Lecture 5

Audition

CogS17 * UCSD
Sound Waves

Increased Pressure  Decreased Pressure  Atmospheric Pressure

Motion of air molecules associated with sound.

Propagation of sound
Frequency = \# Cycles / Second = Hz

Per speed at which molecules of medium (air) oscillate

1 second

6 cycles / sec = 6Hz
Frequency = # Cycles / Second = Hz

Per speed at which molecules of medium (air) oscillate

.001 second

6000 cycles / sec = 6000Hz = 6kHz
Phase = place in cycle of condensation & rarefaction
**Amplitude** = Distance a given molecule of medium (air) travels during its oscillation

If distance < x meters = Low Amplitude (soft sound)

If distance > x meters = High Amplitude (loud sound)
Auditory Reception

Also called Tympanic Membrane
The Middle Ear

- Auditory ossicles:
  - Malleus (Hammer)
  - Incus (Anvil)
  - Stapes (Stirrup)

- Stabilizing ligaments

- External acoustic meatus

- Tympanic membrane

- Oval window

- Round window

- Tympanic cavity (middle ear)
Ossicles

Convert large vibrations of big **Tympanic Membrane** into smaller, but more powerful vibrations of **Oval Window**

Overcomes **IMPEDANCE MISMATCH**

Air molecules are easy to vibrate, but viscous **COCLEAR FLUID** molecules in Cochlea much harder to vibrate
The Cochlea
The Cochlea

Cross-Section of Cochlea

Tectorial Membrane
Within middle chamber,
Top of Organ of Corti

Basilar Membrane
Floor of middle chamber
& of Organ of Corti,
on which the Hair Cells
(Receptors) sit

Source: Hohmann and Schmuckli 1989.
Organ of Corti

Hair Cells
Auditory Receptors

Stand between Tectorial Membrane above, and Basilar Membrane below.

As membranes vibrate CILLIA (hairs) are bent >> release NT.
Hair Cells

Cilia

Mechanically Gated Channels in Hair Bundles

Tip link
Transduction in Hair Cells is **Potassium (K+)** based (No Na+)

**Cochlear Fluid is rich in Potassium**

When Cillia are bent, K+ gates are pulled opened
Higher Concentration of K+ OUTSIDE cell >> so K+ enters

This change in polarity opens Ca++ gates

Ca++ in, Neurotransmitter out

...a Graded response
Humans hear from 20 Hz to 20,000 Hz (or 20 kHz)

But, we make our most detailed discrimination between frequencies up to ~ 5kHz

The piano keyboard ranges from 27.5 Hz at low end to 4,186 Hz (~4.2 kHz) at high end
Coding for Frequency

- Place Coding
- Temporal (Rate) Coding
Place Coding
Place Coding

Basilar Membrane

BASE
Narrow & Stiff

APEX
Wide & Floppy
Place Coding

Basilar Membrane
(Time lapse image of oscillation)

Narrow & Stiff resonates to **HIGH** Frequencies

Wide & Floppy resonates to **LOW** Frequencies
The more the Basilar Membrane resonates, the farther it moves...

...the more the Cilia of the Hair Cells are BENT against the Tectorial Membrane...

...the more Neurotransmitter the Hair Cells release.
Place Coding

LOW Frequencies resonate APEX of cochlea

So, it is DISTRIBUTION of NT release along Basilar Membrane that codes for Frequency

HIGH Frequencies resonate BASE of cochlea
**Place Coding**

**High frequency sound** = more response from Base than Apex

**Low frequency sound** = more response from Apex than Base

**Mid frequency sound** = more response from Mid-Membrane
Hair Cells accommodate this with a graded response, responding to relative amounts of vibration along Basilar Membrane.

BUT Hair Cells communicate to Spiral Ganglions (whose axons make up the Auditory Nerve) which fire Action Potentials.

Refractory Period for Action Potentials limit how frequently Spiral Ganglions can fire! Maximum ~ 1000/second.

In addition to different "places" resonating more than others, **WHOLE** Basilar Membrane vibrates at rate of input (e.g. 3000 Hz >> 3000 oscillations/sec).

So how can they code for a 3000 Hz tone?!!
Temporal Coding  (Rate Coding)

ANSWER: No single Ganglion cell can! But a group of them working together CAN!!

3000 Hz tone

Spiral Ganglions (ANFs)

<table>
<thead>
<tr>
<th>SGa</th>
<th>Fiber a</th>
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<tbody>
<tr>
<td>SGb</td>
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<td>SGc</td>
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<td>SGd</td>
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All responding to SAME Hair Cell

Overall response from Auditory Nerve

Produces VOLLEYS of activity at rate of input (3000/sec)
Temporal Coding (Rate Coding)

**Volley Principle** – Depends on Ganglions being **Phase Locked**

Spiral Ganglions do not just fire when they are ready, but are locked to the PHASE of input (only fire ~PEAK)

In this way, Auditory Nerve produces VOLLEYS of activity at correct intervals
Localization - via Amplitude differences

"Head Shadow"
Head absorbs some of sound energy, so sound is louder at ear closer to source.

