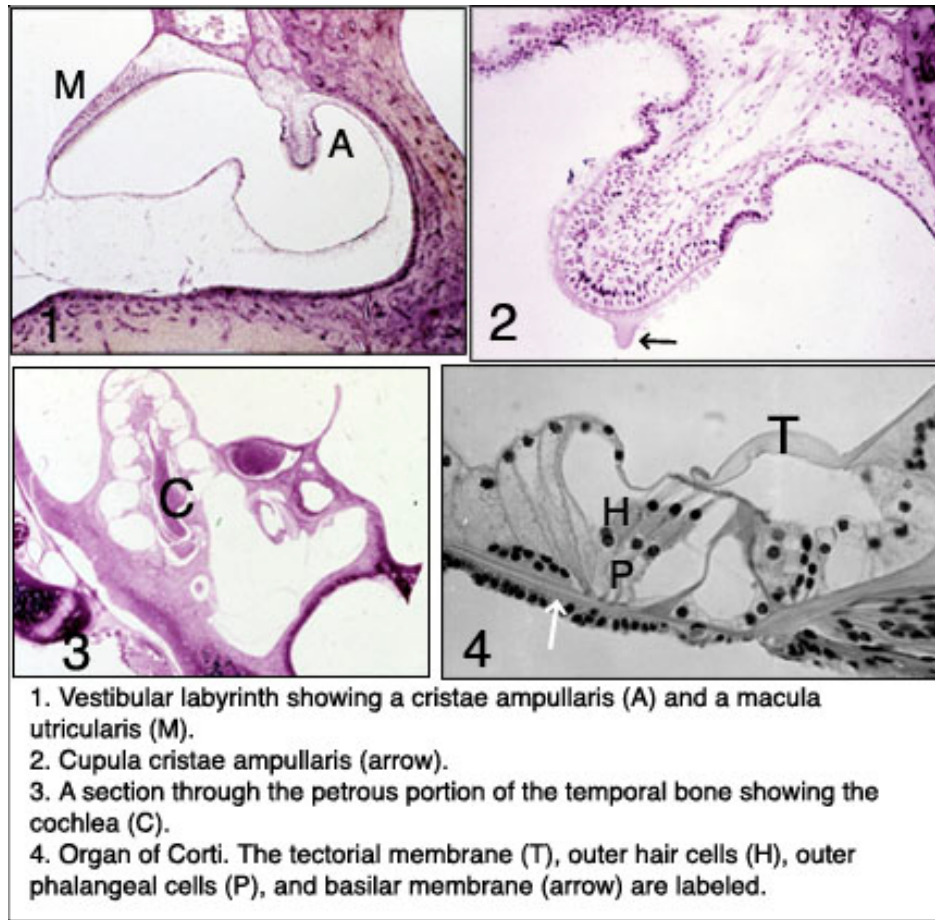
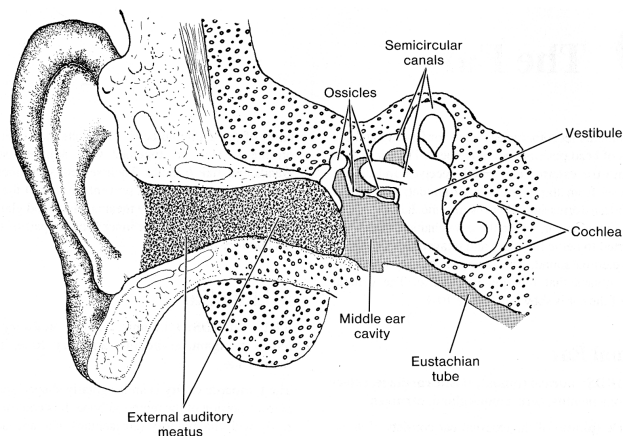


Ear



The ear contains receptors specialized for hearing and for awareness of head position and movement. The ear is subdivided into the external ear, which receives and directs sound waves from the external environment; the middle ear, which transforms sound waves into mechanical vibrations; and the inner ear, where these mechanical vibrations are converted to nerve impulses and relayed to the brain to be interpreted as sound. The inner ear also contains the vestibular organs that function in balance.



A diagrammatic sketch illustrating the general structure of the ear.

