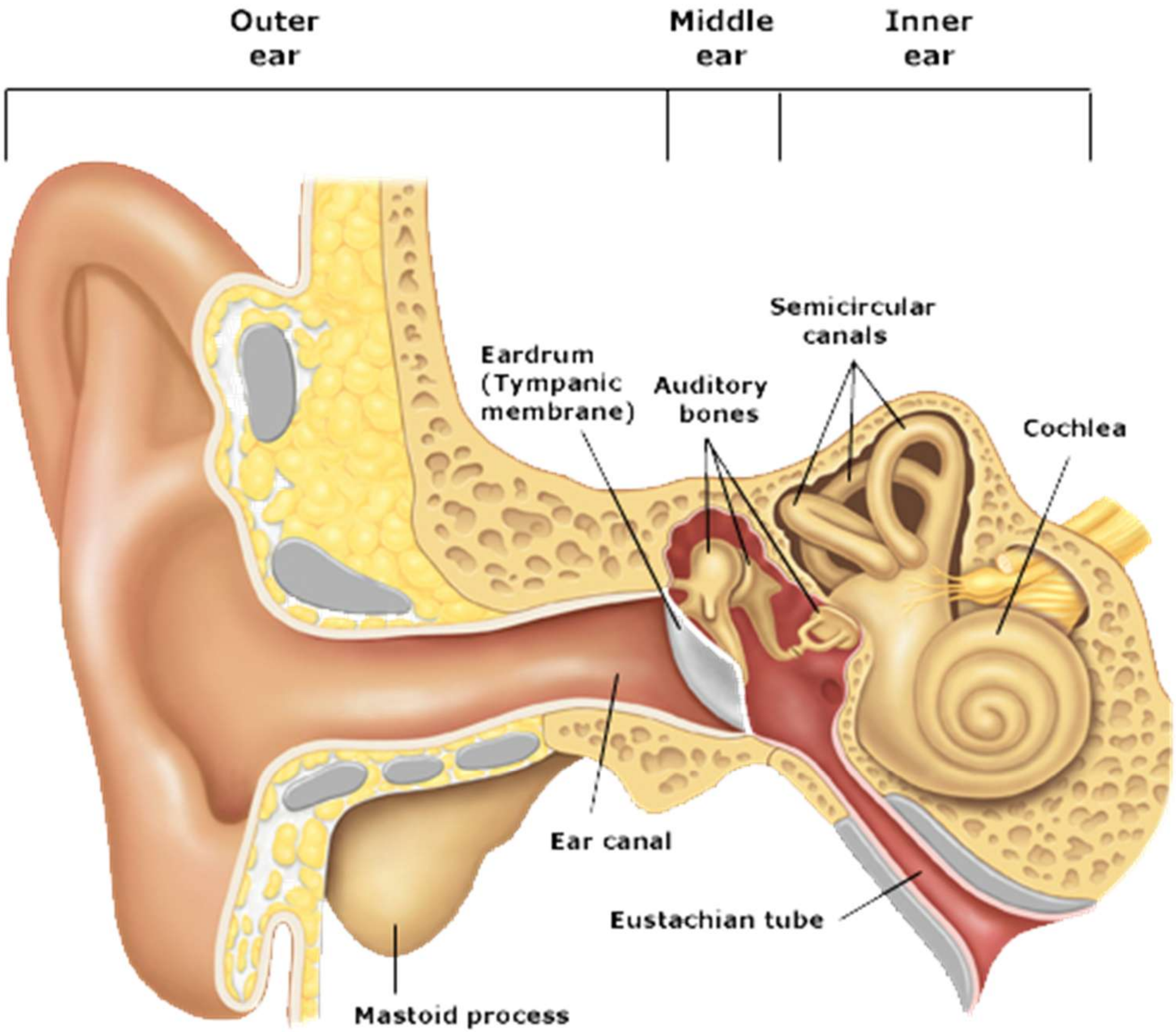
Signals, systems, acoustics and the ear

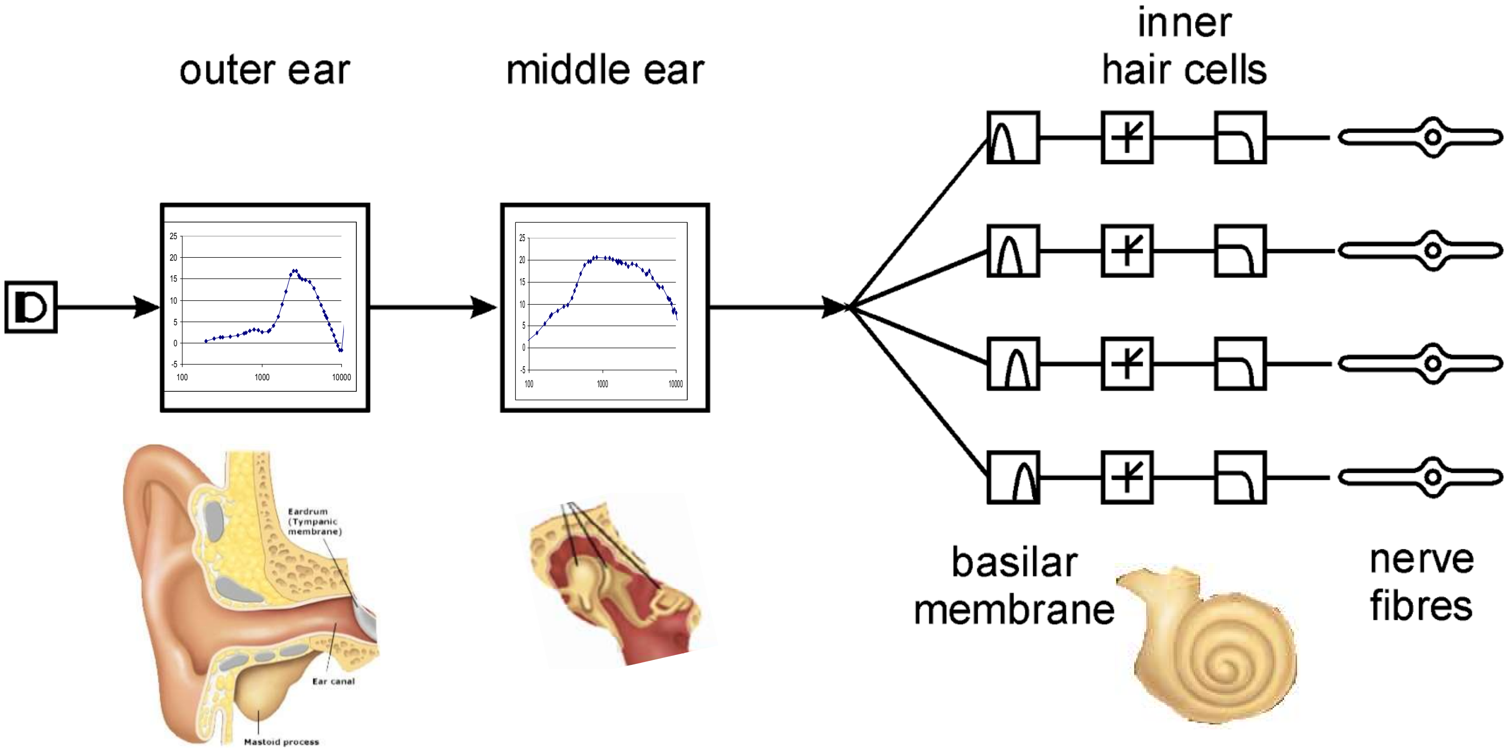
Week 5

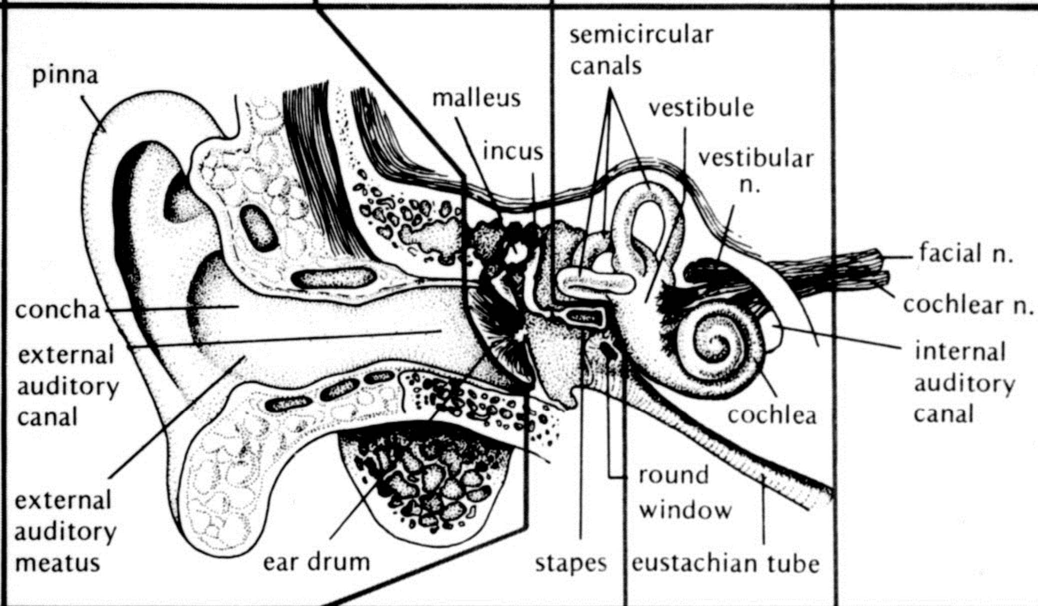
The peripheral auditory system: The ear as a signal processor



Think of this set of organs …

as a collection of 'systems', transforming sounds to be sent to the brain



Gross division	*Outer ear*	*Middle ear*	*Inner ear*	*Central auditory nervous system*
Anatomy				
Mode of operation	*Air vibration*	*Mechanical vibration*	*Mechanical, Hydrodynamic, Electrochemical*	*Electrochemical*
Function	*Protection, Amplification, Localization*	*Impedance matching, Selective oval window stimulation, Pressure equalization*	*Filtering distribution, Transduction*	*Information processing*

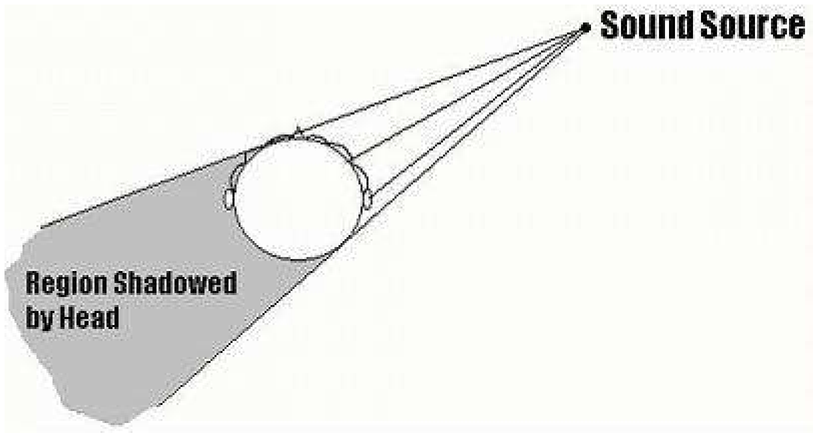
A quick summary of the auditory periphery:

Three main divisions: *Outer, Middle and Inner ear*

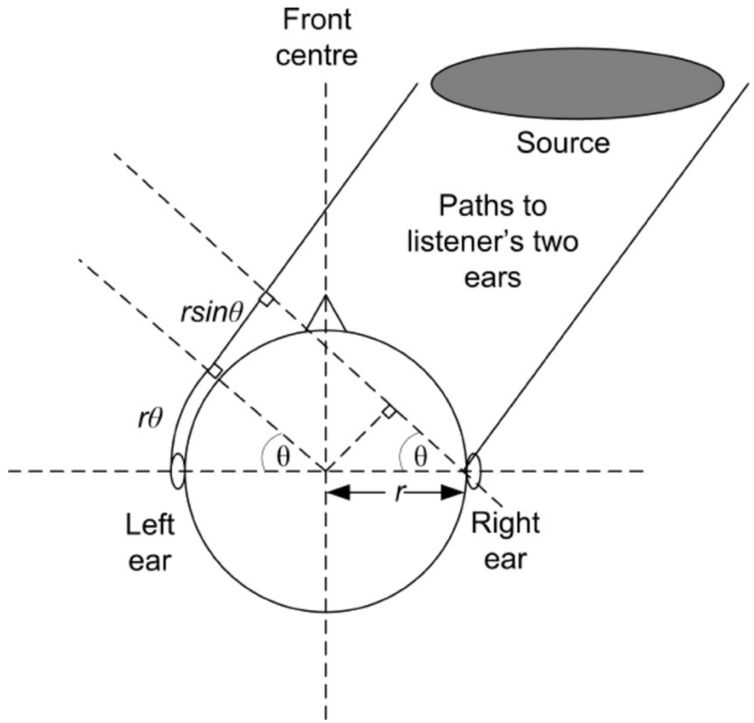
Outer ear

- Funnel shaped pinna “collects” sounds from environment
- Pinna and ear canal affect the frequency content of sounds
  - *filtering*
- Having two ears (instead of one) is important for sound localisation
  - differences between what each ear ‘hears’

Sounds are (often) more intense, and sooner to reach, the closer ear



ILD: Works at mid-high frequencies



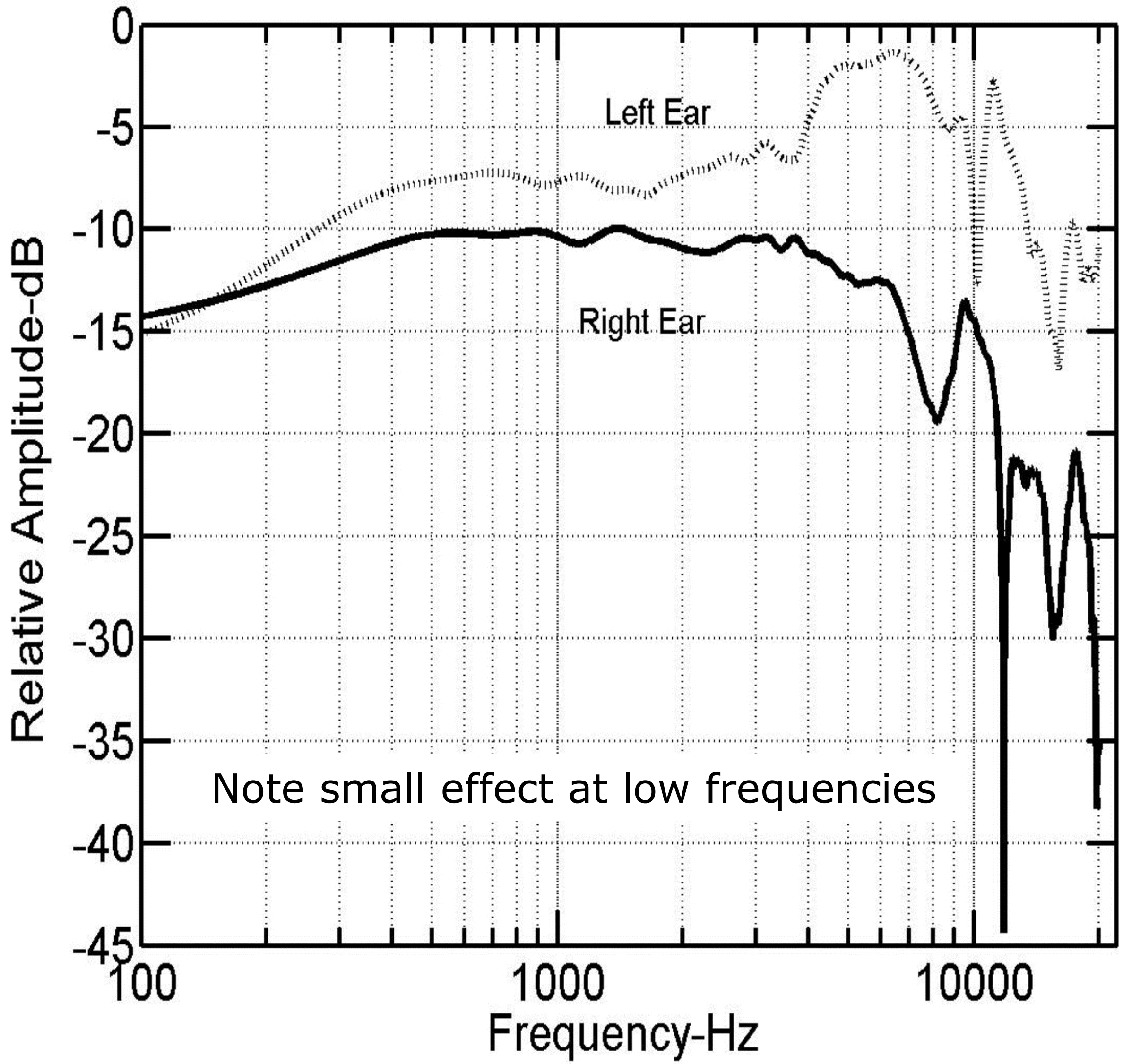
ITD: Works at low-mid frequencies

Why is the maximum *interaural time difference* (ITD) < 1 ms?

