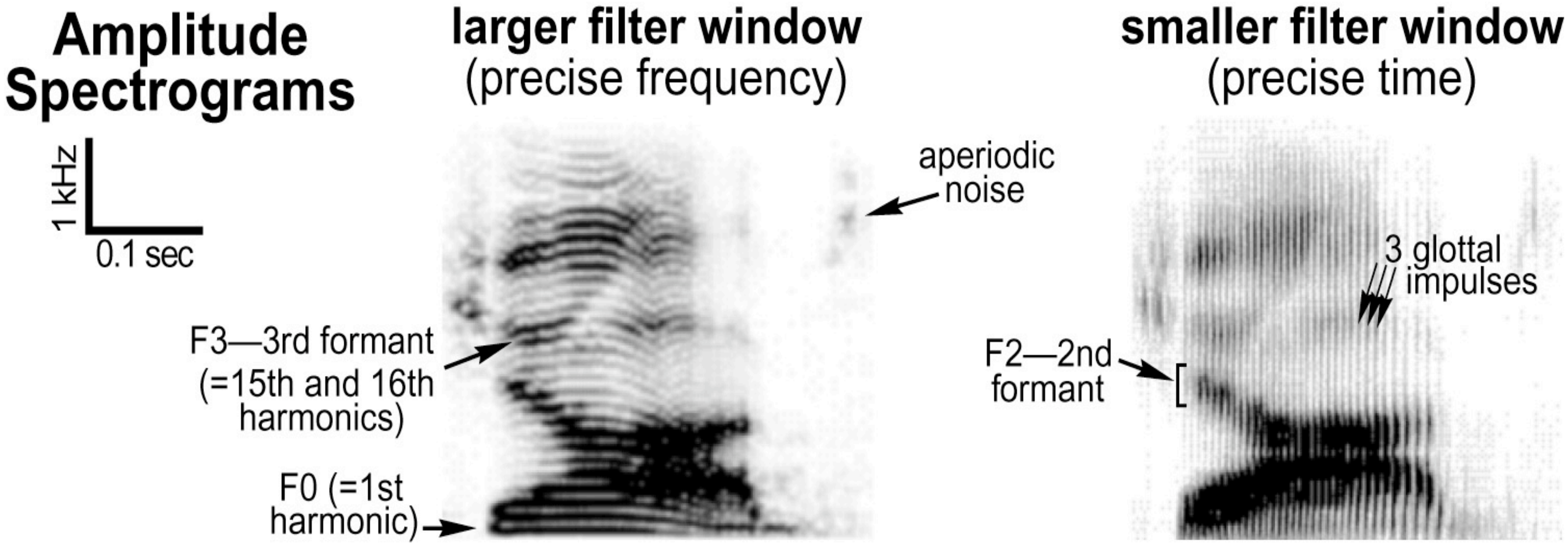


- vowels are characterized by bands of emphasized frequencies (formants), which are produced by the oral/pharyngeal filter, e.g. F1 and F2

Formants for one vowel

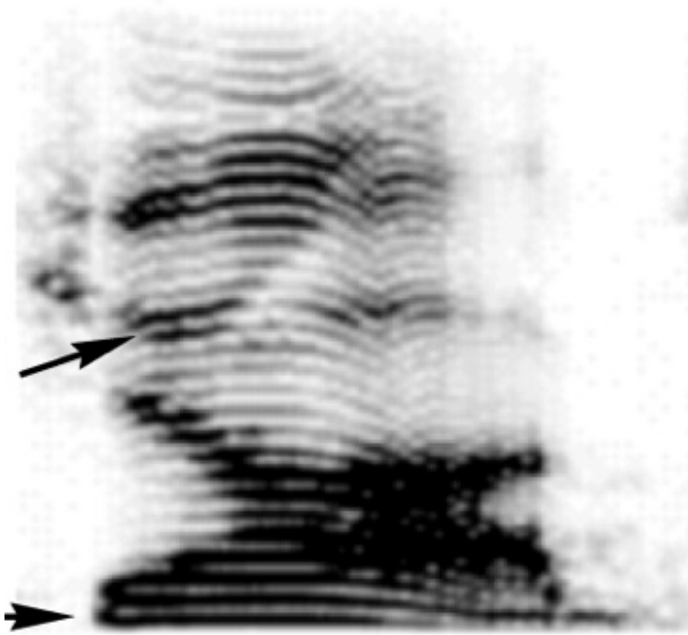
L: blurry time, good freq;
can see individual harmonics of vocal folds

