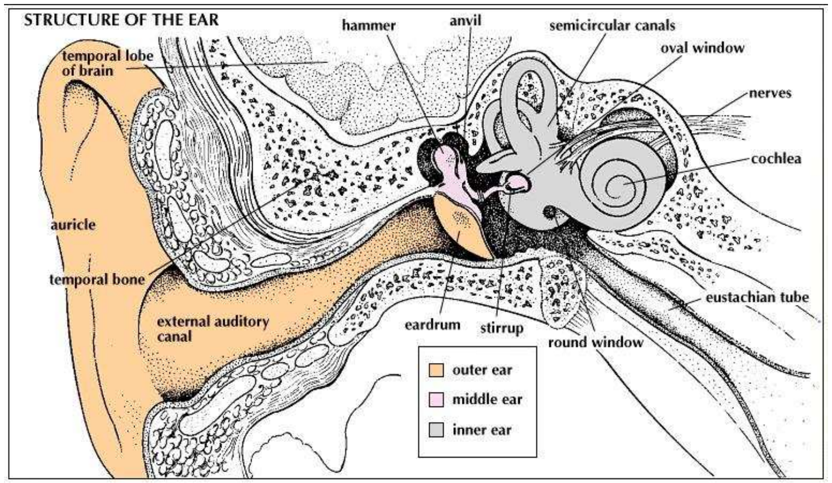
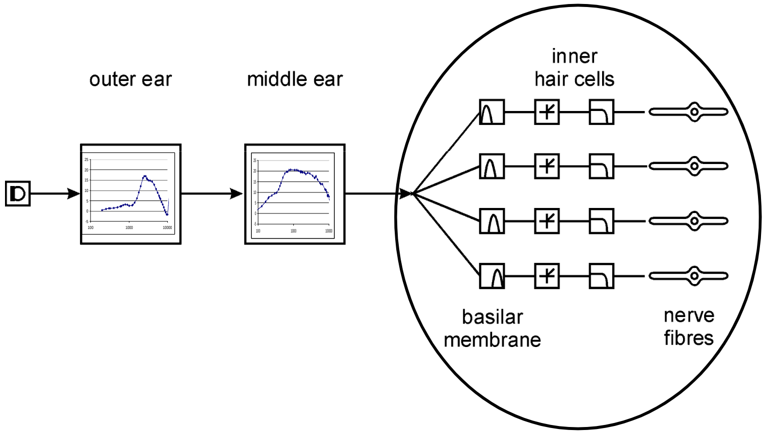
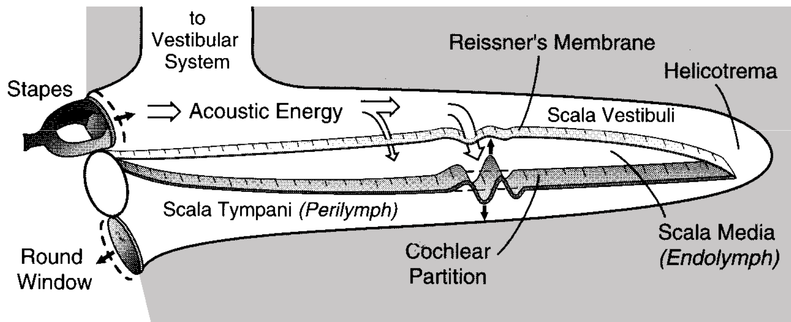
Cochlea & Auditory Nerve: obligatory stages of auditory processing



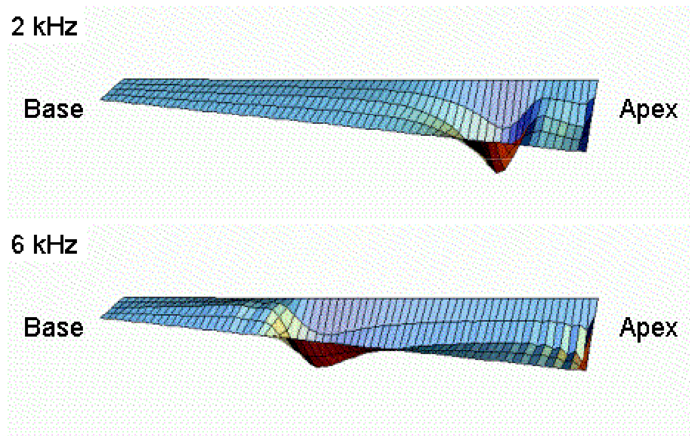
Think of the auditory periphery as a processor of signals



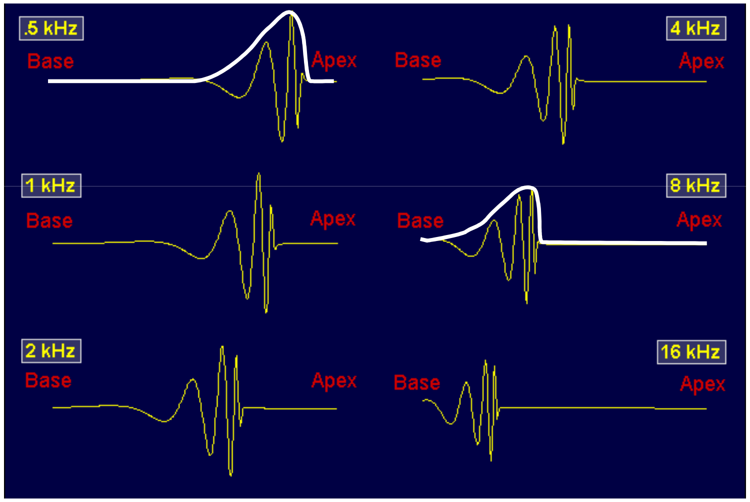
Imagine the cochlea unrolled



Basilar membrane motion to two sinusoids of different frequency

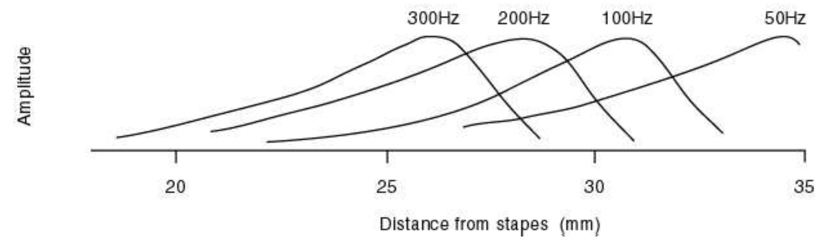


Defining the envelope of the travelling wave



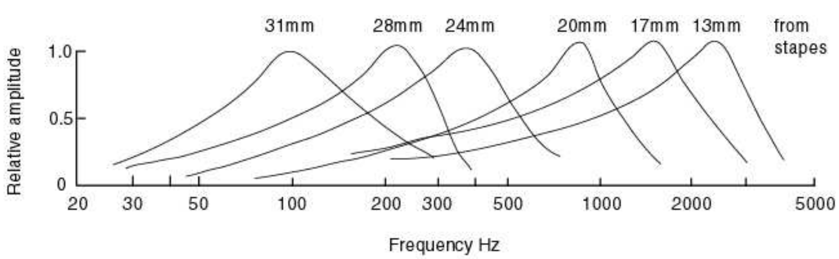
A crucial distinction
excitation pattern vs. *frequency response*

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

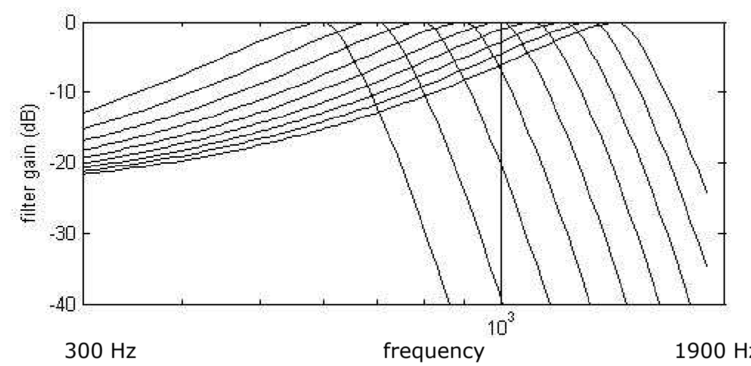


A crucial distinction
excitation pattern vs. *frequency response*

- 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.

