Sensory Receptors

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Sensory Receptors: Introduction

Each type of sensory receptor responds to a particular modality of stimulus by causing the production of action potentials in a sensory neuron.
These impulses are conducted to parts of the brain that provide the proper interpretation of the sensory information when that specific neural pathway is activated.
Our perceptions of the world—its textures, colors, and sounds; its warmth, smells, and tastes—are created by the brain from electrochemical nerve impulses delivered to it from sensory receptors.
These receptors **transduce** (change) different forms of energy in the “real world” into the energy of nerve impulses that are conducted into the central nervous system by sensory neurons. Different *modalities* (forms) of sensation—sound, light, pressure, and so forth—result from differences in neural pathways and synaptic connections.

Categories of Sensory Receptors

Sensory receptors can be categorized on the basis of **structure** or various **functional** criteria.
Structurally, the sensory receptors may be the dendritic endings of sensory neurons. These dendritic endings may be free, such as those that respond to pain and temperature, or encapsulated within nonneural structures, such as those that respond to pressure. The photoreceptors in the retina of the eyes (rods and cones) are highly specialized neurons that synapse with other neurons in the retina. In the case of taste buds and of hair cells in the inner ears, modified epithelial cells respond to an environmental stimulus and activate sensory neurons.

Functional Categories

Sensory receptors can be grouped according to the type of stimulus energy they transduce. These categories include

- **chemoreceptors,** which sense chemical stimuli in the environment or the blood (e.g., the taste buds, olfactory epithelium, and the aortic and carotid bodies);
- **photoreceptors**—the rods and cones in the retina of the eye;
- **thermoreceptors,** which respond to heat and cold; and
- **mechanoreceptors,** which are stimulated by mechanical deformation of the receptor cell membrane (e.g., touch and pressure receptors in the skin and hair cells within the inner ear).
- **nociceptors** are pain receptors that depolarize in response to stimuli that accompany tissue damage. These stimuli include noxiously high heat or pressure, acid, and a variety of chemicals such as bradykinin, prostaglandins, nitric oxide, adenosine, and ATP.

Functional Categories # 2

Receptors also can be grouped according to the type of sensory information they deliver to the brain.

Proprioceptors include the muscle spindles, Golgi tendon organs, and joint receptors. These provide a sense of body position and allow fine control of skeletal movements.

Cutaneous (skin) **receptors** include

- touch and pressure receptors,
- heat and cold receptors, and
- pain receptors.

The receptors that mediate sight, hearing, equilibrium, taste, and smell are grouped together as the **special senses.**

Functional Categories # 3

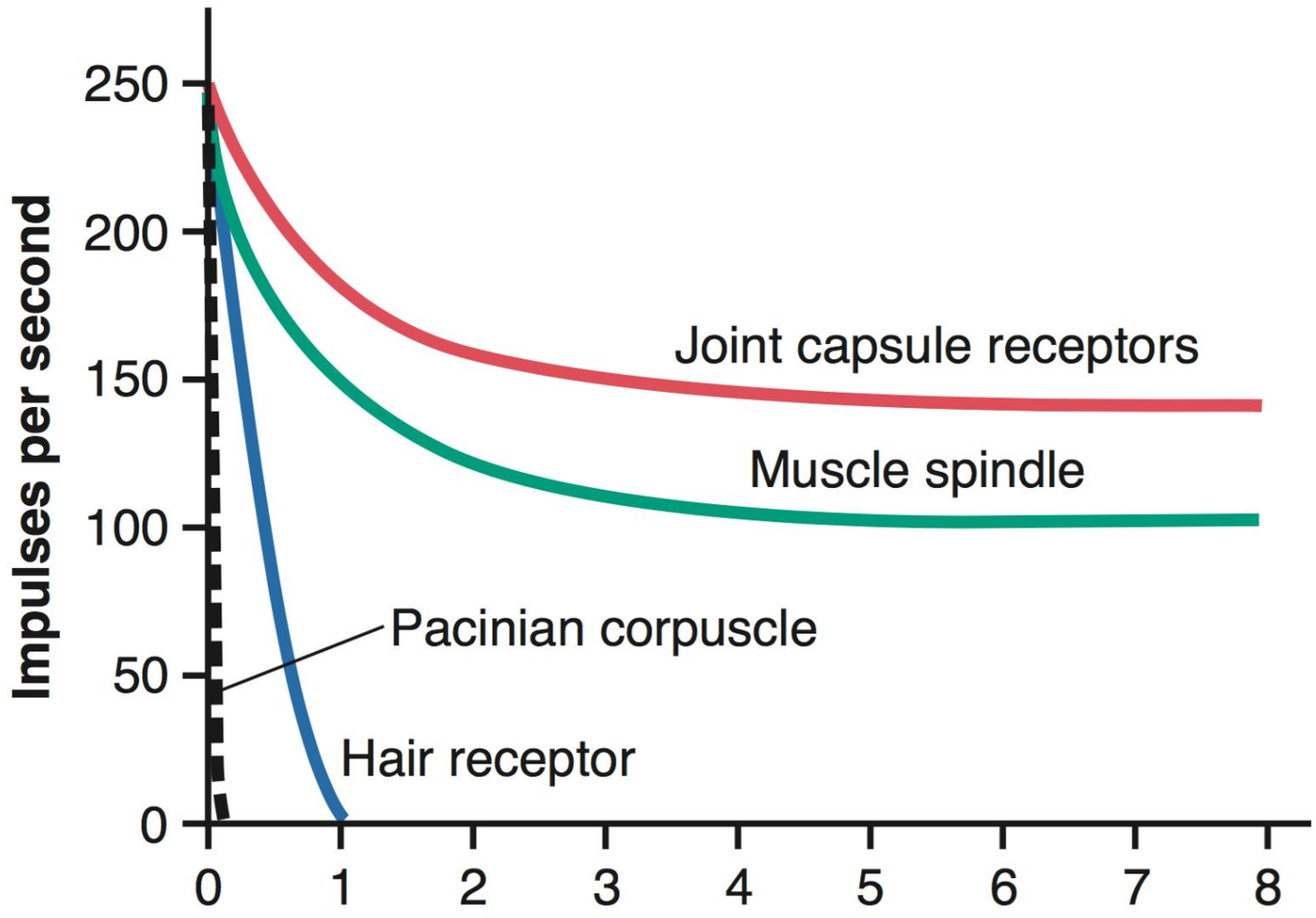
In addition, receptors can be grouped into
exteroceptors, which respond to stimuli from outside of the body (such as those involved in touch, vision, and hearing), and
interoceptors, which respond to internal stimuli. Interoceptors are found in many organs, and include mechanoreceptors and chemoreceptors. An example of mechanoreceptors are those in blood vessels that respond to stretch induced by changes in blood pressure, and chemoreceptors include those that monitor blood pH or oxygen concentration in the regulation of breathing.

Tonic and Phasic Receptors

Some receptors respond with a burst of activity when a stimulus is first applied, but then quickly decrease their firing rate— adapt to the stimulus—if the stimulus is maintained. Receptors with this response pattern are called **phasic receptors**. An example of a phasic receptor is a pacinian corpuscle (a pressure receptor). Some other phasic receptors respond with a quick, short burst of impulses when a stimulus is first applied, and then with another quick short burst of impulses when the stimulus is removed. These phasic receptors thus provide information regarding the “on” and “off” of a stimulus. Those receptors that maintain their higher firing rate the entire time that a stimulus is applied are known as **tonic receptors**.

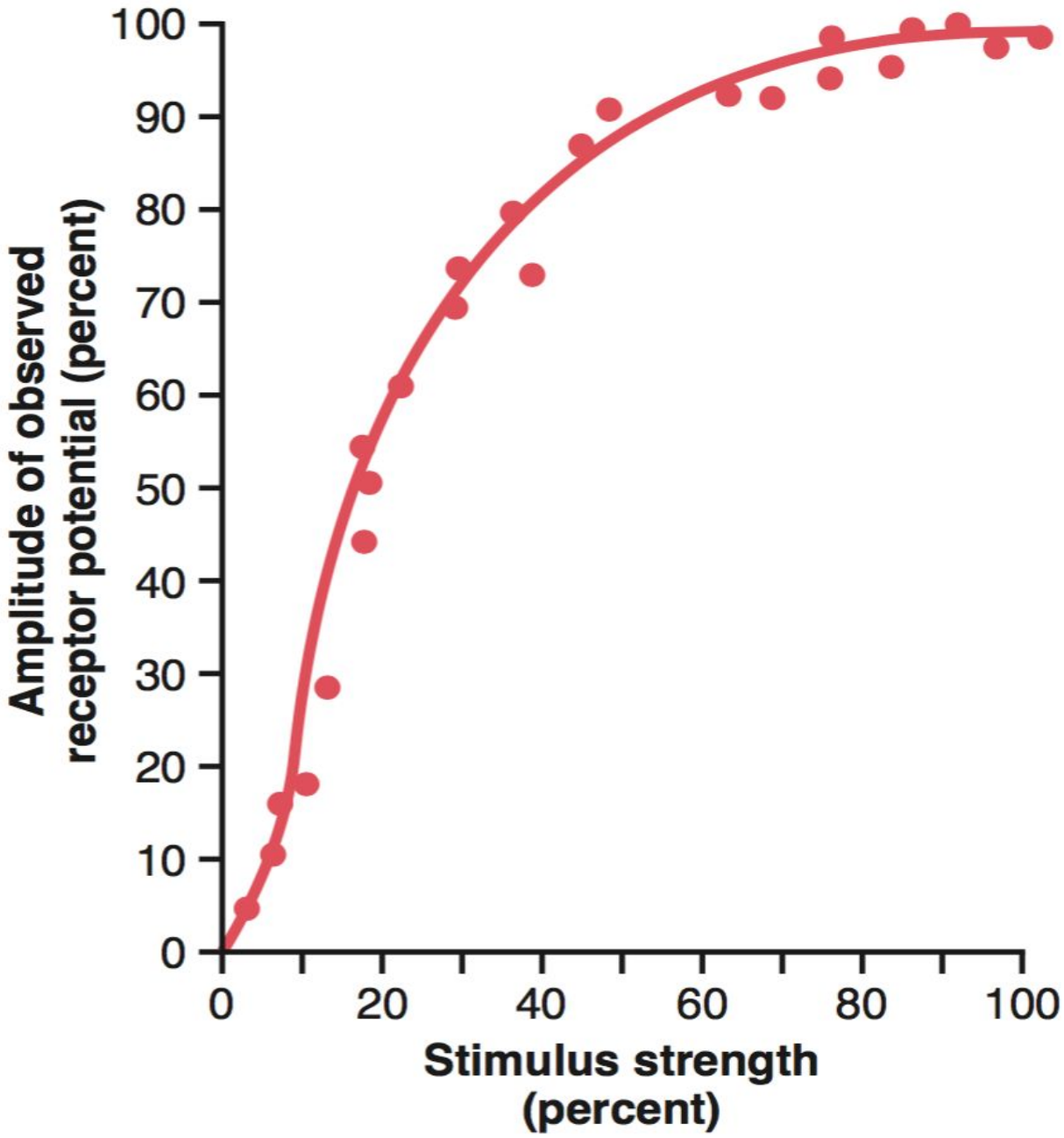
Adaptation of Receptors

Figure 1 shows typical adaptation of certain types of receptors.
Adaptation of different types of receptors showing rapid adaptation of some receptors and slow adaptation of others.



Relation between Stimulus Intensity and the Receptor Potential

The amplitude increases rapidly at first but then progressively less rapidly at high stimulus strength.
In turn, the *frequency of repetitive action potentials* transmitted from sensory receptors increases approximately in proportion to the increase in receptor potential.
Putting this principle together with the data in **Figure**, one can see that very intense stimulation of the receptor causes progressively less and less additional increase in numbers of action potentials. This exceedingly important principle is applicable to almost all sensory receptors. It allows the receptor to be sensitive to very weak sensory experience and yet not reach a maximum ring rate until the sensory experience is extreme. This feature allows the receptor to have an extreme range of response, from very weak to very intense.