External Ear

The auricle (pinna) of the external ear consists of an irregular plate of elastic cartilage surrounded by a thick perichondrium rich in elastic fibers. The covering skin contains a few small hairs, their associated sebaceous glands, and an occasional eccrine sweat gland. The skin adheres tightly to the perichondrium except on the posterior surface, where a subcutaneous layer is present. The auricle is associated with sheets of skeletal muscle. The external auditory meatus is about 2.5 cm long and follows an open S-shaped course. It consists of an outer part whose cartilaginous walls are continuous with the auricular cartilage and an inner portion whose walls are formed by the temporal bone. The external auditory meatus is lined by keratinized stratified squamous epithelium that is continuous with the epidermis of the auricle. The epithelium is firmly anchored to the surrounding perichondrium or periosteum by dense collagenous connective tissue. Numerous small hairs are present in the epithelium of the outer part of the meatus and are associated with large sebaceous glands in the underlying connective tissue. A special form of simple coiled tubular apocrine sweat gland, the ceruminous gland, occurs in the skin that lines the meatus. Depending on the state of activity, the secretory cells may vary in shape from cuboidal to columnar. A network of myoepithelial cells that lies between the basal lamina and the bases of the epithelial cells surrounds each secretory tubule. The ducts may open directly on the surface or, together with adjacent sebaceous glands, into hair follicles. Their secretory product is cerumen, a waxy material that prevents drying of the skin that lines the external auditory meatus. Hairs and glands occur primarily along the roof of the inner (bony) part of the external auditory meatus.

Middle Ear

The tympanic cavity is an irregularly shaped space in the petrous portion of the temporal bone. It is continuous anteriorly with the auditory (eustachian) tube and posteriorly with the mastoid air cells (cavities) of the temporal bone. The lateral wall consists chiefly of the tympanic membrane (ear drum), which forms a partition separating the tympanic cavity from the external auditory meatus. The inner, bony wall of the middle ear makes contact with the inner ear via two small, membrane-covered openings called the oval and round windows. The membrane of the oval window contains the base of an auditory ossicle, the stapes. The membrane that covers the round window often is referred to as the secondary tympanic membrane. The tympanic cavity contains the auditory ossicles, a chain of three bones (malleus, incus, and stapes) that unites the tympanic membrane of the middle ear with the oval window of the inner ear. The ossicles consist of compact bone and are united by small synovial joints. The bones are suspended in the air-filled tympanic cavity by thin strands of connective tissue called ligaments. Small skeletal muscles, the tensor tympani and stapedius, are associated with two of the ossicles; the tendon of the tensor tympani attaches to the malleus, and the tendon from the stapedius attaches to the stapes. The bulk of the muscles themselves are contained within small canals in the temporal bone. The auditory ossicles, their suspending ligaments, and the inner walls of the tympanic cavity are covered by a thin mucous membrane that consists of a simple squamous epithelium lying on a thin layer of connective tissue. The mucous membrane is firmly attached to the periosteum of the temporal bone, lines the interior of the mastoid air cells, and covers the inner surface of the tympanic membrane. Where the tympanic cavity joins the auditory tube, the lining epithelium becomes ciliated columnar, interspersed with secretory cells. The auditory tube (eustachian tube) is about 4 cm long and connects the anterior part of the tympanic cavity with the nasopharynx. The auditory tube acts as a passageway to ventilate the tympanic cavity and allows equalization of pressure between the middle ear and pharynx.