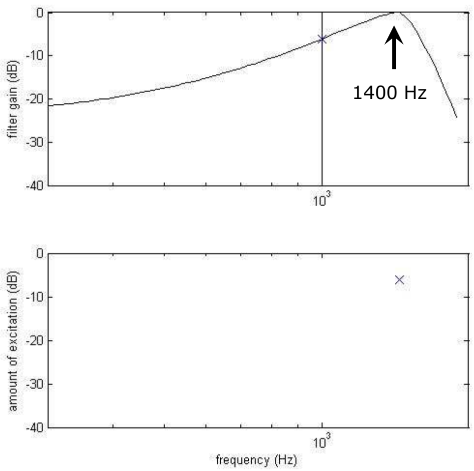


Two sides of the same coin:
Deriving excitation patterns for a 1 kHz sinusoid from frequency responses

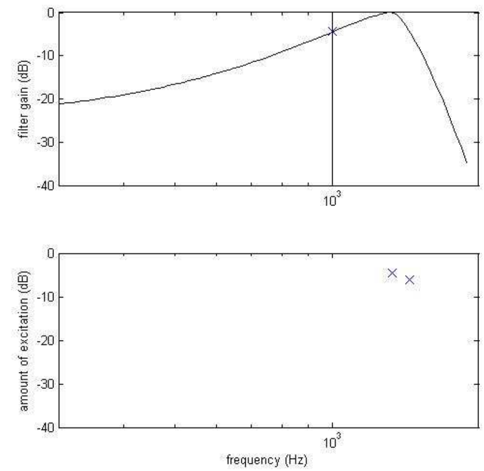


Note shallower slope to lower frequencies (left) for frequency responses

Frequency responses with centre frequencies running from 1400 – 600 Hz



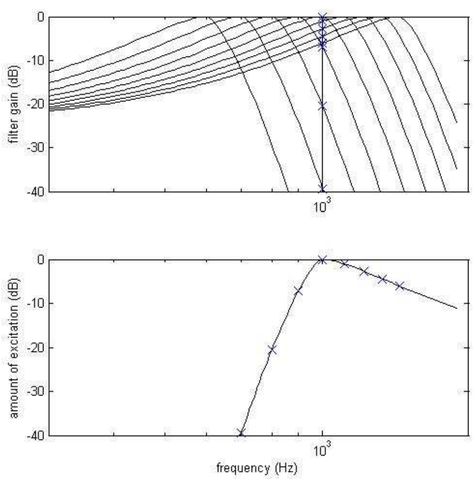
Frequency responses with centre frequencies running from 1400 – 600 Hz



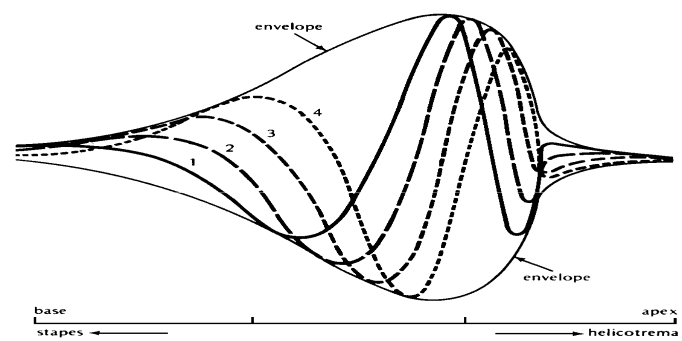
Deriving excitation pattern from auditory filters

Note shallower slope to left

Note shallower slope to right



Now the other way around: filter shapes from excitation patterns

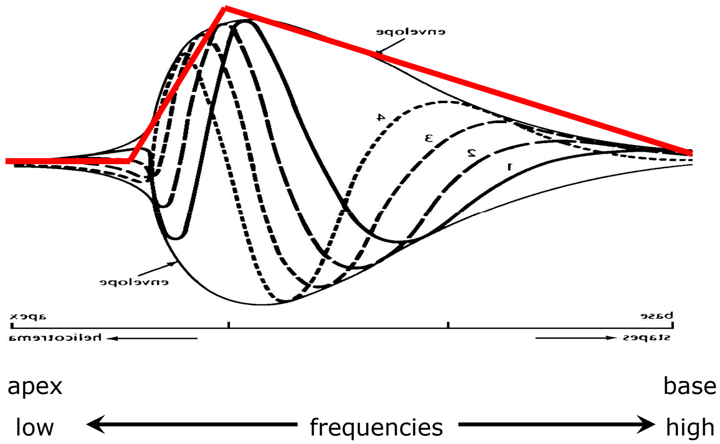


base apex

high ← frequencies → low

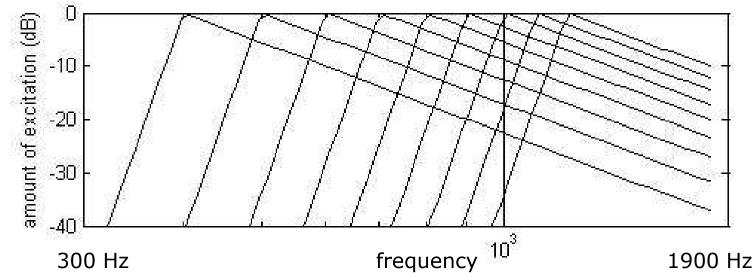
Note shallower slope to left

Flip the orientation of the axis and schematise



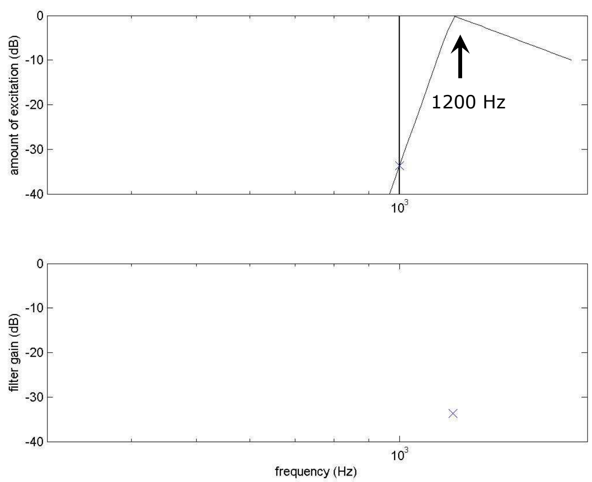
Note shallower slope to right

The other side of the coin: Deriving a frequency response at 1 kHz from excitation patterns

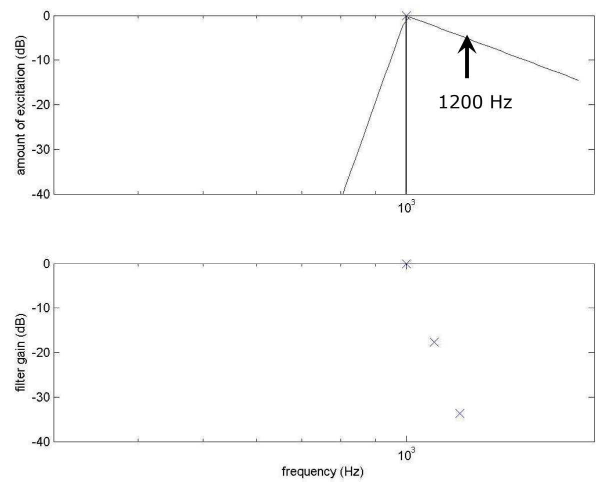


Note shallower slope to higher frequencies (right) for excitation patterns

Excitation patterns with centre frequencies running from 1200 – 400 Hz



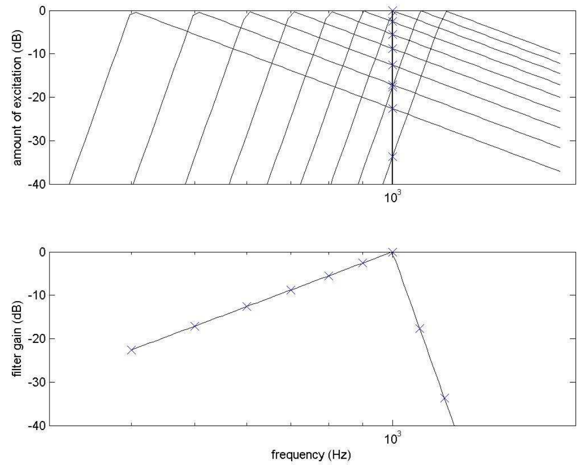
Excitation patterns with centre frequencies running from 1200 – 400 Hz



