Auditory Physiology

Outline

- **Basic Anatomy**
  - Where things are located inside your head
- **Normal Physiology**
  - How we extract information about sounds
- **Impaired Physiology**
  - How it can all go wrong

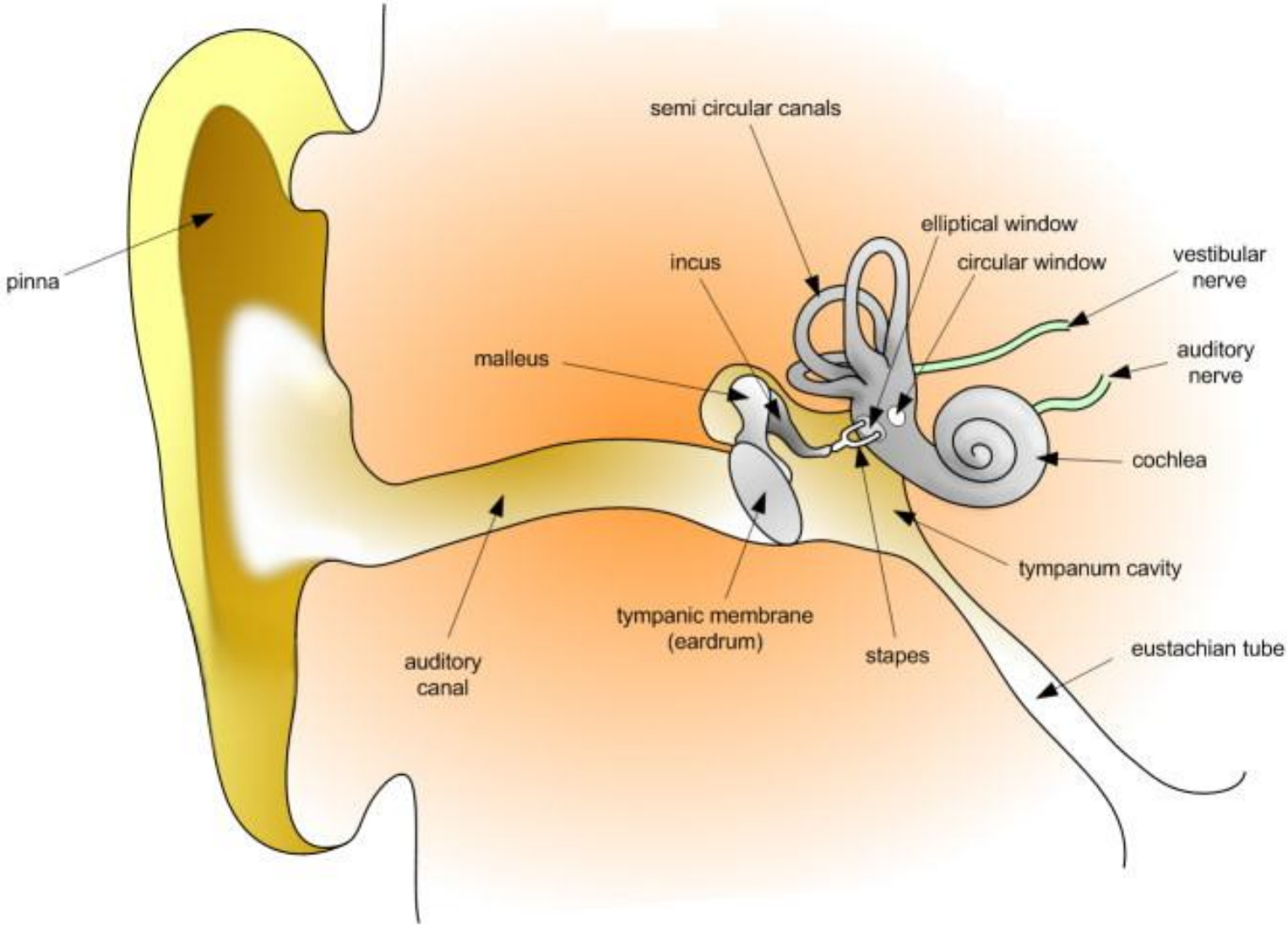
Outline

- **Basic Anatomy**
  - Where things are located inside your head
- Normal Physiology
  - How we extract information about sounds
- Impaired Physiology
  - How it can all go wrong

Auditory Transduction

[video]

The Ear


semi circular canals
elliptical window
incus
circular window
vestibular nerve
pinna
malleus
auditory nerve
cochlea
tympanum cavity
tympanic membrane (eardrum)
stapes
eustachian tube
auditory canal

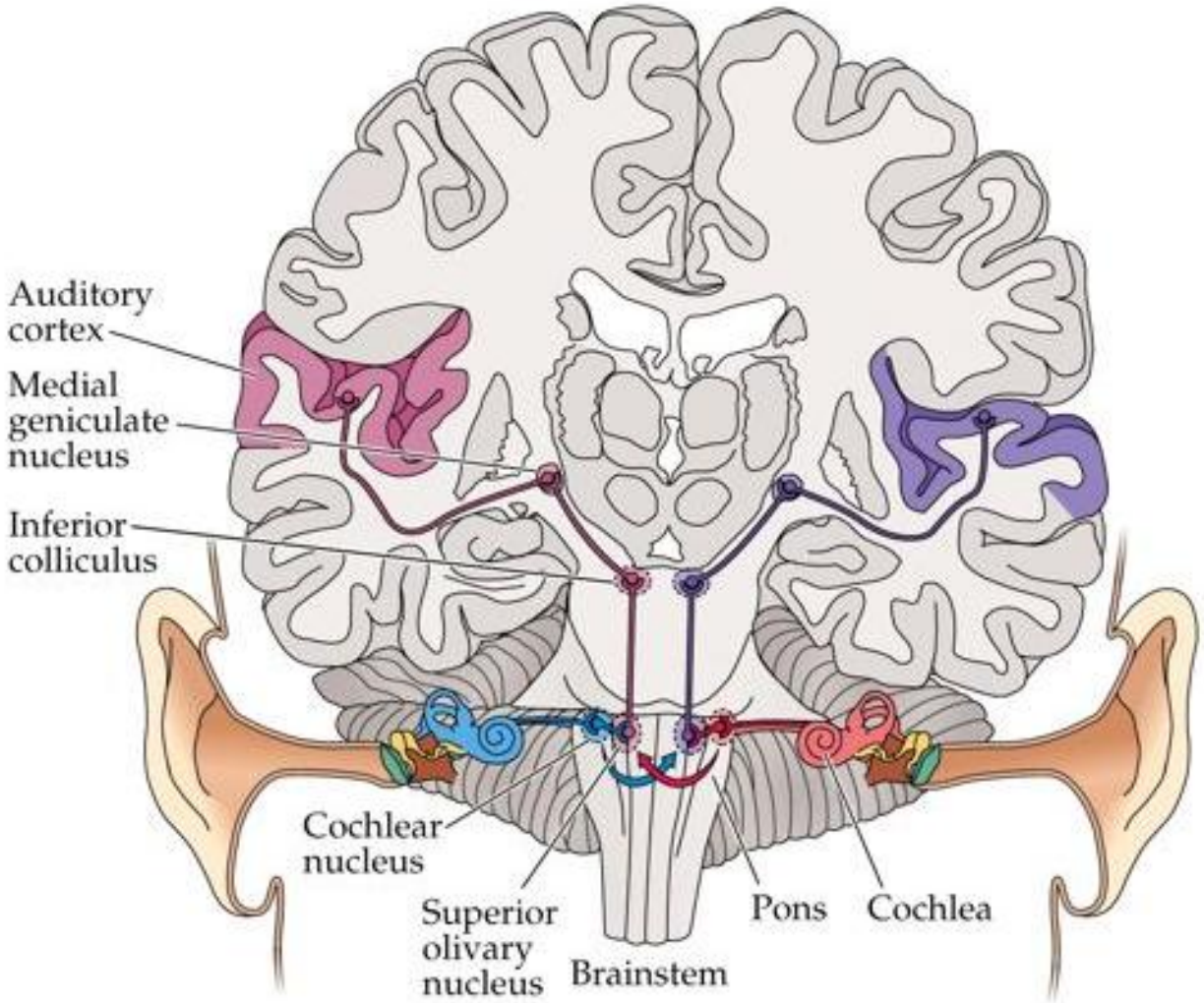


Image from http://www.cns.nyu.edu/~david/courses/perception/lecturenotes/localization/localization.html

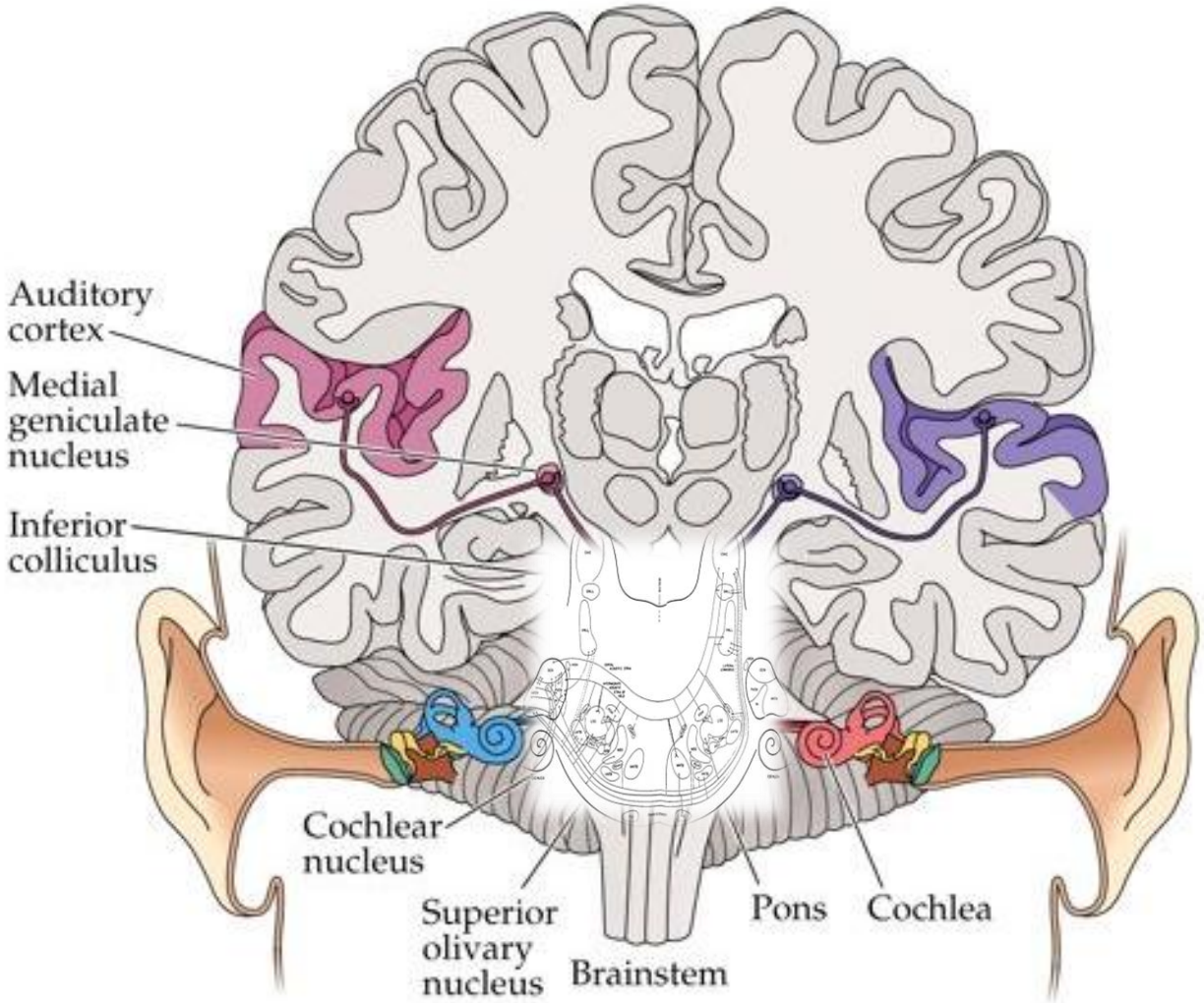
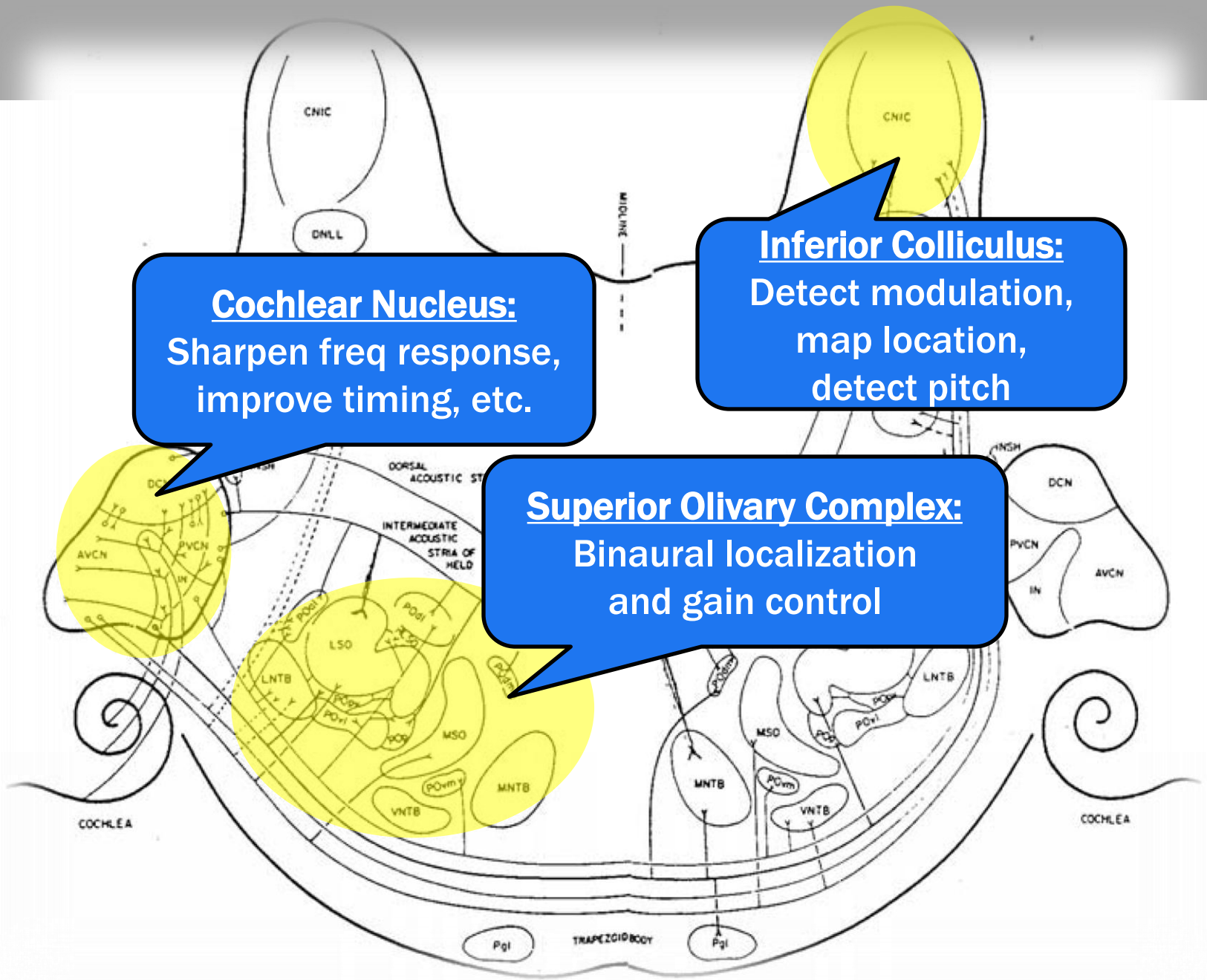
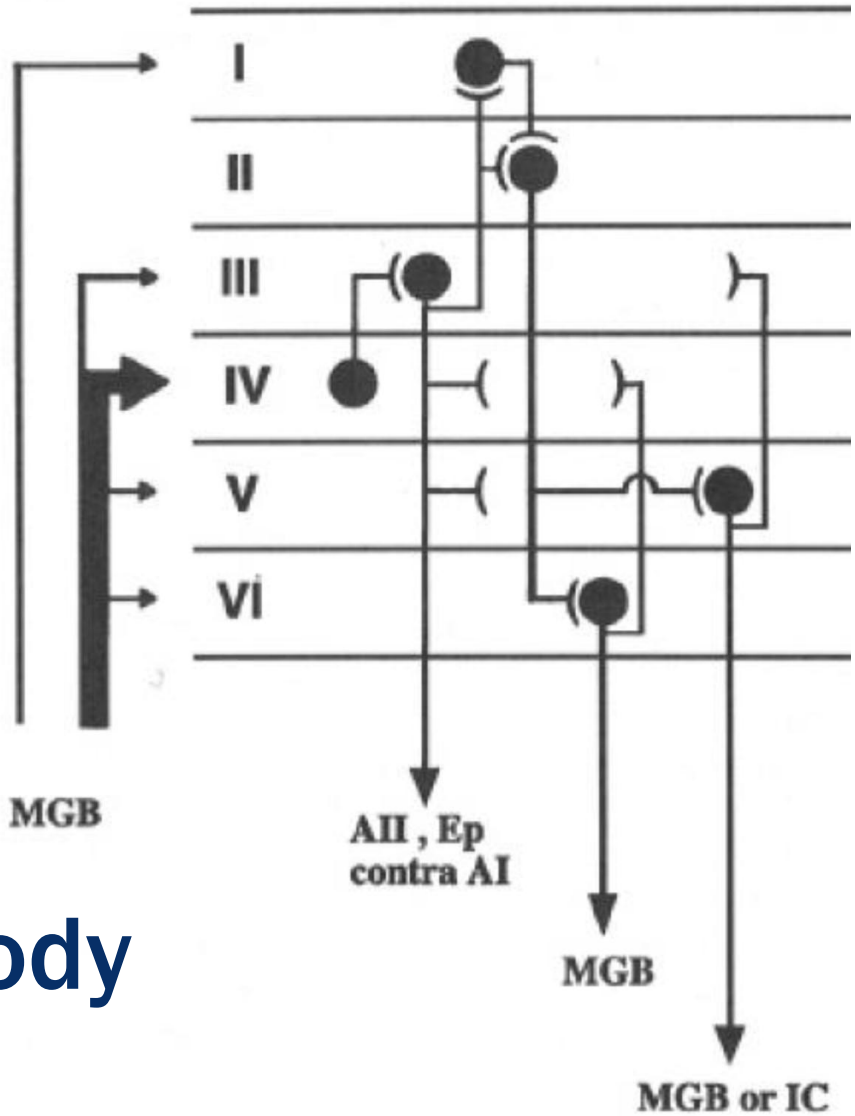


Image from http://www.cns.nyu.edu/~david/courses/perception/lecturenotes/localization/localization.html


CNIC
DNLL
MIDLINE
CNIC
Inferior Colliculus:
Detect modulation,
map location,
detect pitch
Cochlear Nucleus:
Sharpen freq response,
improve timing, etc.
DORSAL
ACOUSTIC ST
INTERMEDIATE
ACOUSTIC
STRIA OF
HELD
DCN
PVCN
AVCN
IN
Superior Olivary Complex:
Binaural localization
and gain control
LSO
LNTB
MSO
MNTB
VNTB
COCHLEA
COCHLEA
TRAPEZOID BODY
Pgl
Pgl

Auditory Cortex

Pattern Recognition



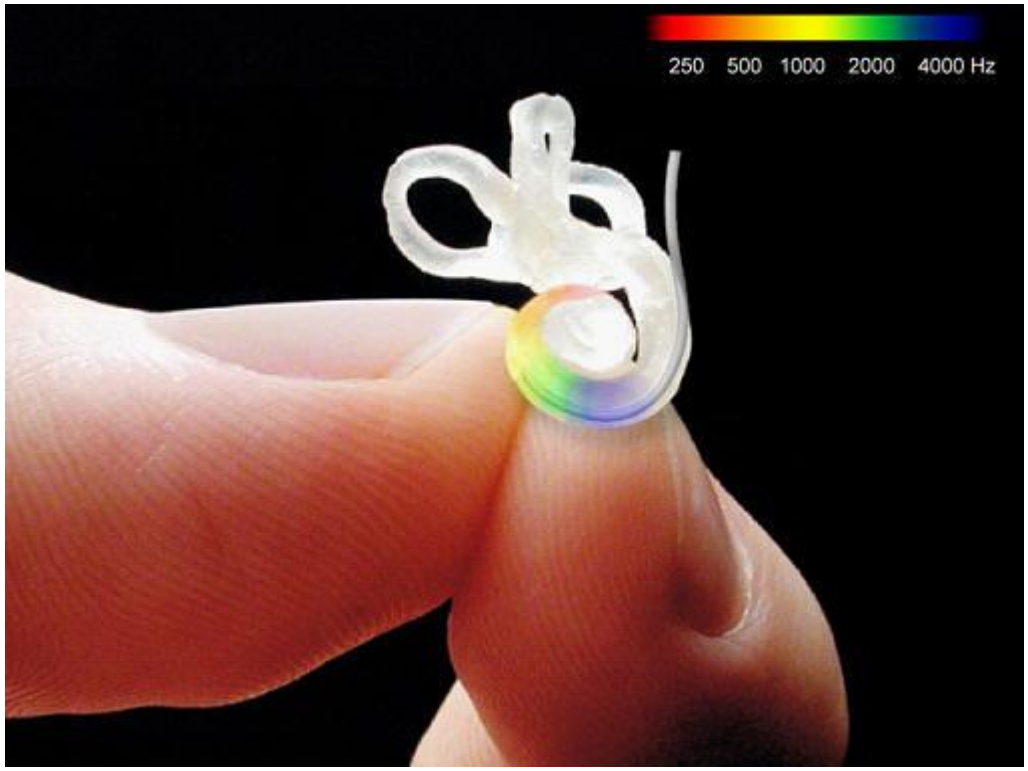
Medial Geniculate Body

Relative intensity & duration

Outline

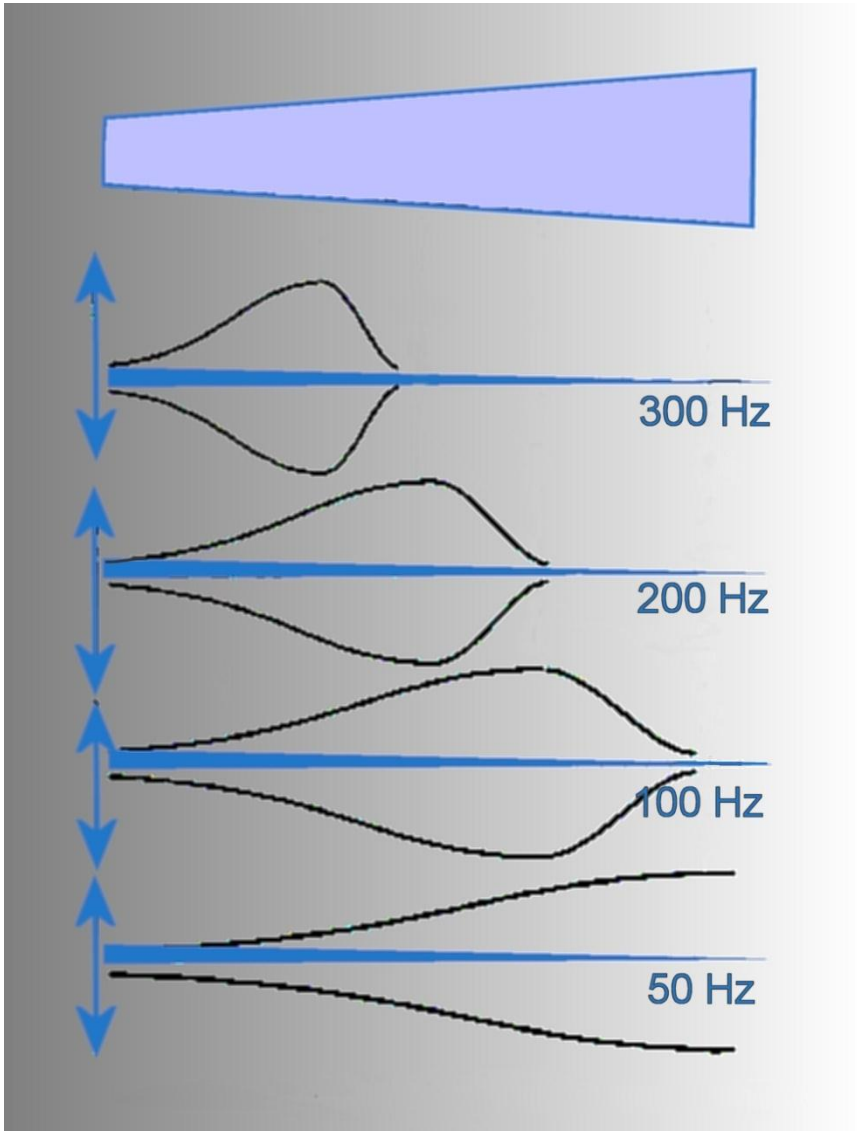
- Basic Anatomy
  - Where things are located inside your head
- **Normal Physiology**
  - **How we extract information about sounds**
- Impaired Physiology
  - How it can all go wrong

