Overview of Questions

- What is it that makes sounds high pitched or low pitched?
- How do sound vibrations inside the ear lead to the perception of different pitches?
- How are sounds represented in the auditory cortex?
Pressure Waves and Perceptual Experience

- Two definitions of the word “sound”
  - Physical definition - sound is *pressure changes* in the air or other medium
  - Perceptual definition - sound is the *experience* we have when we hear

Sound Waves

- Loud speakers produce sound by
  - The diaphragm of the speaker moves out, pushing air molecules together
  - The diaphragm also moves in, pulling the air molecules apart
  - The cycle of this process creates alternating high- and low-pressure regions that travel through the air
Sound Waves

- Pure tone - created by a sine wave
  - Amplitude: difference in pressure between high and low peaks of wave
Frequency and Pitch

The psychological experience of *pitch* is related to the temporal *frequency* of vibrations of the air hitting the eardrum.

Doubling the frequency increases the pitch by one octave. The tone *chroma* is the same.

Perception of *amplitude* is *loudness*

Decibel (dB) is used as the measure of loudness

Number of dB = 20 \log_{10}(p/p_o)

The decibel scale relates the amplitude of the stimulus to the psychological experience of loudness
Table 11.1 | Relative amplitudes and decibels for environmental sounds

<table>
<thead>
<tr>
<th>Sound</th>
<th>Relative amplitude</th>
<th>Decibels (dB)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Barely audible (threshold)</td>
<td>1</td>
<td>0</td>
</tr>
<tr>
<td>Leaves rustling</td>
<td>10</td>
<td>20</td>
</tr>
<tr>
<td>Quiet residential community</td>
<td>100</td>
<td>40</td>
</tr>
<tr>
<td>Average speaking voice</td>
<td>1,000</td>
<td>60</td>
</tr>
<tr>
<td>Express subway train</td>
<td>100,000</td>
<td>100</td>
</tr>
<tr>
<td>Propeller plane at takeoff</td>
<td>1,000,000</td>
<td>120</td>
</tr>
<tr>
<td>Jet engine at takeoff (pain threshold)</td>
<td>10,000,000</td>
<td>140</td>
</tr>
<tr>
<td>Spacecraft launch at close range</td>
<td>100,000,000</td>
<td>160</td>
</tr>
</tbody>
</table>
Range of Hearing

- Human hearing range - 20 to 20,000 Hz (dogs 40KHz, cats 50KHz)
- Audibility curve - shows the threshold of hearing
  - Changes on this curve show that humans are most sensitive to frequencies in the range of 2,000 to 4,000 Hz

Auditory response area (blue) falls between the audibility curve (green) and the threshold for feeling (blue)
Range of Hearing

- Equal loudness curves - determined by using a standard 1,000 Hz tone
  - Almost equal loudness at 80 dB
  - High and low frequencies sound softer at 40 dB than the rest of the tones in the range
Hearing loss compared to 20 year olds

Standard NTSC televisions ‘whine’ at 15,735 Hz. Can you hear it?

Environmental noise affects hearing. Easter Island residents who spent more years off of the relatively quiet island had relatively worse hearing.
Additive synthesis - process of adding harmonics to create complex sounds

(a) 

(b) 

(c) 

(d)
Sound Quality: Timbre

- All other properties of sound except for loudness and pitch constitute timbre
- Timbre is created partially by the multiple frequencies that make up complex tones
  - Fundamental frequency is the first (lowest) harmonic
  - Musical tones have additional harmonics that are multiples of the fundamental frequency

![Guitar](image)

![Time graphs](image)
Sound Quality: Timbre

- Frequency spectrum - display of harmonics of a complex sound
- Attack of tones - buildup of sound at the beginning of a tone
- Decay of tones - decrease in sound at end of tone

Timbre

- Pure tone (262 Hz, C4)
- Tenor saxophone
  - $f = 262$ Hz, C4
- Trombone
  - $f = 262$ Hz, C4
- Piano
  - $f = 262$ Hz, C4
The Ear

- **Outer ear** - pinna and auditory canal
  - Pinna helps with sound location
  - Holds glasses on your head.
  - Auditory canal - tube-like 3 cm long structure
    - Protects the tympanic membrane at the end of the canal
    - Resonant frequency of the canal amplifies frequencies between 2,000 and 5,000 Hz
The Middle Ear

