Sensation & Perception: Other Physical Sense

Chapter 8

Sensory systems

- First, the incoming signal must reach a cell (generally called a transducer) that changes its electrical properties
- Then, information initiates a series of signals into the CNS
- Not all sensations are perceived

Contents

The Auditory System

- Sound waves are compressions and rarefractions of a medium (for us, often air)
  - No medium = no propagation
- All sounds are contained in their corresponding sound waves

Three components of sound waves: 1

- Frequency - How often do the sound waves compress?
  - More often they repeat, higher the pitch
  - Range for humans:
20 - 20,000 Hz
  - Common to lose high frequency hearing as we age
  - Doubling frequency changes tone by an octave

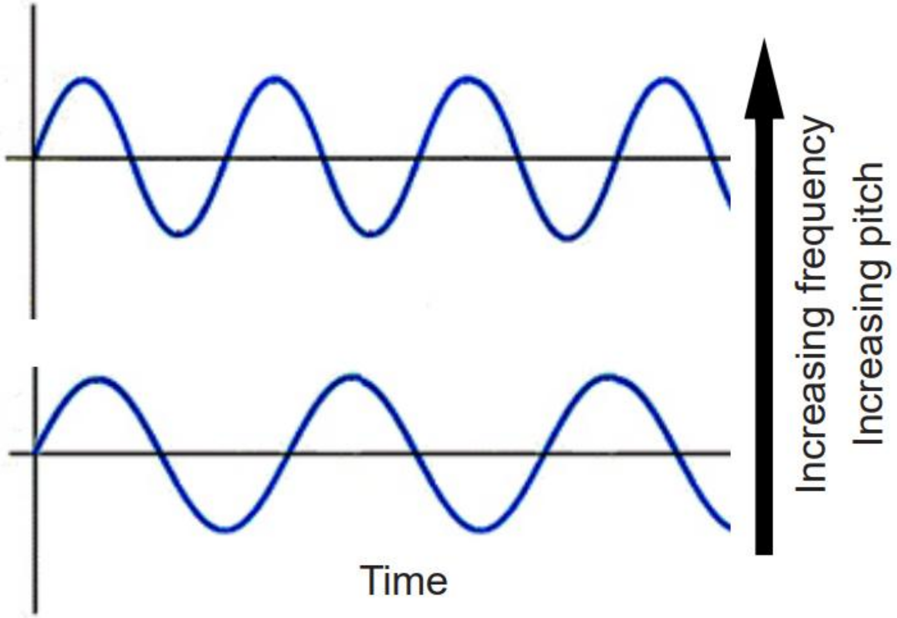


Figure 8.1 Pitch is a result of increased frequency of displacement.

Three components of sound waves: 2

- Amplitude – How much do the wave displace the medium from baseline?
  - Larger the amplitude, louder the sound
    - ~40 dB: ex. background noise in library
    - ~60 dB: ex typical conversation
    - 100-110 dB: ex. rock concert or lawnmower
  - dB (decibel) scale is logarithmic
    - A sound at 20 dB is 10 times more intense than a sound at 10 dB
  - Prolonged exposure to high amplitude sounds can lead to permanent damage (hearing loss or tinnitus)

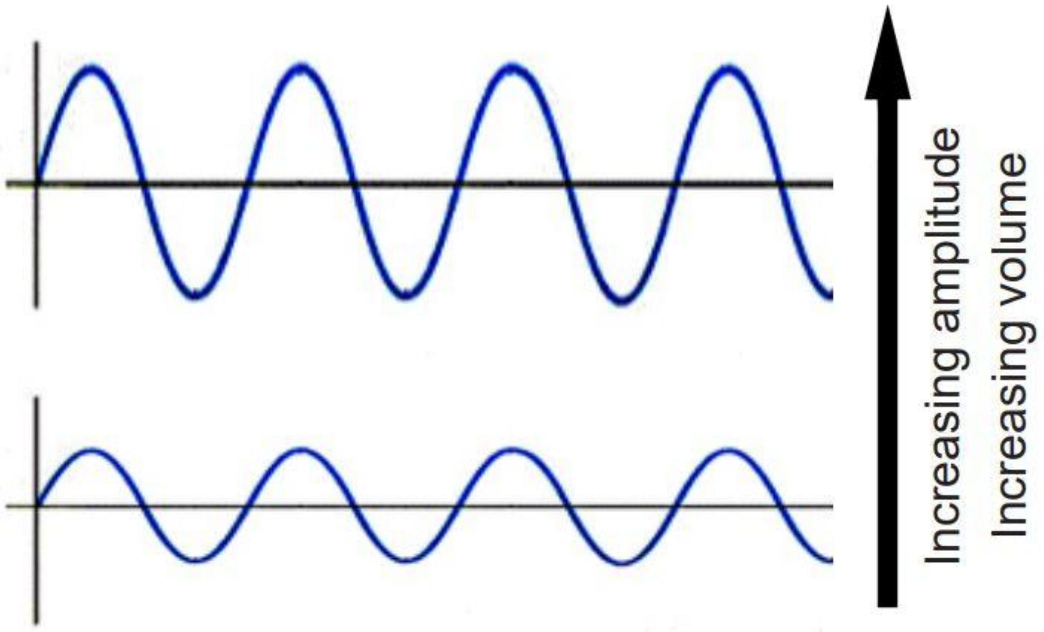


Figure 8.2 Volume is a result of increased amplitude of displacement.

Three components of sound waves: 3

- Timbre – How complex is the wave form?
  - Timbre refers to "color" or "character" of the sound
  - While notes contain the same frequency, each wave of an instrument differs in number of other high frequency components called overtones
  - Overtones oscillate at a frequency that are multiples of a fundamental frequency
  - Pure tone, or sine wave tone = sound wave without any overtone frequencies

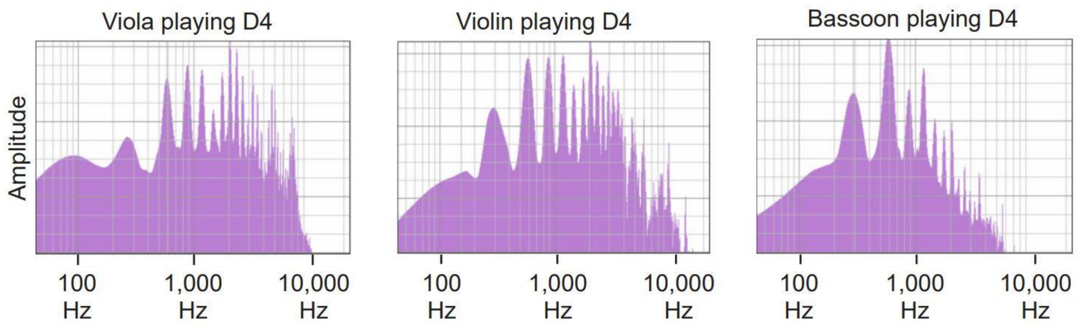


Figure 8.3 Timbre refers to the complexity of the waveform. Instruments sound different because the they produce peaks at different frequencies related to the fundamental frequency.

Physical structures of auditory system: Outer ear

- Pinna (AKA auricle): ear
  - Shape functions as a funnel capturing sound waves
  - Asymmetrical shape helps us determine where sound is coming from
  - Serves these and other functions in other animals (ex. Excess heat dispersion; display of emotion)
- Auditory canal: second part of outer ear

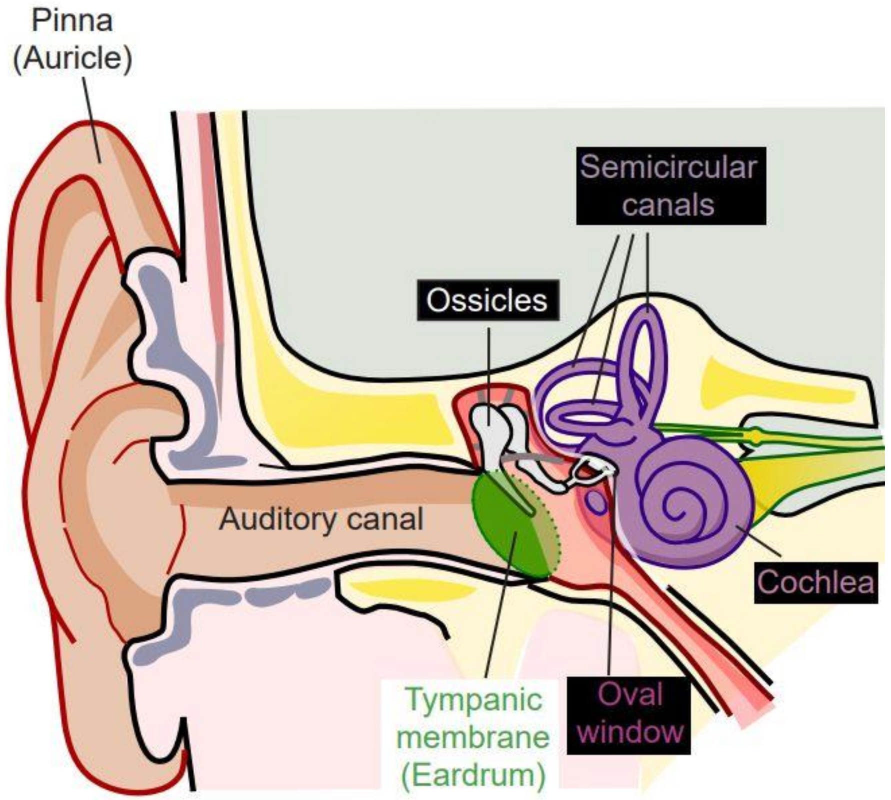


Figure 8.4 Anatomy of the auditory system.

Physical structures: Middle ear

- **Tympanic membrane** (AKA ear drum)
  - Delicate piece of tissue (0.1 mm thin)
  - **Vibrates to meet frequency, amplitude, and timbre of incoming sound waves**
  - Boundary between outer and middle ear

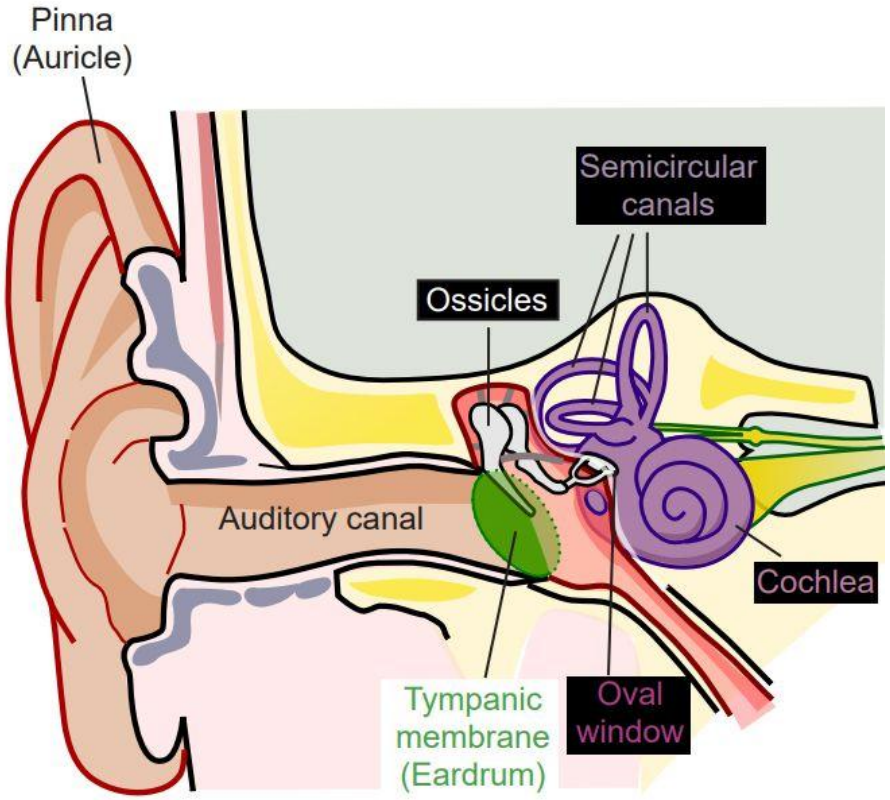


Figure 8.4 Anatomy of the auditory system.

Bones of middle ear

- Attached to tympanic membrane, ossicles
- Three bones that convey vibrational sound information
    - **Malleus**
    - **Incus**
    - **Stapes**
- Bones amplify incoming sounds by a tenfold difference; important because inner ear is a denser medium (liquid)

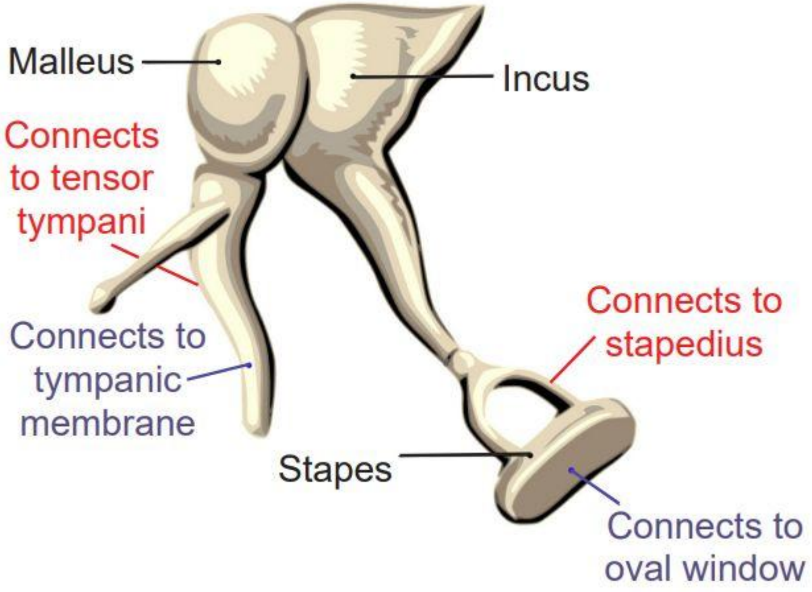


Figure 8.5 Anatomy of the ossicles, found in the middle ear. Bones are labeled in black, connections to membrane labeled in blue, and connections to muscle labeled in red.

