Neuroscience 500

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The Auditory and Vestibular Systems

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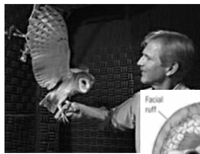
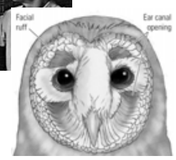
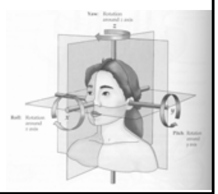
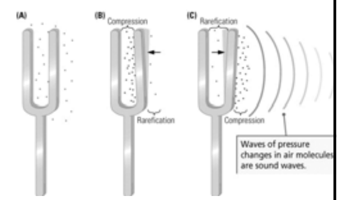






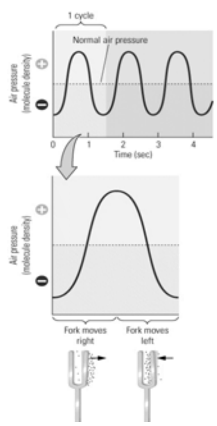
What is sound?

- Pressure waves generated by vibrating air molecules.
- Propagate in 3 dimensions
- Molecules of air alternatively compressed and released (rarefaction)



Features of sound waves

1. Amplitude (measured in dB) *Loudness*
2. Frequency (measured in Hz) *Pitch*
3. Waveform (e.g., simple versus complex). *Timbre*
4. Phase



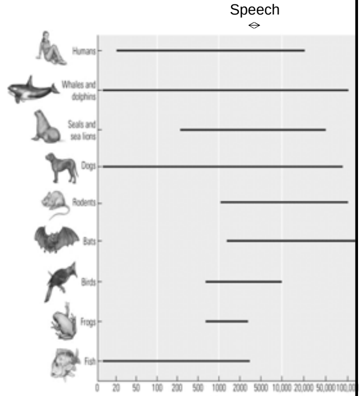
- 200 Hz
- 500 Hz
- 1 kHz
- 5 kHz
- 10 kHz
- 15 kHz
- 16 kHz
- 17 kHz
- 18 kHz
- 19 kHz
- 20 kHz

Capacity of auditory system. Part 1

Loudness can vary over a range of 120 dB (about 10^{12})

Sensitive to vibrations down to the diameter of an atom of gold

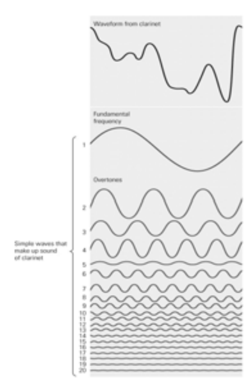
Frequency can vary between 20-20,000 Hz



Capacity of auditory system. Part 2

Most sounds and complex waveforms composed of multiple frequencies

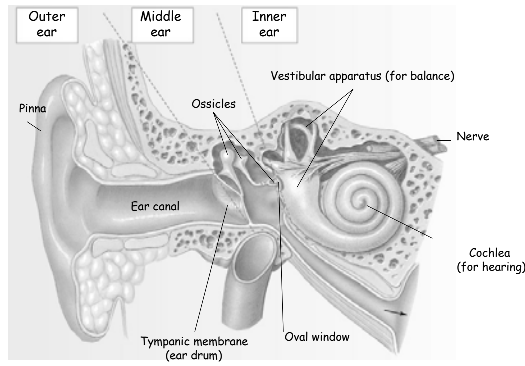
The auditory system performs a type of *Fourier Transform*, breaking such complex waveforms into the component frequencies



Capacity of auditory system. Part 3

- CNS can respond up to ~1,000 Hz max
- How then can the auditory system:
    1. Represent frequencies greater than 1,000 Hz?
    2. Represent loudness over a 120 dB range?
    3. Decode complex waveforms?