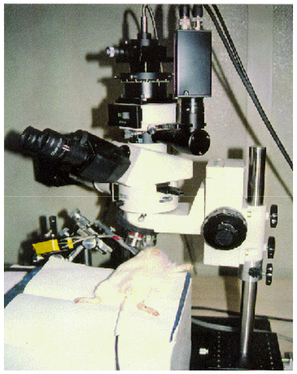
Deriving frequency responses from excitation patterns

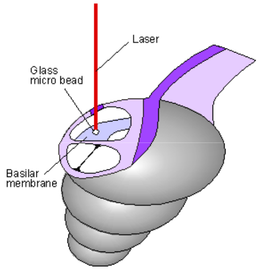
Note shallower slope to right

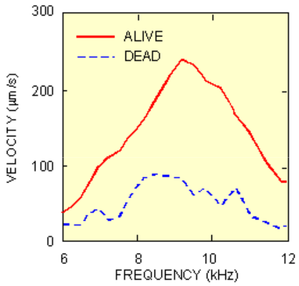
Note shallower slope to left



Laser Doppler Velocimetry







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

Modern measure-ments of the frequency response of the basilar membrane

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

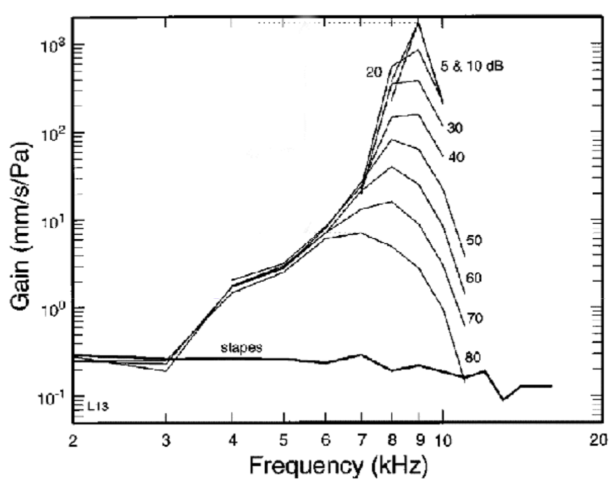


FIG. 10. A family of isointensity curves representing the gain (velocity divided by stimulus pressure) of basilar-membrane responses to tone pips as a function of frequency (abscissa) and intensity (parameter, in dB SPL). The thick line at bottom indicates the average motion of the stapes (Ruggero *et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

input/ output functions on the basilar membrane

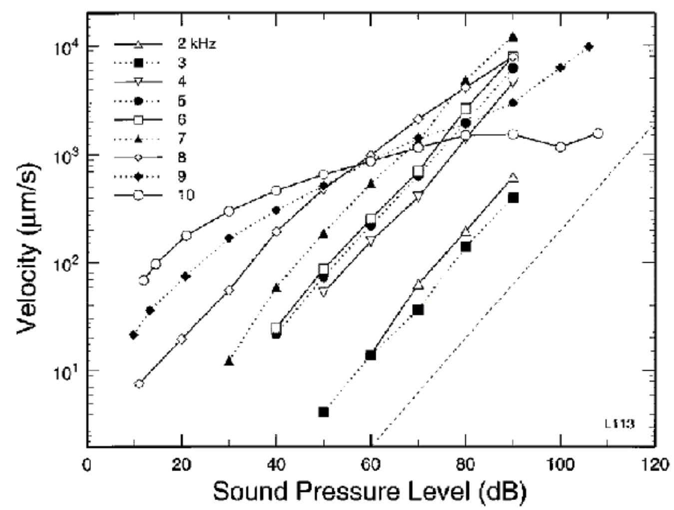
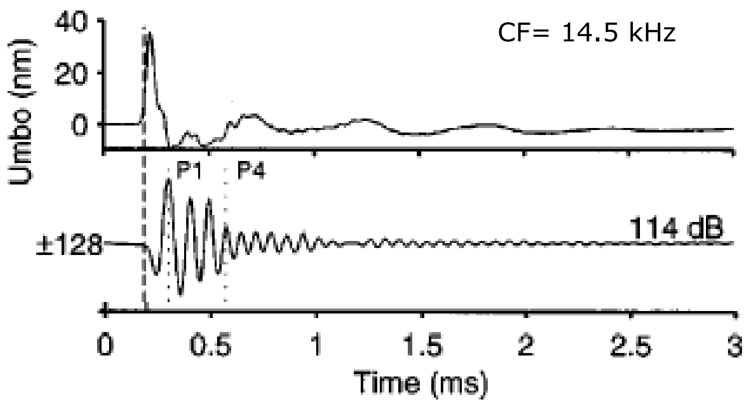
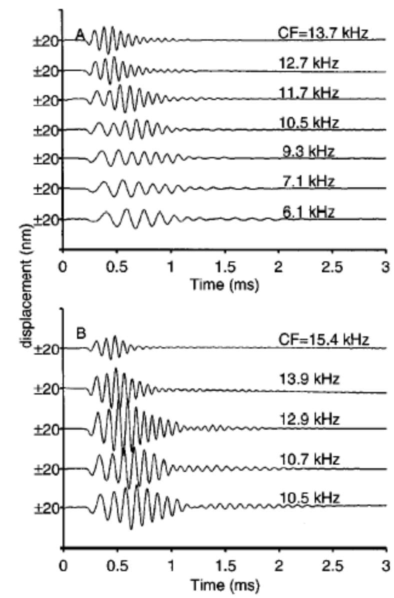


FIG. 7. Velocity-intensity functions of basilar-membrane responses to tones with frequency equal to and lower than CF (10 kHz). The straight dashed line at right has a linear slope (1 dB/dB).

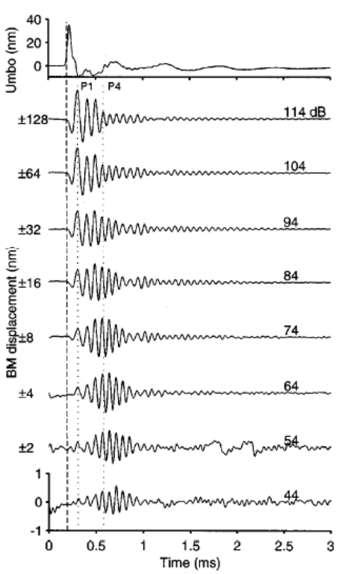
Waveform of response to clicks on the basilar membrane (a.k.a. ?)



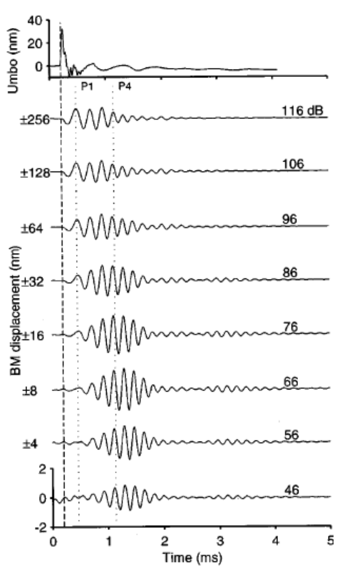
Click responses at various BM places



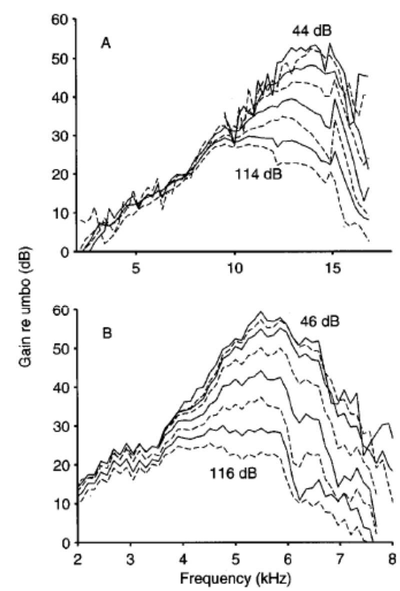
CF = 14.5 kHz



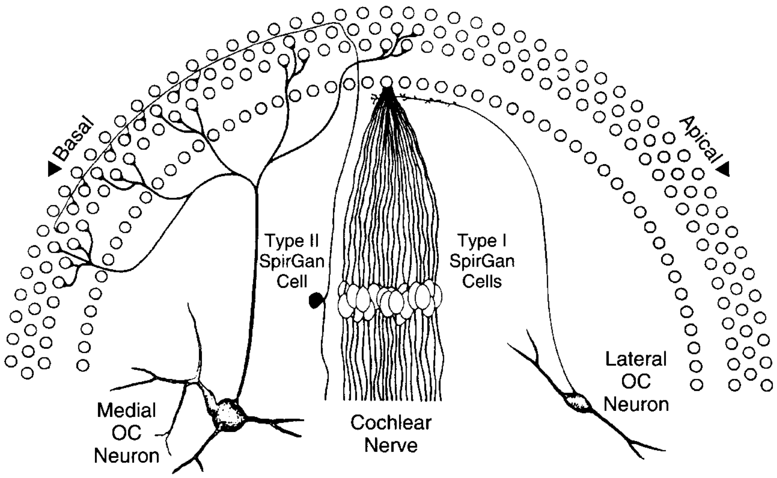
CF = 5.5 kHz



What else can you do to impulse responses (and why)?