Near the tympanic cavity the supporting wall consists of compact bone, whereas in its medial two-thirds, a J-shaped elastic cartilage supports the auditory tube. The bony portion is lined by a simple columnar epithelium that becomes ciliated pseudostratified columnar epithelium in the cartilaginous part. Cilia beat toward the pharynx. Goblet cells are present in the lining epithelium near the pharynx, and mixed, compound, tubuloalveolar glands often are found in the underlying connective tissue. A mass of lymphoid tissue, the tubal tonsil, fills the connective tissue and infiltrates the lining epithelium near the pharyngeal opening of the eustachian tube. The tympanic membrane forms most of the lateral wall of the tympanic cavity and is made up of three layers. The outer layer consists of stratified squamous epithelium, which reflects onto the tympanic membrane from the external auditory meatus. Two layers of collagenous fibers and fibroblasts form the middle layer. In the external layer, the fibers are arranged radially, whereas those of the inner layer run a circular pattern. A simple squamous epithelium and its supporting connective tissue form the third layer and are continuous with the mucosa lining the tympanic cavity. The fibrous layers of the tympanic membrane enter an encircling ring of fibrocartilage that unites the eardrum to the surrounding bone. The inner surface of the tympanic membrane attaches to the malleus. Sound waves received by the tympanic membrane cause it to vibrate slightly. The vibrations then are transmitted to the fluid-filled chambers of the inner ear via the ossicles. The tympanic membrane is about 18 times as large as the oval window of the inner ear, which contains the footplate of the stapes. Because of this arrangement, the eardrum and auditory ossicles act as a piston that exerts pressure on the confined fluid of the inner ear. Thus, the tympanic membrane and auditory ossicles not only transmit vibrations but also are able to amplify weak forces of sound waves without expending energy. The tensor tympani and stapedius muscles protect delicate structures in the inner ear by dampening ossicle movement resulting from loud or sudden noises. They also are thought to regulate the degree of tension in the tympanic membrane so that sounds of moderate intensity can be picked up in a noisy environment.

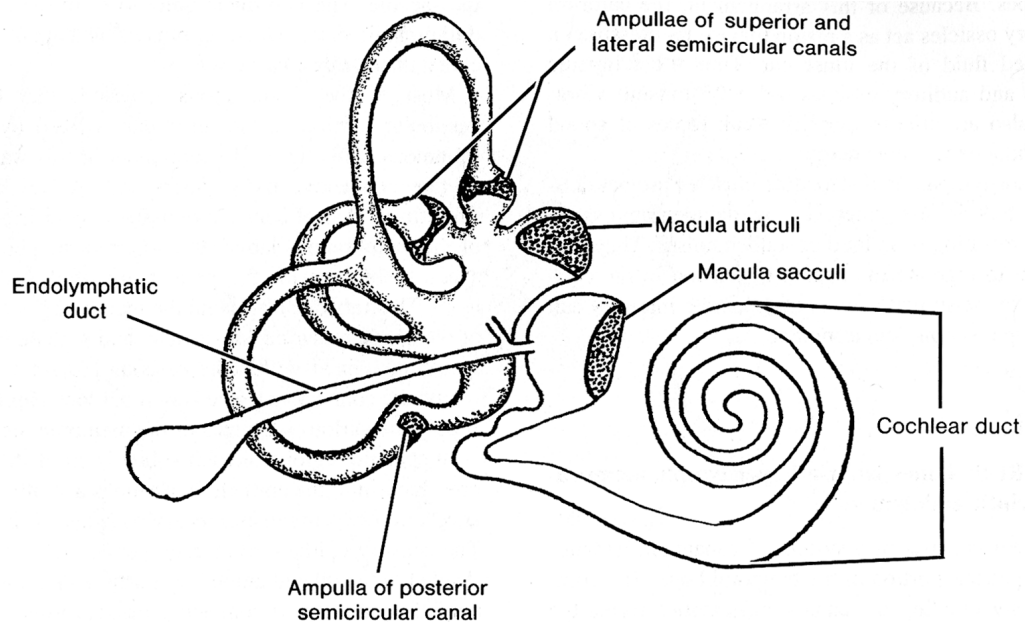
Inner Ear

The inner ear consists of a hearing receptor organ, the cochlea, and five vestibular sense organs devoted to balance and head position. It is made up of a system of canals and cavities within the petrous portion of the temporal bone. The compact bone immediately surrounding the canals and cavities forms the bony labyrinth and is filled with a fluid called perilymph. A series of fluid-filled membranous structures, collectively called the membranous labyrinth, lie suspended in the perilymph. The membranous labyrinth is filled with endolymph, a fluid with an ionic composition similar to that of intracellular fluid, being rich in potassium ions and low in sodium ions. Perilymph resembles extracellular fluid, having a high content of sodium ions and a low concentration of potassium ions. An area of the cochlear duct called the stria vascularis produces endolymph; the exact site of perilymph formation is unknown. The bony and membranous labyrinths consist of two major components: the vestibular labyrinth, which contains sensory elements for equilibrium, and the cochlea, which contains sensory structures for hearing.