The human ear is a sense organ specialized for hearing and balance



Outer ear

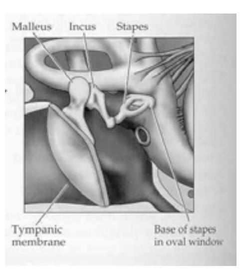
- Pinna
    - Helps direct sound into ear canal, amplifying certain frequencies (eg, 3kHz)
    - Aids in sound localization of vertical targets
- Auditory canal
    - Funnels and modulates incoming sounds
- Tympanic membrane (eardrum)
    - converts air pressure changes into mechanical vibrations

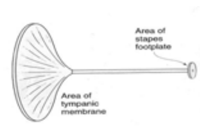
Middle ear

- Interface between air in outer ear and fluid in inner ear
- Fluids usual have a much higher *impedance* than air (~99% of sound waves in air reflect off water)
- The Middle Ear acts as an *impedance matcher*, so that sound waves in the air are changed into pressure waves in the inner ear fluid

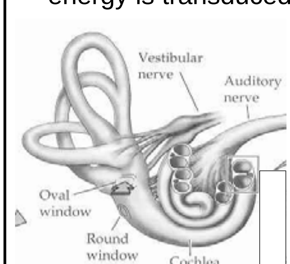
Middle ear

- Essentially an amplifier
- 3 small bones (the "ossicles": malleus, incus and stapes) transmit sound vibrations mechanically to the cochlea
- Amplification due to:
    - 1. Leverage (malleus moves more than stapes)
    - 2. Force focusing device (Tympanic area > stapes footplate)



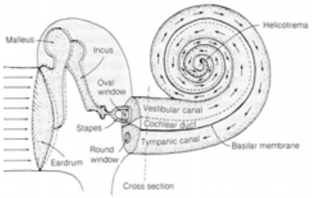


- The inner ear is where the mechanical energy is transduced into neural signals



- Inner ear has two main components:
    - cochlea (for hearing).
    - vestibular labyrinth
- Both are filled with endolymph, which has a high K+ concentration

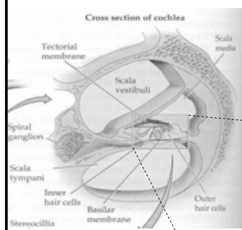
Transducing auditory signals:



- The cochlea has three canals separated by membranes
  - **scala vestibuli**
  - **scala tympani**
  - **scala media (cochlear duct)**
- **Basilar membrane** forms base of scala media

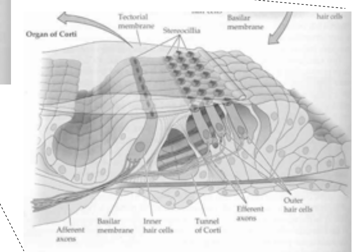
- Movement of stapes displaces **oval window**
- This sends a pressure wave, which is released at **round window**
- The pressure wave displaces the **basilar membrane**

The Organ of Corti



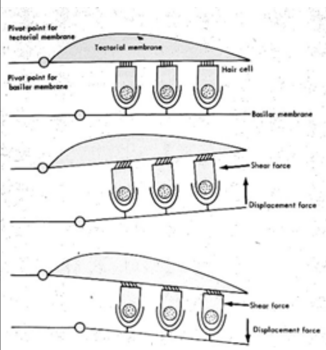
-Rests on basilar membrane

-Contains the **hair cells** receptors



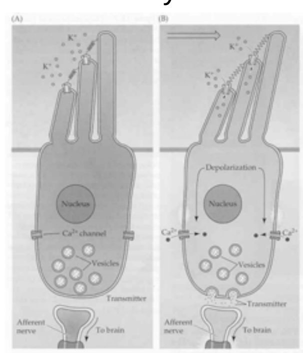
Stereocilia of hair cells embedded within ***Tectorial Membrane***

Auditory transduction:



- The shearing motion of the hair cells generates a neural signal in the auditory nerve

Inner Hair cell transduction: auditory and vestibular systems

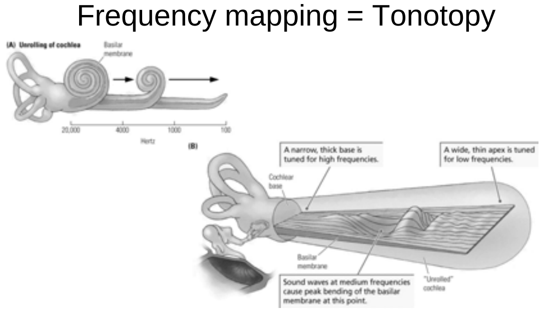


-Mechanically-linked K+ channels

-Bending of stereocilia towards kinocilium (largest one) opens channel, **depolarizing** hair cell, increasing neurotransmitter release

