principle of the week: Active Sensing
basic characterization of sound waves

<table>
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<th>Physical Dimension</th>
<th>Perceptual Dimension</th>
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<td>Amplitude (intensity)</td>
<td>Loudness</td>
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<tr>
<td>Frequency</td>
<td>Pitch</td>
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<tr>
<td>Complexity</td>
<td>Timbre</td>
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- **Loudness**: low, high
- **Pitch**: low, high
- **Timbre**: simple, complex

**Diagram**:
- **Compressed sound waves**
- **Rarefied (negative pressure)**
- **Eardrum**

**Graph**:
- Power (dB) vs. Frequency (kHz)
- Log S(f) (dB)

- Power (dB): -16 to 0
- Frequency (kHz): 1.0 to 5.0
outer ear (pinna) shape reflects sound from different sources in different ways providing a possible source for localization of the height of a sound source.
middle ear bones amplify sound in a frequency-dependent fashion

frequency-dependence of amplification is, in turn, modulated by middle ear muscle contractions
basilar membrane vibration is transduced into neural signals by hair cells

[Diagram of cochlear hair cells and their components, including stereocilia, kinocilia, microvilli, cuticular plate, basal body, tight junction, and supporting cell.]

[Diagram showing the interaction between the basilar membrane and the tectorial membrane, with an arrow indicating the direction of movement and tip links.]
the inner ear – transformation of pressure waves (sound) and their frequency characteristics (spectra) into neural signals
varying stiffness of the basilar membrane results in a Fourier transform of the vibrations of the endolymph
Segregation of cochlear ganglion cell outputs to cochlear nucleus according to the position of their hair cell inputs – creation of a topographic representation of sound (tonotopy) that ultimately reaches primary auditory cortex.
cochlear nucleus neurons exhibit heterogeneous responses to inputs from ganglion cells. 

the response fields of each are described in frequency X amplitude response plots.
ascending pathways of the mammalian auditory system
the ‘where’ of sound – sound source localization by comparison of inputs to the left and right ears

interaural time difference (ITD)

interaural level difference (ILD)

not useful for persistent high frequency sounds (>2000 Hz) as hair cell responses do not oscillate in response to high frequency tones

not useful for low frequency sounds as their amplitude is less impacted by the head

what about sound source height?
brainstem processing of auditory information yields sound source localization
the organization of cochlear nucleus outputs to the brainstem yields responses to
interaural time differences in medial superior olive neurons and interaural level
differences in lateral superior olive neurons.
brainstem processing of auditory information yields sound source localization

the organization of cochlear nucleus outputs to the brainstem yields responses to interaural time differences in medial superior olive neurons and interaural level differences in lateral superior olive neurons.
timing of spikes in A1 can be very consistent even for highly complex auditory sequences
multiple sub-regions of auditory cortex: most contain a tonotopic map – responses to different sound intensities are heterogenous
timing matters: A1 responses to pure tones are modulated by the frequency ordering of preceding tones

A1 preferred frequency map (tonotopy)
preferred frequency = pitch for which amplitude necessary to give a response is lowest

A1 preferred ‘sweep direction’ map
preferred direction = ordering (low→high vs. high→low) of frequencies in a frequency sweep that produces the strongest response to the preferred frequency
history-dependence of A1 response fields: order-dependent excitation
history-dependence of A1 response fields: order-dependent suppression
temporal dependence of response to preferred frequencies means that auditory ‘objects’ can be registered by the patterns of firing of A1 neurons

vocalization of a monkey can be considered an auditory object (similar, in principal, to a spoken word)

both the ordering of tones and their temporal relationships alter A1 responses
bat echolocation: finding and tracking the location of prey through comparison of sound time signatures
What Can the Bat Tell from an Echo?

Distance to target – FM delay

Absolute target size - amplitude

Azimuth and elevation- ITD, ILD

Velocity of target- CF Doppler shift

Flutter of target (i.e., wing beat) – modulation of echo delay
The stiffness of the basilar membrane is best at 60 kHz and 62 kHz, which are the frequencies for membrane oscillation.
target proximity: utilization of the FM component delay

bat cortex area 4 contains neurons which recognize the FM component of a call AND register its delay from the time of the call
target speed: utilization of changes in pitch of the CF component between call and echo (i.e., detecting the Doppler shift in frequency)
take-homes:

• A1 neurons respond best to sounds at particular frequencies, but those responses can vary greatly according to:
  • sound amplitude – neurons may exhibit a linear increase in response to increasing amplitude of a preferred-frequency tone or may exhibit highest firing at some intermediate amplitude and less at lower and higher amplitudes
  • the temporal ordering of sound – neurons may exhibit very different responses to a preferred-frequency tone depending on the tones that precede and accompany it
• the basilar membrane of a bat has extra space devoted to regions responding to sounds near 60 kHz (in the range of its calls) – in this sense, it can be considered the bat’s auditory fovea
• bats use long ‘CF’ calls to assess Doppler shift and, in turn, the movement speed of their prey
• bats use shorter ‘FM’ sweeps to assess their proximity to their prey
• prey size can be determined by the echo amplitude (closer = louder)