

The Auditory Periphery: An Overview

Paul Fuchs
955-3877
pfuchs1@jhmi.edu
818 Ross

Websites:

Promenade 'round the cochlea (http://www.iurc.montp.inserm.fr/cric/audition/english/start.htm)

Auditory Animations, Univ. of Wisconsin
(http://www.neurophys.wisc.edu/animations/)

Texts (at Welch or Eisenhower):

From Sound to Synapse, C. D. Geisler, New York: Oxford Univ. Press, 1998

An Introduction to the Physiology of Hearing, J. O. Pickles, New York: Academic Press, 1982

Fundamentals of Hearing: An Introduction (3rd ed.), W. A. Yost, San Diego: Academic Press, 1994

Objectives:

1. Identify gross structure and function of the outer, middle, and inner ear components.
 2. Identify micro-structures of the Organ of Corti (sensory and non-sensory cells)
 3. Define basic cochlear mechanics terms (place coding, traveling wave, tuning)
 4. Describe locale, construct, and electrical potentials of inner ear fluids: perilymph and endolymph
-

Cochlear tasks

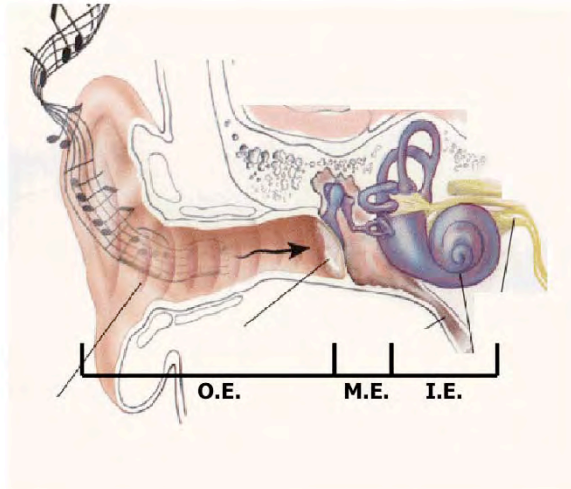
- Sensitivity
- Frequency selectivity
- Timing

What are the tools?

Structure and Function of the Auditory and Vestibular System - 1

Lecture outline

- Outer Ear
 - pinna, canal
- Middle Ear
 - Tympanic Membrane
 - Middle Ear Bones
 - Middle Ear Muscles
- Inner Ear (cochlea)
 - Cochlear Duct
 - Hair Cells
 - Innervation
 - Mechanics
 - Cochlear Fluids



The ear is divided into three components: the outer, middle, and inner ear.

The auditory periphery transforms sound waves into neural signals. Three characteristics of this 'transformation' are:

1. preserving the temporal structure of the acoustic signal
2. encoding changes in (rather than absolute) stimulus intensity
3. performing amplitude compression to encode stimulus intensities over 7-orders of magnitude.

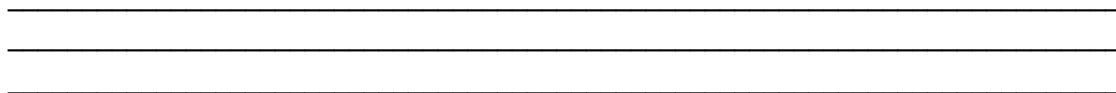
COLLECTION: The primary function of the outer ear is for protection, funneling sound, and performing spectral filtering for sound localization.

CONDUCTION: The middle ear serves as an impedance matching device, allowing for adequate transfer of energy from air-borne sound to the fluid-filled cochlea.

TRANSDUCTION: The inner ear is the sensory element of the auditory/vestibular periphery, transducing sound-driven vibrations, gravity, and acceleration into neural stimuli via the activity of inner ear hair cells.

In this lecture, we will consider the anatomical structure of each of these components and will briefly introduce functional aspects along the way.

(images: adapted from *Promenade*, S. Blatrix)



Structure and Function of the Auditory and Vestibular System - 1

The mammalian (guinea pig) cochlea

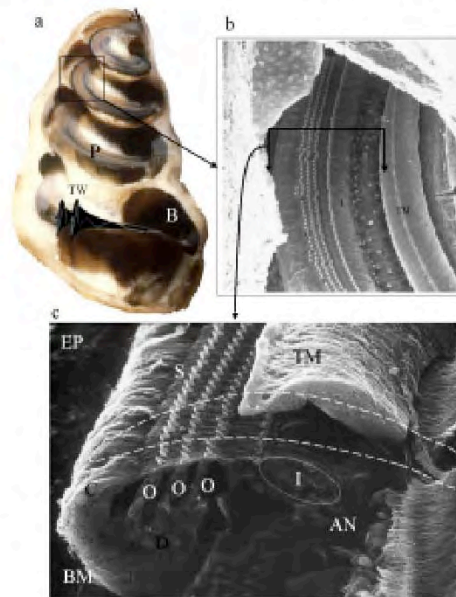
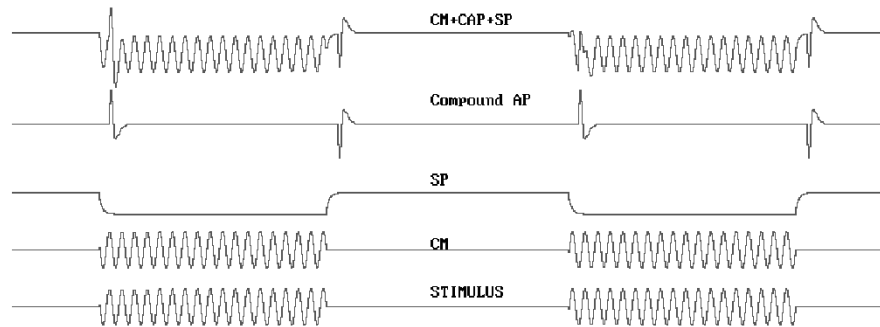


Figure 1 The cochlea as a mechanism for sound processing; illustrated with a guinea pig ear. a) the whole cochlea with bony encapsulation removed to show the spiral cochlear partition (P) incorporating the basilar membrane and making $3 \frac{1}{2}$ turns from the basal end (B) to the apex (A). SV indicates the position of the stria vascularis which spirals around the outer wall. Photograph kindly supplied by Ade Pye. Superimposed on this photograph is a computer graphic showing two travelling waves of slightly differing high frequency forming peak vibrations at two places. Note that the waves are grossly enlarged of illustration purposes and in fact the greatest vibration sound creates in the cochlea is of less than cellular dimensions. From D.T. Kemp, "Otoacoustic emissions and evoked potentials", in *The Ear*, volume 1 of the Oxford University Press Handbook of Auditory Sciences, (P. Fuchs, ed.) to be published in 2009.