Back to the ear…



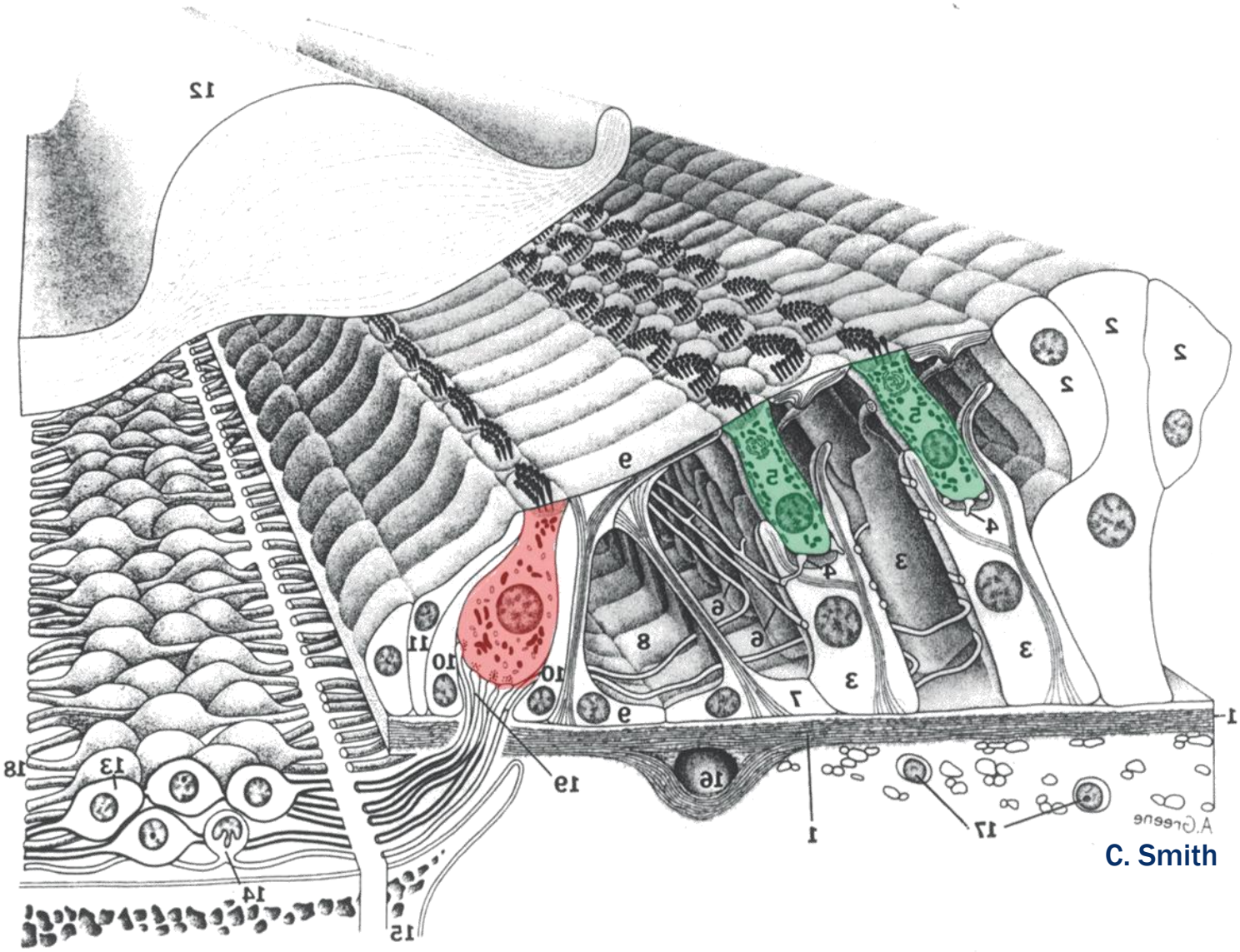
http://graemeclarkfoundation.org

Basilar Membrane



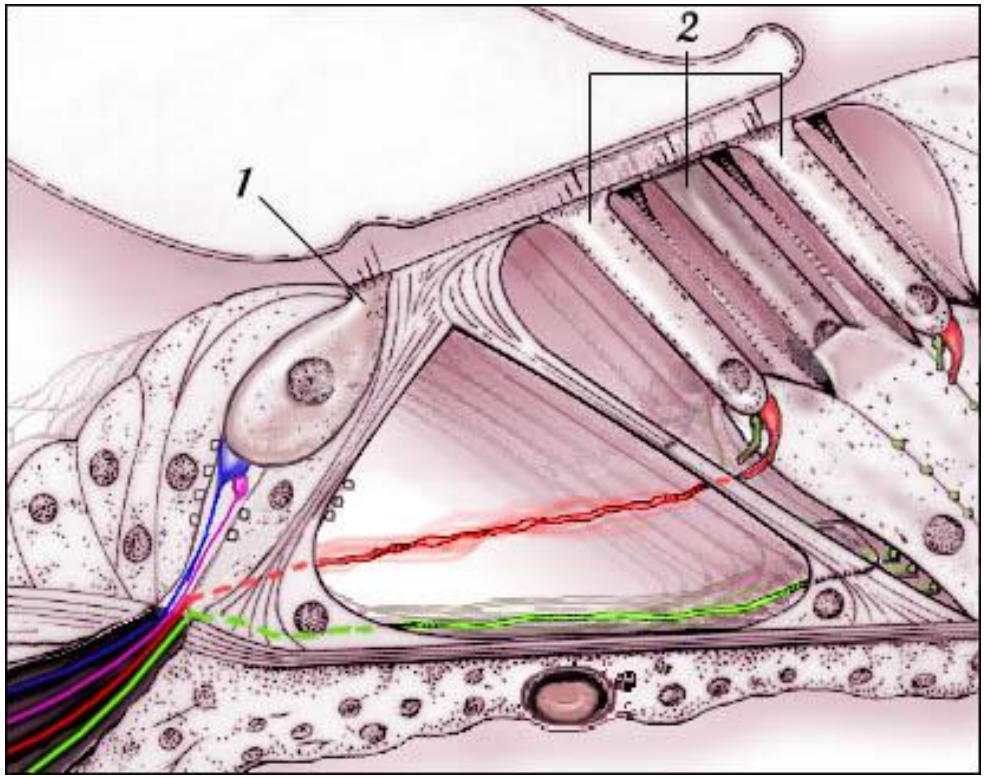
http://commons.wikimedia.org/wiki/File:Vibrations_of_basilar_membrane.jpg

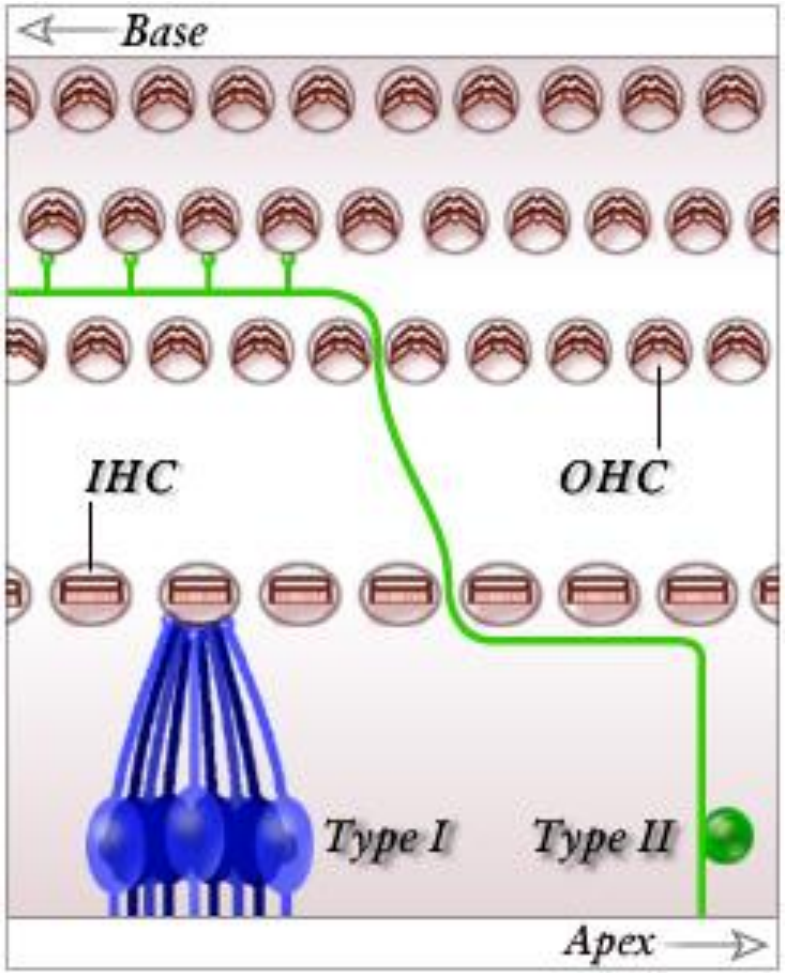
Organ of Corti



C. Smith

Neural Connections

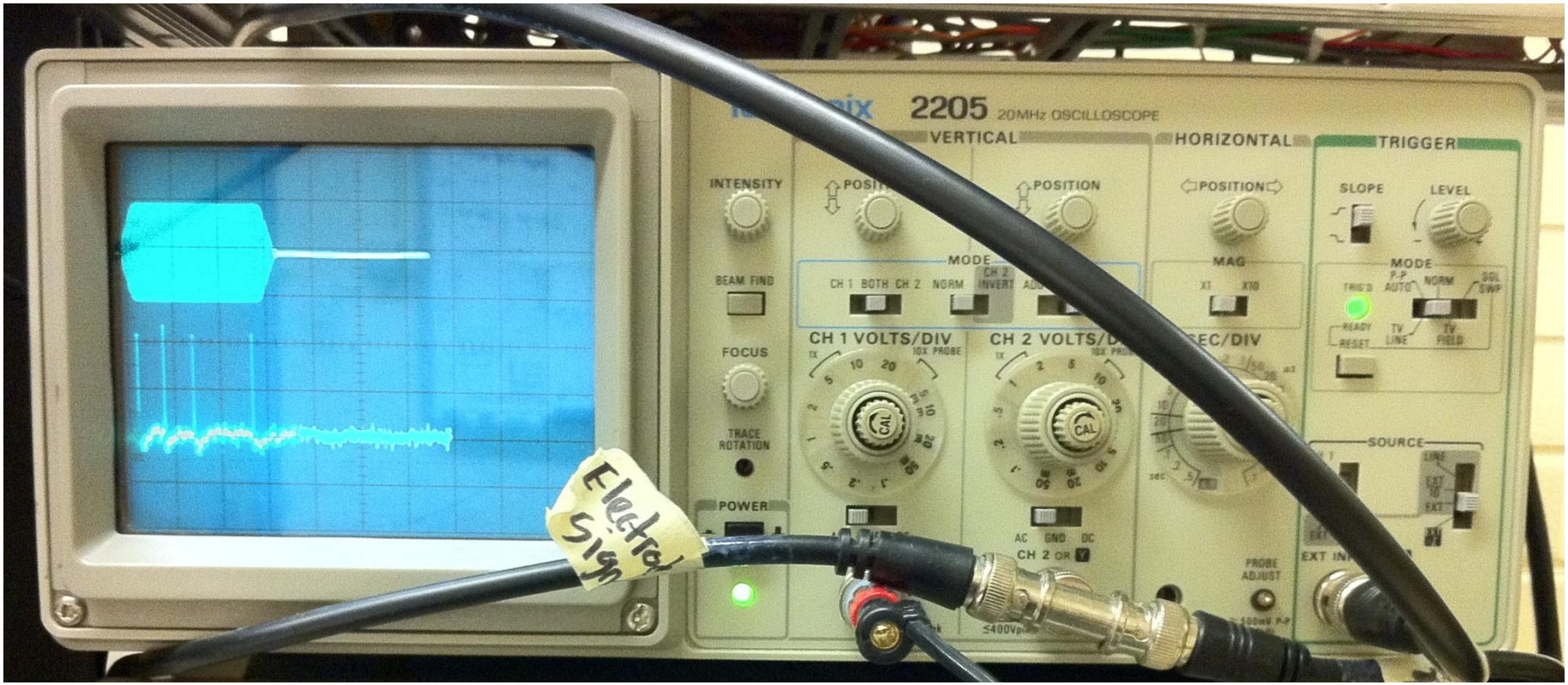




95% of auditory nerve fibers send signals to the brain

images from http://cochlea.org

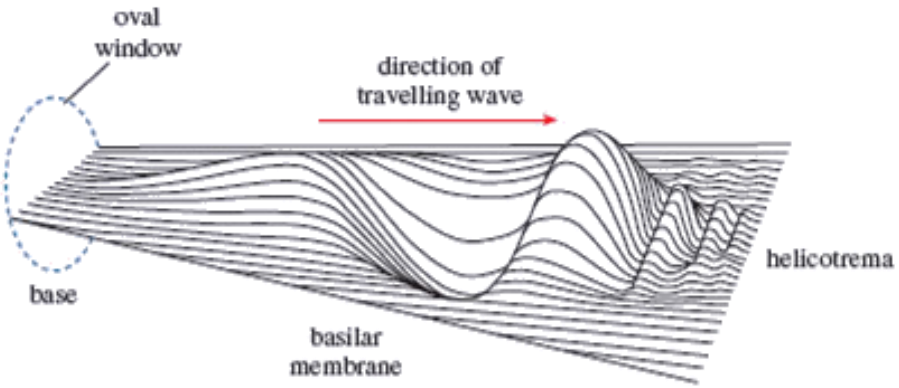
... in the lab


2205 20MHz OSCILLOSCOPE
VERTICAL
HORIZONTAL
TRIGGER
INTENSITY
POSITION
POSITION
POSITION
SLOPE
LEVEL
BEAM FIND
MODE
CH 1 BOTH CH 2 NORM
MAG
X1 X10
MODE
FOCUS
CH 1 VOLTS/DIV
CH 2 VOLTS/DIV
SEC/DIV
TRACE ROTATION
SOURCE
POWER
AC GND DC
CH 2 OR Y
PROBE ADJUST
EXT IN
Electrol
Sign

A quick note on neural coding…

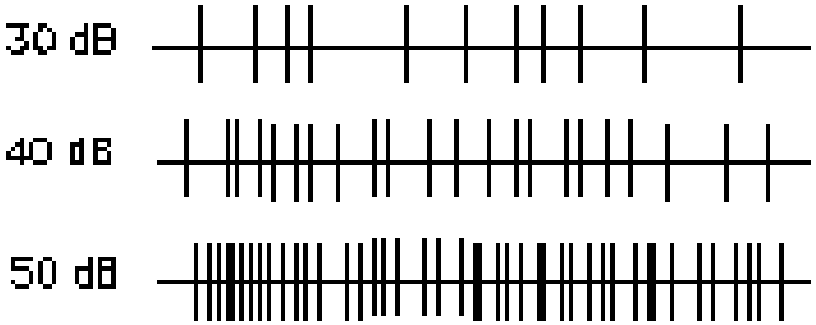
Place Code

- Location = Frequency



Rate Code

- Intensity Information

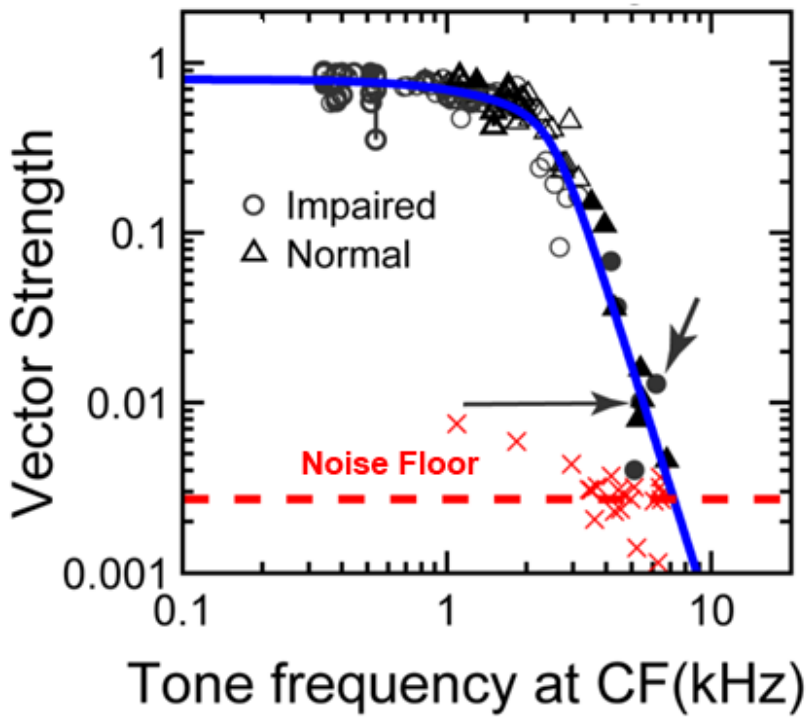


Temporal Code

- Nerve spikes are phase-locked to audio input

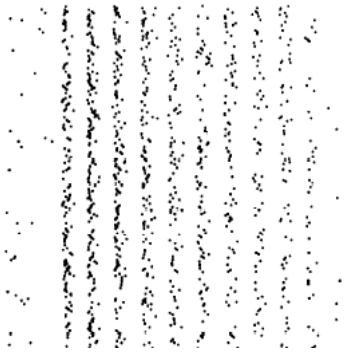
Phase locking decreases at high freqs

Kale, 2010 dissertation



Joris et al, 1994

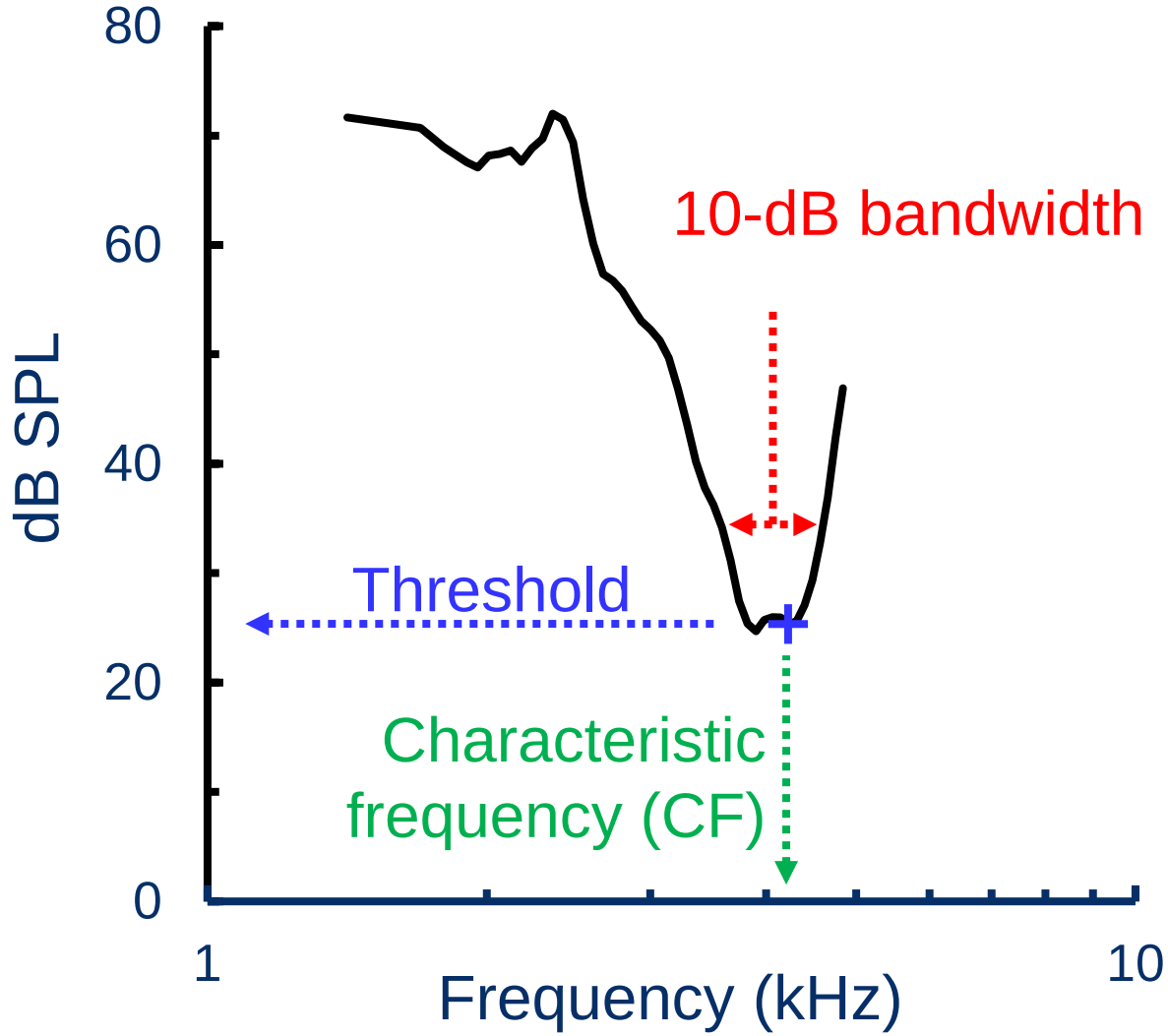
AN

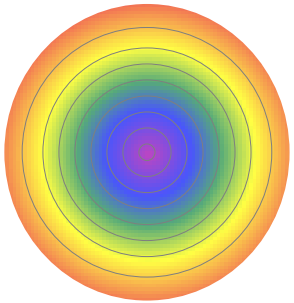


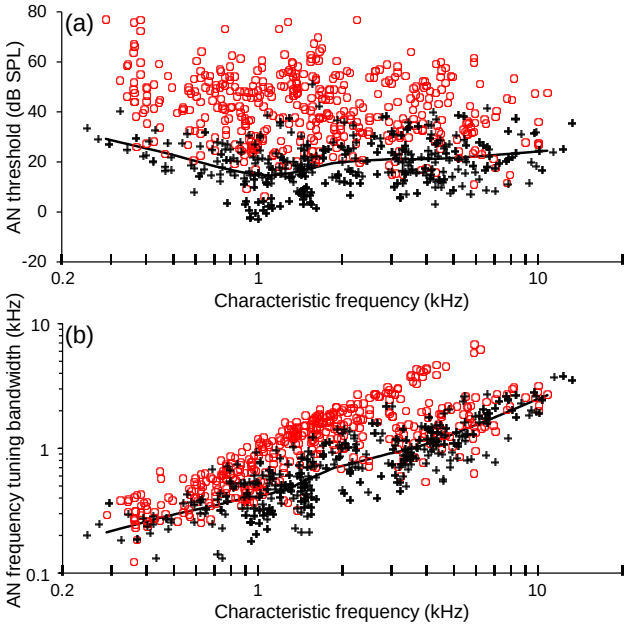
CN

Joris, Philip X., et al. "Enhancement of neural synchronization in the anteroventral cochlear nucleus. I. Responses to tones at the characteristic frequency." *Journal of neurophysiology* 71.3 (1994): 1022-1036.