Movement of ossicles

- Movement of ossicles is partially regulated by 2 muscles:
  - **Tensor tympani** – connects with malleus
  - **Stapedius** – connects to the stapes
- Contractions of muscles → ossicles move less → decreased intensity of loud sounds **(acoustic reflex)**
  - Decreases sound by about 15 dB

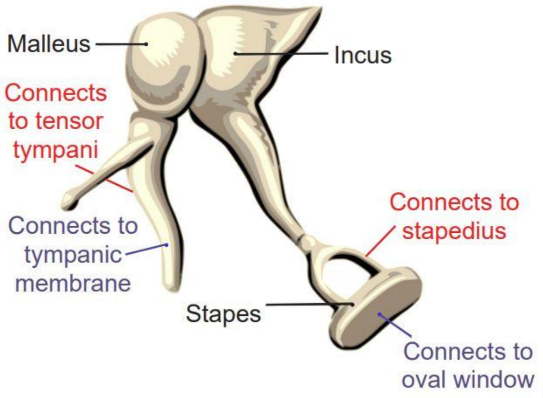
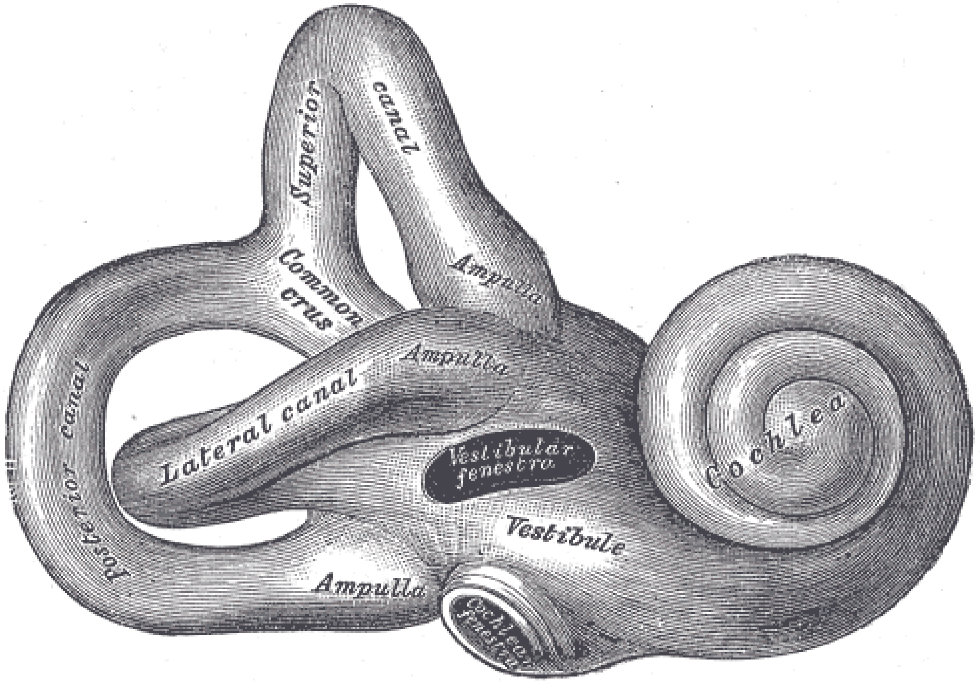


Figure 8.5 Anatomy of the ossicles, found in the middle ear. Bones are labeled in black, connections to membrane labeled in blue, and connections to muscle labeled in red.

https://www.flickr.com/photos/specialk-files/428060061/

Physical structures: Inner ear

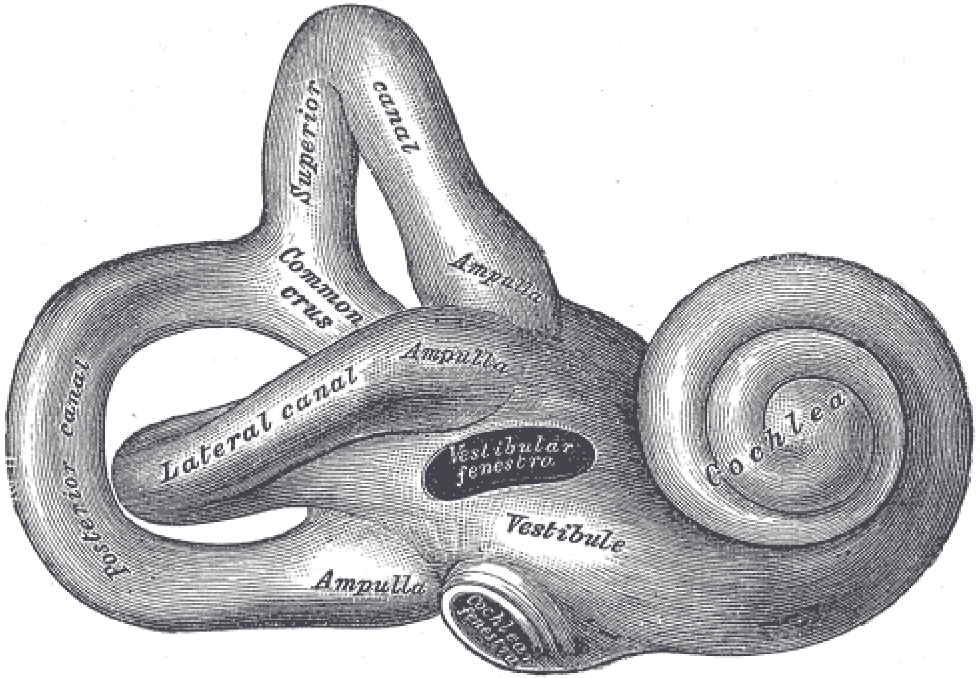
- **Oval window** – thin membrane that is the entrance to inner ear; entrance to vestibular labyrinth
- **Vestibular labyrinth** – main auditory structure of inner ear; hollow bone; auditory portion of it is **cochlea**



Henry Gray. (1918). Anatomy of the Human Body. Public Domain.

Physical structures: Inner ear

- Cochlea (ancient Greek word for "snail shell") - spiral shaped structure; rolled-up cone that makes 2 ¾ turns
  - If unrolled (impossible), **base** (widest diameter portion) would be closest to oval window and **apex** (narrowest portion) would be at center of spiral
  - Objects with different stiffness vibrate at different frequencies; base is stiffer than apex; base vibrates at higher frequencies than apex; different points of cochlea respond to different vibrations



Henry Gray. (1918). Anatomy of the Human Body. Public Domain.

Physical structures: Inner ear continued

- **Organ of Corti** – specialized epithelial membrane inside cochlea
- First nervous system structure processing physical vibrations and converting into signals NS can interpret

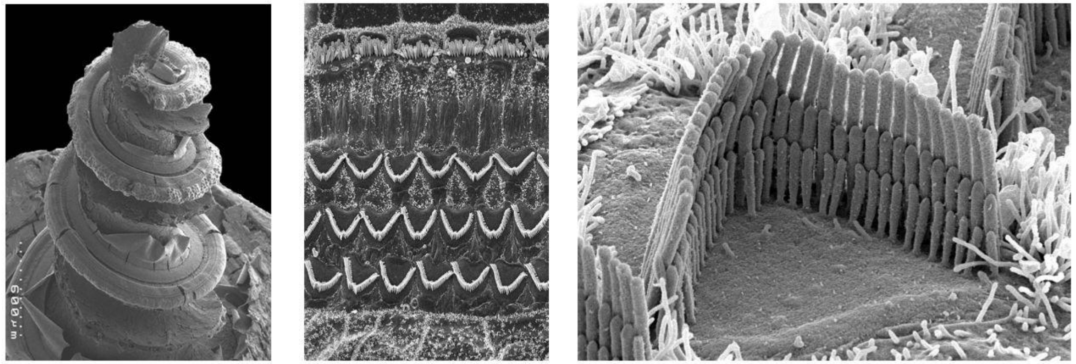
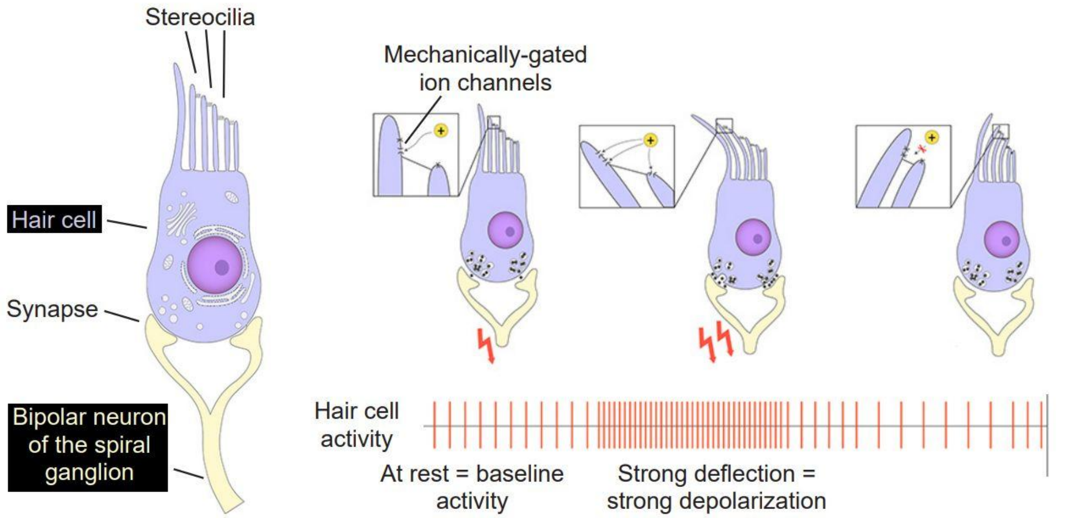


Figure 8.6 Anatomy of the Organ of Corti and hair cells under progressively higher magnifications in an electron microscope. The Organ of Corti is a spiral structure (left). The three rows of the outer hair cells and the single row of inner hair cells can be seen by zooming in (middle). At highest magnification, the stereocilia can be seen (right).

Neural components of auditory system

- Organ of Corti
  - converts sound waves into action potentials
  - adjacent to endolymph – high K^+, low Na^+ extracellular solution
- Somata of hair cells are embedded on interior surface of organ of Corti
- Hair cell
  - **Primary sensory neurons** to interpret physical movement
  - 30 – a few hundred **stereocilia** protrude away from organ of Corti and into endolymph

Figure 8.7 Physiology of hair cells. Physical deflection causes the opening of the mechanically-gated ion channels, which allows movement of K^+ into the hair cells, causing excitation.