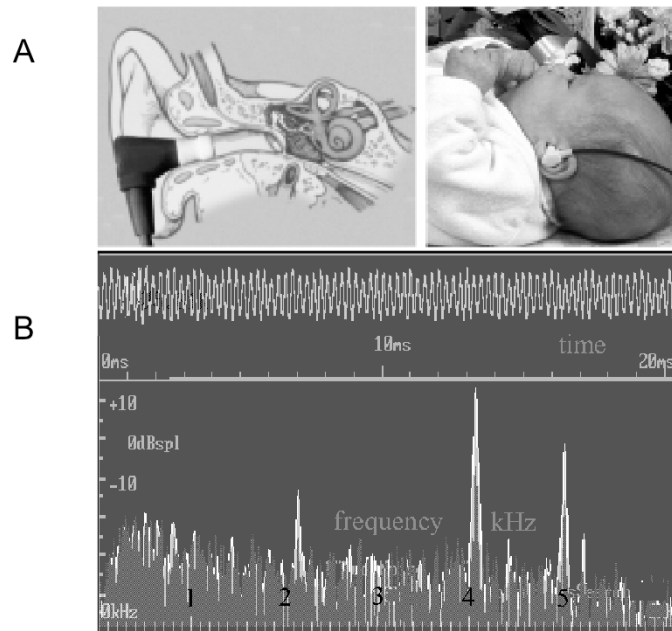
Evoked electrical responses of the cochlea



Schematic representation of externally recorded electrical cochlear response waveforms and their relations to each other. The stimulus consists of two bursts lasting about 18 ms. The second tone burst is inverted in polarity with respect to the first. From the bottom up, the cochlear microphonic response CM exactly follows both stimulus waveforms. The summing potential SP is by definition non oscillatory and follows the envelope of the stimulus. The compound or whole nerve action potential CAP is present only at the start and end of stimulation. The top trace shows the composite electrical signal as it would actually be recorded. The CM, SP and CAP traces are simply added. The composite responses to the two stimuli are different only because of the polarity inversion of CM. Subtraction of the two composite waveforms would leave only the CM trace, whereas adding them together would eliminate CM and leave the sum of SP and CAP traces. (From D.T. Kemp, "Otoacoustic emissions and evoked potentials", in *The Ear*, volume 1 of the Oxford University Press Handbook of Auditory Sciences, (P. Fuchs, ed.) to be published in 2009.)

Structure and Function of the Auditory and Vestibular System - 1

Spontaneous oto-acoustic emissions from a newborn human



A, left. An otoacoustic emission probe inserted in the ear canal communicates acoustically with the cochlea through the middle ear. There are no electrodes. The probe contains a miniature microphone and one or two miniature loudspeakers as used in hearing aids. A, right. An infant fitted with an OAE probe for hearing screening. A tight and deep probe fit is valuable in gaining a good signal to noise ratio.

B.)

Examples of spontaneous otoacoustic emissions from an infant ear.

Upper trace. The waveform of sound in the ear canal showing the periodicity of the dominant component at 4.1 kHz. The modulation of intensity is due to the presence of other smaller spontaneous emissions.

Lower trace: the frequency spectrum of this sound showing three clear peaks at 2.2, 4.1 and 5 kHz. The largest has an amplitude of 10 dB SPL. The dark shading is the noise contamination assessed by subtracting repeat recordings.

(From D.T. Kemp, "Otoacoustic emissions and evoked potentials", in *The Ear*, volume 1 of the Oxford University Press Handbook of Auditory Sciences, (P. Fuchs, ed.) to be published in 2009.)

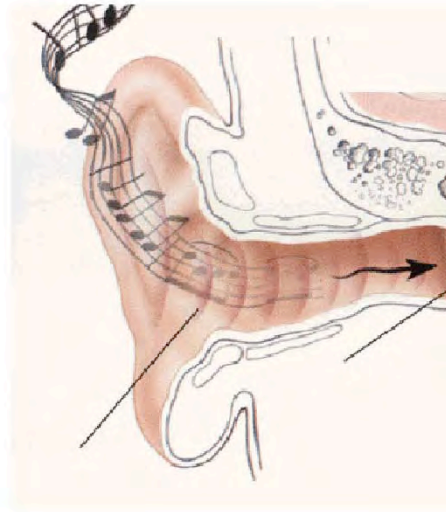
Outer ear structure

Structure

- Pinna
- External Auditory Meatus

Function

- Protection
- Funnel Sound
- Spectral Cues



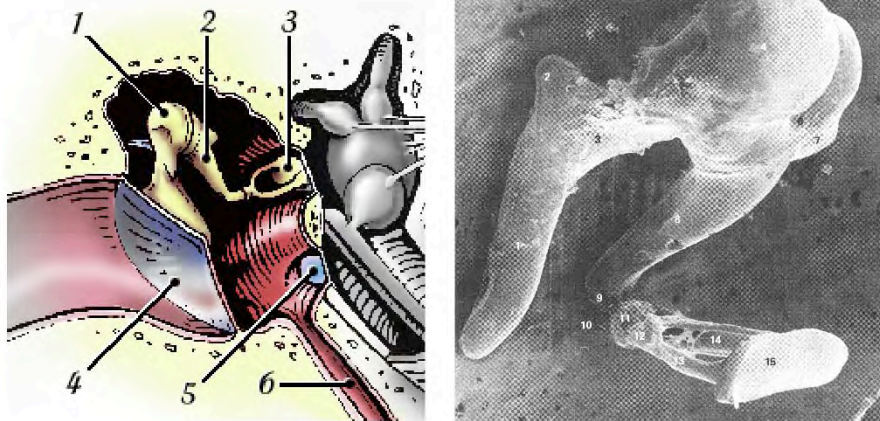
The pinna and external auditory meatus (auditory canal) of vertebrates come in a variety of shapes and sizes. Note that most reptiles and amphibians do not possess an outer ear. Instead, their tympanic membrane is flush with the surface of the skin. Is the outer ear just an adornment? Like other anatomical elements, we see that the structure of the outer ear in mammals is intimately tied with function.