- 2 cubic centimeter cavity separating inner from outer ear
- It contains the three ossicles (the smallest bones in the body!)
  - Malleus - moves due to the vibration of the tympanic membrane
  - Incus - transmits vibrations of malleus
  - Stapes - transmit vibrations of incus to the inner ear via the oval window of the cochlea
Function of Ossicles

- Outer and inner ear are filled with air
- Inner ear filled with fluid that is much denser than air
- Pressure changes in air transmit poorly into the denser medium
- Ossicles act to amplify the vibration for better transmission to the fluid
The Cochlea
- Fluid-filled snail-like structure set into vibration by the stapes
- Divided into the scala vestibuli and scala tympani by the cochlear partition
- Cochlear partition extends from the base (stapes end) to the apex (far end)
- Organ of Corti contained by the cochlear partition

The Organ of Corti
- Key structures
  - Basilar membrane vibrates in response to sound and supports the organ of Corti
  - Inner and outer hair cells are the receptors for hearing
  - Tectorial membrane extends over the hair cells
- Transduction at the hair cells takes place due to the interaction of these structures
Békésys' Place Theory of Hearing

- Frequency of sound is indicated by the place on the organ of Corti that has the highest firing rate
Békésys' Place Theory of Hearing

- Frequency of sound is indicated by the place on the organ of Corti that has the highest firing rate
- Békésy determined this in two ways
  - Direct observation of the basilar membrane in a cadaver
  - Building a model of the cochlea using the physical properties of the basilar membrane

Békésys' Place Theory of Hearing

- Envelope of the traveling wave
  - Indicates the point of maximum displacement of the basilar membrane
  - Hair cells at this point are stimulated the most strongly leading to the nerve fibers firing the most strongly at this location
  - Position of the peak is a function of frequency
Békésy’s Place Theory of Hearing

• Physical properties of the basilar membrane
  – Base of the membrane (by stapes) is
    • 3 to 4 times narrower than at the apex
    • 100 times stiffer than at the apex
  • Both the model and the direct observation showed that the vibrating motion of the membrane is a traveling wave

Evidence for Place Theory

• Tonotopic map
  – Cochlea shows an orderly map of frequencies along its length
    • Apex responds best to low frequencies
    • Base responds best to high frequencies

Tonotopic map of the guinea pig cochlea.
Updating Békésy’s Place Theory

- Békésy used unhealthy basilar membranes and his results showed no difference in response for close frequencies that people can distinguish.
- New research with healthy membranes show that the entire outer hair cells respond to sound by slight tilting and a change in length
  - This is called the motile response and helps to amplify action on the membrane
Hearing becomes less sensitive with age, particularly for high frequencies.

Environmental noise affects hearing. Easter Island residents who spent more years off of the relatively quiet island had relatively worse hearing.
Response of Basilar Membrane to Complex Tones

- Fourier analysis - mathematic process that separates complex waveforms into a number of sine waves
- Research on the response of the basilar membrane shows the highest response in auditory nerve fibers with characteristic frequencies that correspond to the sine-wave components of complex tones
- Thus the cochlea is called a frequency analyzer

The Cochlea automatically breaks down complex tones into their component frequencies – it’s performing Fourier Analysis.
**Effect of the Missing Fundamental**

- The fundamental frequency is the lowest frequency in a complex tone
- When the fundamental and other lower harmonics are removed, the perceived pitch is the same, but the timbre changes
- The pitch perceived in such tones is called periodicity pitch

![400 Hz Diagram](image)

**Missing Fundamental: evidence against Place Theory**

- Pattern of stimulation on the basilar membrane cannot explain this phenomenon since removing the fundamental and harmonics creates different patterns
- Periodicity pitch is perceived even when the tones are presented to two ears

![Missing Fundamental Diagram](image)
Neural Signals for Frequency

- There are two ways nerve fibers signal frequency
  - *Which* fibers are responding
    - Specific groups of hair cells on basilar membrane activate a specific set of nerve fibers (*Bekesy*)
  - *How* fibers are firing
    - Rate or pattern of firing of nerve impulses
Timing of Neural Firing and Frequency

- **Phase locking**
  - Nerve fibers fire in bursts
  - Firing bursts happen at or near the peak of the sine-wave stimulus
  - Thus, they are "locked in phase" with the wave
  - Groups of fibers fire with periods of silent intervals creating a pattern of firing

![Graphs showing phase locking](image-url)
Two tone suppression

- low level test tone is presented
- Masking tones are presented with frequencies above and below the test tone
- Measure the level of each masking tone needed to eliminate the perception of the test tone
- Assumption is that the masking tones must be causing activity at same location as test tone

Can you hear the 400Hz tone?