Law of Specific Nerve Energies

Stimulation of a sensory nerve fiber produces only one sensation—touch, or cold, or pain, and so on.
According to the **law of specific nerve energies,** the sensation characteristic of each sensory neuron is that produced by its normal stimulus, or **adequate stimulus**. Also, although a variety of different stimuli may activate a receptor, the adequate stimulus requires the least amount of energy to do so. The adequate stimulus for the photoreceptors of the eye, for example, is light, where a single photon can have a measurable effect. If these receptors are stimulated by some other means—such as by the high pressure produced by a punch to the eye—a flash of light (the adequate stimulus) may be perceived.
The effect of **paradoxical cold** provides another example of the law of specific nerve energies. When the tip of a cold metal rod is touched to the skin, the perception of cold gradually disappears as the rod warms to body temperature. Then, when the tip of a rod heated to 45C is applied to the same spot, the sensation of cold is perceived once again. This paradoxical cold is produced because the heat slightly damages receptor endings, and by this means produces an “injury current” that stimulates the receptor.

Generator (Receptor) Potential

The electrical behavior of sensory nerve endings is similar to that of the dendrites of other neurons. In response to an environmental stimulus, the sensory endings produce local graded changes in the membrane potential. In most cases, these potential changes are depolarizations that are analogous to the excitatory postsynaptic potentials (EPSPs). In the sensory endings, however, these potential changes in response to stimulation are called **receptor,** or **generator, potentials** because they serve to generate action potentials in response to the sensory stimulation. Because sensory neurons are pseudounipolar, the action potentials produced in response to the generator potential are conducted continuously from the periphery into the CNS.

Taste

Gustation, the sense of taste, is evoked by receptors that consist of barrel-shaped **taste buds**. Located primarily on the dorsal surface of the tongue, each taste bud consists of 50 to 100 specialized epithelial cells with long microvilli that extend through a pore in the taste bud to the external environment, where they are bathed in saliva.

These sensory epithelial cells are not neurons, they behave like neurons; they become depolarized when stimulated appropriately, produce action potentials, and release neurotransmitters that stimulate sensory neurons associated with the taste buds.

Because of this, some scientists classify the taste cells as *neuroepithelial cells.*

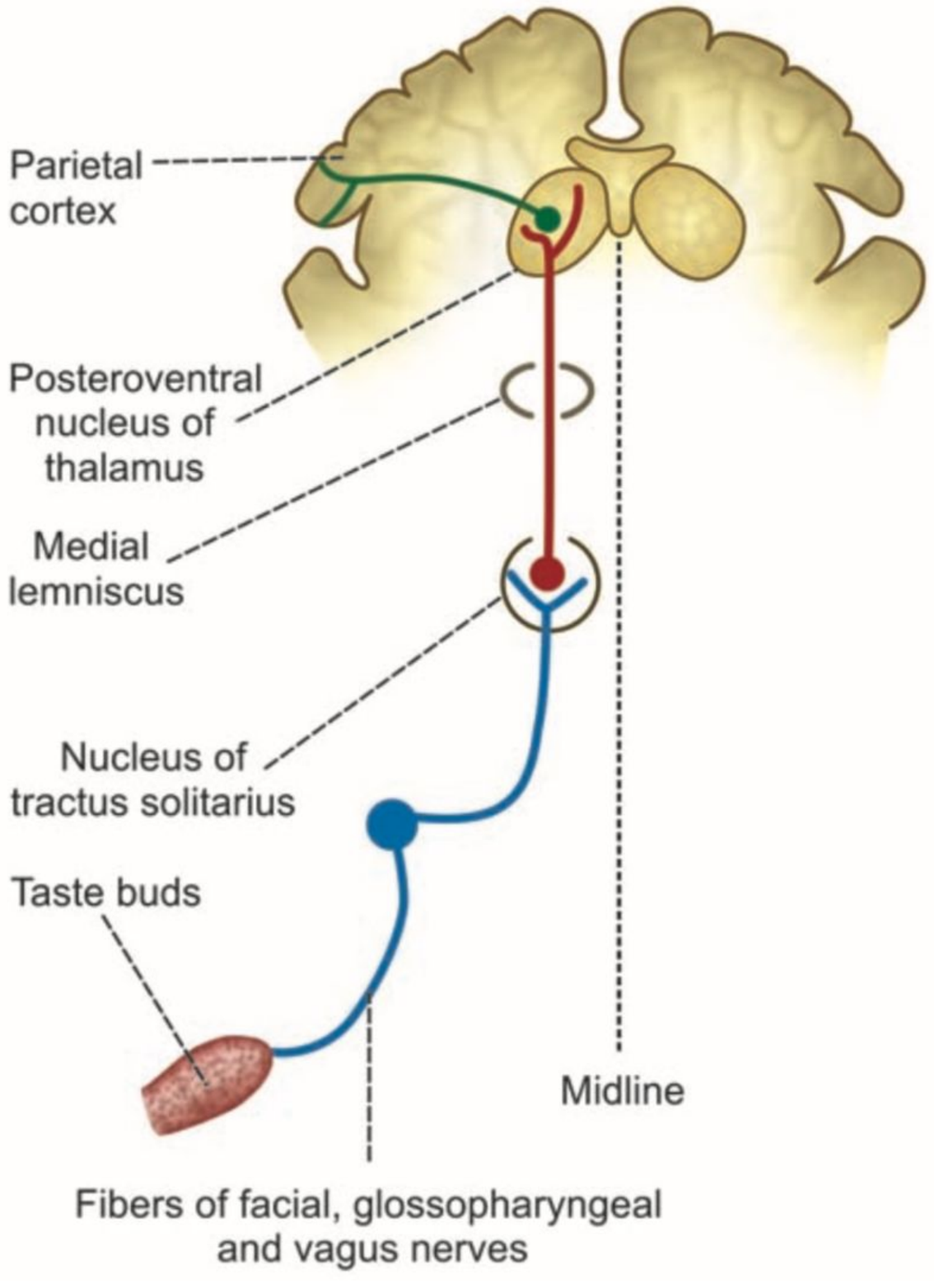
Taste buds are located mainly within epithelial papillae.

These include

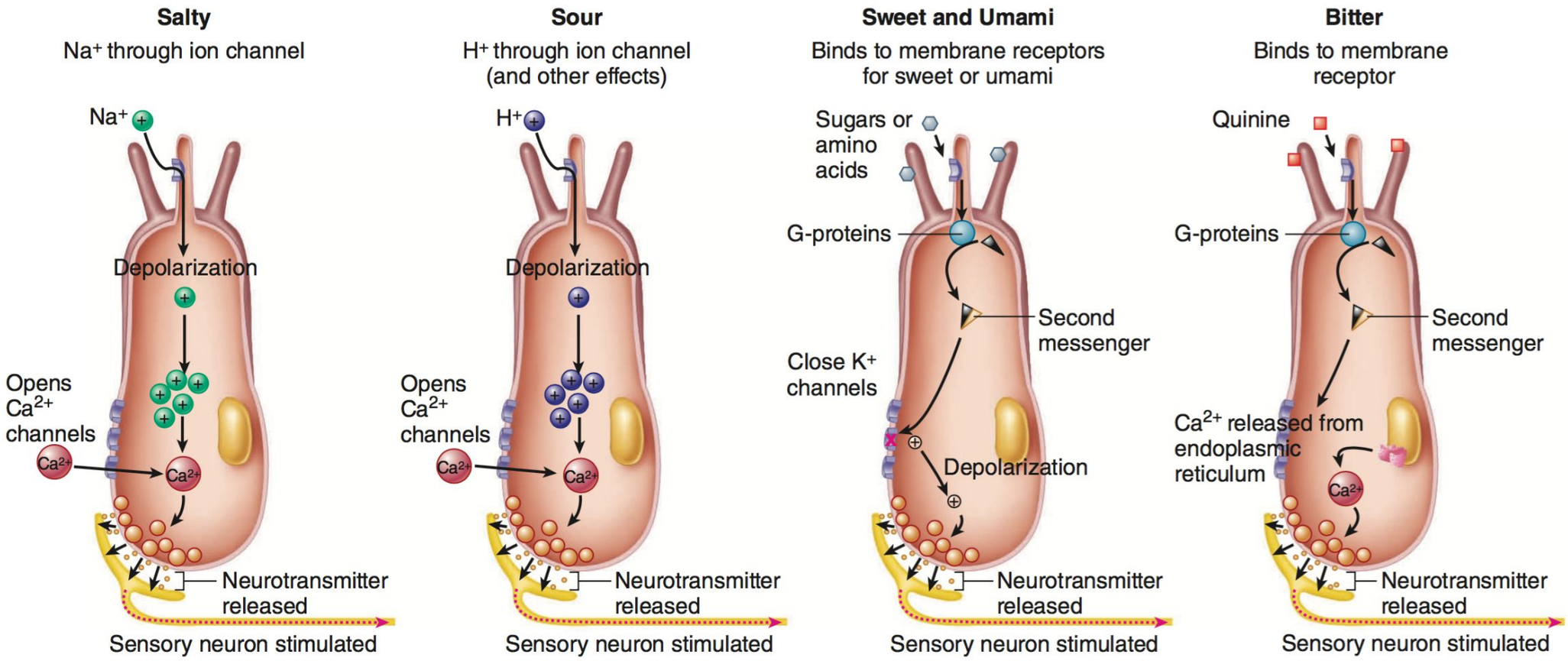
- *fungiform papillae* on the anterior surface of the tongue;
- *circumvallate papillae* on the posterior surface of the tongue;
- *foliate papillae* on the sides of the tongue.

Pathway for taste sensation

Information regarding taste is transmitted from the taste buds on the fungiform papillae via the **chorda tympani branch** of the **facial nerve (VII)** and from the taste buds on the circumvallate and foliate papillae via the **glossopharyngeal nerve (IX).** These nerves carry taste information to a nucleus of second-order neurons in the medulla oblongata. From there, the second-order neurons project to the thalamus, which serves as a switchboard for directing sensory information to the cerebral cortex. Third-order neurons from the thalamus convey taste information to the **primary gustatory cortex** in the insula, and to the somatosensory cortex of the postcentral gyrus devoted to the tongue. Information is also sent to the prefrontal (orbitofrontal) cortex, which is important for taste associations and the perception of flavor.



Taste



The five major categories of taste. Each category of taste activates specific taste cells by different means. Notice that taste cells for salty and sour are depolarized by ions (Na^+ and H^+, respectively) in the food, whereas taste cells for sweet, umami, and bitter are depolarized by sugars, the amino acids glutamate and aspartate (not shown), and quinine, respectively, by means of G-protein-coupled receptors and the actions of second messengers.

Smell

The receptors responsible for **olfaction** are located in the olfactory epithelium.
The olfactory apparatus consists of *receptor cells* (which are bipolar neurons), *supporting (sustentacular) cells,* and *basal stem cells.*
The stem cells generate new receptor cells every one to two months to replace the neurons damaged by exposure to the environment.
The supporting cells are epithelial cells rich in enzymes that oxidize hydrophobic volatile odorants, thereby making these molecules less lipid-soluble and thus less able to penetrate membranes and enter the brain.
Each bipolar sensory neuron has one dendrite that projects into the nasal cavity, where it terminates in a knob containing cilia. It is the plasma membrane covering the cilia that contains the receptor proteins that bind to odorant molecules. The axon of each olfactory neuron thereby conveys information relating only to the specific odorant molecule that stimulated that neuron.
The olfactory receptors are G-protein-coupled receptors. This means that before the odorant molecule binds to its receptor, the receptor is associated with the three G-protein subunits (a, b, and g). When an odorant molecule binds to its receptor, these subunits dissociate, move in the plasma membrane to adenylate cyclase, and activate this enzyme. Adenylate (or adenyl) cyclase catalyzes the conversion of ATP into cyclic AMP (cAMP) and PPi (pyrophosphate). The cAMP serves as a second messenger, opening ion channels that allow inward diffusion of Na^+ and Ca^{2+}. This produces a graded depolarization, the receptor potential, which then stimulates the production of action potentials.
Up to 50 G-proteins may be associated with a single receptor protein.