Function of the Mammalian Outer Ear:

1. Protection
 - Foreign bodies, change in temp & humidity
 - Cerumen (Wax), fights infection and removes debris. Wax is produced by small glands in the ear canal to keep it moist.
2. Funnels sound
 - 10 to 15 dB amplification for 1.5 kHz to 7 kHz
 - Gain due to combined resonance of concha and ear canal
3. Head-Related Transfer Function
 - Spectral cues for sound localization, especially for animals with mobile pinnae
(images: adapted from *Promenade*, S. Blatrix)

Structure and Function of the Auditory and Vestibular System - 1

Middle ear structure:
ossicles (malleus, incus and stapes)



The auditory canal is bounded medially by the tympanic membrane. This membrane consists of three layers (squamous epithelium, a fibrous layer, and respiratory mucosa). The central fibrous layer thickens laterally to form the annulus, a tougher ring that supports the tympanic membrane and connects it to adjacent bone.

The three middle ear bones (ossicles) are the malleus, incus, and stapes. The malleus is in direct contact with the tympanic membrane (TM). The malleus' extension into the center of the TM (the manubrium) creates the conical form of the TM.

- | | |
|---------------------|----------------------|
| 1. Malleus (Hammer) | 4. Tympanic Membrane |
| 2. Incus (Anvil) | 5. Round Window |
| 3. Stapes (Stirrup) | 6. Eustachian Tube |

The stapes ends in a footplate, which is implanted in the Oval Window of the cochlea, supported by an annular ligament. Thus, the tympanic membrane is mechanically coupled to the cochlea's oval window via the middle ear bones.

Note the 3D structure in the SEM figure. Movement of the middle ear bones is largely accomplished through rotations about parallel axes, thus translational movements are in the same plane.

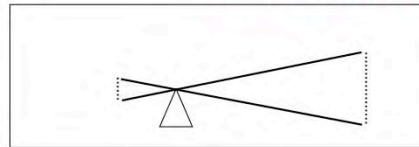
Finally, the middle ear cavity is connected to the nasopharynx by the eustachian tube. This connection serves to equalize the air pressure on either side of the tympanic membrane and allows for fluid buildup in the middle ear cavity to drain down the throat. The 'fullness' in the ear felt during air flight is a direct result of pressure imbalance between the atmosphere and middle ear. 'Back pressure' forced up through the eustachian helps correct.

(images: left: adapted from *Promenade*, S. Blatrix; right: Yost, pg 64.)

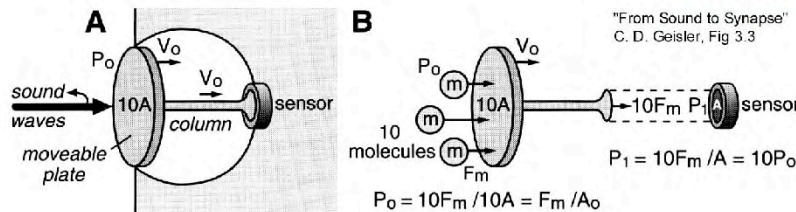
Middle ear function

- Overcoming an impedance mismatch
- In humans...
 - Lever Ratio (1.3:1)
 - Area Ratio (20:1)

Lever Ratio



Area Ratio



Acoustic transmission through the middle ear can be achieved by: (1) bone conduction, (2) conduction through the air in the middle ear cavity, or (3) by means of the ossicular chain. The ossicular chain is the most effective means of conducting sound to the inner ear, because it overcomes in part the impedance mismatch between air and fluid.

The density of water is far greater than the density of air. Thus, when an air-borne pressure wave encounters a fluid surface, 99% of the wave's energy is reflected (rather than transmitted).

The impedance mismatch is overcome in part through two central mechanisms: the lever ratio and area ratio.

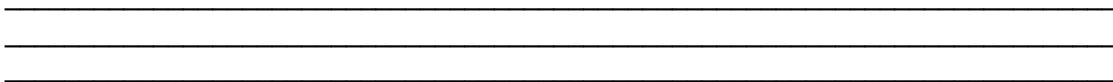
Lever Ratio:

The movement of the human stapes is about 1.3 times that of the tympanic membrane due to the 'effective' lever ratio of the ossicular chain, determined by the lengths of the bones and pivot points (like in the see-saw example above).

Area Ratio:

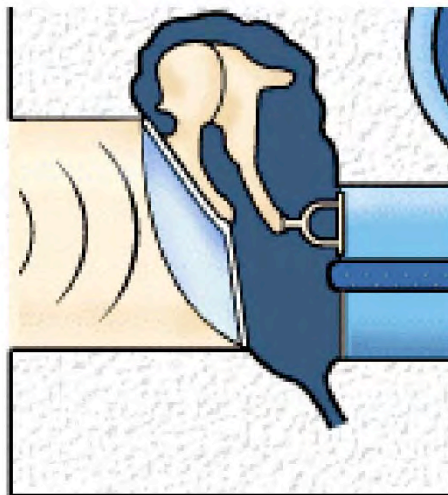
The surface area of the tympanic membrane is about 20 times that of the oval window. If we consider the middle ear system as a rigid link between these two membranes (as illustrated above), then the pressure at the stapes is about 20 times that at the TM.

(images: lower image from Geisler, pg 26)



Middle ear function: movement of ossicles

- Pivot about ligaments
- Rocking of stapes
- Note incompressible cochlear fluids



Animation demonstrates movement of the ossicular chain.