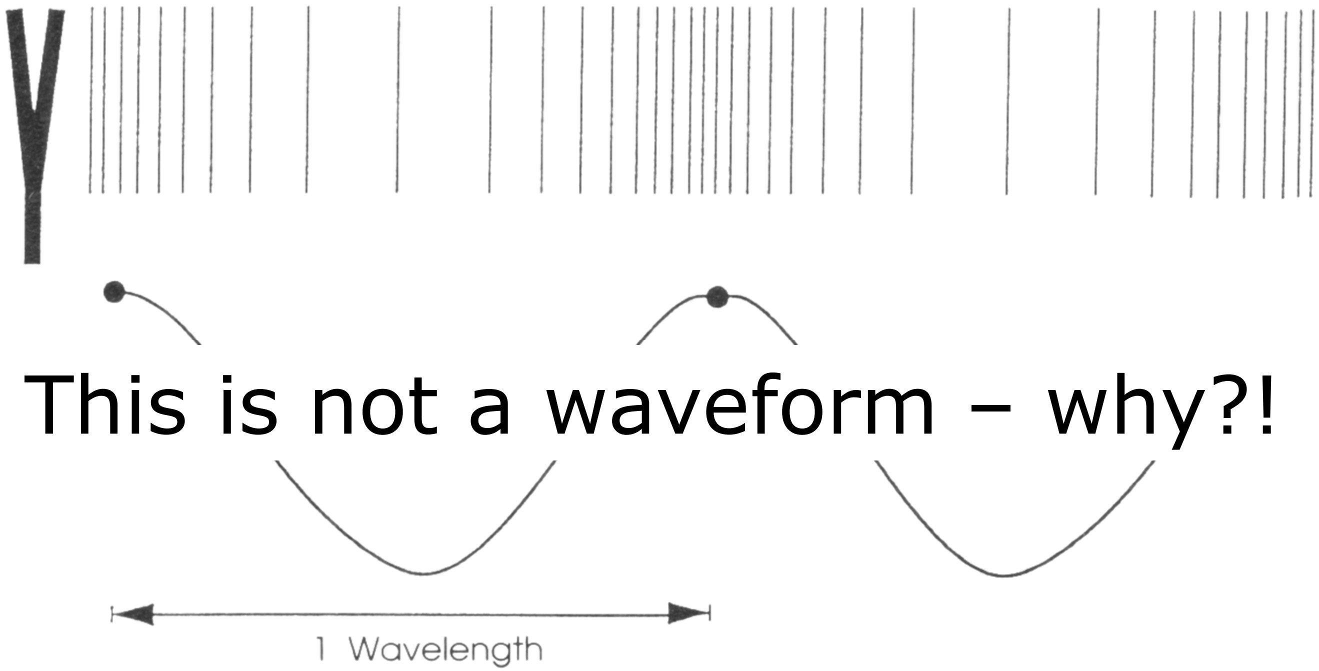
Graphic from: Glackin B et al (2010) A spiking neural network model of the medial superior olive using spike timing dependent plasticity for sound localization. *Front Comp Neuro, 4*.

Measure sound fields at entrance to both ear canals

Head-Related Transfer Functions (HRTFs) for a narrow pulse opposite the L ear (measured at entrance to the ear canal).



Wavelength



This is not a waveform – why?!

wavelength = distance = time x c (speed of sound)

wavelength = period x c = c/f

speed of sound = 344 m/s (770 mph)

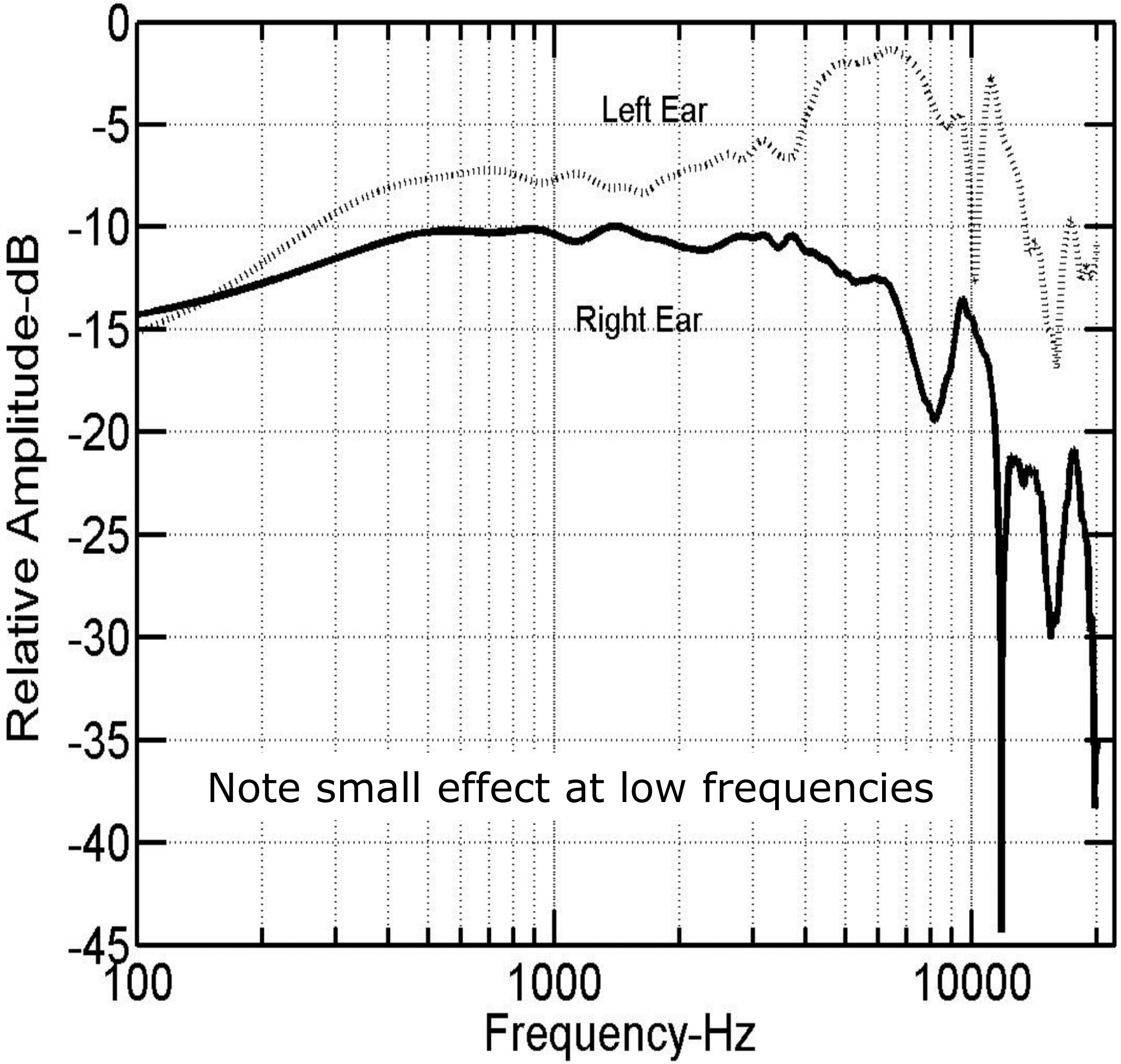
So for 1 kHz, wavelength = .344 m ≈ 13.5 in

Why is wavelength important?

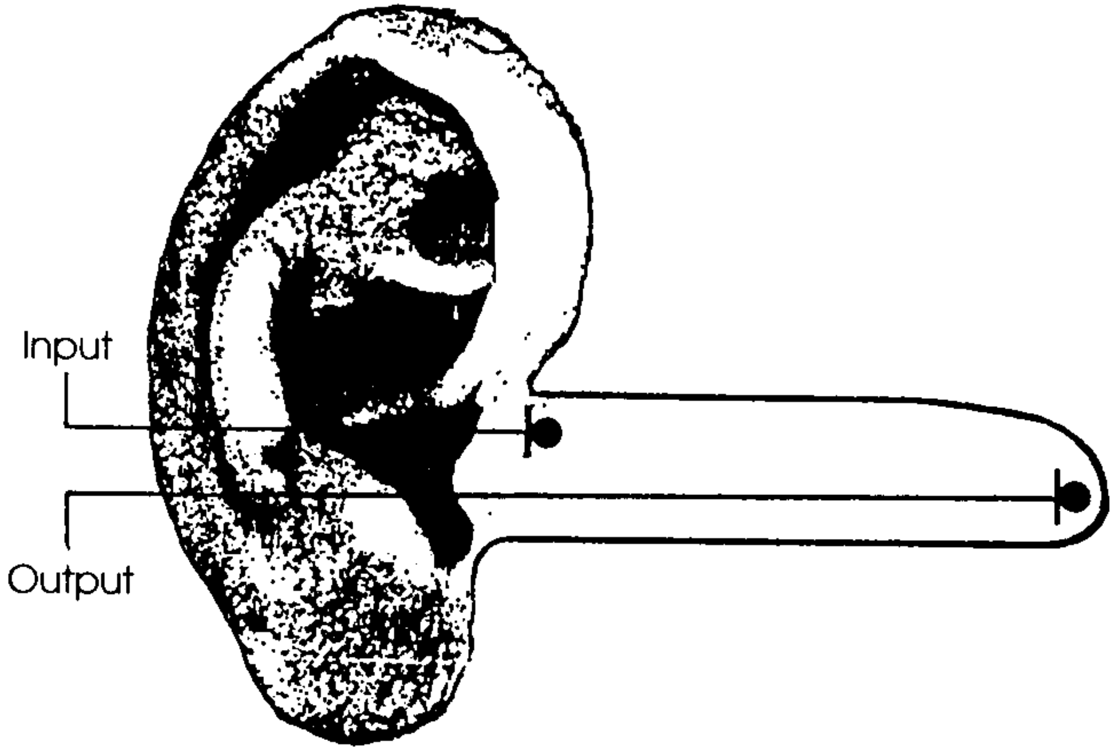
- Objects only have an effect on sinusoids whose wavelength is comparable to the dimensions of the object.
- So, a 100 Hz sinusoid will not be affected by any human body part because its wavelength is …

  ≈ 3.44 m or > 11 feet

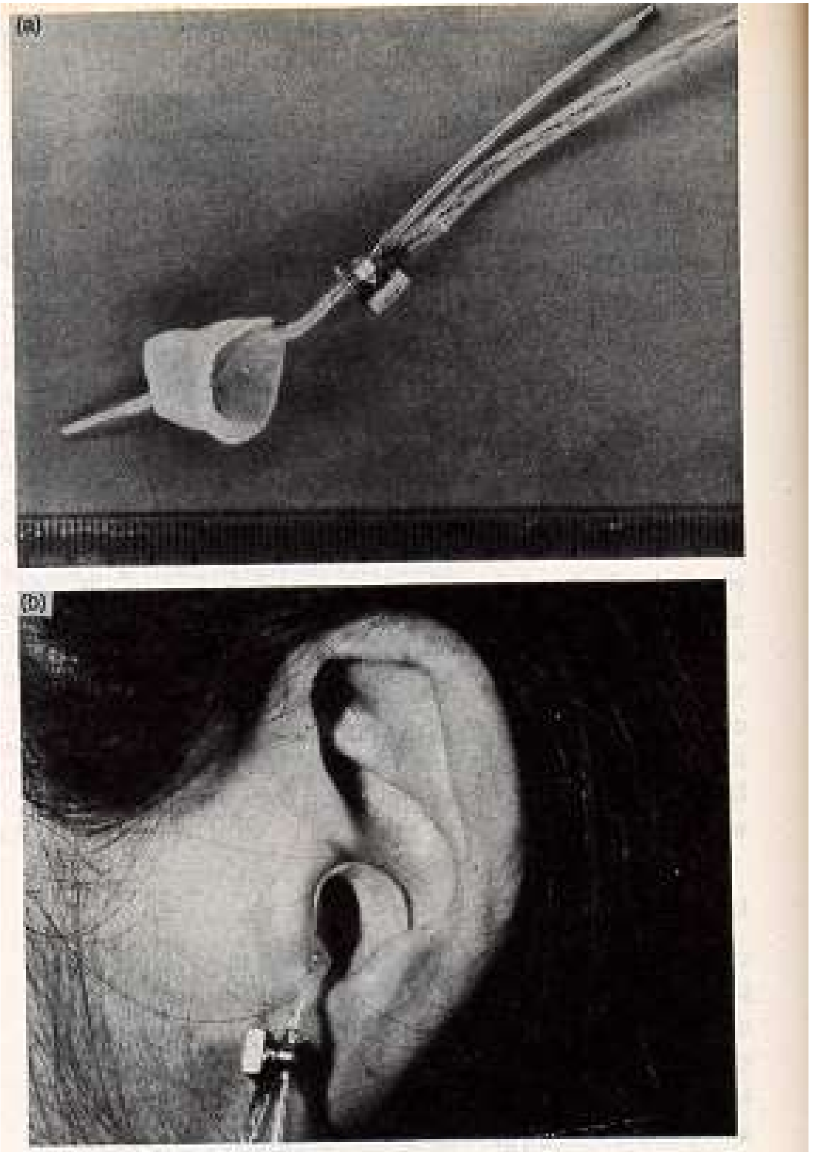
Head-Related Transfer Functions (HRTFs) for a narrow pulse opposite the L ear (measured at entrance to the ear canal).