Innervation of the cochlea



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

Four aspects of firing patterns on the auditory nerve

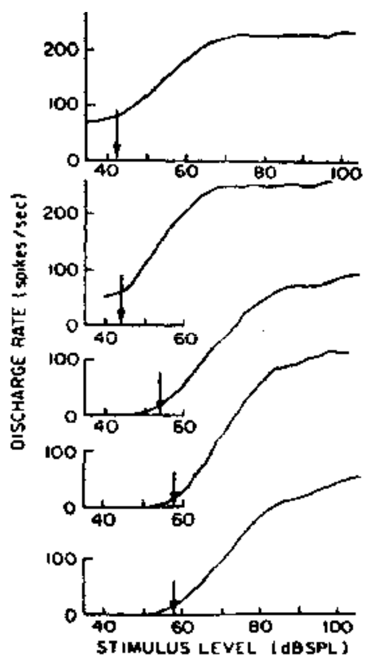
- The coding of intensity.
- The representation of the place code.
- The representation of temporal fine structure (for intervals ranging up to ≈20 ms).
- The representation of gross temporal structure.

Intensity

Rate-level functions for auditory nerve fibres

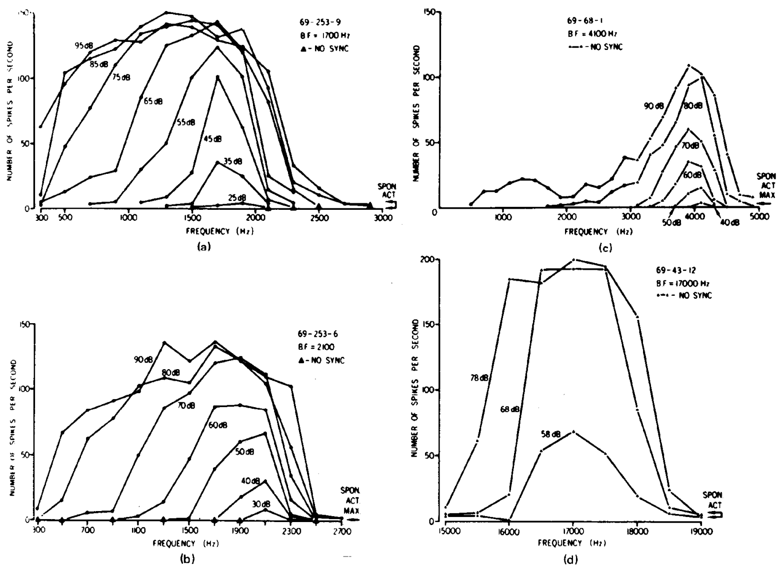
Observe!

- Threshold
- Saturation
- Limited dynamic range

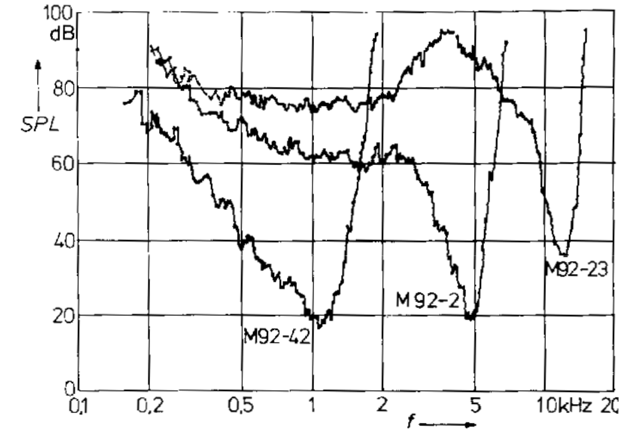


However, firing rates depend not only on sinusoidal sound intensity but also on sound ...

Firing rate across frequency and level

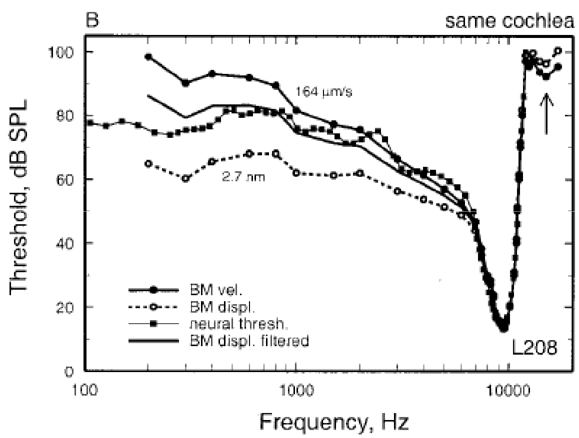


'Audiograms' of single auditory nerve fibres reflect BM tuning



The 'best' frequency of a particular tuning curve depends upon the BM position of the IHC to which the afferent neuron is synapsing

BM and neural tuning compared

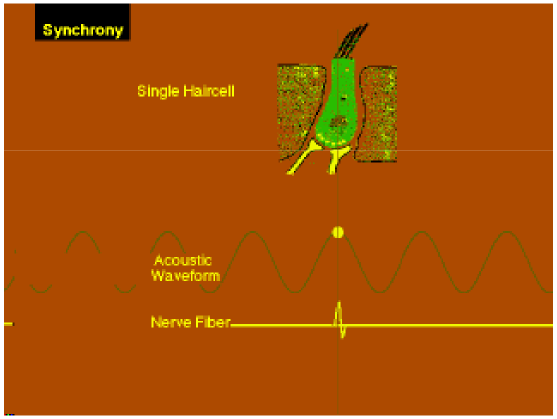


'filtered' is high-pass filter at 3.8 dB/octave. From Ruggero *et al*. 2000

Temporal coding (up to ≈ 5 kHz)

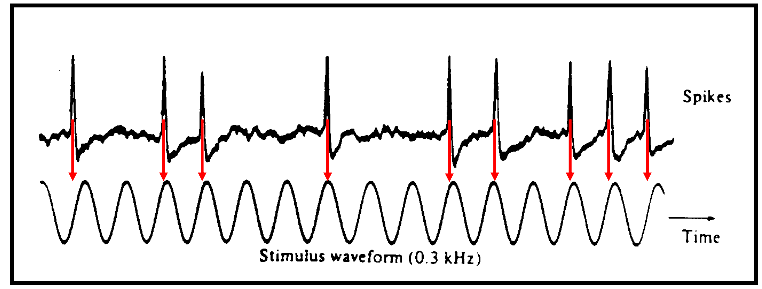
Information about stimulus frequency is not only coded by *which* nerve fibres are active (the *place* code) but also by *when* the fibres fire (the *time* code).

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*).



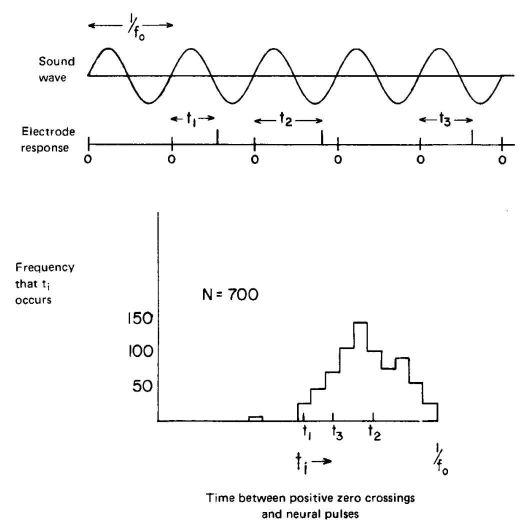
Not the same as firing *rate*!