Vestibular Labyrinth

The vestibular labyrinth consists of three semicircular canals that are continuous with an elliptical structure called the utricle. The utricle in turn unites with an anteromedial spherical part of the vestibular system called the saccule by a thin duct that joins with a similar duct from the saccule. The two ducts unite to form the slender endolymphatic duct, which terminates as

a small expansion called the endolymphatic sac. Most of the membranous labyrinth that forms the vestibular portion of the inner ear is lined by a simple squamous epithelium. The remainder of this wall consists of fine connective tissue fibers and stellate fibroblasts. Thin trabeculae of connective tissue extend from the wall of the membranous labyrinth and cross the perilymphatic space to blend with the periosteum of the surrounding bone. The trabeculae suspend the membranous component of the semicircular canals, utricle, and saccule in the perilymph contained within the osseous labyrinth. The perilymphatic connective tissue is rich in blood capillaries that supply the various segments of the membranous labyrinth. In specific regions of each subdivision of the membranous labyrinth, the epithelium assumes a stratified appearance and serves in sensory reception. The sensory epithelium of each semicircular canal is restricted to the dilated ampullary portion and, together with an underlying core of connective tissue, forms a transverse ridge that projects into the lumen of the ampulla. The connective tissue contains many nerve fibers. These sensory neuroepithelial regions of the semicircular canals form the cristae ampullaris. Similar raised regions of neuroepithelium are found in the utricle and saccule and form the macula utriculi and the macula sacculi, respectively. The macula utriculi cover an area approximately 2 mm square along the superoanterior wall. It lies on a plane perpendicular to the macula sacculi, which occupies an area measuring 2 x 3 mm on the anterior wall of the saccule. The macula of the utricle lies on a horizontal plane positioned at a right angle to the macula of the utricle. The macula of the saccule lies on a vertical plane at a right angle to the macula of the utricle. The sensory epithelium of the cristae and maculae consists of type I and type II sensory hair cells and supporting (sustentacular) cells.



A diagrammatic sketch illustrating the locations of the sensory regions in the membranous labyrinth (stippled area).

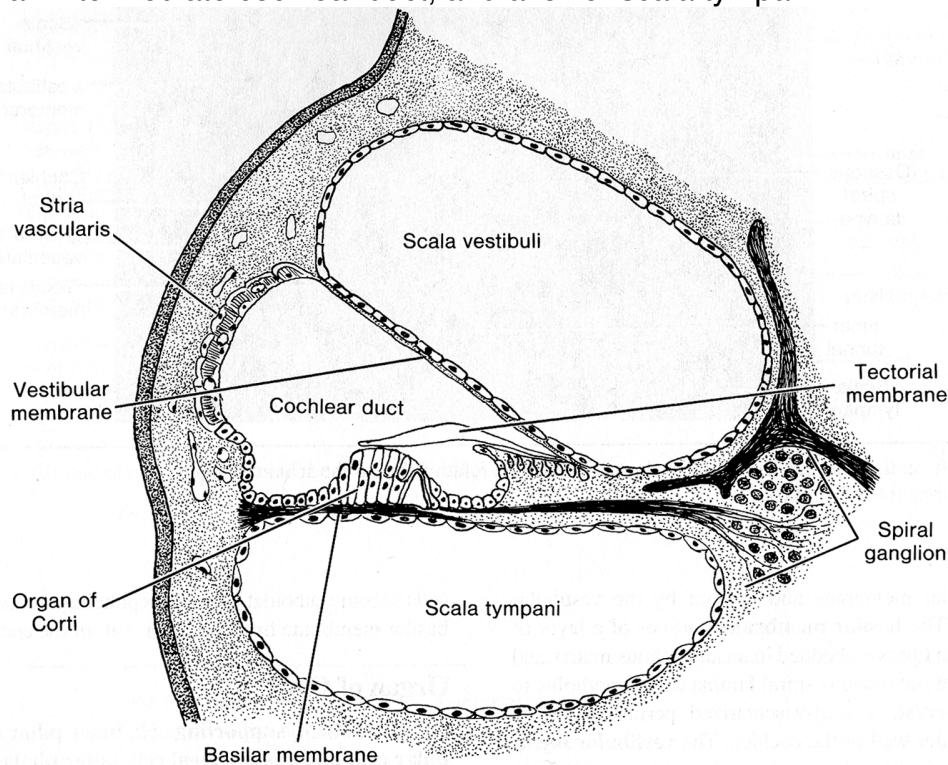
The type I hair cell is flask-shaped with a narrow apical region and a rounded base that contains the nucleus. A large part of the cell is enveloped by a cup-like afferent nerve ending (calyx). Nearby efferent nerve endings may synapse with the nerve calyx but do not directly contact the type I hair cell; a narrow intercellular cleft, 30 nm wide, separates the hair cell from