Auditory Nerve Tuning Curve







Tonotopic Mapping

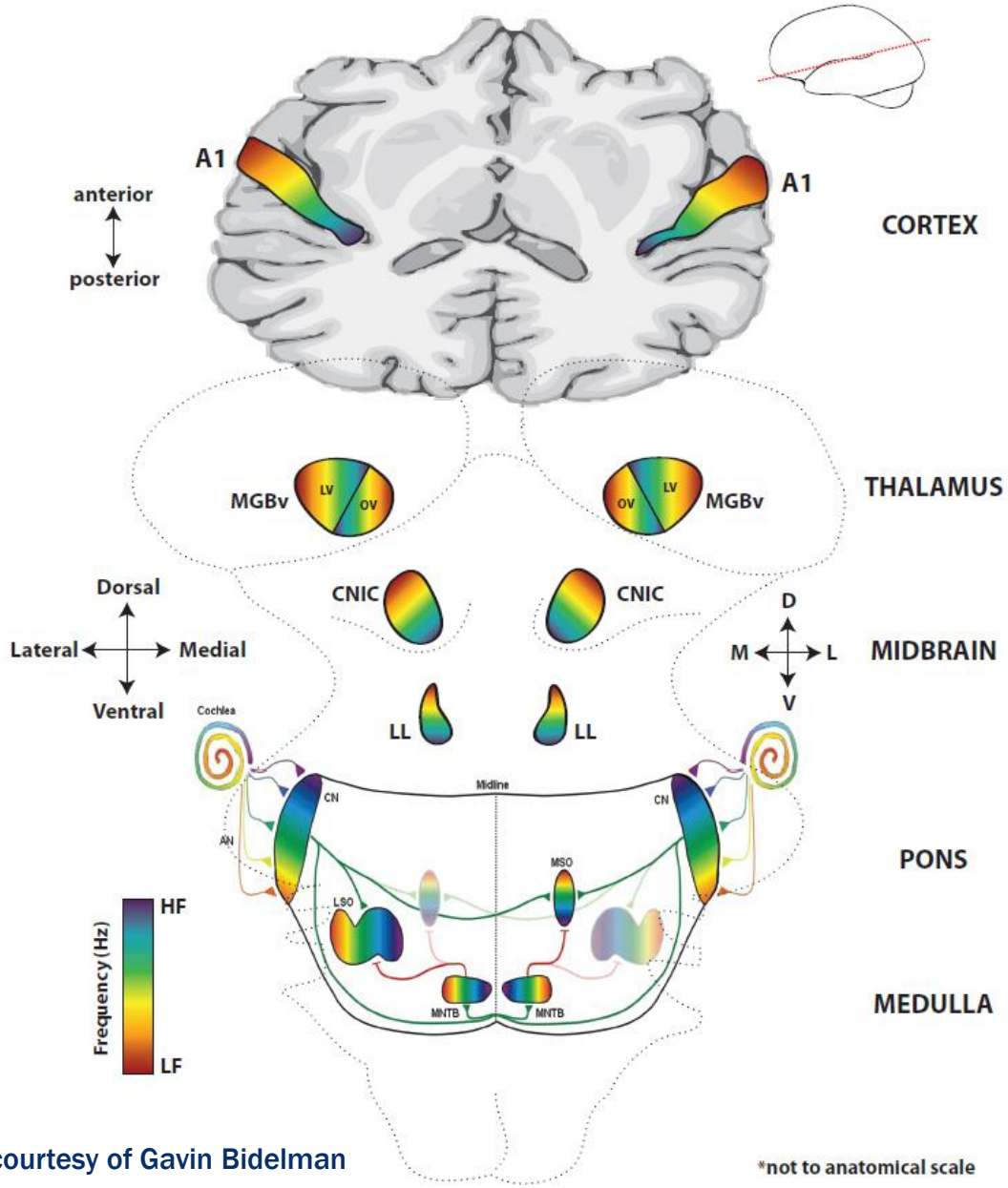


Image courtesy of Gavin Bidelman

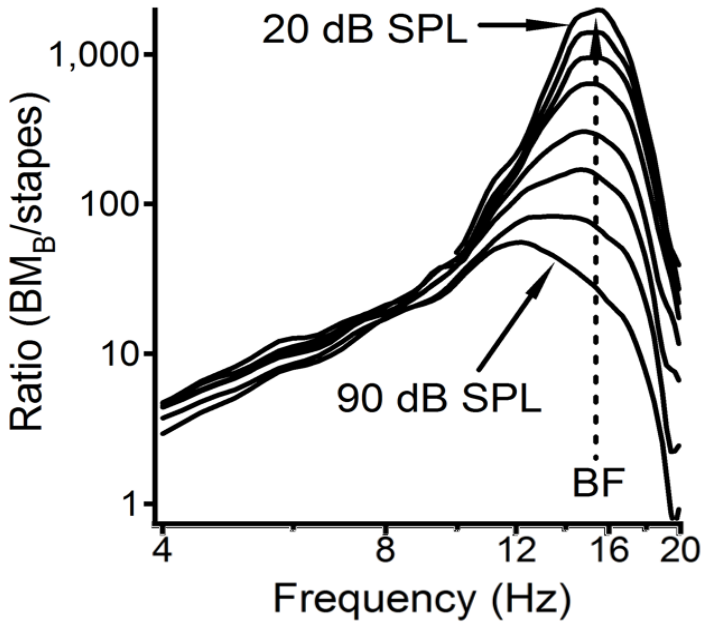
*not to anatomical scale

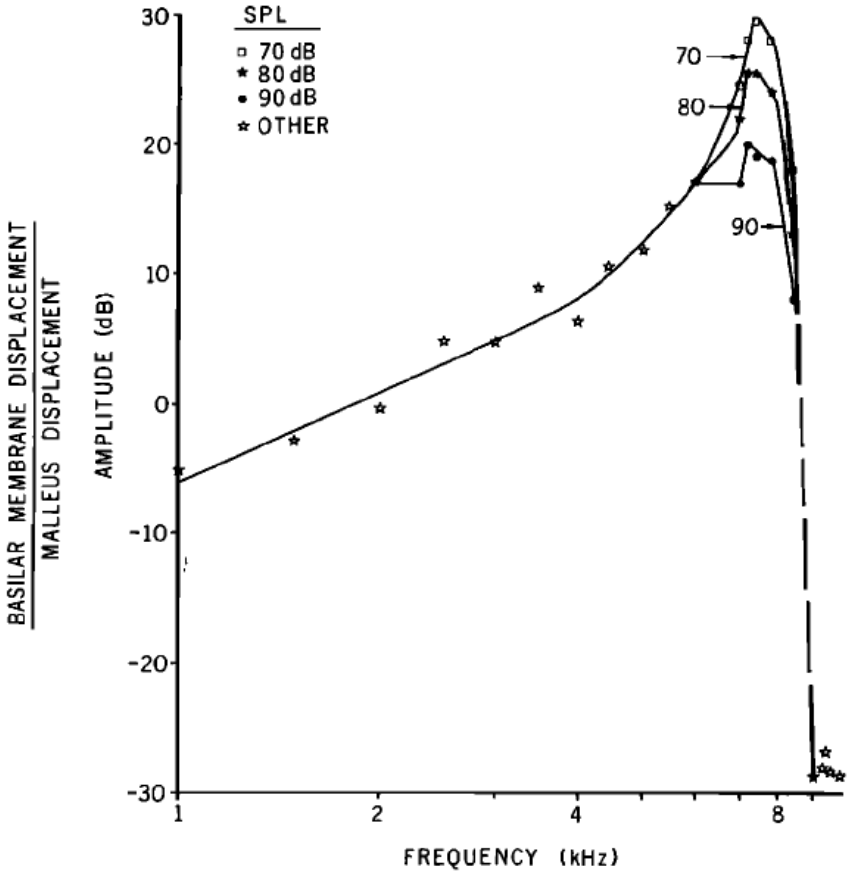
Cochlear Amplifier

Gain = $\frac{\text{BASILAR MEMBRANE DISPLACEMENT}}{\text{MALLEUS DISPLACEMENT}}$

At low levels, we see a lot of gain

At higher levels, not so much



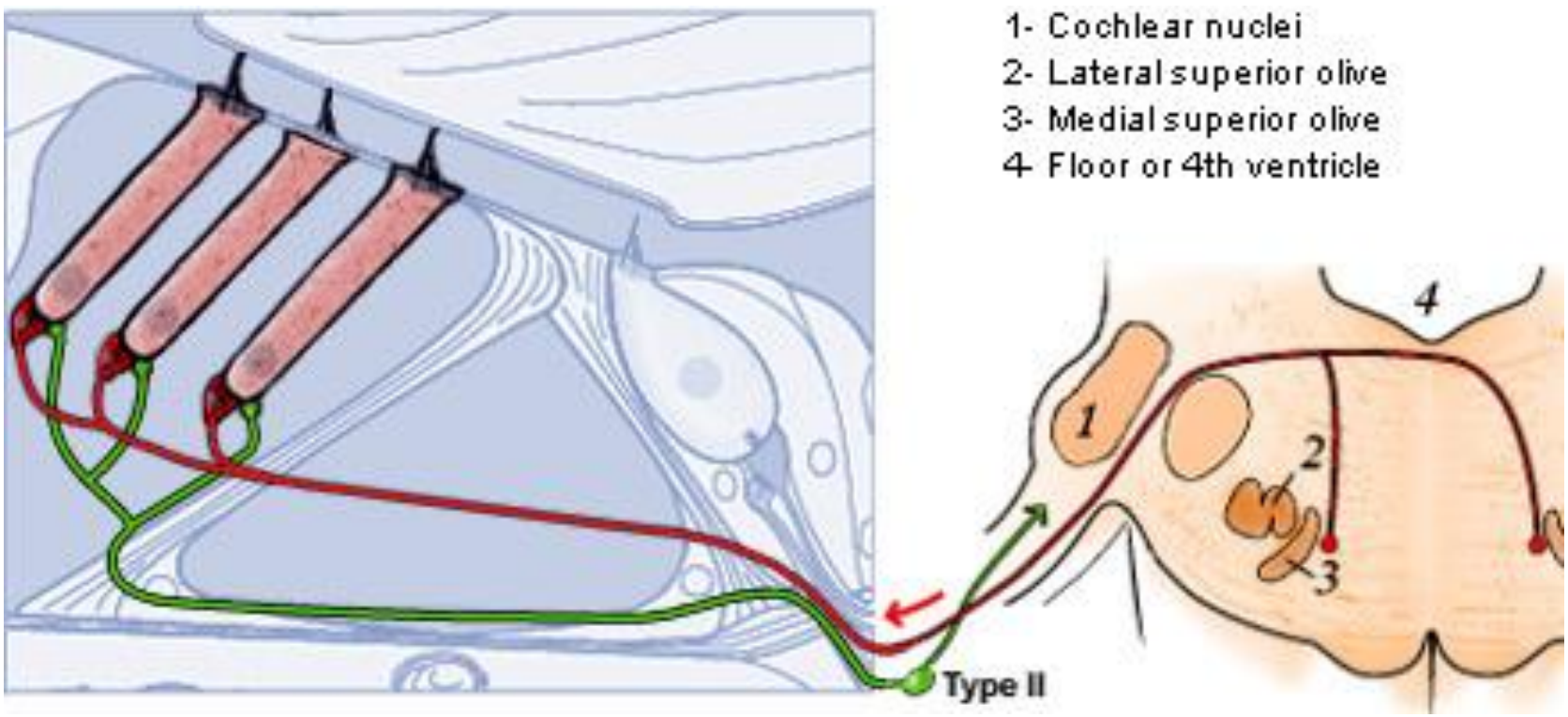


Rhode, W. S. (1971). Observations of the vibration of the basilar membrane in squirrel monkeys using the Mössbauer technique. *J Acoust Soc Am*, *49*(4).
Ren, Tianying, Wenxuan He, and Edward Porsov (2011). "Localization of the cochlear amplifier in living sensitive ears." *PloS one* 6.5: e20149.

OHC Motility

[video]

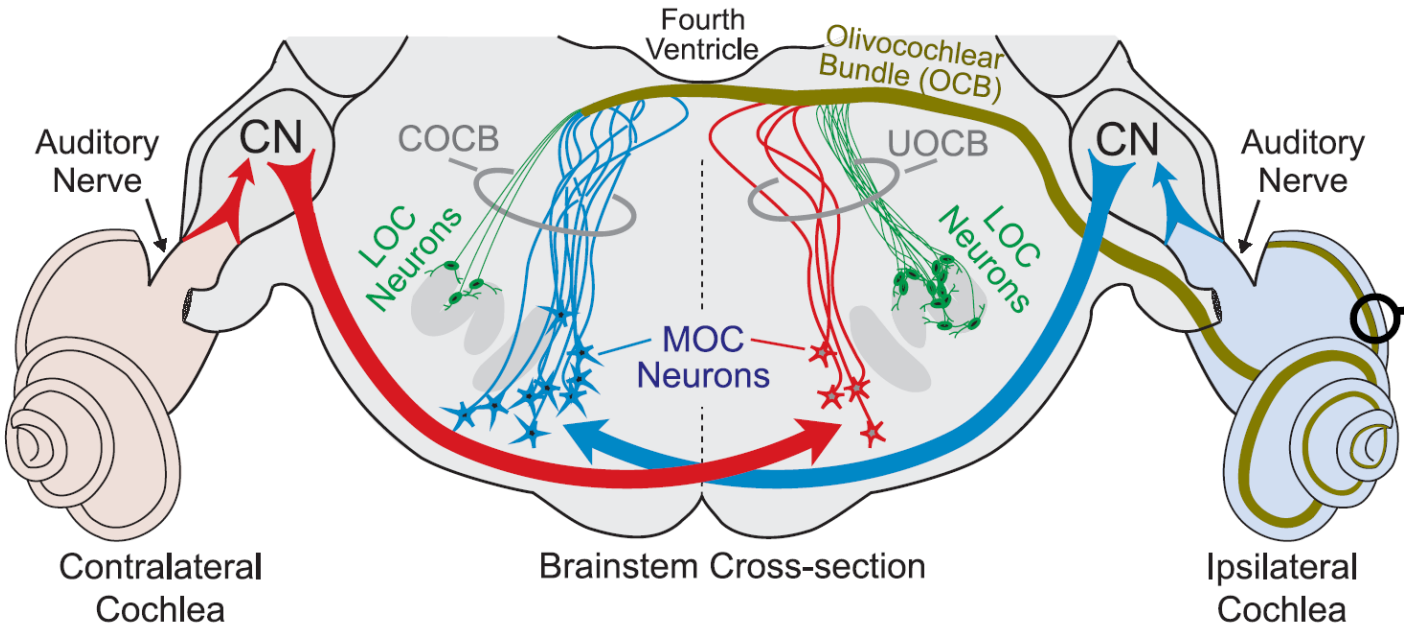
Neural Feedback (Automatic Gain Control)

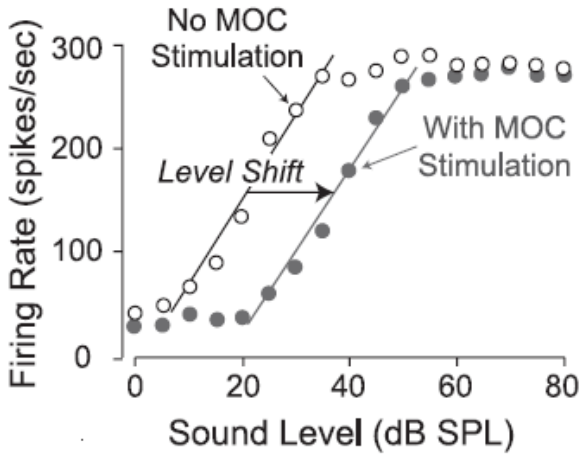


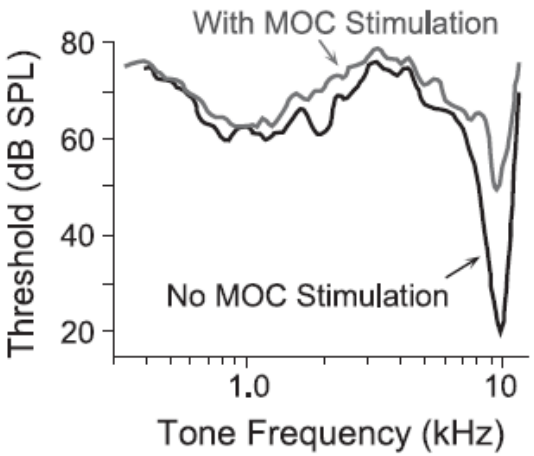
5% of auditory nerve fibers send signals back to the cochlea

images from http://cochlea.org

Adaptive Gain Control

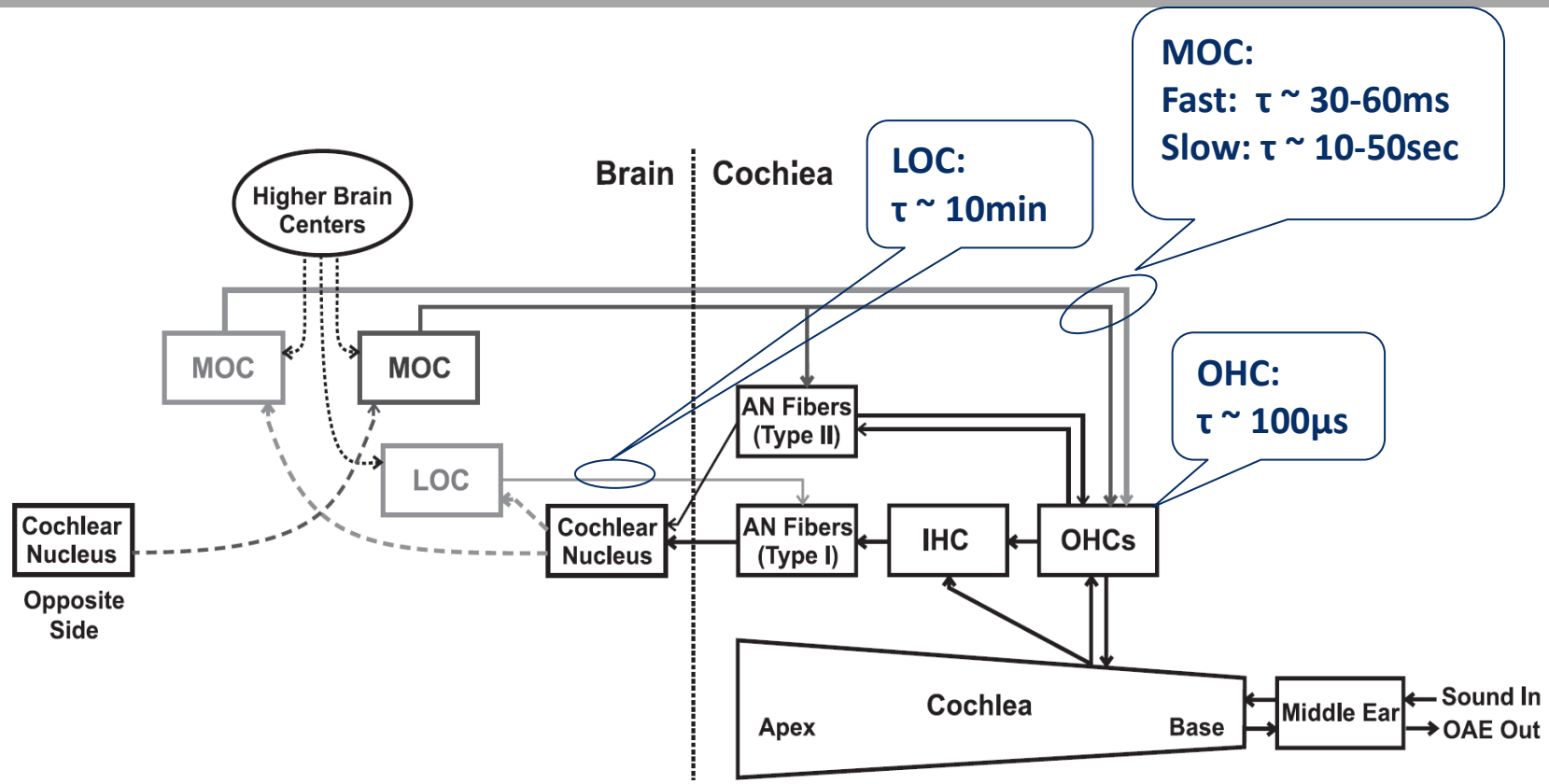






Guinan, J. J. (2006). Olivocochlear efferents: anatomy, physiology, function, and the measurement of efferent effects in humans. *Ear Hear*, *27*(6), 589–607.

Cochlear Feedback Loops



- **LOC pathway balances interaural sensitivity** (originates near ILD sensitive neurons)
  - (e.g., if you have an infection in one ear)

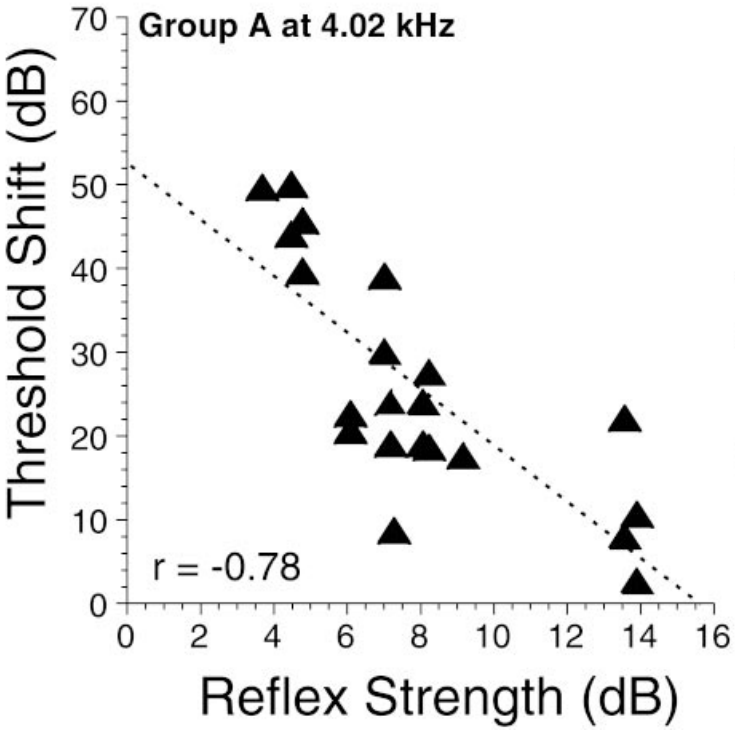
Guinan, J. J. (2006). Olivocochlear efferents: anatomy, physiology, function, and the measurement of efferent effects in humans. *Ear Hear*, *27*(6), 589–607.

Darrow, K. N., Maison, S. F., & Liberman, M. C. (2006). Cochlear efferent feedback balances interaural sensitivity, *9*(12), 1474–1476.

Feedback as a protective mechanism

Tough vs. tender ears

- Some ears appear to have more active feedback than others
- The feedback may serve to protect the cochlea from damage
- This may account for individual differences in susceptibility to hearing loss



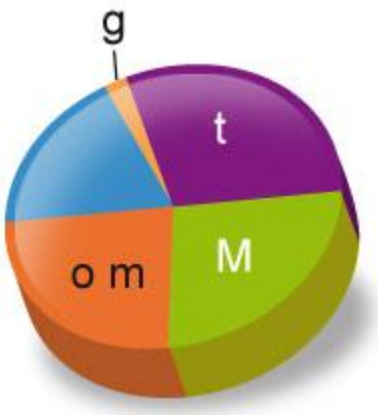
Maison, S. F., & Liberman, M. C. (2000). Predicting vulnerability to acoustic injury with a noninvasive assay of olivocochlear reflex strength. *J Neurosci*, *20*(12), 4701–4707.