Acoustic effects of ear canal

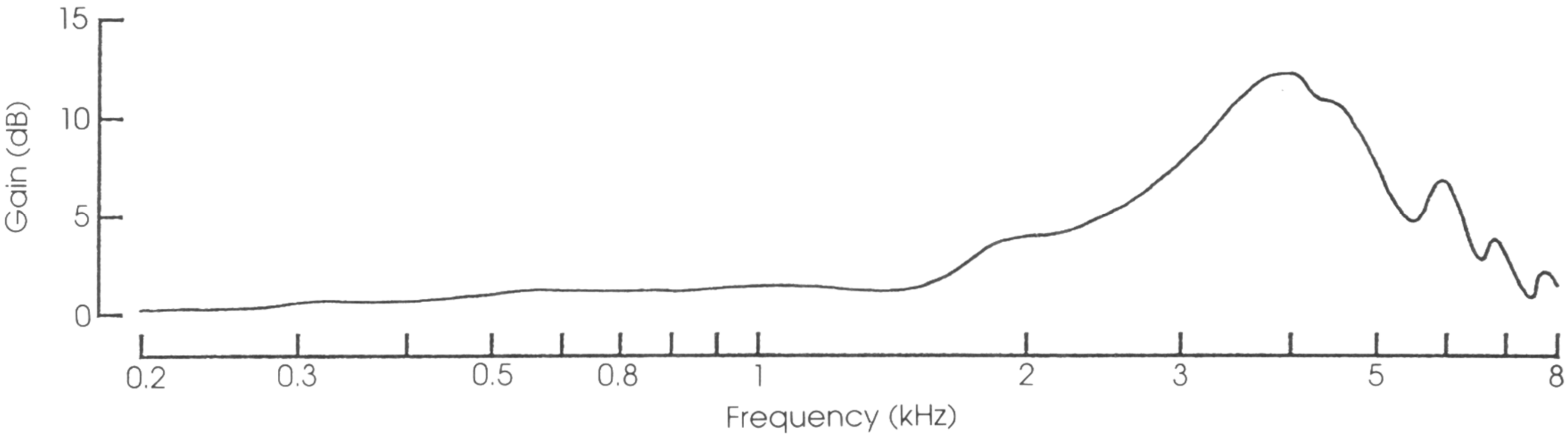


A tube closed at one end and open at the other.

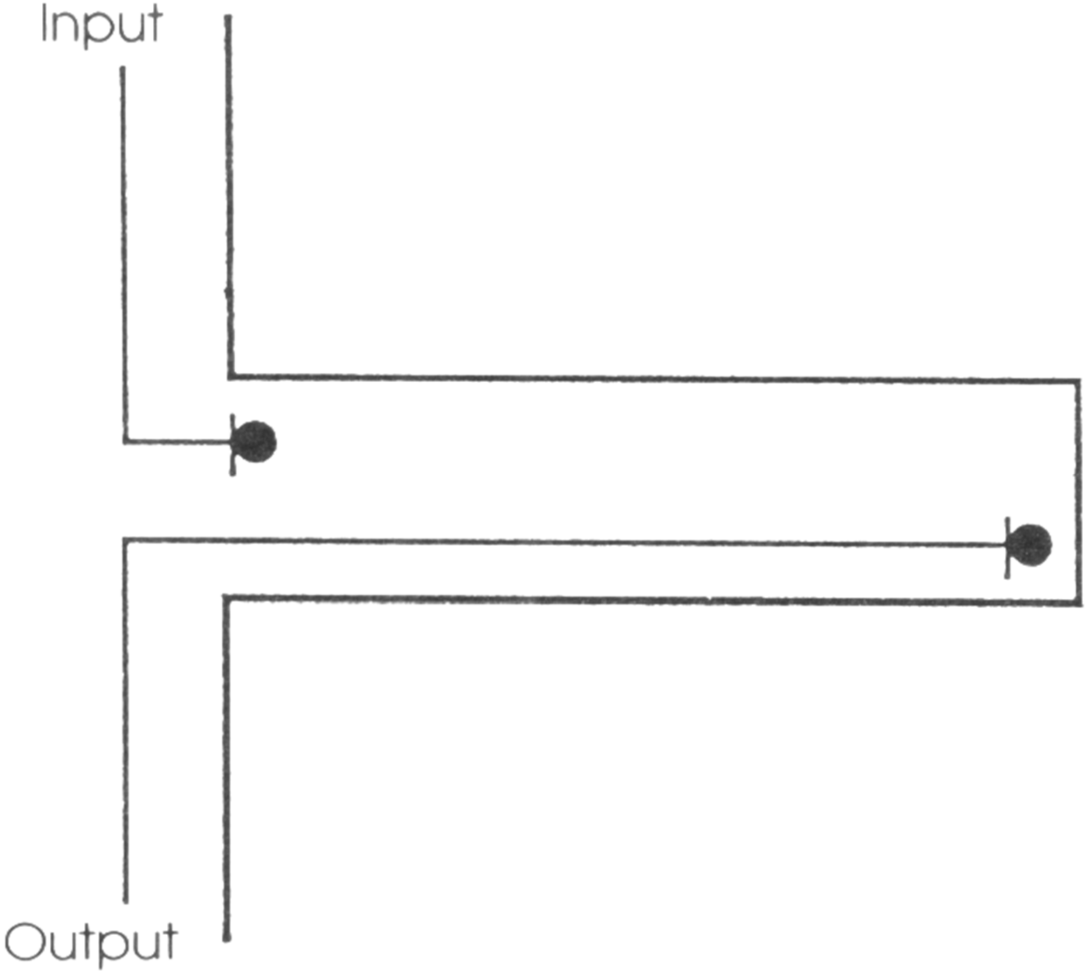


Need to measure sounds down in the ear canal

Acoustic effects of ear canal

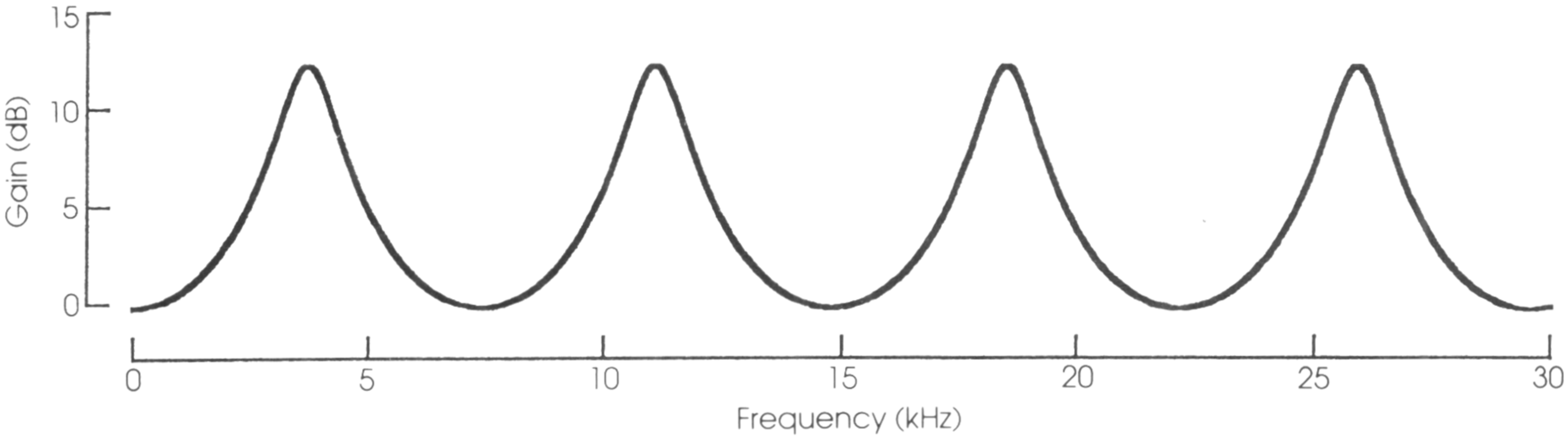


Over this frequency range, the ear canal is a simple resonator (with more resonances at high frequencies)



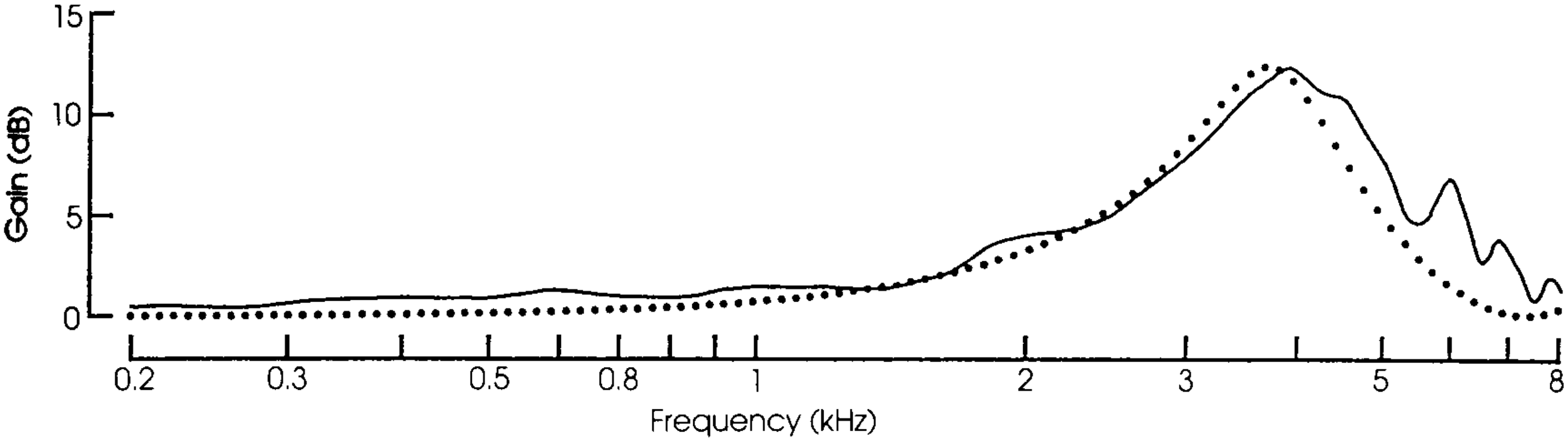
Think of the ear canal as a tube closed at one end and open at the other

amplitude response of an acoustic tube closed at one end and open at the other



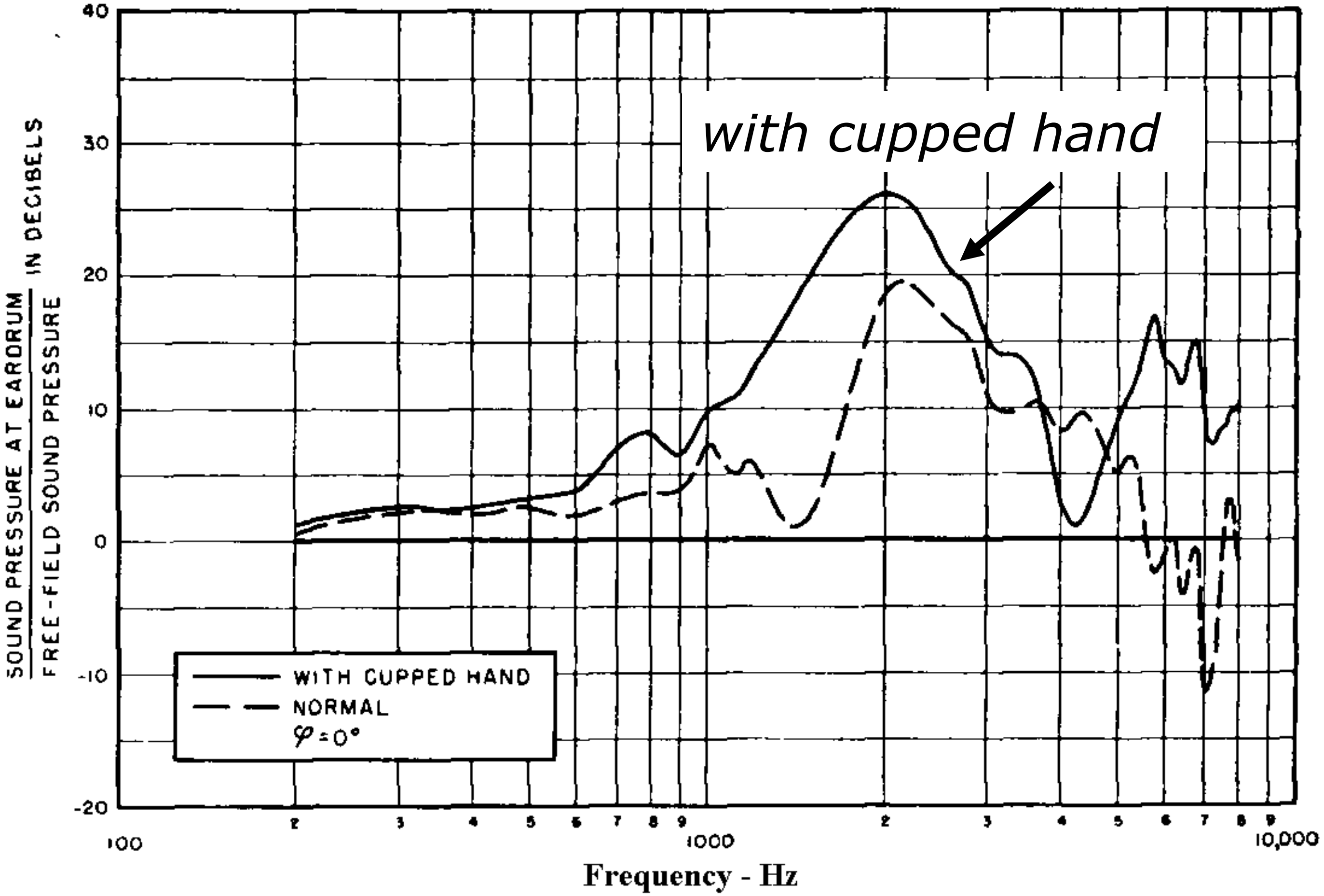
A series of *resonances*

Acoustic effects of ear canal



Original measurements plus simple model

Why cupping a hand behind your ear helps

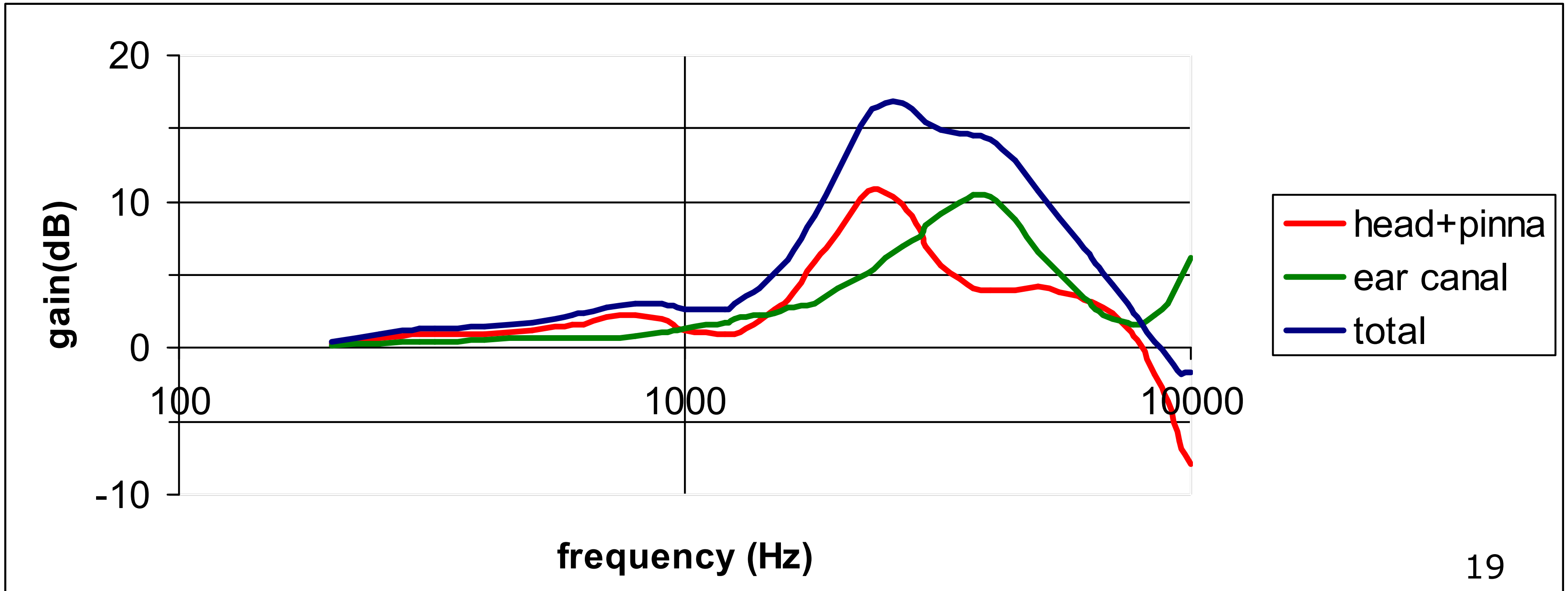


Weiner & Ross (1946) JASA

Frequency responses for:

$\frac{\text{ear-canal entrance}}{\text{free-field pressure}}$ $\frac{\text{near the ear drum}}{\text{ear-canal entrance}}$

Total Effect: $\frac{\text{near the ear drum}}{\text{free-field pressure}}$



Move on to the middle ear

- Provides coupling from eardrum to cochlea.
- Impedence matching through 20:1 area ratio, and lever ratio.
- Stapedius reflex provides protection of cochlea from intense sounds

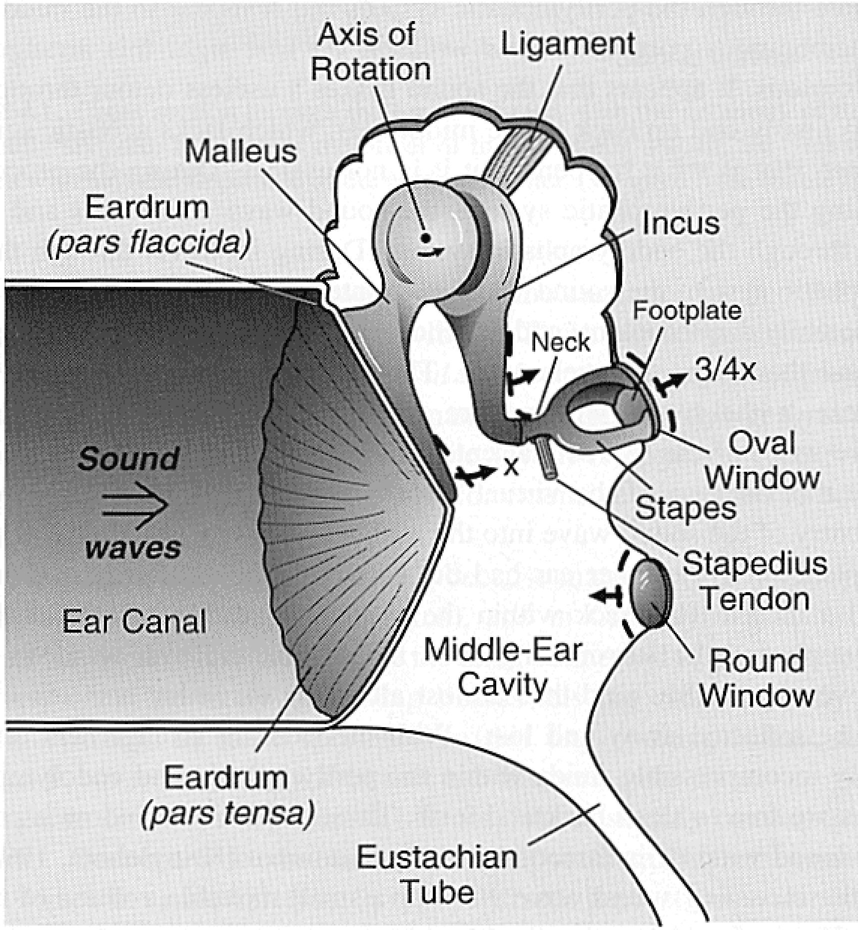


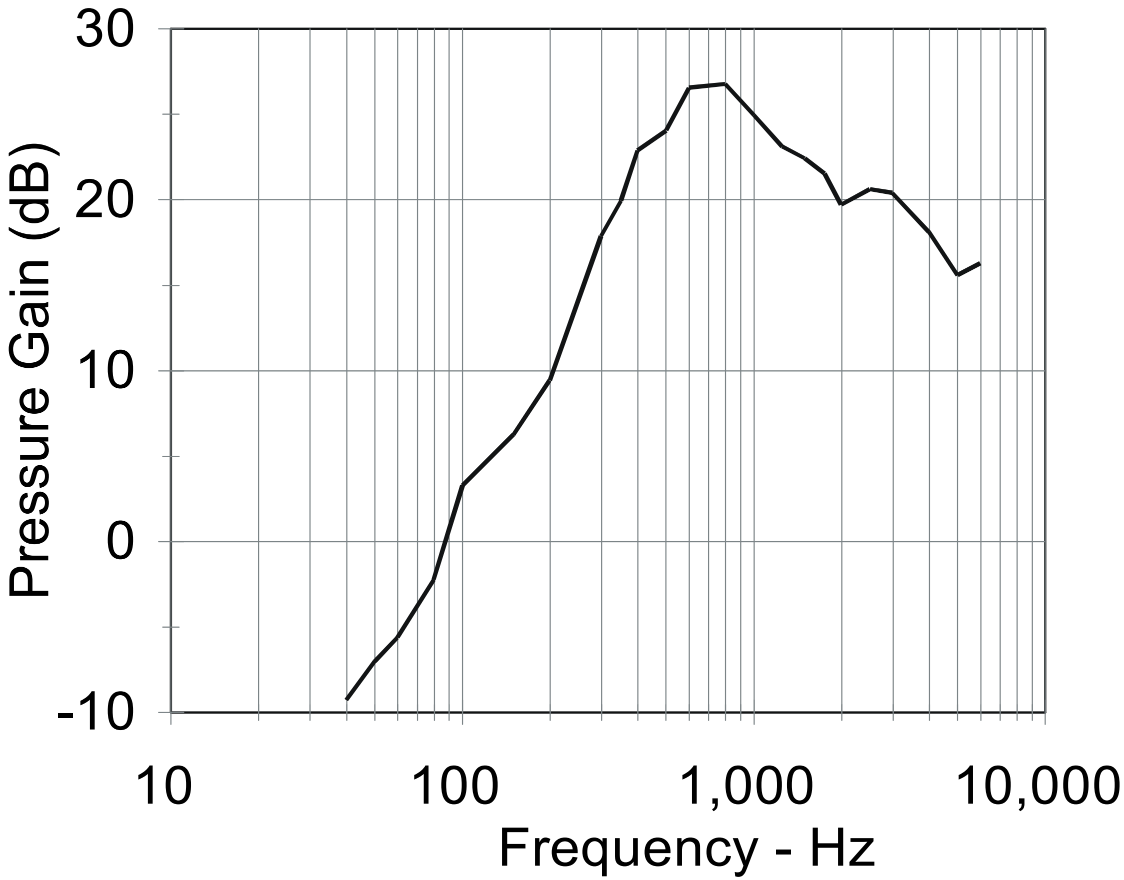
Figure 4.2. Cross section through the human middle ear. The oval window vibrates with three-fourths the amplitude of the eardrum center. Note that the axis of rotation passes through the main concentration of ossicular mass. The *pars flaccida* is a small, limp section of the eardrum that is unconnected to the ossicles. It appears to have several functions, including the release of static pressure within the middle ear (Teoh et al., 1997). (Adapted from Goodhill, 1979.)

Frequency response of the middle ear

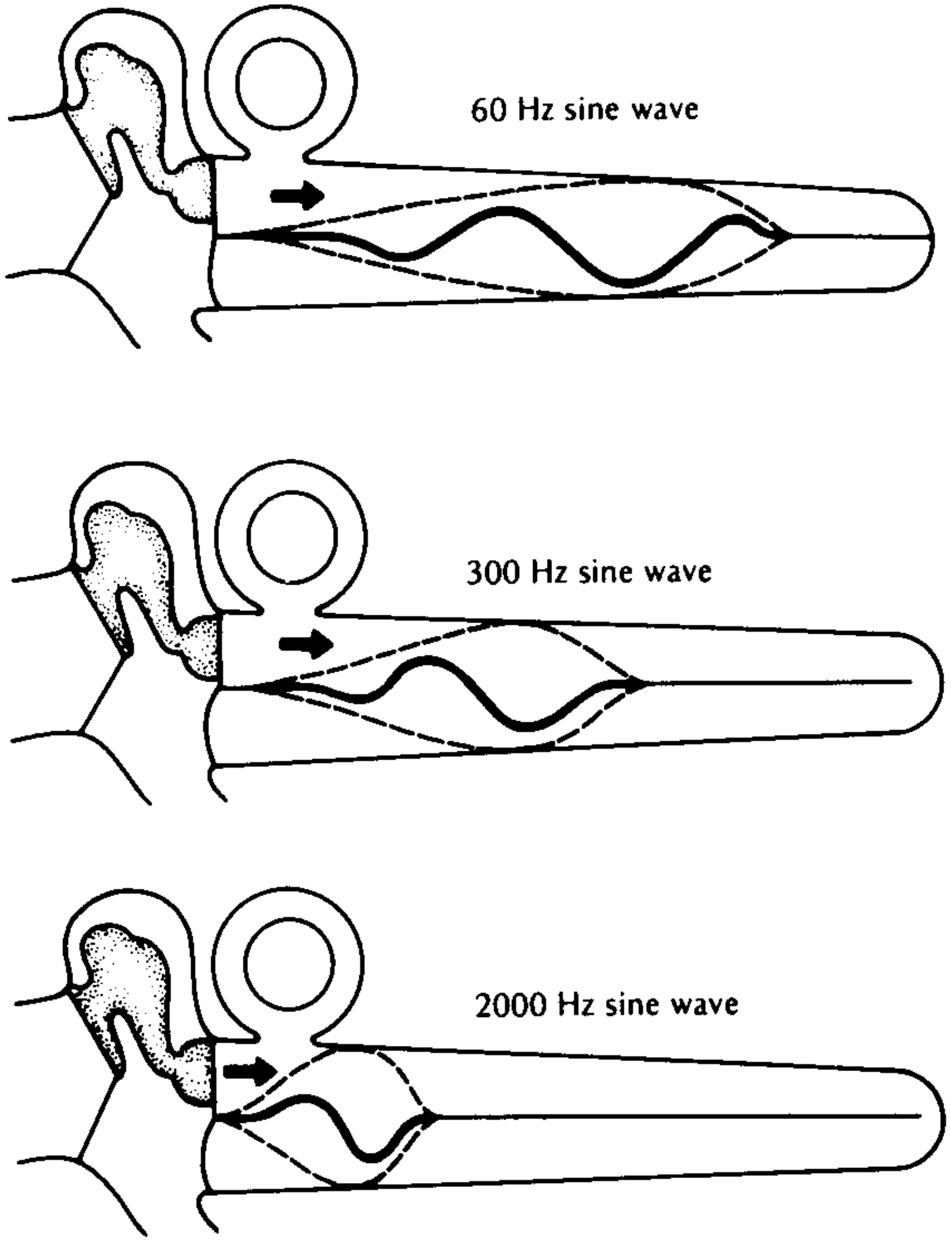
$$\frac{\text{pressure in cochlear fluids}}{\text{pressure at ear drum}}$$

What kind of filter is this?

bandpass filter

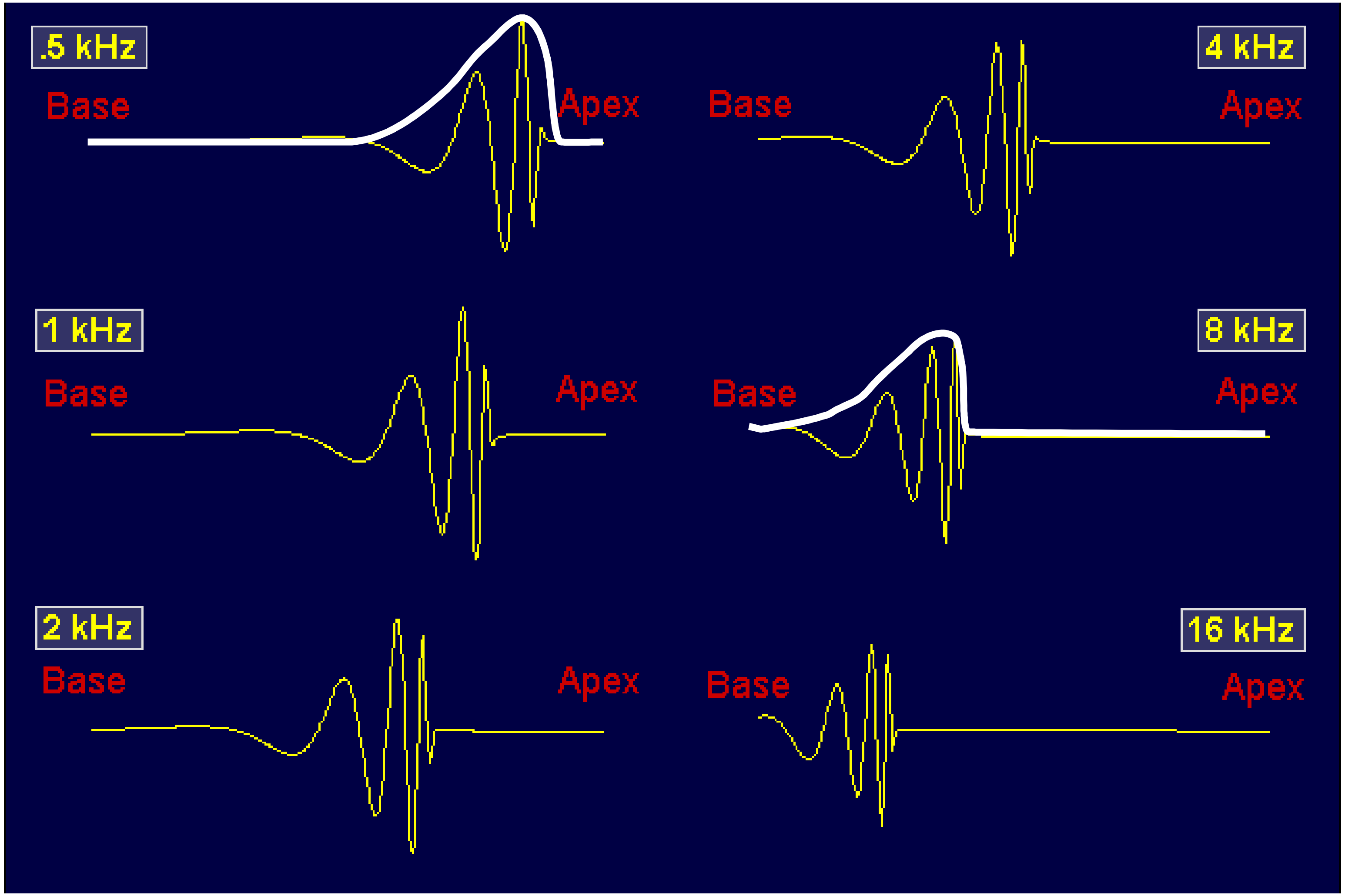


Moving into the inner ear ...