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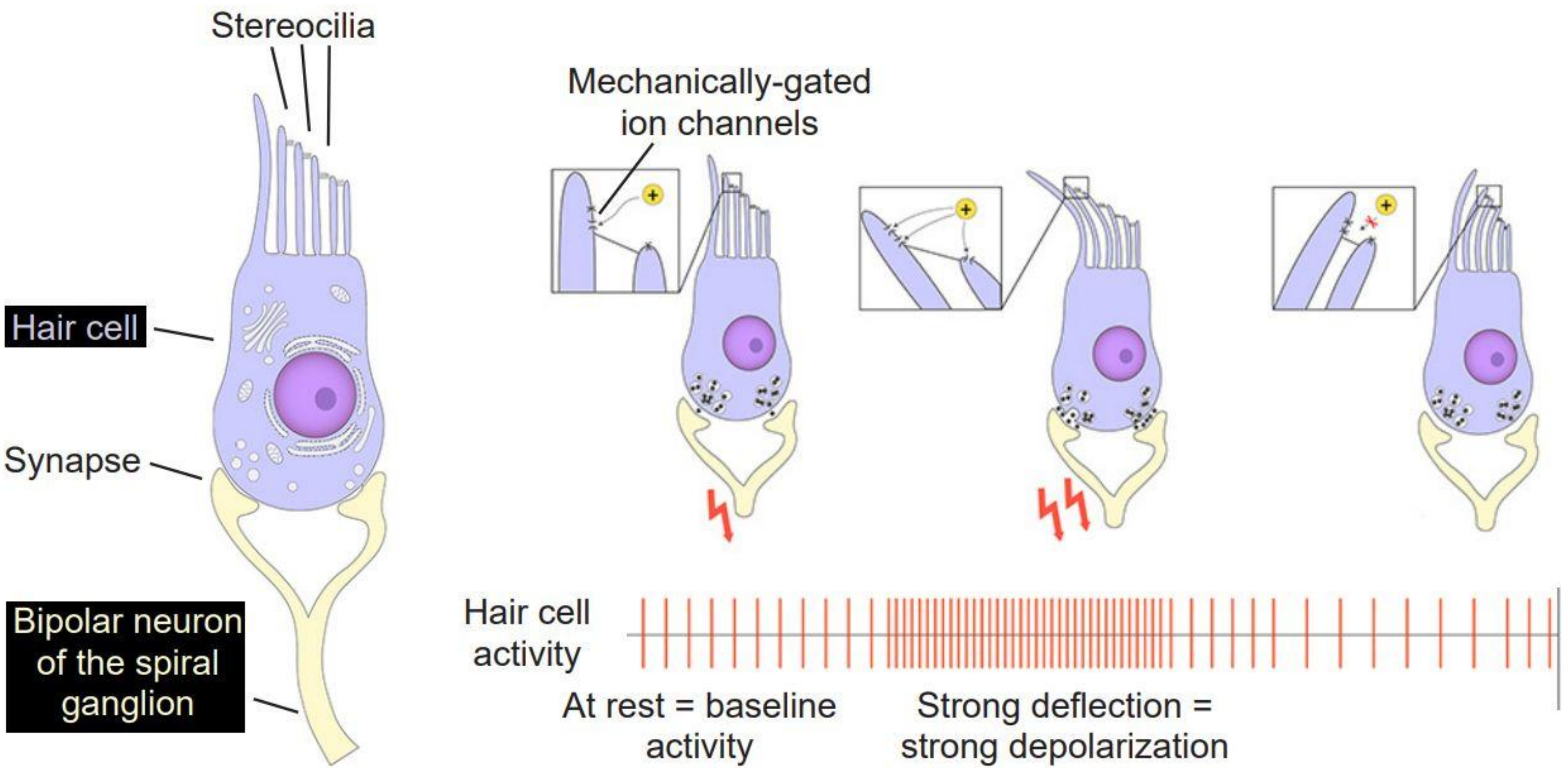
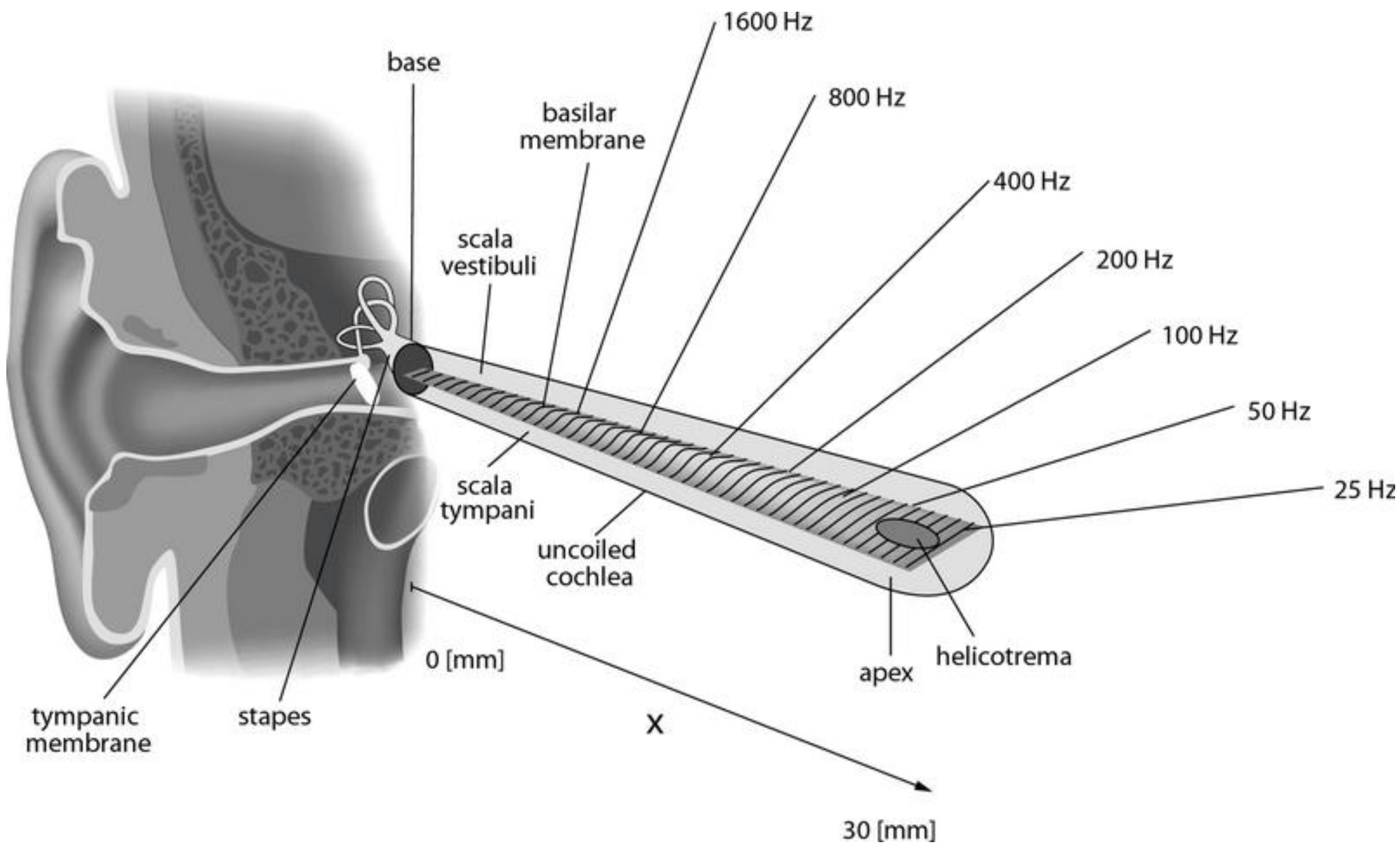


More on hair cells: Inner hair cells

- 2 different populations: inner and outer
- When vibration reaches oval window, endolymph also vibrates, displacing stereocilia
- Movement causes opening of **mechanically-gated ion channels** (**mechanotransduction**) → K^+ enters → cell depolarizes → neurotransmitter is released
- Hair cells are very sensitive to stereocilia movement; deflection on order of 100s of picometers (1 picometer = 1 trillionth of a meter) causes changes in electrical signaling in hair cell
  - Shorter hair cells respond to high-pitch sounds (base)
  - Longer hair cells are more sensitive to lower pitched sounds (apex)
- As such, position along spiral and length of stereocilia allow "tuning" in cochlea

Unrolled / Uncoiled Cochlea Depicted



Kern A, Heid C, Steeb W-H, Stoop N, Stoop R. 2008. Biophysical Parameters Modification Could Overcome Essential Hearing Gaps. License: CC-BY-2.5

Outer hair cells

- Function as amplifier to increase intensity of vibrations
- Estimate: increase sound by 20-80 dB
- Three rows
- Form glutamatergic synapses onto **bipolar neurons** of the spiral ganglion

More neural components

- **Spiral ganglion**
- Axons = **Vestibulocochlear nerve** (AKA auditory nerve; CN VIII)
  - Carries vestibular information
  - Some of these project to
    - Superior olive – a pontine area; an integrative center that receives bilateral input
    - Cochlear nuclear complex – in rostral medulla; carries out some auditory processing functions

Clinical connection: Hearing loss

- Permanent hearing loss
- Two classifications:
  - **Conductive hearing loss** – changes to auditory system up to oval window (ex. Tumor in ear canal, tympanic membrane perforation, changes to middle ear pressure)
  - **Sensorineural hearing loss** – changes from inner ear up to neural pathway (ex. hair cell damage, brain tumor, bacterial or viral infections, exposure to toxins or drugs)

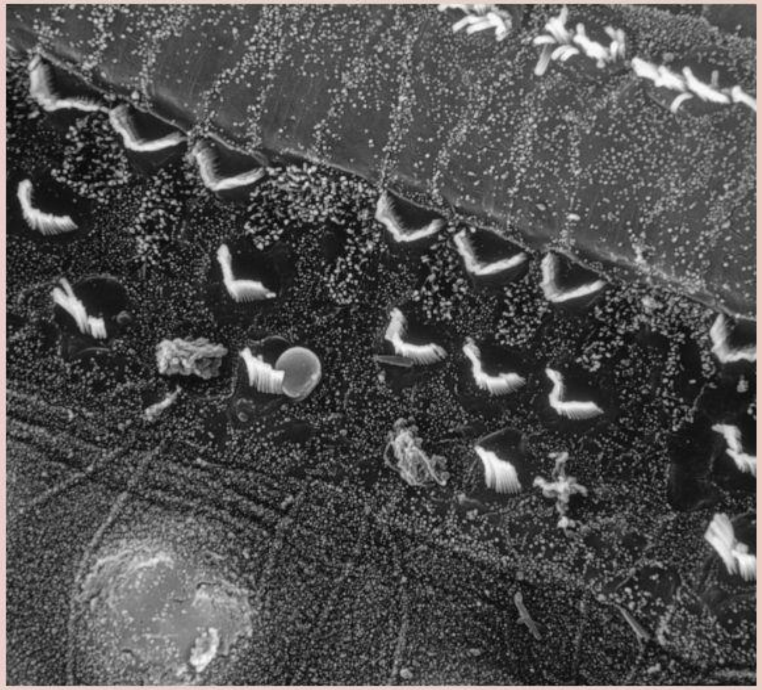
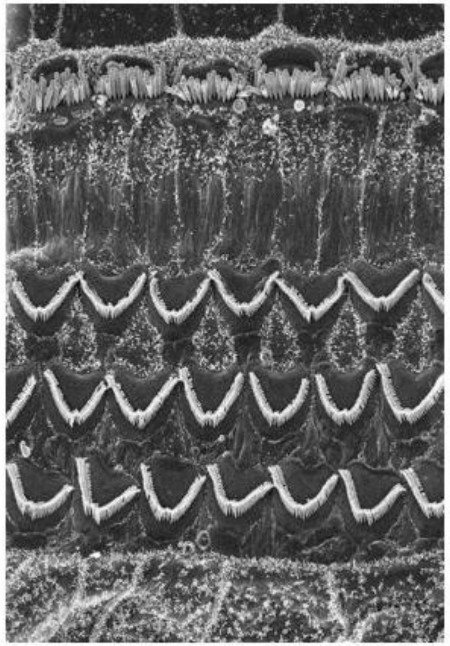


Figure 8.8 Damaged hair cells under an electron microscope.



Hearing loss reversal

Suggested additions to watch list:
Sound of Metal
A Quiet Place

- Most common cause of hearing loss = **excessive noise exposure**
  - Preventable by earing appropriate protection
- Another common cause – **aging**
  - Born with 15, 000 hair cells; damage throughout life; shorter hair cells are more sensitive to injury (lose sensitivity to high-frequency sounds)
- Partial hearing loss can be reversed
  - **Hearing aid** – process that helps filter out background noise, decrease pitch, and amplify incoming sounds
  - **Cochlear implant** – surgically-implanted devices that receives incoming sound and directly stimulates auditory nerve (bypassing external components of auditory system)

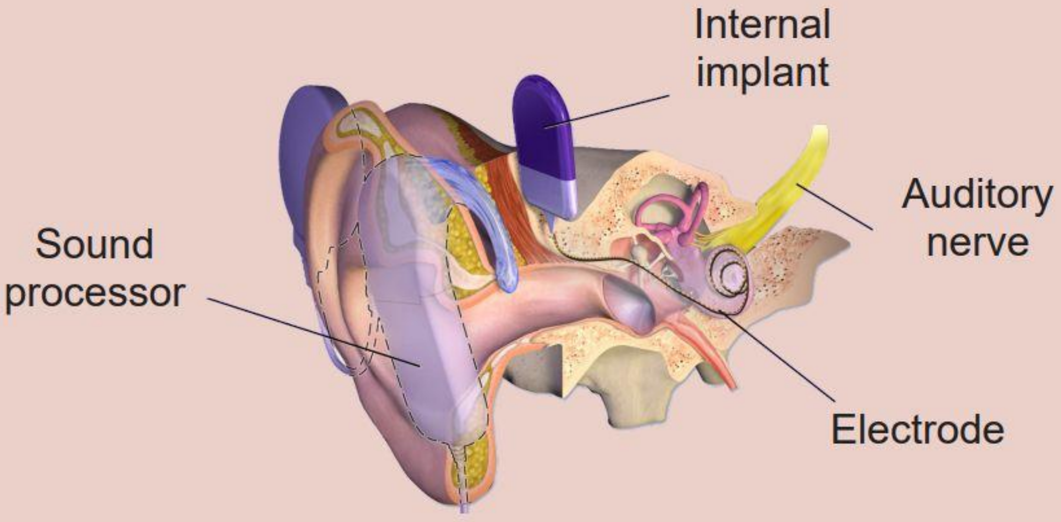


Figure 8.9 A cochlear implant directly stimulates the neural components of the auditory system.

Superior olives

- Help us figure out if sound originates from left or right side
- Two calculations:
  - **Interaural level difference**
    - Difference in volume between left and right ears
    - Evaluated by neurons in the lateral superior olive
  - **Interaural time difference**
    - Difference in when sound reaches ear
    - Assessed by medial superior olive
- Sound localization when sound is above or below ears: tilting of head
  - A different strategy in owls: https://youtu.be/8SI73-Ka51E?t=127

Pathway continued

- **Inferior colliculi**
  - Important for interactions between multiple sensory inputs and motor response
  - Particularly responsive to biologically-relevant sounds (ex. focus on a predator)
- **Medial geniculate body** (thalamic nuclei)
- **Primary auditory cortex** (A1; historically called Herschel's gyrus) - dorsal-most part of temporal lobe

- Many components (organ of Corti, spiral ganglion, and A1) are **tonotopically organized** (adjacent physical areas are responsible for information from adjacent frequencies)

- **Secondary and tertiary auditory cortices**
  - Evidence to support dual stream organization: dorsal (location of sounds, speech production, and language related memory) and ventral (sound recognition and sentence comprehension)