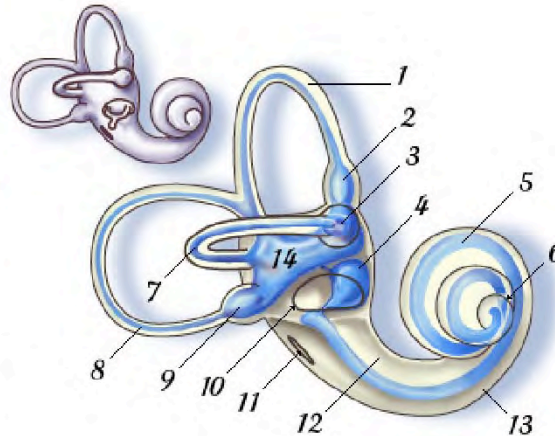
(images: adapted from *Promenade*, S. Blatrix)

ADDED NOTE:

When middle ear function is degraded, it results in a “conductive” hearing loss. A common cause is otosclerosis in which bony growth impedes the movement of the middle ear ossicles. Conductive hearing loss can be distinguished from “sensorineural” hearing loss (the loss of hair cells and/or nerve fibers such as occurs with sound damage) by comparing the audibility of a tuning fork held in the air, or pressed against the skull. In conductive hearing loss, the latter position is effective at presenting sound by bone conduction, thus overcoming the conductive loss pertaining to air-borne sound. If the loss is sensorineural, then bone conduction doesn’t help. Dr. Howard Francis will elaborate on hearing loss and cochlear pathology in a later lecture.

Inner ear structure

1. Superior SCC
2. Ampulla
3. Ampulla
4. Sacculus
5. Cochlear Partition
6. Helicotrema
7. Horizontal SCC
8. Posterior SCC
9. Ampulla
10. Oval Window
11. Round Window
12. Scala Vestibuli
13. Scala Tympani
14. Utricle



© S. Blatrix/CRIC 99

The inner ear consists of vestibular and auditory end-organs. For this lecture, we are interested in the anatomy of the auditory periphery and will confine our discussion to the coiled, 3-chamber tube called the cochlea. Later, Dr. John Carey will take up the vestibular portion.

Oval Window:

Note the orientation of the stapes with regard to the membranous inner ear. The stapes sits at the base of the cochlea, pressing against the oval window. The oval window is the boundary for one of the three fluid-filled cochlear chambers.

Scala Vestibuli and Scala Tympani:

Pressure waves setup by movement of the stapes are transmitted through the fluid-filled chambers of the cochlea, first through scala vestibuli. As you saw in the animated movements of the ossicular chain, movement of the stapes into the oval window results in the **Round Window** bulging outward. This is due to the incompressible nature of the fluid. So, pressure waves that enter scala vestibuli escape through scala tympani. Pressure moves from one chamber to the other via the cochlear partition or the helicotrema.

Helicotrema:

Static pressure and waves of very low frequency (<20 Hz) pass from scala vestibuli to scala tympani via a physical connection at the apex of the cochlea, called the helicotrema.

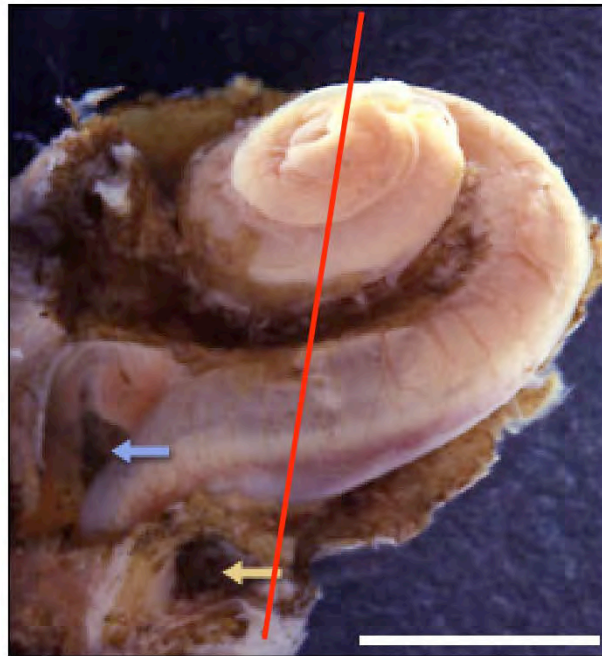
Cochlear Partition:

The cochlear partition contains the sensory structure of the cochlea (the Organ of Corti). Pressures waves from 20 Hz to 20,000 Hz (in humans) pass from scala vestibuli to scala tympani by setting this partition in motion. This motion results in the stimulation of sensory hair cells and the transduction of acoustic signals into a neural response.

(images: adapted from *Promenade*, S. Blatrix)

Structure and Function of the Auditory and Vestibular System - 1

The cochlea of a human fetus (5 months). Scale bar 5 mm. Arrows point to the oval window (blue) and round window (yellow).
M. Levigne-Rebillard

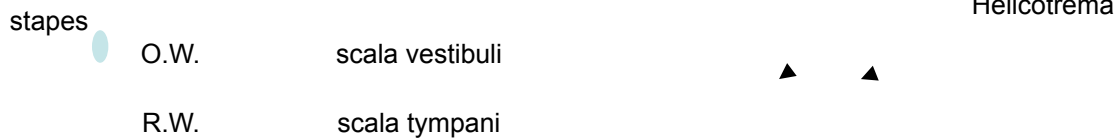
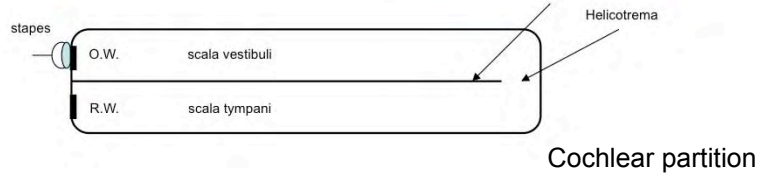
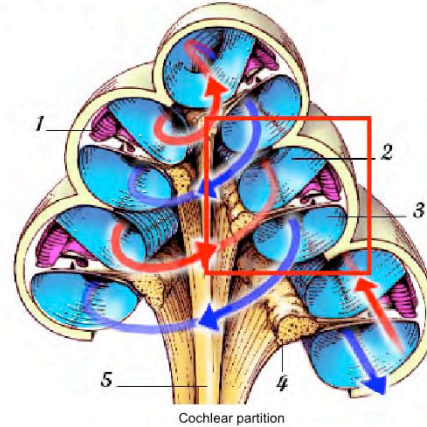


Example of the human cochlea obtained from a 5 month old fetus. The coil provides a continuous pathway for sound wave propagation. The stapes footplate moves into and out of the oval window (blue arrow), driving fluid motion that is relieved (at steady-state) at the round window (yellow arrow).