Maison, S. F., Usubuchi, H., & Liberman, M. C. (2013). Efferent Feedback Minimizes Cochlear Neuropathy from Moderate Noise Exposure. *Journal of Neuroscience*, *33*(13), 5542–5552

Outline

- Basic Anatomy
  - Where things are located inside your head
- Normal Physiology
  - How we extract information about sounds
- **Impaired Physiology**
  - How it can all go wrong

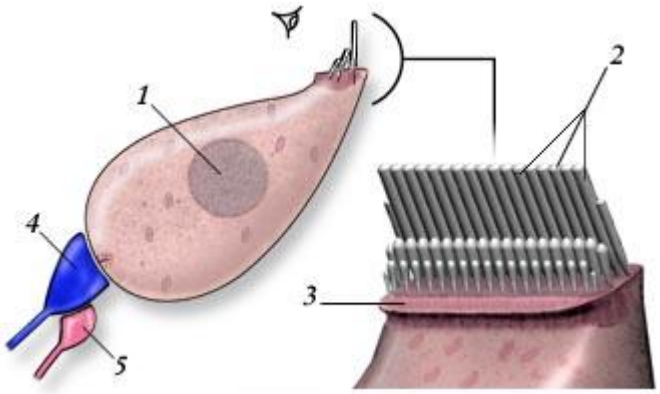
Hearing ~~Loss~~ Impairment

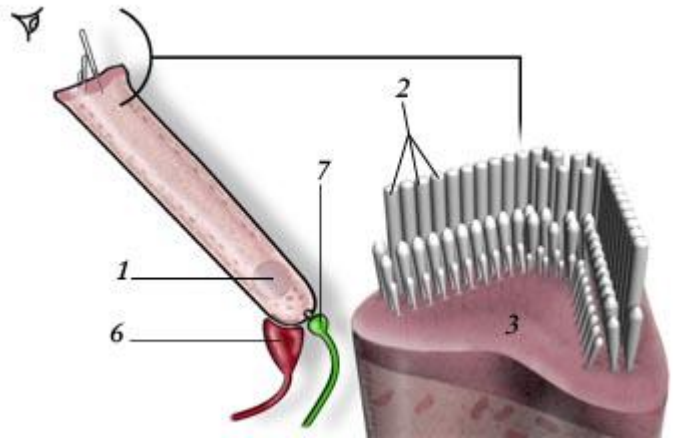


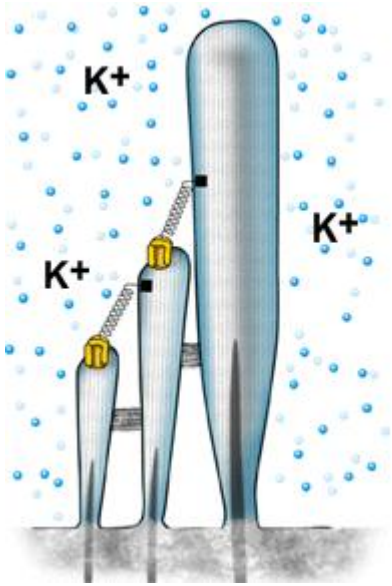
- Conductive Hearing Loss
  - Ear Wax
  - Middle Ear Infection (otitis media)
  - Bone dislocation, fracture, growth, etc
- Sensorineural Hearing Loss
  - Damaged tip links and/or stereocilia
  - Dead hair cells (e.g., excitotoxicity / ototoxicity)
  - Reduced endocochlear potential
  - Auditory nerve degeneration

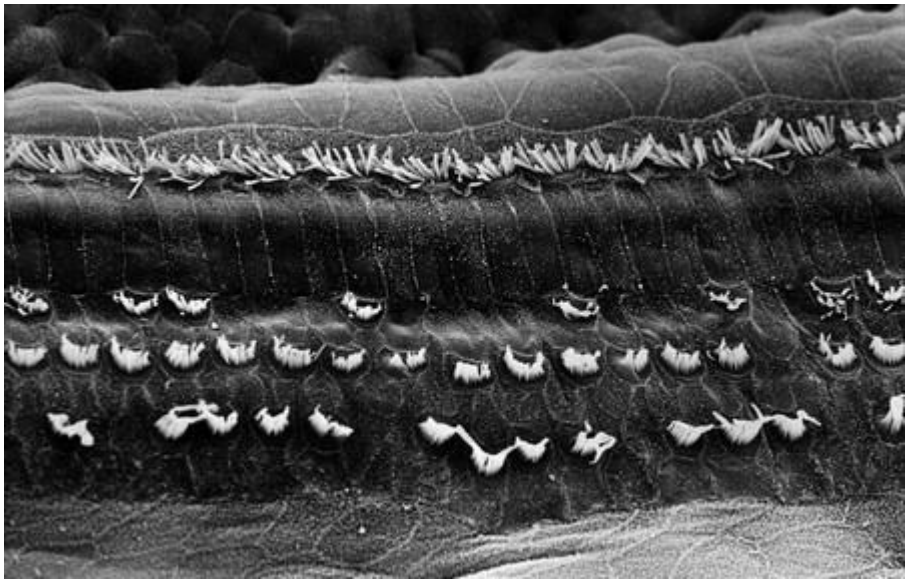
- … and of coursed, mixed conductive & sensorineural

Hair Cells, Stereocilia, and Tip Links









images from http://cochlea.org

Endocochlear potential

Aging causes the *stria vascularis* to atrophy

- the predomininent problem seen in elderly cochleae
- reduces the endocochlear potential
  (the "battery" for the organ of Corti)

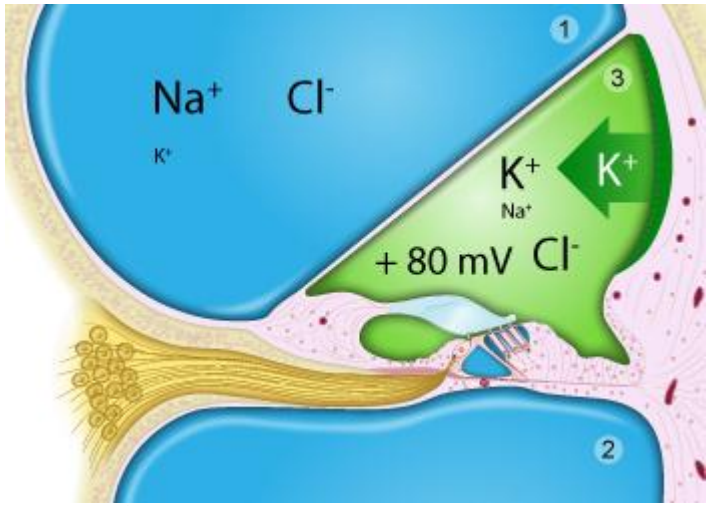
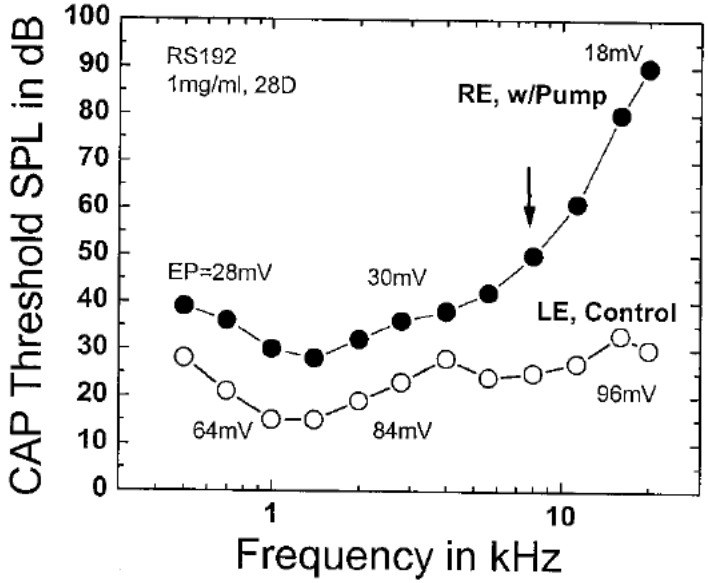


image from http://cochlea.org



Schuknecht, et al. (1974). Atrophy of the stria vascularis, a common cause for hearing loss. *Laryngoscope*, *84*(10), 1777–1821.
Schuknecht and Gacek (1993). Cochlear pathology in presbycusis *The Annals of otology, rhinology, and laryngology* 102.1 Pt 2: 1.
Schmiedt, R. A., Lang, H., Okamura, H., & Schulte, B. A. (2002). Effects of furosemide applied chronically to the round window: a model of metabolic presbyacusis. *J Neurosci*, *22*(21), 9643–9650.

Behavioral estimates of IHC/OHC dysfunction

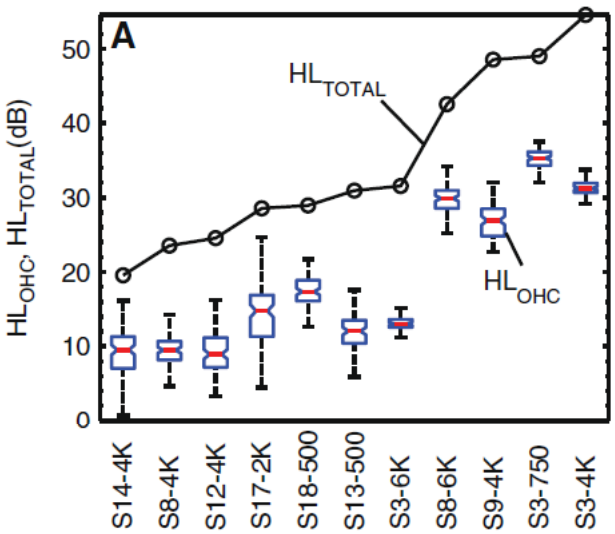
A recent study found that, on average:

- 60% of threshold shift is due to OHC dysfunction
- 40% of threshold shift is due to IHC dysfunction

... but there can be a lot of individual variability

- in some cases, IHCs appeared to contribute >60%

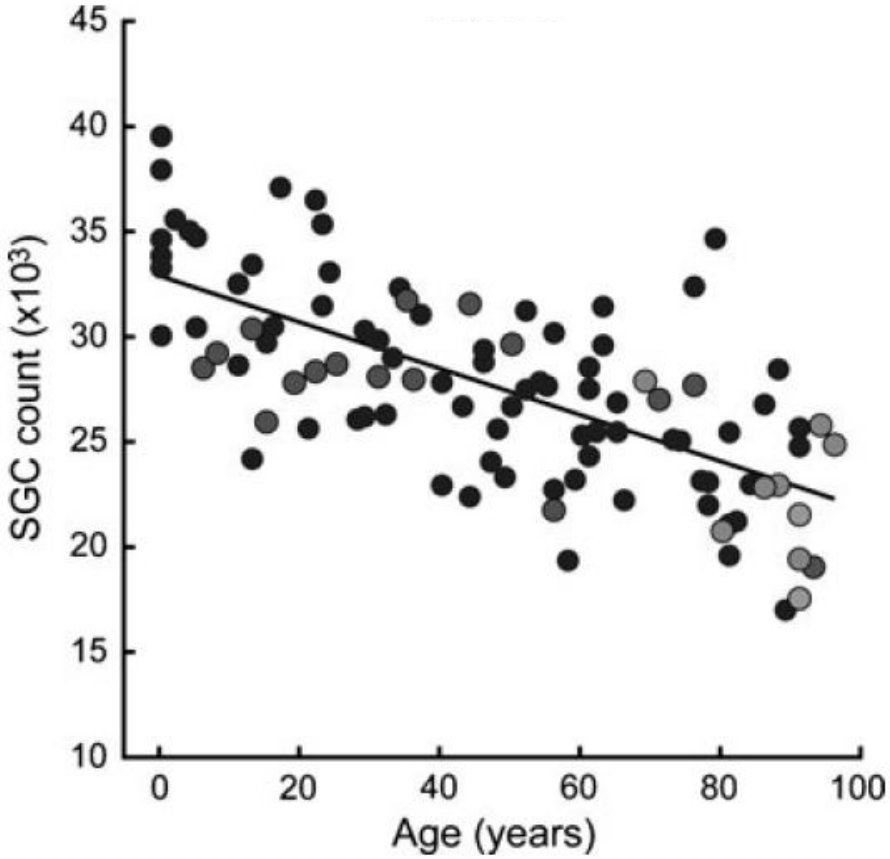
Note: reduced cochlear potential probably impairs both IHCs & OHCs



Lopez-Poveda, Enrique A., and Peter T. Johannesen. "Behavioral Estimates of the Contribution of Inner and Outer Hair Cell Dysfunction to Individualized Audiometric Loss." *Journal of the Association for Research in Otolaryngology*13.4 (2012): 485-504.

Auditory nerve degeneration

People tend to lose 100 nerve fibers per year as they age (even when hair cells remain fully intact)



Makary, C. A., Shin, J., Kujawa, S. G., Liberman, M. C., & Merchant, S. N. (2011). Age-Related Primary Cochlear Neuronal Degeneration in Human Temporal Bones. *Journal of the Association for Research in Otolaryngology JARO, 717*, 711–717

Auditory Nerve Degeneration

Auditory nerve fibers disappear with noise exposure

- Specifically, fibers with high thresholds (Furman et al, 2013)

<u>Perceptual effects</u>:

- Audiometric thresholds are barely affected (if at all)
- Auditory filters don't get any wider
- Speech intelligibility is degraded (Lorenzi et al, 2008; Leger et al, 2012)
    - Lopez-Poveda has recently developed a simulation of this

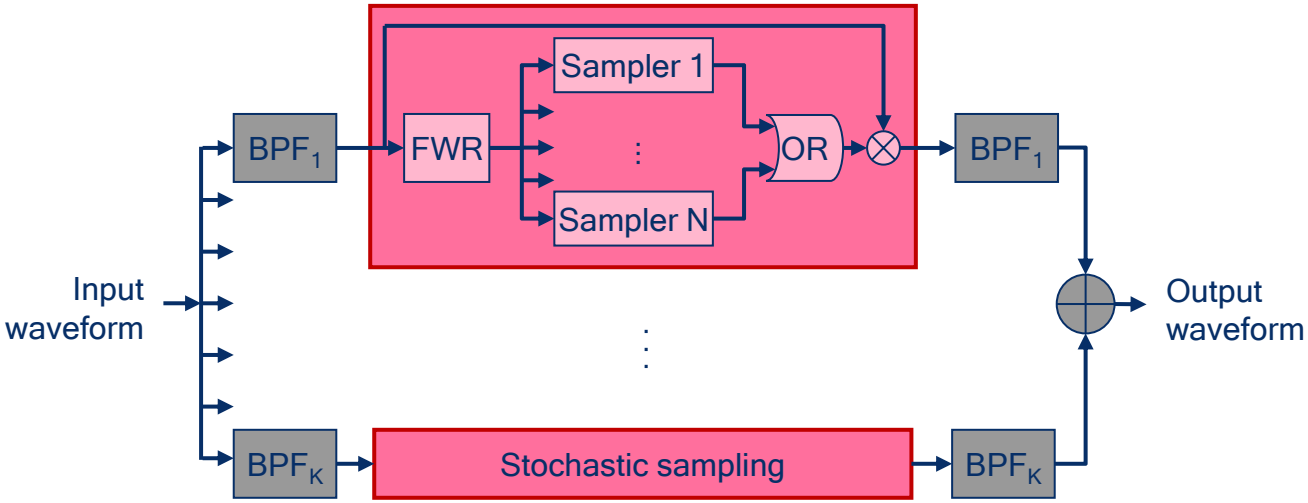
Furman, Adam C., Sharon G. Kujawa, and M. Charles Liberman. "Noise-induced cochlear neuropathy is selective for fibers with low spontaneous rates." *Journal of Neurophysiology* (2013).

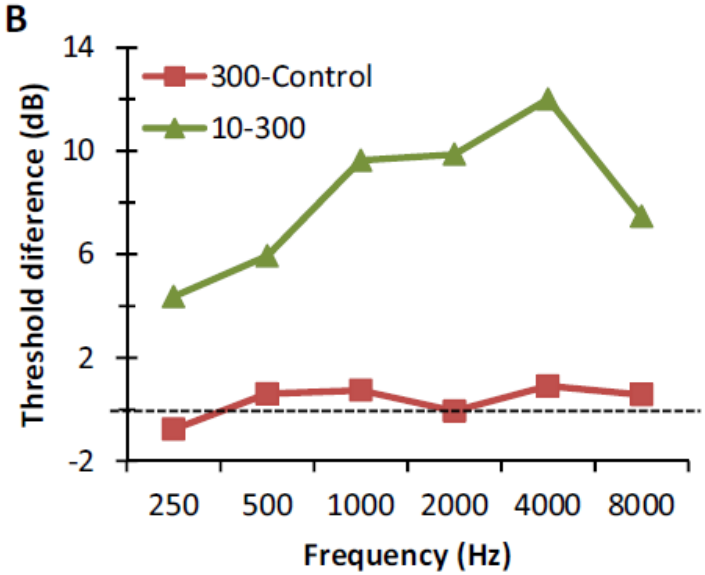
Lorenzi, C., Debruille, L., Garnier, S., Fleuriot, P., & Moore, B. C. J. (2009). Abnormal processing of temporal fine structure in speech for frequencies where absolute thresholds are normal. *The Journal of the Acoustical Society of America*, *125*(1), 27–30.

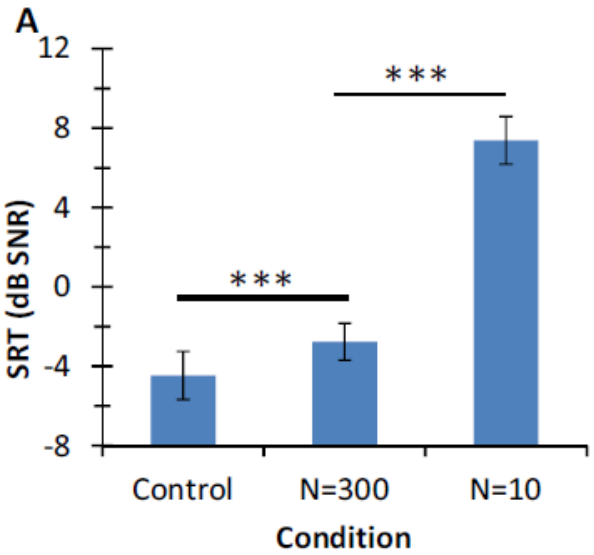
Léger, A. C., Moore, B. C. J., Gnansia, D., & Lorenzi, C. (2012). Effects of spectral smearing on the identification of speech in noise filtered into low- and mid-frequency regions. *The Journal of the Acoustical Society of America*, *131*(5), 4114–23.

Lopez-Poveda, E. A., & Barrios, P. (2013). A perceptual model of auditory deafferentation. *Proceedings of Meetings on Acoustics* (Vol. 19, pp. 050181–050181). Acoustical Society of America.

Lopez-Poveda Vocoder







Lopez-Poveda, E. A., & Barrios, P. (2013). A perceptual model of auditory deafferentation. *Proceedings of Meetings on Acoustics* (Vol. 19, pp. 050181–050181). Acoustical Society of America.

Tinnitus

Tinnitus is often associated with hearing loss

- Temporarily elevated thresholds (Emmerich et al., 2002)
- Elevated thresholds (Roberts et al., 2008)
- Cochlear dead regions (Weisz et al., 2006)
- Outer hair cell damage (Job et al., 2007)

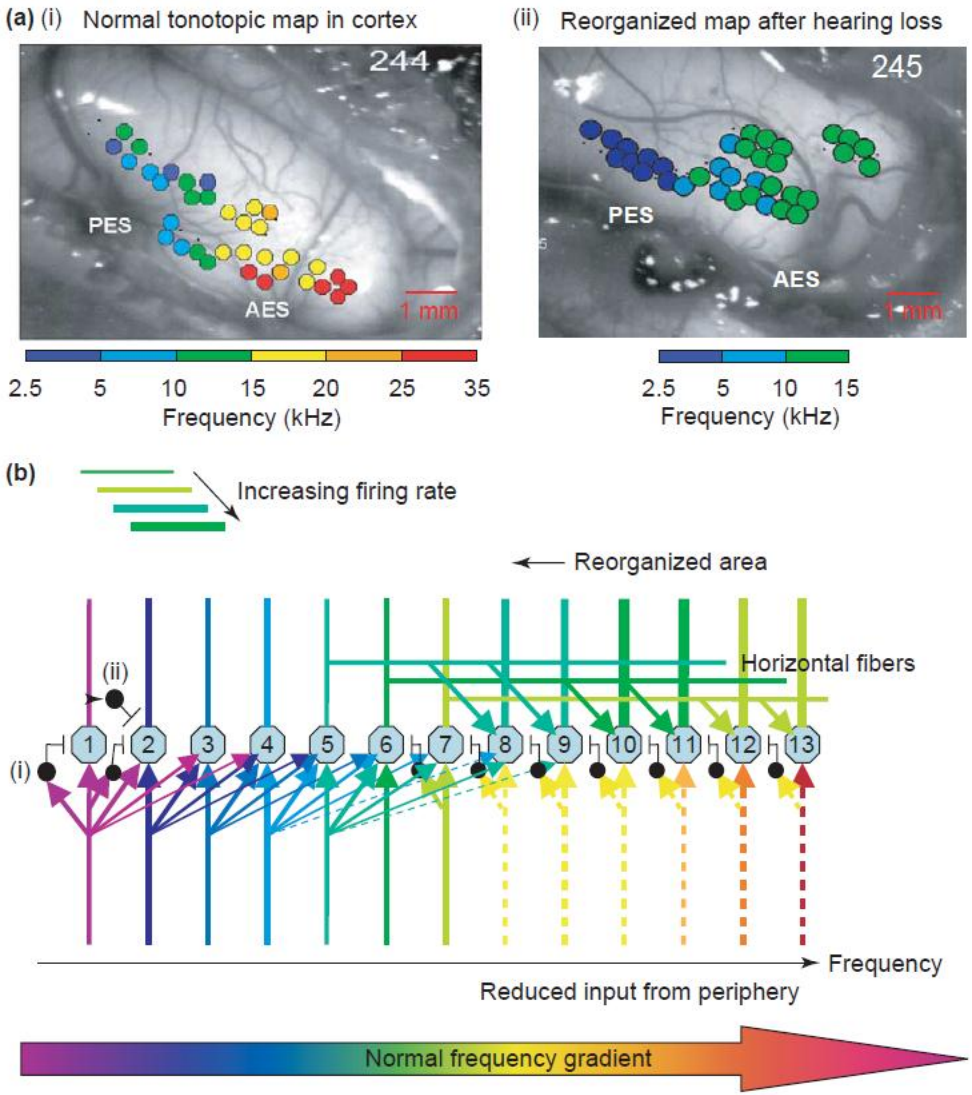
Cutting the auditory nerve often induces tinnitus

(House and Brackmann, 1981; Berliner et al., 1992)

Roberts, L., & Eggermont, J. (2010). Ringing ears: the neuroscience of tinnitus. *Journal of Neuroscience*.

Tinnitus… reduced inhibition?

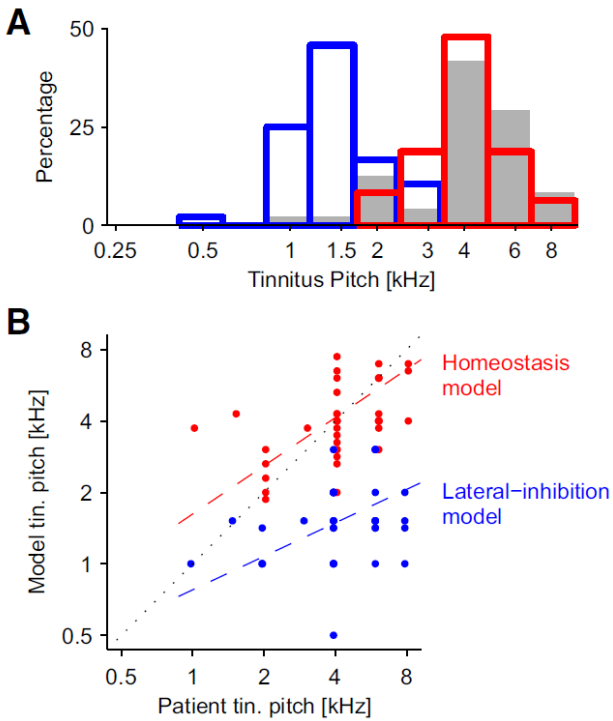
- **Reduced input from the ear** may cause
- **Reduced inhibition** which may cause
- **Increased activation in the absence of a stimulus**

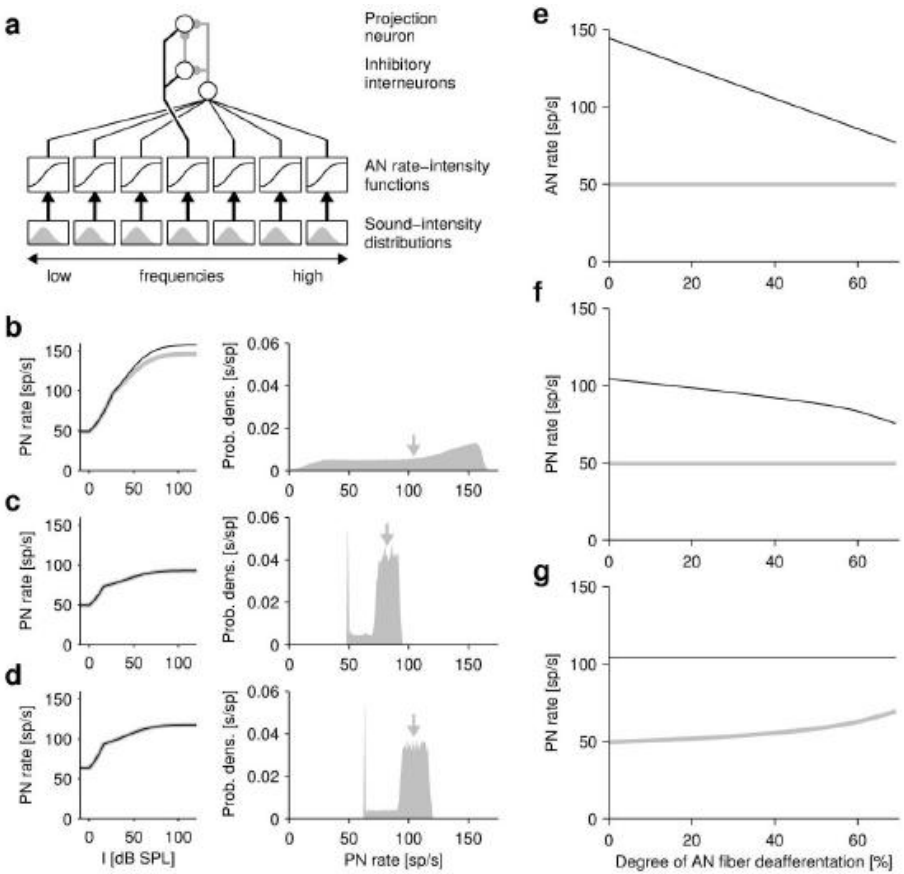


Eggermont, J., & Roberts, L. (2004). The neuroscience of tinnitus. *Trends in Neurosciences*.

