Part 4, Sensory and Motor Systems

4.1. Somatic sensory system

Sensation and sensory processing

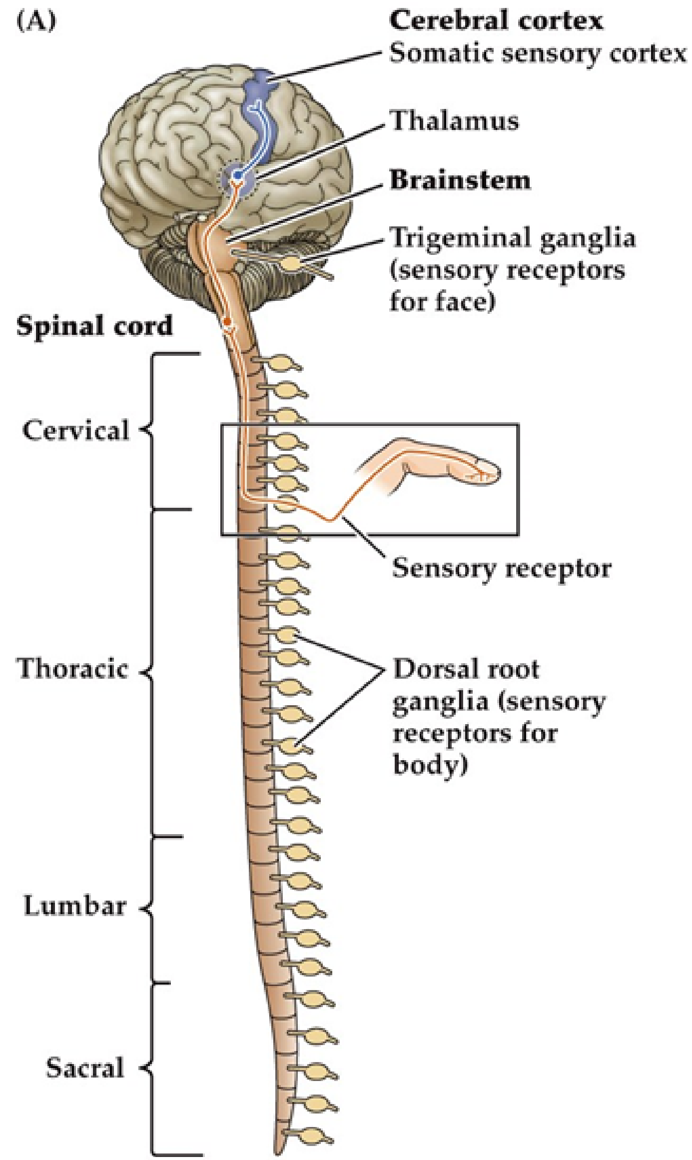
- Sensation entails the ability to transduce, encode, and ultimately perceive information generated by stimuli arising from both the external and internal environments.
- Although the basic senses--somatic sensation, vision, audition, vestibular sensation, and the chemical senses--are very different from one another, a few fundamental rules govern the way the nervous system deals with each of these diverse modalities.
- Highly specialized nerve cells called receptors convert the energy associated with mechanical forces, light, sound waves, odorant molecules, or ingested chemicals into neural signals--afferent sensory signals--that convey information about the stimulus to the brain.
- Afferent sensory signals activate central neurons capable of representing both the qualitative and quantitative aspects of the stimulus (what it is and how strong it is) and, in some modalities (somatic sensation, vision, and audition) the location of the stimulus in space (where it is).

Sensation and sensory processing

- The somatic sensory system is arguably the most diverse of the sensory systems, mediating a range of sensations--touch, pressure, vibration, limb position, heat, cold and pain.
- These sensations are transduced by receptors within the skin or muscles and conveyed to a variety of central nervous system targets.
- This complex neurobiological machinery can be divided into functionally distinct subsystems with distinct sets of peripheral receptors and central pathways:
    1. Transmitting information from cutaneous mechanoreceptors and mediating the sensations of fine touch, vibration and pressure.
    2. Originating in specialized receptors that are associated with muscles, tendons, and joints and is responsible for proprioception--our ability to sense the position of our own limbs and other body parts in space.
    3. Arising from receptors that supply information about painful stimuli and changes in temperature as well as coarse touch.