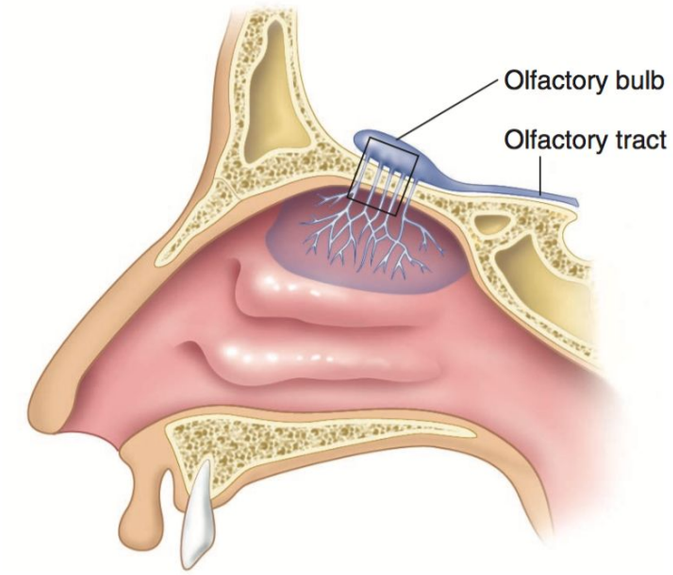
The Neural Pathway of Smell

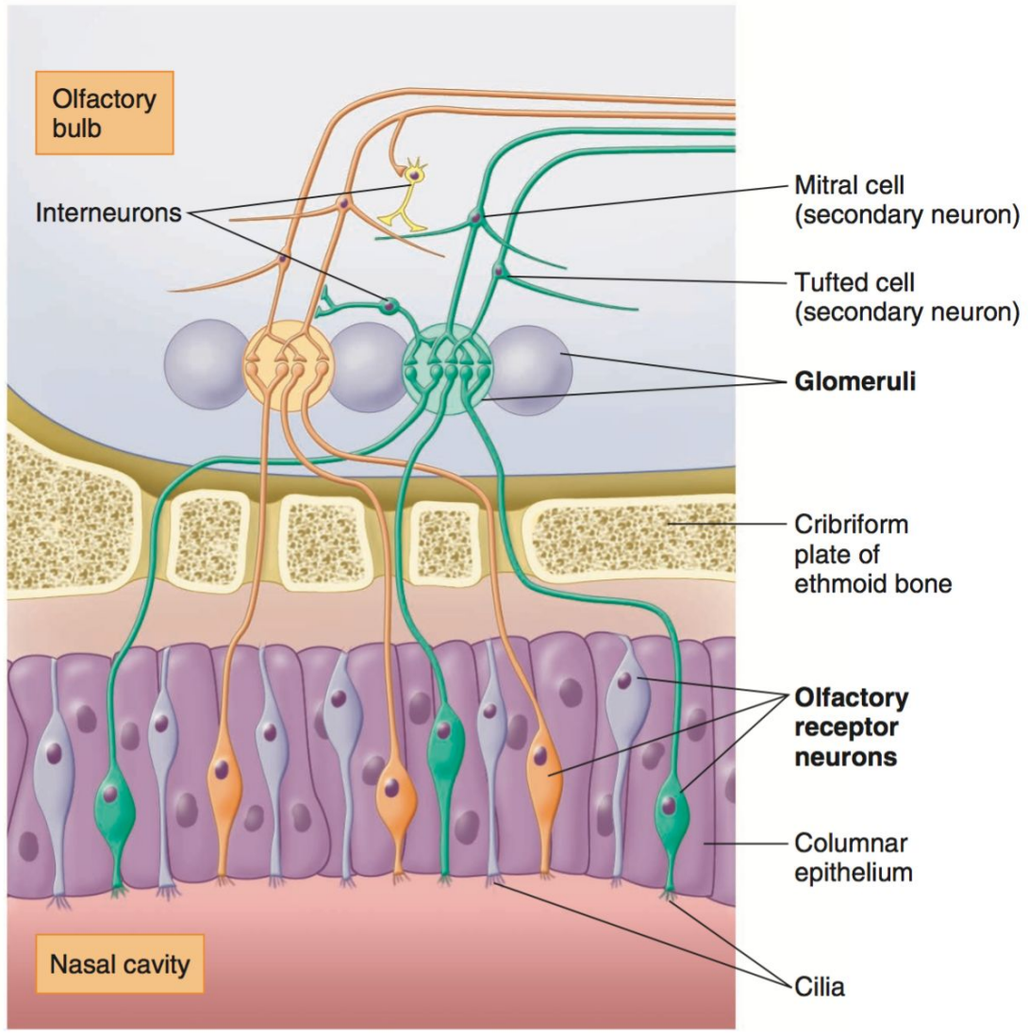
The processing of olfactory information begins in the olfactory bulb, where the bipolar sensory neurons synapse with neurons located in spherically shaped arrangements called glomeruli. Evidence suggests that each glomerulus receives input from one type of olfactory receptor. Identification of an odor is improved by inhibition provided by GABA released from periglomerular cells that surround the glomerulus and make dendrodendritic synapses with the second-order neurons within the glomerulus (termed mitral and tufted cells).

The mitral and tufted neurons of the olfactory glomeruli in the olfactory bulb send axons through the lateral olfactory tracts to numerous brain regions of the frontal and medial temporal lobes that comprise the primary olfactory cortex. There are interconnections between these regions and the amygdala, hippocampus, and other structures of the limbic system. For example, the piriform cortex, a pear-shaped region at the medial junction of the frontal and temporal lobes, receives projections from the olfactory bulb and makes reciprocal connections with the prefrontal cortex and amygdala, among other structures.

The prefrontal cortex receives information regarding taste as well as smell; perhaps this is why olfactory stimulation during eating can be perceived as taste rather than smell.

Smell





The neural pathway for olfaction.
The olfactory epithelium contains receptor neurons that synapse with neurons in the olfactory bulb of the cerebral cortex.
The synapses occur in rounded structures called glomeruli.
Secondary neurons, known as tufted cells and mitral cells, transmit impulses from the olfactory bulb to the olfactory cortex in the medial temporal lobes.
Each glomerulus receives input from only one type of olfactory receptor, regardless of where those receptors are located in the olfactory epithelium.

VESTIBULAR APPARATUS AND EQUILIBRIUM

The sense of equilibrium, which provides orientation with respect to gravity, is due to the function of an organ called the **vestibular apparatus.** The vestibular apparatus and a snail-shaped structure called the *cochlea,* which is involved in hearing, form the **inner ear** within the temporal bones of the skull.

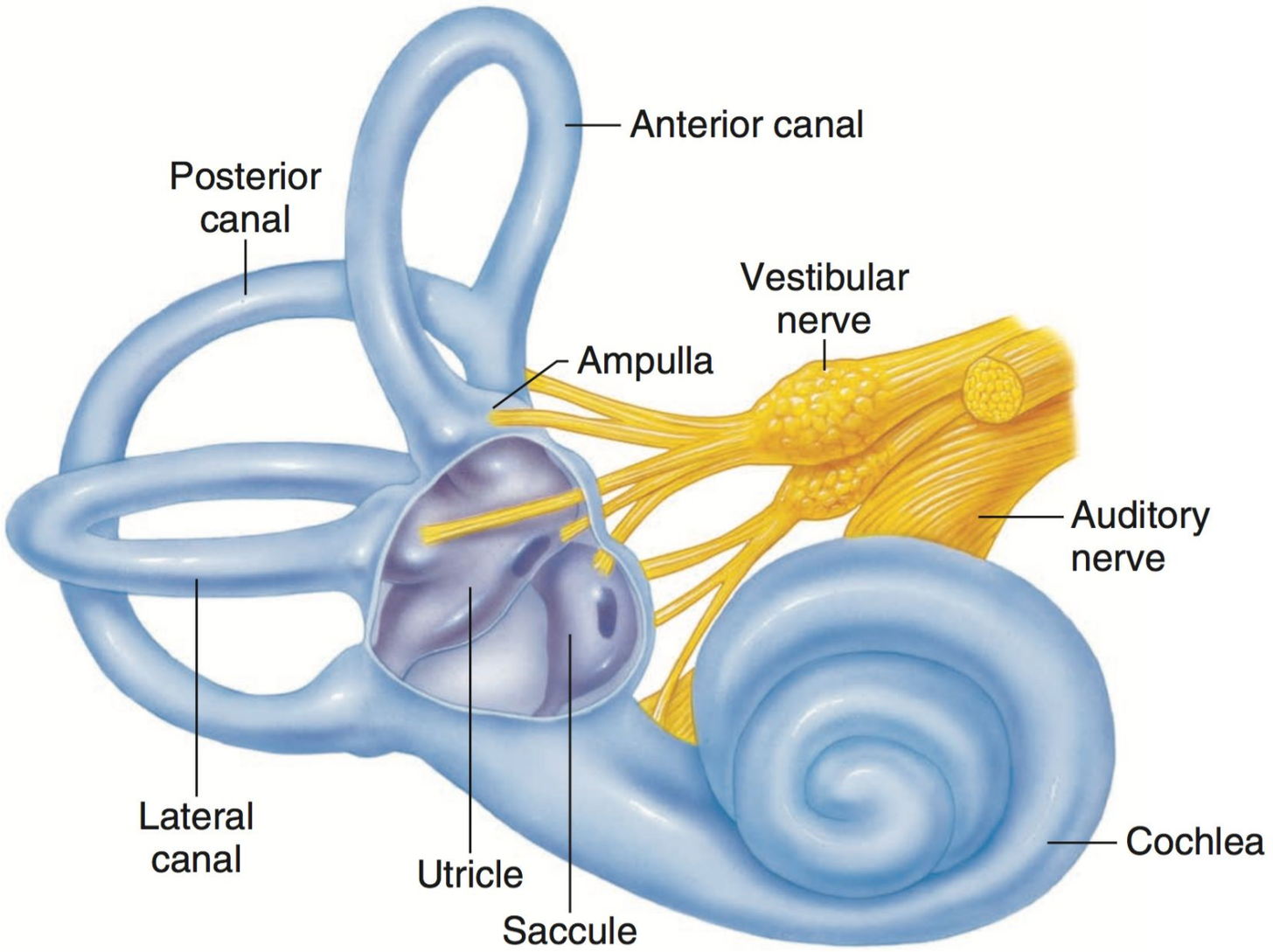
The vestibular apparatus consists of two parts:

- the *otolith organs,* which include the *utricle* and *saccule,*
- the *semicircular canals*

The sensory structures of the vestibular apparatus and cochlea are located within the **membranous labyrinth**, a tubular structure that is filled with a fluid called **endolymph.** Endolymph is unlike any other extracellular fluid: it has a higher K^+ concentration (higher even than in the intra-cellular compartment) and much lower concentrations of Na^+ and Ca^{2+} than do other extracellular fluids.

The membranous labyrinth is located within a bony cavity in the skull, the **bony labyrinth.** Within this cavity, between the membranous labyrinth and the bone, is a fluid called **perilymph.** Unlike endolymph, perilymph is fairly typical of extracellular fluids such as cerebrospinal fluid.

The cochlea and vestibular apparatus of the inner ear



The vestibular apparatus consists of the utricle and saccule (together called the otolith organs) and the three semicircular canals. The base of each semicircular canal is expanded into an ampulla that contains sensory hair cells

Sensory Hair Cells of the Vestibular Apparatus

The utricle and saccule provide information about *linear acceleration*—changes in velocity when traveling horizontally or vertically. We therefore have a sense of acceleration and deceleration when riding in a car or when skipping rope. A sense of *rotational,* or *angular, acceleration* is provided by the semicircular canals, which are oriented in three planes like the faces of a cube. This helps us maintain balance when turning the head, spinning, or tumbling.

The receptors for equilibrium are modified epithelial cells. They are known as **hair cells** because each cell contains 20 to 50 hairlike extensions. These are actually modified microvilli called **stereocilia** arranged in rows of increasing height. Touching the stereocilia of the tallest row is an even taller true cilium called a **kinocilium**.

When the stereocilia are bent in the direction of the kinocilium, the plasma membrane is depressed and ion channels for K^+ are opened, allowing K^+ to passively enter and depolarize the hair cell. This causes the hair cell to release a synaptic transmitter that stimulates the dendrites of sensory neurons that are part of the *vestibulocochlear nerve (VIII).*

When the stereocilia are bent in the opposite direction, the membrane of the hair cell becomes hyperpolarized and, as a result, releases less synaptic transmitter. In this way, the frequency of action potentials in the sensory neurons that innervate the hair cells carries information about the direction of movements that cause the hair cell processes to bend.

Utricle and Saccule

The otolith organs, the **utricle** and **saccule,** each have a patch of specialized epithelium called a *macula* that consists of hair cells and supporting cells. The hair cells project into the endolymphfilled membranous labyrinth, with their hairs embedded in a gelatinous **otolithic membrane**.
The otolithic membrane contains microscopic crystals of calcium carbonate (otoliths) from which it derives its name (*oto* = ear; *lith* = stone). These stones increase the mass of the membrane, which results in a higher inertia (resistance to change in movement).
Because of the orientation of their hair cell processes into the otolithic membrane, the utricle is more sensitive to horizontal acceleration and the saccule is more sensitive to vertical acceleration.