Tinnitus… homeostatic plasticity?

Tinnitus can be predicted from hearing impairment (even supra-threshold)





Schaette, Roland, and Richard Kempter. "Predicting tinnitus pitch from patients' audiograms with a computational model for the development of neuronal hyperactivity." *Journal of neurophysiology* 101.6 (2009): 3042-3052.

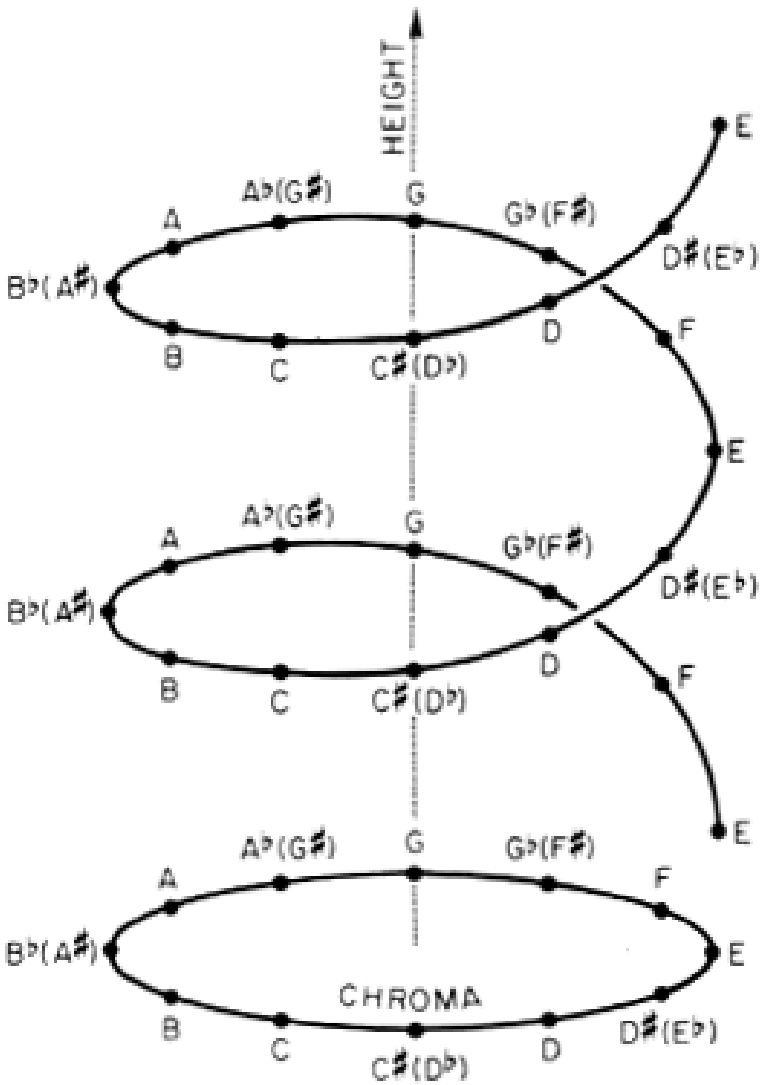
Schaette, Roland. "Computational modelling of tinnitus development."*Proceedings of Meetings on Acoustics*. Vol. 19. 2013.

Extras

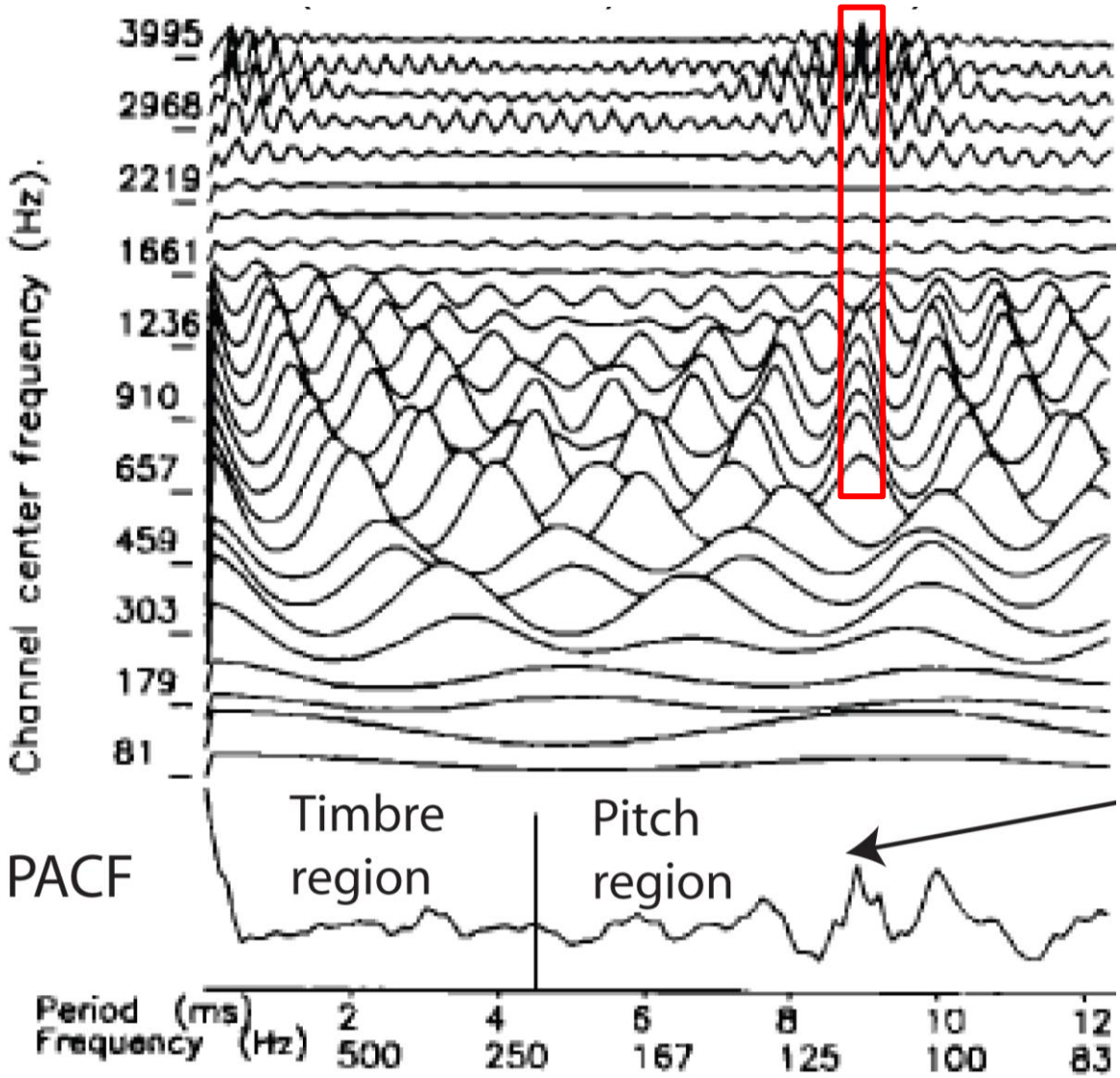
- Neural Basis for Perception
  - Pitch
  - Loudness
  - Masking
  - Localization
- Neural Basis for some auditory ‘illusions’
  - Octave stretch
  - Huggins pitch

Duplex theory of pitch perception

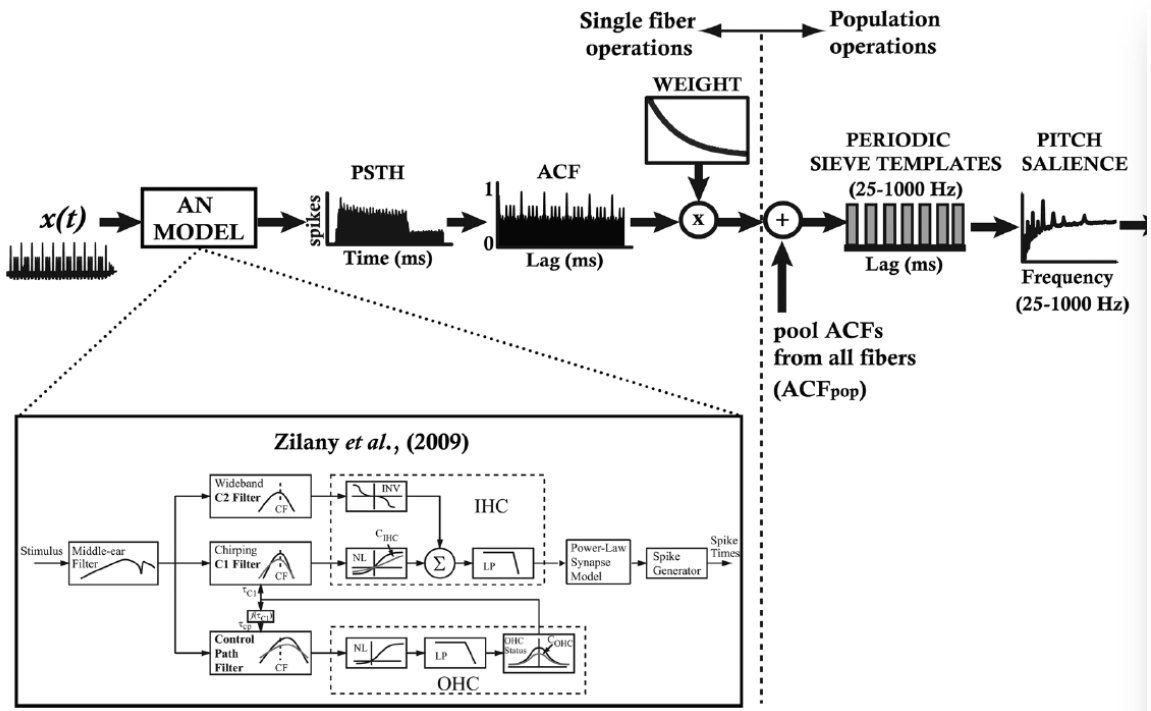
- Rate-Place Coding
  - Pitch Height
- Temporal Coding (Periodicity)
  - Pitch Chroma

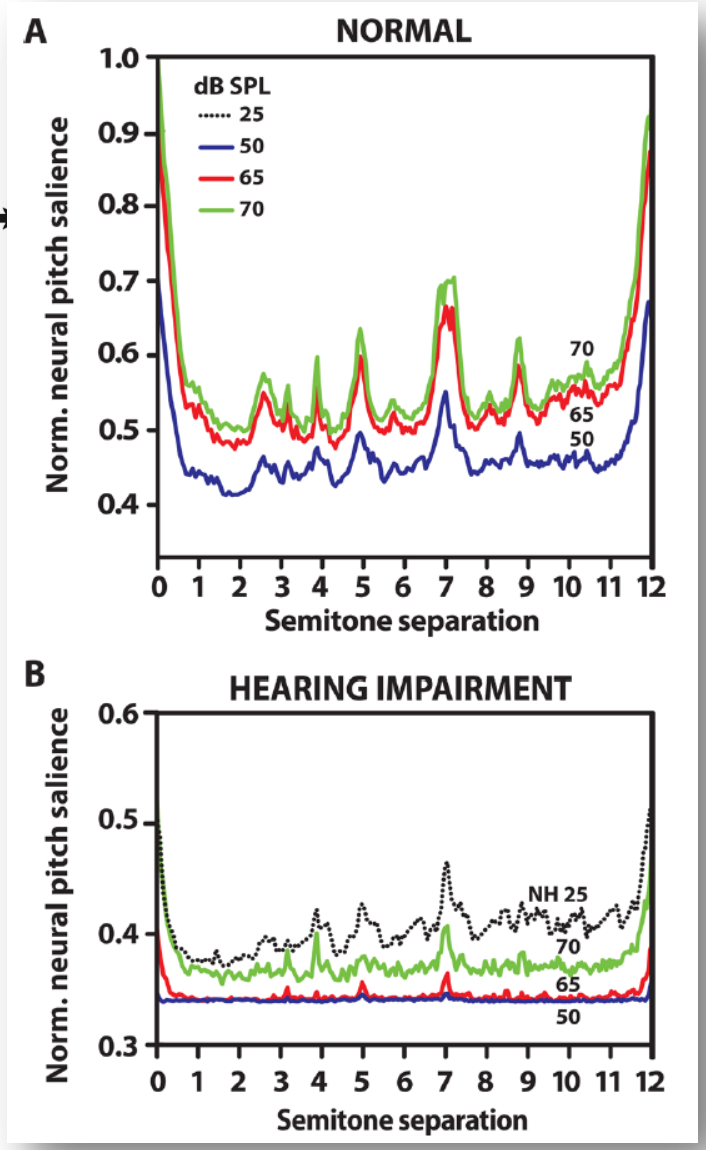


Rate, Place, and Periodicity



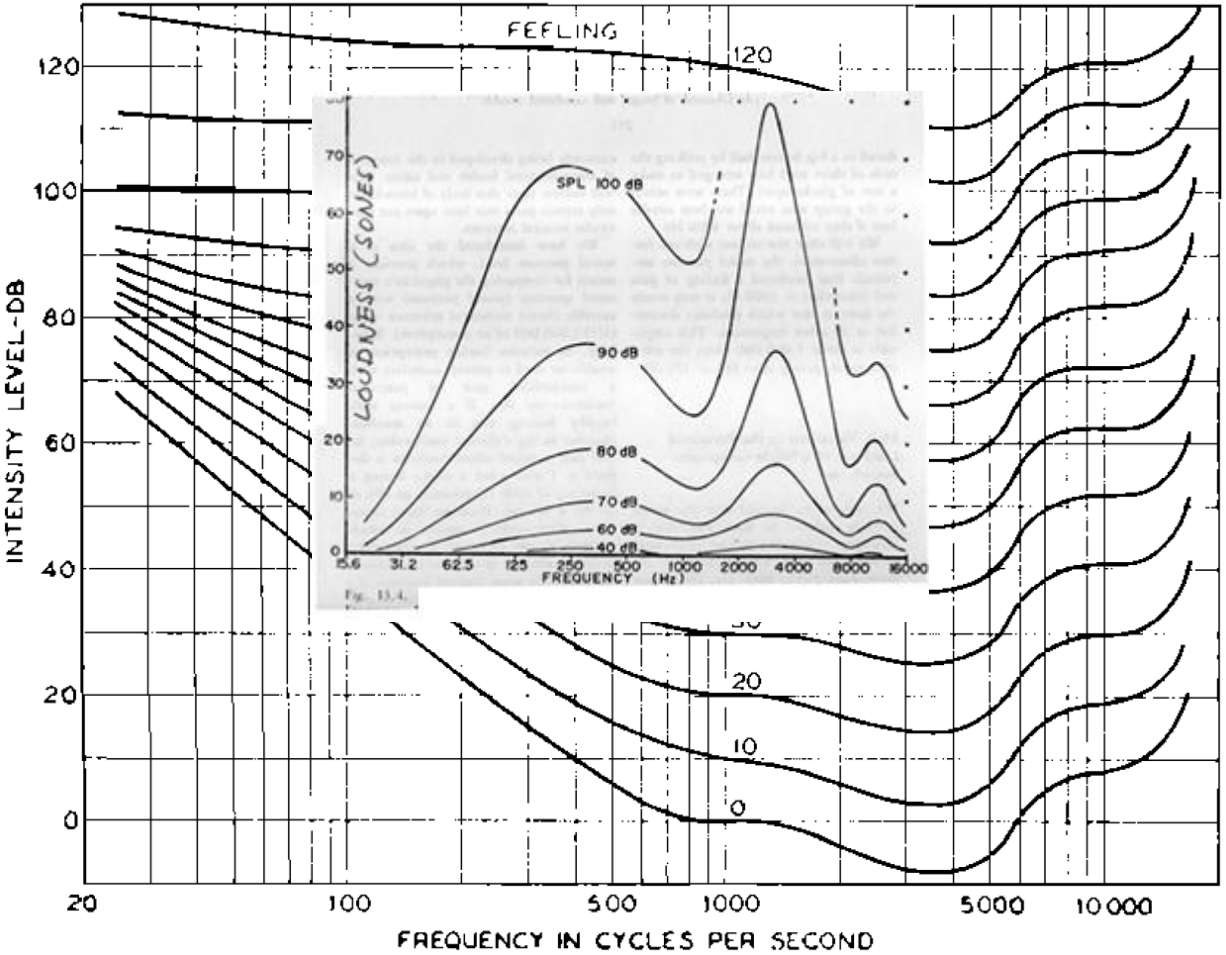
Pitch Salience





Bidelman, G. M. & Heinz, M. G. (2011). Auditory-nerve responses predict pitch attributes related to musical consonance-dissonance for normal and impaired hearing. *Journal of the Acoustical Society of America*,130(3), 1488-1502.

