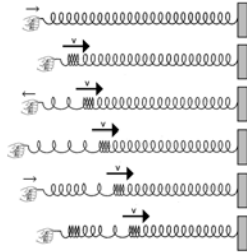


Auditory System: Introduction

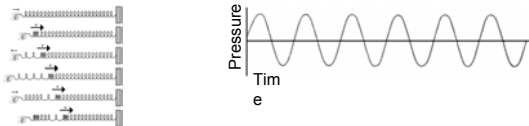
- Sound: Physics; Salient features of perception.
 - Weber-Fechner laws, as in touch, vision
- Auditory Pathway: cochlea – brainstem – cortex
 - Optimal design to pick up the perceptually salient features
 - Coding principles common to other sensory systems:
 - sensory or "place" maps,
 - receptive fields,
 - 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

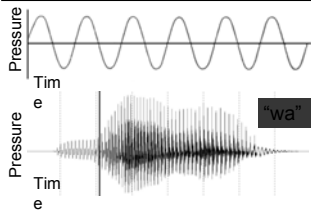


Pitch (Frequency): heard in Octaves



- 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

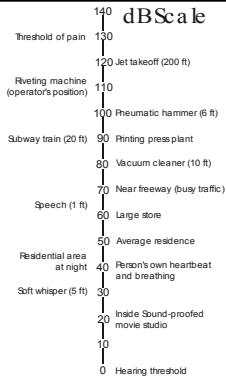
Complex sounds: Multiple frequencies



- 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)

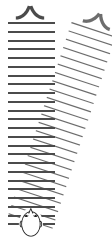
Loudness: Huge range; logarithmic

- 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: $10 \log_{10} (I / I_0)$
 - Threshold: 0 dB: $(1/10^{10})$ atmospheric pressure
 - Max: 5,000,000 larger in amplitude, 10^{13} in power
 - HUGE range.
- Encodes loudness
- Adapts to this huge range

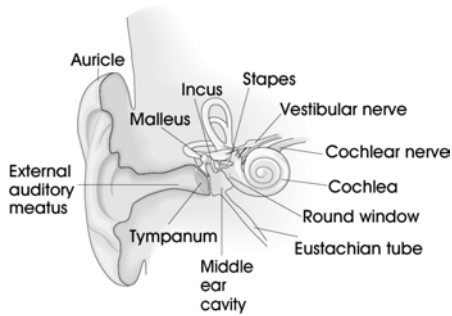


Timing: Used to locate sound sources

- 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



Principles of Neural Science (PNS) Fig 30-1

Middle Ear: Engineering; diseases



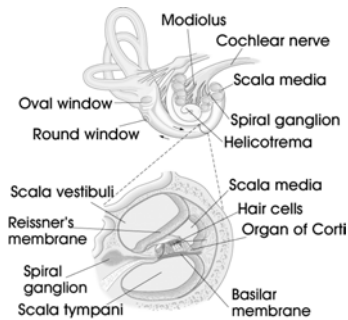
- Perfect design to transmit tiny vibrations from air to fluid inside cochlea
- Stapedius muscle: damps loud sounds, 10 ms latency.

- 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

Principles of Neural Science (PNS) Fig 30-2

Inner ear: Cochlea

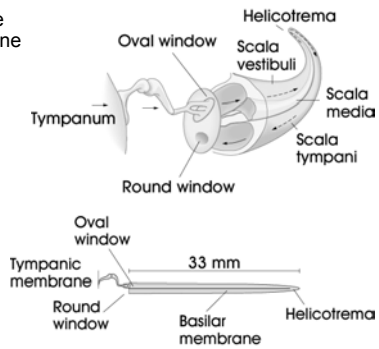
- 3 fluid-filled cavities
- Transduction: organ of Corti: 16,000 hair cells, basilar membrane to tectorial membrane



PNS Fig 30-2

Basilar Membrane

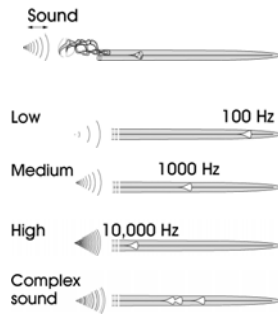
- Incompressible fluid, dense bone (temporal).



