COGS17 Neurobiology of Cognition

Lecture 5: **Perception: Audition**

ANATOMY OF AUDITORY SYSTEM

Pinna - Outer ear; individually distinct; We learn to use echoes in localization; Most mammals can orient pinna to sound

Auditory Canal - Air channel leading to. . . **Tympanic Membrane** (Eardrum)

Ossicles - 3 tiniest bones in body (*Malleus*/Hammer, *Incus*/Anvil, *Stapes*/Stirrup), jointed into a **lever system** that converts vibration of large Tympanic Membrane into high intensity vibration of**…**

Oval Window = a membrane at the Base of the upper chamber of the …

Cochlea = snail-shaped (coiled) tube w/3 fluid-filled chambers: top (*Scala Vestibuli*), mid (*S. Media*), bottom (*S. Tympani*)
- Fluid is vibrated by oscillation of *Stapes* against Oval Window
- Vibration travels from Base of top chamber to Apex (tip), around to Round Window at Base of bottom chamber, and back
- This sets up a vibration in the *Scala Media,* where **Transduction** (conversion of env energy into neural signal) occurs

ORGAN OF CORTI

- The floor of the central *Scala Media* (or "Cochlear Canal") is the **Basilar Membrane**, its ceiling is the **Tectorial Membrane**
  - The Auditory Receptor Cells - the **HAIR CELLS** - are located between these two membranes
  - This chamber is filled with a viscous, non-compressible, Potassium (K+) rich fluid called **Endolymph**
- Vibration causes Basilar Membrane to move up and down and Tectorial Membrane to move left and right
  - **Cilia** of Hair Cells (arranged short to long) are **bent** between these two membranes
    - If Cilia bent as little as 10^{-10} m = 0.1 nm = diameter of an atom, can trigger a response!
  - When bent toward longest cilium, K+ gates open, since K+ in higher concentration outside, **K+ enters cell**
    - NOTE: Unlike in a prototypical neuron, Na+ is NOT involved in this transduction, only K+
    - Influx of K+ **decreases polarity** from –60mV
      - => Chain reaction involving Second Messengers allows Ca++ to enter cell ==> release excitatory NT (**Glutamate**)
    - The farther the cilia are bent, the greater the impact on the polarity and thus the on the release of NT
  - When cilia bent toward shortest cilium, K+ leaves cell (per gradients) and Ca++ is actively pumped out, restoring **polarity**
    - Typically, Hair Cell potential oscillates (polarized/depolarized/polarized/etc), repeatedly releasing at least some NT
- So, Hair Cells show **graded** hypo-polarization and thus graded release of NT, depending on how far & often Cilia are bent
  => to **Spiral Ganglions** (**= ANFs** = Auditory Nerve Fibers) which may then fire **Action Potentials** along axons to Brain

CODING FOR FRQUENCY – Auditory Systems codes the freq of a sound in two ways: **Place Coding & Temporal Coding**

Place Coding: The physical structure of the **Basilar Membrane** influences the neurological response to incoming sound.
  - The **BASE** (near Oval Window) is narrow and stiff; *resonates* with/is most displaced by HIGH frequencies
  - The **APEX** (far end of Cochlea) is wide and floppy, *resonates* with/is most displaced by LOW frequencies
  - Places in-between *resonate* with/are most displaced by the respective "in-between" frequencies (mid by MID etc)
- The greater the displacement of the Basilar Membrane => the farther the Cilia located at that place will be bent
  => the more NT the Hair Cells will release => the more likely Spiral Ganglions will reach threshold for Action Potentials
- So, a given freq produces a place of max displacement (& max NT release) & adjacent places of less displacement (& less NT)
  - Thus, as always, stimulus is coded by relative distribution of activity across multiple cells = **Across Fiber Coding**
- Note that as many sounds have complex frequency profiles, there can often be multiple maxima
  - So, auditory (like visual) system does a **Fourier Analysis** of sound, filtering multiple, simple, component frequencies

Temporal Coding (or "Frequency Theory") for frequencies < 4 kHz
- Another physical feature of Basilar Membrane is that the input frequency affects the **Rate** at which the membrane vibrates
  - e.g. When play sound of 500 Hz, whole membrane moves up and down 500 times per second
    When play sound of 3000 Hz, whole membrane moves up and down 3000 times per second, etc…
      - Note: Membrane moves (is displaced) farther at some places than others, but at same rate thru-out
  - So, auditory system can *also* use rate of Action Potentials along Auditory Nerve to code for frequency
- But, altho we can discriminate between frequencies very well up to about 4000 Hz (note: highest piano key is 4186 Hz)
  Spiral Ganglions are limited to firing at most 1000 times/second because of their **Refractory Period**
  - So, how can Timing Code be used for frequencies above 1000 Hz if no cell can fire faster than that???
- Answer: **Volley Principle**: One cell can't, but several working in concert CAN! Another e.g. of **Across Fiber Coding**
  - e.g. For a 3000 Hz tone => a volley of activity from one subset of Spiral Ganglions is followed, 1/3000 sec later, by a volley from another subset (while first subset is recovering), followed by another, etc. etc.
    - This activity is **Phase Locked** such that the Ganglions can only fire at the same phase (e.g. peak) of the input freq
  - As a result, these volleys occur at a rate that corresponds to the rate of the input frequency