Neural pathways depicted

Note there is an extra synapse on this figure

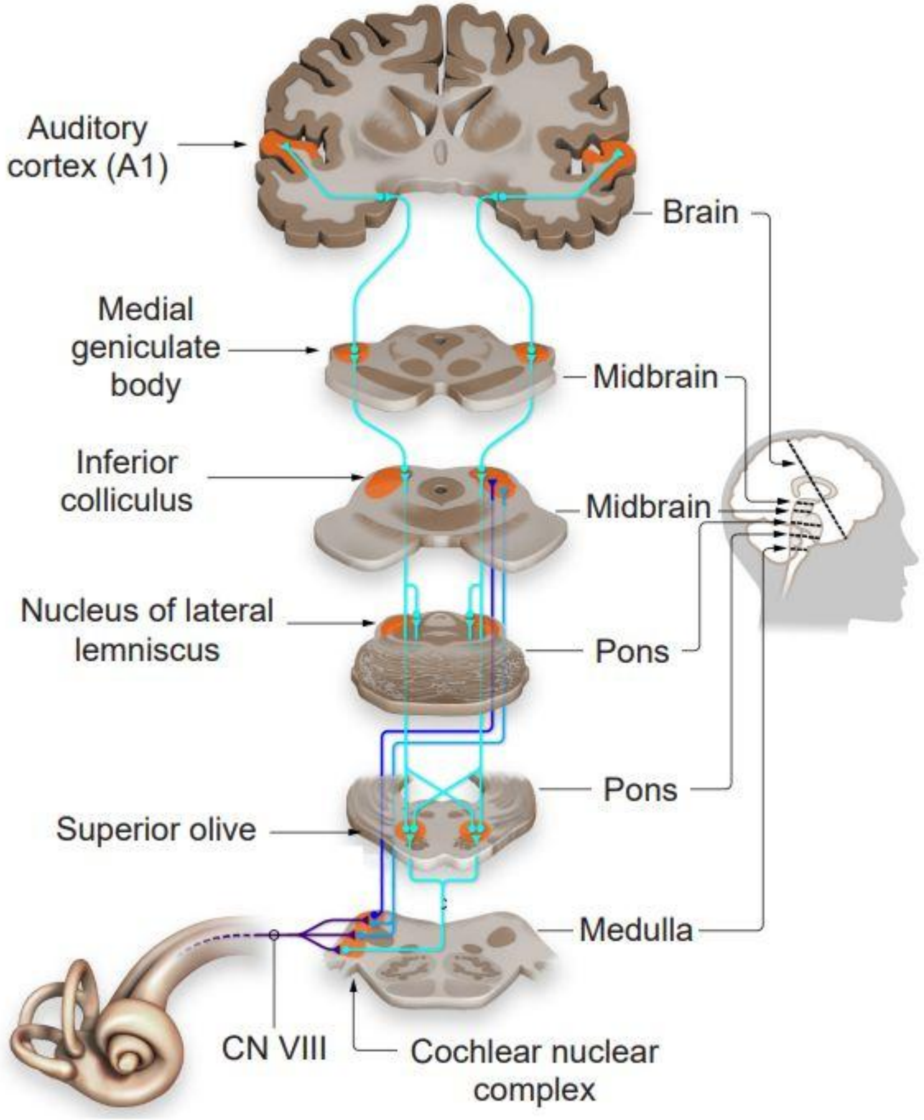
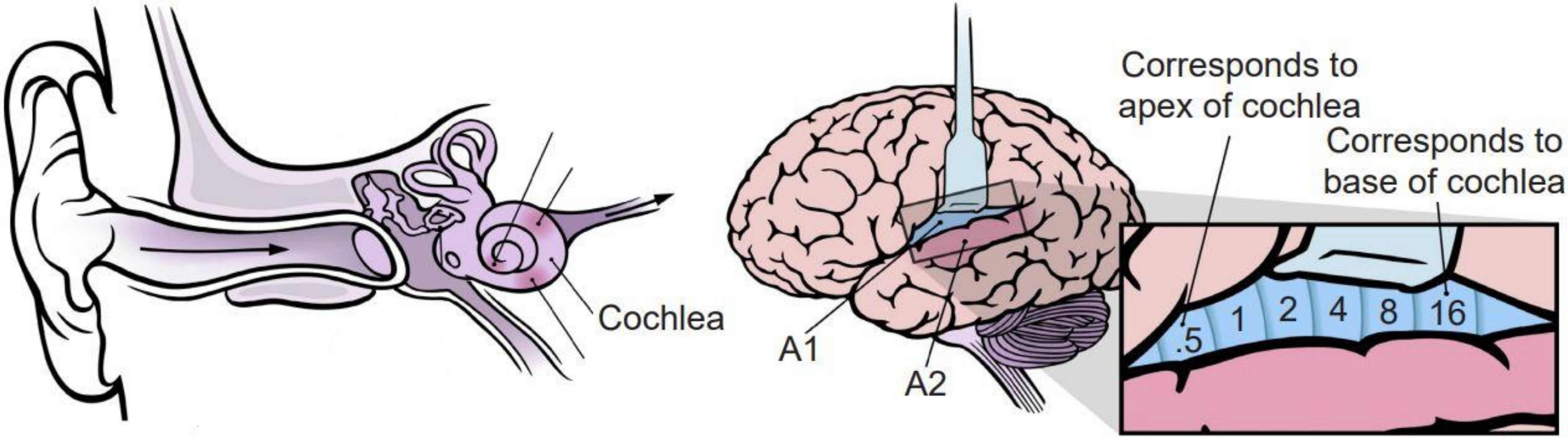


Figure 8.10 The neural pathways involved in the auditory system.

Tonotopy depicted

Figure 8.11 Tonotopy is maintained across many of the auditory neural structures, from the cochlea to the auditory cortex.



Dual stream organization

- Evidence for dual stream in auditory processing
  - **dorsal auditory stream**
    - helps identify the location of sounds (analogous to the ***where*** pathway), speech production, and language related memory
  - **ventral auditory stream**
    - contributes to sound recognition (similar to the ***what*** pathway) and sentence comprehension

Clinical connection: Tinnitus

- Tinnitus: condition characterized by occasional perception of ringing, whistling, buzzing, or clicking sound in absence of a genuine stimulus
- Estimated 15% of people experiences some tinnitus and ~2% have clinically significant tinnitus
- Common predictor: hearing loss
- Leading theory: phantom sounds originating in brain as a result of faulty plasticity

The Vestibular System

- Acts like a 3-D compass that can detect head movement and help us balance ourselves in changing conditions

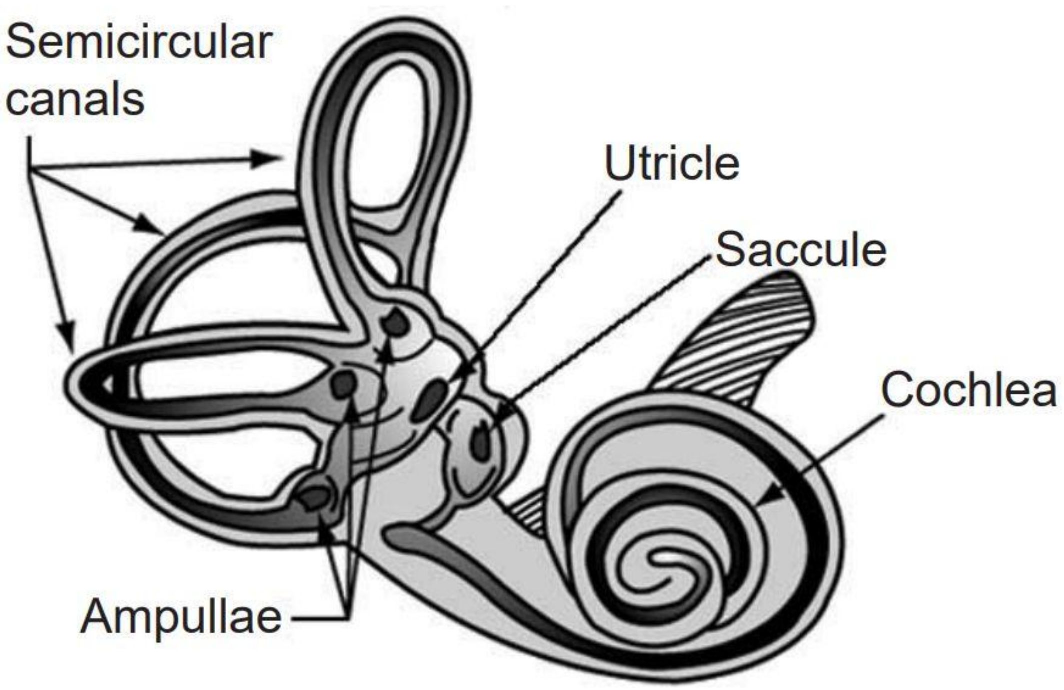


Figure 8.12 Anatomy of the vestibular system.

Organs of the vestibular system

- **Otolith organs**
  - Next to cochlea and within vestibular labyrinth; two sacs that determine changes in inertia
    - **Saccule** – more sensitive to vertical movements
    - **Utricle** – more responsive to horizontal movements
  - **Otoliths** (small calcium carbonate crystals; oto- means "ear" and –lith means "rock") within these sacs and embedded within gelatinous membrane
  - **Stereocilia of hair cells** are also in the membrane; deflection of these allows K^+ in surrounding endolymph to enter cells through mechanically-gated ion channels (shifting of physical weight of otoconia is what causes hair cell movement)
  - Information from hair cells is sent to brain via branch of **vestibulocochlear nerve** (CN VIII)
  - Axons reach **cerebellum** (important to balance), **reticular formation** of brain stem, **spinal cord**, and **thalamus**

Organs of vestibular system continued

- **Semi-circular canals**: Responsible for detecting head rotation
  - Series of 3 arch-shaped membranous tubes within vestibular labyrinth, oriented at a right angles to each other
  - Due to shape, can convey information about roll, pitch, and yaw (any direction of head movement)
  - Filled with **endolymph** (like cochlea)
  - At end of three canals, **ampulla** (swelling)
  - Within ampulla, **cupula** (gelatinous membrane)
  - Hair cells extend **stereocilia and kinocilium** (another cellular protrusion) into cupula
  - When we tilt head, endolymph in semicircular canals flows in the ampulla, physically displacing cilia
  - These hair cells have mechanically-gated ion channels working on a push-pull system
    - Hairs deflected in one direction, hair cells depolarize; deflection in opposite direction causes hyperpolarization

Pitch, roll, and yaw:
https://images.app.goo.gl/4bG4q5UEbwutNBup7
https://images.app.goo.gl/SZbZdh1h5Un5eZQD7

Vestibular reflexes: 1. Righting reflex

- Righting reflex
  - Animals correct their body position if they are in an abnormal orientation
  - Knowing up from down depends on afferent vestibular signals, but performance of motor task also requires integration of visual and somatosensory inputs

Vestibular reflexes: 2. Vestibulo-ocular reflex

- **Vestibulo-ocular reflex (VOR)**
  - Eyes stay fixed on target while head moves
  - Rapid head impulse test (diagnostic assessment) - physician shakes head
  - Response is driven through series of 3 synapses
    1. Axonal projections from neurons of vestibular system to neurons of vestibular brainstem nuclei
    2. Vestibular brainstem nuclei send axonal projections to contralateral hemisphere - form synaptic connections with two populations of neurons in contralateral pons
       - Motor neurons excite extraocular muscle opposite of the eye movement (right head turn triggers excitation of lateral rectus of left eyeball, pulling eyeball in temporal direction (left)
       - Interneurons excite medial rectus of right eyeball, the extraocular muscles that pull the right eyeball in the nasal direction (left, again)
    - Simultaneously, inhibitory circuits act at opposite muscles to inhibit eye from moving in same direction as turn
    - Operates on ~10 ms span; fast reflex

VOR circuitry

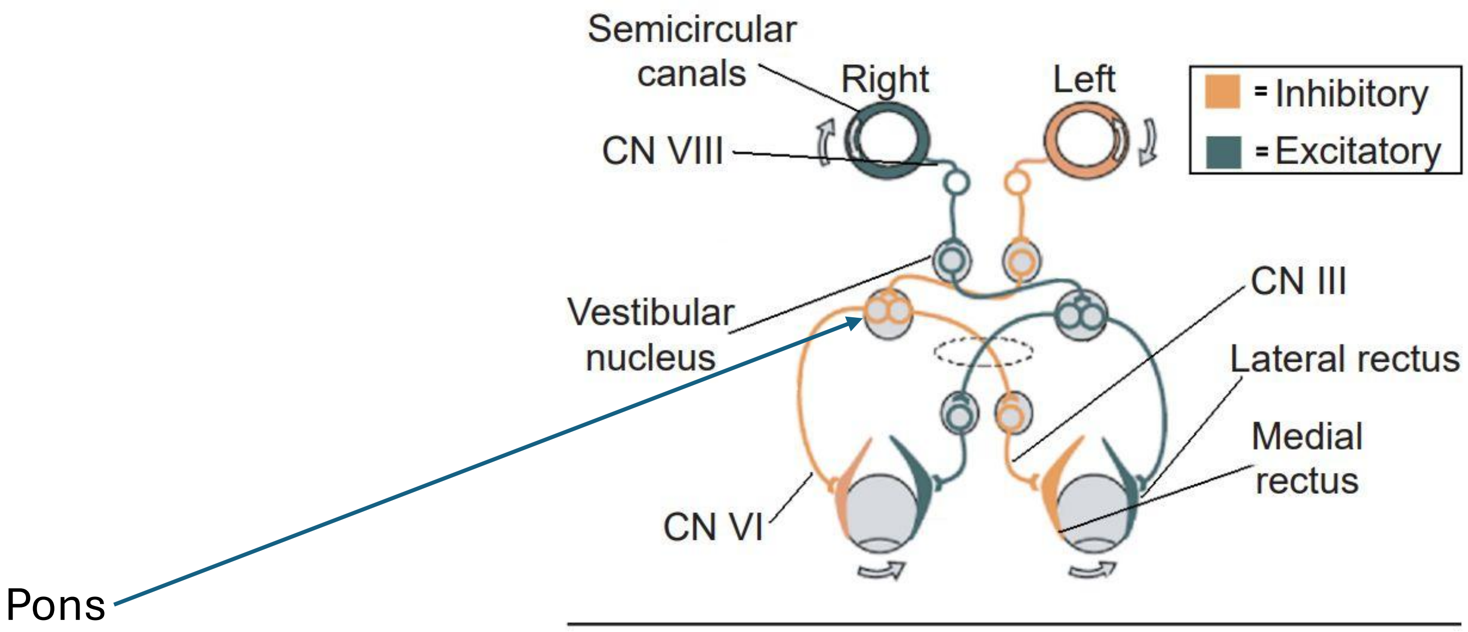


Figure 8.13 Neural circuitry underlying the vestibulo-ocular reflex (VOR) originates at the semicircular canals that detect head movement and ends with compensatory extraocular muscle activation.

