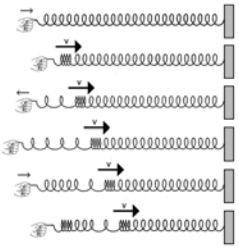
Auditory System: Introduction

- 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 + range

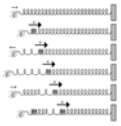


Pitch (Frequency): heard in Octaves

- PITCH: our subjective perception is a LOGARITHMIC FUNCTION of the physical variable (frequency). Common Principle
- Pitch perception in OCTAVES: "Equal" intervals actually MULITPLES.

Sound "Do" in musical scales:

C1. 32.703 Hz.
C2. 65.406.
C3. 130.81.
C4. 261.63. (middle C)
C5. 523.25.
C6. 1046.5.
C7. 2093.



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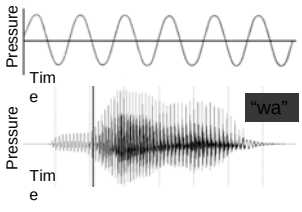
C7. 2093.

- Two-tone discrimination: like two-point discrimination in the somatosensory system. Proportional to the frequency (~ 5%).
- Weber-Fechner Law
- WHY? Physiology: "place" map for frequency coding from the cochlea up to cortex; sizes of receptive fields. Just like somatosensory system

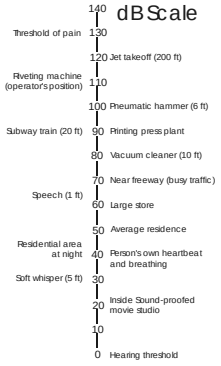
Complex sounds: Multiple frequencies



- Natural sounds:
  - multiple frequencies (music: piano chords, hitting keys simultaneously; speech). We hear it as a "whole" not parts.
  - 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)

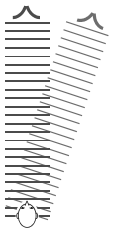
Loudness: Huge range; logarithmic

- 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 (Bel)
  - 10 $\log_{10}$ (I / I_{th}) Decibels:
  - 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 (like light intensity)



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 midsaggital 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)

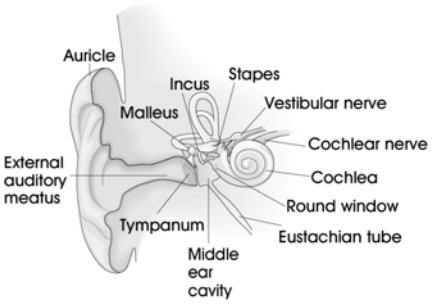


Auditory System: Demands

- Frequency (logarithmic, octave scale)
- Complex sounds: multiple & changing frequencies.
- Loudness (logarithmic scale; extending over a range of 5,000,000 in amplitude, i.e. 2.5 x 10^{13} in intensity)
- (properties analogous to touch and vision)

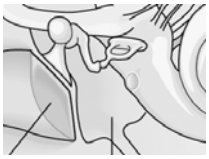
- Timing, to 10 microsecond accuracy

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.

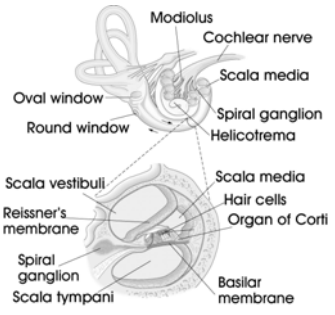
- CONDUCTIVE (vs. SENSORINEURAL) hearing loss
  - Scar tissue due to middle-ear infection (otitis media)
  - Ossification of the ligaments (otosclerosis)
- Rinne test: compare loudness of (e.g.) tuning fork in air vs. placed against the bone just behind the auricle.
- Surgical intervention usually highly effective

Principles of Neural Science, Chapter 30

Inner ear: Cochlea

- 3 fluid-filled cavities

- Transduction: organ of Corti: 16,000 hair cells, basilar membrane to tectorial membrane

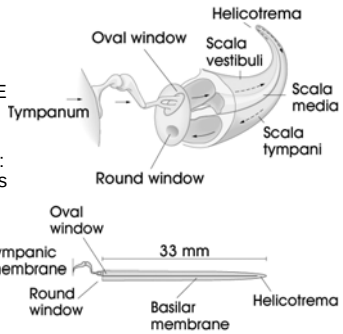


PNS Fig 30-2

Basilar Membrane

- Incompressible fluid, dense bone (temporal).
- Traveling wave (vibrations) IN THE FLUID

- Basilar membrane: Individual elements (vibraphone, not didgeridoo).