the nerve ending. The space narrows to approximately 5 nm at gap junctions that are scattered between the two compartments. Synaptic ribbons often are found in the cytoplasm of type I hair cells, immediately adjacent to the plasmalemma. Mitochondria are concentrated around the nucleus and at the cell apex, and numerous microtubules are present, especially in the apical region. The cytoplasm of the nerve calyx shows scattered mitochondria and many vesicles that range from 50 to 200 nm in diameter. The apical cell membrane of the type I hair cell bears 50 to 100 large, specialized microvilli, known as "hairs". These nonmotile elements are limited by a plasmalemma, have cytoplasmic cores that contain numerous fine filaments, and are constricted at their base just before they join the rest of the cell. The longitudinal filaments leave the microvilli and enter into a thick mat of filaments that forms a terminal web in the apical cytoplasm of the cell. The microvilli progressively increase in height from about 1 μm on one side to about 100 μm on the opposite side of the cell. Fine extracellular filaments link individual microvilli in each row. A single, eccentrically placed cilium is present on the apical surface and is peculiar in that the two central microtubules end shortly after originating from the basal body. The cilium is believed to be non-motile and often is called a kinocilium. Type II hair cells are simple columnar cells surrounded by numerous separate afferent and efferent nerve endings, rather than by a single afferent nerve ending as seen surrounding type I hair cells. The type II hair cell also bears a single, eccentrically placed, nonmotile cilium and 50 to 100 large microvilli that are arranged identically to those of type I cells. The cytoplasm contains scattered profiles of granular endoplasmic reticulum, abundant mitochondria, smooth-surfaced tubules, and numerous vesicles 20 nm in diameter. A well-developed Golgi complex occupies a supranuclear position. Synaptic ribbons are present in the cytoplasm of type II hair cells, immediately opposite the surrounding nerve terminals. Adjacent columnar-shaped supporting cells (sustentacular cells) extend from the basal lamina to the free surface of the sensory epithelium. They follow a very irregular course throughout the epithelium and in electron micrographs show a well-developed terminal web at the cell apex, a prominent Golgi complex, numerous secretory granules, and bundles of microtubules that extend from the basal cytoplasm to the terminal web. The microtubules form an integral part of the cytoskeleton and provide rigidity to the supporting cells. Although the function of the supporting cells is uncertain, it has been suggested that they are concerned with the metabolism of endolymph or that they contribute to the nutrition of hair cells. The supporting cells at the periphery of the sensory epithelium form a simple columnar layer, the planum semilunatum, which lacks hair cells. The microvilli of the hair cells in the cristae are embedded in a gelatinous structure called the cupula cristae ampullaris, which is composed of viscous proteoglycans that project from the surface of the crista into the ampullary lumen of each semicircular canal. Supporting cells in the sensory epithelium also may contribute to the cupula. The sulfated proteoglycans may be secreted by the planum semilunatum. The tallest row of microvilli of the hair cells from the maculae of the utricle and saccule also are embedded in a viscous proteoglycan that forms the otolithic membrane. Additionally, numerous crystalline bodies called otoliths (otoconia) are suspended in this layer. These bodies consist of protein and calcium carbonate. The gelatinous cupula of the cristae projects across the lumen of the ampullary region of the semicircular canal like a swinging door. During angular movement of the head, the cupula is displaced by the motion of endolymph contained within this part of the membranous labyrinth. Displacement of the cupula excites the sensory hair cells, which, in turn, generate an action potential that is received by surrounding nerve terminals. Similarly, gravitational forces on the otolithic membrane and the otoconia embedded within it cause a shearing action on the microvilli of the underlying hair cells in the macula. Linear acceleration also results in stimulation of hair cells in the macula. Although the exact mechanism is unknown, the sensory epithelium in the