PNS, Fig 30-3

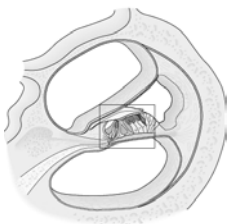
Basilar Membrane: tonotopy, octaves

- 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



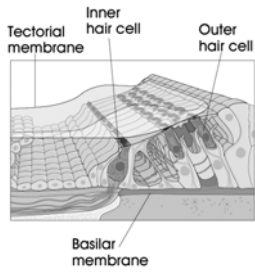
PNS Fig 30-3

Organ of Corti



Organ of Corti

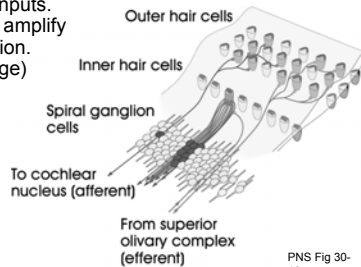
- Inner hair cells: single row, ~3500 cells, stereocilia free in fluid.
- Outer hair cells: 3 (to 4) rows, totalling ~ 12000, stereocilia embedded in gelatinous overlying tectorial membrane
- From basilar membrane vibration, adjacent hair cells differ ~0.2% in **CHARACTERISTIC FREQUENCY (freq at which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



PNS Fig 30-4

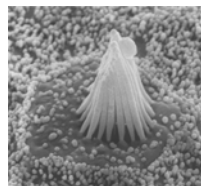
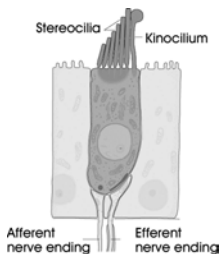
Transduction: inner hair cells

- 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)



PNS Fig 30-10

Auditory System: Hair Cells

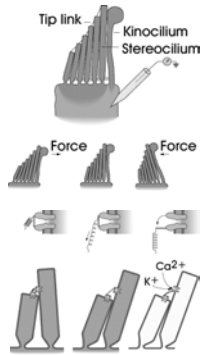


Auditory system AND Vestibular system (semicircular canals)

PNS Fig 31-1

Auditory System: Hair Cells

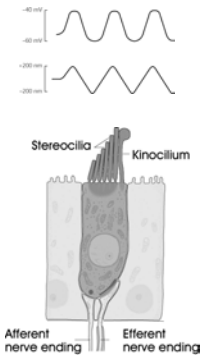
- Force towards kinocilium opens channels & K^+ , Ca^{2+} enter, depolarizing cell by 10s of mV. Force away shuts channels.
- Tip links (em): believed to connect transduction channels (cation channels on hairs)



PNS Fig 31-2, 31-3

Auditory System: Hair Cells

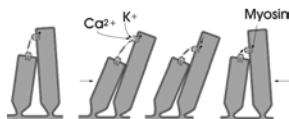
- Force towards kinocilium opens channels & K^+ , Ca^{2+} enter, depolarizing cell by 10s of mV. Force away shuts channels.
- Tip links (em): believed to connect transduction channels (cation channels on hairs)
- Cell depolarized / hyperpolarized
 - frequency: basilar membrane
 - timing: locked to local vibration
 - amplitude: loudness
- Neurotransmitter (Glu?) release
- Very fast (responding from 10 Hz – 100 kHz i.e. 10 μ sec accuracy).



PNS Fig 31-2

Hair Cells: Tricks to enhance response:

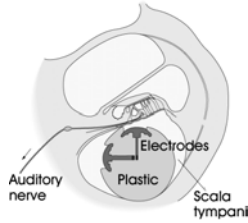
- To enhance frequency tuning:
 - Mechanical resonance of hair bundles: Like a tuning fork, hair bundles near base of cochlea are short and stiff, vibrating at high frequencies; hair bundles near the tip of the cochlea are long and floppy, vibrating at low frequencies.
 - Electrical resonance of cell membrane potential
- Synaptic transmission speed:
 - Synaptic density: for speed ?
- Adapting to large displacement:
 - Ca^{2+} -driven shift in tip link insertion site, myosin motor on actin in hair bundles.