Evans (1975)

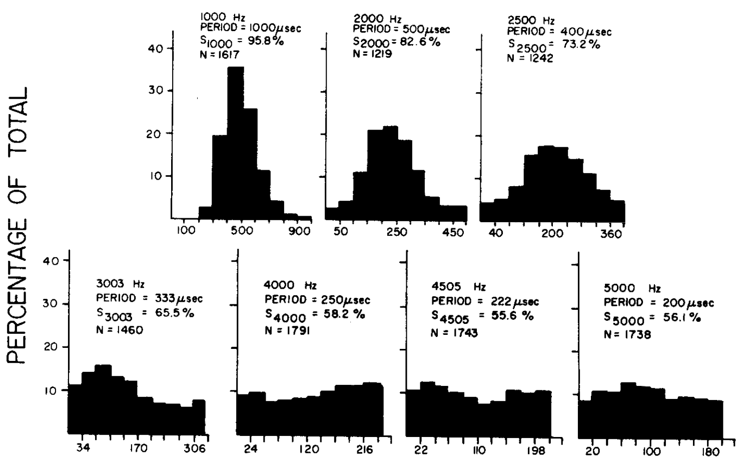
But phase-locking is limited to lower frequencies ...

- 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.

… as readily seen in a *period histogram*

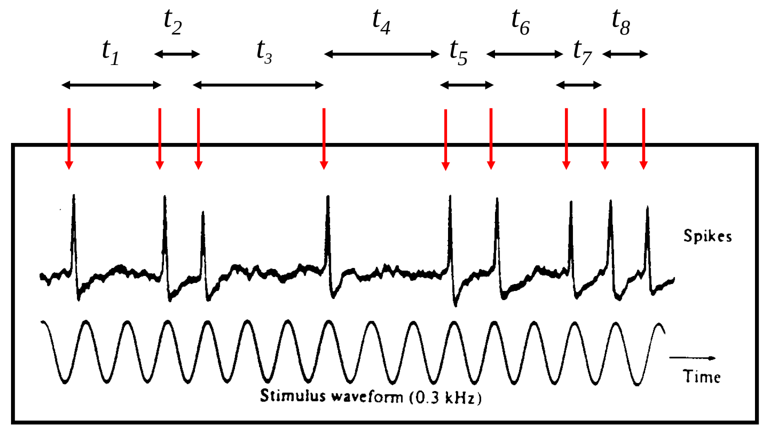


Period histograms across frequency

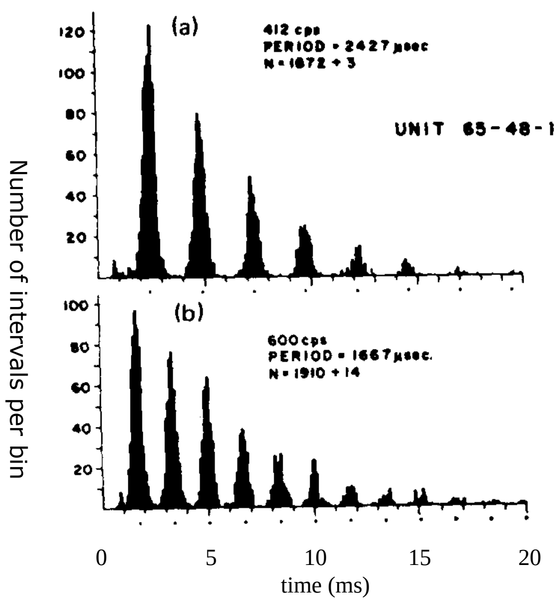


Note half-wave rectification and *synchrony index*

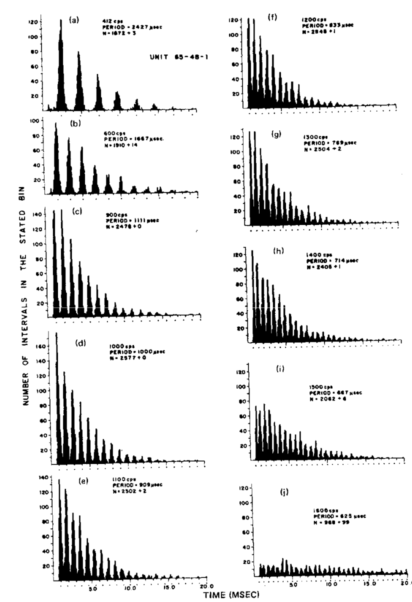
Constructing an *interval histogram*



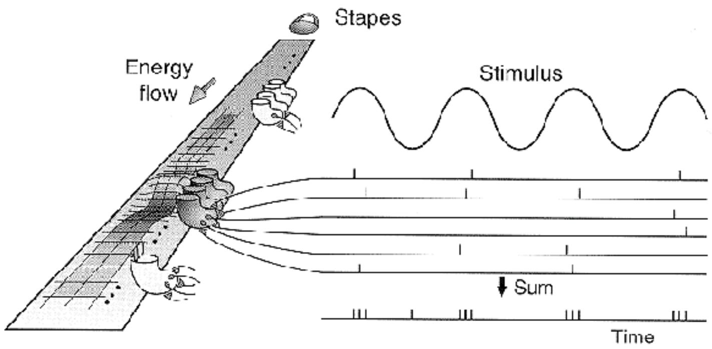
Interval histograms for a single AN fibre at two different frequencies



Interval histograms for a single AN fibre across frequency

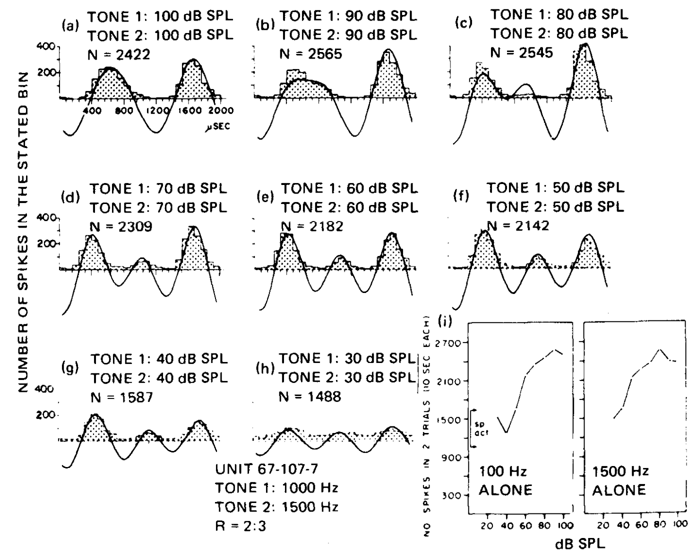


Neural stimulation to a low frequency tone

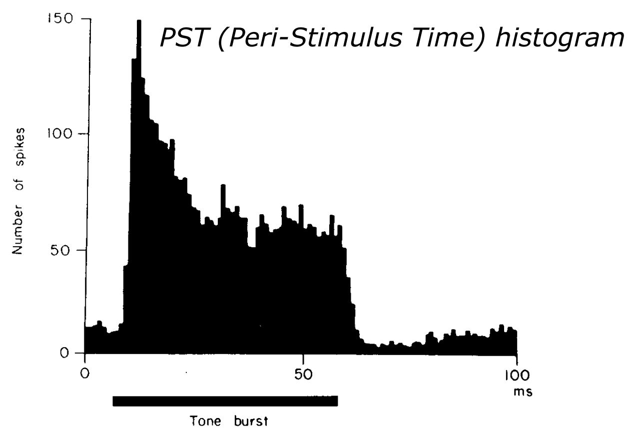


Sound energy propagates to the characteristic place of the tone where it causes deflection of the cochlear partition. Neural spikes, when they occur, are synchronized to the peaks of the local deflections. The sum of these neural spikes tends to mimic the wave shape of the local deflections.