- Bending in opposite direction will **hyperpolarize** hair cell, decreasing neuotransmitter release

Frequency mapping = Tonotopy



Sound produces a travelling wave along the basilar membrane

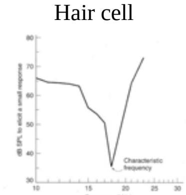
The location of maximum displacement varies with frequency

Tonotopy is maintained throughout auditory system

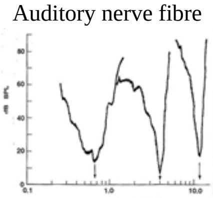
How does the brain encode high frequencies > 1kHz?

- Both hair cells and auditory nerve fibres respond best to a narrow range of frequencies
- Activation of a particular nerve fibre is **interpreted** at a particular frequency, regardless of rate of action potential

Hair cell



Auditory nerve fibre

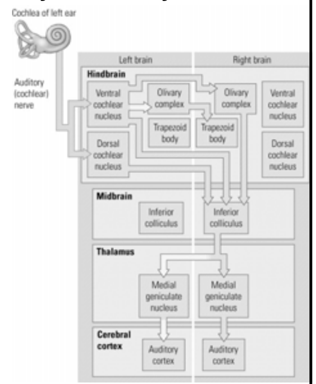


How does the brain represent loudness over a 120 dB range?

- Loudness coding cannot be a simple result of increases in neural firing rate
- Several other mechanisms:
  - Multiple sets of neurons with different thresholds
  - Recruitment of additional neurons as loudness increases

Central Auditory Pathways

- Ascending pathways pass through several different nuclei before reaching the cortex
- Parallel pathways
- All information leaving the ear projects bilaterally



How does the brain localize sound?

- Several cues available to localize sound direction
  - Interaural time differences
  - Interaural intensity differences
  - Pinna cues

Interaural time differences

- Sound takes longer to reach one ear than another
- Timing differences are typically very small (e.g., ~700 μs). Humans are sensitive to differences of around 10 μs (1 degree)
- Better for low frequency sounds < 3kHz
- Binaural “Coincidence detectors” in auditory brainstem

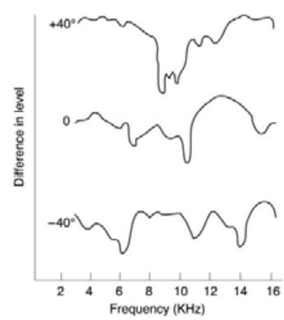
Interaural intensity differences

- Head “shadows” sound: greater differences for more lateralized sounds
- More effective for high frequency sounds > 3kHz
- Due to binaural interactions in auditory brainstem

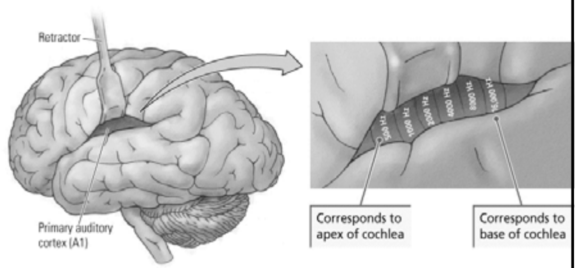
Pinna cues

- Time and intensity cues only give information about horizontal position, not the vertical plane
- The convolutions of the pinna sets up a characteristic pattern of reflections
- Sound stimuli *must* contain multiple frequencies

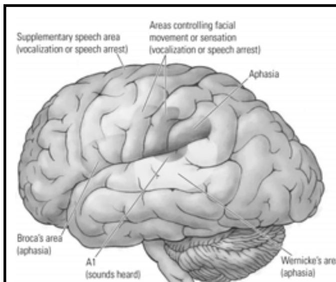
“Head-related transfer function”