Structure and Function of the Auditory and Vestibular System - 1

Cochlear cross-section

1. Cochlear Partition
2. Scala Vestibuli
3. Scala Tympani
4. Spiral Ganglion
5. Auditory Nerve Fibers



This image is of a mid-modiolar cross-section of the coiled cochlea. The modiolus is the central axis of the cochlear coil. A number of anatomical objects are labeled as inner or outer, meaning that they lie along the inner part of the spiral (near the modiolus) or along the outer part of the spiral.

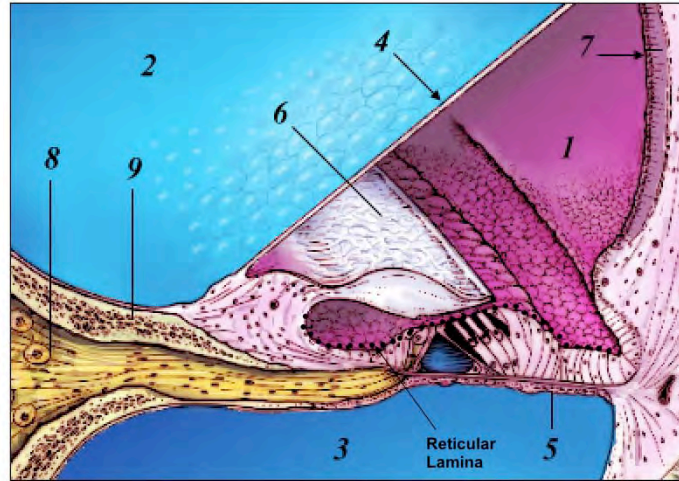
It is often convenient to consider the cochlea as though it were unrolled from its coil.

(see drawing on board)

At each turn, three fluid-filled chambers can be identified. Scala vestibuli and scala tympani are contiguous, with mixing occurring at the helicotrema. Scala media is found within the cochlear partition. The coiled nature of the cochlea can be seen by following the arrows in the slide. Note that the direction of the arrow changes at the apex (at the helicotrema).

Cochlear Cross-Section At a Single Turn

1. Scala media
2. Scala vestibuli
3. Scala tympani
4. Reissner's membrane
5. Basilar membrane
6. Tectorial membrane
7. Stria Vascularis
8. Auditory Nerve
9. Bony Spiral Lamina



We are moving deeper into the structures of the cochlear partition, where the sensory components are located. This image illustrates a cross-section at a single cochlear turn.

Three Fluid Chambers:

Scala vestibuli and scala tympani contain perilymph, a fluid similar to CSF.

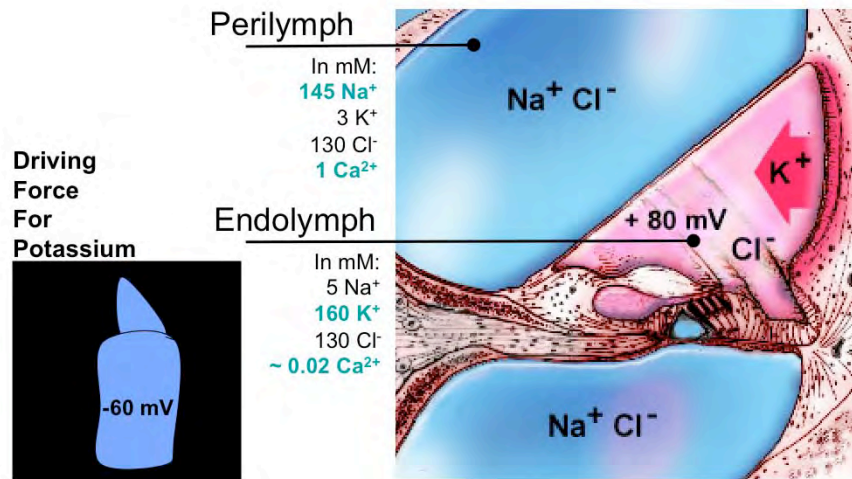
Scala media contains endolymph, a fluid similar to intracellular environments (high potassium). We'll learn more about these fluids later. Note that scala media is bounded by Reissner's membrane, the stria vascularis (secretes potassium), and the reticular lamina (not the basilar membrane). The reticular lamina is formed by tight junctions between hair cells and supporting cells (dotted line in figure), creating an impermeable barrier between scala media and scala tympani.

Cochlear Partition:

The cochlear partition largely consists of the sensory and non-sensory structures of the Organ of Corti, bounded by the tectorial and basilar membranes. Auditory nerve fibers extend from the sensory hair cells, out the habenular perforata, and into the modiolus gathering together to form the auditory nerve.

(slide image: adapted from *Promenade*, S. Blatrix)

Cochlear fluids: endolymphatic potential



We have already noted the two types of cochlear fluids, perilymph and endolymph, and how separate portions of the hair cells (in fact, ALL hair cells) are exposed to these solutions.

Perilymph is similar to most extracellular fluids (e.g. CSF), being high in Na and low in K. Recall that this solution bathes the basolateral surface of hair cells (i.e. the barrier to endolymph is the reticular lamina, not the basilar membrane).

Endolymph is a highly unusual extracellular fluid, being high in K, low in Na, and very low in Ca. This is very similar to most intracellular environments, where potassium is the dominant ion. Thus, the transduction current into hair cells is largely a potassium current. But without a concentration gradient, there must be another driving force to get potassium into the cell. This driving force is generated by two electrical potentials.

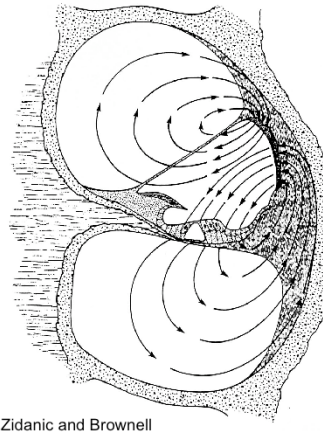
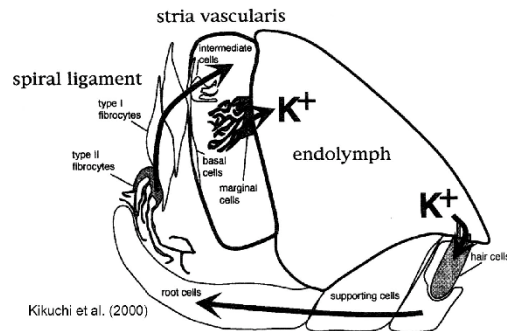
First, the hair cell's resting potential is between -40 and -60 mV due to ion channels in the basolateral portion of the membrane. Second, there exists an endolymphatic potential that is +80 mV with respect to the vascular system. This so-called endocochlear potential combines with the hair cell's resting potential for an ~140 mV driving force pushing potassium into the hair cell. The source of the endocochlear potential remains unclear, though it is intimately tied to the stria vascularis which secretes potassium into the endolymphatic space.