R: good freq, blurry time;
can see individual time-resolved taps of each opening and closing of the vocal folds



Formants for one vowel

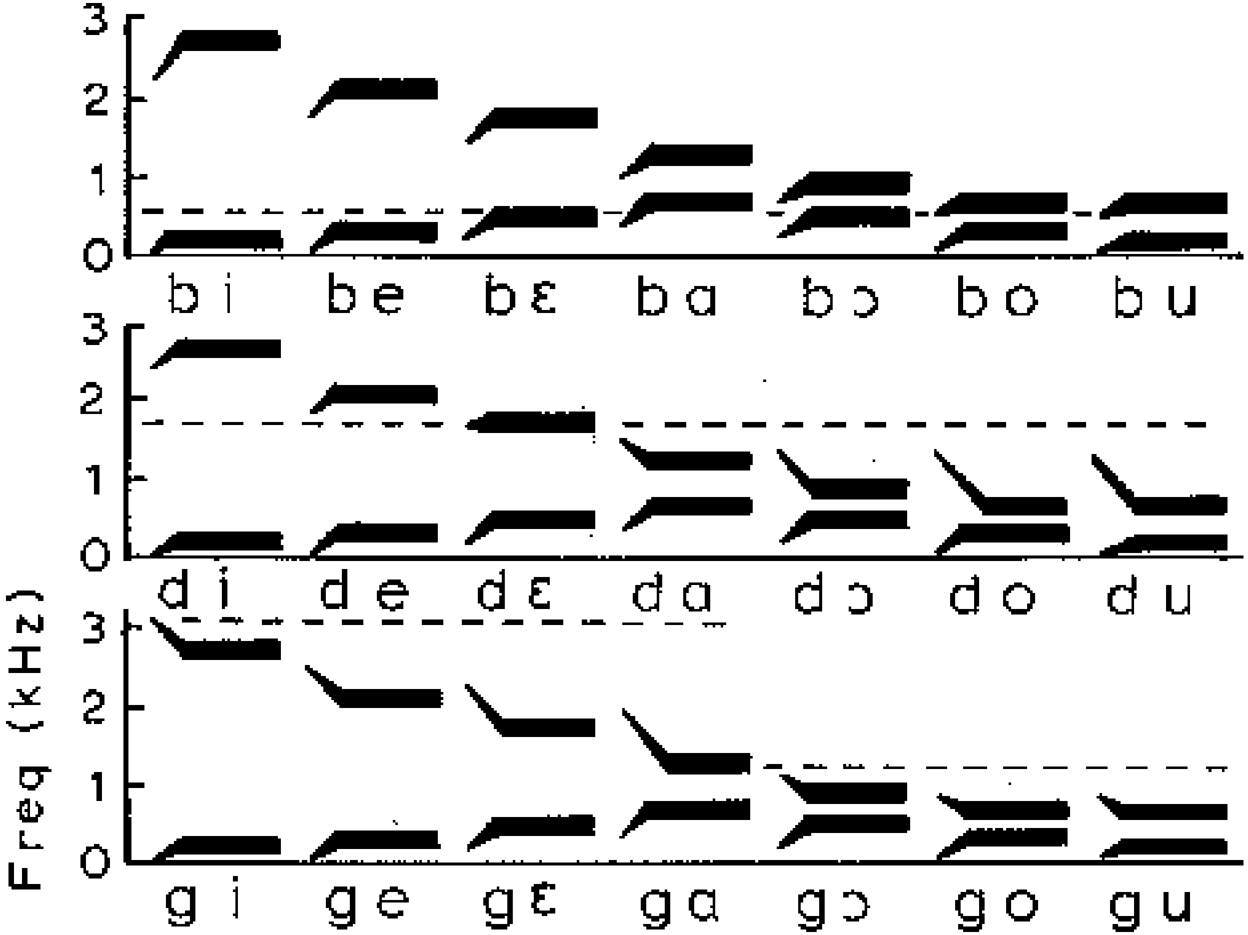
Frequencies contained in the vocal
tract when a vowel is pronounced:



Vowel formant centers

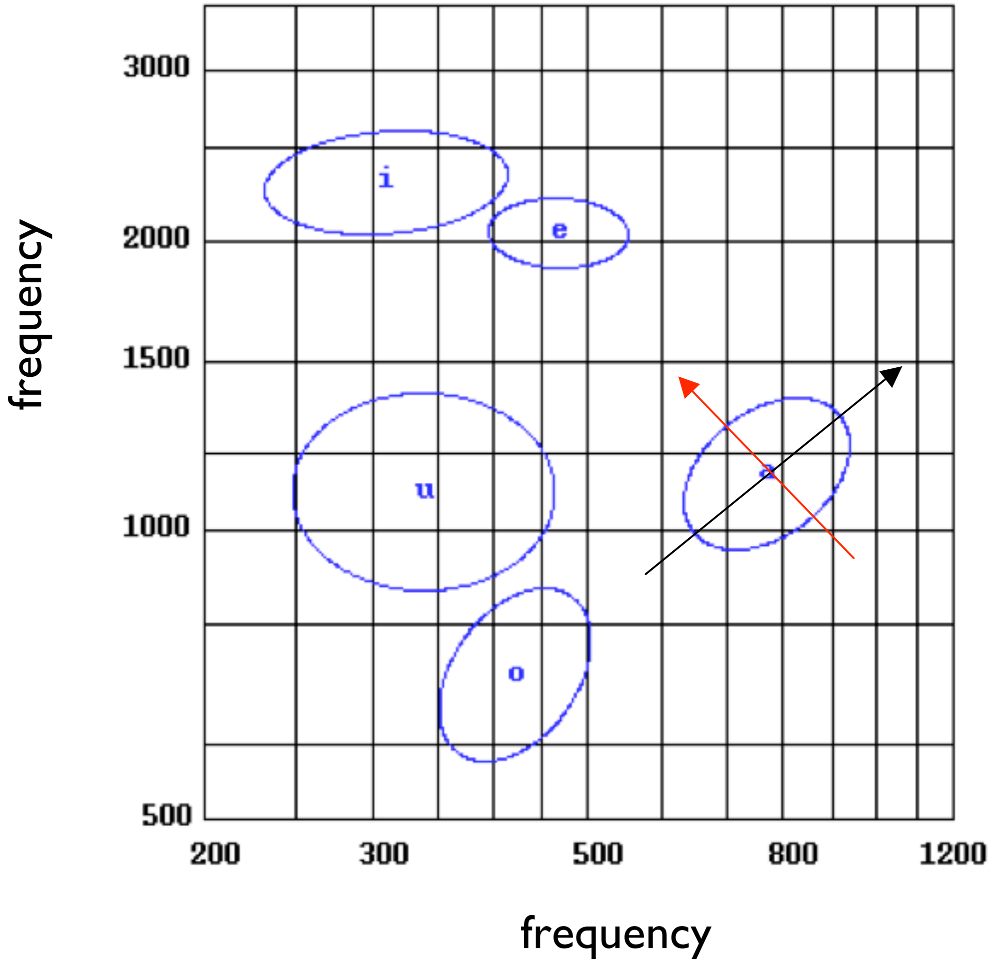
Vowel	IPA	Formant f_1	Formant f_2
u	u	**320 Hz**	800 Hz
o	o	**500 Hz**	1000 Hz
ɑ	ɑ	**700 Hz**	1150 Hz
a	a	**1000 Hz**	1400 Hz
ø	ø	500 Hz	**1500 Hz**
y	y	320 Hz	**1650 Hz**
æ	ɛ	700 Hz	**1800 Hz**
e	e	500 Hz	**2300 Hz**
i	i	320 Hz	**2500 Hz**