Period histograms to more complex sounds



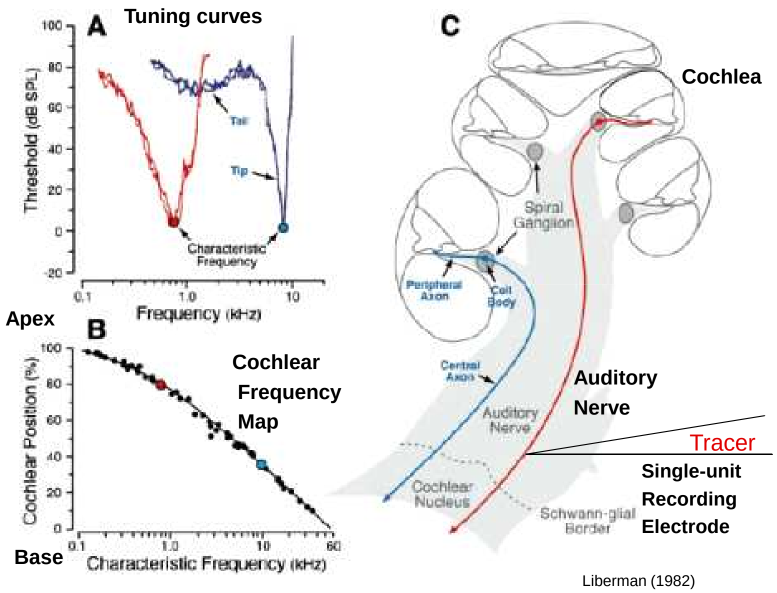
Gross temporal structure
Enhanced response to sound onsets: The value of novelty



Where we've got to …

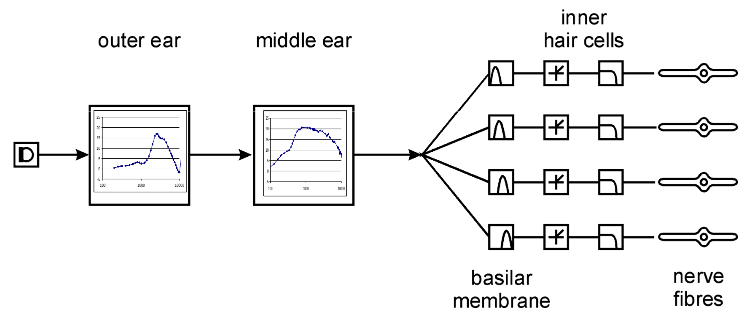
- Outer ear channels sound to the middle ear, and can be characterized as a bandpass filter.
- Middle ear effects an efficient transfer of sound energy into the inner ear, again with the characteristics of a bandpass filter.
- Inner ear
  - Transduces basilar membrane movements into nerve firings …
  - which are synchronised to peaks in the stimulating waveform at low enough frequencies
  - Performs a mechanical frequency analysis, which can be envisioned as the result of analysis by a *filter bank.*

Auditory Nerve Structure and Function



Liberman (1982)

A systems model of the auditory periphery

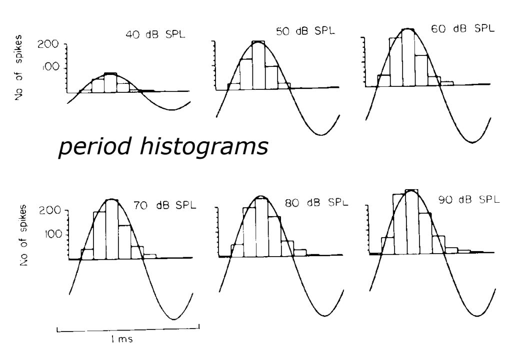


What properties should the filter bank have?

- Filter spacing
  - *Corresponding to tonotopic map*
- Filter bandwidth
  - *vary with frequency as on the basilar membrane*
- Filter nonlinearity
  - *vary gain and bandwidth with level as on the basilar membrane*

Modelling the hair cell/auditory nerve synapse

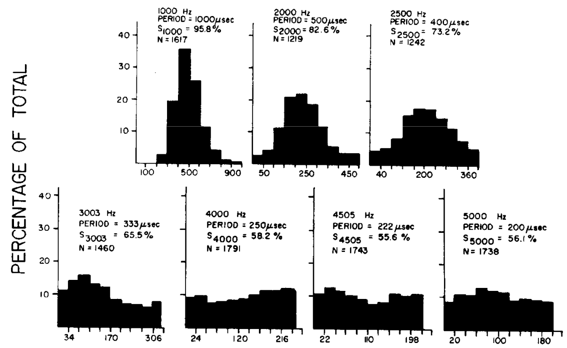
- Neuro-transmitter is released when cilia are pushed in one direction only, tied to polarity of basilar membrane motion
  - *half-wave rectification*



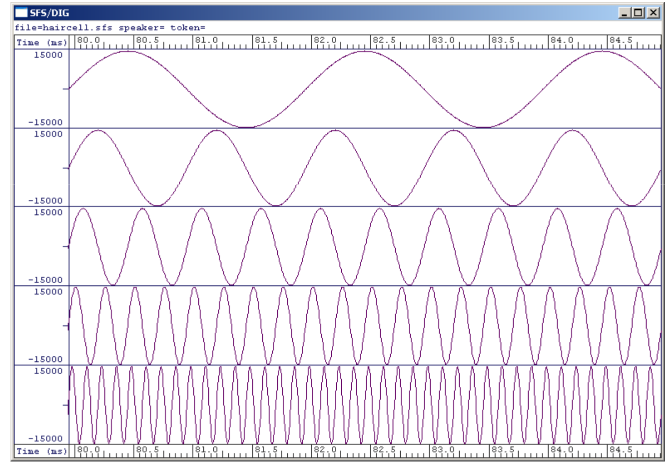
Modelling the hair cell/auditory nerve synapse