Primary auditory cortex: Percepetion



- Located on superior temporal gyrus
- Tonotopically organized
- “Stripes” of neurons excited by both ears (“EE cells”), alternating with stripes excited by one ear and inhibited by the other (“EI cells”)

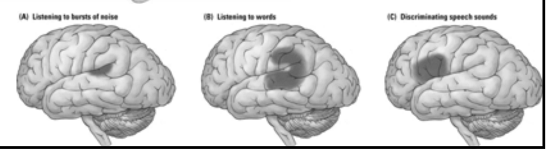


Aphasia = language disorder

Caused by focal brain lesions (e.g., strokes or head injury)

Wernike’s aphasia: impaired comprehension. “Nonsense” words

Broca’s aphasia: Non-fluent, effortful speech. Good comprehension



Wernicke’s aphasia

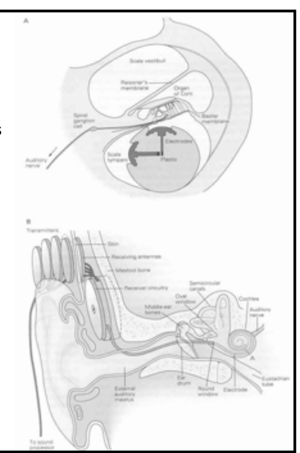
Broca’s aphasia

Types of hearing loss

1. Conductive: Sound is unable to be transmitted through outer or middle ear. A mechanical defect.
   - extremely loud sounds rupture eardrum or damage ossicles
   - infection fills middle ear with fluid
   - ear wax!
2. Sensorineural: damage to structures of inner ear that affects hair cells, or to auditory nerve (nerve deafness). A transductive and/or peripheral defect.
   - extremely loud sounds damage Organ of Corti
   - ototoxic drugs that damage hair cells
   - presbycusis (aging) due to atherosclerotic damage to microvasculature of inner ear
   - auditory nerve tumour
3. Central: Damage to auditory pathways upstream from cochlea. A defect in the Central Nervous system.
   - e.g., tumours or strokes in the central auditory pathways

Cochlear prosthetic

- Array of tiny electrodes implanted into scala tympani. Between 8-20 electrodes “wound” into cochlea
- Incoming sounds analyzed by receiver circuitry, and decomposed into frequency components
- Extracellular stimulation excites nearby auditory nerve fibers
- Exploits tonotopic organization of frequency
- Users must relearn the auditory world, but can have amazing long-term recovery of function.

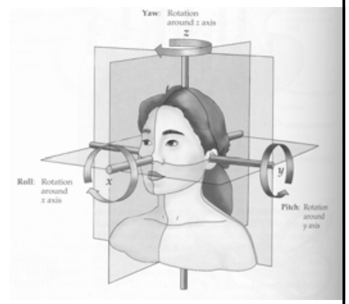


5 minute break??

The Vestibular system

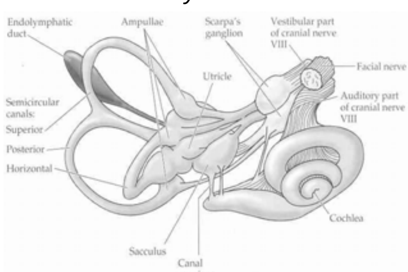
- Provides sense of balance and body position in space
- Bodies move in 6 degrees of freedom:
  - 3 rotational
  - 3 translational

How is this information derived from the vestibular organs?



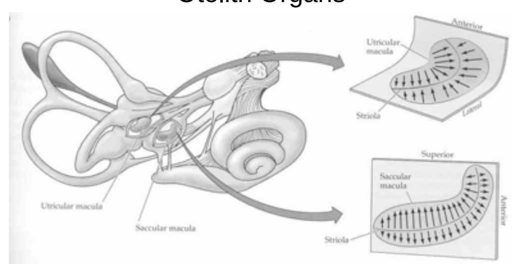
The sense of balance originates within the *Vestibular Labyrinth*

Each labyrinth consists of 2 *otolith organs* (the utricle and the saccule) and 3 *semicircular canals*