Works best with **Higher Frequencies** (shorter wavelengths) since lower frequencies pass around head, less likely to be absorbed.

- High frequency sounds have **short** wavelengths
- Low frequency sounds have **long** wavelengths
Localization - via Phase differences
Localization - via Phase differences

Works best with Lower Frequencies (longer wavelengths)

Small-headed animals do not use phase, since often ambiguous

Note PHASE difference at two ears
Localization - via **Timing** Differences

Each Cochlear Nucleus axon branches to synapse on one of many Superior Olive cells.
Localization - via **Timing** Differences

Axon from COCHLEAR NUCLEUS

Sound came to the **LEFT** ear first

**Superior Olive** (Medulla)

Axon from COCHLEAR NUCLEUS

**Right** Ear
Localization - via Timing Differences

If the RIGHT side of Superior Olive fires, sound came to the LEFT ear first.

Only when input from BOTH ears converges will Superior Olive fire.
Localization – via Timing Differences

Axon from COCHLEAR NUCLEUS

If LEFT side of Superior Olive fires, sound came to the RIGHT ear first

Sound came to the RIGHT ear first

Superior Olive (Medulla)

Axon from COCHLEAR NUCLEUS

Right Ear
Localization – via **Timing** Differences

If **MIDDLE** of **Superior Olive** fires, sound came to **BOTH** ears at same time.
Auditory Pathways

Begin with 

Hair Cells
(Receptors) in Cochlea
Hair Cells – Auditory Receptors

Cochlea

Organ of Corti

Source: Hohmann and Schmiedt 1989.
**Hair Cells – Auditory Receptors**

**Inner** Hair Cells

“Divergent” Connection 1:8

Spiral Ganglions

Axons make up Auditory Nerve

Cochlear Nucleus (in Medulla)

**Outer** Hair Cells

“Convergent” Connection 20:1

Spiral Ganglion

Cochlear Nucleus (in Medulla)

For Details (e.g. Diff Freqs)

NOT for Details (e.g. Amp)
Auditory Pathways

Monaural
i.e. each Auditory Nerve connects only to IPSI-lateral side
Cochlear Nucleus Cells

Each Spiral Ganglion synapses on **multiple** Cochlear Nucleus Cells

Spiral Ganglion (ANF)
Auditory Pathways

Fibers from Cochlear Nucleus go to IPSI-lateral and CONTRA-lateral Superior Olives in Cerebellum

Combining info from both ears allows for localization. Thus, these, and all subsequent connections, are Binaural.
Auditory Pathways

**Onset** signal from Cochlear Nucleus . . .

. . . is input to Superior Olive localization circuit
Auditory Pathways

From Superior Olives, connect to Inferior Colliculi in Midbrain

These communicate with Superior Colliculi (visual motion maps) and Tegmentum, to direct eyes to source of sound.
Auditory Pathways

From Inferior Colliculi to Medial Geniculate Nucleus (MGN) of Thalamus
MGN
Medial Geniculate Nucleus
MNEMONICS: Nuclei of the Thalamus

- **LGN** (Lateral Geniculate Nucleus)  
  - L is for Light (Visual)

- **MGN** (Medial Geniculate Nucleus)  
  - M is for Music (Auditory)

- **VPN** (Ventral Posterior Nucleus)  
  - VP is for Very Personal (Touch)

- **DMN** (Dorsal Medial Nucleus)  
  - DM is for Dog Muzzle (Smell)

- **VLN** (Ventro Lateral Nucleus)  
  - VL is for Victory Lap (Motor)

- **MDN** (Medial Dorsal Nucleus)  
  - MD is for Memory Doctor (Memory)

*Others?!*
Topological Maps in Auditory System

In the Auditory system, such Topological maps are called "Tonotopic Maps"

Distribution of activity across the Basilar Membrane ("Place-coded" frequency) is preserved up the pathway.

High frequency sound

High Frequency

Low Frequency

Basilar Membrane (Cochlea)

Spiral Ganglion (Cochlea)

Cochlear Nucleus (Medulla)

Superior Olive (Medulla)

Inferior Colliculus (Midbrain)

MGN (Thalamus)

A1 (Cortex)
Auditory Pathways

Auditory Cortex

From MGN to A1 (Primary Projection Area) in Medial Temporal Cortex
Primary Projection Area for Audition

On Medial face of Temporal Lobe, in Lateral Fissure
**A1** – Primary Projection Area for Audition in Cortex

**Topological Frequency Map**

- 500 Hz, High Amp
- 500 Hz, Low Amp
- 1600 Hz, High Amp

All cells in each column (through 6 layers, below each dot) have same preferred stimulus.
**A2** – Secondary Auditory Cortex

**A1** – Responds best to single frequency

**A2** – Responds best to changing frequency
Wernicke’s Area

Wernicke’s Area – Specialized for comprehending SPEECH

Interacts with Broca's Area in Prefrontal Cortex, for speech Production