It should be noted that the endocochlear potential itself is not necessary to proper hair cell function since this potential is only a few mV in the vestibular system. Yet, if the stria is damaged or the endocochlear potential is eliminated, auditory sensitivity is reduced. It may be that the high frequency environment of the cochlea and voltage-dependent motility of some hair cells benefit from the added 'push' of the endocochlear potential.

(right slide image: adapted from *Promenade*, S. Blatrix)

Cochlear fluids: potassium recycling

Theoretical model for the recycling of endolymphatic potassium



The recycling of potassium and the homeostasis of endolymph is of particular interest, since a stable ionic environment is critical for proper hair cell function.

The endolymphatic compartments of each inner ear organ and a separate endolymphatic sack are contiguous. While some secretion and resorption of potassium may occur by the flow of endolymph through this network, there is strong evidence that the recycling of potassium is under local control.

The illustrations above depict current theories, where potassium is secreted by the stria, taken up by hair cells in transduction, released from the hair cell's basolateral surface, and recirculated to endolymph via a system of gap junctions between epithelial supporting cells and connective tissues at the spiral ligament. From the fibrocytes of the spiral ligament, potassium presumably enters the stria again by gap junctions. The combination of Na,K-ATPase and Na-K-Cl cotransporters in the marginal cells of the stria enable the accumulation of potassium in these cells (indeed they have a highly positive resting potential). Slowly gating potassium channels on the endolymph-facing surface of marginal cells leads to the accumulation of potassium in endolymph.

Immunoreactivity supports connexins as likely components in this network of gap junctions. Mutation of the connexin 26 gene leads to non-syndromic sensorineural hearing loss and the loss of endolymphatic potential.

The sensory epithelium – organ of Corti

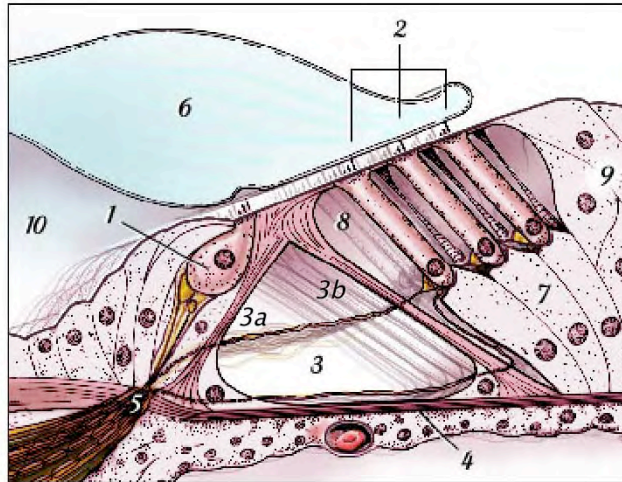
SEM of rat organ of Corti. Scale bar 2 mm.
M. Lenoir



The sensory epithelium, the organ of Corti, extends throughout the length of the coiled cochlea.

Organ of Corti

1. IHC
2. OHC
3. Tunnel of Corti: (a) inner and (b) outer pillar cells
7. Basilar membrane
8. Habenula perforata



Inner Hair Cells (IHC; ~3,500 in the human cochlea):

Inner hair cells are the focal points for the transduction of mechanical stimuli from acoustic waves to electrical neural output (mechano-electrical transduction). These cells sit in the inner (modiolar) part of the cochlear spiral, with a single row spanning from base to apex. They are flask shaped and form tight junctions with surrounding supporting cells. Apical surfaces are flat, except for the tuft of microvilli (stereocilia), which extend from the apical surface.

Outer Hair Cells (OHC; ~12,000 in the human cochlea):

Outer hair cells lie along the outside of the spiral, extending in three rows (sometimes four) from base to apex. These cells also form tight junctions with neighboring cells and have protruding stereocilia. Primarily efferently innervated.

Tunnel of Corti:

Inner and outer pillar cells, consisting of interlaced microfibrils and microtubules, create a stiff truss and a cell free space called the tunnel of Corti. (note: also called "rods of Corti"). Pillar cells provide structural stability, ensuring that movement of the basilar membrane is transmitted to the reticular lamina.

Basilar Membrane:

The structural platform of the cochlear partition. It is not a true membrane, but an acellular sheet of fibers (collagen). It is thick and narrow at the base, thin and wide at the apex. The differential stiffness results in the passive mechanical tuning of the cochlea.

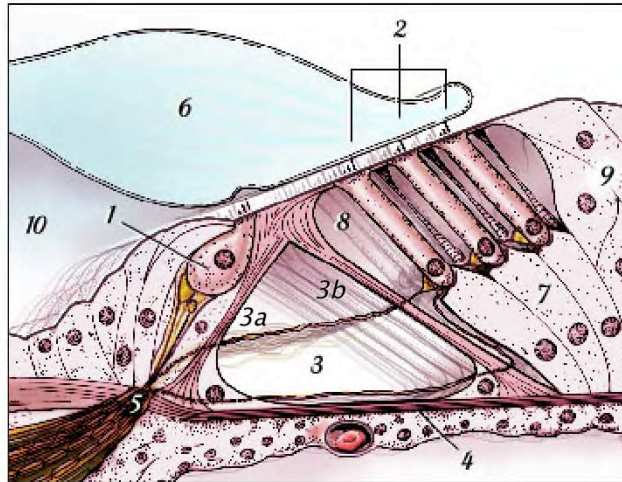
Habenula Perforata:

Holes in the bony spiral lamina are present along the cochlea, providing passage to extending auditory nerve fibers.