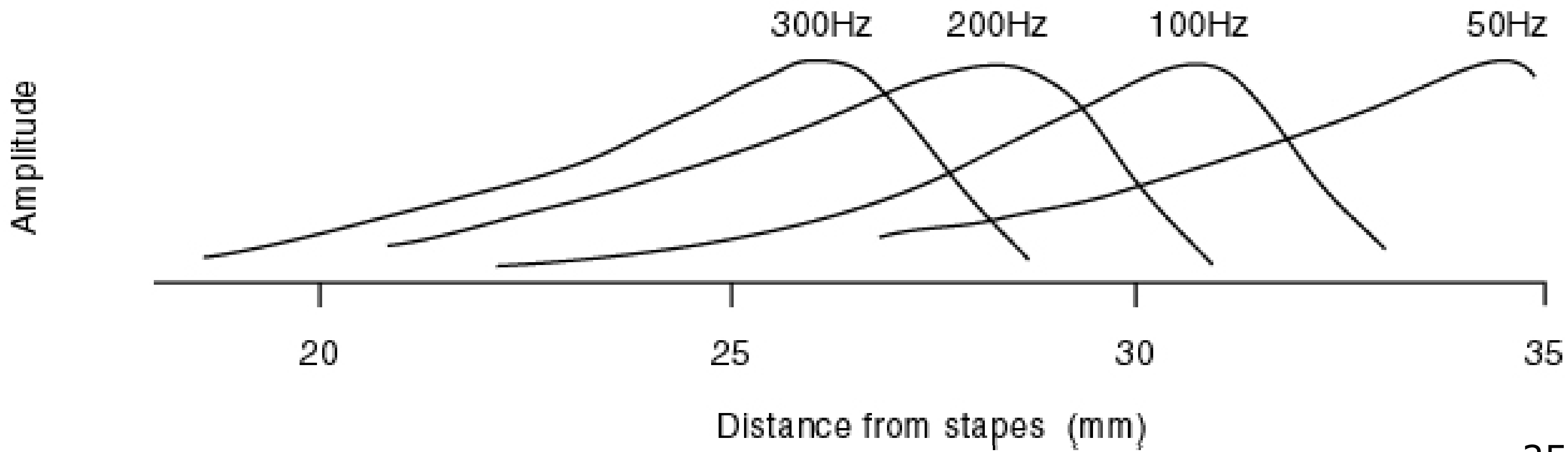
Basilar membrane vibration to sinusoids varies with frequency because its mechanical properties vary along its length: wider at the apex (most responsive to low frequencies) and stiffer at the base (most responsive to high frequencies) .

The *envelope* of the travelling wave



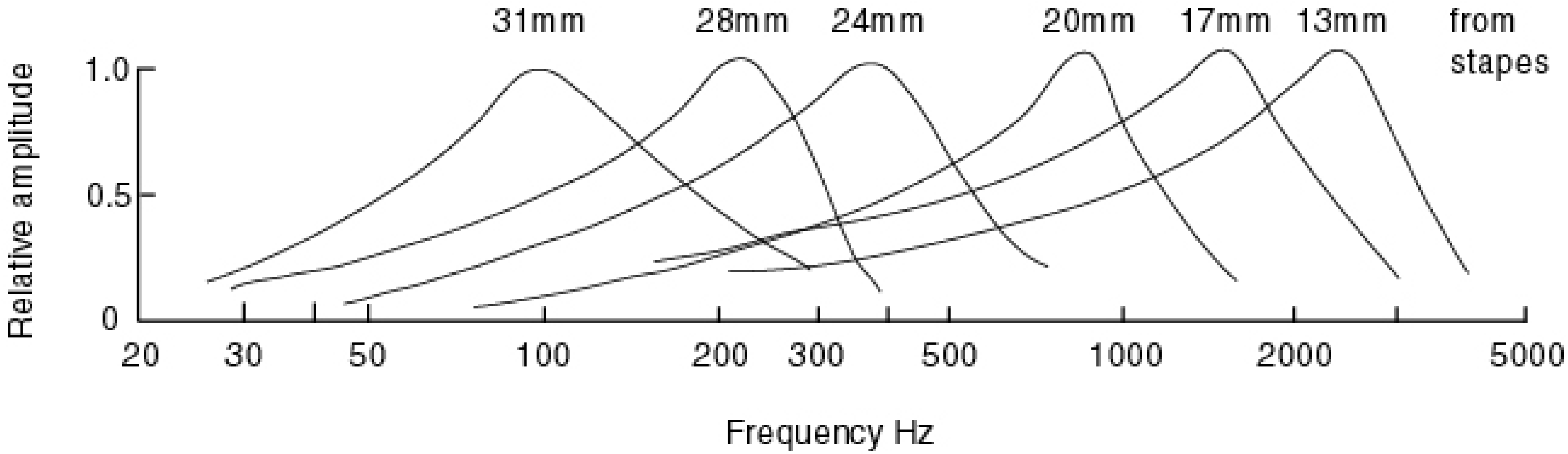
A crucial distinction
<u>*excitation pattern*</u> vs *frequency response*

- Excitation pattern — the vibration pattern across the basilar membrane to a single sound.
  - Input = 1 sound.
  - Measure at many places along the BM.
- Related to a *spectrum* (amplitude by frequency).



A crucial distinction
excitation pattern vs *frequency response*

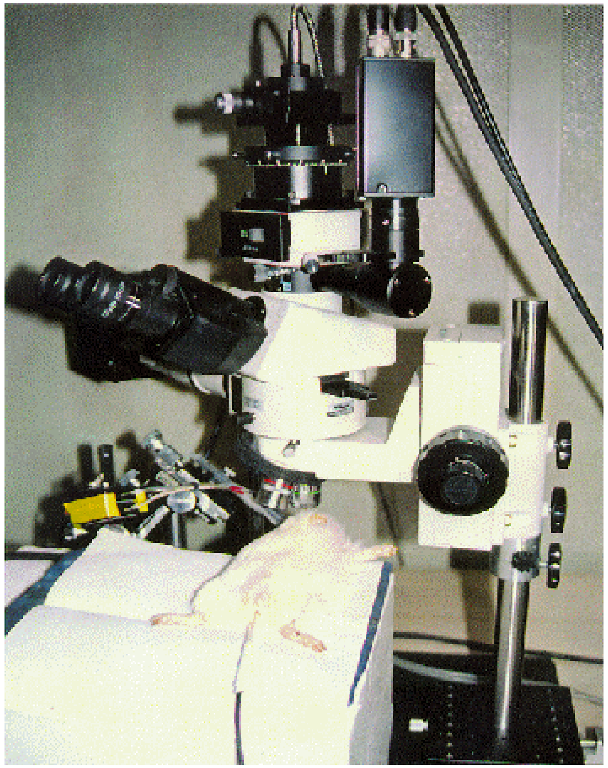
- Frequency response — the amount of vibration shown by a particular place on the BM to sinusoids of varying frequency.
  - Input = many sinusoids.
  - Measure at a single place on the BM.
  - Band-pass filters at each position along the basilar membrane.

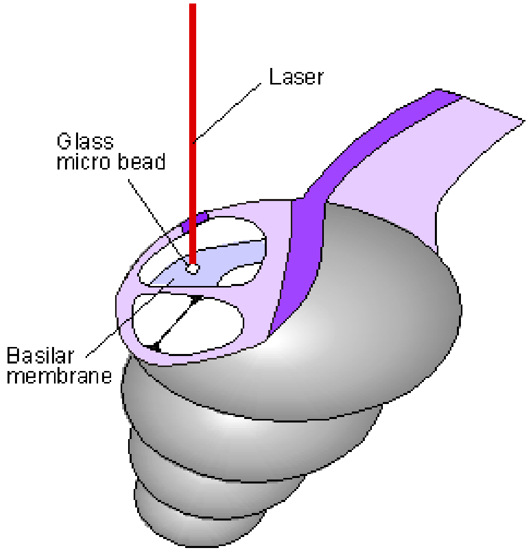


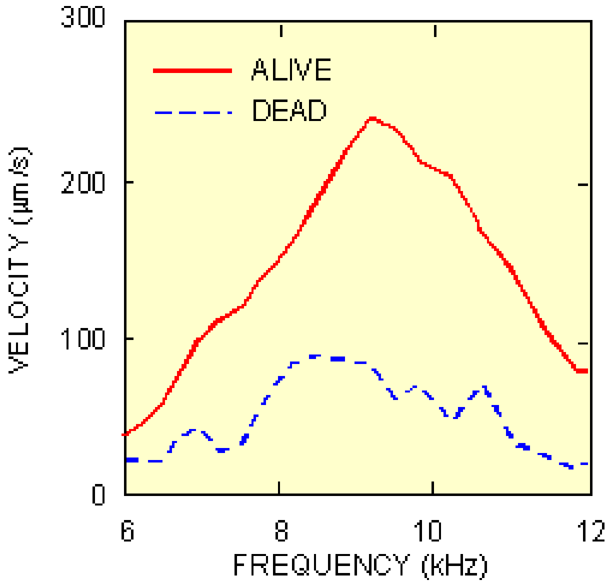
Modern measurements of basilar membrane movement

- Measure the movement of one point on the BM at a time *(frequency response).*
- Technically difficult, although lots easier than before!
- Access difficult to anything but the most basal end of the cochlea …
  - so most measurements are made at high frequencies.

Laser Doppler Velocimetry







http://www.wadalab.mech.tohoku.ac.jp/bmldv-e.html

Modern measurements of the frequency response of the basilar membrane

Consider the frequency response of a *single place* on the BM

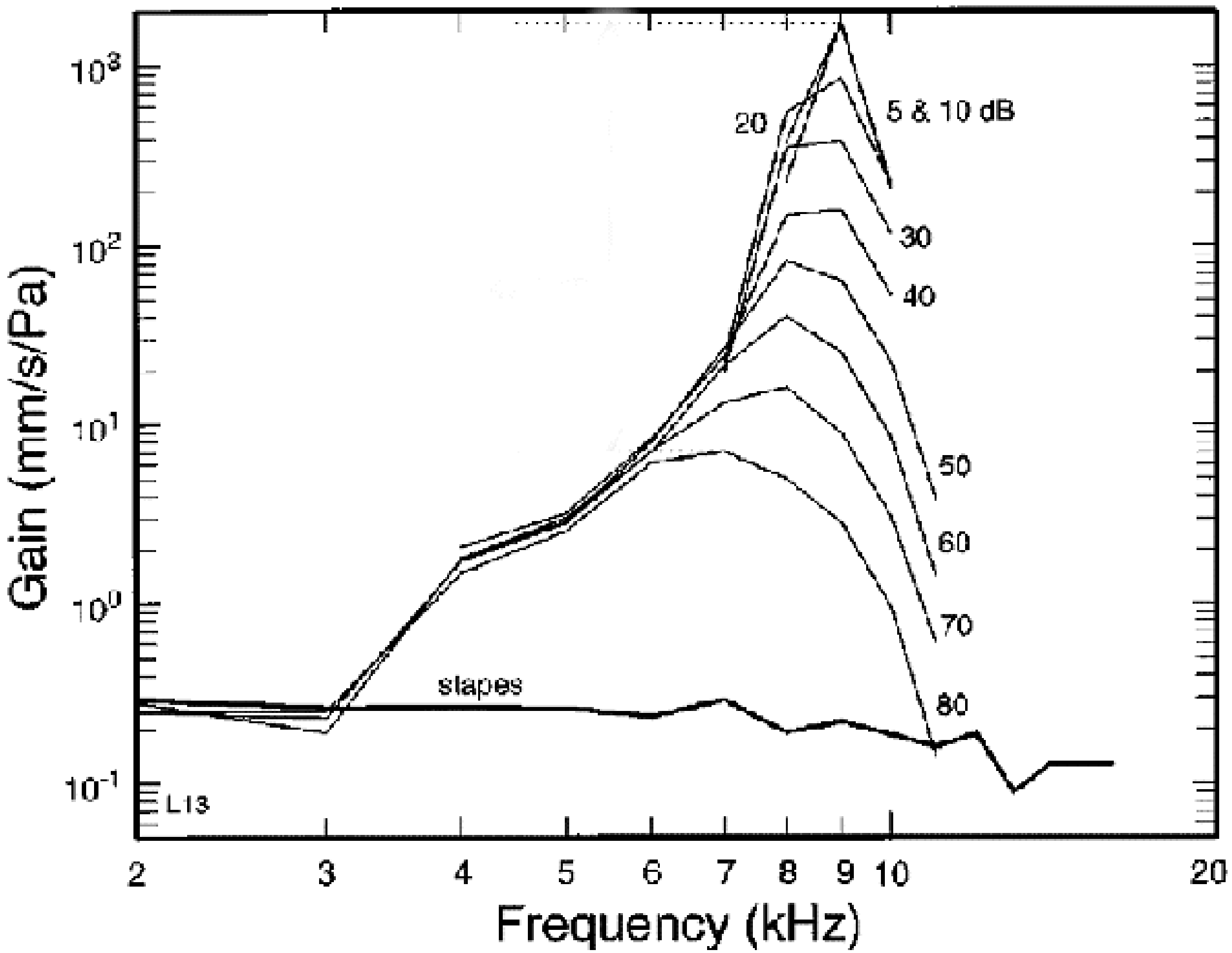


FIG. 10. A family of isointensity curves representing the gain (velocity divided by stimulus pressure) of basilar-membrane responses to tone pips as a function of frequency (abscissa) and intensity (parameter, in dB SPL). The thick line at bottom indicates the average motion of the stapes (Ruggero *et al.*, 1990). Data recorded in cochlea L13.