Semicircular Canals

The three **semicircular canals** project in three different planes at nearly right angles to each other.
Each canal contains an inner extension of the membranous labyrinth called a *semicircular duct,* and at the base of each duct is an enlarged swelling called the *ampulla.*
The *crista ampullaris,* an elevated area of the ampulla, is where the sensory hair cells are located. The processes of these cells are embedded in a gelatinous membrane, the **cupula**, which has a higher density than that of the surrounding endolymph. Like a sail in the wind, the cupula can be pushed in one direction or the other by movements of the endolymph.

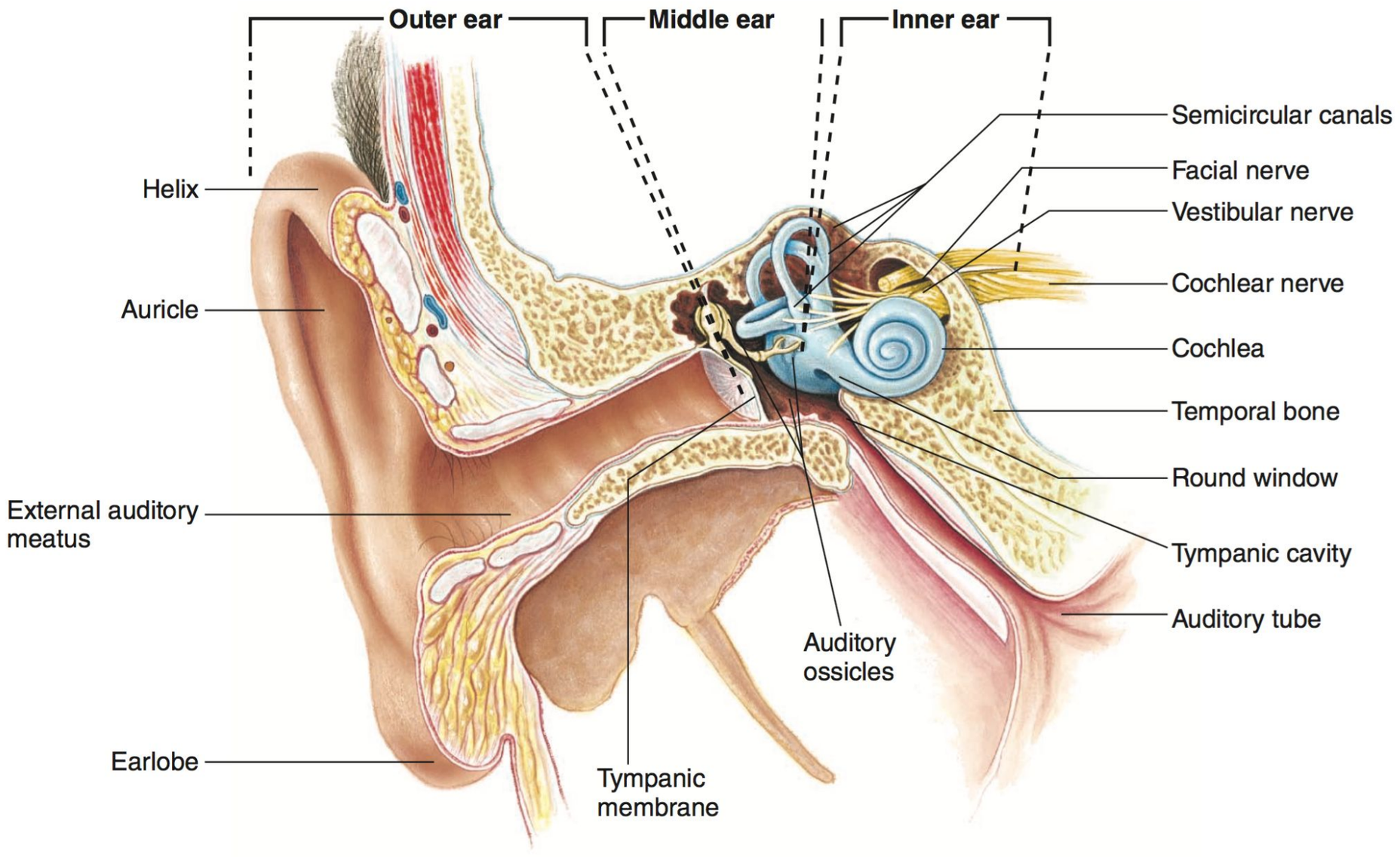
Neural Pathways

Stimulation of hair cells in the vestibular apparatus activates sensory neurons of the vestibulocochlear nerve (VIII). These fibers transmit impulses to the cerebellum and to the vestibular nuclei of the medulla oblongata.
The vestibular nuclei, in turn, send fibers to the oculomotor center of the brain stem and to the spinal cord.
Neurons in the oculomotor center control eye movements, and neurons in the spinal cord stimulate movements of the head, neck, and limbs.
Movements of the eyes and body produced by these pathways serve to maintain balance and “track” the visual field during rotation.

THE EARS AND HEARING

Sound waves are alternating zones of high and low pressure traveling in a medium, usually air or water.
These waves are characterized by their frequency and intensity.
The **frequency** is measured in *hertz (Hz),* which is the modern designation for *cycles per second (cps).* The *pitch* of a sound is directly related to its frequency—the greater the frequency of a sound, the higher its pitch.
The **intensity,** or loudness, of a sound is directly related to the amplitude of the sound waves and is measured in units called *decibels (dB).* A sound that is barely audible—at the threshold of hearing—has an intensity of zero decibels. Every 10 decibels indicates a tenfold increase in sound intensity; a sound is 10 times louder than threshold at 10 dB, 100 times louder at 20 dB, a million times louder at 60 dB, and 10 billion times louder at 100 dB.
The ear of a trained, young individual can hear sound over a frequency range of 20 to 20,000 Hz, yet still can distinguish between two pitches that have only a 0.3% difference in frequency.
The human ear can detect differences in sound intensities of only 0.1 to 0.5 dB, while the range of audible intensities covers 12 orders of magnitude (1012), from the barely audible to the limits of painful loudness. Human hearing is optimal at sound intensities of 0 to 80 dB.

Outer Ear

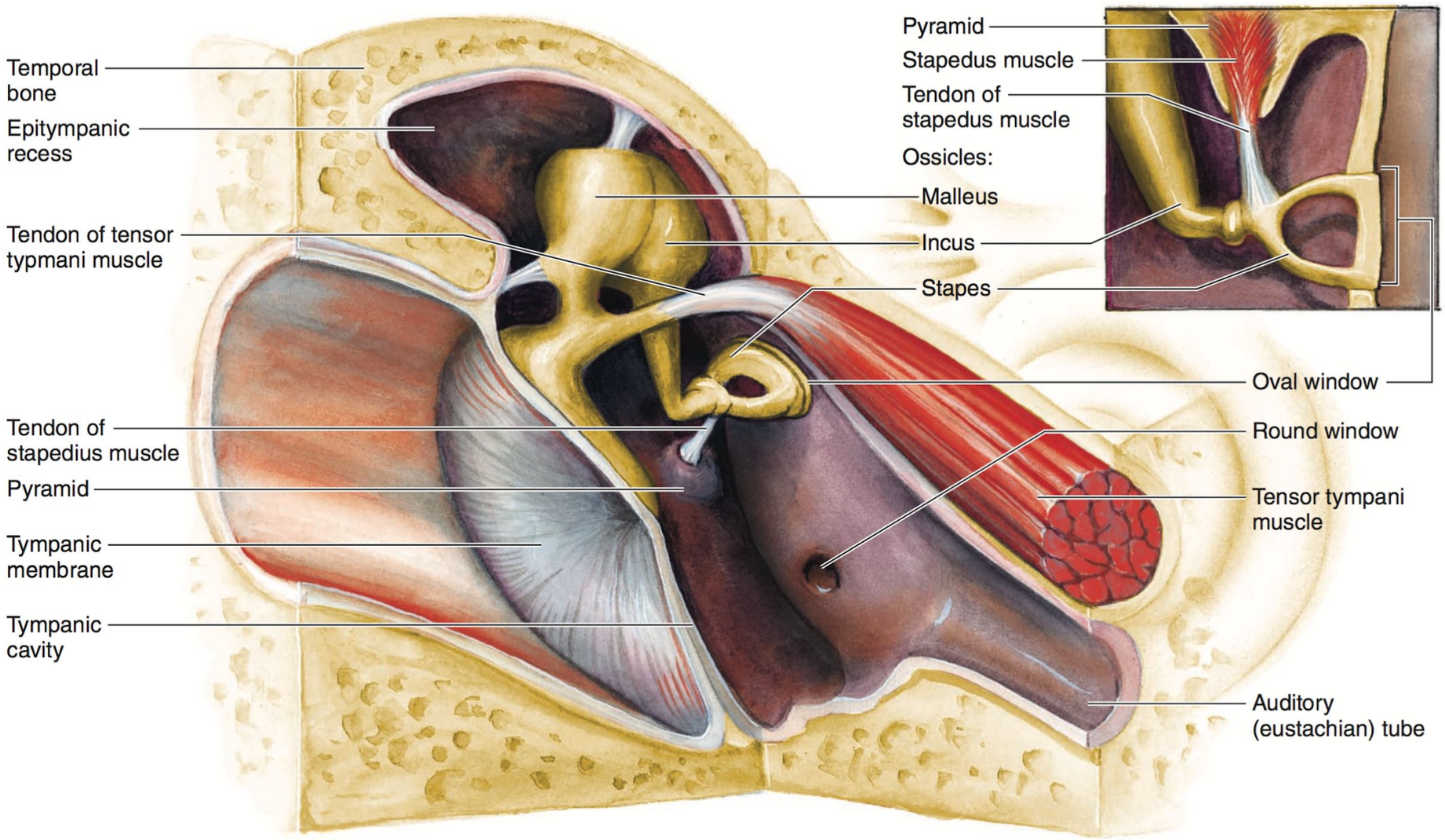


Sound waves are funneled by the *pinna,* or *auricle,* into the *external auditory meatus*. These two structures form the **outer ear.**
The external auditory meatus channels the sound waves to the eardrum, or **tympanic membrane.** Sound waves in the external auditory meatus produce extremely small vibrations of the tympanic membrane; movements of the eardrum during speech (with an average sound intensity of 60 dB) are estimated to be about the diameter of a molecule of hydrogen.

Middle Ear

The **middle ear** is the cavity between the tympanic membrane on the outer side and the cochlea on the inner side.
Within this cavity are three **middle-ear ossicles**—the *malleus* (hammer), *incus* (anvil), and *stapes* (stirrup). The malleus is attached to the tympanic membrane, so that vibrations of this membrane are transmitted via the malleus and incus to the stapes. The stapes, in turn, is attached to a membrane in the cochlea called the *oval window,* which thus vibrates in response to vibrations of the tympanic membrane.
The fact that vibrations of the tympanic membrane are transferred through three bones instead of just one affords protection. If the sound is too intense, the ossicles may buckle. This protection is increased by the action of the *stapedius muscle,* which attaches to the neck of the stapes. When sound becomes too loud, the stapedius muscle contracts and dampens the movements of the stapes against the oval window. This action helps to prevent nerve damage within the cochlea. If sounds reach high amplitudes very quickly, however the stapedius muscle may not respond soon enough to prevent nerve damage.

A medial view of the middle ear



The locations of auditory muscles, attached to the middle-ear ossicles, are indicated.