LOCALIZATION - Localization can use Intensity differences, Phase differences, or Timing differences to the two ears

- i.e. Just as in visual system, a disparity between the inputs to two receptors (2 eyes, 2 ears, etc) is used to perceive depth
- **Intensity Differences** Sound at ear closer to source is slightly more intense (louder) than at other ear, because of Head Shadow
  - Works best for higher frequencies, since these most likely to be absorbed by head
- **Phase Differences** For lower frequencies, can detect difference in peak vs. trough of wave reaching two ears
  - Peak = oscillating molecules most condensed Trough = oscillating molecules most rarefied – widely spread out
- **Timing Differences** to the two ears via "Interaural Time-Disparity Detectors" found in monkey Superior Olive (& A1)
  - e.g. If sound reaches right ear first, "Onset" cells in right Cochlear Nucleus fire before those in left Cochlear Nucleus
  - Onset signals **race** to same Superior Olive nucleus; Signal travels on axon with a branch to each Sup. Olive cell in array
    - e.g. If right signal arrives *long before* left, it travels farther along array toward left side where left signal soon enters
      - Since input from both right and left Onset cells are required to trigger a response from a Superior Olive cell, only a cell at the left of the array (in the above example) will fire, indicating sound source reached right ear first
    - If sound arrives *slightly before* other, right and left Onset signals will meet closer to center of Superior Olive array, etc.
    - If Onset signals arrive at Superior Olive at same time, meet in center of array, sound localized equi-distant from 2 ears
      - Note: Above for left/right distinction; Sound from ahead/behind disambiguated by other cues, e.g. Intensity diffs
- Thus, these detector cells respond to different ranges *and* directions of disparity in arrival time to the two ears.

AUDITORY PATHWAY Starts with two types of **Hair Cells** in Cochlea

- **Inner Hair Cells** (IHC)- about 3,500 per ear. Connectivity: **Divergent,** 1:Many (1 IHC: Up to 30, avg 8 Spiral Ganglions)
  - Responsible for coding frequency with little or no loss of information (highly redundant system)
- **Outer Hair Cells** (OHC)- about 12,000 per ear. Connectivity: **Convergent,** Many:1 (Avg ~20 OHC: 1 Spiral Ganglion)
  - Cannot encode detailed frequency info, but can convey some amplitude info

=> **Spiral Ganglions**, Axons of which form Auditory Nerve (part of 8th Cranial Nerve) also called Auditory Nerve Fibers (**ANF**s)

- Note, no Lateral Inhibition in Cochlea, but can get Negative Feedback (Inhibition) from downstream Superior Olive

=> **Cochlear Nucleus** (in Medulla) - **Monaural** site (Left Cochlear Nucleus receives from left ear only, right from right only)

- Also, each Spiral Ganglion has up to 5 branches that synapse onto diff Cochlear Nucleus cells; Begin sub-pathways for diff info
  - That is, a sequence of Action Potentials from a single Spiral Ganglion might be:
    - e.g. Faithfully reproduced by a "**Primary Like**" Cochlear Nucleus cell (e.g. for preserving Tonotopic Map)
    - e.g. Transformed into a continually increasing graded response by a "**Build-Up**" cell (e.g. for Amplitude?)
    - e.g. Transformed into a single onset signal by an "**Onset**" Cochlear Nucleus cell (e.g. for Localization – see above)

=> **Superior Olive** (also in Medulla)- Some Cochlear Nucleus axons cross-over to contra-lateral Superior Olive, others to ipsi-lateral

- So, this is first **Biaural** site along pathway (i.e. info from both ears is first combined here); Critical for **localizing** (see above)

=> **Inferior Colliculus** (in Tectum of Midbrain) - These, like all subsequent sites along pathway, are binaural

- Some from contra-lateral Cochlear Nucleus; Most from ipsi-lateral Superior Olive
- Inferior Colliculus integrates with visual info in Superior Colliculus, help map source of sight/sound

=> **Medial Geniculate Nucleus** (**MGN**) of Thalamus includes **Tonotopic Map** (as do other previous & subsequent sites)

- i.e. Cells that respond to highest frequencies next to cells that respond to medium-high, next to medium, etc.

=> **A1** (Primary Projection Area, along Lateral Sulcus of Temporal Cortex)

- **Tonotopic/Amplitude Map** (High to low frequency : anterior to posterior; High to low amplitude : lateral to medial)
- Some cells respond best to simple (sine-wave) tones, others to more complex sounds (e.g. "sweeps" that rise or fall in freq)
- Other A1 areas respond per **location** of sound source (depends on comparing info to two ears – see above)

=> **A2** (Secondary Auditory Cortex, also in Temporal Lobe) - Most respond best to **complex** sounds (familiar noises, speech sounds)

- Damage to A2 not necessarily result in deafness, but **Auditory Agnosia** = inability to recognize/identify familiar sounds

=> Higher Auditory – Processes complex patterns; Integrates auditory input with other perceptual and cognitive activity

- e.g. **Wernicke's Area** for comprehension of speech, esp in left hemisphere - e.g. Music, esp in right hemisphere

NOTE: Auditory Pathway has much more **sub**-cortical processing than Visual; Cortical mainly for complex combos, sequences

- e.g. Unlike visual system, auditory localization is by primitive hindbrain (Medulla) for survival: "Orienting Reflex" (HEY!!!)