input/
output
functions
on the
basilar
membrane

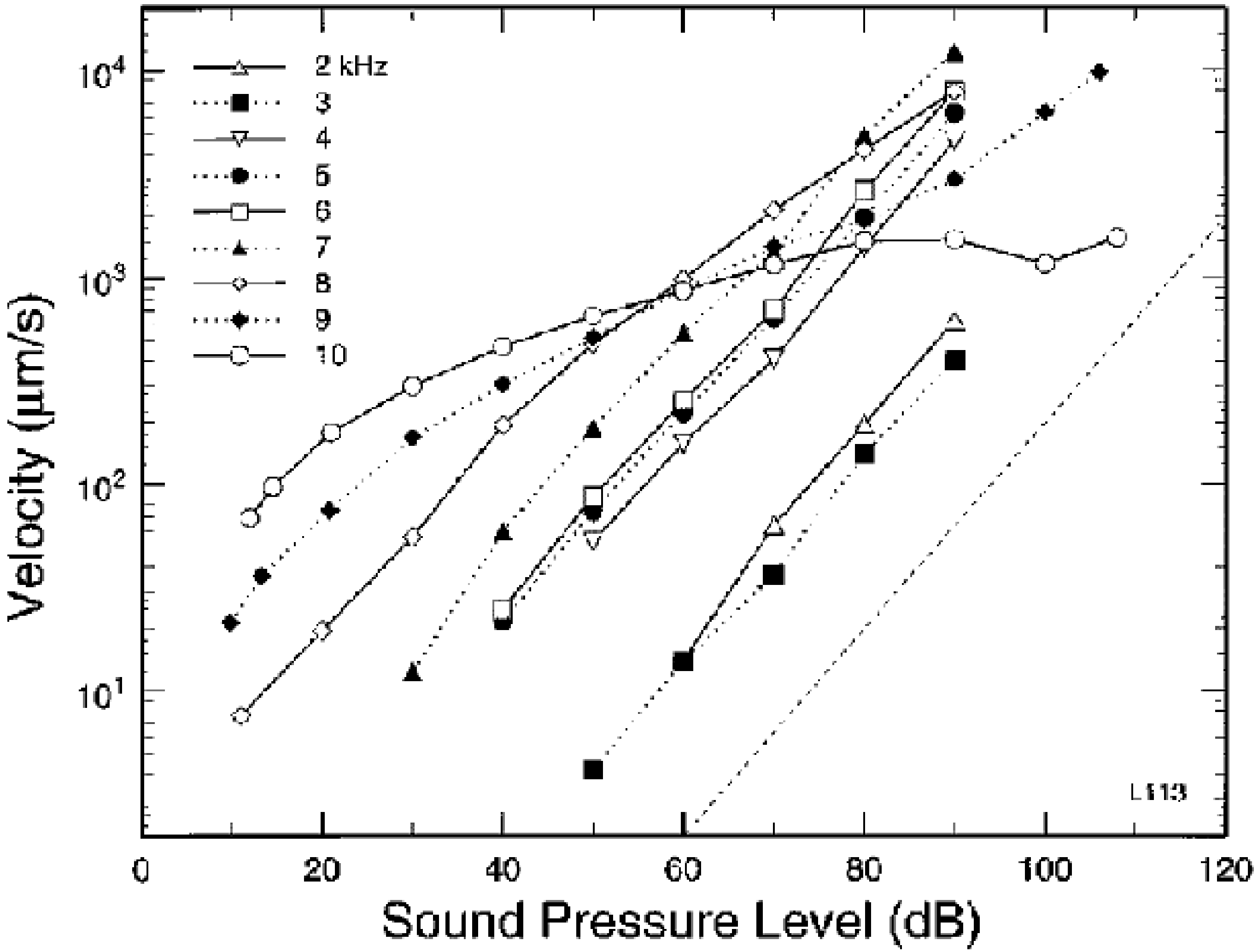
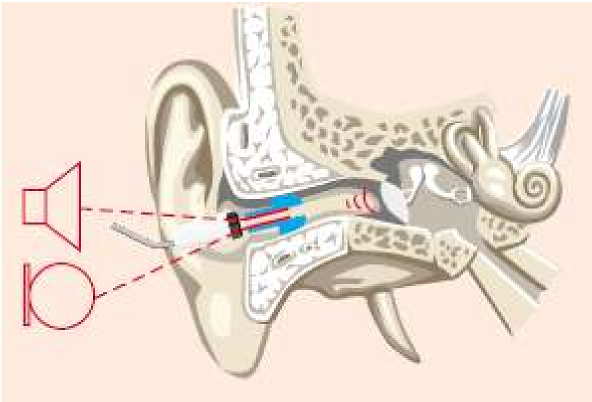
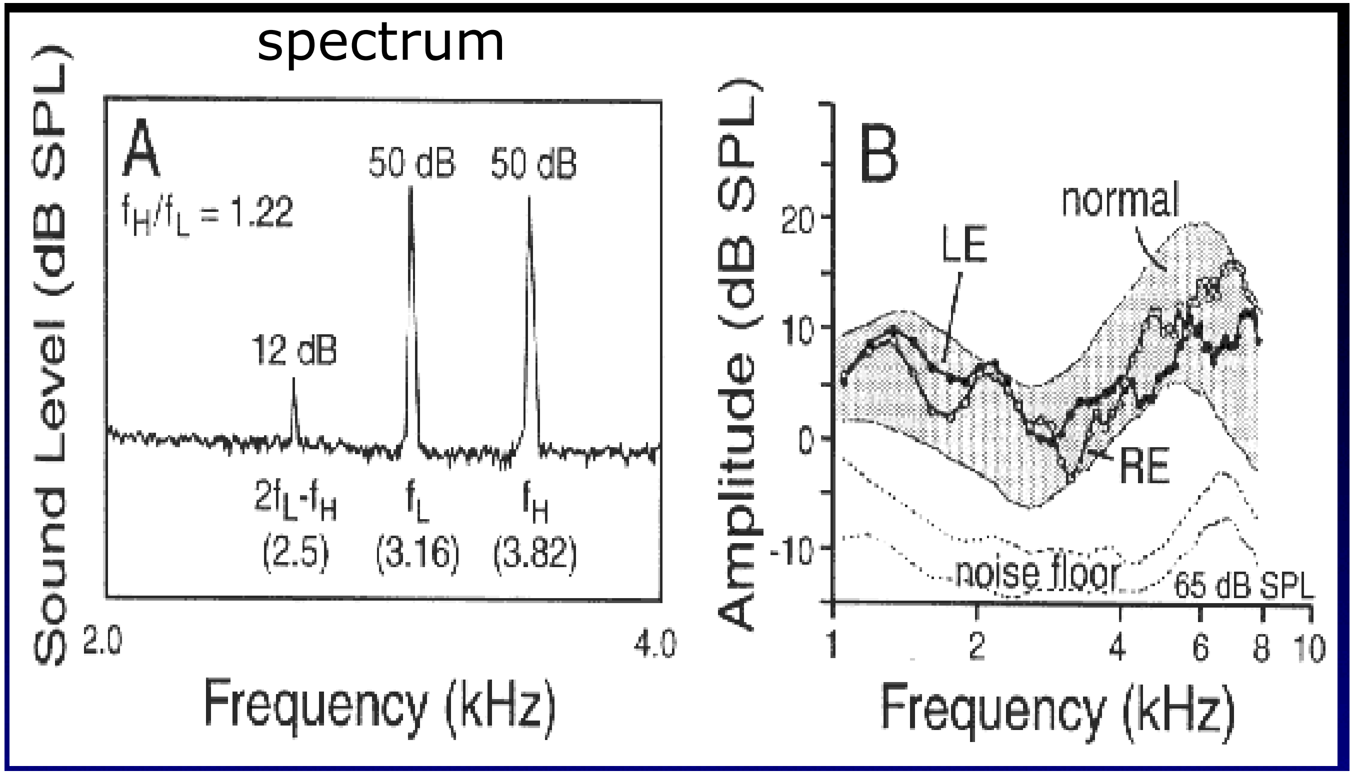


FIG. 7. Velocity-intensity functions of basilar-membrane responses to tones with frequency equal to and lower than CF (10 kHz). The straight dashed line at right has a linear slope (1 dB/dB).

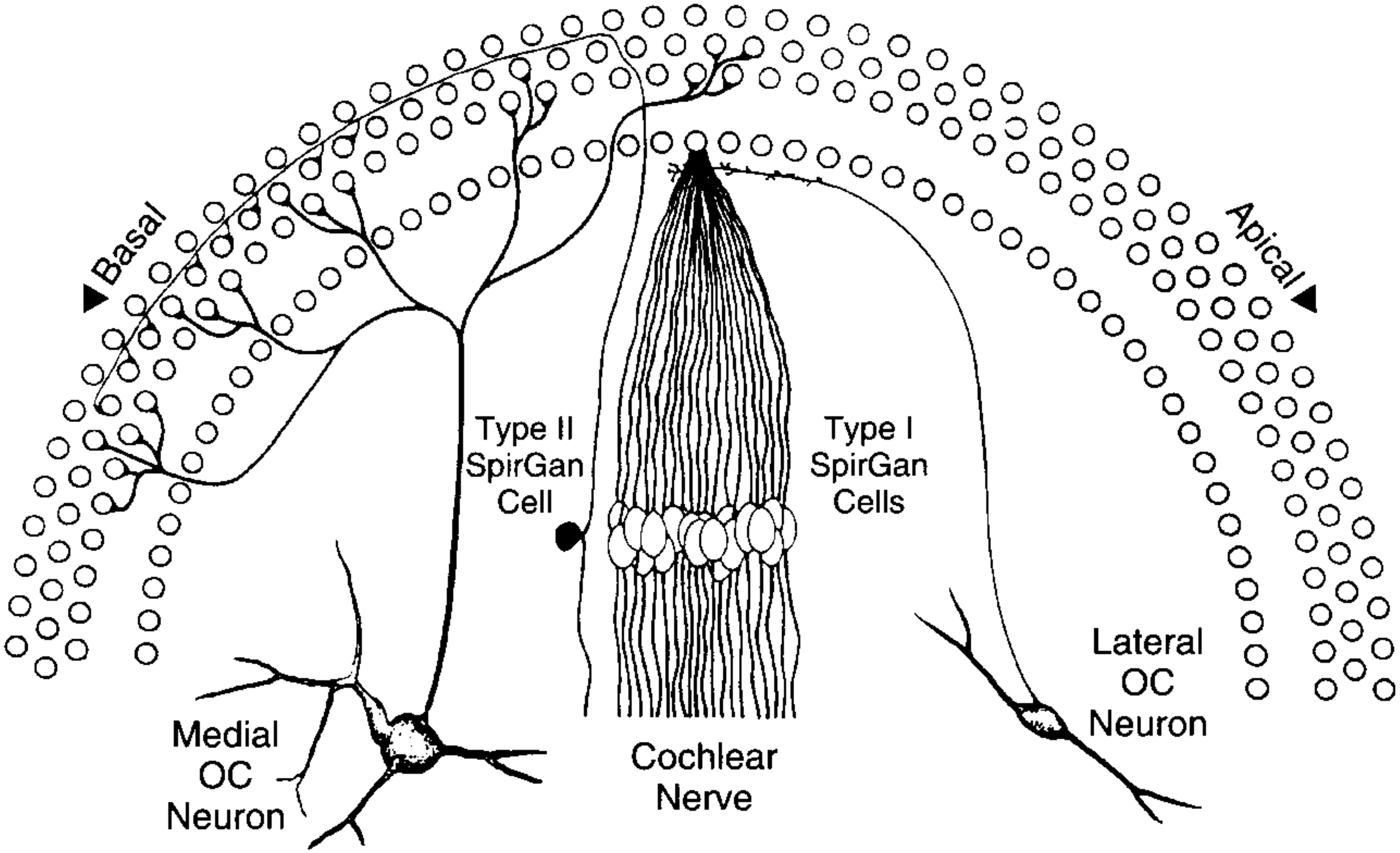
Distortion product otoacoustic emissions



- Play two tones simultaneously into an ear
- Record the sound in the ear canal using a microphone
- Calculate the spectrum of the output



Innervation of the cochlea

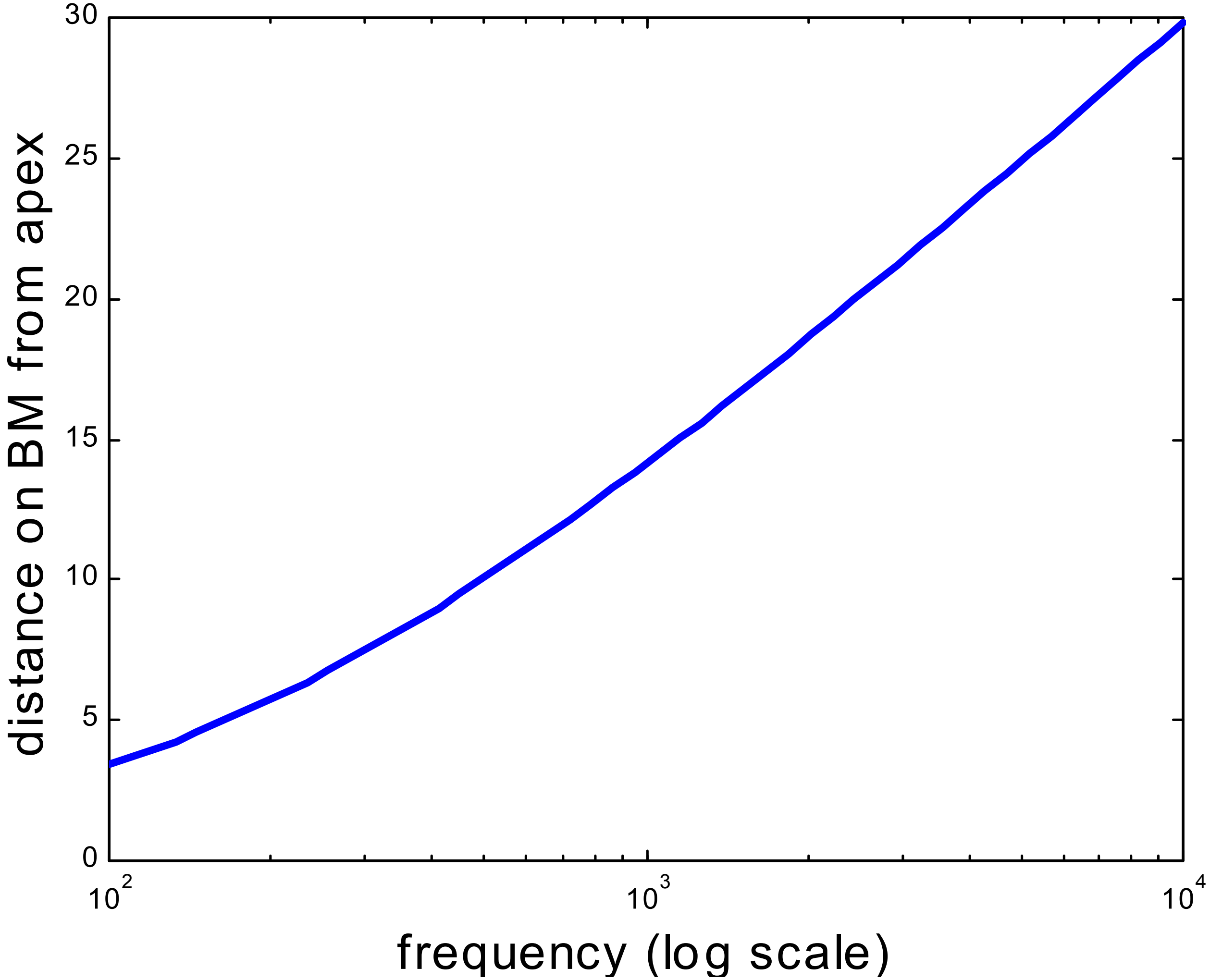


90-95% of afferents are myelinated, synapsing with a single inner hair cell (IHC).

The cochlea as a filterbank

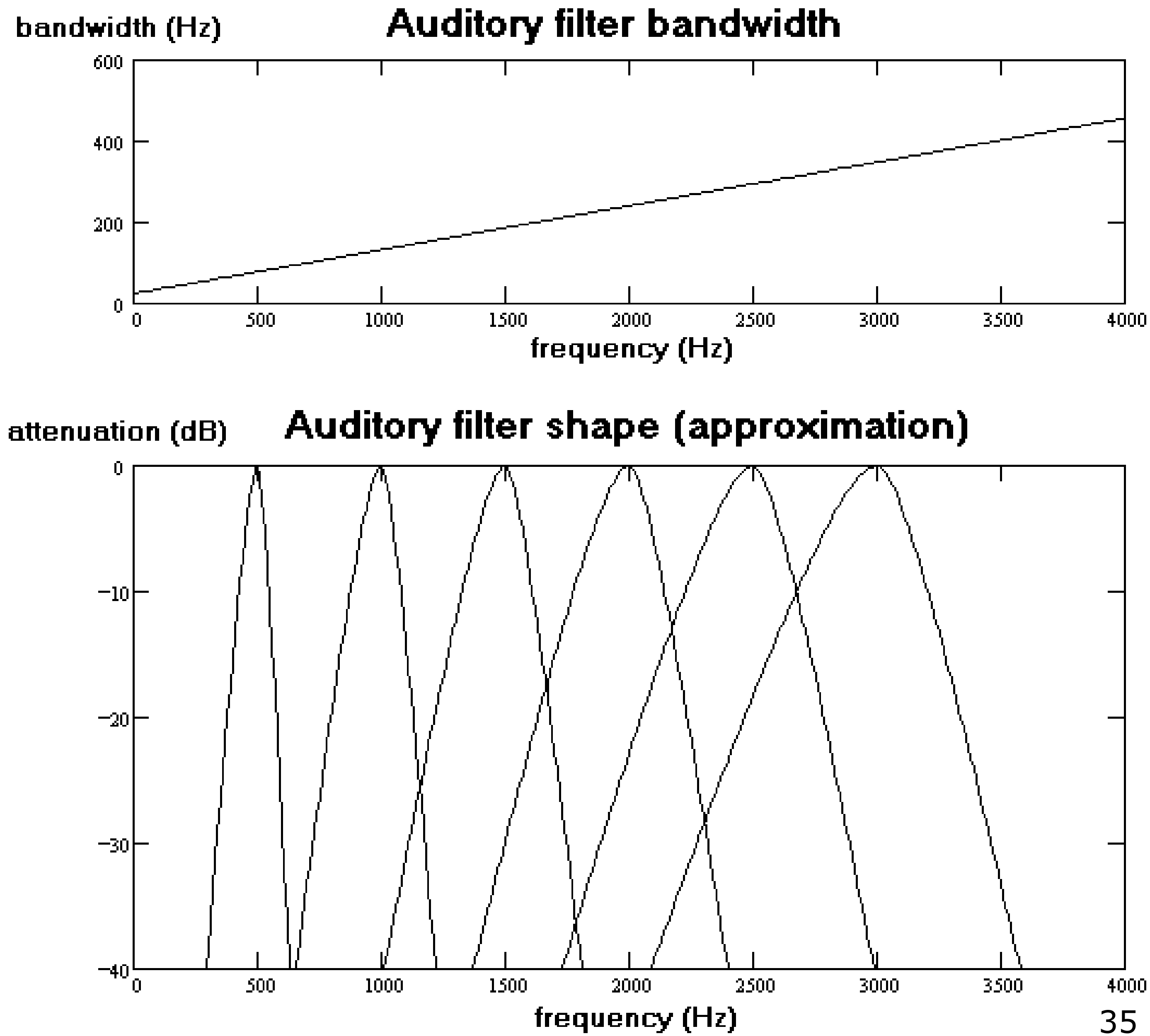
- Auditory nerve fibres do not differ with centre frequency.
- So all tuning to frequency arises from the filtering of the basilar membrane.
- Imagine that each auditory nerve fibre is preceded by a bandpass filter.
- Then imagine many filters in parallel (*a filterbank*) each feeding a single (or a number of) auditory nerve fibres.
- *place* or *tono-topic* coding.