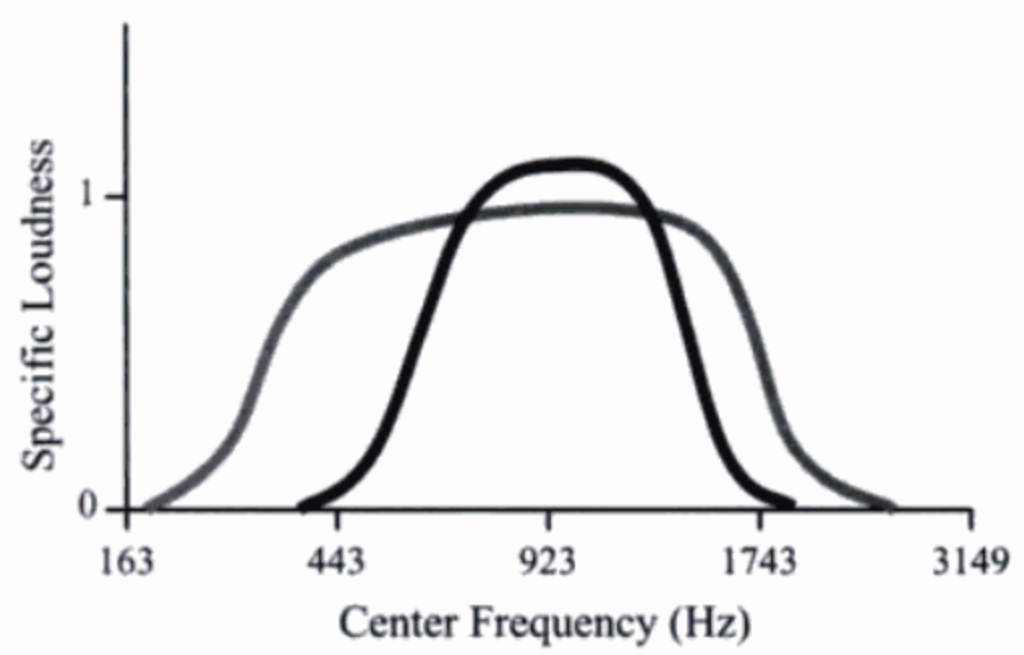
Loudness



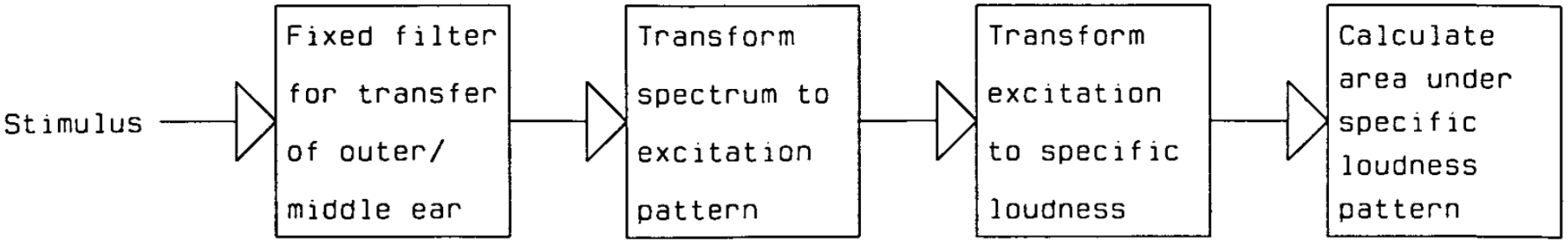
Fletcher & Munson 1933

Specific Loudness

Loudness as a function of frequency

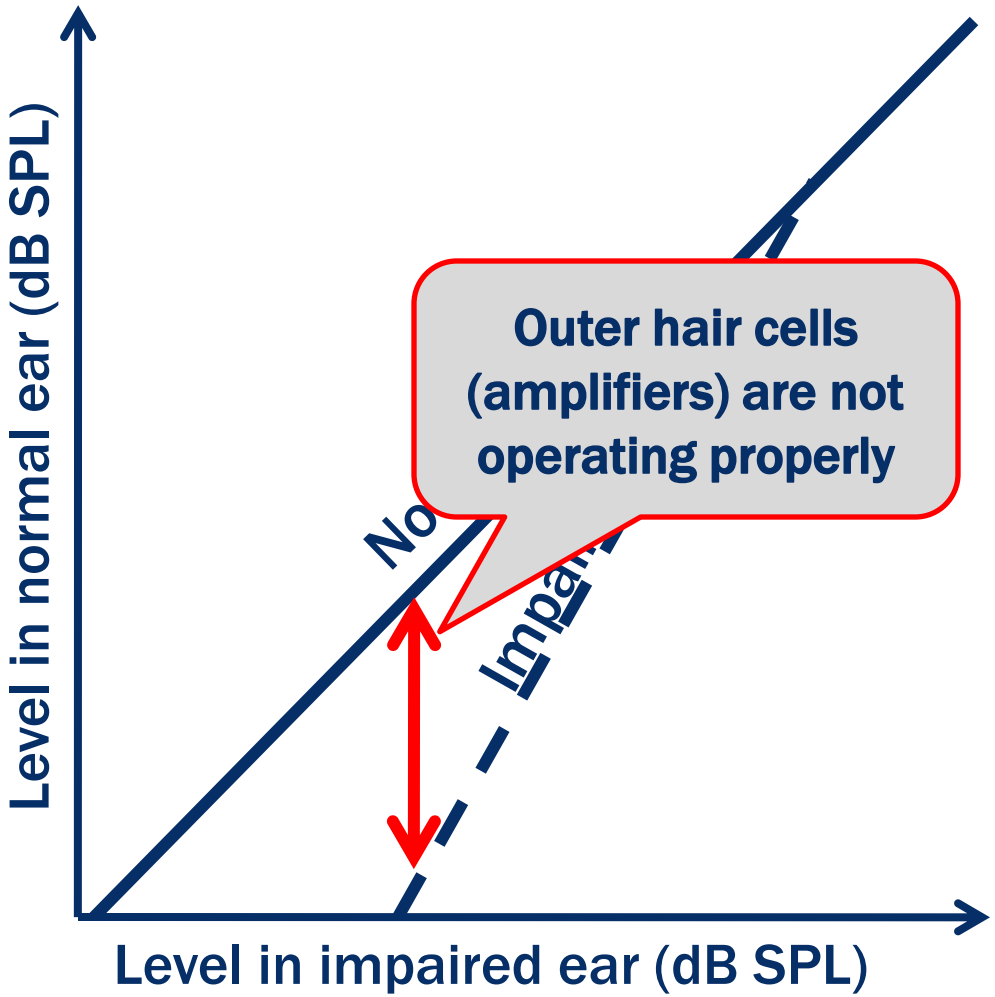


Plack, C. The Sense of Hearing. 2005

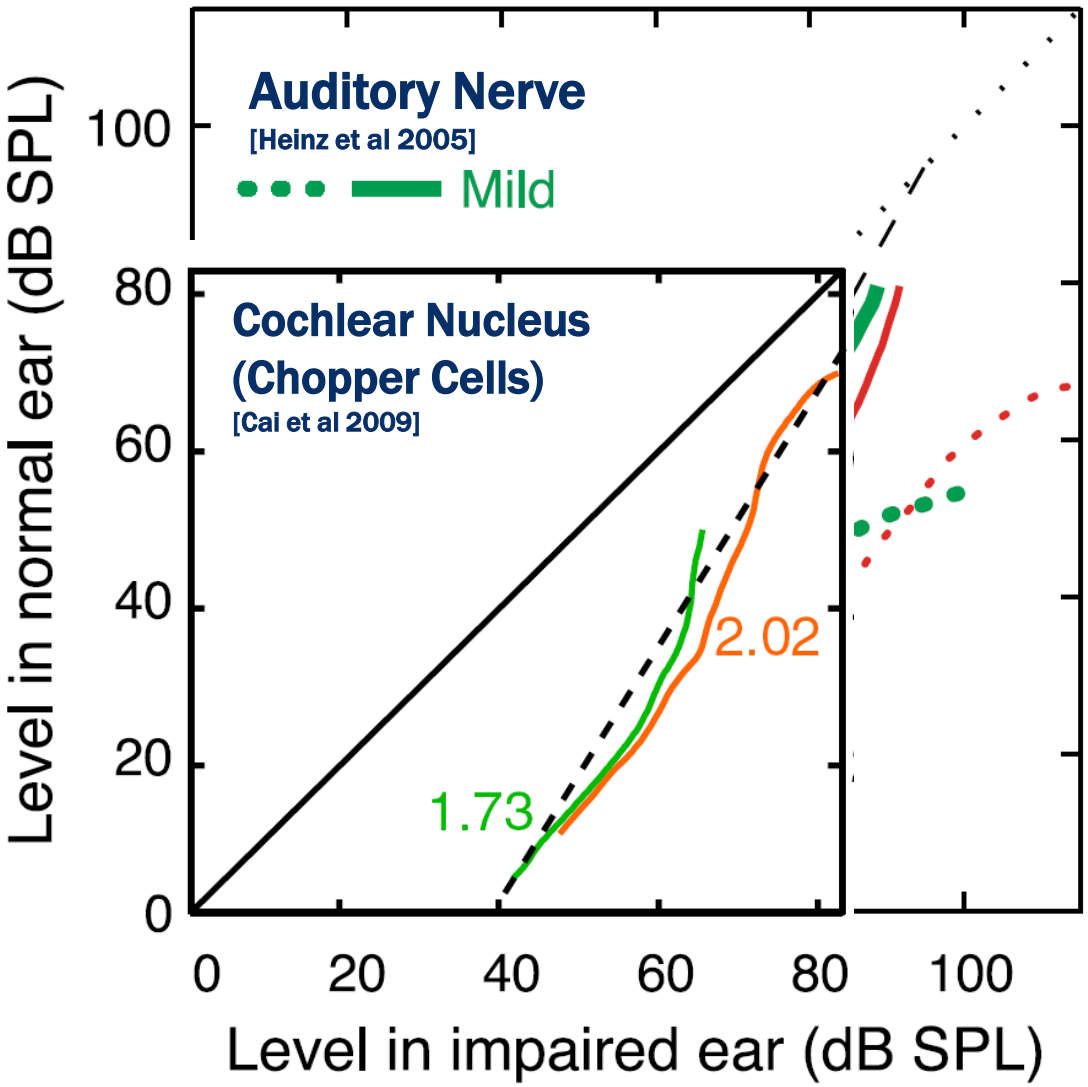


Zwicker, 1958/1965/1990; Moore & Glasberg 1996

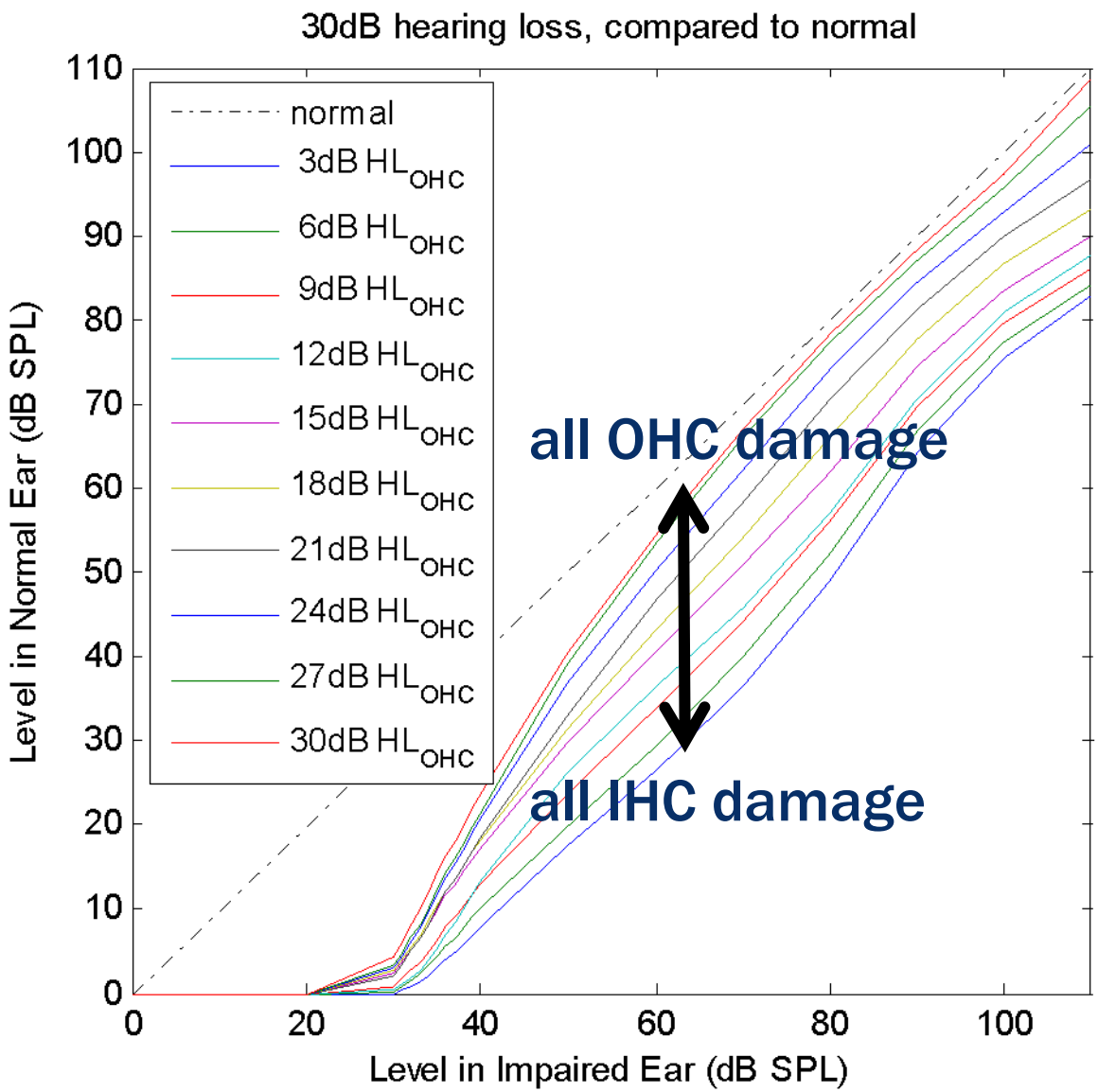
Impaired Loudness (Recruitment)



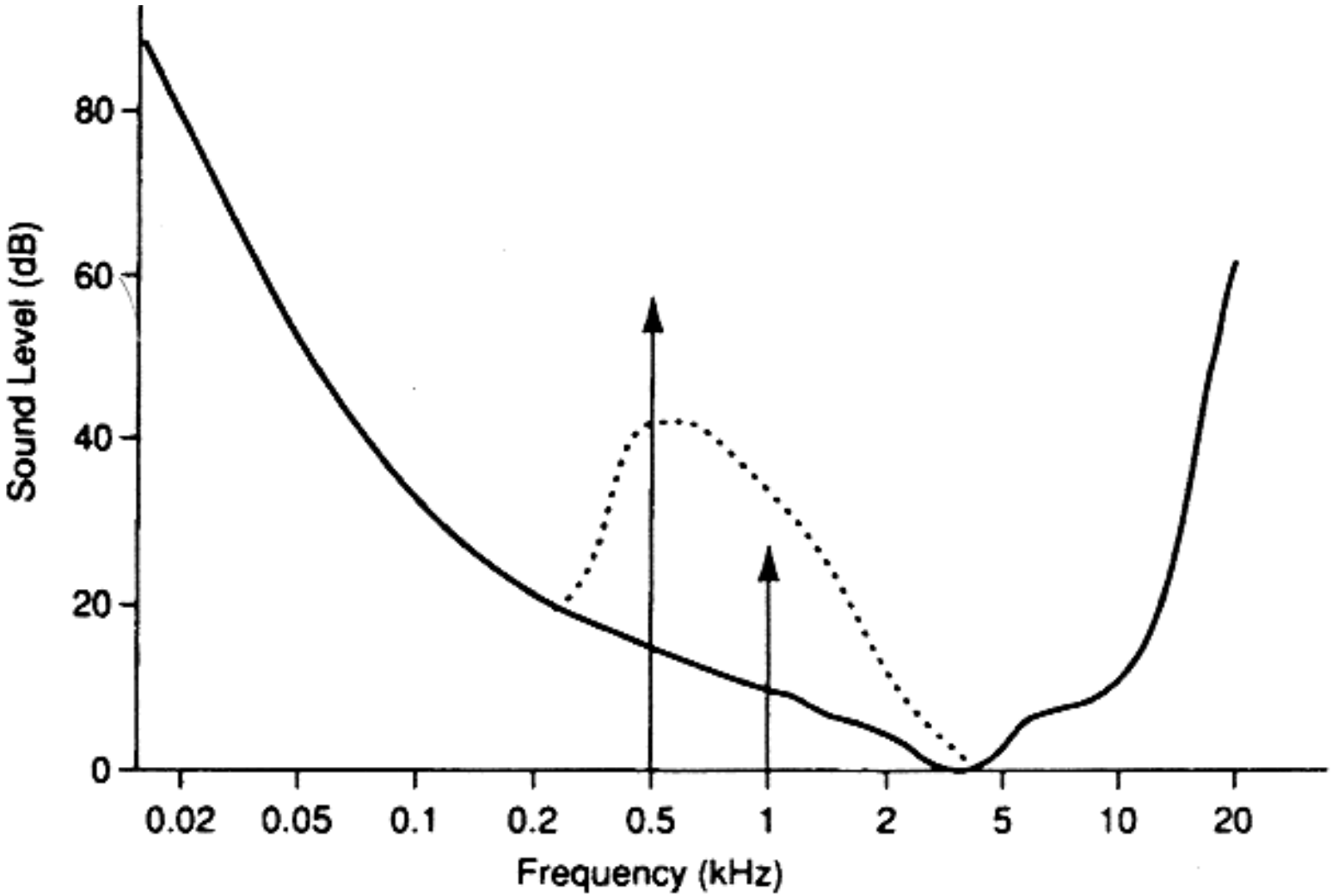
Impaired Loudness



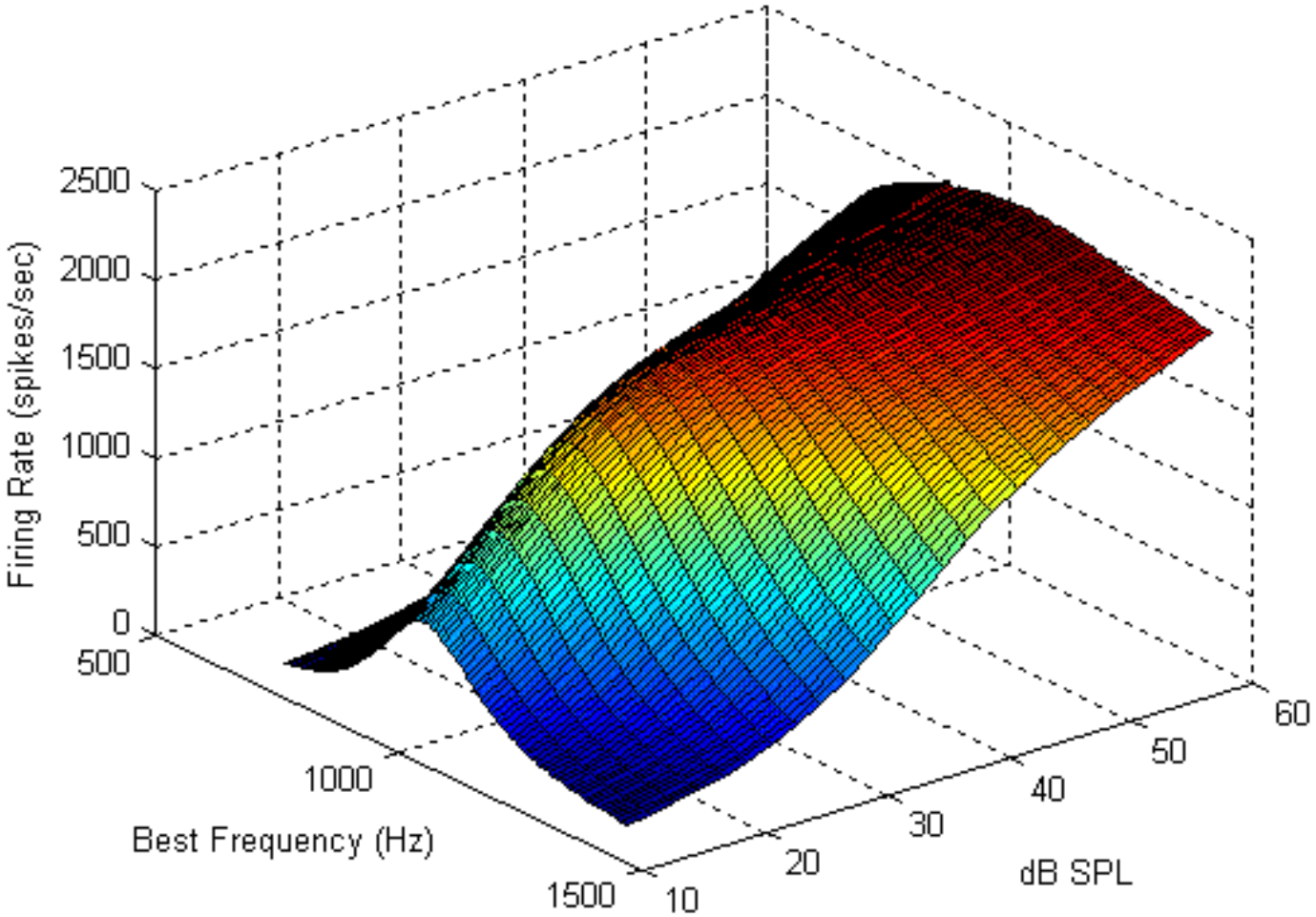
Recruitment with IHC/OHC Damage



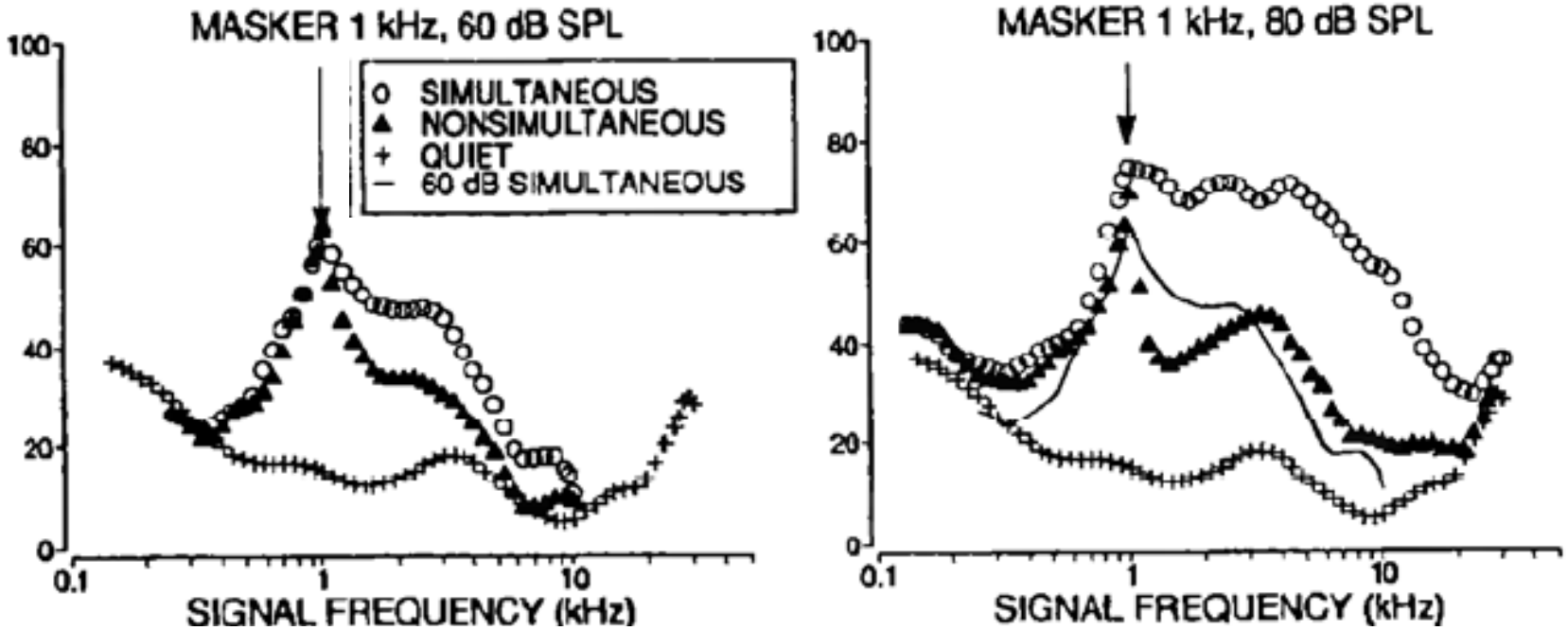
Masking


Sound Level (dB)
80
60
40
20
0
0.02
0.05
0.1
0.2
0.5
1
2
5
10
20
Frequency (kHz)

Masking


Firing Rate (spikes/sec)
2500
2000
1500
1000
500
0
500
1000
1500
Best Frequency (Hz)
10
20
30
40
50
60
dB SPL

Excitation vs. Suppression



Delgutte, B. (1990), 'Physiological mechanisms of psychophysical masking: observations from auditory-nerve fibers', *JASA,* 87(2), 791–809.

Also see:
Oxenham, A.J. Plack, C.J. (1998) 'Suppression and the upward spread of masking', JASA, 104 (6) 3500–3510

Two-Tone Suppression

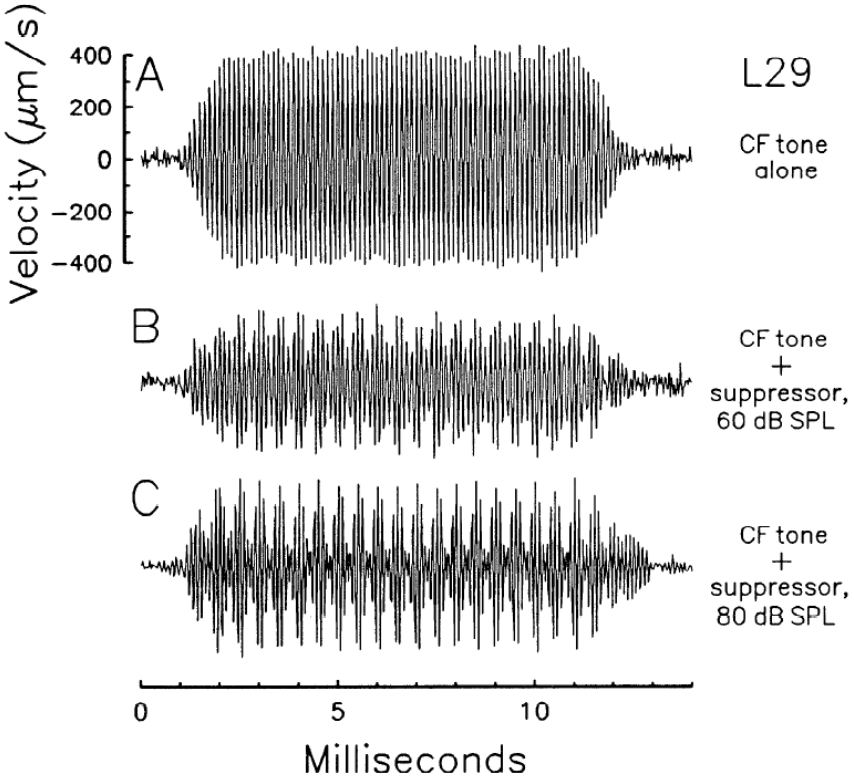
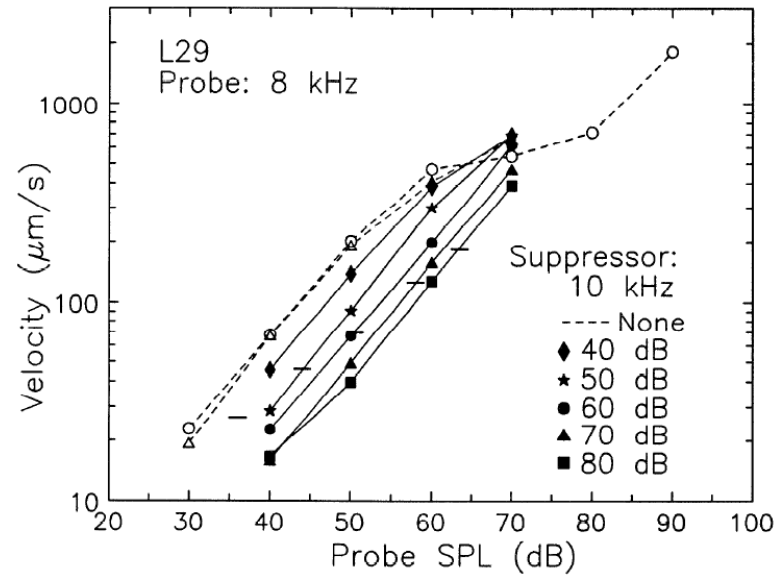
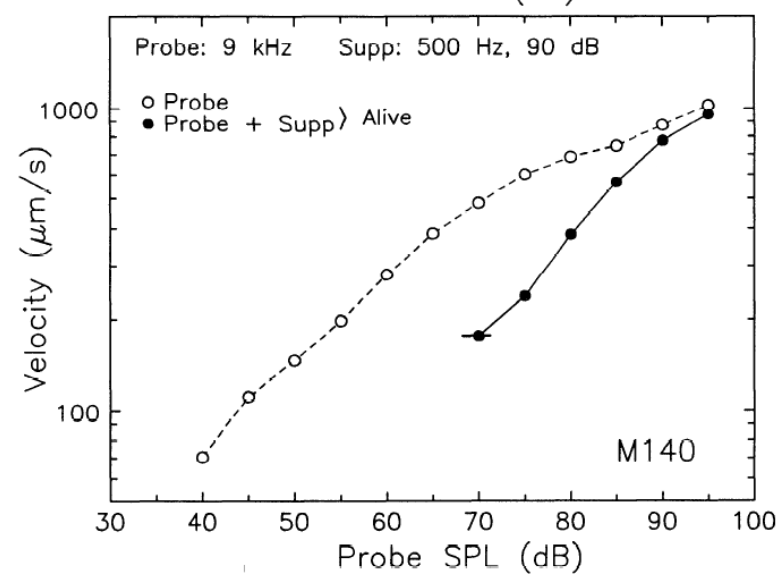


FIG. 1. Two-tone suppression in the vibrational response of the basilar membrane. *A*: averaged response to a characteristic frequency (8-kHz) tone burst presented at 60 dB SPL (peak velocity, 410 μm/s). *B*: averaged response to a pair of equal-intensity tones (8 and 10 kHz, 60 dB SPL) gated simultaneously. Response velocities at 8 and 10 kHz were 199 and 71 μm/s. *C*: averaged response to a pair of tones (8 kHz, 60 dB SPL and 10 kHz, 80 dB SPL) gated simultaneously. Response velocities at 8 and 10 kHz were 128 and 187 μm/s, respectively.