- 400 Hz
- 400 & 500 Hz
- 400 & 2000 Hz
Firing rate plotted against sound intensity for six auditory nerve fibers:
Pathway from the Cochlea to the Cortex

- Auditory nerve fibers synapse in a series of subcortical structures
  - Cochlear nucleus
  - Superior olivary nucleus (in the brain stem)
  - Inferior colliculus (in the midbrain)
  - Medial geniculate nucleus (in the thalamus)
  - Auditory receiving area (A1 in the temporal lobe)
Auditory Areas in the Cortex

- Hierarchical processing occurs in the cortex
  - Neural signals travel through the core, then belt, followed by the parabelt area
  - Simple sounds cause activation in the core area
  - Belt and parabelt areas are activated in response to more complex stimuli made up of many frequencies
Perceiving Pitch and Complex Sounds

• Tonotopic maps are found in A1
  – Neurons that respond better to low frequencies are on the left and those that respond best to high frequencies are on the right
  – However, early research did not show a direct relationship between pitch perception and the tonotopic map

Recent Evidence of Pitch Perception in A1

• Effect of training on tonotopic maps
  – Owl monkeys were trained to discriminate between two frequencies near 2,500 Hz
  – Trained monkeys showed tonotopic maps with enlarged areas with neurons that responded to 2,500 Hz compared to untrained monkeys
**Masking**

- The amplitude needed to hear a test tone is measured as a function of the bandwidth of a noise mask.
- Assumption is that when the detection curve levels off, the masking noise is no longer affecting the neurons responsible for detecting the test tone.
What and Where Streams for Hearing

- **What** or ventral stream starts in the anterior portion of the core and belt and extends to the prefrontal cortex
  - It is responsible for identifying sounds
- **Where** or dorsal stream starts in the posterior core and belt and extends to the parietal and prefrontal cortices
  - It is responsible for locating sounds
- Evidence from neural recordings, brain damage, and brain scanning support these findings

Does auditory cortex respond to visual stimuli in deaf observers?

Found area that activated to music/white noise in the hearing (amplitudes significantly > 0)

Projected that area onto hearing, deaf & CODAs
Defining auditory ROIs

+ scanner noise

(scanner noise)

(done in hearing subjects only)

auditory ROI
Differentially activated by visual input in the deaf
Caused by auditory deprivation, not sign-language

- Visual stimulus
- Auditory stimulus

% signal change

DEAF  HEAR  CODA
Cochlear Implants

- Electrodes are inserted into the cochlea to electrically stimulate auditory nerve fibers
- The device is made up of
  - A microphone worn behind the ear
  - A sound processor
  - A transmitter mounted on the mastoid bone
  - A receiver surgically mounted on the mastoid bone

Cochlear Implants

- Implants stimulate the cochlea at different places on the tonotopic map according to specific frequencies in the stimulus
- These devices help deaf people to hear some sounds and to understand language
- They work best for people who receive them early in life or for those who have lost their hearing, although they have caused some controversy in the deaf community
**Auditory recovery - cochlear implant**

Activation of auditory cortex, and ability to understand speech declines with duration of deafness.

<table>
<thead>
<tr>
<th>Duration of deafness</th>
<th>CI D scores (years of training)</th>
</tr>
</thead>
<tbody>
<tr>
<td>6.5 yr</td>
<td>90% (3.8 yr)</td>
</tr>
<tr>
<td>6.5 yr</td>
<td>67% (1.1 yr)</td>
</tr>
<tr>
<td>11.2 yr</td>
<td>7% (1.4 yr)</td>
</tr>
<tr>
<td>20.3 yr</td>
<td>0% (1.9 yr)</td>
</tr>
</tbody>
</table>

Lee et al., Nature, 2001

![Graph showing speech ability and CI D scores](image)

**Speech ability**

Low metabolism in auditory cortex pre-implantation