(slide image: adapted from *Promenade*, S. Blatrix)

Organ of Corti

- 6. Tectorial membrane
- 7. Dieters' cells
- 8. Spaces of Nuel
- 9. Hensen's cells
- 10. Inner spiral sulcus



Tectorial Membrane:

Not a true membrane (acellular, gelatinous structure, collagen?). This structure extends from supporting cells along the modiolar side and overlays the sensory hair cells. It is integral to the mechanical stimulation of hair cell hair bundles. Note the notch above the inner hair cells, called Hensen's stripe. The tips of the tallest stereocilia of outer hair cell hair bundles are in contact with the tectorial membrane, while the stereocilia of inner hair cells are not.

Dieters' Cells:

Inner hair cells are in contact with supporting cells on all sides. Outer hair cells are supported only at their bases by Dieters' cells, leaving the sides exposed to the perilymphatic fluid of scala tympani. A phalangeal process extends from the apical surface of each Dieters' cell, ending at the reticular lamina maintaining tight junctions with neighboring outer hair cells. Some efferent contact; purpose unknown.

Spaces of Nuel:

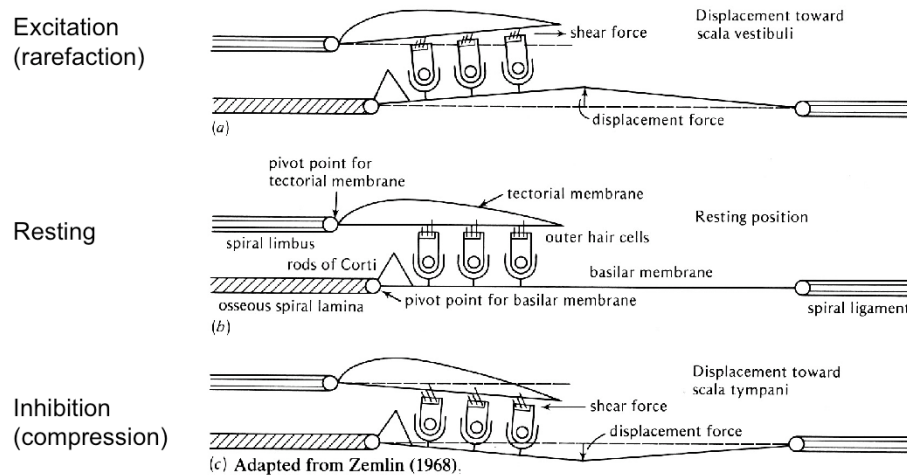
This refers to the fluid filled space surrounding the sides of outer hair cells.

Hensen's Cells:

These supporting cells have a number of interesting anatomical characteristics (i.e. some efferent contact and connection to tectorial membrane), but their purpose is largely unknown.

(slide image: adapted from *Promenade*, S. Blatrix)

Cochlear function: hair cell stimulation



Hair Cell Excitation (Transduction):

Deflection toward tallest row – depolarization, increased transmitter release

Deflection toward shortest row – hyperpolarization, decreased transmitter release

Mechanism in future lecture.

Yet, how is the vertical motion of the basilar membrane translated into horizontal motion of the stereocilia?

Deflection of outer hair cell stereocilia:

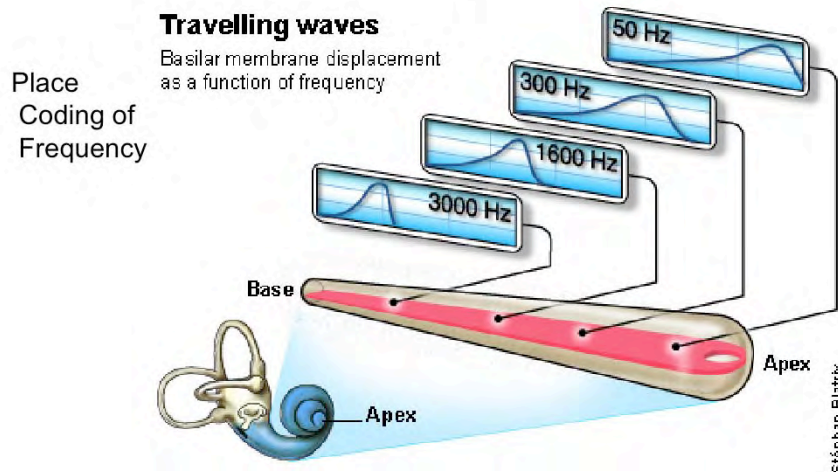
An increase in pressure from movement of the stapes into the oval window results in the displacement of the basilar membrane toward scala tympani. Since the tectorial and basilar membranes are hinged, and since the tips of the stereocilia of the outer hair cells are embedded in the tectorial membrane, the hair bundles are displaced toward the modiolus (toward shortest stereocilia, inhibitory) by the resulting shear. Displacement of the basilar membrane toward scala vestibuli results in excitatory displacement of the outer hair cell hair bundles.

Deflection of inner hair cell stereocilia:

The movement of the inner hair cell hair bundle is less direct since these stereocilia do not contact the tectorial membrane. Presumably, fluid is displaced by the OHC hair bundles. Inertial forces and viscous drag from this fluid results in displacement of the IHC hair bundles.

Now, take time to review in a bulleted outline how hearing happens (at least in the periphery) from, say a pure tone at 1,000 Hz.

Cochlear function: tonotopic organization, mechanical tuning



A brief introduction to cochlear mechanics:

We have already seen that very low frequency waves (<20 Hz) travel down the extent of the cochlea and pass from one chamber to the other via the helicotrema. We've also mentioned that the audible frequency spectrum for humans is limited to 20 Hz to 20,000 Hz. But, how is the frequency information of an acoustic signal represented in the cochlea?

Complex acoustic stimuli, from voice to car horns to violins, are generated by the combination of simple tones of various amplitude, frequency, and phase ($\sum A_i \cdot \cos[\omega_i t - \phi_i]$). The cochlea acts as a frequency analyzer, breaking the complex wave into frequency components. A given frequency in the 20 Hz to 20,000 Hz spectrum excites a particular location along the cochlea best. If one were to map those locations along the cochlea, you would see a logarithmic progression of best frequency from highest to lowest as you moved from base to apex. This is called the "place code of frequency", or tonotopic map (tonos – tone; topia – place).