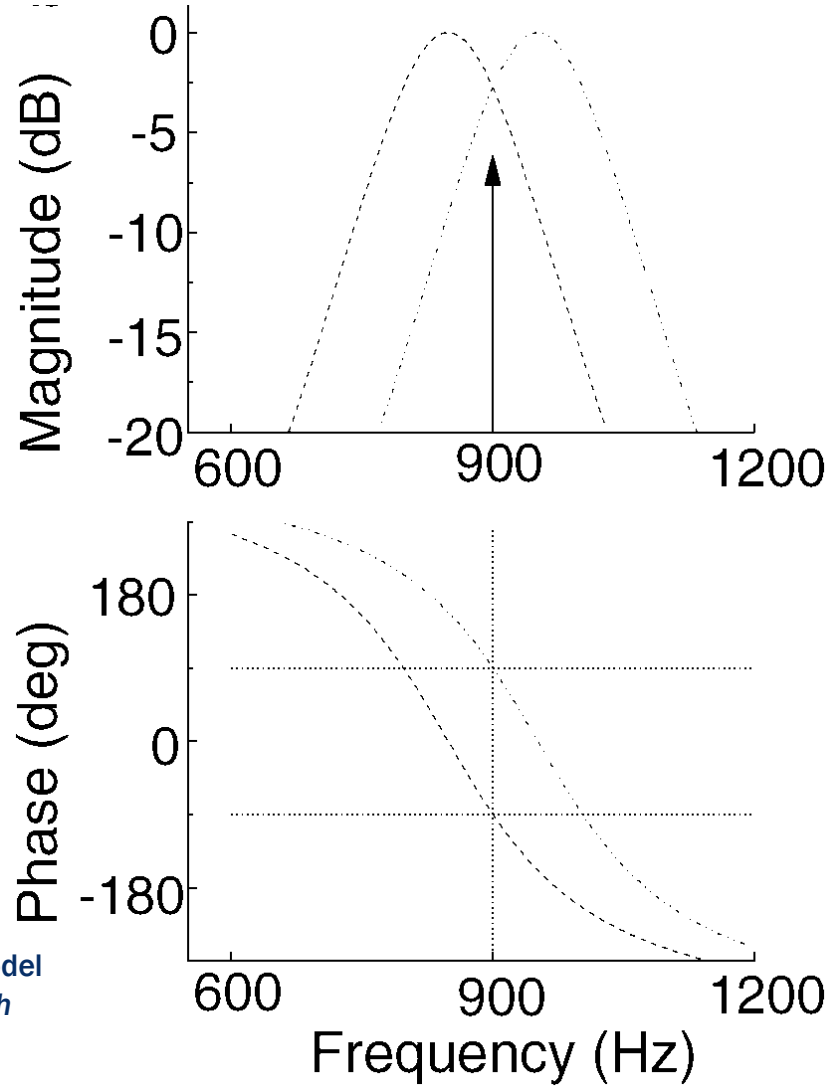




Ruggero, M. A., Robles, L. U. I. S., & Rich, N. C. (1992). Two-tone suppression in the basilar membrane of the cochlea: Mechanical basis of auditory-nerve rate suppression. *Journal of Neurophysiology*, *68*(4), 1087-1099.

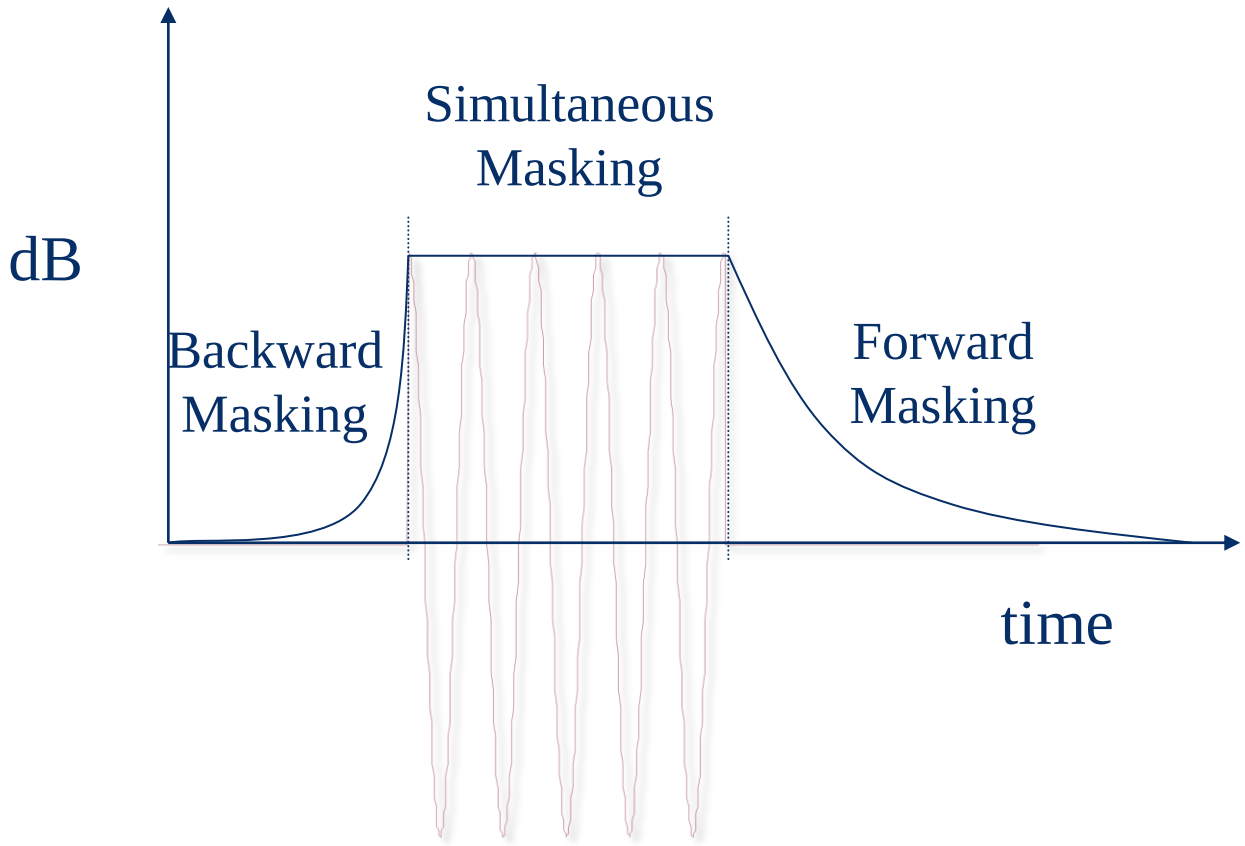
Masking & Phase

We can detect signals that would otherwise be masked by detecting phase differences between nerve fibers



Carney, Laurel H., et al. "Auditory phase opponency: A temporal model for masked detection at low frequencies." *Acta Acustica United with Acustica* 88.3 (2002): 334-347.

Temporal Masking



Temporal Masking

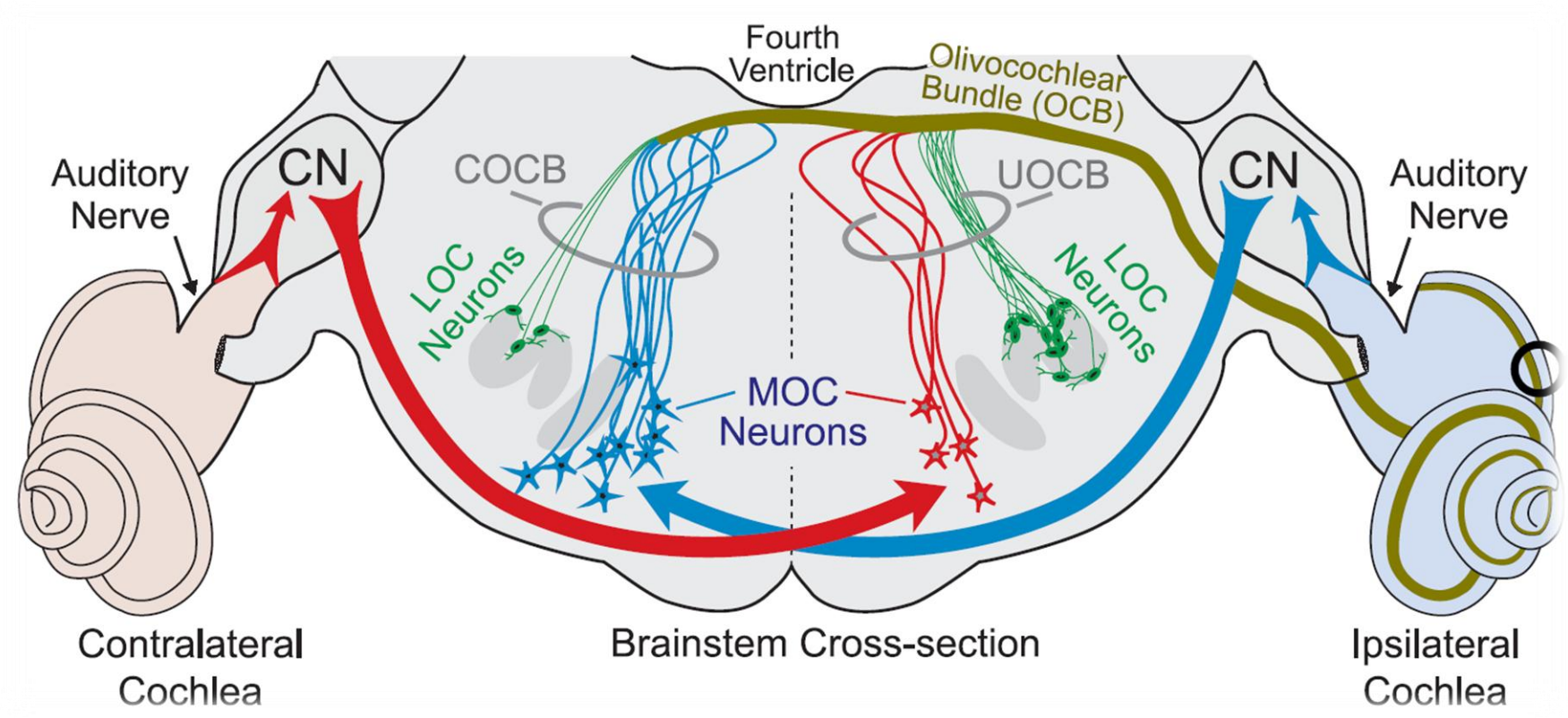
Backward Masking

- Nobody knows what causes it
- With practice, you can learn to get rid of it

Forward Masking

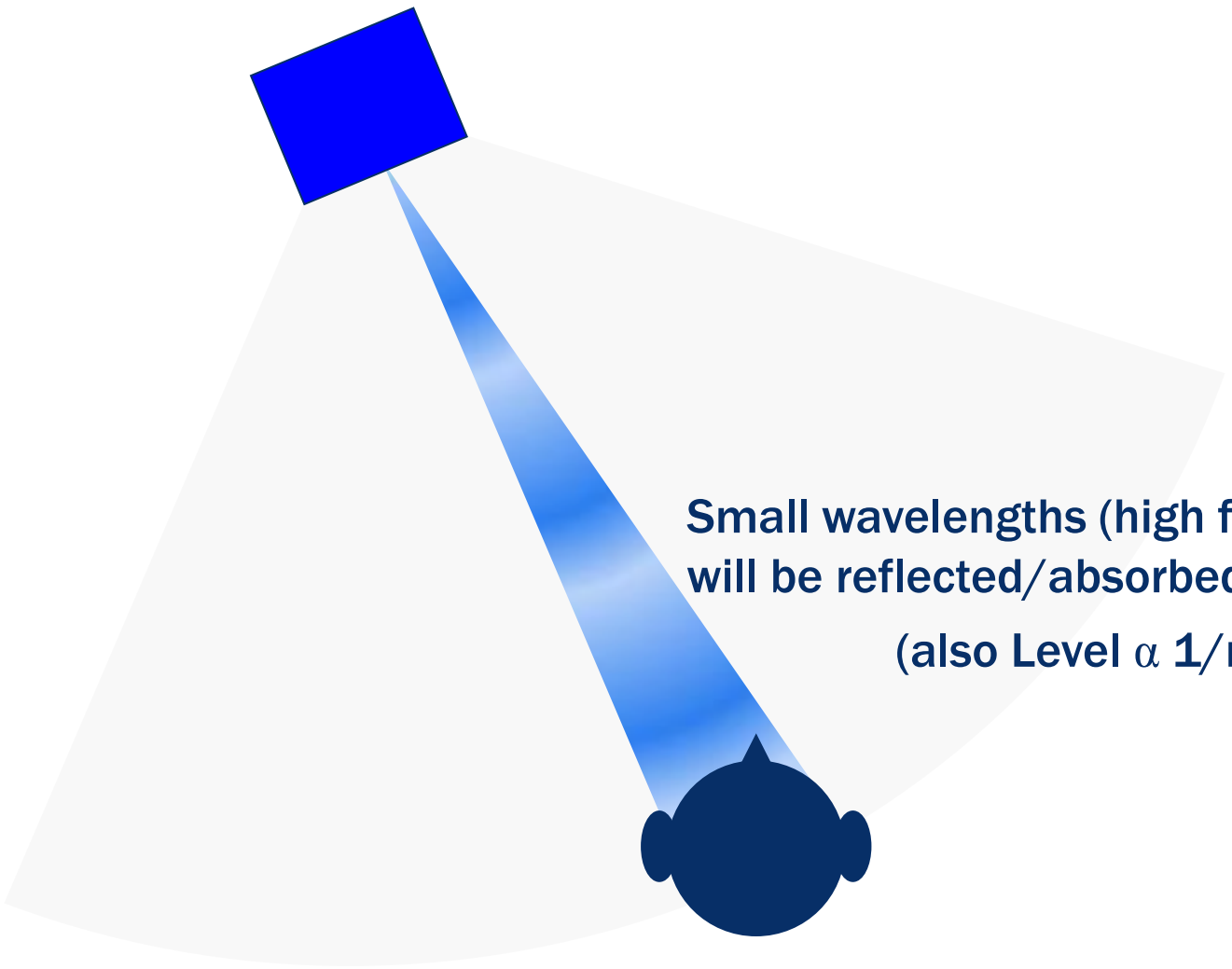
- Nobody knows what causes it
- Theories:
  - Neural adaptation (in the cochlea)
  - Persistence of excitation (temporal integration)
  - Gain control (neural feedback)

Adaptive Gain Control Neural Circuit



Guinan (2006)

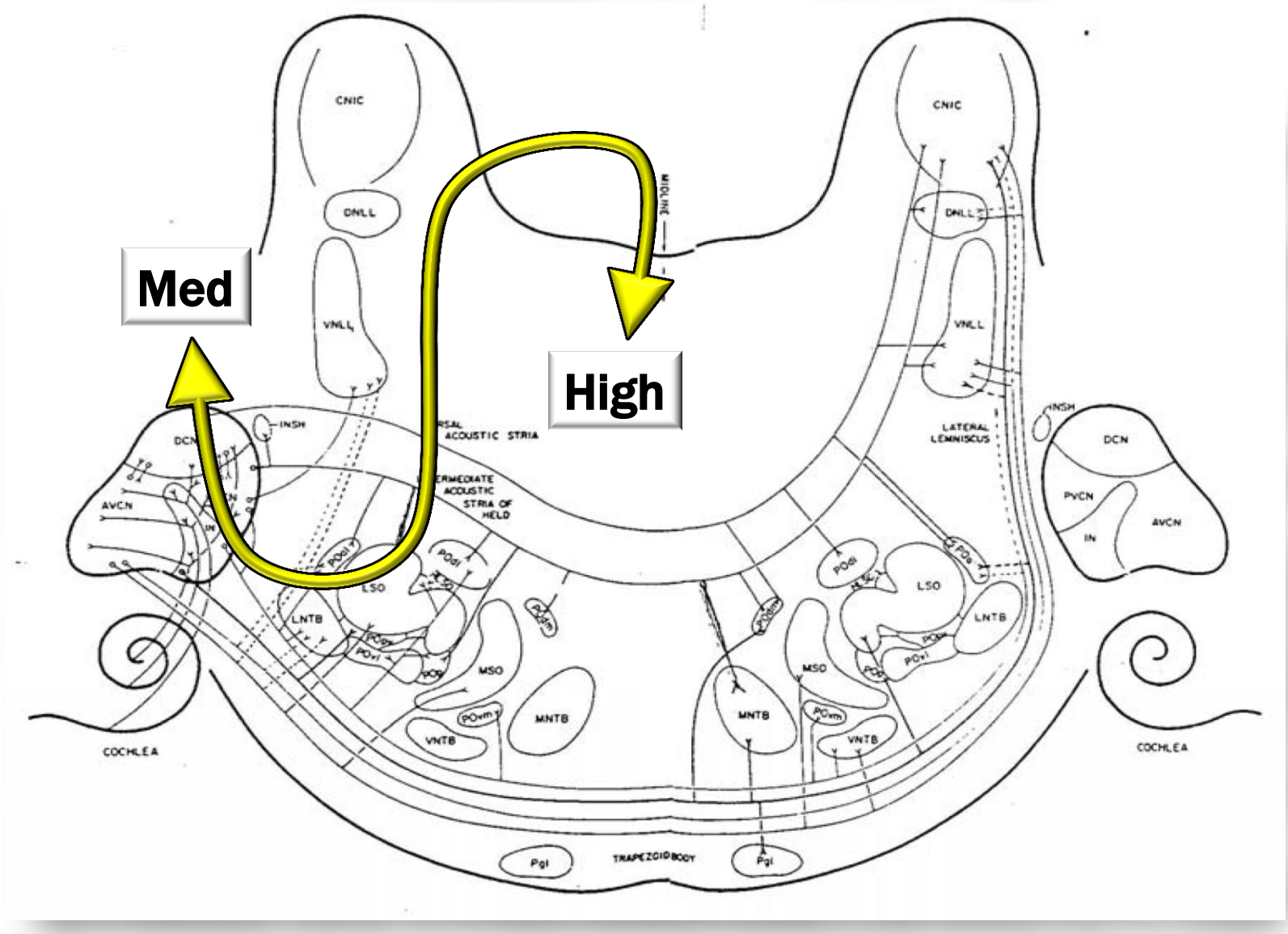
Interaural Level Difference



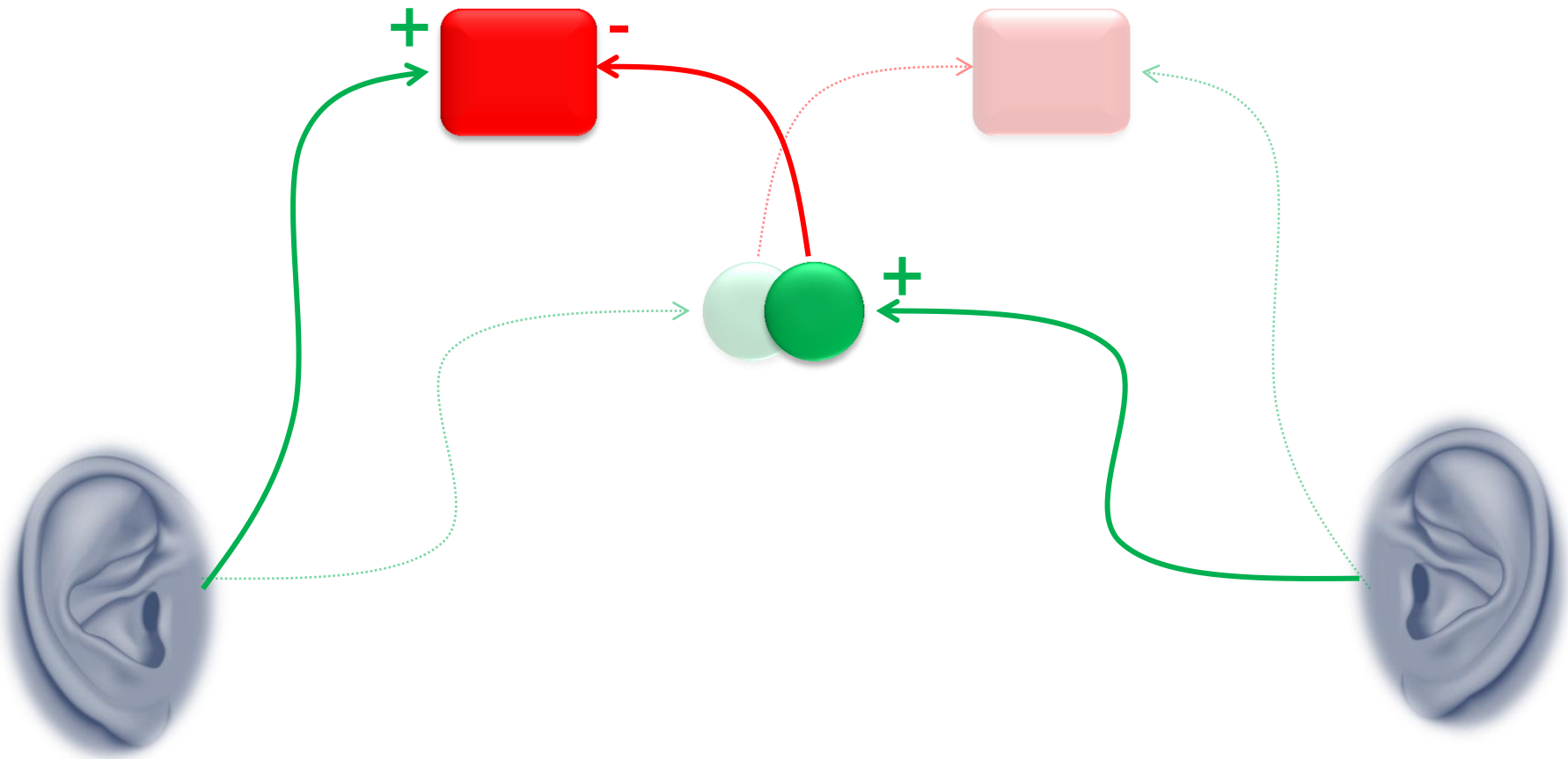
Small wavelengths (high frequencies) will be reflected/absorbed by the head

(also Level α $1/r^2$)