Cochlea

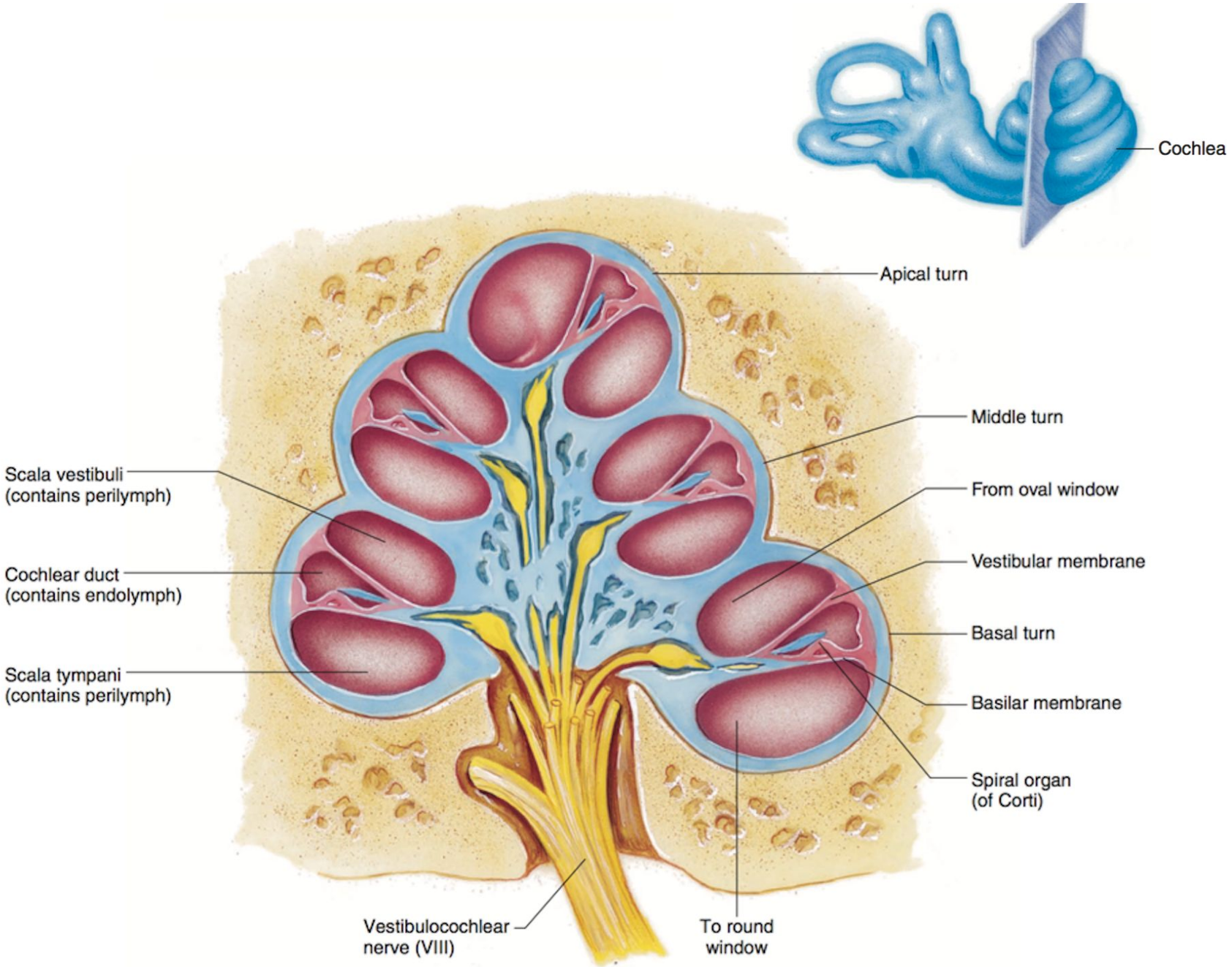
Encased within the dense temporal bone of the skull is an organ called the **cochlea,** about 34 mm long (the size of a pea) and shaped like the shell of a snail. Together with the vestibular apparatus, it composes the **inner ear.** Vibrations of the stapes and oval window displace perilymph fluid within a part of the bony labyrinth known as the **scala vestibuli,** which is the upper of three chambers within the cochlea. The lower of the three chambers is also a part of the bony labyrinth and is known as the **scala tympani.** The middle chamber of the cochlea is a part of the membranous labyrinth called the **cochlear duct,** or **scala media.** Like the cochlea as a whole, the cochlear duct coils to form three turns, similar to the basal, middle, and apical portions of a snail shell. Because the cochlear duct is a part of the membranous labyrinth, it contains endolymph rather than perilymph.

The perilymph of the scala vestibuli and scala tympani is continuous at the apex of the cochlea because the cochlear duct ends blindly, leaving a small space called the *helicotrema* between the end of the cochlear duct and the wall of the cochlea. Vibrations of the oval window produced by movements of the stapes cause pressure waves within the scala vestibuli, which pass to the scala tympani.

Cochlea # 2

Movements of perilymph within the scala tympani, in turn, travel to the base of the cochlea where they cause displacement of a membrane called the *round window* into the middle-ear cavity. This occurs because fluid, such as perilymph, cannot be compressed; an inward movement of the oval window is thus compensated for by an outward movement of the round window.
Sound waves transmitted through perilymph from the scala vestibuli to the scala tympani thus produce displacement of the vestibular membrane and the basilar membrane. Although the movement of the vestibular membrane does not directly contribte to hearing, displacement of the basilar membrane is central to pitch discrimination. Each sound frequency produces maximum vibrations at a different region of the basilar membrane. Sounds of higher frequency (pitch) cause maximum vibrations of the basilar membrane closer to the stapes.

A cross section of the cochlea



In this view, its three turns and its three compartments—the scala vestibuli, cochlear duct (scala media), and scala tympani—can be seen.

Spiral Organ (Organ of Corti)

The sensory *hair cells* are located on the basilar membrane with their “hairs” projecting into the endolymph of the cochlear duct. The hairs are actually stereocilia, which are large, specialized microvilli arranged in bundles. The stereocilia increase in size stepwise within each bundle, as they do in the vestibular apparatus; however, unlike the case in the vestibular apparatus, the cochlear hair cells lack kinocilia.

There are two categories of hair cells, inner and outer.
Inner hair cells, about 3,500 per cochlea, form one row that extends the length of the basilar membrane. The hair bundles on the inner hair cells are mechanosensory: they transform sound waves in cochlear fluid into nerve impulses. Their stereocilia are interconnected near their tips with filaments that are coupled to mechanotransduction channels in the plasma membrane. These channels open when the stereocilia within each bundle are bent in the direction of their tallest members, allowing the movement of K^+ across the plasma membrane as will be described shortly. Each of the inner hair cells is innervated by 6–20 sensory neurons of cranial nerve VIII from the spiral ganglion, which transmit sound information to the brain. The number of synapses with afferent neurons depends on the location of the inner hair cells along the basilar membrane, with those in the middle having the greatest number of synapses and the highest sensitivity to sound.

Spiral Organ (Organ of Corti) # 2

There are also about 11,000 **outer hair cells** arranged in multiple rows: three rows in the basilar turn, four in the middle turn, and five in the apical turn of the cochlea. The outer hair cells are innervated primarily by motor neurons that originate in the olivary nuclei of the medulla oblongata. These depolarize or hyperpolarize the outer hair cells, causing them to shorten when they are depolarized or lengthen when they are hyperpolarized. Such movements are believed to aid the sensory function of the inner hair cells.
The stereocilia of the hair cells are embedded in a gelatinous **tectorial membrane** (*tectum* = roof, covering), which overhangs the hair cells within the cochlear duct. The association of the basilar membrane, inner hair cells with sensory fibers, and tectorial membrane forms a functional unit called the **spiral organ,** or **organ of Corti**. When the cochlear duct is displaced by pressure waves of perilymph, a shearing force is created between the basilar membrane and the tectorial membrane. This causes the stereocilia to bend, and this mechanical process opens K^+ channels in the plasma membrane covering the tops of the stereocilia.
These K^+ channels face endolymph, which uniquely has a high concentration of K^+ similar to that of the intracellular compartment. Also, the endolymph of the cochlea (but not the vestibular apparatus) has an amazingly high positive potential: 1100 mV. Combined with the negative resting membrane potential of the hair cells, this produces an extremely steep electrochemical gradient favoring the entry of K^+.
So, when the K^+ channels in the bent stereocilia open, K^+ moves passively down its electrochemical gradient into the hair cells. This depolarizes the hair cells and stimulates them to release glutamate, which stimulates the associated sensory neurons. The K^+ that entered the hair cells at their apical surface can then move passively out through channels in their basal surface, which face perilymph in the scala tympani. Perilymph, as previously mentioned, has a low K^+ concentration typical of extracellular fluids.

Spiral Organ (Organ of Corti) # 3

The greater the displacement of the basilar membrane and the bending of the stereocilia, the greater the amount of transmitter released by the inner hair cell, and therefore the greater the generator potential produced in the sensory neuron. By this means, a greater bending of the stereocilia will increase the frequency of action potentials produced by the fibers of the cochlear nerve that are stimulated by the hair cells. Experiments suggest that the stereocilia need bend only 0.3 nanometers to be detected at the threshold of hearing! A greater bending will result in a higher frequency of action potentials, which will be perceived as a louder sound.

As mentioned earlier, traveling waves in the basilar membrane reach a peak in different regions, depending on the pitch (frequency) of the sound. High-pitched sounds produce a peak displacement closer to the base, while sounds of lower pitch cause peak displacement further toward the apex. Those neurons that originate in hair cells located where the displacement is greatest will be stimulated more than neurons that originate in other regions. This mechanism provides a neural code for **pitch discrimination.**

Neural Pathways for Hearing

Sensory neurons in the spiral ganglion of each ear send their axons in the vestibulocochlear nerve (VIII) to one of two *cochlear nuclei* in the junction of the medulla and pons of the brain stem. Neurons in the cochlear nuclei send axons either directly to the *inferior colliculi* of the midbrain or to the *superior olive,* a collection of brain stem nuclei. Axons from the superior olive pass through the *lateral lemniscus* to the inferior colliculus. Whatever the route, all auditory paths synapse in the inferior colliculus. Neurons in the inferior colliculus then send axons to the *medial geniculate body* of the thalamus, which in turn projects to the *auditory cortex* of the temporal lobe.

The cochlea is a frequency analyzer, in that different frequencies (pitches) of sound stimulate different sensory neurons that innervate the basilar membrane. This is because hair cells located in different places along the basilar membrane are most effectively stimulated by different frequencies of sound. This is known as the *place theory* of pitch, and has been previously described. Sensory neurons stimulated by low-frequency sounds, and those stimulated by high-frequency sounds, project their axons to different regions of the cochlear nucleus. The cochlear nucleus displays a **tonotopic organization,** in that different regions represent different “tones” (pitches). This separation of neurons by pitch is preserved in the tonotopic organization of the auditory cortex, which allows to perceive the different pitches of sounds.

THE EYES AND VISION

The eyes transduce energy in the electromagnetic spectrum into nerve impulses. Only a limited part of this spectrum can excite the photoreceptors—electromagnetic energy with wavelengths between 400 and 700 nanometers (1 nm = 10^{-9} m, or one-billionth of a meter) constitutes *visible light.*
Light of longer wavelengths in the infrared regions of the spectrum is felt as heat but does not have sufficient energy to excite the photoreceptors.

WALL OF THE EYEBALL

Wall of the eyeball is composed of three layers

□□

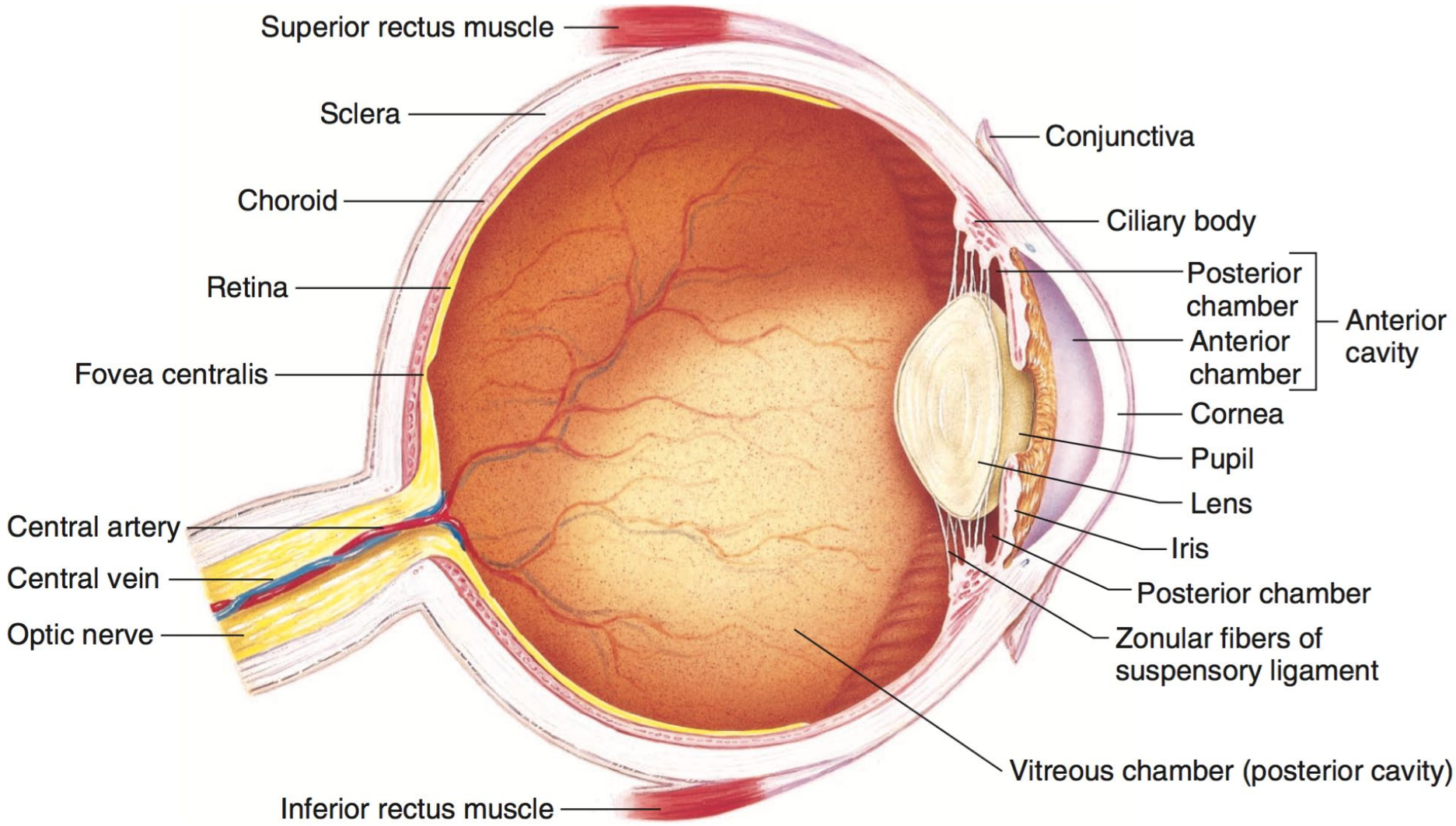
□. □outer layer, which includes cornea and sclera
□. m□iddle layer, which includes choroid, ciliary body and iris
□. Inner layer, the retina.