The auditory filter bank has three special properties

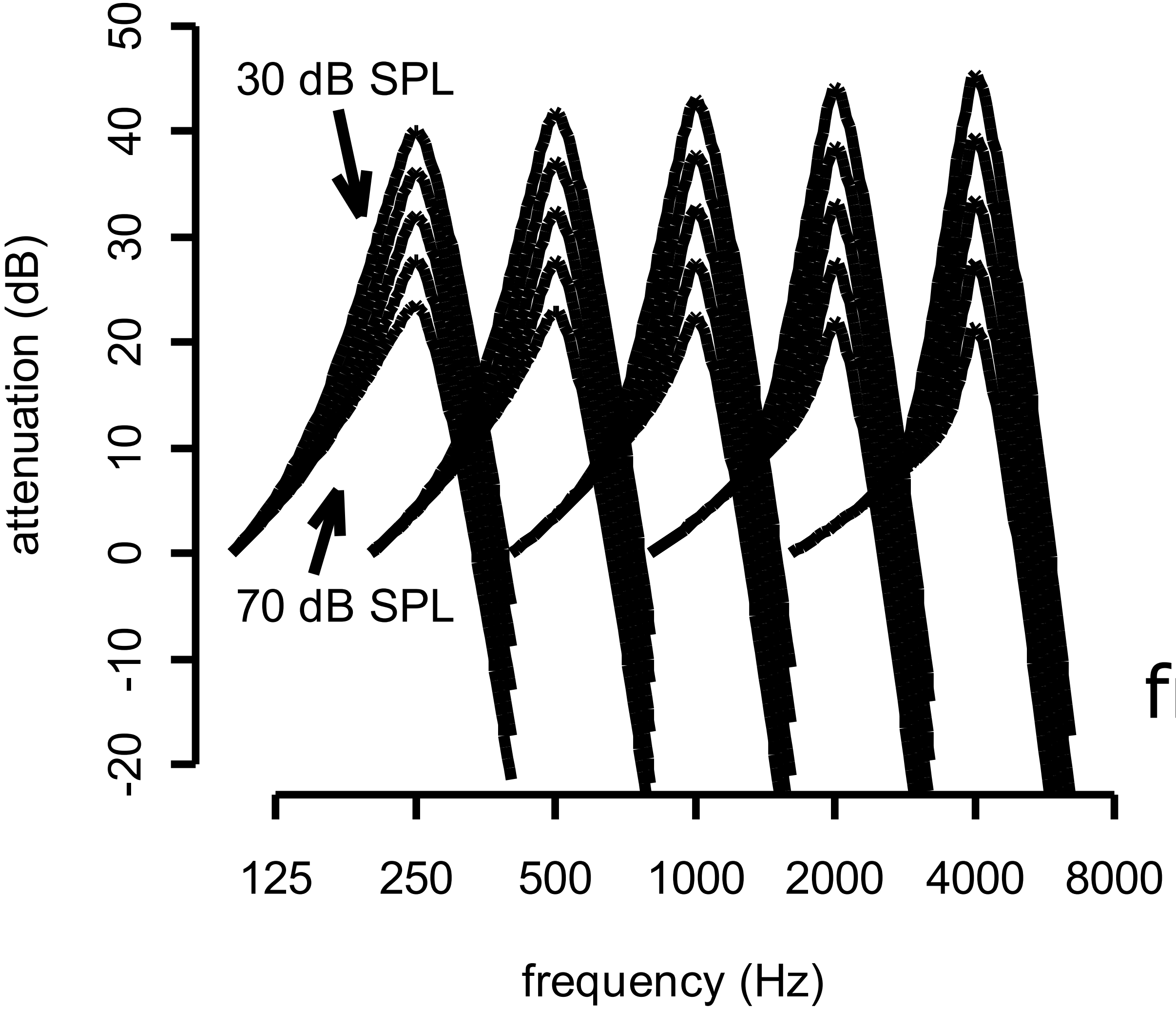


Sinusoidal *frequency* maps on to *place* in a quasi-logarithmic way

Auditory filter band-widths vary with frequency (note linear frequency scale)



Auditory filters vary with level (they are *nonlinear*)

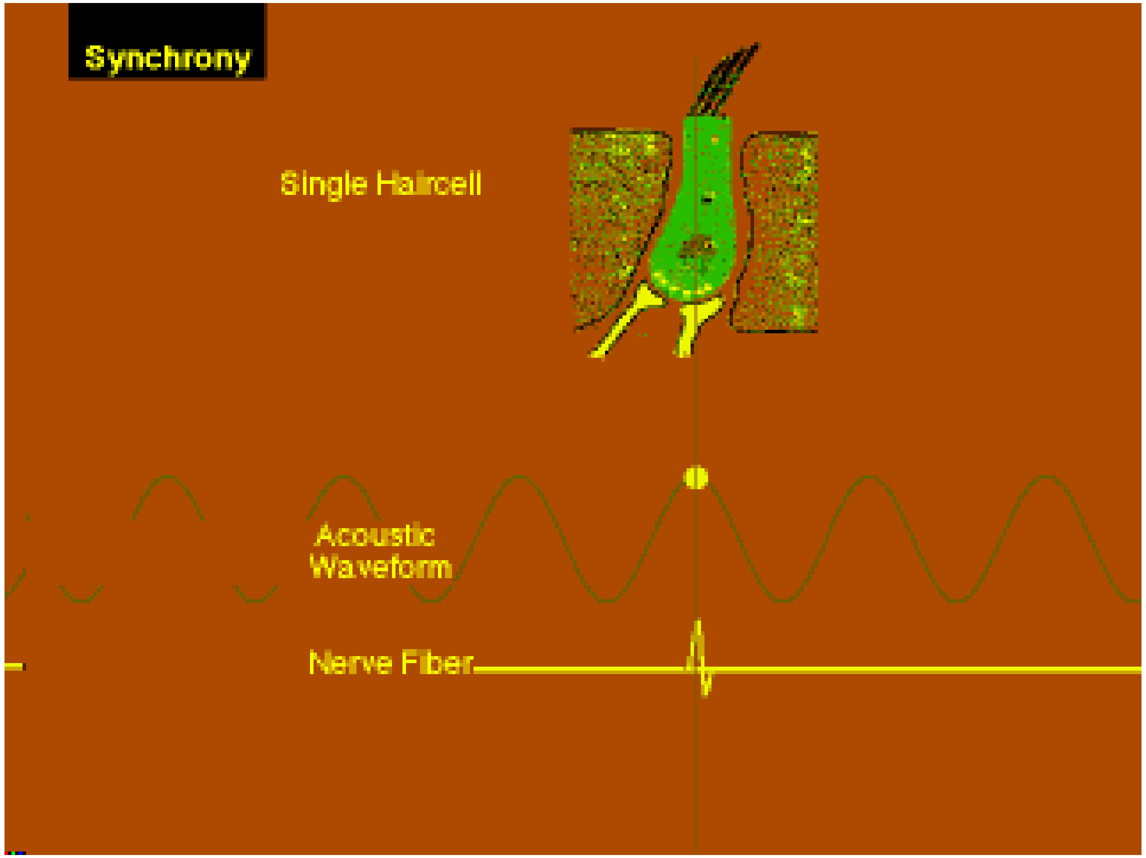


note log frequency scale

Temporal coding
(up to ≈ 5 kHz)

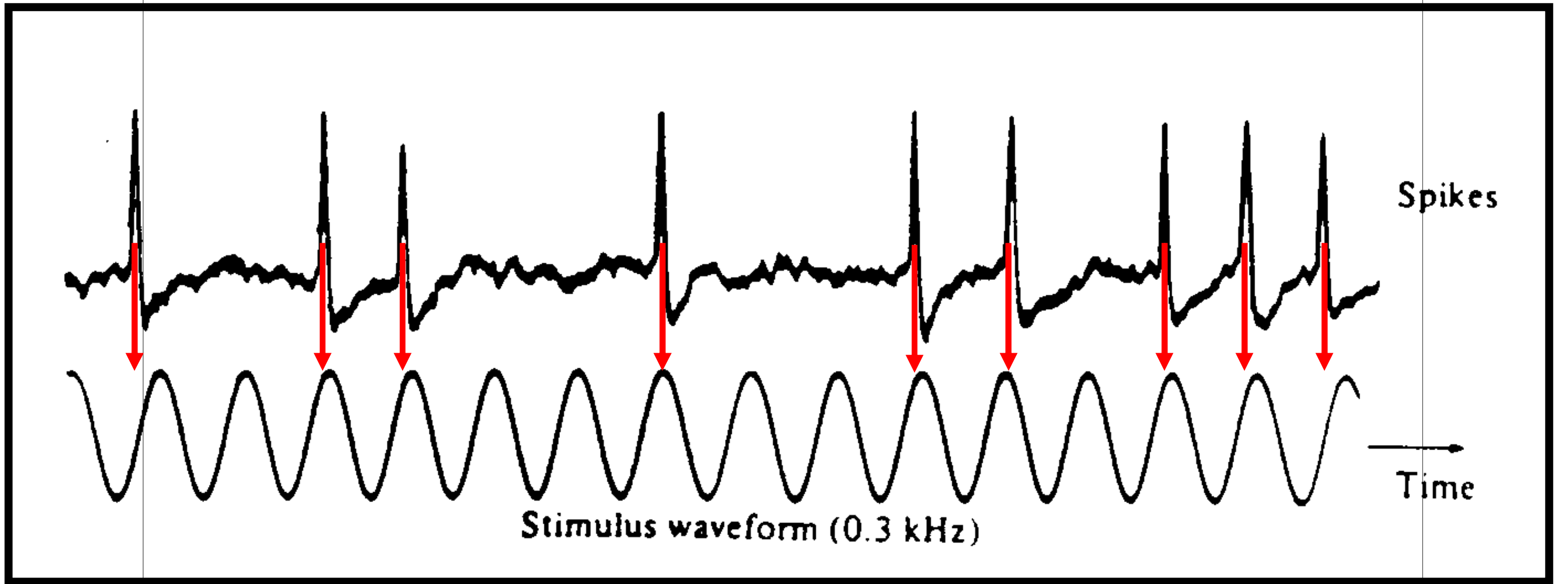
Information about stimulus frequency is not only coded by *which* nerve fibres are active (the *place* code) but also by *when* the fibres fire (the *time* code).

The firing of auditory nerve fibres is synchronized to movements of the hair cell cilia (at low enough frequencies)



Play transdct.mov

Auditory nerves tend to fire to low-frequency sounds at particular waveform times (*phase locking*).



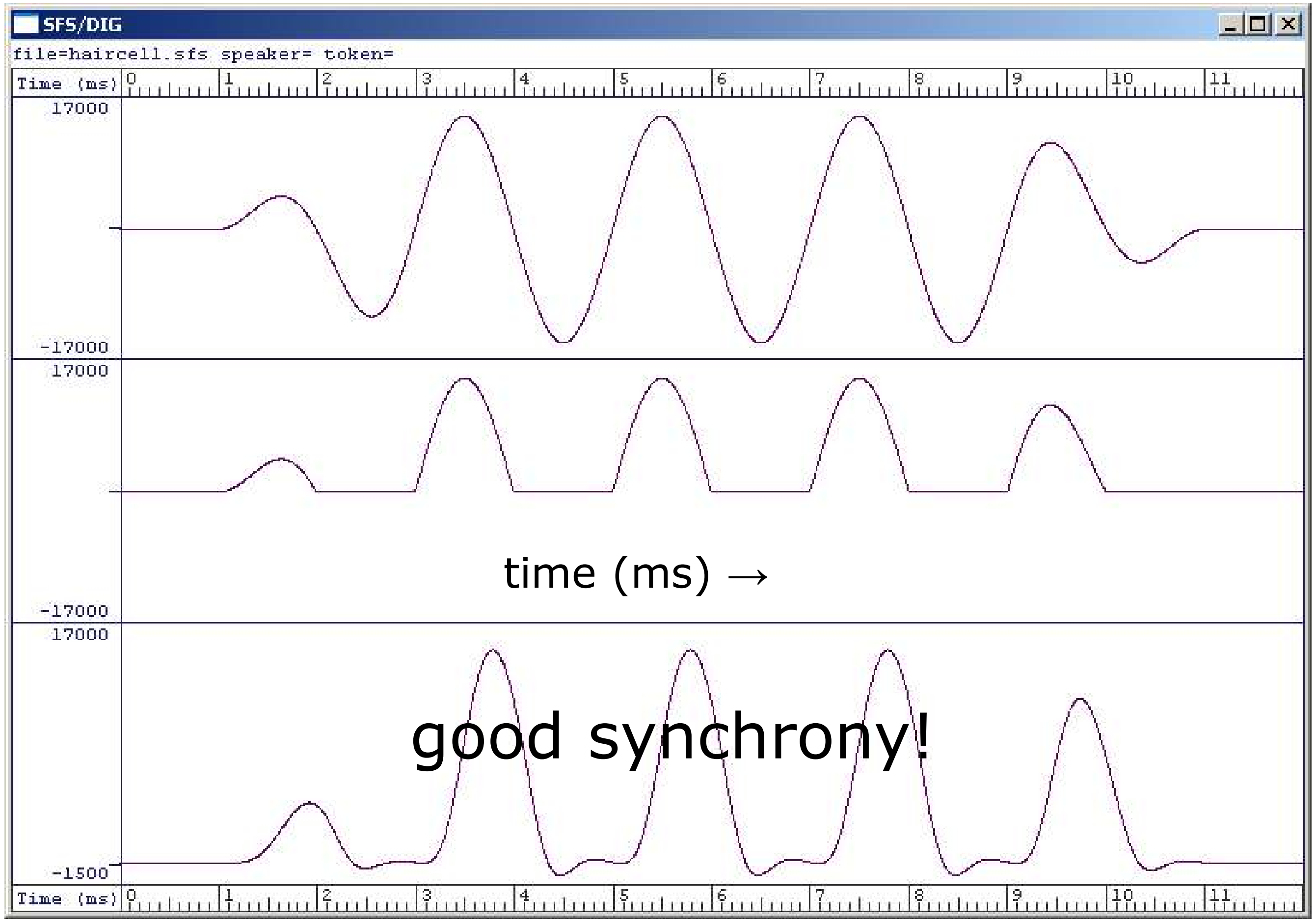
Not the same as firing *rate*!

Evans (1975)

But phase-locking is limited to lower frequencies ...

- Synchrony of neural firing is strong up to about 1-2 kHz.
- There is no evidence of synchrony above 5 kHz.
- The degree of synchrony decreases steadily over the mid-frequency range.