PNS, Fig 30-3

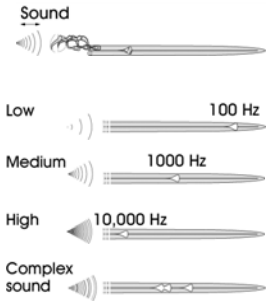
Basilar Membrane: tonotopy, octaves

- Thick & taut near base
- Thin & floppy at apex
- Couples with vibrating fluid to give local peak response.

PNS Fig 30-3

Basilar Membrane: tonotopy, octaves

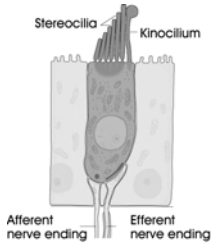
- Thick & taut near base
- Thin & floppy at apex
- Couples with vibrating fluid to give local peak response.
- Tonotopic PLACE map (...homunculus)
- LOGARITHMIC: 20 Hz -> 200 Hz -> 2kH -> 20 kHz, each 1/3 of the membrane
- Two-tone discrimination
- Timing

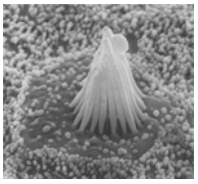


PNS Fig 30-3

Organ of Corti

Auditory System: Hair Cells



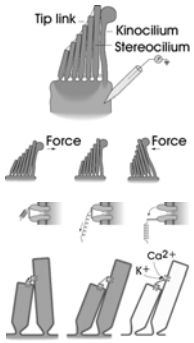


Auditory system AND Vestibular system (semicircular canals)

PNS Fig 31-1

Auditory System: Hair Cells

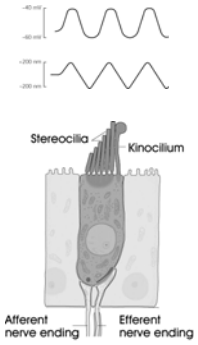
- Force towards kinocilium opens channels & K^+, Ca^{2+} enter, depolarizing cell by 10s of mV. Force away shuts channels.
- Tip links (em): believed to connect transduction channels (cation channels on hairs)



PNS Fig 31-2, 31-3

Auditory System: Hair Cells

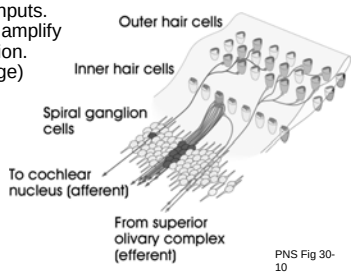
- Force towards kinocilium opens channels & K^+, Ca^{2+} enter, depolarizing cell by 10s of mV. Force away shuts channels.
- Tip links (em): believed to connect transduction channels (cation channels on hairs)
- Cell depolarized / hyperpolarized
  - frequency: basilar membrane
  - timing: locked to local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



PNS Fig 31-2

Hair Cells: Tricks to enhance response

- 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

Hair Cells: Tricks to enhance response

- 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)
- To enhance frequency tuning:
  - Mechanical resonance of hair bundles: Like a tuning fork, hair bundles of cells 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 (in mammals?)
  - An AMAZING feat of development.
- Synaptic transmission speed (10 μs):
  - Synaptic density: for speed? (normal synapse: 1 to 100s of ms)

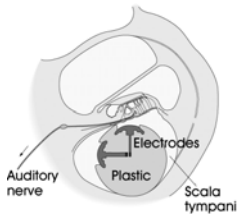
Ear: a finely tuned machine

Optimally engineered to:

- pick up the very faint vibrations of sound &
- extract perceptually relevant features
  - pitch
  - loudness
  - complex patterns
  - timing

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.