vestibular organs transforms the mechanical energy of endolymph movement into the electrical energy of a nerve impulse. The bending or displacement of microvilli is thought open mechanoreceptors which results in the depolarization of hair cells, the action potential being transferred to surrounding nerve endings to result in the generation of a nerve impulse. Efferent nerve endings probably have inhibitory functions to control the threshold of activity of hair cells. It is thought that movement of microvilli towards the tallest row of microvilli depolarizes (excites) the hair cell whereas movement of microvilli towards the shortest row hyperpolarizes (inhibits) hair cell activity.

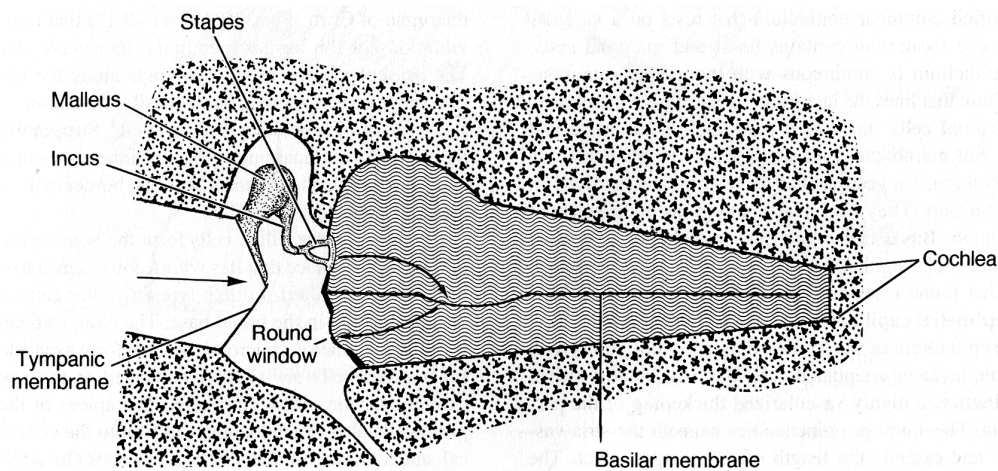
Cochlea

Like the vestibular portion of the inner ear, the cochlea consists of an outer portion of compact bone and a central membranous part contained in perilymph. The osseous part of the cochlea spirals for two and three-fourths turns around a cone-shaped axis of spongy bone called the modiolus. Blood vessels, nerve fibers, and the perikarya of afferent bipolar neurons, called the spiral ganglion, lie within the boney substance of the modiolus. A projection of bone, the spiral lamina, extends from the modiolus into the lumen of the cochlear canal along its entire course. A fibrous structure, the basilar membrane, extends from the spiral lamina to the spiral ligament, a thickening of periosteum on the outer boney wall of the cochlear canal. The thin vestibular membrane extends obliquely across the cochlear canal from the spiral lamina to the outer wall of the cochlea. The basilar and vestibular membranes divide the cochlear canal into an upper scala vestibuli, an intermediate cochlear duct, and a lower scala tympani.



A diagrammatic sketch illustrating a cross sectional view of the cochlear canal.

The cochlear duct is part of the endolymphatic system and is connected to the saccule of the membranous labyrinth by the small ductus reuniens. The opposite end of the cochlear duct terminates at the apex of the cochlea as the blindly ending cecum cupulare. The scala vestibuli and the scala tympani contain perilymph and communicate at the apex of the cochlea through a small opening called the helicotrema. At the base of the cochlea, the scala tympani is closed by the secondary tympanic membrane, which fills the round window. This membrane separates the perilymph in the scala tympani from the middle ear. The scala vestibuli extends through the perilymphatic channels of the vestibule to end at the oval window, which is closed by the foot of the stapes. Movement of the stapes in the oval window exerts pressure on the perilymph in the scala vestibuli. Because fluid cannot be compressed, waves of pressure either pass through the cochlear duct, displacing it to enter the scala tympani, or enter the scala tympani directly through the helicotrema. The pressure is released from the confined perilymphatic spaces of the cochlea by the elasticity of the secondary tympanic membrane, which bulges into the tympanic cavity of the middle ear.