- Semi-circular canals: sensitive to angular rotations
- Otolith organs: sensitive to linear accelerations and static position of the head relative to gravity

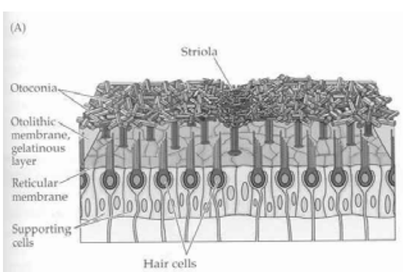
Otolith Organs



The otolith organs are two membranous sacs call the **utricle** and the **saccule**.

In each, a portion of the membrane is thickened (the **macula**) and contains the hair cells innervated by neurons of the 8th nerve

Otolith transduction



- The hairs of the hair cells project into the **otolithic membrane**, a gelatinous material embedded with calcium carbonate stones (**otoconia** = ear stones).
- Hair cell transduction in the vestibular organs is the same as in the cochlea

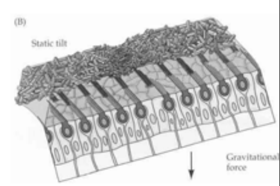
What bends the hairs?

At rest, the vestibular afferents have a baseline firing of ~100 Hz

When the head moves, the inertia of the crystals bends the hair cells in the opposite direction

When the head tilts, gravity "pulls" the crystals downwards

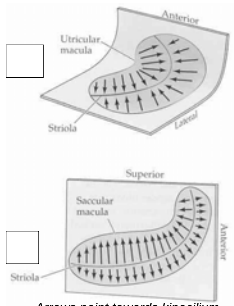
Rules of transduction similar to auditory system:
- Toward kinocilium → increase APs freq.
- Away from kinocilium → decrease AP freq.



A given vestibular afferent can therefore signal motion or tilt in ***two*** directions

Orientation of utricle and saccule

- With the head upright, the macula of the utricle senses horizontal translations (left/right and front/back)
- The macula of the saccule is on the side, and sense vertical translations (up/down and front/back).
- In each macula, the hair cells are oriented in all possible directions. All possible tilt or translation directions can therefore be represented across both sides of the head



Arrows point towards kinocilium

TILT-TRANSLATION AMBIGUITY

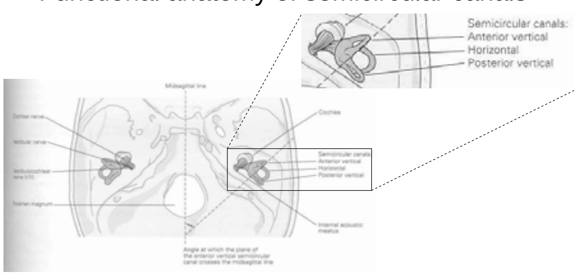
• Linear accelerometers detect net acceleration regardless of its source (Einstein's equivalence principle)

• For the otolith organs, this introduces an ambiguity between *tilt* and *linear acceleration*

Real world examples?

Pilots must learn to ignore perception of excessive tilt during period of high linear acceleration…

Functional anatomy of semicircular canals



• 3 semicircular canals per side

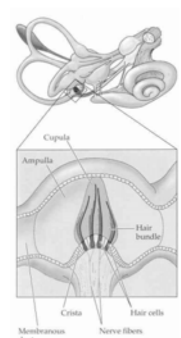
• One lies approximately in the horizontal plane. The others, the anterior and the posterior, are aligned vertically and lie perpendicular to each other

How the semicircular canals sense rotations

Each canal has a swelling called the **ampulla**

A pliable membrane called the **cupula** spans and seals the inner diameter of the ampulla.