Wall of the eyeball

- **Outer layer (Tunica externa or tunica fibrosa)**
  - **Cornea**
    1. Stratified epithelium
    2. Bowman membrane
    3. Substantia proper
    4. Descement layer
    5. Endothelium
  - **Sclera**
    1. Fibrous tissues
    2. Elastic tissues
- **Middle layer (Tunica media or tunica vasculosa)**
  - **Choroid**
    1. Arteries
    2. Capillary plexus
    3. Veins
  - **Ciliary body**
    1. Orbiculus ciliaris
    2. Ciliary body proper
    3. Ciliary processes
  - **Iris**
    1. Constrictor pupillae
    2. Dialator pupillae
- **Inner layer (Tunica interna or tunica nervosa or retina)**

  Layers of retina (from outside in):
  1. Layer of pigment epithelium
  2. Layer of rods and cones
  3. External limiting membrane
  4. Outer nuclear layer
  5. Outer plexiform layer
  6. Inner nuclear layer
  7. Inner plexiform layer
  8. Ganglion cell layer
  9. Layer of nerve fibers
  10. Internal limiting membrane

The internal anatomy of the eyeball



Light passes through the cornea to enter the *anterior chamber* of the eye. Light then passes through an opening called the *pupil,* which is surrounded by a pigmented muscle known as the *iris.* After passing through the pupil, light enters the *lens.*

The iris is like the diaphragm of a camera; it can increase or decrease the diameter of its aperture (the pupil) to admit more or less light.

Structures of the Eyeball

Constriction of the pupils is produced by contraction of circular muscles within the iris; dilation is produced by contraction of radial muscles. Constriction of the pupils results from parasympathetic stimulation through the occulomotor (III) nerve, whereas dilation results from sympathetic stimulation.
The posterior part of the iris contains a pigmented epithelium that gives the eye its color. The color of the iris of the eye is determined by the amount of pigment—blue eyes have the least pigment, brown eyes have more, and black eyes have the greatest amount of pigment. In the condition of *albinism*—a congenital absence of normal pigmentation caused by an inability to produce melanin pigment—the eyes appear pink because the absence of pigment allows blood vessels to be seen.
The lens is composed of living cells but is avascular (lacking in blood vessels), requiring its own microcirculatory system to sustain its cells.

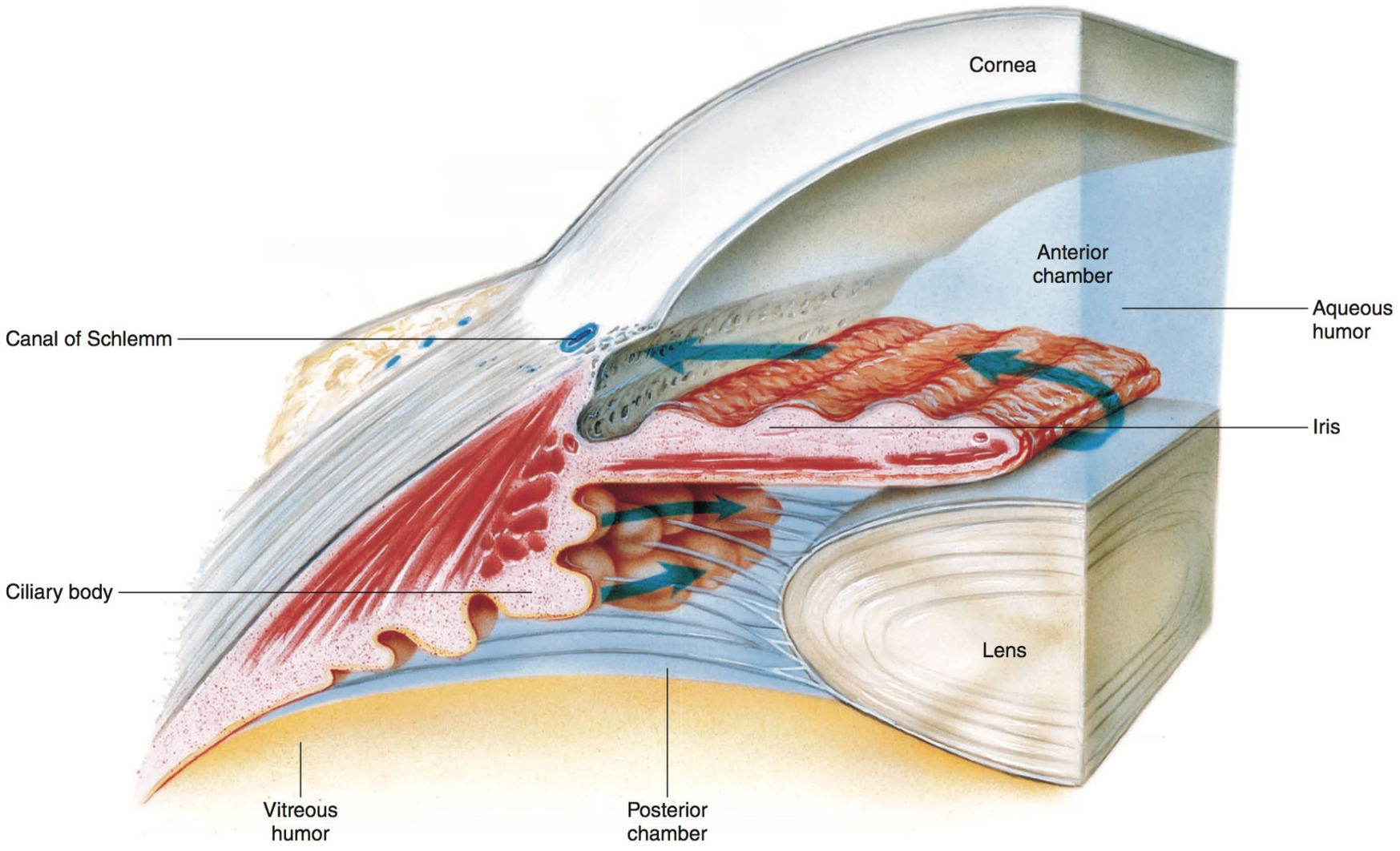
Structures of the Eyeball # 2

The lens is suspended from a muscular process called the **ciliary body,** which connects to the sclera and encircles the lens. *Zonular fibers* (*zon* = girdle) suspend the lens from the ciliary body, forming a **suspensory ligament** that supports the lens. The space between the cornea and iris is the *anterior chamber,* and the space between the iris and the ciliary body and lens is the *posterior chamber.*

The anterior and posterior chambers are filled with a fluid called **aqueous humor.** This fluid is secreted by the ciliary body into the posterior chamber and passes through the pupil into the anterior chamber, where it provides nourishment to the avascular lens and cornea. The aqueous humor is drained from the anterior chamber into the *scleral venous sinus (canal of Schlemm),* which returns it to the venous blood.

The portion of the eye located behind the lens is filled with a thick, viscous substance known as the **vitreous body,** or **vitreous humor.** Light from the lens that passes through the vitreous body enters the neural layer, which contains pho- toreceptors, at the back of the eye. This neural layer is called the **retina.** Light that passes through the retina is absorbed by a darkly pigmented *choroid layer* underneath. While passing through the retina, some of this light stimulates photoreceptors, which in turn activate other neurons. Neurons in the retina contribute fibers that are gathered together at a region called the **optic disc**, where they exit the retina as the optic nerve. This region lacks photoreceptors and is therefore known as the *blind spot.* The optic disc is also the site of entry and exit of blood vessels.

The production and drainage of aqueous humor



Aqueous humor maintains the intraocular pressure within the anterior and posterior chambers. It is secreted into the posterior chamber, flows through the pupil into the anterior chamber, and drains from the eyeball through the canal of Schlemm.

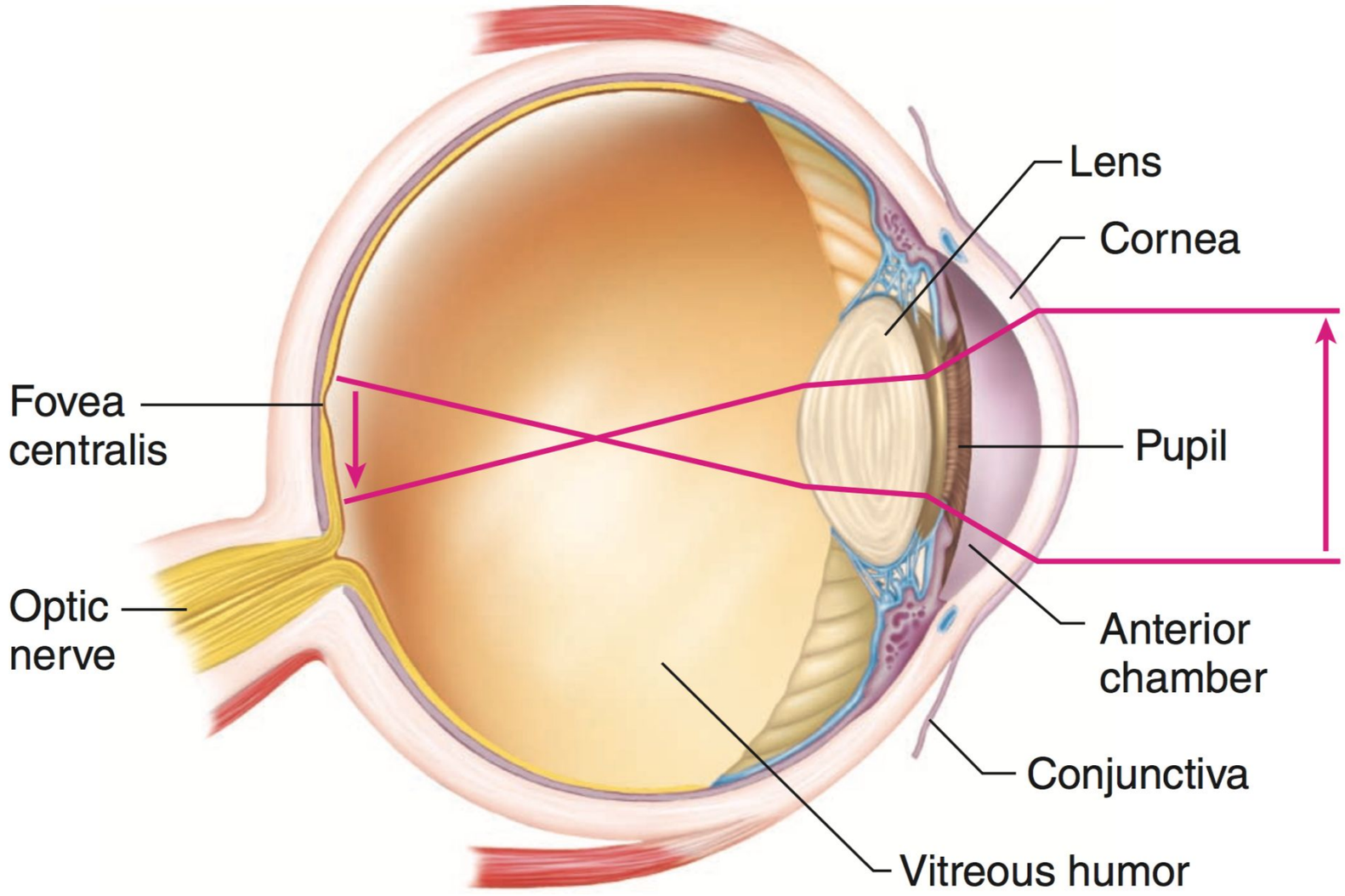
Refraction

Light that passes from a medium of one density into a medium of a different density is *refracted,* or bent. The degree of refraction depends on the comparative densities of the two media, as indicated by their *refractive index.* The refractive index of air is set at 1.00; the refractive index of the cornea, by comparison, is 1.38; and the refractive indices of the aqueous humor and lens are 1.33 and 1.40, respectively. Because the greatest difference in refractive index occurs at the air-cornea interface, the light is refracted most at the cornea.