Formants



3
2
1
0
b i
b e
b ɛ
b ɑ
b ɔ
b o
b u
d i
d e
d ɛ
d ɑ
d ɔ
d o
d u
g i
g e
g ɛ
g ɑ
g ɔ
g o
g u
Freq (kHz)

Formants



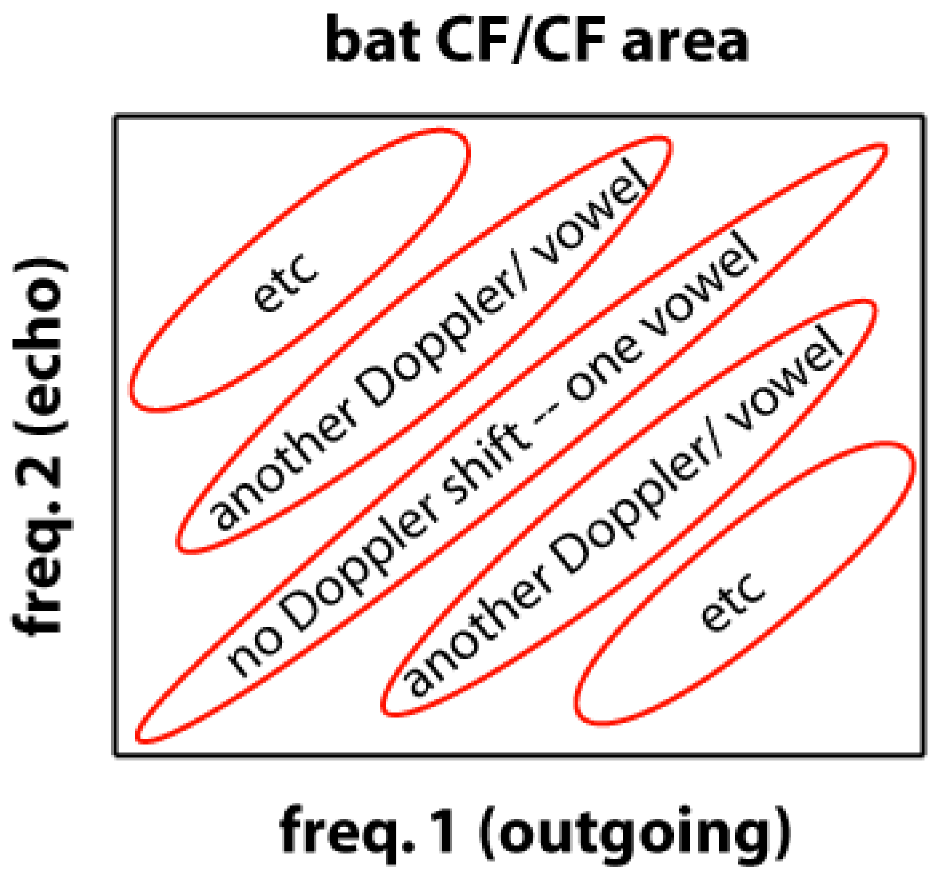
Variation in this direction reflects differences in vocal tract size

This direction optimal to distinguish between vowels

Vowel formants and gender

- depending on vocal tract size, vowel formants will be shifted up or down (females have high-pitch voice, format bands are shifted up → higher frequencies)
- how do we still recognize a vowel spoken by different speakers?
- → Suga (1988): perhaps combination-sensitive neurons in human auditory cortex detect relative spacing between formant bands, just like bats detect Doppler shift: F1 compared with F2
- same "frequency ratio" F1: F2 despite upward/downward shift

Formants vs. Doppler shift



- similar auditory area in humans?