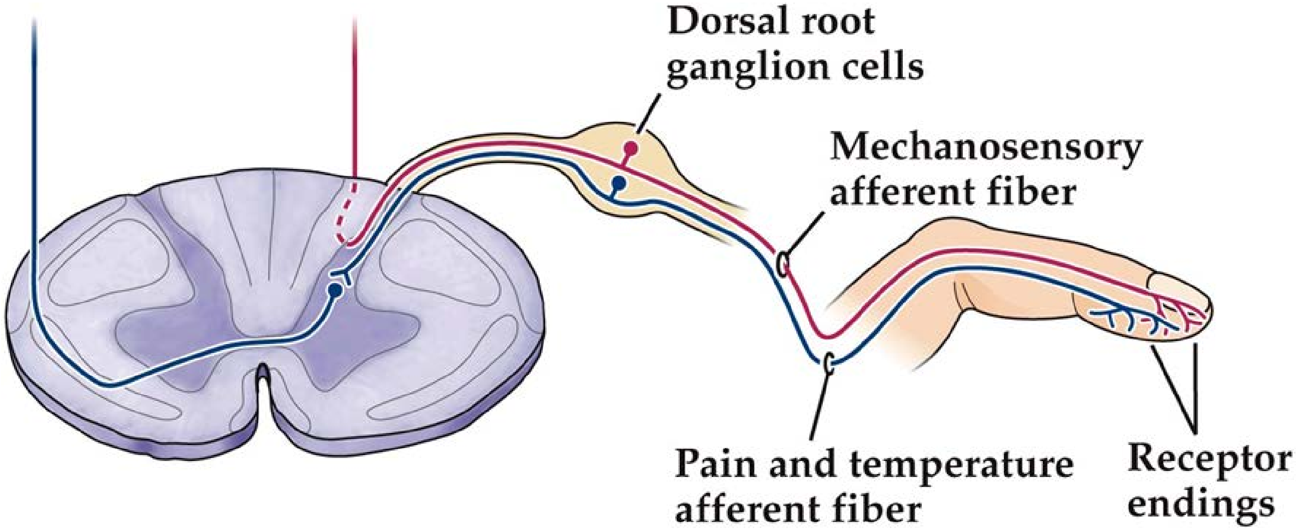
Somatic sensory afferent fibers

- Somatic sensation originates from the activity of afferent nerve fibers whose peripheral processes ramify within the skin or in muscle.
- The cell bodies of afferent fibers reside in a series of ganglia that lie alongside the spinal cord and the brainstem and are considered part of the peripheral nervous system.
- Neurons in the dorsal root ganglia and in the cranial nerve ganglia (for the body and head, respectively) are the critical links supplying central nervous system circuits with information about sensory events that occur in the periphery.