Clinical connection: Vertigo

- Vertigo: sensation of spinning or movement while standing still
- Leads to dizziness, imbalance, ear pain, nausea, or vomiting
- A symptom, rather than a disease
- Estimated 7% of people experience vertigo in their lives, affecting woman ~3 times more often than men
- Potential causes
  - Benign paroxysmal positional vertigo
  - Meniere's disease (often experience other ear-related problems)
  - Bacterial or viral infections
  - Excessive alcohol intoxication
  - Severe head trauma

The Somatosensory System

- Afferent branch of somatic NS (part of PNS) = nerves that receive somatosensory inputs
- These nerves provide information about physical stimuli, including pressure, stretch, vibration, heat, and pain
- Minimal processing in spinal cord
- Information ascends through brain stem and passes through thalamus before reaching primary somatosensory cortex, S1 (anterior-most gyrus of parietal lobe)
    - Different types of sensory receptors – labelled line principle (theory about separate but parallel paths)
    - Somatotopic organization for spinal cord, thalamus, and S1 neurons
    - Two types of information are kept together: type of stimulus and location

Somatotopic organization at S1

- Mapping was discovered by neurosurgeon Wilder Penfield who electrically stimulated patients who had epilepsy surgery
- Key observation: volume of brain region corresponding to body parts is not necessarily proportional to area of skin
  - Large portion of cortex is dedicated to sensory information from lips and fingertips

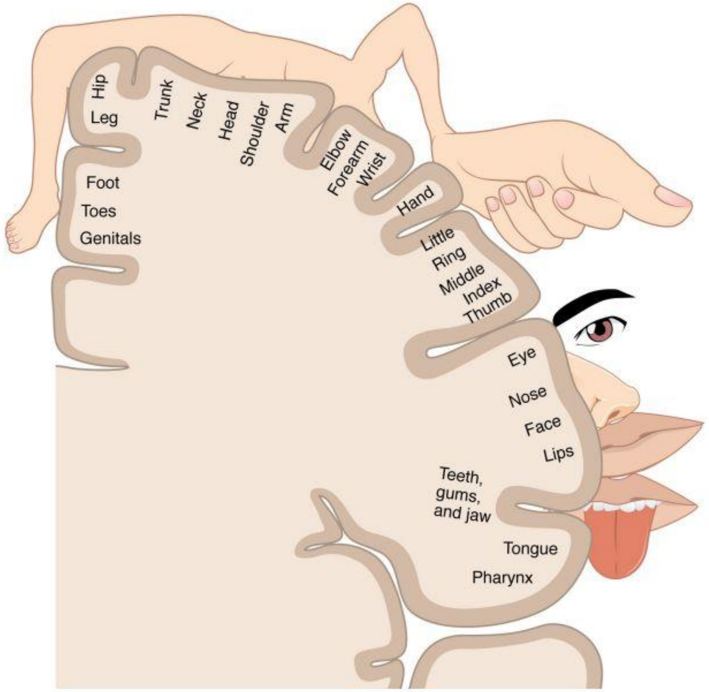


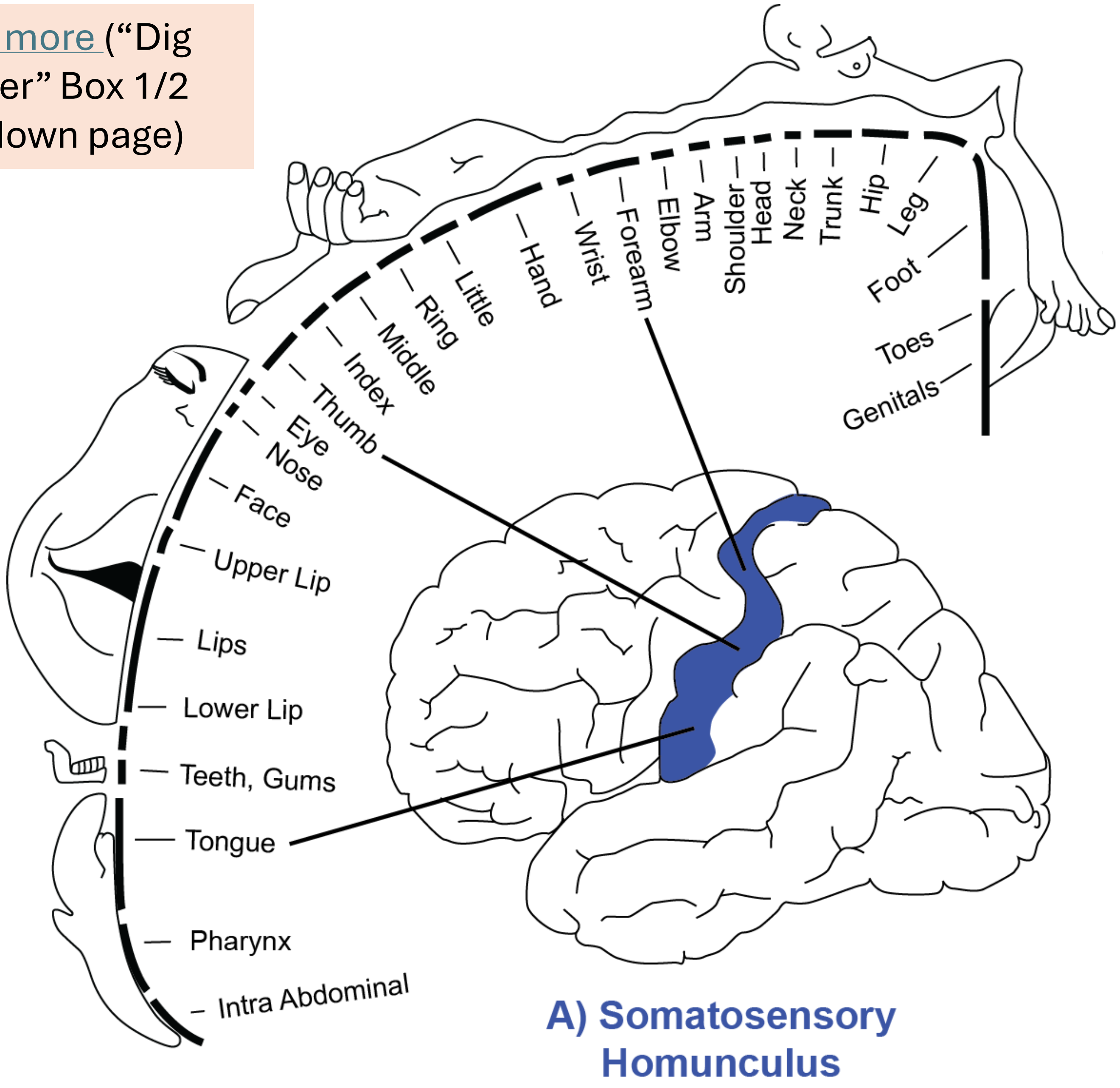
Figure 8.14 Different parts of the body ultimately send their signals through to different areas of the somatosensory cortex.

Sensory homunculus

- Person drawn to scale of how large dedicated area of S1 is

Figure 8.15 The somatosensory homunculus shows which parts of the body are heavily represented in somatosensory cortex, like the hands or mouth.

Read more ("Dig Deeper" Box 1/2 way down page)



Gender bias in neuroscience

Often, the homunculus is presented as a demonstration of neural organization in a *neutral* human body, even though it depicts a person with a penis and testicles. What about bodies that don't have those parts? Glaringly, Penfield didn't make a homunculus with breasts, vagina, clitoris, uterus or ovaries (Di Noto et al., 2012), even though he studied people with those body parts. (reproduced from https://caul-cbua.pressbooks.pub/intropsychneuro/chapter/the-brain-and-spinal-cord/, CC-BY 4.0)

Image courtesy Nancy Shie

Figure BB. 17: (A) 3D model of the H.P. Cantiles somatosensory homunculus. These sculptures depict the homunculus as an anatomically distorted 'little man', with the sizes of body parts corresponding to the amount of representation they have in the somatosensory cortex (adapted from creative commons, author Mpj29). (B) Representation of a 3D female somatosensory homunculus created by Haven Wright (adapted from Wright & Foerder, 2021). (reproduced from https://caul-cbua.pressbooks.pub/intropsychneuro/chapter/the-brain-and-spinal-cord/, CC-BY 4.0)

Continued processing

- Some outputs project into secondary somatosensory cortex, S2 (located posteriorly in parietal lobe), for higher-order processing

Cutaneous receptors

- Sensory receptors just under surface of skin (cutis refers to skin)
- Three categories of receptors
    1. Mechanoreceptors – detect mechanical changes to skin (ex. pressure or stretch)
    2. Thermoreceptors – detect temperature
    3. Nociceptors – detect pain

Mechanoreceptors

- Work via physical distortion of mechanically-gated ion channels
- When pressure is applied to protein, gate opens, Na^+ moves down electrochemical gradient, and depolarization occurs

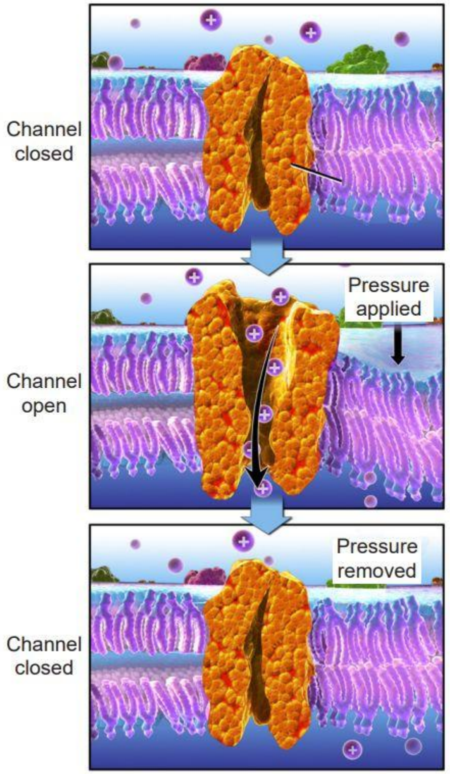
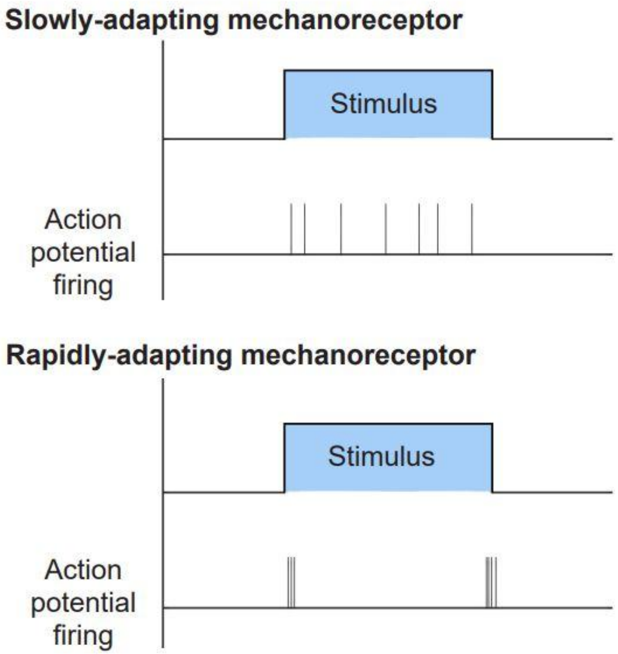


Figure 8.16 Mechanoreceptors respond to a physical distortion of the channels.

Classes of mechanoreceptors

1. Slowly-adapting (aka tonic receptors)
   - Change action potential firing rate as long as stimulus is present
2. Rapidly-adapting (aka phasic receptors)
   - Change activity the moment there is a change is stimulus
   - Signal change is status

Figure 8.17 Slowly-adapting mechanoreceptors modify their action potential firing as long as a stimulus is present, while rapidly-adapting mechanoreceptors do so only at the moments when a stimulus is changed.



Four different types of mechanoreceptors

- Different shapes
- Detect different stimuli
- 2 tonic, 2 phasic

1. Tactile epithelial cells (Merkel's discs)
2. Lamellar corpuscles (Pacinian corpuscles)
3. Tactile corpuscles (Meissner's corpuscles)
4. Bulbous corpuscles (Ruffini endings)

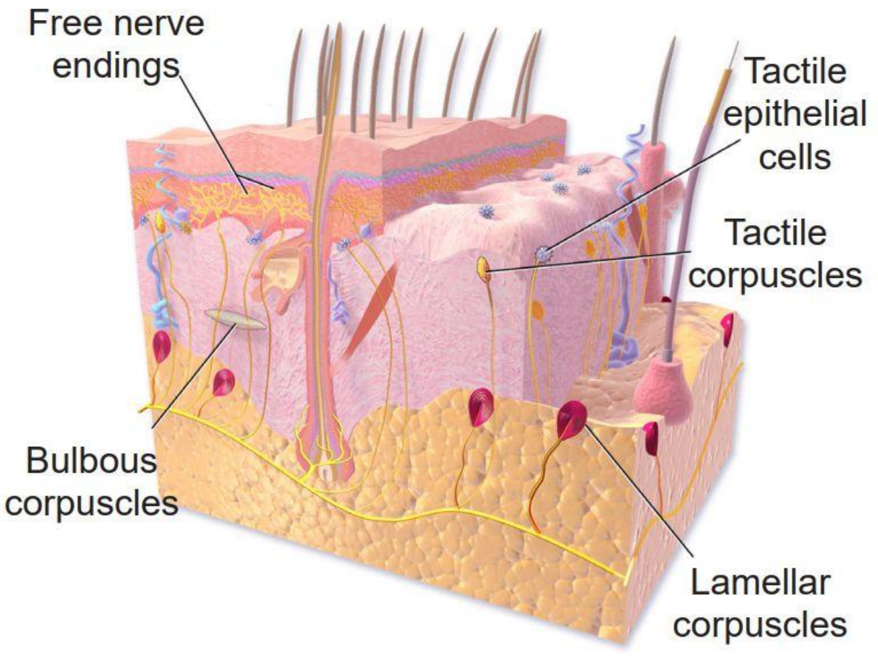
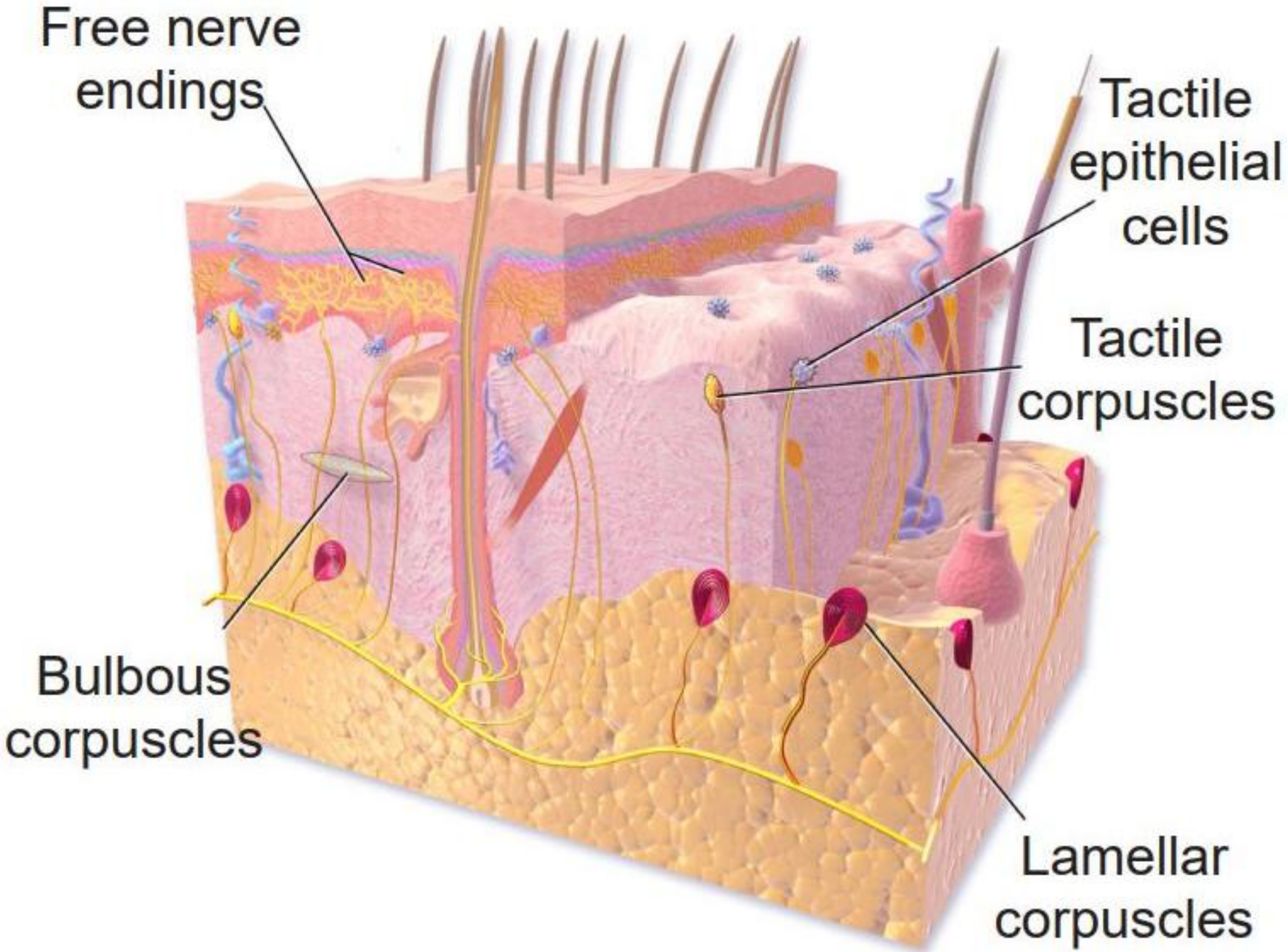