Simulating hair cell transduction at 500 Hz



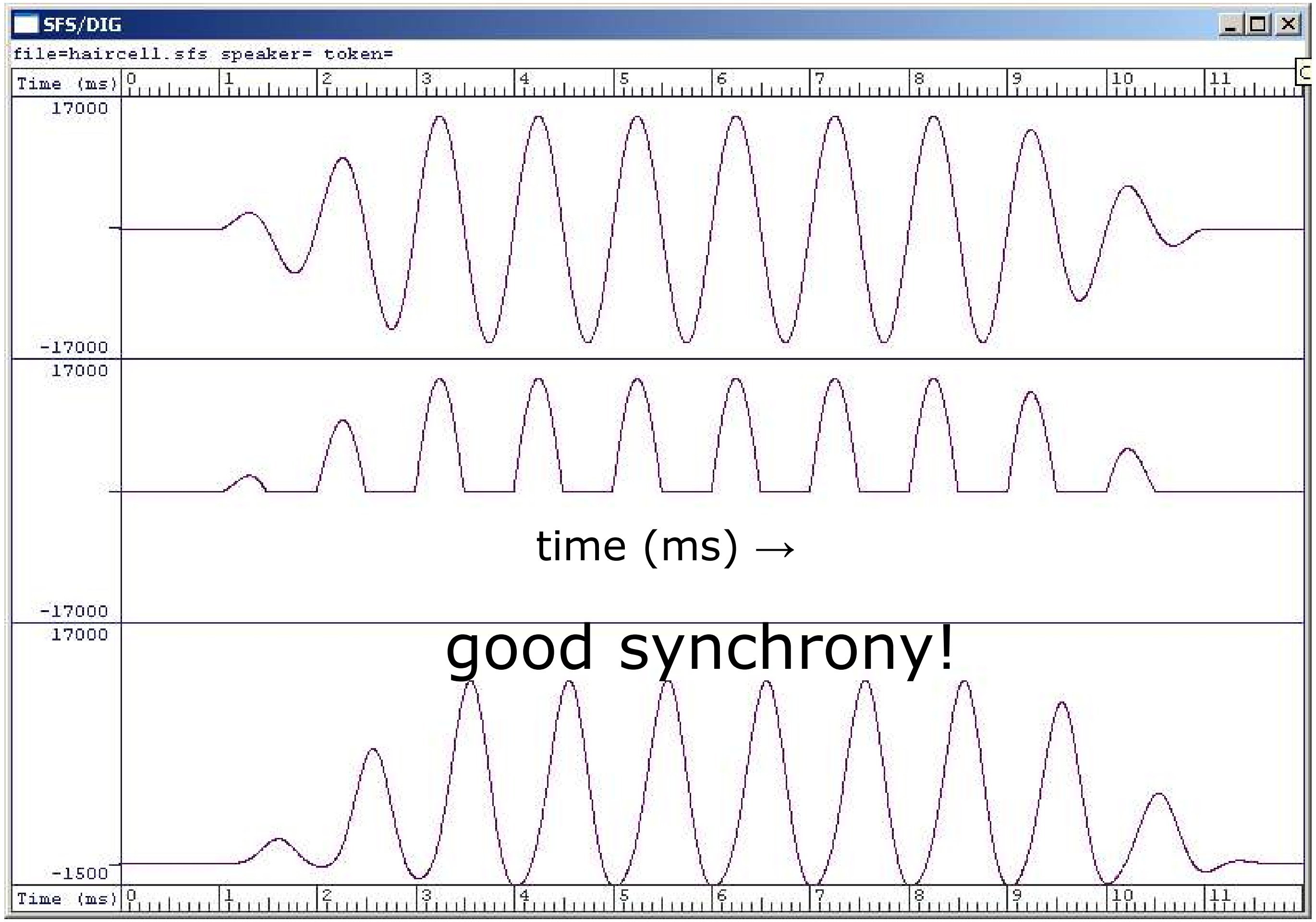
input wave

½–wave rectification

smoothing with a 1.5 kHz lowpass filter

think of this last wave as driving the auditory nerve
(e.g., as the amount of neurotransmitter in the synaptic cleft)

Simulating hair cell transduction at 1000 Hz

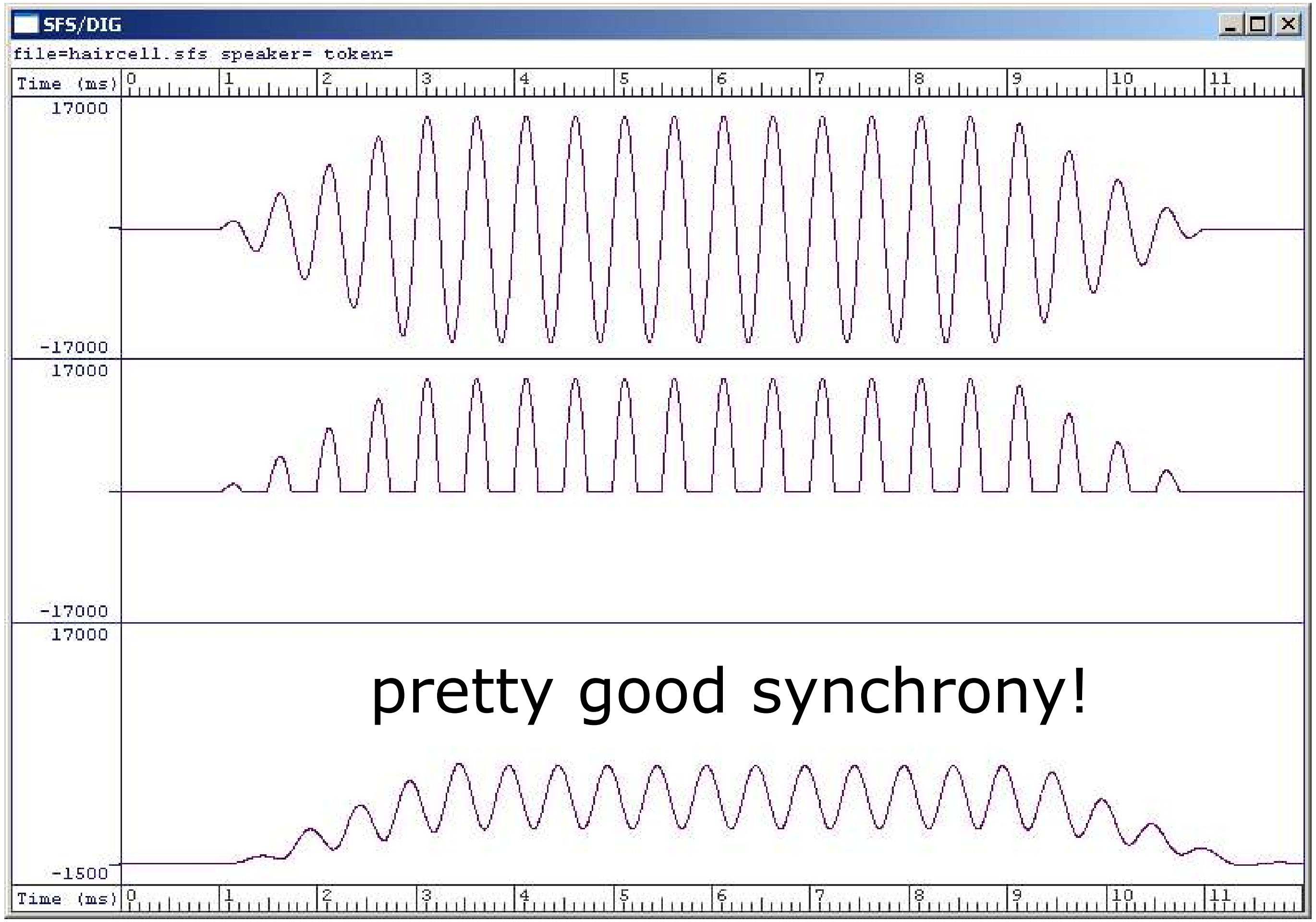


input wave

½–wave rectification

smoothing with a 1.5 kHz lowpass filter

Simulating hair cell transduction at 2000 Hz



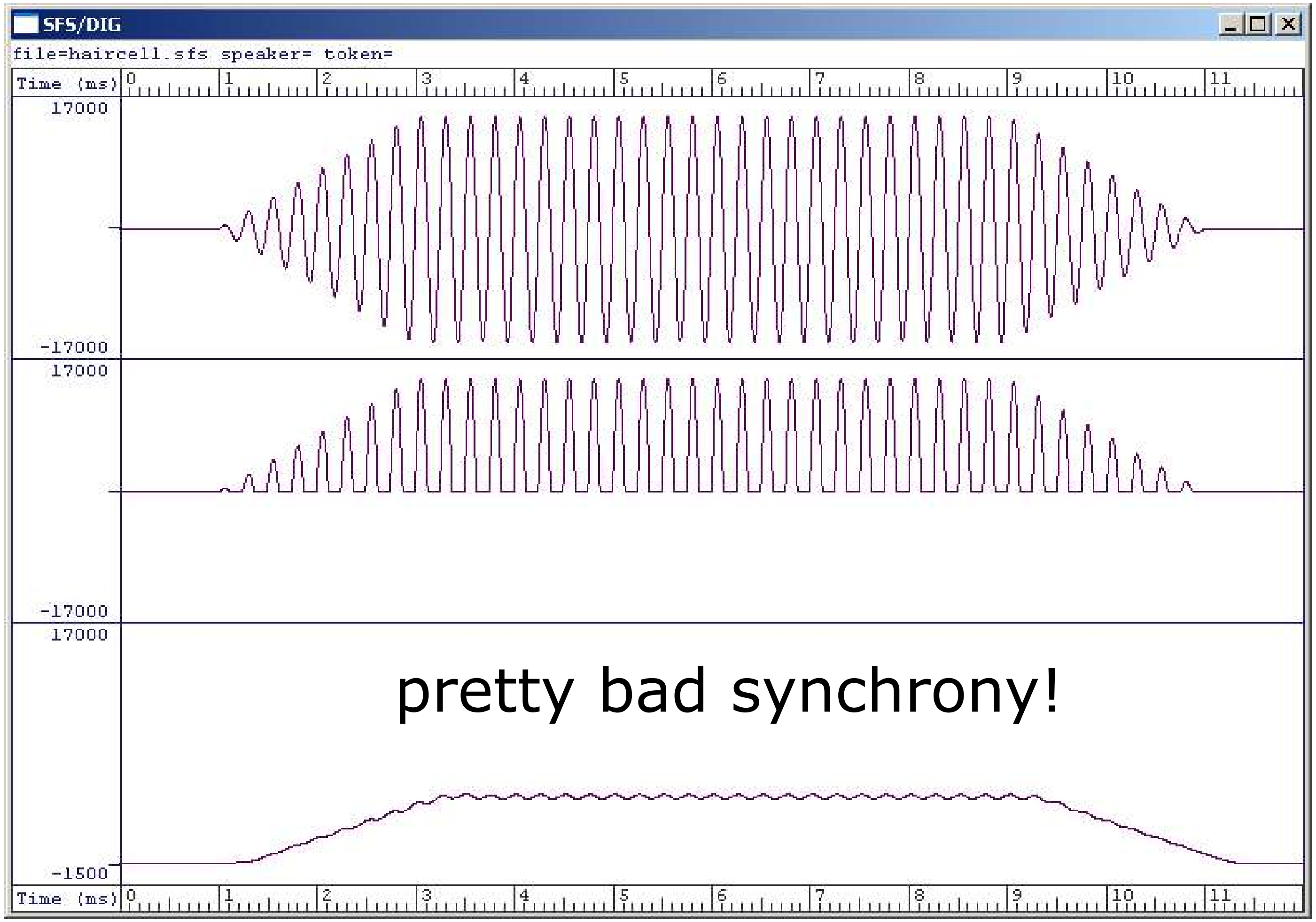
input wave

½–wave rectification

smoothing with a 1.5 kHz lowpass filter

pretty good synchrony!

Simulating hair cell transduction at 4000 Hz

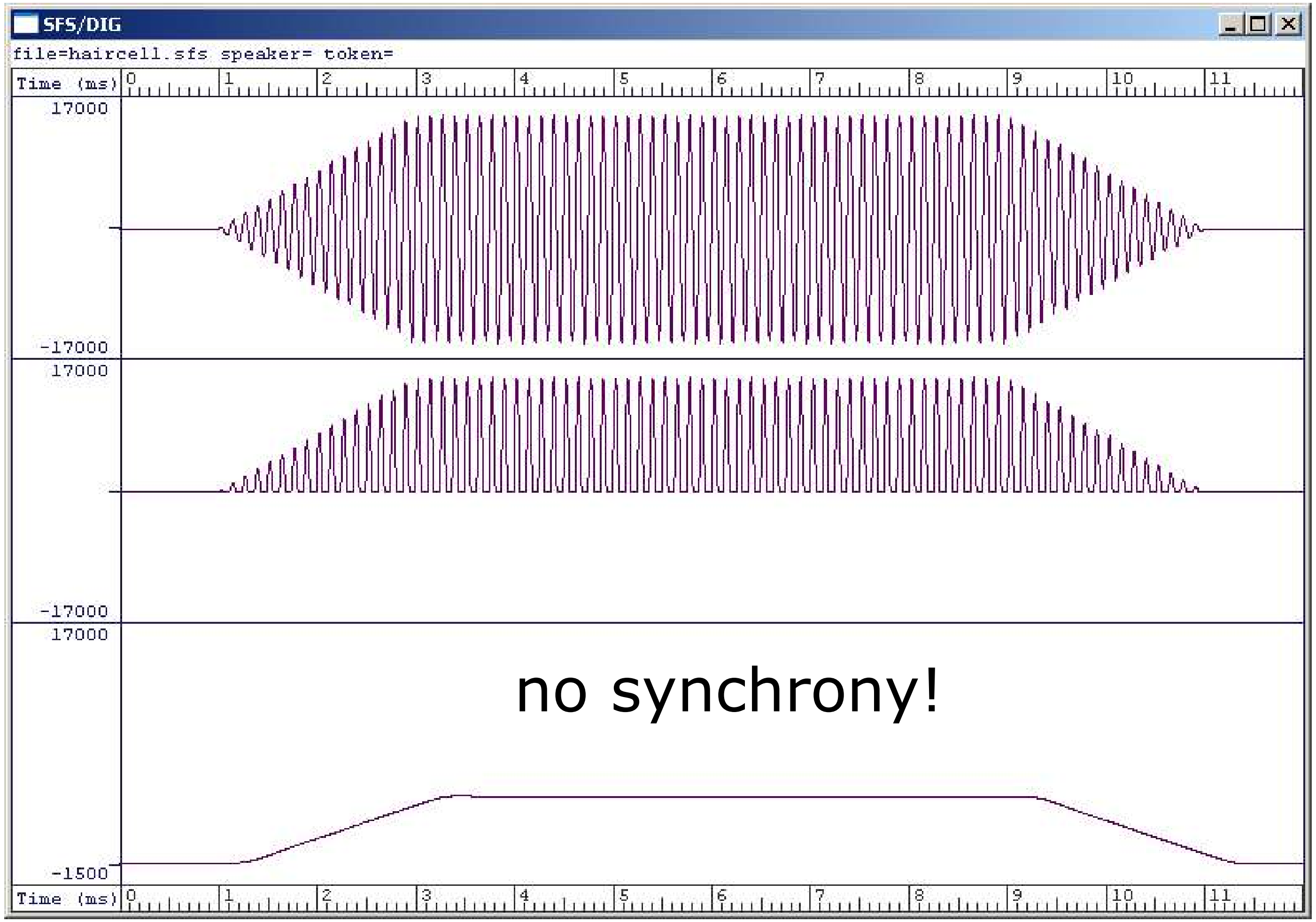


input wave

½–wave rectification

smoothing with a 1.5 kHz lowpass filter

Simulating hair cell transduction at 8000 Hz



input wave

½–wave rectification

smoothing with a 1.5 kHz lowpass filter

Neural stimulation to a low frequency tone