- Phase-locking is limited to low frequencies
  - *low-pass filtering*

period histograms across frequency

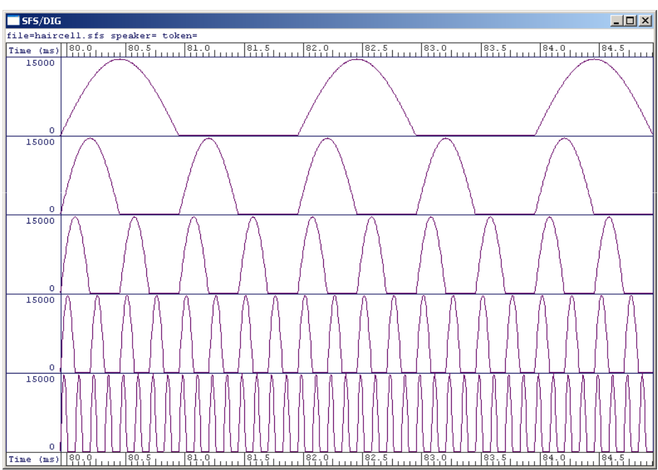


Input sinusoids



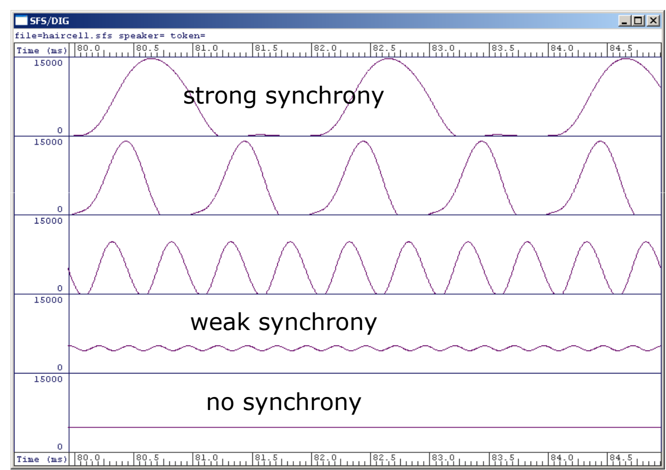
0.5 kHz
1.0 kHz
2.0 kHz
4.0 kHz
8.0 kHz

Half-wave rectification



0.5 kHz
1.0 kHz
2.0 kHz
4.0 kHz
8.0 kHz

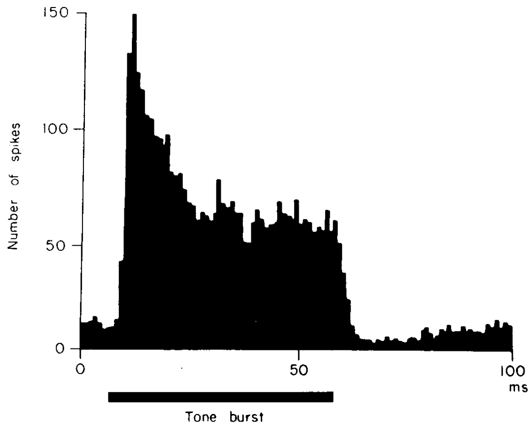
Smoothing



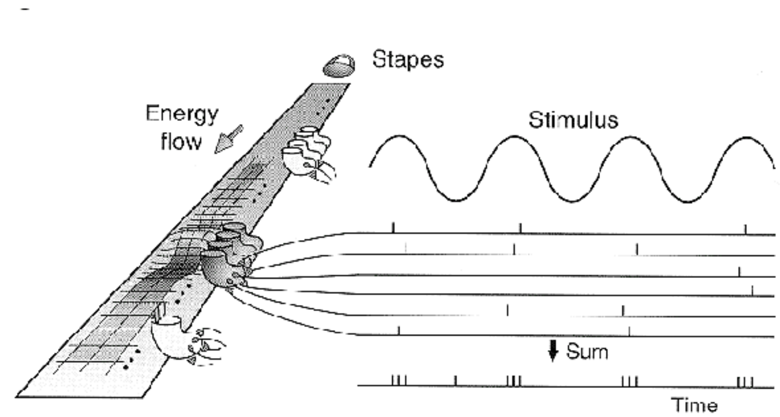
0.5 kHz
1.0 kHz
2.0 kHz
4.0 kHz
8.0 kHz

Modelling the hair cell/auditory nerve synapse

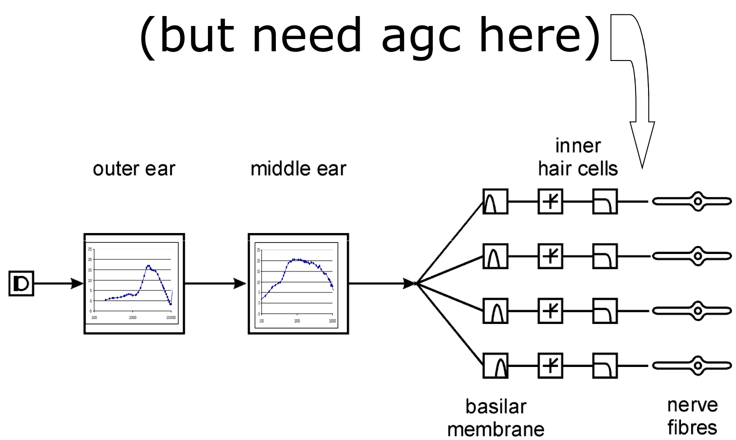
- Rapid adaptation
  - *need some kind of automatic gain control (agc)*



Neural stimulation to a low frequency tone



We're done! (but need agc here)

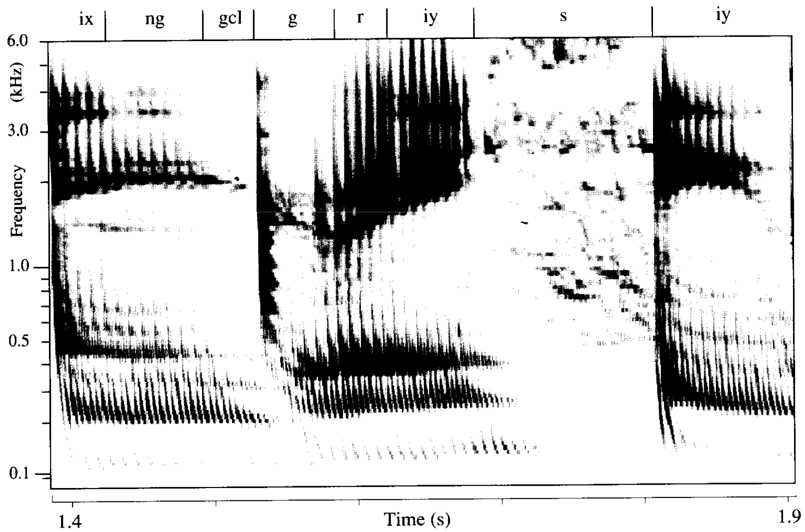


A spectrogram with 'ear-like' processing (Giguere & Woodland, 1993)

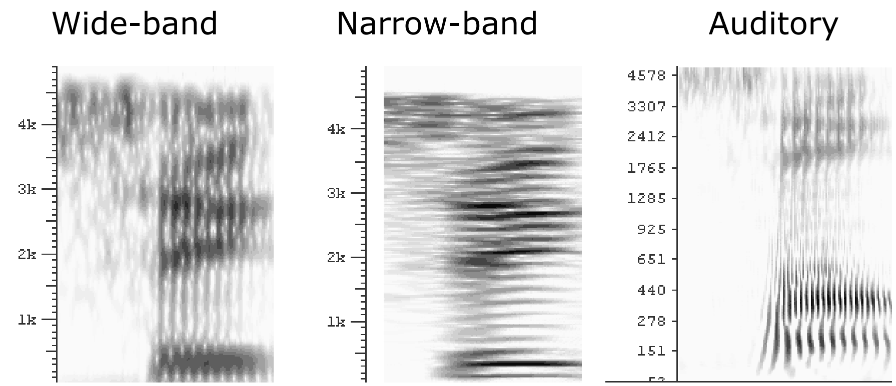
(*typical spectrogram properties in italics)*

- A first-stage broad band-pass linear filter to mimic outer and middle ear effects *(pre-emphasis filter).*
- A filterbank whose centre frequencies are arranged in the same way as the human tonotopic (frequency to place) map ... *(equal spacing of filters in Hz).*
- with non-linear filters whose bandwidths increase as level increases (*linear filters with a fixed bandwoidth)*.
- Smearing of temporal information so as to mimic the frequency limitation of phase locking in the auditory nerve *(smearing by choice of temporal window/filter bandwidth — no extra processing)*.

An auditory spectrogram

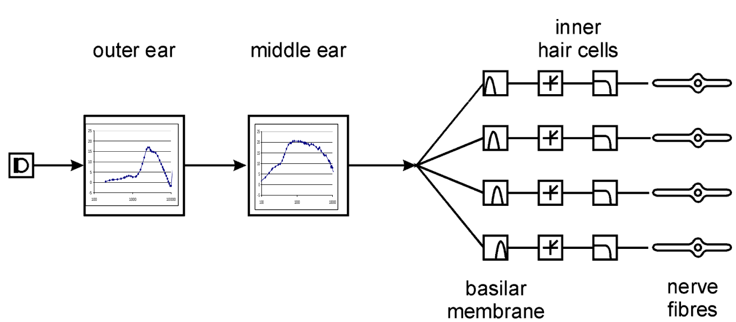


Types of Spectrogram

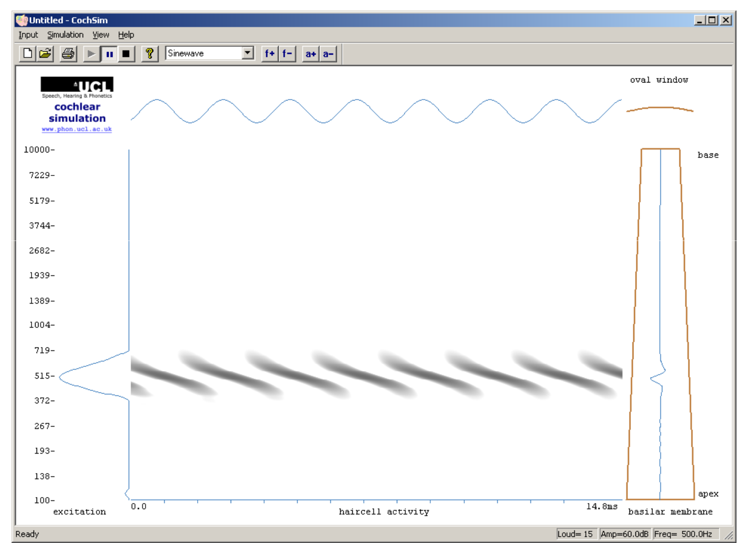


An auditory spectrogram looks like a wide-band spectrogram at high frequencies and a narrow-band spectrogram at low frequencies (but with more temporal structure).

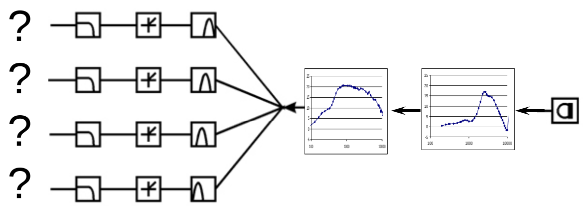
Next lab: A computer implementation of essentially this model



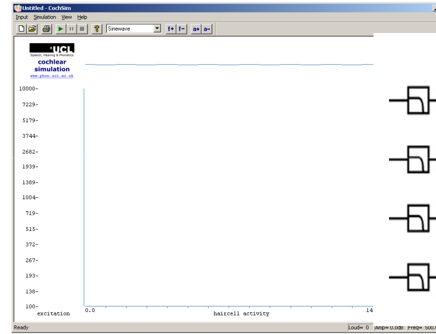
A cochlear simulation

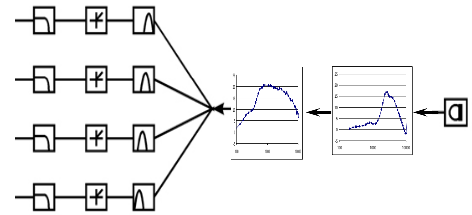


Flip it around



A cochlear simulation

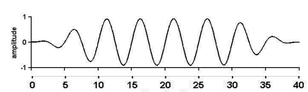


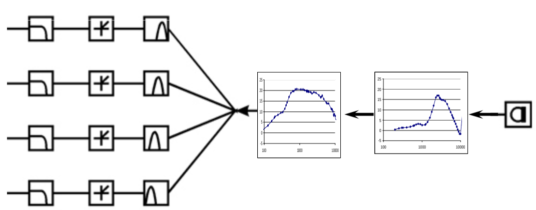


How should we look at the output of the model?