PNS Fig 31-5

Cochlear prosthesis

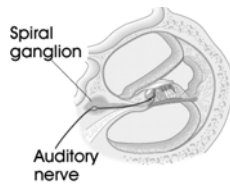
- Most deafness: **SENSORI-NEURAL** hearing loss.
- Primarily from loss of cochlear hair cells, which do not regenerate.
- Hearing loss means problems with language acquisition in kids, social isolation for adults.
- When auditory nerve unaffected: cochlear prosthesis electrically stimulating nerve at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



PNS Fig 30-18

Auditory Nerve (VIII cranial nerve)

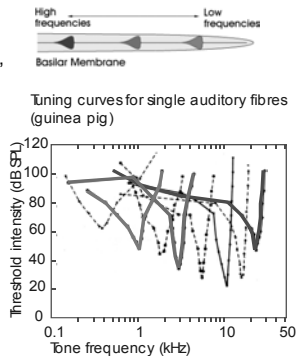
- Neural information from inner hair cells: carried by cochlear division of the VIII Cranial Nerve.
- Bipolar neurons, cell bodies in spiral ganglion, proximal processes on hair cell, distal in cochlear nucleus.



PNS Chapter 30

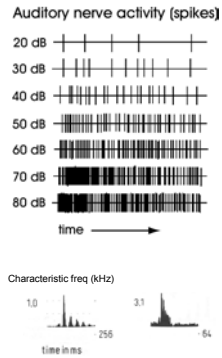
Auditory Nerve (VIII): Receptive fields

- Receptive fields: **TUNING CURVE** from hair cell
- "Labeled line" from "place" coding.
- Note: bandwidths equal on log frequency scale. Determines two-tone discrimination.



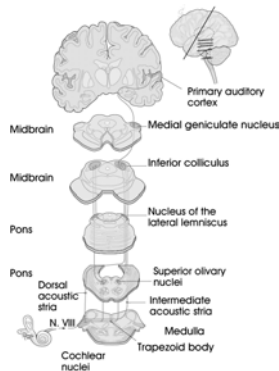
Auditory Nerve (VIII): Receptive fields

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



Auditory System: Central Pathways

- Very complex. Just some major pathways shown.

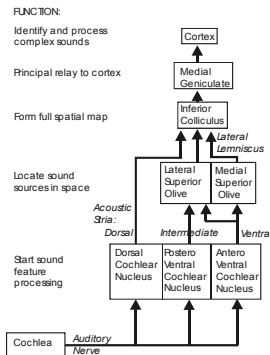


PNS Fig 30-12

Auditory System: Central Pathways

General principles.

- Parallel pathways, each analysing a particular feature
- Streams separate in cochlear nucleus: different cell types of 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.



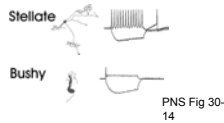
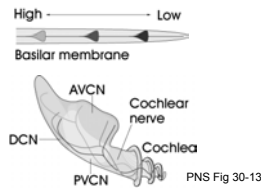
Cochlear Nucleus:

- VIII nerve: branches -> 3 cochlear nuclei.

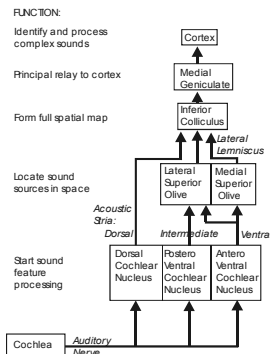
- Dorsal Cochlear Nucleus (DCN)
- Posteroventral Cochlear Nucleus (PVCN)
- Anteroventral Cochlear Nucleus (AVCN)

- 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.

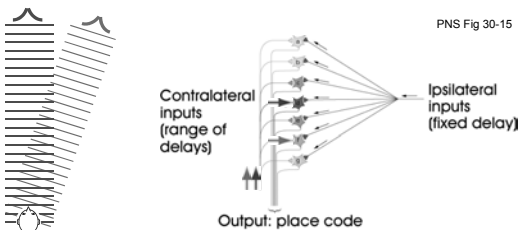


Auditory System: Central Pathways



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:



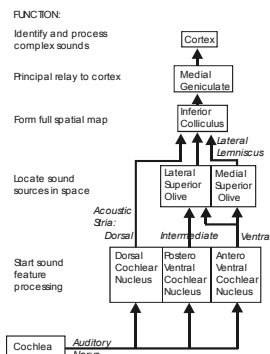
Superior Olive: locates sound sources

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

Principles of Neural Science, Chapter 30

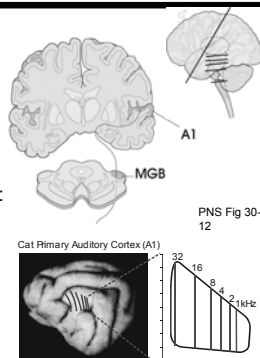
Auditory System: Midbrain

- 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?