A diagrammatic sketch illustrating the mechanics of hearing.

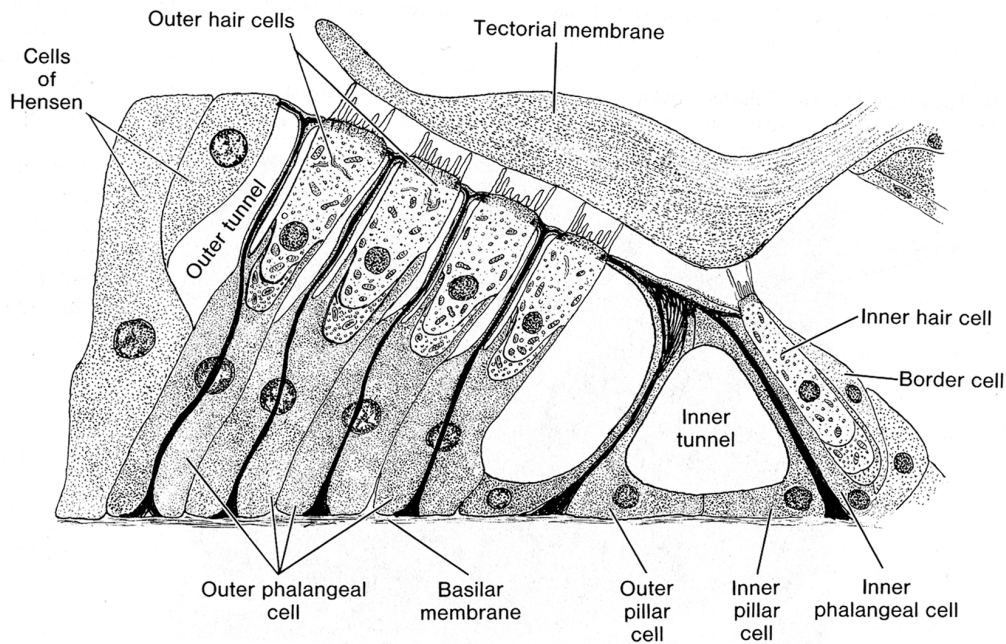
Cochlear Duct

The cochlear duct is a triangular space that follows the spiral course of the cochlea. Its floor is formed by the basilar membrane and its roof by the vestibular membrane. The basilar membrane consists of a layer of collagen-like fibers embedded in an amorphous matrix and extends from the osseous spiral lamina of the modiolus to the spiral crest, a well-vascularized periosteal region along the outer wall of the cochlea. The vestibular membrane consists of two layers of simple squamous cells separated mainly by their basal laminae. A vascular area called the stria vascularis forms the outer wall of the cochlear duct. It occurs along the entire length of the cochlear duct and consists of a pseudostratified columnar epithelium that rests on a vascular connective tissue and contains basal and marginal cells. The epithelium is continuous with the simple squamous epithelium that lines the interior of the vestibular membrane. Marginal cells show deep infoldings of the basal and lateral cell membranes and are associated with numerous mitochondria, suggesting that these cells are involved in fluid transport. They may participate in the elaboration of endolymph. Basal cells show few mitochondria or basal infoldings. The epithelium of the stria vascularis differs from that found

elsewhere in the body in that it contains intraepithelial capillaries. The epithelium of the stria vascularis is continuous with a simple layer of attenuated cells that overlies the spiral prominence, a highly vascularized thickening of the periosteum. The spiral prominence lies beneath the stria vascularis and extends the length of the cochlear duct. The cells become cuboidal where the epithelium reflects onto the basilar membrane from the outer wall of the cochlear duct.