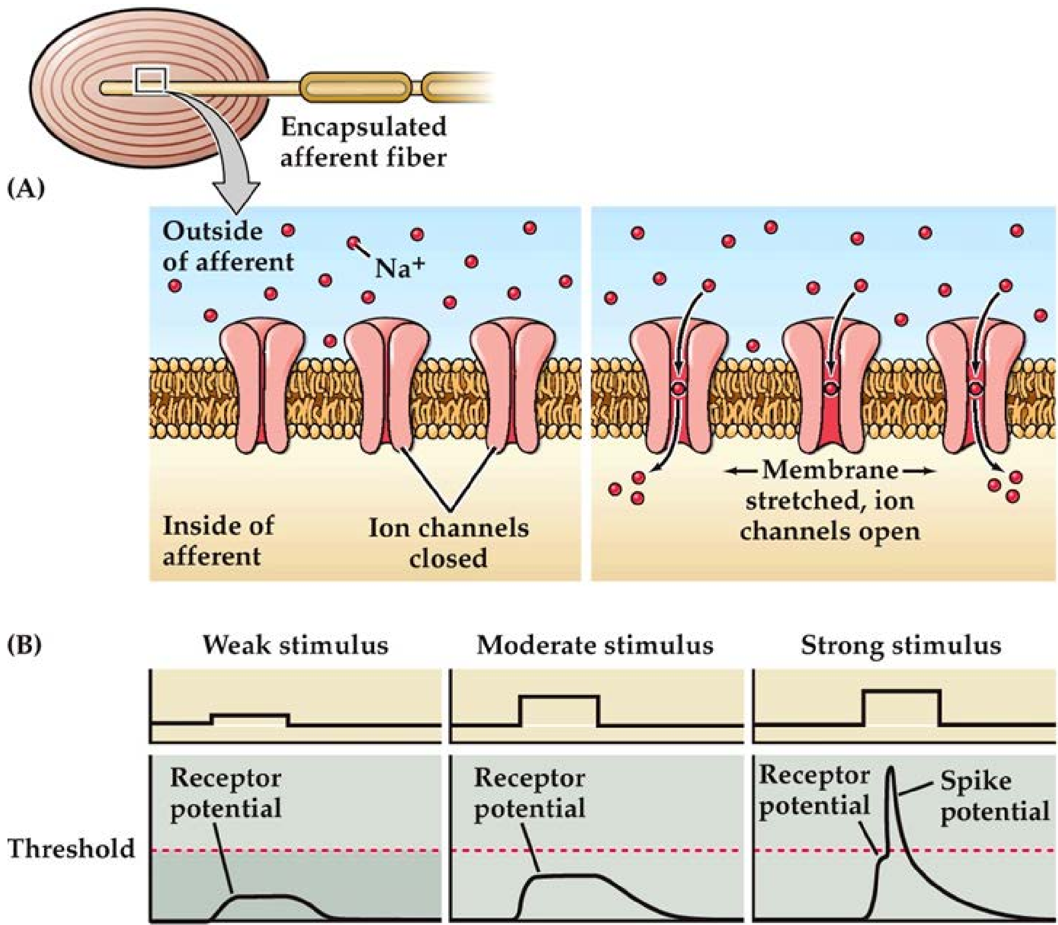
Pseudounipolar neurons

- Action potentials generated in afferent fibers by events that occur in the skin or in muscle propagate along the fiber and past the location of the cell body in the ganglia until they reach the fibers' synaptic terminals, which are located in various target structures of the central nervous system.
- Peripheral and central components of afferent fibers are continuous, attached to the cell body in the ganglia by a single process.
- Neurons in the dorsal root ganglia are often called **pseudounipolar**.
- Because of this configuration, conduction of electrical activity through the membrane of the cell body is not an obligatory step in conveying sensory information to central targets.



Sensory transduction

- **Sensory transduction**: a stimulus alters the permeability of cation channels in the afferent nerve endings, generating a depolarizing current known as a **receptor** (or **generator**) **potential**.
- If sufficient in magnitude, the receptor potential reaches threshold for the generation of action potentials in the afferent fiber.
- Afferent fibers are often encapsulated by specialized receptor cells called **mechanoreceptors** that help tune the afferent fiber to particular features of somatic stimulation.
- Afferent fibers that lack specialized receptor cells are referred to as **free nerve endings** and are especially important in the sensation of pain.



Somatic sensory afferents

- Somatic sensory afferents differ significantly in their response properties. These differences, taken together, define distinct classes of afferents, each of which makes unique contributions to somatic sensation.
- <u>Axon diameter</u> is one factor that differentiates classes of somatic sensory afferents:
  - The largest-diameter sensory afferents (**Ia**) are those that supply the sensory receptors in the muscles.