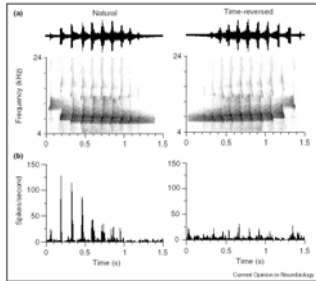
Auditory Cortex: Complex patterns

- 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).
- A1: Primary Auditory Cortex: logarithmic map of frequency.
- Perpendicular to freq axis:
 - binaural interactions: EE, EI,
 - rising or falling pitch
 - connections across octaves



Auditory Cortex: Complex patterns

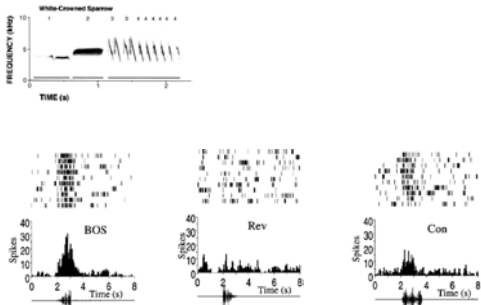
- Cortical cells: tuned to precise sequence of complex sounds
- Particularly, ethologically important sounds



- Marmoset A1 response to its own twitter call

A.A. Ghazanfar & M.D. Hauser: *Current Opinion in Neurobiology*, Vol 11: 712-720 (2001)

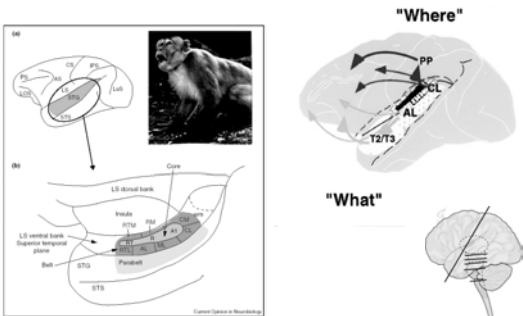
Auditory Cortex: Complex patterns



- Birdsong brain centers: HVC response; "accents"

F.E. Theunissen & A.J. Doupe: *J. Neurosci.* Vol 18: 3786-3802 (1998)

Auditory Cortex: "What vs. Where"



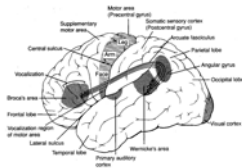
- Rhesus monkey: "belt" or secondary auditory cortex

J.P. Rauschecker & B. Tian: *Proc. Nat. Acad. Sci.* Vol 97: 11800-6 (2000)

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



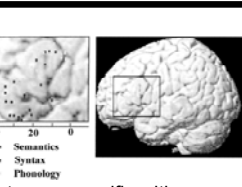
- Current understanding: not uniform areas. Rather, category-specific with strongest activation proximal to the sensory or motor area associated with that category:
 - Words for manipulable objects (tools) activate reaching / grasping motor areas
 - Words for movement activate next to visual motion areas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

Ref: fMRI of language: Susan Bookheimer, *Ann. Rev. Neurosci.* 25:151-88, 2002

Auditory System: Speech Areas

- Classical division on basis of aphasia following lesions:

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- Not monolithic areas. Rather, category-specific with strongest activation spatially proximal to the sensory or motor area associated with that category:
 - Words for manipulable objects (tools) activate reaching / grasping motor areas
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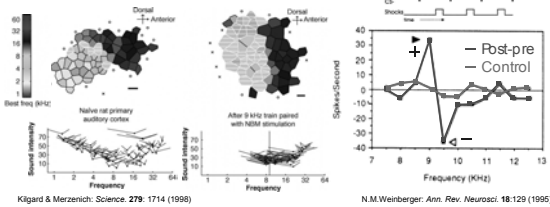
Ref: fMRI of language: Susan Bookheimer, *Ann. Rev. Neurosci.* 25:151-88, 2002

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).