Figure 8.18 Cutaneous mechanoreceptors in the skin have different physiological properties and respond to different types of stimuli.


Free nerve endings
Tactile epithelial cells
Tactile corpuscles
Bulbous corpuscles
Lamellar corpuscles

Slowly-adapting receptors (tonic)

- Tactile epithelial cells (Merkel's discs)
  - Densely populated under skin layers
  - Sense pressure
  - Help us perceive edges, points, and corners (help with reading Braille)
  - Most precise mechanoreceptors (resolution at the level of 0.5 mm)
  - Release serotonin at synapses
- Bulbous corpuscles (Ruffini endings)
  - Respond to stretching of skin (ex. object slipping out of grasp)

Rapidly-adapting receptors

- Lamellar corpuscles (Pacinian corpuscles)
  - Wrapped in several layers of connective tissue
  - Mostly respond to high-frequency vibrations and deep pressure
  - Deepest of cutaneous receptors
- Tactile corpuscles (Meissner's corpuscles)
  - Highly sensitive to light touch, skin movement, and low-frequency vibration
  - Found in superficial skin layers
  - Concentrated heavily at fingertips

Cutaneous mechanoreceptors continued

- Receptive field = particular patch of skin that responds to particular cutaneous stimuli
- Smaller the receptive field, better brain can distinguish between two different adjacent tactile stimuli
- Different sizes of receptive fields throughout body
  - Receptive field at fingertips and lips are very small (~10 mm^2)
  - Receptive field on back is much larger
- Different classes of mechanoreceptors have different receptive field sizes (deeper structures, like lamellar corpuscles, have larger fields)
- Approximate size of receptive field is assessed via two-point discrimination task

Receptive fields depicted

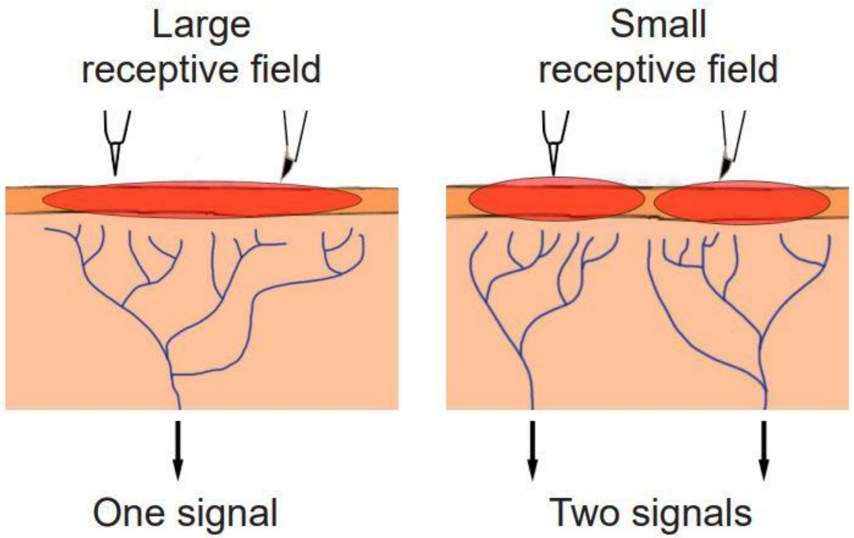


Figure 8.19 In skin areas with a large receptive field (left), two adjacent stimuli may feel like one. Skin areas with small receptive fields (right) are better able to distinguish two similarly-spaced points.

Afferent pathways from mechanoreceptors

- Cell bodies of receptors in dorsal root ganglion (DRG)
- Pseudounipolor neurons with single protrusion branching in two directions
  - One towards skin surface terminating as one of the mechanoreceptors
  - Other direction towards spinal cord
- Mechanosensory information travels via large Aβ axons (~10 μm in diameter) that send signals on order of 50 m/s

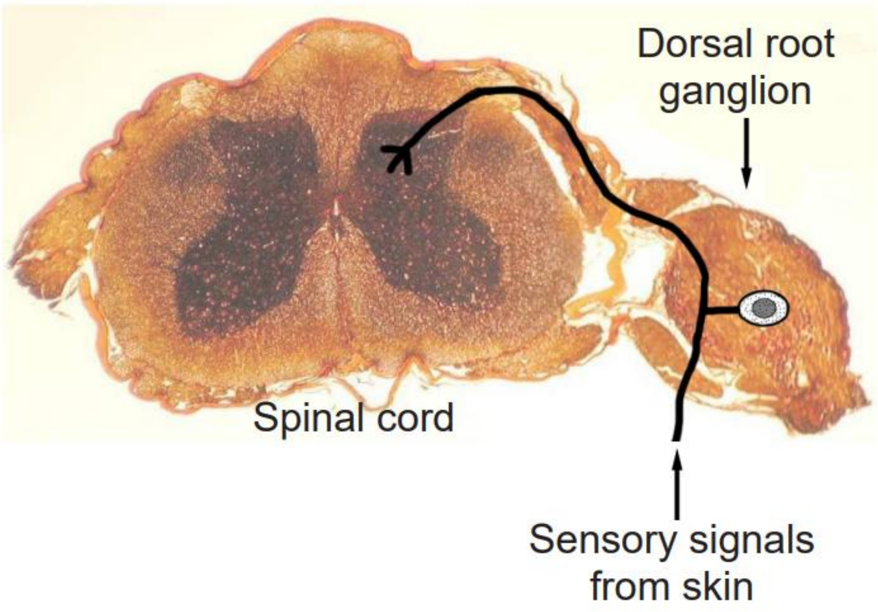
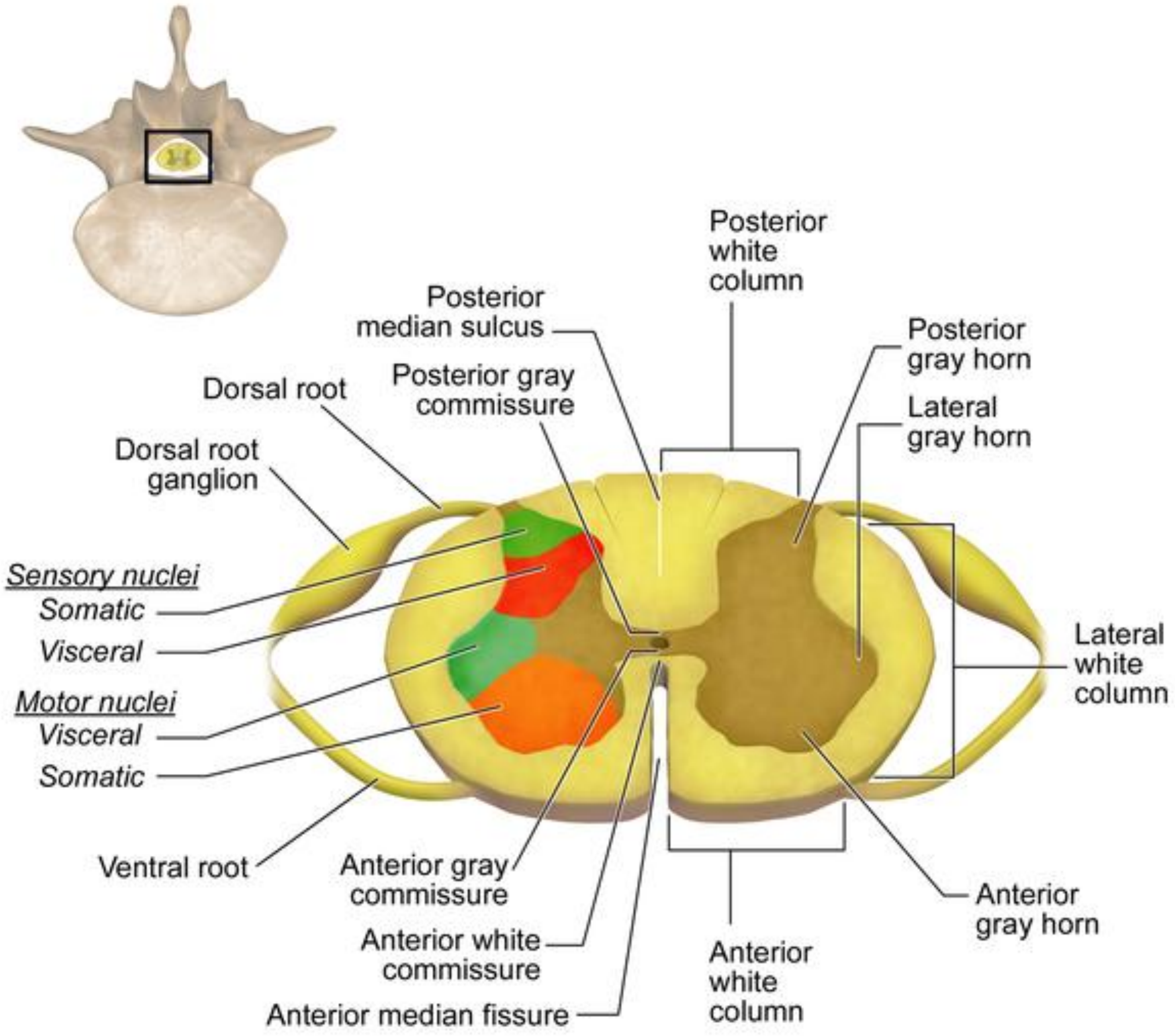


Figure 8.20 Somatosensory neurons are pseudounipolar, and have their cell bodies in the dorsal root ganglion. **Spinothalamic tract**



Sectional Organization of the Spinal Cord

Afferent pathway continued

- *Next, neurons with cell bodies in dorsal horn of spinal cord send ascending information through 2 different pathways*

1. Dorsal-column medial lemniscus (DCML) tract – projects through ipsilateral white matter
    - Carries crude touch, pressure, vibration, and two-point discrimination information
    - Form synapses with neurons in medulla, and then decussate
    - Ascend further into ventral posterior lateral (VPL) nucleus of thalamus
2. Spinothalamic tract – projects upward through contralateral white matter
    - Carries light touch and pressure information
    - Form synapses in dorsal horn, decussate, and project directly into thalamus

