Auditory System: Introduction

- Sound: Physics; Salient features of perception.
  - Weber-Fechner laws, as in touch, vision
- Auditory Pathway: cochlea – brainstem – cortex
  - Optimal design to pick up the perceptually salient features
  - Coding principles common to other sensory systems:
    - sensory or “place” maps,
    - receptive fields,
    - hierarchies of complexity.
  - Coding principles unique to auditory system: timing
  - Physiology explains perception
- fMRI of language processing
- Plasticity (sensory experience or external manipulation).
- Diseases:
  - Hearing impairment affects ~ 30 million in the USA

Sound: a tiny pressure wave

- Waves of compression and expansion of the air
  - (Imagine a tuning fork, or a vibrating drum pushing the air molecules to vibrate)
- Tiny change in local air pressure:
  - Threshold (softest sounds): $1 / 10^{10}$ Atmospheric pressure
  - Loudest sounds (bordering pain): $1 / 1000$ Atmospheric pressure
- Mechanical sensitivity

Pitch (Frequency): heard in Octaves

- PITCH: our subjective perception is a LOGARITHMIC FUNCTION of the physical variable (frequency). Common Principle
- Pitch perception in OCTAVES: “Equal” intervals actually MULTIPLES.
- Two-tone discrimination: like two-point discrimination in the somatosensory system. Proportional to the frequency (~ 5%).
- Weber-Fechner Law
- WHY? Physiology: “place” coding for frequency coding in cochlea up to cortex; sizes of receptive fields. Just like somatosensory system
Complex sounds: Multiple frequencies

- Natural sounds:
  - multiple frequencies (music: piano chords, hitting keys simultaneously; speech)
  - constantly changing (prosody in speech; trills in bird song)
- Hierarchical system, to extract and encode higher features (like braille in touch, pattern motion in vision)

Loudness: Huge range; logarithmic

- Why DECIBELS?
- LOUDNESS perception: also LOGARITHM of the physical variable (intensity).
  - Fechner (1860) noticed: “equal” steps of perceived loudness actually multiples of each other in intensity. Logarithmic.
  - Defined: log scale Decibels:
    - $10 \log (I/I_0)$
    - Threshold: 0 dB: (1/10 atmospheric pressure)
    - Max: 10^13 larger in amplitude, 10^10 in power
    - HUGE range.
- Encodes loudness
- Adapts to this huge range

Timing: Used to locate sound sources

- Not PERCEIVED directly, but critical for LOCATING sources of sound in space:
  - Interaural Time Difference (ITD) as a source moves away from the midsagittal plane.
  - Adult humans: maximum ITD is 700 microseconds.
  - We can locate sources to an accuracy of a few degrees. This means we can measure ITD with an accuracy of ~ 10 microseconds.
  - Thus, auditory system needs to keep track of time to the same accuracy.
  - Unique to auditory system (vs. visual or touch)
**Auditory System: Ear**

- **Ear**
  - **Middle Ear**
    - Engineering; diseases
      - Perfect design to transmit tiny vibrations from air to fluid inside cochlea
      - Stapedius muscle: damps loud sounds, 10 ms latency.
      - CONDUCTIVE (vs. SENSORINEURAL) hearing loss
        - Scar tissue due to middle-ear infection (otitis media)
        - Ossification of the ligaments (otosclerosis)
      - Rinne test: compare loudness of (e.g.) tuning fork in air vs. placed against the bone just behind the auricle.
      - Surgical intervention usually highly effective

**Middle Ear: Engineering; diseases**

**Inner ear: Cochlea**

- 3 fluid-filled cavities
- Transduction: organ of Corti: 16,000 hair cells, basilar membrane to tectorial membrane
Basilar Membrane

- Incompressible fluid, dense bone (temporal).

