The Auditory and Vestibular Senses

Introduction

Our ability to hear (auditory) and to determine our balance (vestibular) depends on structures in the ear:

- Hearing (Auditory information) is detected by hair cells in the cochlea.
- Balance (Vestibular information) is detected by hair cells in the vestibular organs.

Hearing

Sounds

Sounds arise from audible variations in air pressure:

- Frequency – number of compressed patches of air that go by our ears each second (hertz (Hz)).
    - High or low pitch is determined by frequency.
    - High pitch = high frequency
    - Low pitch = low frequency
    - Humans hear about 20Hz to 20,000Hz
- Amplitude – difference in pressure between compressed and non-compressed patches of air.
- Most sounds are the combination of many different frequency waves of different intensities (amplitudes).

The Structure of the Auditory System

The ear is divided into three parts:

- The Outer Ear which includes the:
    - Pinna
    - External Auditory Canal
    - Tympanic Membrane (eardrum)
- The Middle Ear, which includes the:
    - Auditory Ossicles – the Malleus, the Incus, and the Stapes.
- The Inner Ear, which includes the:
    - Oval Window
    - Cochlea

Briefly, sound is detected through the following steps:

- Sound waves are collected by the Pinna and External Auditory Canal.
- Sound waves move the Tympanic Membrane.
- Movement of the Tympanic Membrane moves the Auditory Ossicles.
- Movement of the Auditory Ossicles moves the membrane of the Oval Window.
- Movement of the Oval Window moves fluid in the Cochlea.
- Movement of fluid in the Cochlea is detected by Hair Cells.

Structures responsible for conveying and processing auditory information involve neurons of the Spiral Ganglia, the Cochlear nerve, the Cochlear Nucleus of the brain stem, the Inferior Colliculus of the midbrain, the Medial Geniculate Nucleus of the Thalamus, and the Primary Auditory Cortex.

The Middle Ear

Auditory Ossicles

The Auditory Ossicles include the Malleus, Incus and the Stapes which are critical for sound amplification and attenuation.

Amplification by Ossicles

- The surface area of the Oval Window is less than the Tympanic Membrane.
- Without the Ossicles most of sound energy would be reflected back from the Oval Window.
- The Ossicles act like levers and work together to make the pressure at the Oval Window about 20 times greater than at the Tympanic Membrane.

Attenuation Reflex

- Movement of the Malleus is controlled by the Tensor Tympani muscle.
- Movement of the Stapes is controlled by the Stapedius muscle.
- Contraction of these muscles restrains the movement of the Ossicles and reduces the movement of the Oval Window.
    - There is a delay in the

The Inner Ear

Anatomy of the Cochlea

The Cochlea is spiraled and looks something like a “cinnamon roll” or a “snail”. Spiraling through the Cochlea are three chambers:

- The Vestibular Duct which begins with the Oval Window.
- The Cochlear Duct which contains the Organ of Corti with Hair Cells.
- The Tympanic Duct which end with the Round Window.
- A thin Vestibular Membrane separates the Vestibular Duct and the Cochlear Duct.
- A variable thickness Basilar Membrane separates the Cochlear Duct and the Tympanic Duct.

Physiology of the Cochlea

Fluids in the Cochlea

- The Vestibular Duct and Tympanic Duct are filled with Perilymph, an extracellular fluid which is similar to Cerebral Spinal Fluid.
    - Low K^+ (7 mM)

  - High Na^+ (140 mM)
- The Cochlear Duct is filled with Endolymph, an extracellular fluid which is similar to intracellular fluids:
  - High K^+ (150 mM).
  - Low Na^+ (1 mM).

Movement of Fluids and the Basilar Membrane

- Inward motion of the Oval Window pushes Perilymph into the Vestibular Duct and a complimentary motion at the Round Window.
- When the perilymph is displaced in the Vestibular Duct Endolymph is displaced in the Cochlear Duct because the Vestibular Membrane is very flexible.
- Von Bėkėsy determined that the movement of the Endolymph makes the Basilar Membrane bend near its base, starting a wave that propagates toward the apex.
  - The Basilar membrane is wider at the apex than at the base by a factor of about 5.
  - The Basilar membrane is stiffer at the base than at the apex by a factor of about 100
- The distance the wave travels depends on the frequency of the sound.
- The Basilar Membrane establishes a place code in which locations are deformed maximally at different sound frequencies
  - High frequencies are detected close to the base.
  - Low frequencies are detected close to the apex.

Organ of Corti and Hair Cells

- The organ of Corti contains hair cells, each with about 100 stereocilia.
- A reticular lamina covers the hair cells; the stereocilia pass through and extend above this layer.
- The organ of Corti contains:
  - One row of inner hair cells (3500 hair cells)
  - Three rows of outer hair cells (15,000 to 20,000 hair cells)
- Hair cells synapse with neurons whose cell bodies are in the Spiral Ganglion.
  - Axons of Spiral Ganglion neurons enter the Cochlear nerve (part of the Vestibulocochlear nerve, cranial n. VIII) which then synapse in the cochlear nuclei of the medulla.

Transduction by Hair Cells

- Movement of the Basilar Membrane moves the organ of Corti.
- Upward movement moves the reticular lamina up and centrally; inward with regard to the Tectorial membrane, forcing the stereocilia to bend outward.
- The stereocilia contain gated TRPA1 channels for K^+ (Remember that the Endolymph has a high [K+].
  - Each channel is connected by an elastic filament called a "tip link."
  - When the cilia are straight the K^+ channels are partially open.
  - When the cilia are bent one way the K^+ channels close.
  - When the cilia are bent the other way the K^+ channels open.