TABLE 9.1 Somatic Sensory Afferents that Link Receptors to the Central Nervous System

SENSORY FUNCTION	RECEPTOR TYPE	AFFERENT AXON TYPE[a]	AXON DIAMETER	CONDUCTION VELOCITY
Proprioception	Muscle spindle	 Ia, II	13–20 μm	80–120 m/s
Touch	Merkel, Meissner, Pacinian, and Ruffini cells	 Aβ	6–12 μm	35–75 m/s
Pain, temperature	Free nerve endings	 Aδ	1–5 μm	5–30 m/s
Pain, temperature, itch	Free nerve endings (unmyelinated)	C	0.2–1.5 μm	0.5–2 m/s

Somatic sensory afferents

- Most of the information subserving touch is conveyed by slightly smaller diameter fibers (**Aβ** afferents).
- Information about pain and temperature is conveyed by even smaller diameter fibers (**Aδ** and **C**).

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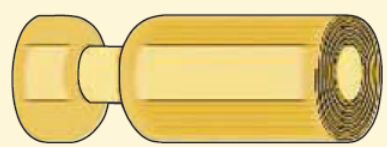
Touch	Merkel, Meissner, Pacinian, and Ruffini cells	 Aβ	6–12 μm	35–75 m/s
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Somatic sensory afferents

- Another distinguishing feature of sensory afferents is the size of the receptive field—the area of the skin surface over which stimulation results in a significant change in the rate of action potentials.

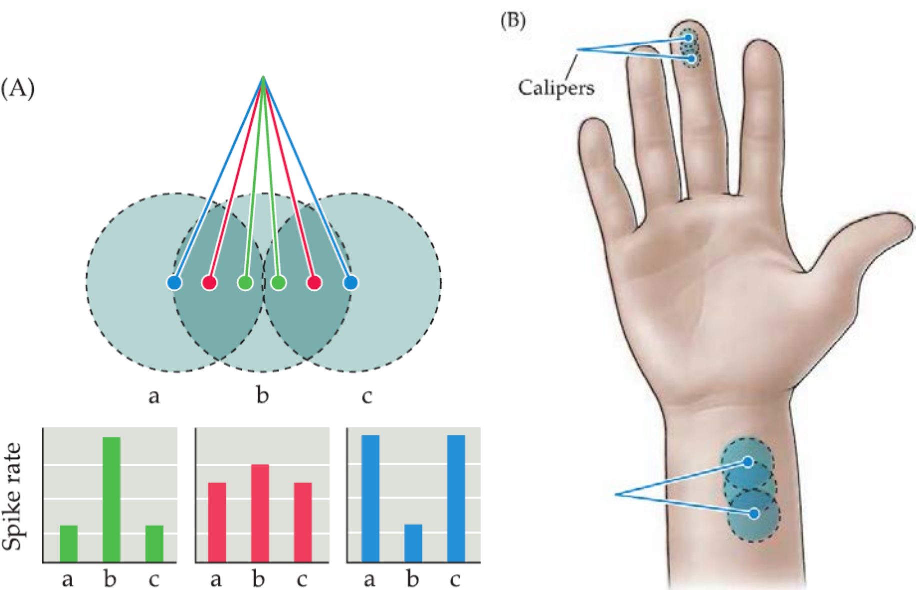
  - The size of the receptive field is largely a function of the branching characteristics of the afferent within the skin; smaller arborizations result in smaller receptive fields.