Could look at the output waveforms

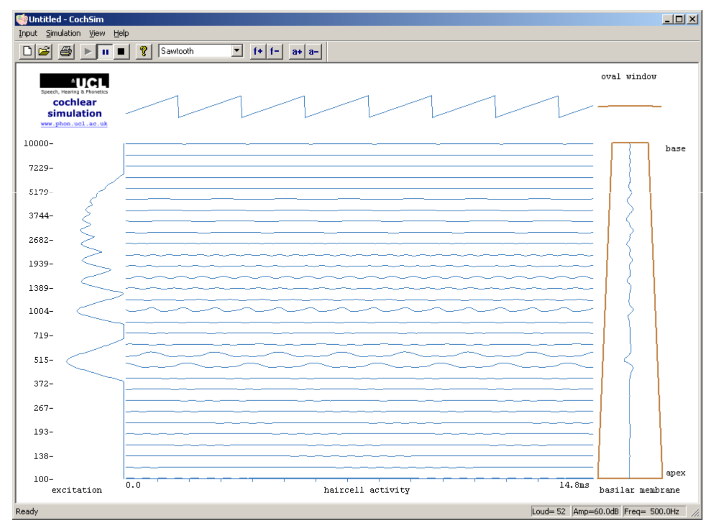
input signal



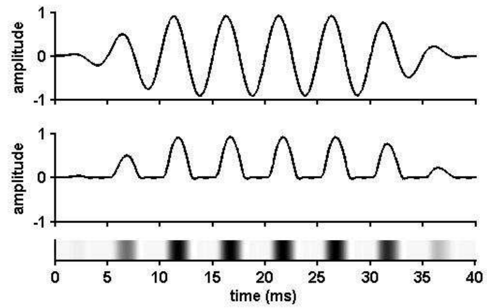


output signal

But hard to see what is going on (especially for complex waves)



Solution: encode wave amplitude in a different way



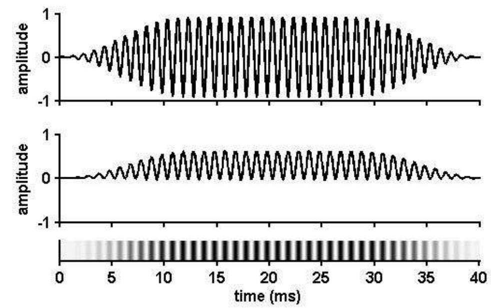
waveform at 200 Hz

rectified & smoothed

spectrographic

waveform amplitude is recoded as
the darkness of the trace

Encode wave amplitude as trace darkness

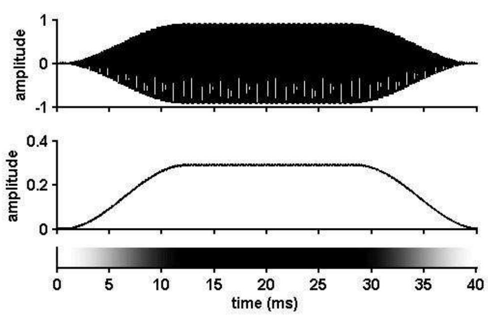


waveform at 1 kHz

rectified & smoothed

spectrographic

Encode wave amplitude as trace darkness



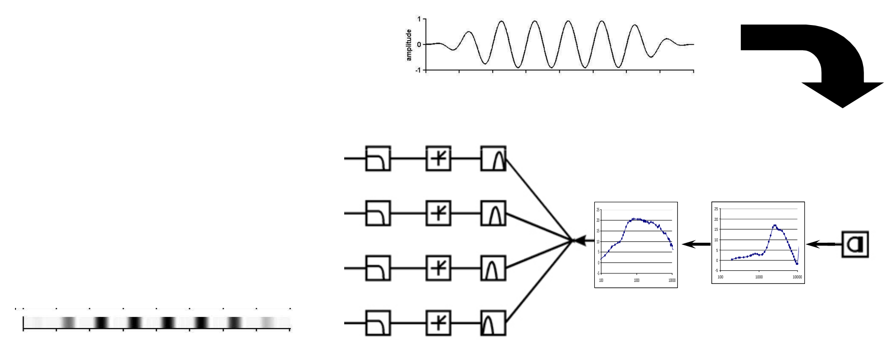
waveform at 4 kHz

rectified & smoothed

spectrographic

Construct the output display one strip at a time

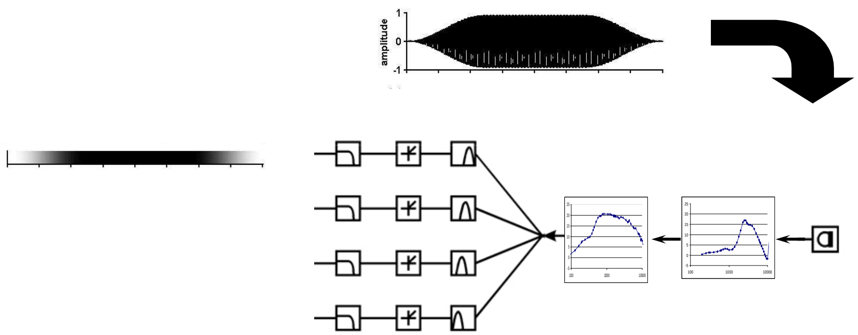
input signal at 200 Hz



output display

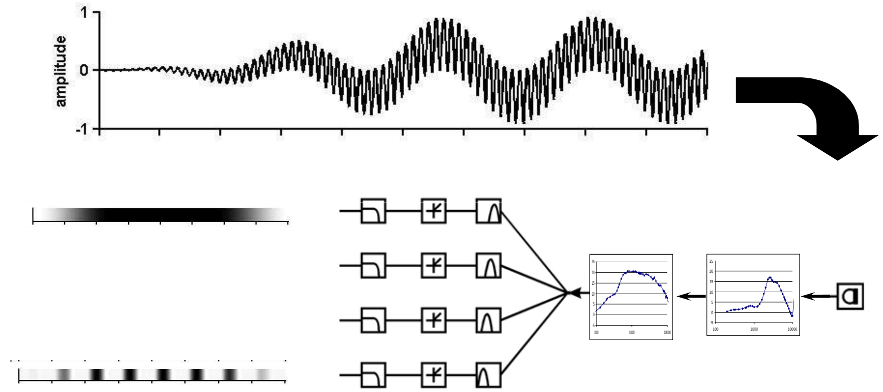
Construct the output display one strip at a time

input signal at 4 kHz



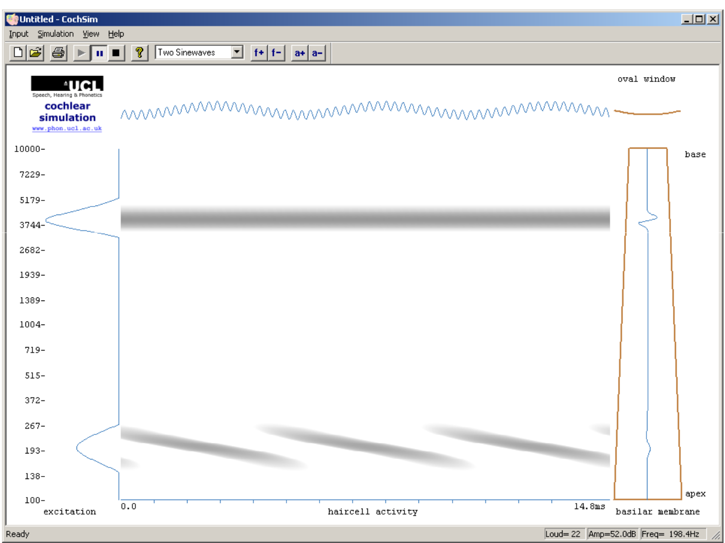
output display

4 kHz + 200 Hz



output display

4 kHz + 200 Hz



Auditory and ordinary spectrograms