Basilar Membrane: tonotopy, octaves

- Thick & taut near base
- Thin & floppy at apex
- Piano strings, or xylophone (vibraphone).
- Tonotopic PLACE map
- LOGARITHMIC: 20 Hz -> 200 Hz -> 2kHz -> 20 kHz, each 1/3 of the membrane
- Two-tone discrimination
- Complex sounds
- Timing

Organ of Corti
Organ of Corti

- Inner hair cells: single row, ~3500 cells, stereocilia free in fluid.
- Outer hair cells: 3 (to 4) rows, totalling ~12000, stereocilia embedded in gelatinous overlying tectorial membrane
- From basilar membrane vibration, adjacent hair cells differ ~0.2% in CHARACTERISTIC FREQUENCY (freq at which most sensitive).
  (Piano strings: 6% apart)

Transduction: inner hair cells

- Inner hair cells: MAIN SOURCE of afferent signal in auditory (VIII) nerve. (~10 afferents per hair cell)
- Outer hair cells: primarily get EFFERENT inputs. Control stiffness, amplify membrane vibration.
  (5,000,000 X range)

Auditory System: Hair Cells

Auditory system AND Vestibular system (semicircular canals)
Auditory System: Hair Cells

- Force towards kinocilium opens channels & K⁺, Ca²⁺ enter, depolarizing cell by 10s of mV. Force away shuts channels.
- Tip links (em): believed to connect transduction channels (cation channels on hairs)

Auditory System: Hair Cells

- Force towards kinocilium opens channels & K⁺, Ca²⁺ enter, depolarizing cell by 10s of mV. Force away shuts channels.
- Tip links (em): believed to connect transduction channels (cation channels on hairs)
- Cell depolarized / hyperpolarized
  - frequency: basilar membrane
  - timing: locked to local vibration
  - amplitude: loudness
- Neurotransmitter (Glu?) release
- Very fast (responding from 10 Hz — 100 kHz i.e. 10 µsec accuracy).

Hair Cells: Tricks to enhance response:

- To enhance frequency tuning:
  - Mechanical resonance of hair bundles: Like a tuning fork, hair bundles near base of cochlea are short and stiff, vibrating at high frequencies; hair bundles near tip of cochlea are long and floppy, vibrating at low frequencies.
  - Electrical resonance of cell membrane potential
- Synaptic transmission speed:
  - Synaptic density: for speed?
- Adapting to large displacement:
  - Ca²⁺-driven shift in tip link insertion site, myosin motor on actin in hair bundles.
Cochlear prosthesis

- Most deafness: SENSORI-NEURAL hearing loss.
- Primarily from loss of cochlear hair cells, which do not regenerate.
- Hearing loss means problems with language acquisition in kids, social isolation for adults.
- When auditory nerve unaffected: cochlear prosthesis electrically stimulating nerve at correct tonotopic site.

Auditory Nerve (VIII cranial nerve)

- Neural information from inner hair cells: carried by cochlear division of the VIII Cranial Nerve.
- Bipolar neurons, cell bodies in spiral ganglion, proximal processes on hair cell, distal in cochlear nucleus.

Auditory Nerve (VIII): Receptive fields

- Receptive fields: TUNING CURVE from hair cell
- “Labeled line” from “place” coding.
- Note: bandwidths equal on log frequency scale. Determines two-tone discrimination.
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- Loudness: spike rate (+ high-threshold fibers)
- Phase-locking to beyond 3 kHz
- Match: to frequency, loudness and timing

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Auditory System: Central Pathways

- Very complex. Just some major pathways shown.

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Auditory System: Central Pathways

General principles.
- Parallel pathways, each analysing a particular feature
- Streams separate in cochlear nucleus: different cell types project to specific nuclei. Similar to “what” and “where”
- Increasing complexity of responses
- Extensive binaural interaction, with responses depending on interactions between two ears. Unilateral lesions rarely produce unilateral deficits.
Cochlear Nucleus:

- VIII nerve: branches → 3 cochlear nuclei.
  - Dorsal Cochlear Nucleus (DCN)
  - Posteroventral Cochlear Nucleus (PVCN)
  - Anteroventral Cochlear Nucleus (AVCN)
- Tonotopy (through innervation order)
- Start of true auditory feature processing.
  - Distinct cell classes: stellate (encode frequency), bushy (encodes sound onset)
  - Different cell types project to different relay nuclei.