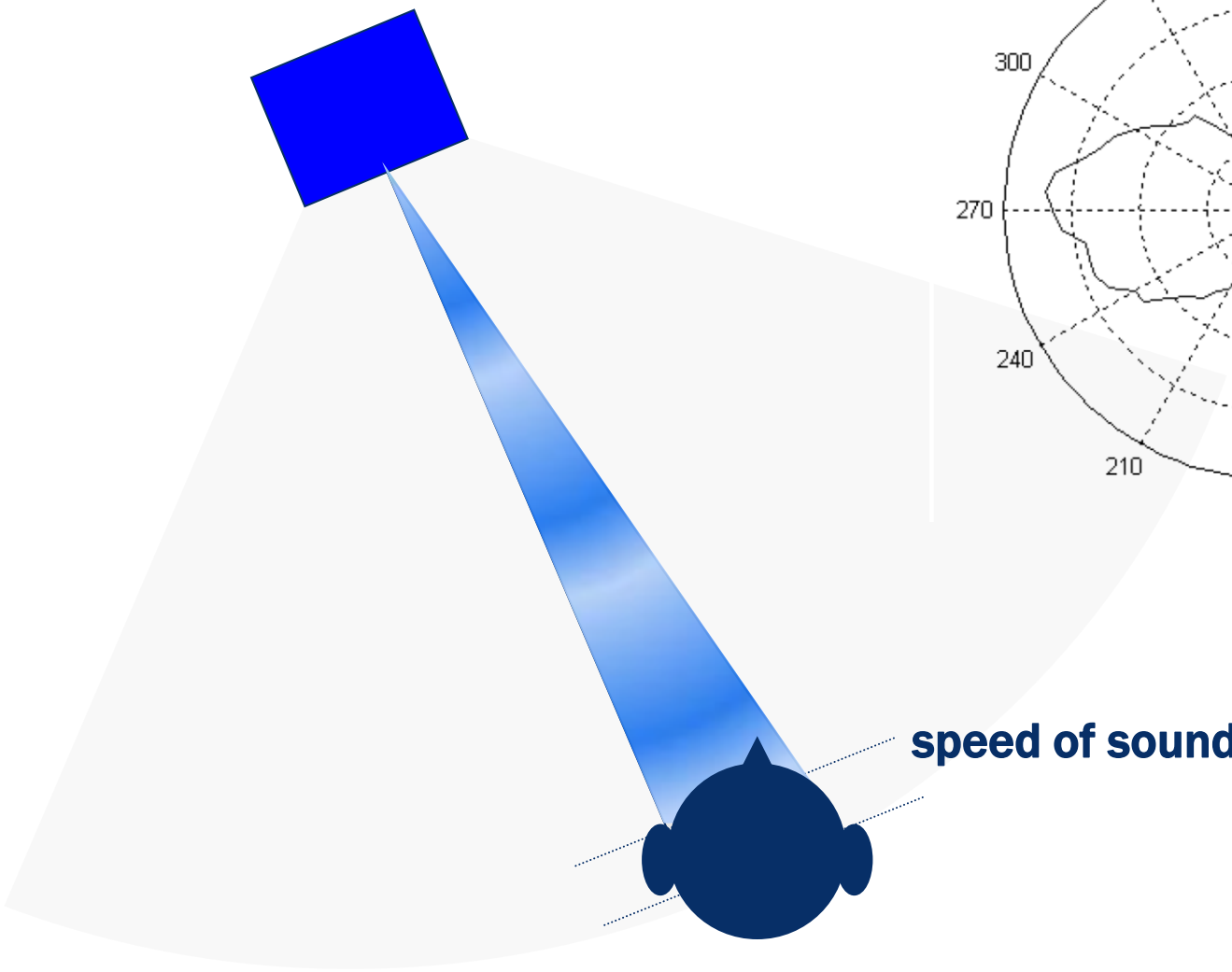
Interaural Level Difference

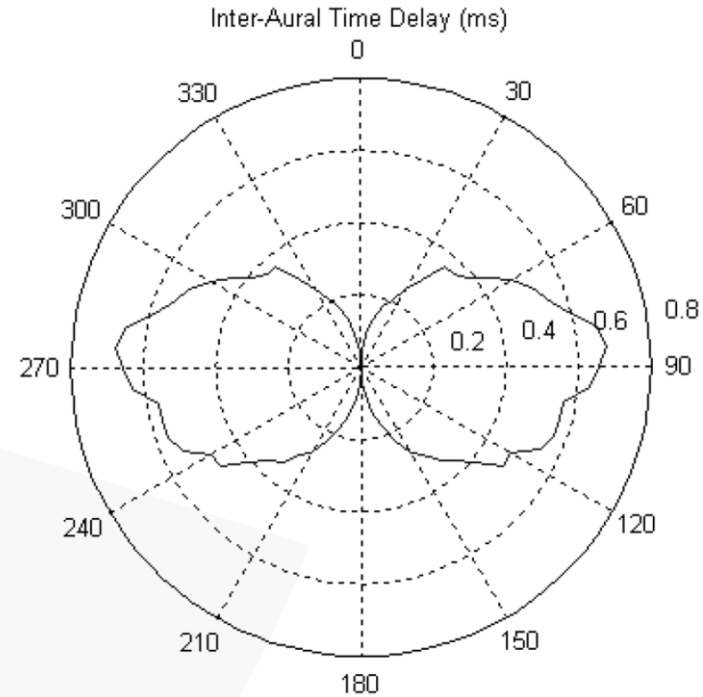


Interaural Level Difference



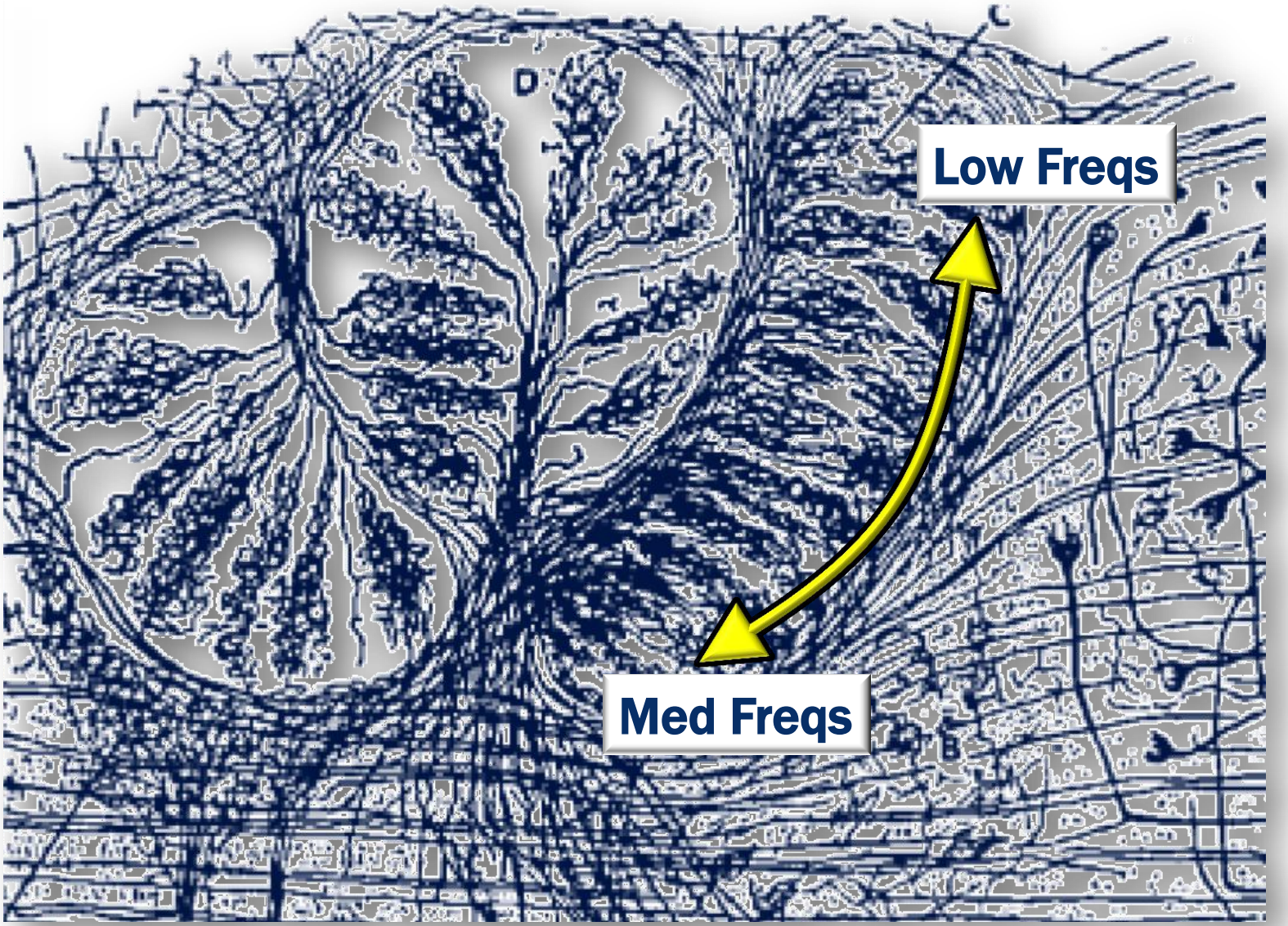
Interaural Time Difference





speed of sound = 340.29 m/s

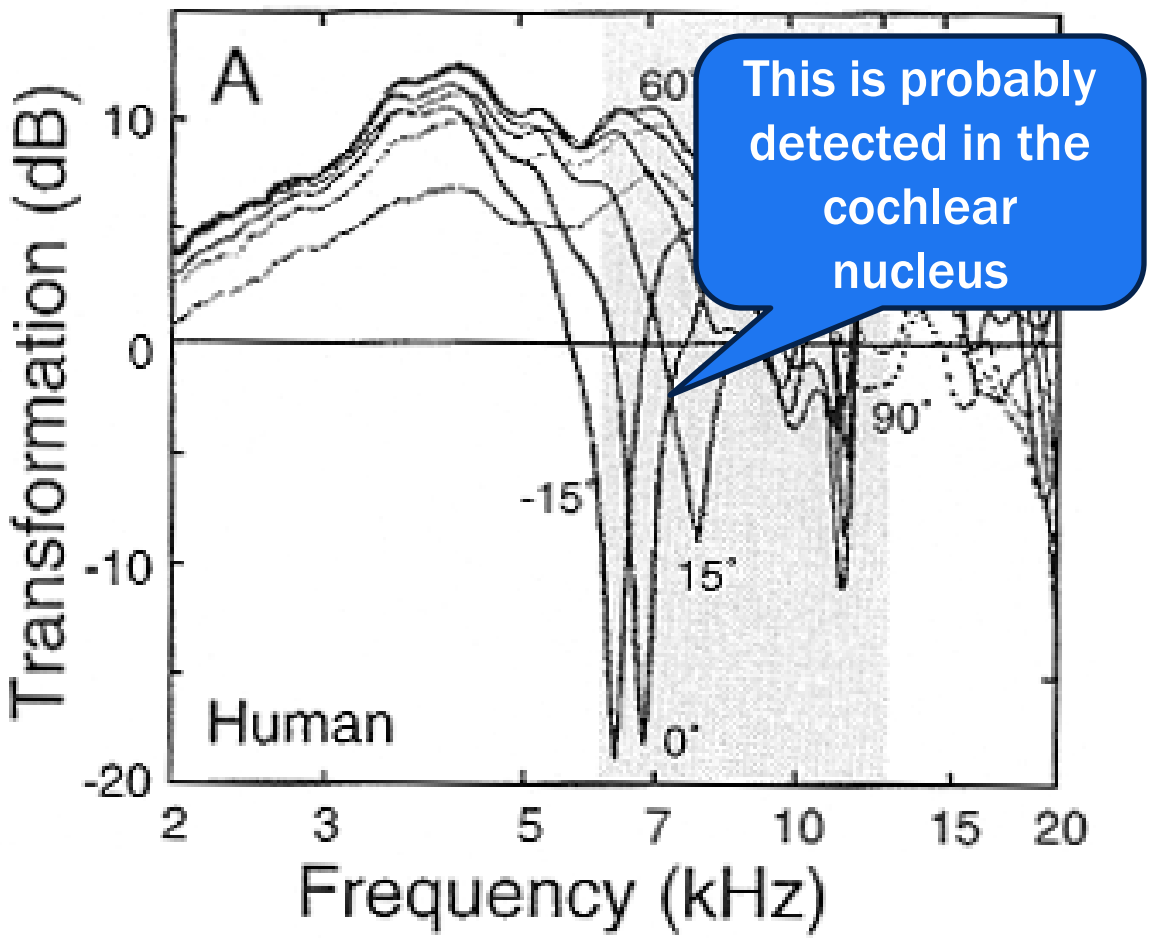
Interaural Time Difference



Jeffress Coincidence Model

[video]

Spectral Localization Cues



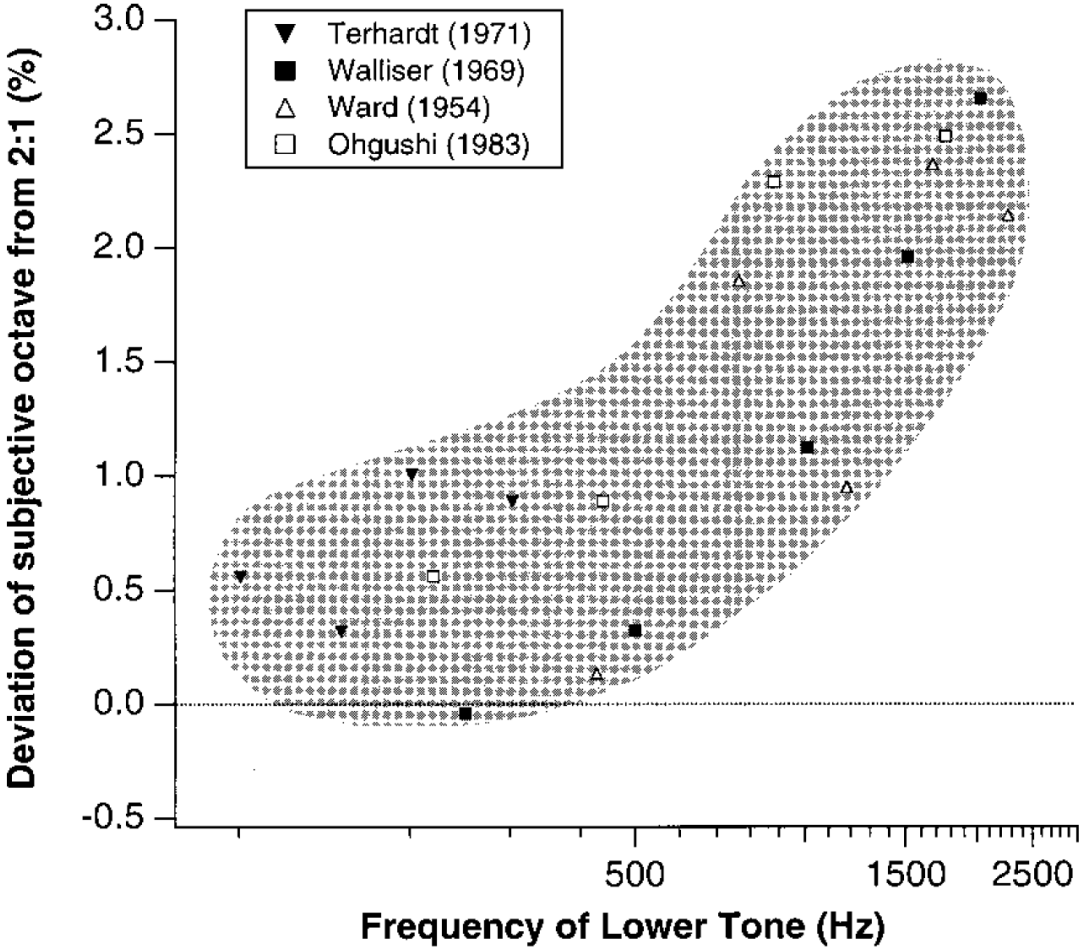
Illusions with a physiological basis

- Octave stretch
- Huggins pitch

Octave Stretch

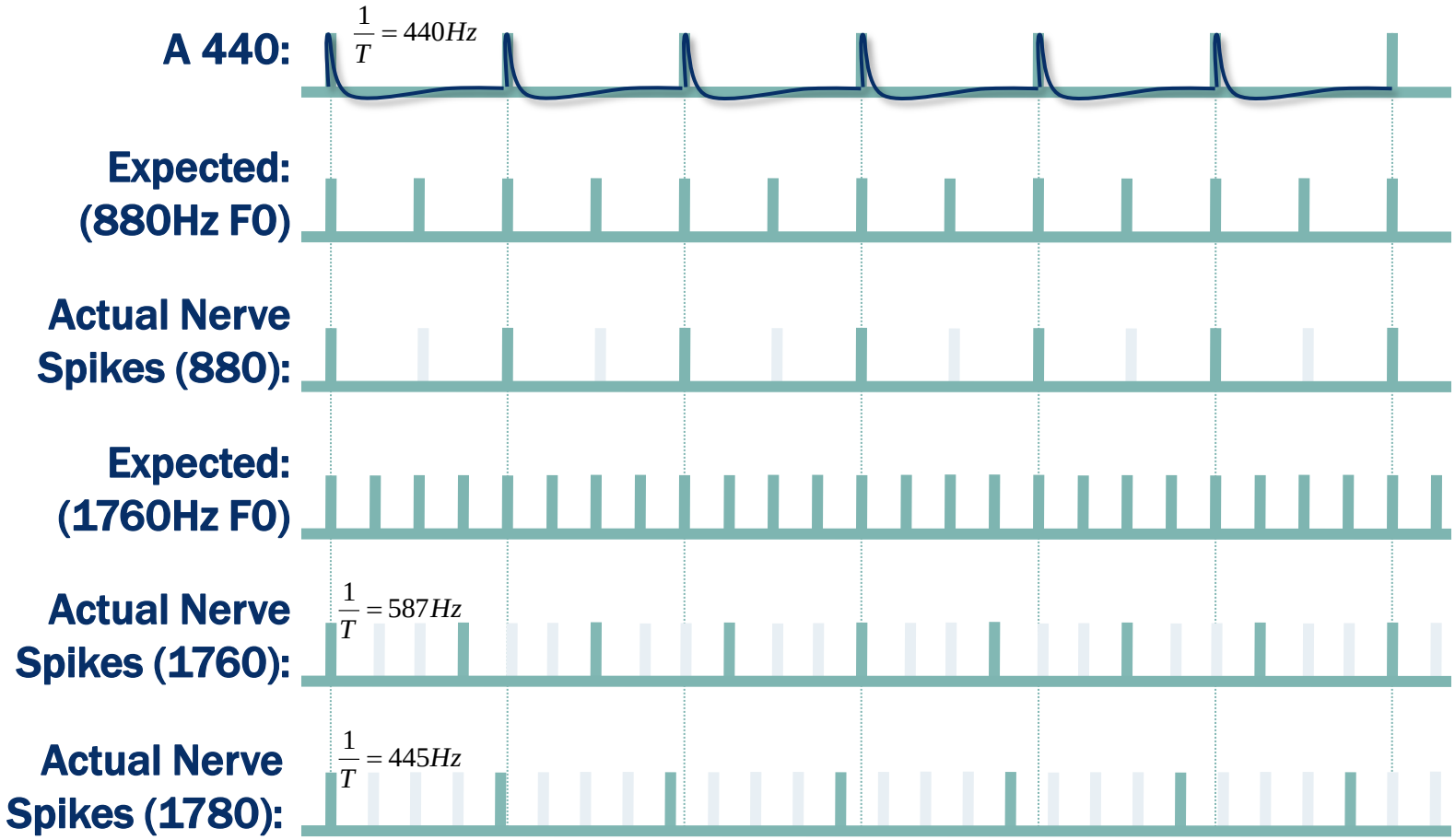
- **Listeners prefer octave ratios slightly greater than 2:1**

(Ward, 1954; Walliser, 1969; Terhardt, 1971; Sundberg and Lindqvist, 1973)



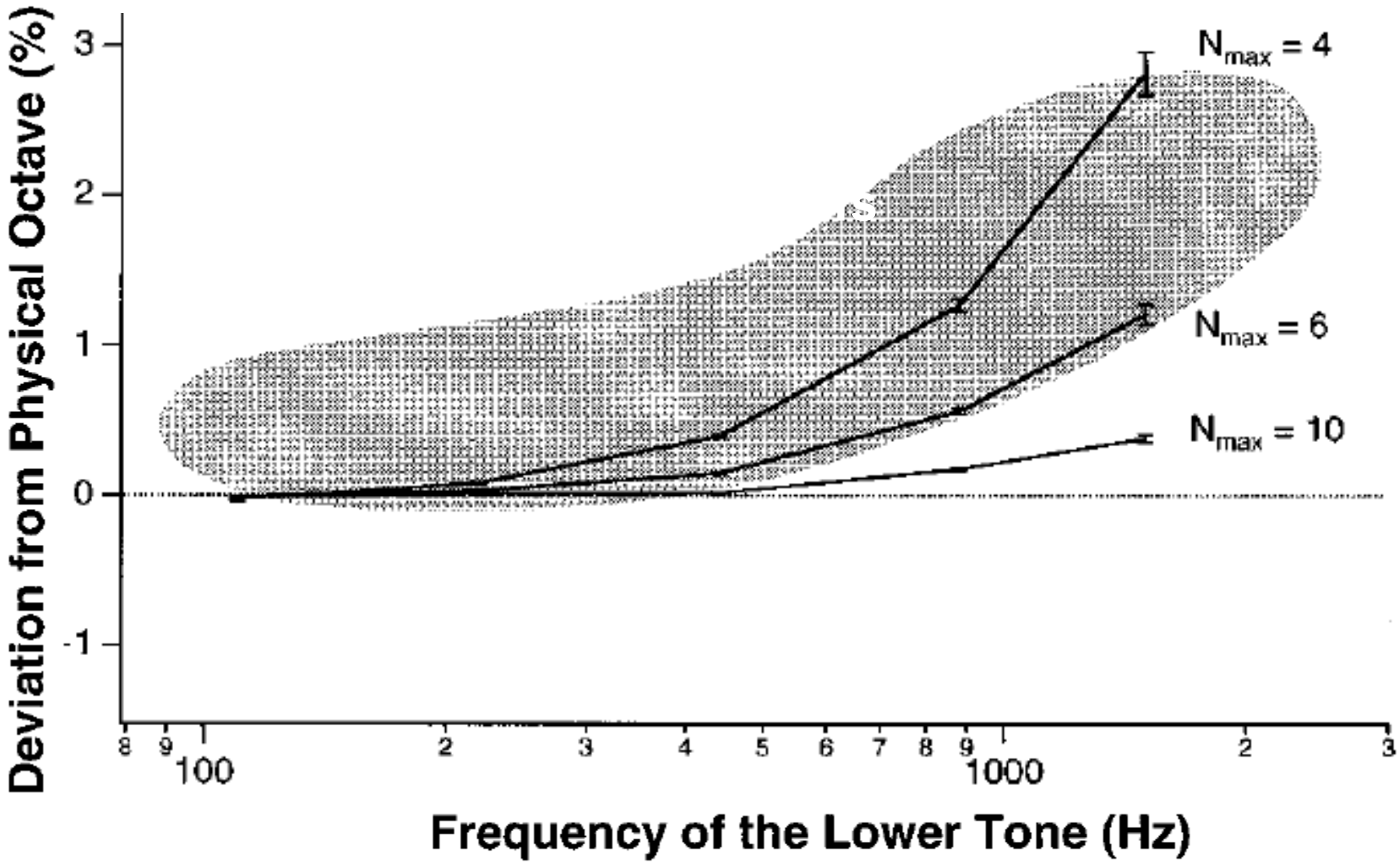
(from McKinney & Delgutte, JASA, 1999)

Octave Stretch



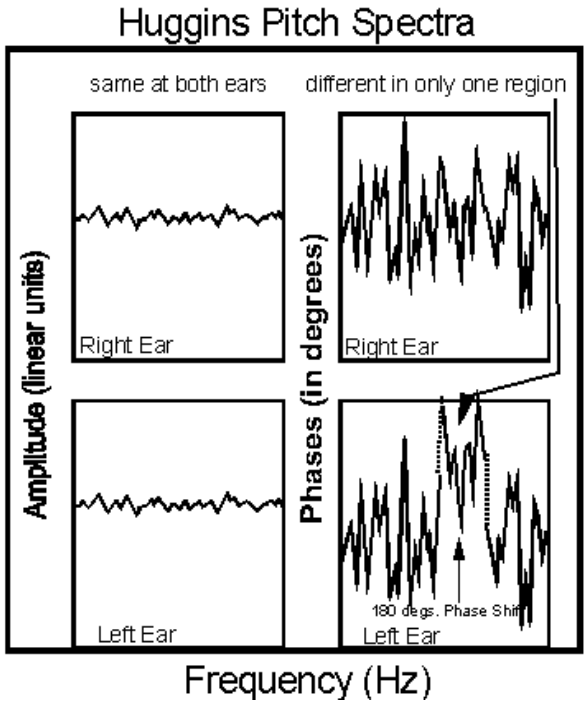
⟶ A slight increase of the frequency improves the periodicity

Octave Stretch



(from McKinney & Delgutte, JASA, 1999)

Huggins Pitch



(use headphones)

- Consistent with Jeffress model of interaural cross-correlation

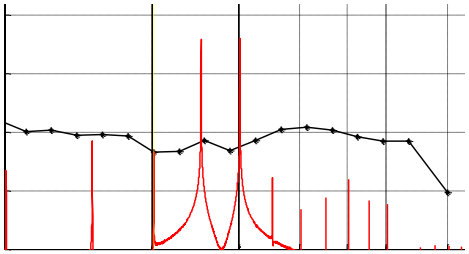
Hancock, Kenneth E., and Bertrand Delgutte. "Neural correlates of the Huggins dichotic pitch." *Association for Research in Otolaryngology Abstracts*. Vol. 25. 2002.

Appendix

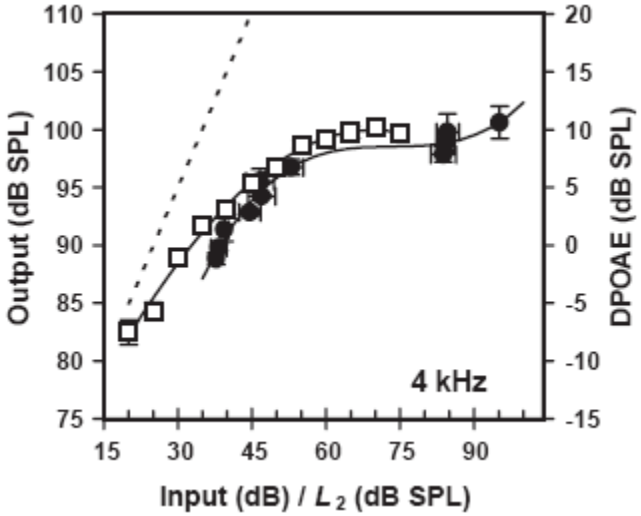
Evoked Responses

DPOAE

- Correlated to behavioral metrics for high frequencies (>4kHz)



Lopez-Poveda, E., P. Johannesen, M, Merchan. Estimation of the degree of inner and outer hair cell dysfunction from distortion product otoacoustic emission input/output functions. Audiological Medicine. 2009; 7: 2228



ABR

- Different 'waves' are thought to originate in different auditory nuclei
- Can measure amplitude, latency, etc
- Wave I latency related to cochlear tuning? But not wave 5?