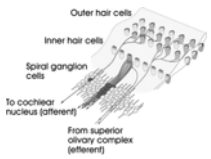


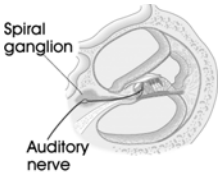
PNS Fig 30-18

Auditory Nerve (VIII cranial nerve)

- Neural information from inner hair cells: carried by cochlear division of the VIII Cranial Nerve.

PNS Chapter 30

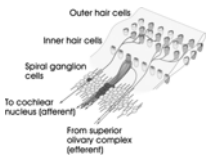


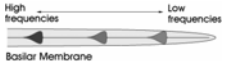


- Bipolar neurons, cell bodies in spiral ganglion, proximal processes on hair cell, distal in cochlear nucleus.

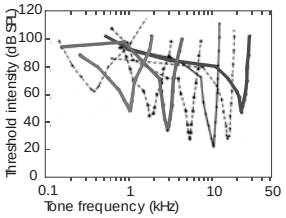
Auditory Nerve (VIII): Receptive fields

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



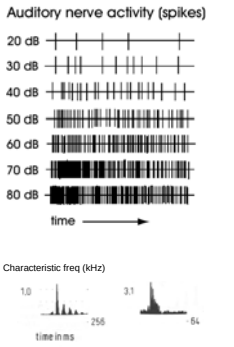


Tuning curves for single auditory fibres (guinea pig)



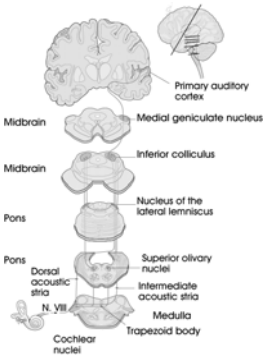
Auditory Nerve (VIII): Receptive fields

- 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.
- Extensive binaural interaction, with responses depending on interactions between two ears. Unilateral lesions rarely produce unilateral deficits.

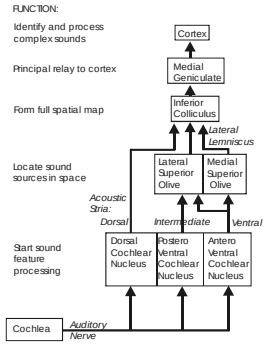


PNS Fig 30-12

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 (like vision, touch)



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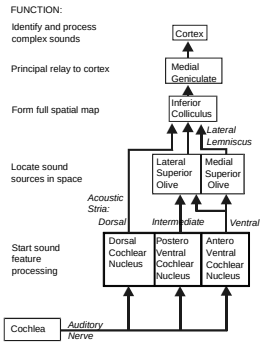
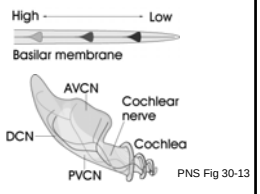
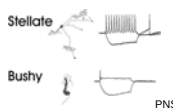


Cochlear Nucleus:

- 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.

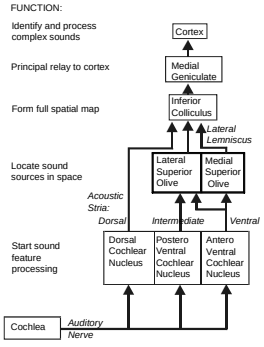


PNS Fig 30-13



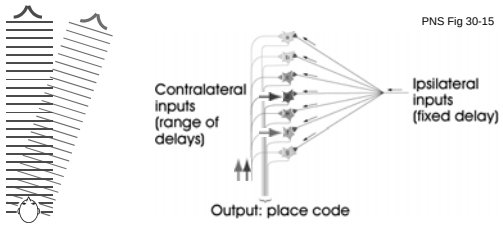
PNS Fig 30-14

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 for angular location.
  - Tonotopic: matching across frequency bands.
- Multiple sclerosis -> sound sources seem centered:



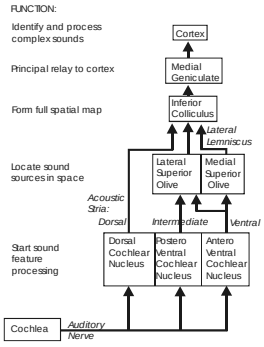
Superior Olive: locates sound sources

- 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?