The degree of refraction also depends on the curvature of the interface between two media. The curvature of the cornea is constant, but the curvature of the lens can vary. The refractive properties of the lens can thus provide fine control for focusing light on the retina. As a result of light refraction, the image formed on the retina is upside down and right to left.

The *visual field*—which is the part of the external world projected onto the retina—is thus reversed in each eye. The cornea and lens focus the right part of the visual field on the left half of the retina of each eye, while the left half of the visual field is focused on the right half of each retina. The medial (or nasal) half-retina of the left eye therefore receives the same image as the lateral (or temporal) half-retina of the right eye. The nasal half-retina of the right eye receives the same image as the temporal half-retina of the left eye.

The image is inverted on the retina



Refraction of light, which causes the image to be inverted, occurs to the greatest degree at the air-cornea interface. Changes in the curvature of the lens, however, provide the required fine focusing adjustments

Accommodation

The ability of the eyes to keep the image focused on the retina as the distance between the eyes and object varies is called **accommodation.** Accommodation results from contrac tion of the ciliary muscle, which is like a sphincter muscle that can vary its aperture. When the ciliary muscle is relaxed, its aperture is wide. Relaxation of the ciliary muscle thus places tension on the zonular fibers of the suspensory ligament and pulls the lens taut.

RETINA

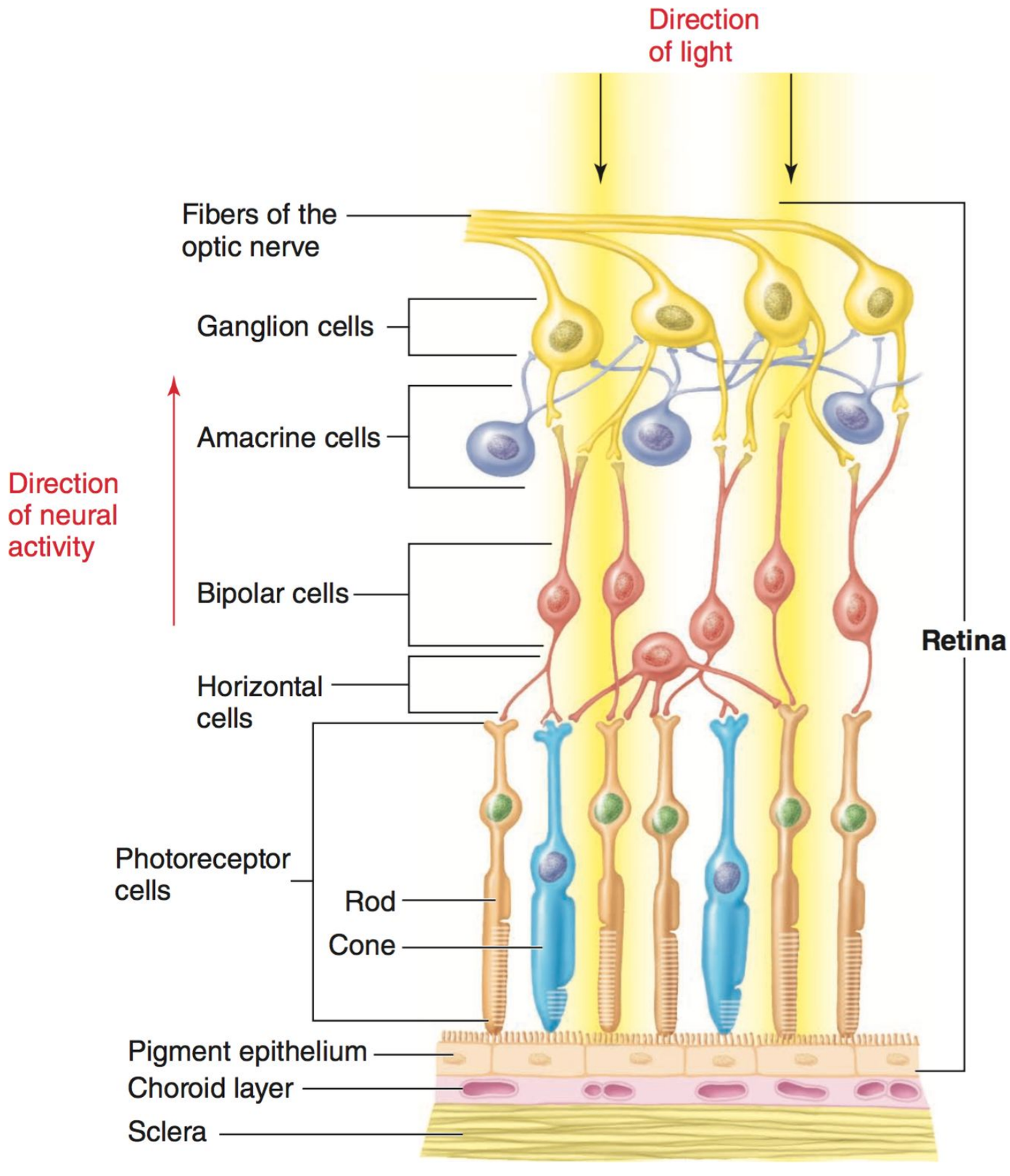
The **retina** consists of a single-cell-thick pigmented epithelium, photoreceptor neurons called **rods** and **cones,** and layers of other neurons. The neural layers of the retina are actually a forward extension of the brain. In this sense, the optic nerve can be considered a tract, and indeed the myelin sheaths of its fibers are derived from oligodendrocytes (like other CNS axons) rather than from Schwann cells.

The outer layers of neurons that contribute axons to the optic nerve are called **ganglion cells.** These neurons receive synaptic input from **bipolar cells,** which in turn receive input from rods and cones. In addition to the flow of information from photoreceptors to bipolar cells to ganglion cells, neurons called *horizontal cells* synapse with several photoreceptors (and possibly also with bipolar cells), and neurons called *ama- crine cells* synapse with several ganglion cells.

Each rod and cone consists of an inner and an outer segment. The *inner segment* contains most of the cell's organelles; the *outer segment* contains hundreds of flattened membranous sacs, or **discs**, where the photopigment molecules required for vision are located. The photoreceptor cells continuously add new discs at the base of the outer segment as the tip regions are removed by the cells of the **retinal pigment epithelium** through a process of phagocytosis. Each retinal pigment epithelial cell is in contact with 50 to 100 photoreceptor outer segments, and daily removes the distal 10% of these outer segments by phagocytosis. This amounts to the phagocytosis of hundreds of thousands of discs over the course of a lifetime by each retinal pigment cell, making these cells the most phagocytically active cells in the body. The photo receptors continuously produce new discs at the base of their outer segments, and these new discs migrate toward the tips to replace the lost material.

Layers of the retina

Because the retina is inverted, light must pass through various layers of nerve cells before reaching the photoreceptors (rods and cones)



Effect of Light on the Rods

The photoreceptors—rods and cones—are activated when light produces a chemical change in molecules of pigment contained within the membranous discs of the outer segments of the receptor cells. Each rod contains thousands of molecules of a purple pigment known as **rhodopsin** in these discs. The pigment appears purple (a combination of red and blue) because it transmits light in the red and blue regions of the spectrum, while absorbing light energy in the green region. The wavelength of light that is absorbed best—the *absorption maximum*—is about 500 nm (blue-green light).

In response to absorbed light, rhodopsin dissociates into its two components: the pigment **retinaldehyde** (also called **retinene** or **retinal**), which is derived from vitamin A, and a protein called **opsin.** This reac- tion is known as the **bleaching reaction.**

Retinal (retinene) can exist in two possible configurations (shapes)—one known as the all-*trans* form and one called the 11-*cis* form. The all-*trans* form is more stable, but only the 11-*cis* form is found attached to opsin. In response to absorbed light energy, the 11-*cis*-retinal is converted to the all- *trans* isomer, causing it to dissociate from the opsin. This dissociation reaction in response to light initiates changes in the ionic permeability of the rod plasma membrane and ultimately results in the production of nerve impulses in the ganglion cells. As a result of these effects, rods provide black-and-white vision under conditions of low light intensity.

Effect of Light on the Rods # 2

The retinal pigment epithelium is needed for the **visual cycle of retinal.** Photoreceptors lack the enzyme *cis-trans* isomerase, which is needed to reisomerize (reconvert) retinal from the all-*trans* form back into the 11-*cis* form. After the absorption of light has caused the formation of the all-*trans* form of retinal, the all-*trans* retinal dissociates from the opsin and is transported from the photoreceptors into the closely associated pigment epithelial cells. There, it is re-isomerized into the 11-*cis* form and then transported back to the photoreceptors. Now, the 11-*cis* retinal can again bind to the opsin and form the active photopigment, able to respond to light. It is this recycling between the photoreceptors and the retinal pigment epithelium that is known as the visual cycle of retinal.

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Cones and Color Vision

Cones are less sensitive than rods to light, but the cones provide color vision and greater visual acuity, as described in the next section. During the day, therefore, the high light intensity bleaches out the rods, and color vision with high acuity is provided by the cones.

Each type of cone contains retinene, as in rhodopsin, but the retinene in the cones is associated with proteins called **photopsins.** It is the three different photopsin proteins (coded by three different genes) that give each type of cone its unique light-absorbing characteristics. Each type of cone expresses only one of these genes to produce only one of these photo- psins. Humans and Old World primates (including chimpanzees, gorillas, and gibbons) have **trichromatic color vision.** We are *trichromats,* with three different types of cones. These may be designated *blue, green,* and *red,* according to the region of the visible spectrum in which each cone's pigment absorbs light best. This is each cone's *absorption maximum.*

The absorption maximum for the blue cones at 420 nanometers (nm) is in the short wavelengths, so these are also known as **S cones.** The absorption maximum for the green cones (at 530 nm) is in the middle wavelengths, and so these are called **M cones.** The red cones (with an absorption maximum of 562 nm) absorb best in the longer wavelengths, and so are **L cones.**

Neural Pathways from the Retina

The visual nerve signals leave the retinas through the optic nerves. At the optic chiasm, the optic nerve fibers from the nasal halves of the retinas cross to the opposite sides, where they join the fibers from the opposite temporal retinas to form the optic tracts. e fibers of each optic tract then synapse in the dorsal lateral geniculate nucleus of the thalamus, and from there, geniculocalcarine fibers pass by way of the optic radiation (also called the geniculocalcarine tract) to the primary visual cortex in the calcarine fissure area of the medial occipital lobe.

Visual fibers also pass to several older areas of the brain (1) from the optic tracts to the suprachiasmatic nucleus of the hypothalamus, presumably to control circadian rhythms that synchronize various physiological changes of the body with night and day; (2) into the pretectal nuclei in the midbrain, to elicit reflex movements of the eyes to focus on objects of importance and to activate the pupillary light reflex; (3) into the superior colliculus, to control rapid directional movements of the two eyes; and (4) into the ventral lateral geniculate nucleus of the thalamus and surrounding basal regions of the brain, presumably to help control some of the body's behavioral functions.