Thalamic neurons = tertiary neurons of somatosensory system; project into S1

Afferent pathway of mechanoreceptors depicted

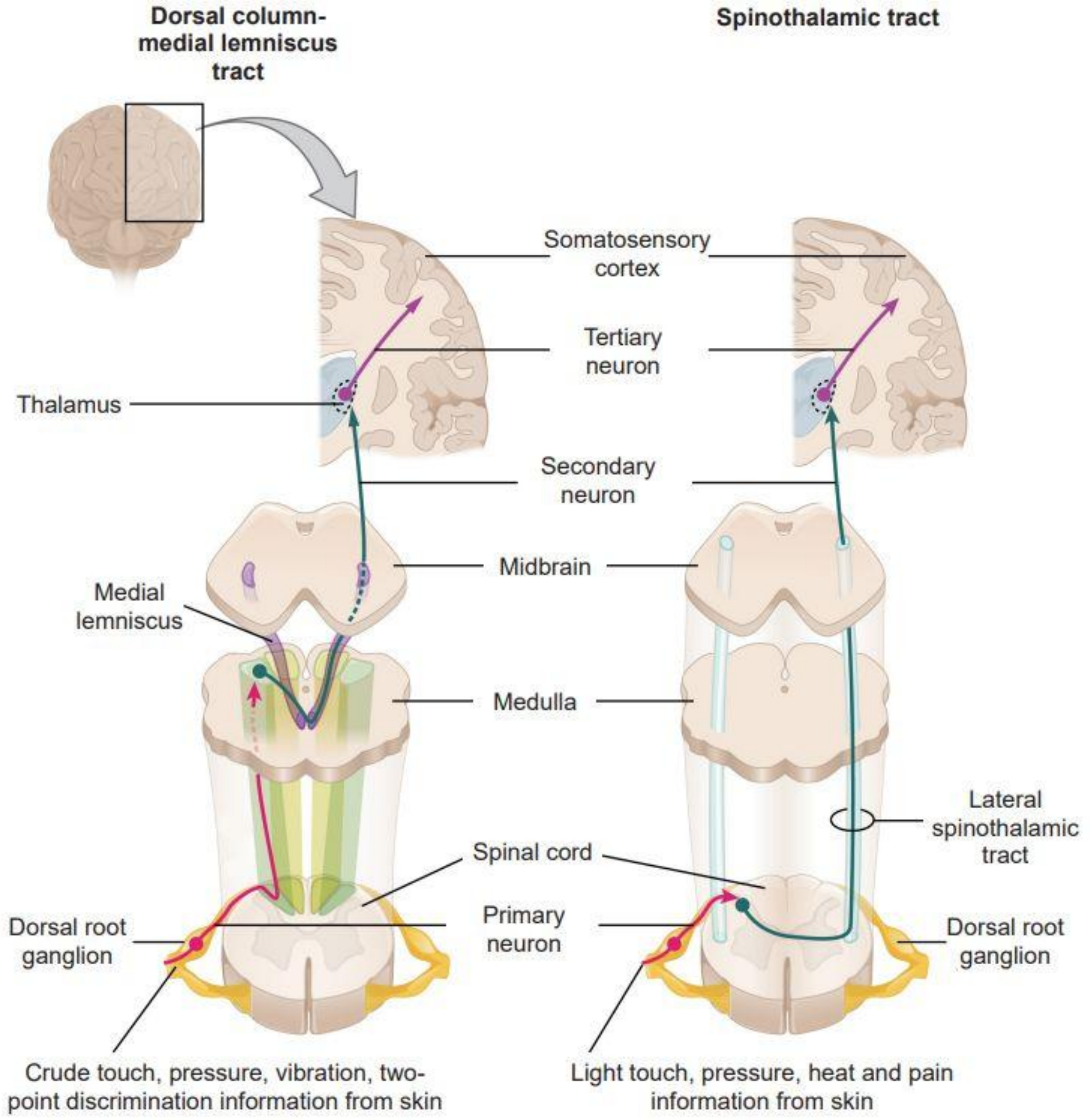


Figure 8.21 Summary of the two major ascending somatosensory pathways, the dorsal column-medial lemniscus (left) and the spinothalamic tract (right).

Thermoreceptors

- Two classes:
  - Low-threshold (15-45 ^{o}C)
    - Detect innocuous, non-harmful temperatures
  - High-threshold (hotter than 45 ^{o}C or colder than 15 ^{o}C)
    - Detect potentially damaging temperatures
- Located in a class of cutaneous receptors called free nerve endings
- Closer to surface of skin than mechanoreceptors
- Free nerve endings are the sensory end of pseudounipolar neurons with somata in DRG (like mechanoreceptors)
- Transient receptor potential receptors (TRP channels) - proteins are sensitive to changes in temperature & change shape more dramatically than other proteins
  - Non-selective cation channels
  - Cold sensations are detected by action of TRPM8 receptor (also activated by menthol)
  - Warm sensations are detected by TRPV1 receptor (also activated by capsaicin)

Thermoreceptors afferent pathway

- Different pathway from mechanoreceptor pathway
- Cool and cold temperature sensation is passed through thinly myelinated Aδ fibers
  - Smaller (~5 μm in diameter)
  - Transmit signals more slowly than to Aβ fibers (~25 m/s)
- Warm and hot temperature sensation is passed through unmyelinated C fibers
  - Even smaller in diameter, ~1 μm
  - With even slower conduction velocity, ~ 1 m/s
- Secondary neurons are within dorsal horn of spinal cord
- Ascending pathway runs through the white matter of the lateral aspect of the spinothalamic tract

Nociceptors

- Detect a variety of noxious stimuli, including crush, acid, and high heat
- Expressed on free nerve endings
- Many of these neurons respond to more than one type of stimulus – polymodal nociceptors
- Send signals through Aδ and C fibers
  - Aδ fibers detect sharp, highly-localized pain
  - C fibers carry dull, throbbing pain that is difficult to pinpoint
- Nociceptive mechanoreceptors can sense crushing, shearing, and cutting of skin
  - May have a high threshold of activity, preventing activation under harmless circumstance
- Acid-sensing ion channels are cation channels that respond to low pH conditions (seen in inflammation related to tissue injury)
  - Inflammation causes release of cellular signaling molecules (ex. prostaglandins and cytokines) which cause sensitization, enhancement of future incoming pain
- High-threshold thermoreceptors (TRP channels) detect painfully cold or painfully hot temperatures

Withdrawal reflex

- Motor response driven by circuit of neurons in the spinal cord
- Mediated independently from descending motor controls from brain
- Nociceptive input from sensory neurons enters spinal cord through dorsal horn, where it forms a synapse onto an excitatory interneuron
- Interneuron signals 2 populations:

1) flexor, muscle that withdraws when contracted
2) an inhibitory interneuron, which innervates the motor neuron controlling the extensor (muscle that functions opposite of flexor)

- Simultaneous activation of flexor and inhibition of extensor result in rapid withdrawal

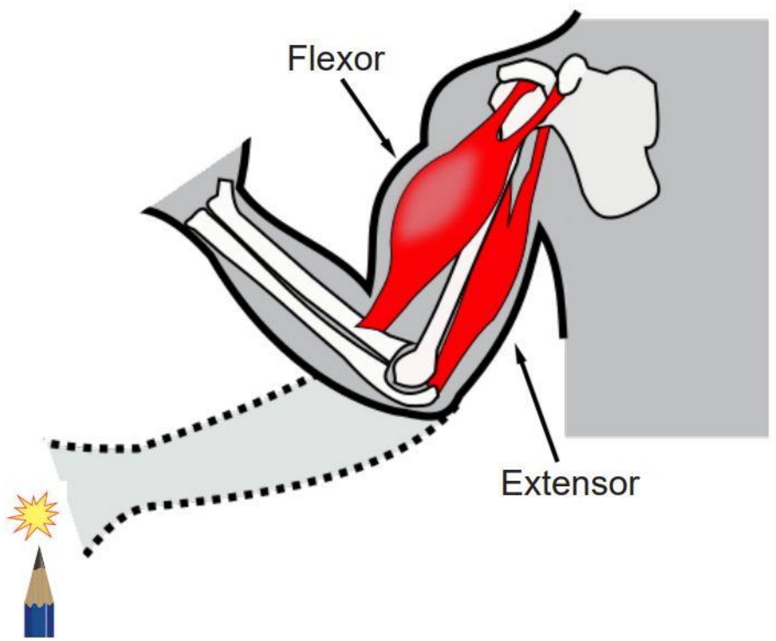
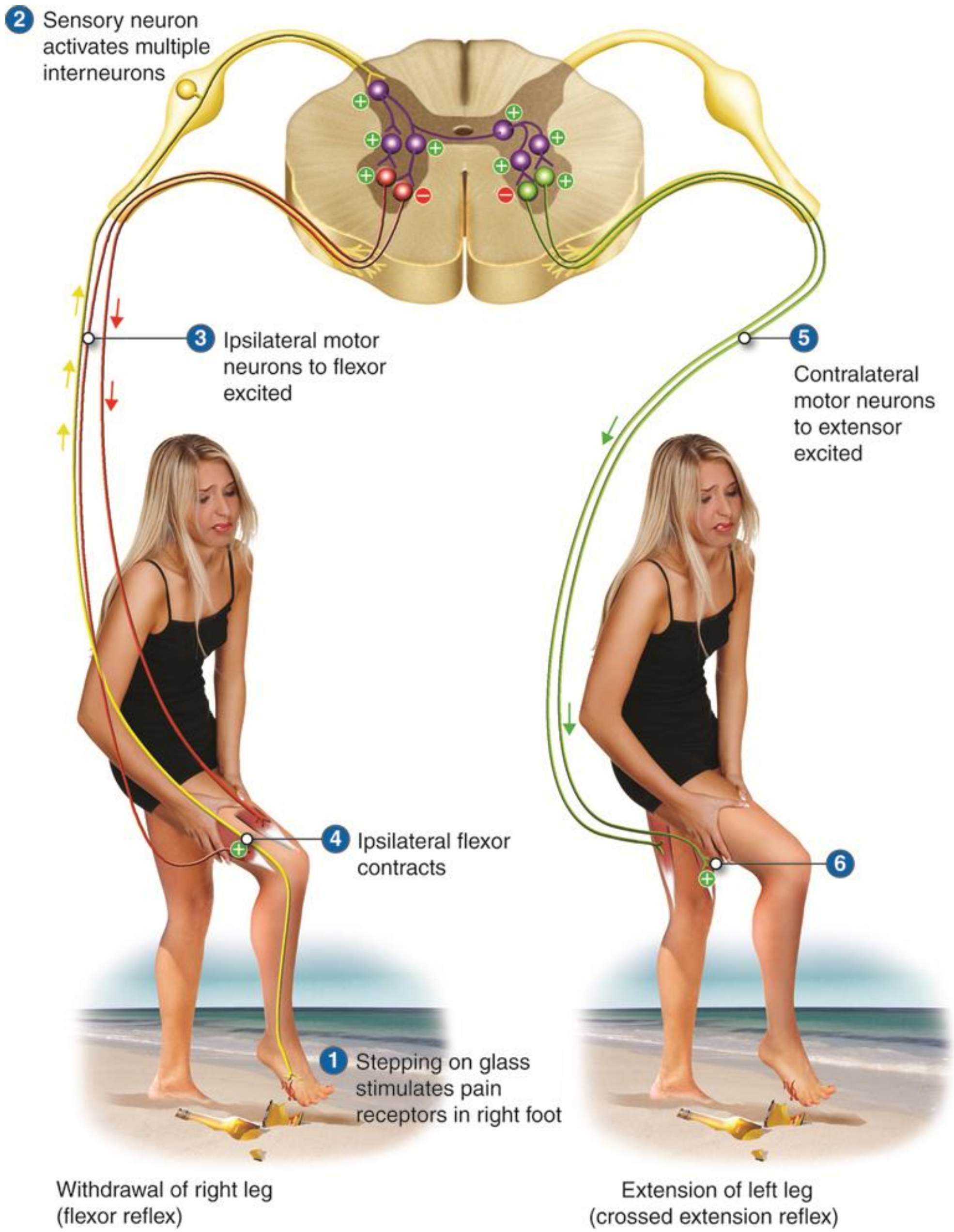


Figure 8.23 A painful stimulus produces a withdrawal reflex, which is driven by the action of skeletal muscles.

This diagram doesn't point out the inhibition of the extensor of the injured side. **Can you find it?**

It also adds the excitation of the contralateral extensor. **Why is that important?**



In addition to the withdraw reflex

- Ascending projections are sent to brain through white matter of lateral spinothalamic tract

Clinical connection: Pain disorders

- Allodynia – disorder where non-injurious tactile stimuli cause pain sensation
- Hyperalgesia – disorder of abnormally heightened perception of pain
- Neuropathic pain – broad category of pain conditions resulting from damage to nervous system
- Chronic pain – longstanding pain that persists beyond the usual recovery period or occurs with a chronic health condition (Johns Hopkins Medicine definition)
- Congenital insensitivity to pain – incapable of perceiving pain, no matter how severe; rare genetic condition
  - Mutations in SCN9A gene
  - The gene codes for a component of voltage-gated Na^+ channels expressed in nociceptors

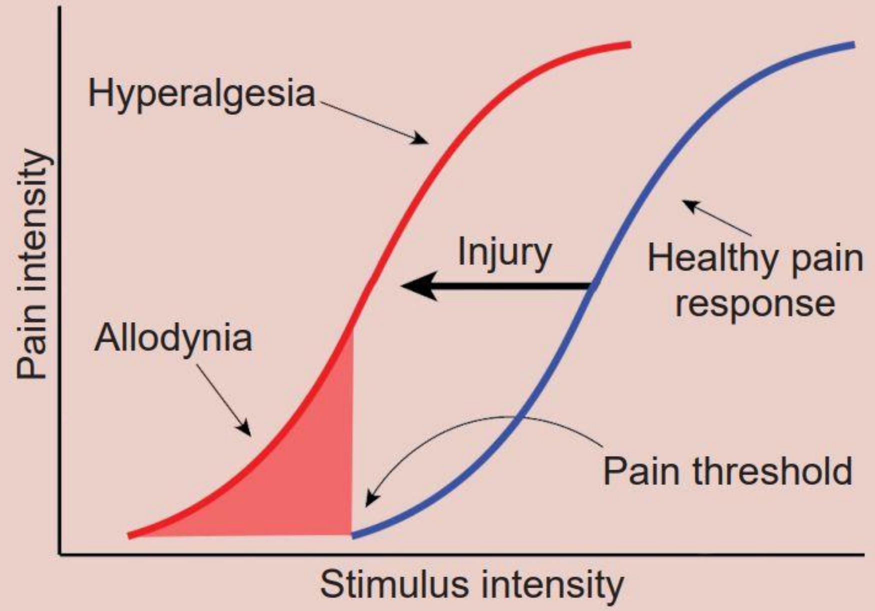


Figure 8.22 Allodynia and hyperalgesia are pain disorders characterized by altered responses to somatosensory stimulation.