Innervation of Hair Cells

- About 95% of the Spiral ganglion neurons synapse with the less numerous inner hair cells.
- The remaining 5% of the Spiral ganglion neurons synapse with the more numerous outer hair cells.
- Apparently the vast majority of the information leaving the cochlea comes from the inner hair cells

Role of Outer Hair Cells

- Outer hair cells seem to act like tiny motors that amplify the movement of the basilar membrane.
  - Respond to sound with both a receptor potential and a change in length.
    - Motor proteins are embedded in the plasma membrane are driven by the receptor potential <u>without</u> the use of ATP.
  - Also are controlled by efferent neurons from the brain stem.

Central Auditory Processes

Auditory Pathways

Primary Ascending Pathways

- Axons of the cochlear nerve ipsilaterally innervate (synapse in) the Dorsal Cochlear Nucleus and the Ventral Cochlear Nucleus
- Neurons in the Ventral Cochlear Nucleus synapse in the Superior Olive of both sides of the brain stem.
- Neurons in each Superior Olive ipsilaterally synapse in the Inferior Colliculus.
- Neurons in the Dorsal Cochlear Nucleus bypass the Superior Olive and synapse in the Inferior Colliculus of both sides of the brain stem.
- All ascending auditory pathways converge onto the Inferior Colliculus.
- Neurons in the Inferior Colliculus synapse onto neurons of the Medial Geniculate Nucleus of the Thalamus, that in turn synapse onto neurons in the Auditory Cortex.

Other Pathways

- Neurons in the Inferior Colliculus also synapse onto neurons in the Superior Colliculus and onto neurons in the Cerebellum.
- Neurons in the Auditory Cortex synapse onto neurons in the Medial Geniculate Nucleus and onto neurons in the Superior Colliculus.
- Neurons in select brain stem nuclei synapse onto the Outer Hair Cells.

Response Properties

- Spiral Ganglion neurons are most responsive to one frequency.
- There is a frequency map of the basilar membrane in the cochlear nucleus, with each of the brainstem nuclei, the Medial Geniculate Nucleus, and the Auditory cortex,
- At low frequency (less than 4 kHz) phase locking is used along with tonotopy.
- At high frequency (greater than 4 kHz) tonotopy only is relied upon.

Sound Localization

- In the horizontal plane interaural time delays ranging from 0 to 0.6 msec and interaural intensity differences are used by the Superior Olive to determine sound localization.
- In the vertical plane subtle differences in sound and/or timing, based upon sound directly striking the ear compared to sound reflected by the Pinna, are used to localize sound.

Auditory Cortex

- Neurons in the Medial Geniculate Nucleus pass through the acoustic radiations and synapse in the Auditory Cortex (A1)of the Temporal Lobe.
- The Auditory Cortex is organized similarly to the Primary Visual Cortex.
  - Layer I has few cell bodies.
  - Layer II and III has mostly small pyramidal cells
  - Layer IV has dense granule cells upon which most axons from the Medial Geniculate Nucleus synapse.
  - Layer V and VI has large pyramidal cells.
- Neurons are relatively sharply tuned for sound frequency in the audible spectrum.
- Low frequencies are represented rostrally and laterally in the auditory cortex.
- High frequencies are represented caudally and medially in the auditory cortex.
- Auditory receptive fields and response characteristics are difficult to categorize.

Vestibular System

The vestibular system monitors the position and movement of the head, gives us sense of balance, and helps coordinate movement and balance.

Vestibular Labyrinth

- Hair cells are contained within sets of interconnected chamber (labyrinths):
  - Otolith organs detect force of gravity and tilts of head.
  - Semicircular Canals detect head rotations

Otolith Organs

- Saccule and Utricle detect changes in head angle in relation to gravity and to changes in linear acceleration.

- The Saccule and Utricle contain a sensory epithelium called the Macula that contains Hair cells:
    - In the Saccule the macula is oriented vertically.
    - In the Utricle the macula is oriented horizontally.
    - The cilia of the Hair cells project into a gelatinous cap.
    - Otoliths (calcium carbonate crystals, 1-5 µm) cover the surface of the gelatinous cap.
    - Bending of the cilia occurs when the otoliths are pulled down against the cilia.
- Bending of Hair cells toward the kinocilium causes depolarization; the opposite bending causes hyperpolarization.

Semicircular Canals

- The semicircular canals are particularly sensitive to angular acceleration of the head in several directions.
- Hair cells are located in a sheet (Crista) in a bulge (Ampulla) along each semicircular canal.
    - The cilia of the hair cells project into a gelatinous cupula.
    - The canals are filled with Endolymph.
    - Bending of the cilia occurs when a canal is rotated around its axis
        - Rotation at a constant velocity makes the Endolymph and cupula move together and the cilia no longer bend.
        - Stopping rotation makes the cupula move and the cilia bend in the opposite direction.
- Bending of Hair cells toward the kinocilium causes depolarization; the opposite bending causes hyperpolarization.
    - Rotation excites hair cells in one canal and inhibits hair cells in the opposite partner canal.

Central Vestibular Pathways

- Primary vestibular neurons make direct connections with the vestibular nucleus and cerebellum on the same side.
- The Lateral Vestibular Nucleus connects with the Vestibulospinal Tract which controls lower body muscles.
- The Medial Vestibular Nucleus connects with the Medial Longitudinal Fasciculus which controls upper body muscles.
- The Vestibular Nuclei connect to the Ventral Posterior Nucleus of the Thalamus that in turn connects with the Primary Somatosensory and Primary Motor Areas.

Vestibular-Ocular Reflex

- Keeps eyes pointed in a particular direction in spite of body movement.