The stereocilia of the hair cells project into the cupula



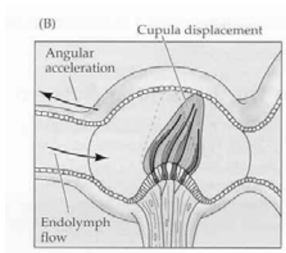
How the semicircular canals sense rotations

• When there is a change in head rotation, the endolymph lags behind because of inertia, distorting the cupula

• Bending of the stereocilia towards the kinocilium increases the firing of vestibular afferents

• Bending away from the kinocilium decreases firing of the vestibular afferents

• Like the otoliths, canal afferents have a baseline firing rate of ~ 100 Hz, and can therefore signal rotations in two directions



Canals have a preferred direction of rotation, and work in pairs

- Three canals per side, oriented roughly orthogonal to each other.
- Each of the 6 canals is best activated by a different direction of head rotation (rotation toward the canal increases afferent firing).
- The canals work together in a push-pull organization. When one canal is maximally active, the other is maximally inhibited.
- For example, for rightward rotation, excitation occurs in the right horizontal canal, and inhibition in the left horizontal canal
- All possible directions of head rotation are covered, and hence can be unambiguously encoded

The Vestibular-Ocular Reflex (VOR)

- The VOR stabilizes the retinal image during head rotations.
- When the head rotates in one direction, the eyes rotate at the same speed in the **opposite** direction (ideal VOR gain = 1).
- This keeps gaze stable in space

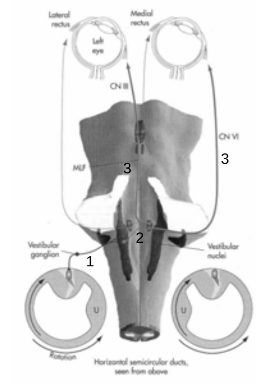
Neural circuit for the VOR

3 neuron arc: Vestibular afferent → interneuron → abducens nerve

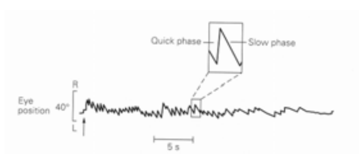
An additional interneuron to the oculomotor nucleus ensures conjugate eye movement

SEQUENCE OF EVENTS:

1. Leftward head rotation increases firing of afferents from left horizontal canal
2. 2nd-order neuron in vestibular nucleus projects to contralateral abducens nucleus
3. Contraction of right lateral rectus muscle, and left medial rectus muscle (via interneuron in the MLF)



NYSTAGMUS (Greek = "Nod")



-Eye position of subject rotated clockwise at a constant rate in the dark

-Slow phase: driven by VOR, matches speed of rotation

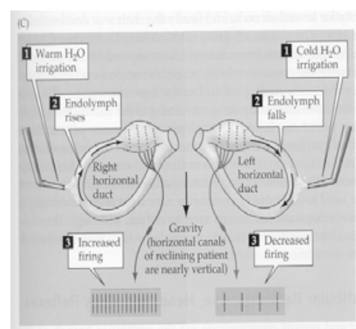
-Quick phase: saccadic eye movements in ***direction of head motion*** to "reset" position of eye in orbit

CAROLIC TESTING OF VESTIBULAR FUNCTION

-Lie subject on back (places horizontal canals vertical)

-Cold water causes convection currents that *decrease* firing

-Warm water causes convection currents that *increase* firing

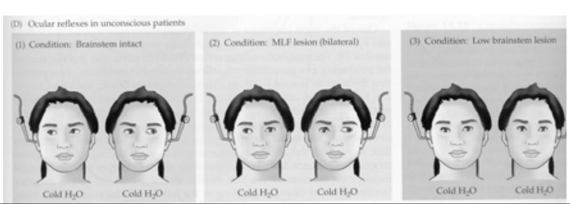


CAROLIC TESTING OF VESTIBULAR FUNCTION

- Used to test brainstem in unconscious patients

- Assess VOR: Look for direction of slow and fast phase of nystagmus and conjugate eye movements

-Indicative of brainstem function (pictures below show slow phase)



Additional Resources

- Chpt 13 and 14 of "Neurosciences, 2nd ed", Purves et al 2001
- Chpt 30, 31 and 40 of "Principles of Neural Science, 4th ed", Kandel, Schwartz and Jessel
- Great animations available at: http://www.physpharm.fmd.uwo.ca/undergrad/sensesweb/ (For this website, concentrate on what we talked about in class!)