Thus, the visual pathways can be divided roughly into an old system to the midbrain and base of the forebrain and a new system for direct transmission of visual signals into the visual cortex located in the occipital lobes. In humans, the new system is responsible for perception of virtually all aspects of visual form, colors, and other conscious vision. Conversely, in many primitive animals, even visual form is detected by the older system, using the superior colliculus in the same manner that the visual cortex is used in mammals.

EYE MOVEMENTS AND THEIR CONTROL

To make full use of the visual abilities of the eyes, almost equally as important as interpretation of the visual signals from the eyes is the cerebral control system for directing the eyes toward the object to be viewed.

The eye movements are controlled by three pairs of muscles:

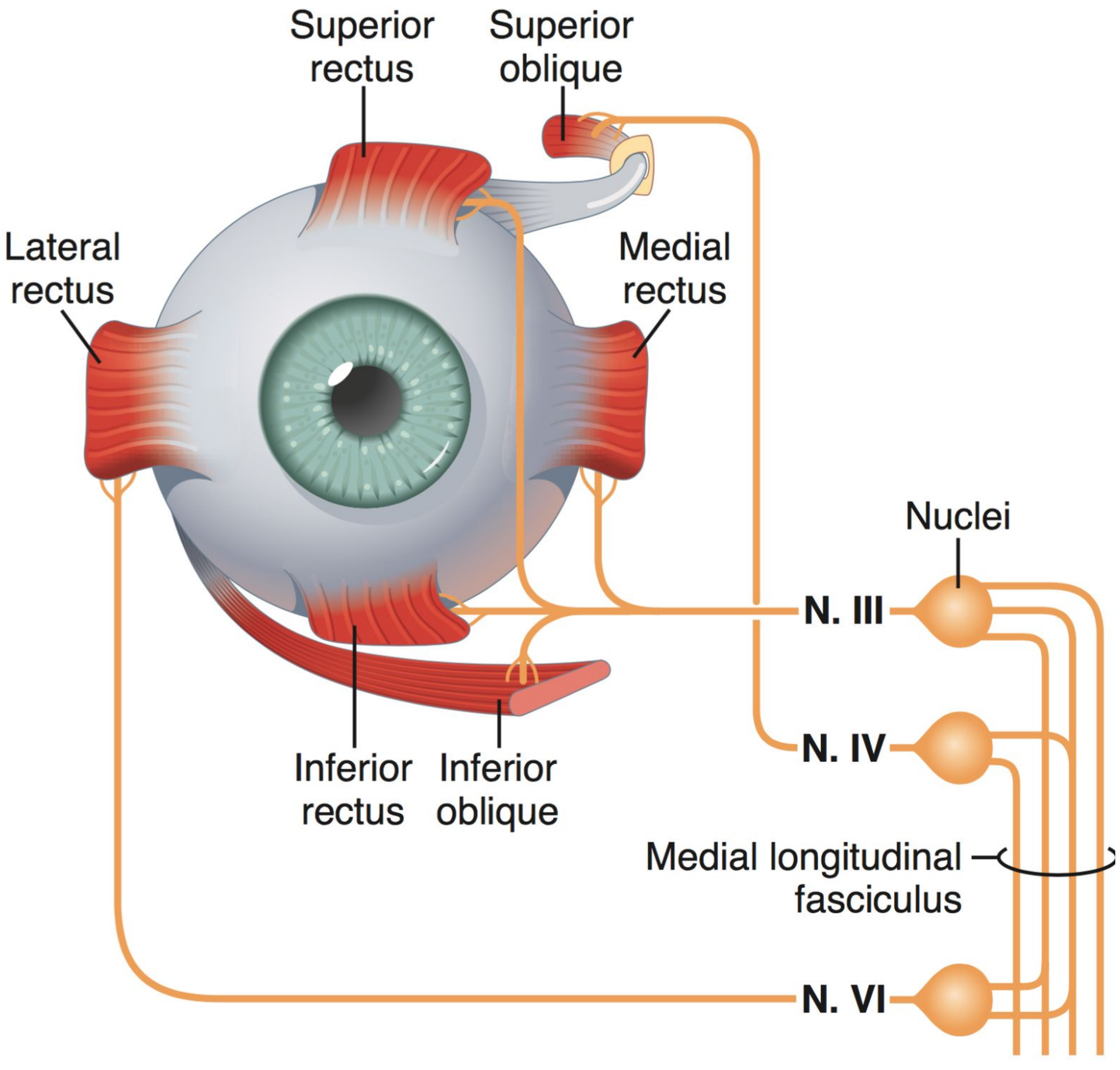
- the medial and lateral recti,
- the superior and inferior recti,
- the superior and inferior obliques.

The medial and lateral recti contract to move the eyes from side to side. e superior and inferior recti contract to move the eyes upward or downward. The oblique muscles function mainly to rotate the eyeballs to keep the visual fields in the upright position.

Neural Control of Eye Movements

There are three types of eye movements coordinated by the brain. **Saccadic eye movements** are very high-velocity movements (400° to 800° per second) of both eyes that target an image on the fovea centralis. For example, saccadic eye movements keep the images of the words you are now reading on or near the fovea, so the words at the middle and end of this sentence can be as clearly seen as those at the beginning. **Smooth pursuit movements** are slower (up to 30° per second), and match the speed of moving objects to keep their images at or near the fovea. **Vergence movements** (30° to 150° per second) cause the eyes to converge so that an image of an object is brought to the fovea of both eyes, allowing the object to be seen more clearly three-dimensionally.

Neural Control of Eye Movements # 2



Anterior view of the right eye showing extraocular muscles of the eye and their innervation.

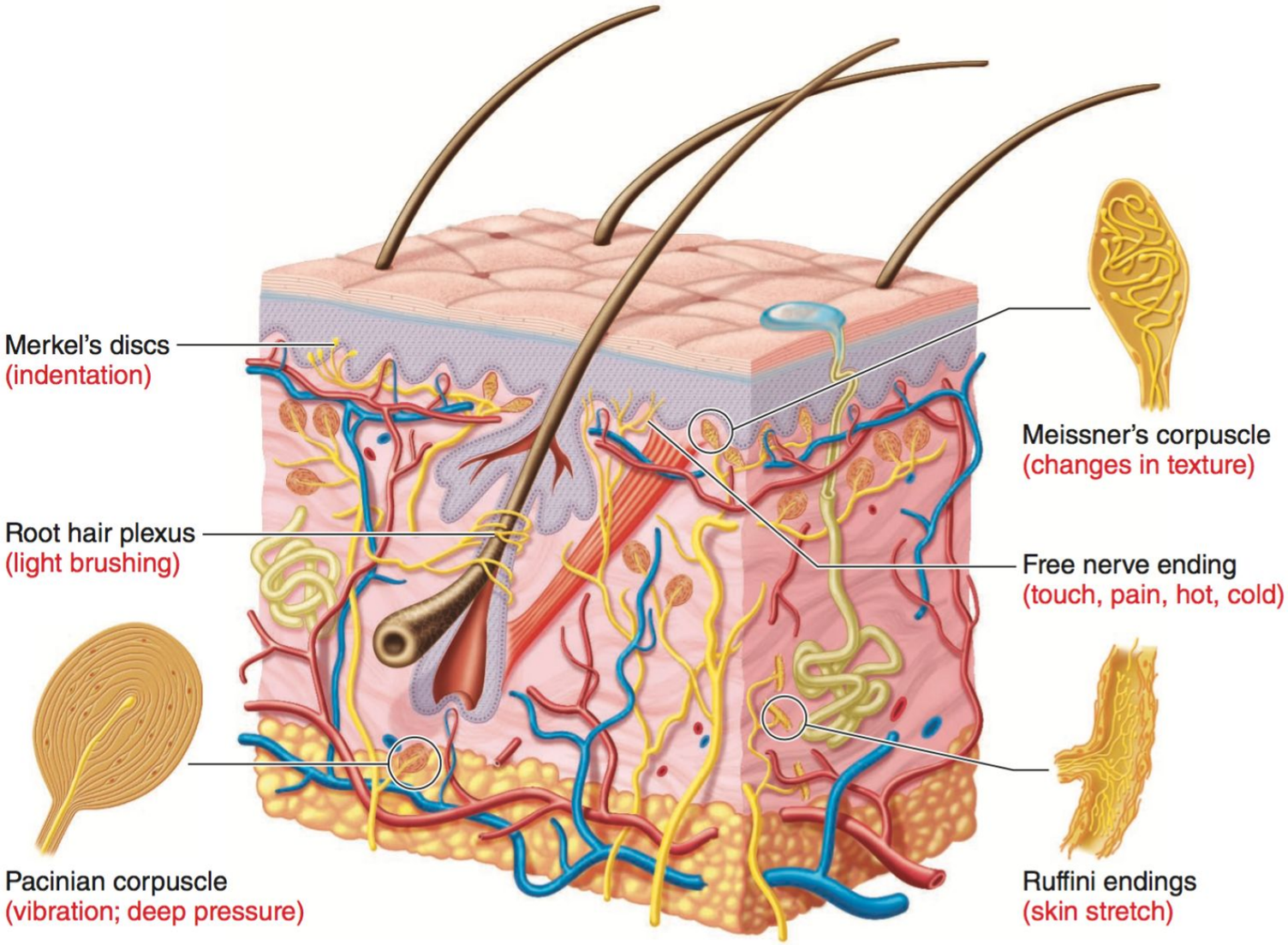
CUTANEOUS SENSATIONS

The **cutaneous sensations** of touch, pressure, heat and cold, and pain are mediated by the dendritic nerve endings of different sensory neurons. The receptors for heat, cold, and pain are simply the naked endings of sensory neurons.
Sensations of touch are mediated by naked dendritic endings surrounding hair follicles and by expanded dendritic endings, called **Ruffini endings** and **Merkel's discs**. Merkel's discs are sensitive to the depth of skin indentation and have the highest spatial resolution of the cutaneous receptors, providing information regarding an object's texture.
The sensations of touch and pressure are also mediated by dendrites that are encapsulated within various structures; these include **Meissner's corpuscles** and **Pacinian (lamellated) corpuscles**. In pacinian corpuscles, for example, the dendritic endings are encased within 30 to 50 onionlike layers of connective tissue. These layers absorb some of the pressure when a stimulus is maintained, which helps accentuate the phasic response of this receptor. The encapsulated touch receptors thus adapt rapidly, in contrast to the more slowly adapting Ruffini endings and Merkel's discs.
There are far more free dendritic endings that respond to cold than to warm. The receptors for cold are located in the upper region of the dermis, just below the epidermis. These receptors are stimulated by cooling and inhibited by warming. The warm receptors are located somewhat deeper in the dermis and are excited by warming and inhibited by cooling.
Nociceptors are also free sensory nerve endings of either myelinated or unmyelinated fibers. The initial sharp sensation of pain, as from a pinprick, is transmitted by rapidly conducting myelinated axons of medium diameter, whereas a dull, persistent ache is transmitted by slower conducting thin unmyelinated axons. These afferent neurons synapse in the spinal cord, using substance P (an eleven- amino-acid polypeptide) and glutamate as neurotransmitters.

Cutaneous Receptors

Receptor	Structure	Sensation	Location
Free nerve endings	Unmyelinated dendrites of sensory neurons	Light touch; hot; cold; nociception (pain)	Around hair follicles; throughout skin
Merkel's discs	Expanded dendritic endings associated with 50–70 specialized cells	Sustained touch and indented depth	Base of epidermis (stratum basale)
Ruffini corpuscles (endings)	Enlarged dendritic endings with open, elongated capsule	Skin stretch	Deep in dermis and hypodermis
Meissner's corpuscles	Dendrites encapsulated in connective tissue	Changes in texture; slow vibrations	Upper dermis (papillary layer)
Pacinian corpuscles	Dendrites encapsulated by concentric lamellae of connective tissue structures	Deep pressure; fast vibrations	Deep in dermis

The cutaneous sensory receptors



Each of these structures is associated with a sensory (afferent) neuron. Free nerve endings are naked, dendritic branches that serve a variety of cutaneous sensations, including that of heat. Some cutaneous receptors are dendritic branches encapsulated within associated structures. Examples of this type include the pacinian (lamellated) corpuscles, which provide a sense of deep pressure, and the Meissner's corpuscles, which provide cutaneous information related to changes in texture.

Dual Pathway for Transmission of Pain Signals

Even though all pain receptors are free nerve endings, these endings use two separate pathways for transmitting pain signals into the central nervous system. The two pathways mainly correspond to the two types of pain— a **fast-sharp pain pathway** and a **slow-chronic pain pathway**.

Preipheral Pain Fibers – „Fast“ and „Slow“ fibers

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