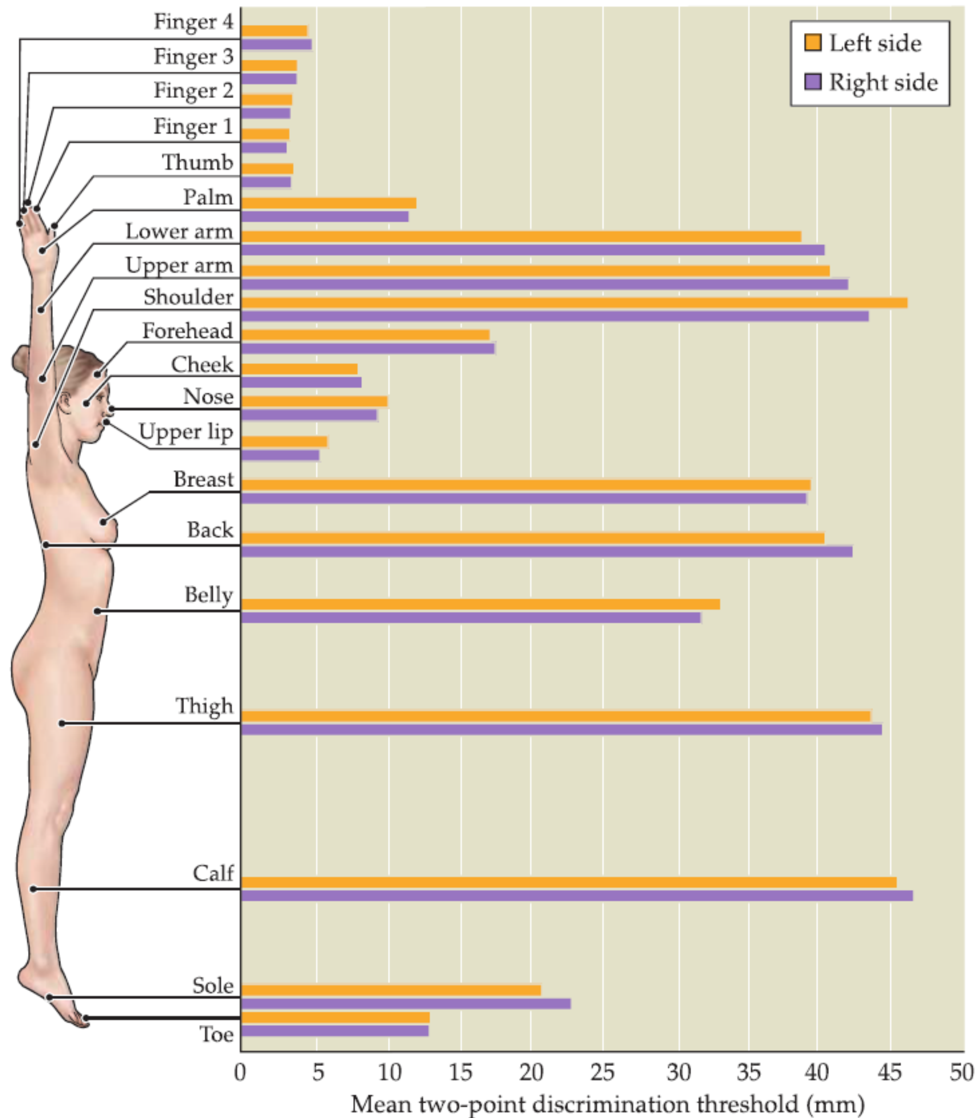
  - The receptive fields in regions with dense innervation (fingers, lips, toes) are relatively small compared with those in the forearm or back that are innervated by a smaller number of afferent fibers.

  - Regional differences in receptive field size and innervation density are the major factors that limit the spatial accuracy with which tactile stimuli can be sensed.

Two-point discrimination

- **Two-point discrimination**: the minimum interstimulus distance required to perceive two simultaneously applied stimuli as distinct.
  - The measures of two-point discrimination vary dramatically across the skin surface.
  - On the fingertips, stimuli are perceived as distinct if they are separated by roughly 2 mm, but the same stimuli applied to the forearm are not perceived as distinct until they are at least 40 mm apart!.