Auditory System: Central Pathways

Superior Olive: Locates sound sources

- **Medial Superior Olive:** interaural time differences:
  - Delay Lines: Coincidence detector (accurate up to 10 ms).
  - Timing code converted to place code.
  - Tonotopic, match across frequencies (better at low frequencies)
- Multiple sclerosis -> sound sources seem centered:
Superior Olive: locates sound sources

- Lateral Superior Olive: interaural intensity differences.
- Works best at high frequencies, the head casts a better shadow.
- Again, organized tonotopically to match across frequencies.

Auditory System: Midbrain

- From superior olives via lateral lemniscus to the inferior colliculus (IC).
  Separate path from DCN.
- Dorsal IC: auditory, touch
- Central Nucleus of IC: combines LSO, MSO inputs to 2-D spatial map; passed on to Superior Colliculus to match visual map
- Medial geniculate body: Principal nucleus; thalamic relay of auditory system. Tonotopic. Other nuclei: multimodal: visual, touch, role in plasticity?

Auditory Cortex: Complex patterns

- Superior temporal gyrus
- Like other sensory cortex:
  - Input layer: IV,
  - V: back project to MGB.
  - VI: back project to IC
- Some 15 distinct tonotopic areas (no timing info).
- Perpendicular to freq axis:
  - binaural interactions: EE, EI,
  - rising or falling pitch
  - connections across octaves
Auditory Cortex: Complex patterns

• Cortical cells: tuned to precise sequence of complex sounds

• Particularly, ethologically important sounds

• Marmoset A1 response to its own twitter call

Auditory Cortex: Complex patterns

• Birdsong brain centers: HVc response; “accents”

Auditory Cortex: “What vs. Where”

• Rhesus monkey: “bell” or secondary auditory cortex
Auditory System: Speech Areas

- Classical division on basis of aphasia following lesions:
  - Broca’s area: understand language but unable to speak or write
  - Wernicke’s area: speaks but cannot understand

- Current understanding: not uniform areas. Rather, category-specific with strongest activation proximal to the sensory or motor area associated with that category:
  - Words for manipulable objects (tools) activate reaching / grasping motor areas
  - Words for movement activate next to visual motion areas
  - Words for complex objects (faces) activate visual recognition areas


Central auditory lesions

- Pure word deafness (but can recognize environmental sounds)
- Specific aphasias (but visual language skills intact)
- Auditory extinction
Auditory System: Cortical Plasticity

- Damage to hair cells in cochlea: remaps neighboring frequencies.
- Train to discriminate tone frequency: increases area of trained frequency.
- Conditioning: pairing tone with stimulus
- Mechanism: corr with ACh release ?
- Pair a tone (9 kHz) with electrical stimulation of Nucleus Basalis (ACh)


Auditory System: Recapitulation:

- Sound: Physics, Perception
  - Characterizing: Frequency (pitch), Loudness
  - Timing (sound source location; discriminating complex sounds)
  - Weber-Fechner law: perceptions are logarithmic; just noticeable differences are proportional to the value (of loudness or pitch)
- Pathway: cochlea – brainstem – cortex
  - Ear: finely engineered to pick up sound
  - Parallel processing of pitch, loudness, timing, (complex sounds)
  - “Physiology explains perception”: receptive fields, tuning curves, place coding for pitch, loudness, sound source location. Similar to sensory systems of vision, touch
  - Higher along pathway -> more complex processing.
- fMRI of language processing
- Plasticity (sensory experience or external manipulation).