Organ of Corti

The cochlear duct contains a region of specialized cells, the organ of Corti, that transforms vibrations of the basilar membrane into nerve impulses. The avascular organ of Corti extends along the length of the cochlear duct and lies on the basilar membrane. It consists mainly of supporting and hair cells. Supporting cells are tall columnar and consist of inner and outer pillar cells, inner and outer phalangeal cells, border cells, cells of Hensen, and cells of Claudius. Inner and outer pillar cells form the boundaries of the inner tunnel, a space that lies within and extends the length of the organ of Corti. In both types of pillar cells, the nucleus is located in the broad base. The elongated cell bodies contain numerous microtubules that form a cytoskeleton. Inner pillar cells are slightly expanded at the apex and extend over the outer pillar cells. The apices of the outer pillar cells also expand slightly to fit into the concave apical undersurface of the inner pillar cells. In addition to forming the boundaries of the inner tunnel, the pillar cells provide structural support for adjacent cells. The phalangeal cells serve as supporting elements for the sensory hair cells. The inner phalangeal cells form a single row immediately adjacent to the inner pillar cells and surround the sensory inner hair cells except at their apical regions. In contrast, the columnar outer phalangeal cells form three or four rows and support outer hair cells, which also are arranged in rows. The apex of each outer phalangeal cell forms a cup-like structure that surrounds the basal one-third of an outer hair cell. Afferent and efferent nerves are located at the base. Each outer phalangeal cell gives rise to a slender cytoplasmic process filled with microtubules. The process extends to the surface, where it expands into a flat plate that attaches to the apical edges of the outer hair cell and is supported laterally by outer phalangeal cells and the outer hair cells in the adjacent row. The apical plates of the outer phalangeal cells provide additional support for the outer hair cells, the upper two-thirds of which are not supported by adjacent cells and are surrounded by large, fluid-filled intercellular spaces. The fluid contained in these spaces is believed to be similar to that within the inner tunnel.



A diagrammatic sketch of the organ of Corti.

Border cells are supporting cells associated with the inner edge of the organ of Corti. These slender cells undergo a transition to the squamous cells that line the inner spiral tunnel. This space is formed by the spiral limbus, which consists of periosteal connective tissue that extends from the osseous spiral lamina and bulges into the cochlear duct. Vertically arranged collagenous fibers, often called auditory teeth, are contained within the substance of the limbus. Interdental cells are specialized cells along the upper surface of the spiral limbus. The cells extend between collagen fibers to reach the lumen of the cochlear duct. On the upper surface of the limbus, they form a continuous sheet and are united by tight junctions. The interdental cells secrete a sheet of material that forms the tectorial membrane, which consists of a gelatinous matrix rich in proteoglycans and a filamentous protein thought to be similar to epidermal keratin. The tectorial membrane extends over the interdental cells and beyond the substance of the spiral limbus to overlie the hair cells of the organ of Corti. The tips of microvilli extending from the outer and inner hair cells contact the undersurface of the tectorial membrane. Near the outer edge of the organ of Corti, immediately adjacent to the outer phalangeal cells, is another group of columnar supporting cells called cells of Hensen. They decrease in height and transform into the adjacent cells of Claudius, which form the outer edge of the organ of Corti. The sensory hair cells are divided into inner and outer hair cells. Inner hair cells form a single row along the inner aspect of the organ of Corti and extend the length of the cochlea. Like type I hair cells of the vestibular labyrinth, the inner hair cells of the cochlea are short, flask-shaped cells with narrow necks. Well-developed microvilli extend from the apical surface of the inner hair cells, but unlike type I hair cells, they lack a kinocilium. The microvilli contain numerous filaments that extend into a dense terminal web in the apical cytoplasm. Mitochondria aggregate just beneath the terminal web and also are scattered throughout the remainder of the cytoplasm, which contains scattered ribosomes and profiles of smooth endoplasmic reticulum. Numerous nerve endings synapse with the bases of the inner hair cells on a plane below the level of the nucleus. The columnar outer hair cells usually form

three or four rows and are supported by the apices of the outer phalangeal cells. Microvilli are arranged in the shape of a V. There is no cilium. Mitochondria aggregate at the base of the outer hair cell, which makes contact with afferent and efferent nerve fibers. In all other respects, the outer hair cells are similar to the inner hair cells, and both are receptors of sound in the organ of Corti.

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