Clinical connection: Referred pain

- Referred pain: feeling of pain at a site separate from where injury is located (ex. pain in shoulders or medial aspect of left arm indicating a heart attack)
- Happens when nervous system is unclear about how to process signals from internal organ and brain interprets afferent signals as bodily pain
- Injuries at different internal organs present as different patterns of somatic pain

Map of referred pain

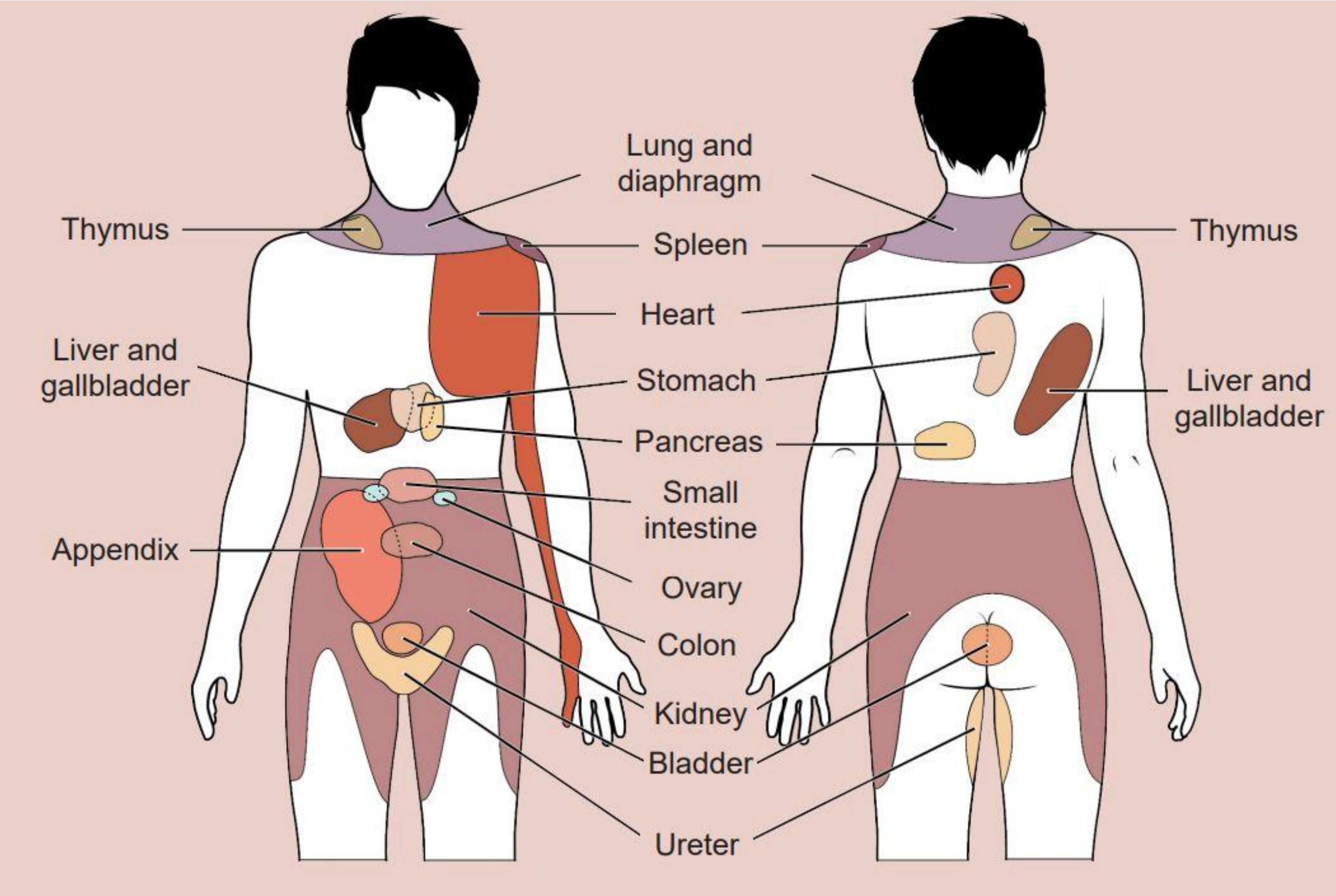


Figure 8.24 A map of referred pain sensations on the body and the corresponding visceral organ that may be triggering the pain.

Convergence theory of referred pain

- Afferent projections from the internal organs and the nociceptive somatosensory neurons of the skin form synapses onto the same population of spinothalamic tract secondary neurons.
- When these secondary neurons project towards the brain, there is no ability to differentiate the origin of the signal coming from the primary neuron.

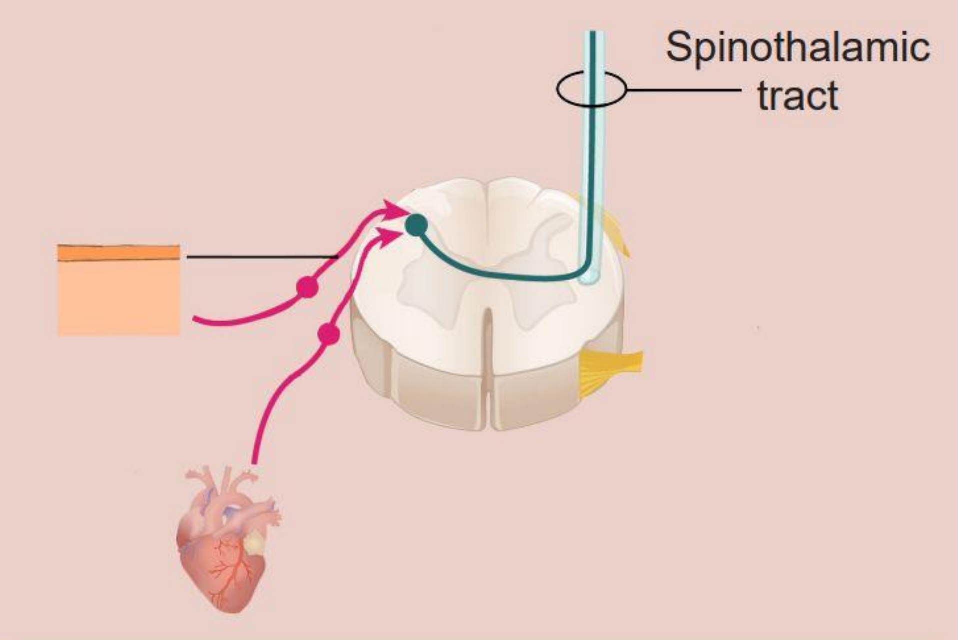


Figure 8.25 The convergence theory suggests that the signals from the internal organs and pain sensory inputs share the secondary neuron.

Central sensitization theory of referred pain

- Neurons of the spinal cord change in their excitability threshold with prolonged exposure to injurious stimuli
- When an injured internal organ repeatedly sends signals to secondary neurons, a host of neurotransmitters cause sensitization of the nociceptive signaling, which are now activated under non-noxious conditions

Proprioception

- Sense of knowing the location and position of your body parts
- Critically important to coordinated movement and motor reflexes that contribute to tiny, rapid adjustments that are made to maintain balance
- Proprioceptive information ascends through spinal cord to brain via the DCML tract
- Processed in S1
- Two main neuron system work to give sense of proprioception: muscle spindles and Golgi tendon organs (GTOs)

Muscle spindles

- Nervous structures wrapped around the skeletal muscle fibers
- Detect the status of muscle
- Each spindle is 6-10 mm long and spirals around thickest part of muscle fiber
- Flexed skeletal muscle becomes shorter and thicker
    - Muscle spindle also changes shape
- Spindles communication this information to the nervous system through action of non-selective cation mechanoreceptors that respond to physical distortion
    - muscle stretching increases firing rate, while muscle flexion decreases firing rate
- Density of muscle spindle is greater for skeletal muscles used for precise movements compared to those for coarse movement

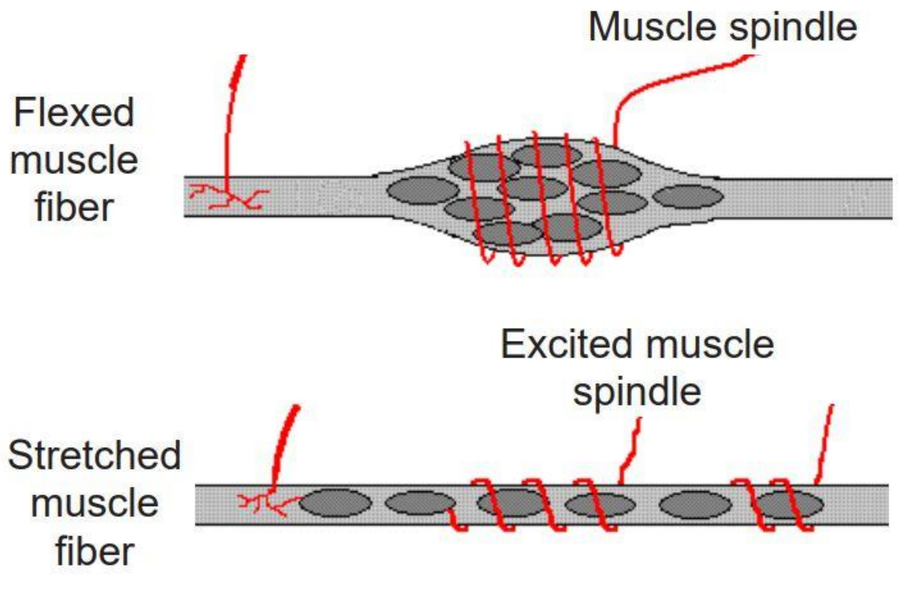


Figure 8.26 Muscle spindles wrap around the center of the inner muscle fibers and detect flexion.

Motor function of muscle spindles

- Communicate with gamma motor neurons that terminate at muscle fibers
- Combination of sensory and motor components allow muscle spindles to function in the stretch reflex (AKA myotatic reflex)
    - A spinal cord-mediated response to muscle stretch that causes flexion to prevent excess stretching which could damage muscle
    - Most well know example: Knee-jerk reflex (AKA patellar tendon reflex) - stretch on quadriceps leading to flexion of quadriceps, which causes foot to kick forward (monosynaptic reflex arc) + hamstring receives information to decrease activity
        - L2, L3, and L4 regions of spinal cord – location of neural circuitry responsible for knee-jerk reflex

Knee-jerk reflex depicted

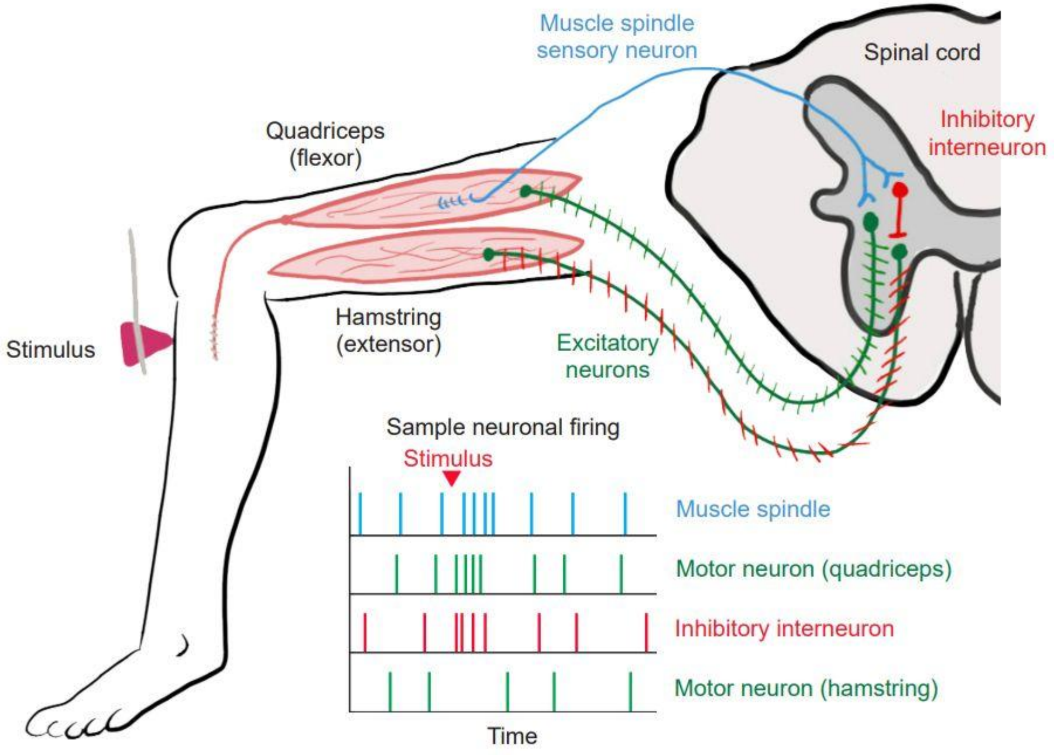


Figure 8.27 The knee jerk reflex is downstream of a series of neural circuits that start with changes in muscle spindle activity.

Golgi tendon organs (GTOs)

- Made up of collagen fibers
- Found at insertion site between muscles and tendons
- Convey information about amount of tension each set of skeletal muscles is experiencing as we move
- Contribute to detection of weight (ex. as we lift objects)
- Each GTO connects to ~20 muscle fibers and is ~0.5 mm long

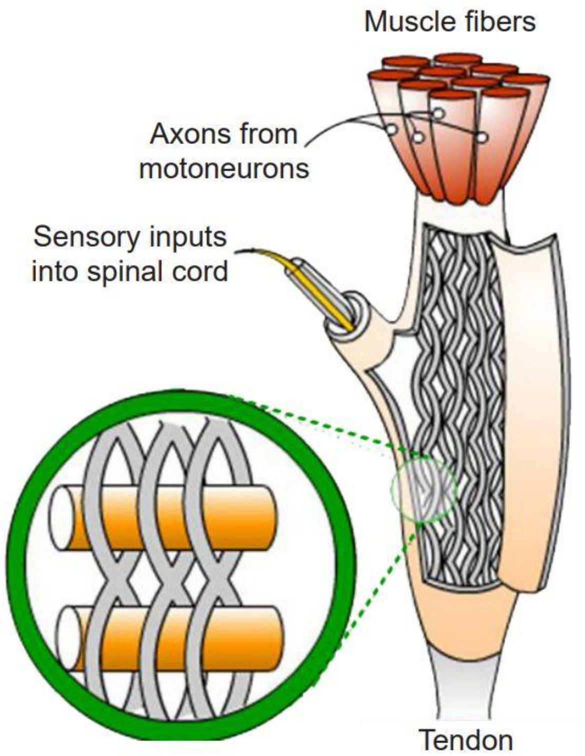


Figure 8.28 Anatomy of the Golgi tendon organ.

GTO pathway

- During muscle contraction, tension in GTO increases
- Opens non-selective cation mechanoreceptors (physical deformation)
- Changes excitability of GTO
- Outputs of GTO communicate with interneurons in spinal cord
- Interneurons inhibit motor neurons that innervate muscle that is "pulling" on the tendons
- GTO communicates via Aα fibers
  - Large diameter (14 μm), heavily myelinated axons
  - Transmit action potentials as fast as 100 m/s (fastest projections in somatosensory system)