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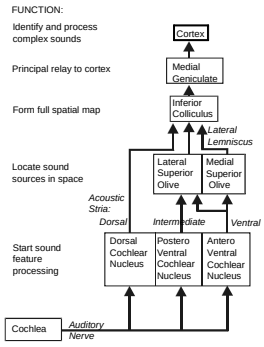
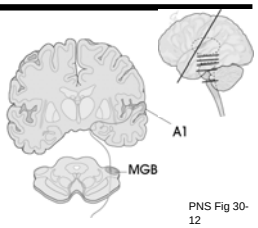
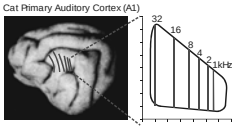


Auditory Cortex: Complex patterns

- Progressively more complex
- 15 distinct tonotopic areas.
- A1: Primary Auditory Cortex: Superior temporal gyrus
- Like other sensory cortex:
  - 6 layers
  - Input layer: IV,
  - V: back project to MGB.
  - VI: back project to IC
  - Cortical columns (map),
- Logarithmic map of frequency.
- Perpendicular to freq axis:
  - binaural interactions: EE, EI,
  - rising or falling pitch

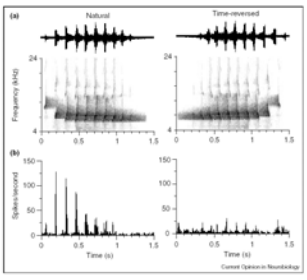


PNS Fig 30-12



Auditory Cortex: Complex patterns

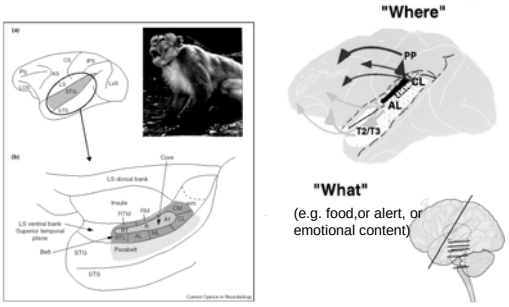
- Cortical cells: tuned to precise sequence of complex sounds
- Particularly, ethologically important sounds



- 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: “What vs. Where”

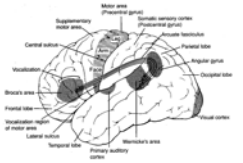


- Rhesus monkey: “belt” or secondary auditory cortex

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

Auditory System: Speech Areas

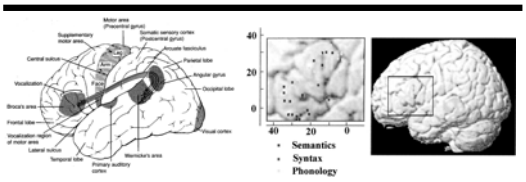
- Classical division on basis of aphasia following lesions:
  - Broca’s area: understand language but unable to speak or write
  - Wernicke’s area: speaks but cannot understand



- 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

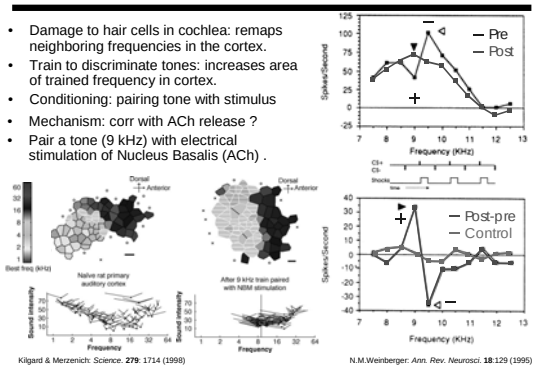


- Not monolithic areas. Rather, category-specific with strongest activation spatially proximal to the sensory or motor area associated with that category:
  - Words for manipulable objects (tools) activate reaching / grasping motor areas
  - Words for movement activate next to visual motion areas
  -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

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

Auditory System: Cortical Plasticity

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



Kilgard & Merzenich: *Science.* **279**: 1714 (1998)

N.M.Weinberger: *Ann. Rev. Neurosci.* **18**:129 (1995)

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)
  - Higher along pathway -> more complex processing.
  - “Physiology explains perception”: receptive fields, tuning curves, place coding for pitch, loudness, sound source location. Similar to sensory systems of vision, touch
- fMRI of language processing
- Plasticity (sensory experience or external manipulation).