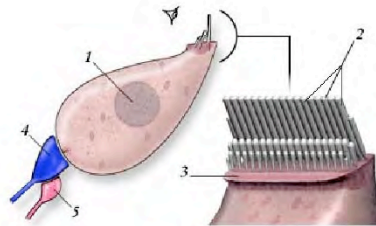
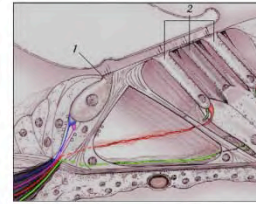
The slide above shows the map for several frequencies. The waveforms represent the envelopes of traveling waves setup by the acoustic stimulus. For more, visit: <http://www.neurophys.wisc.edu/animations/>.

The tonotopic map results from the passive mechanical properties of the cochlear partition, particularly the basilar membrane. This membrane is thick and narrow at the base, thin and wide at the apex. The resulting stiffness gradient is primarily responsible for the map. (Food for thought – could such 'mechanical tuning' underlie the tonotopic map in a turtle ear?).

(slide image: adapted from *Promenade*, S. Blatrix)

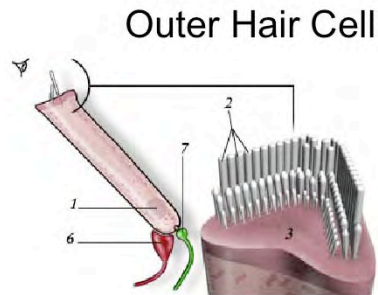
Structure and Function of the Auditory and Vestibular System - 1

Cochlear hair cells



Inner Hair Cell

1. Nucleus
2. Stereocilia
3. Cuticular Plate
4. Type I Afferent
5. Lateral OC Efferent
6. Medial OC Efferent
7. Type II Afferent



Outer Hair Cell

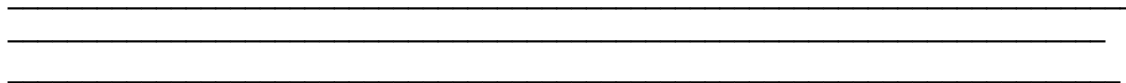
General structure:

Hair cells (regardless of species or organ) possess a tuft of stereocilia (hair bundle) which extend from the apical pole of the hair cell in a 'staircase' array. This hair bundle is tightly anchored to a dense fibrous matrix called the cuticular plate, about which the stiff stereocilia pivot during stimulation. It is the displacement of these stereocilia that initiates the transduction of a mechanical stimulus into neural pulses. More on these cells and the transduction process in upcoming lectures.

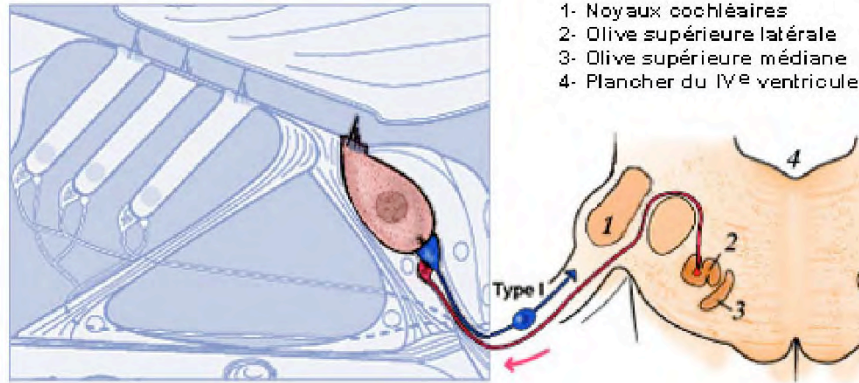
Mammalian hair cells:

Inner (IHC) and outer hair cells (OHC) are named for their positions relative to the modiolus (central axis). **Inner hair cells** are flask-shaped with rows of stereocilia in a straight or slightly curved fashion. They are innervated by Type I afferent fibers (i.e. myelinated prior to entering cochlea). Type I afferents make up 90-95% of all spiral ganglion neurons. In general, a Type I neuron will synapse with a single inner hair cell, and an inner hair cell synapses with 10-30 Type I neurons. Efferents from the lateral olivocochlear system (unmyelinated) appear to synapse directly onto Type I afferents rather than the hair cells themselves. **Outer hair cells** are cylindrically shaped with rows of stereocilia in a V or W shape. They are innervated by Type II afferents (i.e. unmyelinated). A single Type II synapses to 10-20 outer hair cells, and a single OHC makes contact with multiple Type II afferents. Even so, these cells are predominantly innervated by efferents from the medial olivocochlear system (myelinated).

(slide images: adapted from *Promenade*, S. Blatrix)

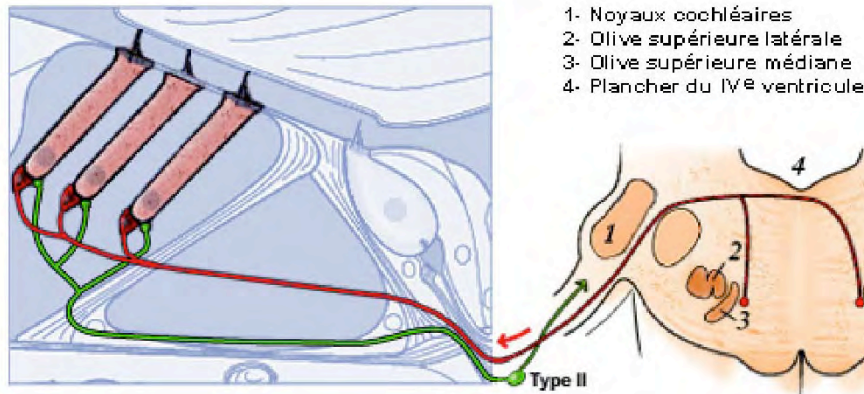


Innervation of inner hair cells



Inner hair cells are the principal source of afferent information to the brainstem. 95% of afferent neurons are postsynaptic to IHCs. Lateral efferent neurons originate in the lateral superior olive.

Innervation of outer hair cells



Outer hair cells are the principal targets of medial olivocochlear efferents to the cochlea, cell bodies near to the medial superior olivary nucleus in the brainstem.