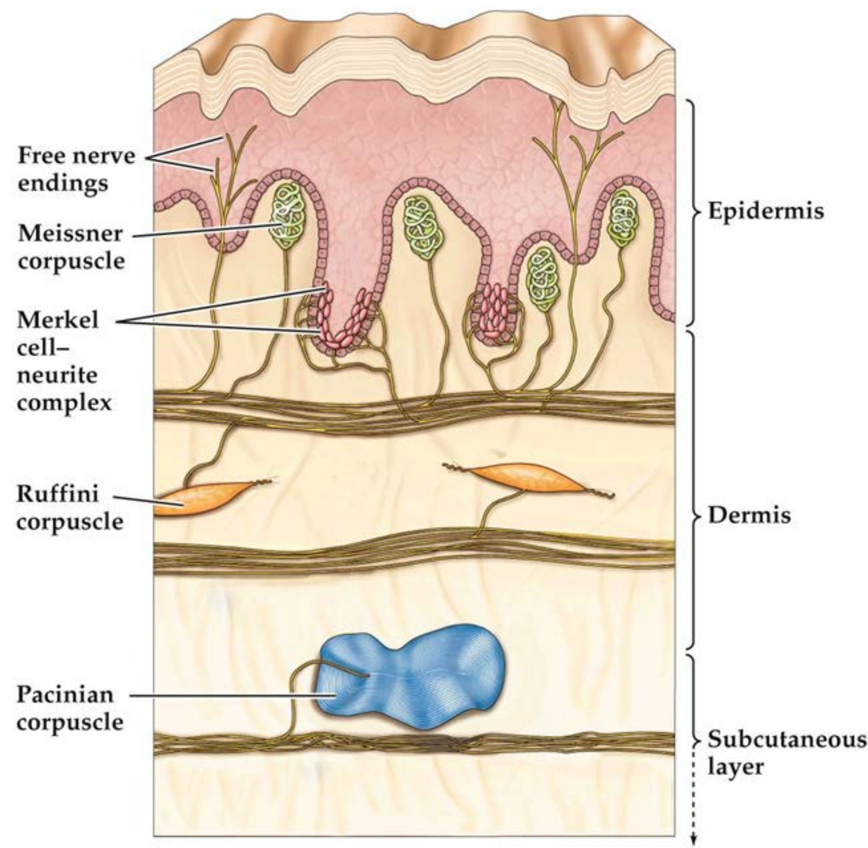
Mechanoreceptors for tactile information

- Active touching, or **haptics**, involves the interpretation of complex spatiotemporal patterns of stimuli that are likely to activate many classes of mechanoreceptors.

- Manipulating an object with the hand can often provide enough information to identify the object, a capacity called **stereognosis**.

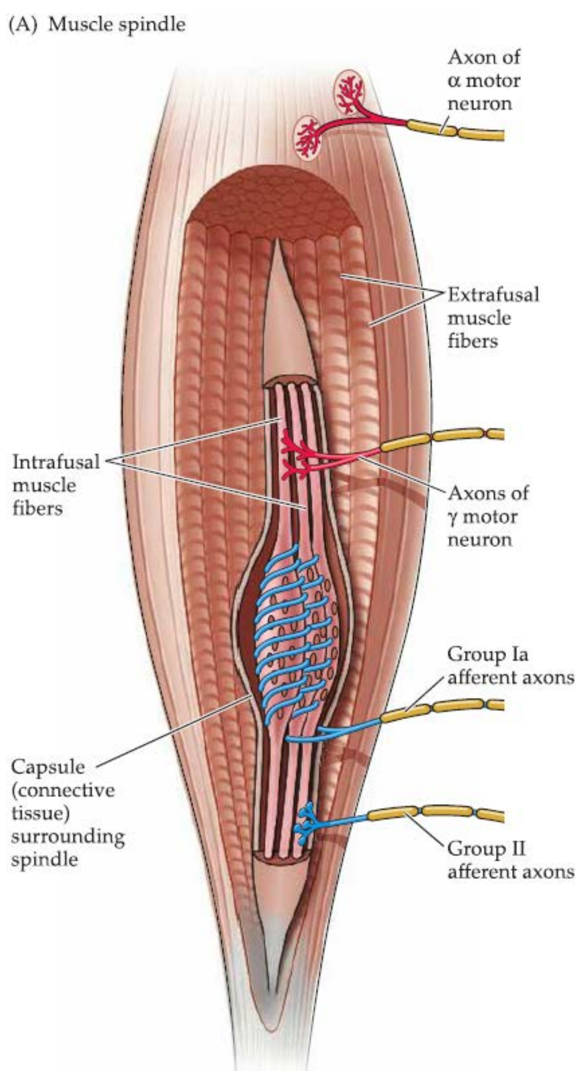
- There are four distinct classes of mechanoreceptive afferents that innervate the glabrous skin of the hand:

  - **Merkel cell afferents**
  - **Meissner afferents**
  - **Pacinian afferents**
  - **Ruffini afferents**



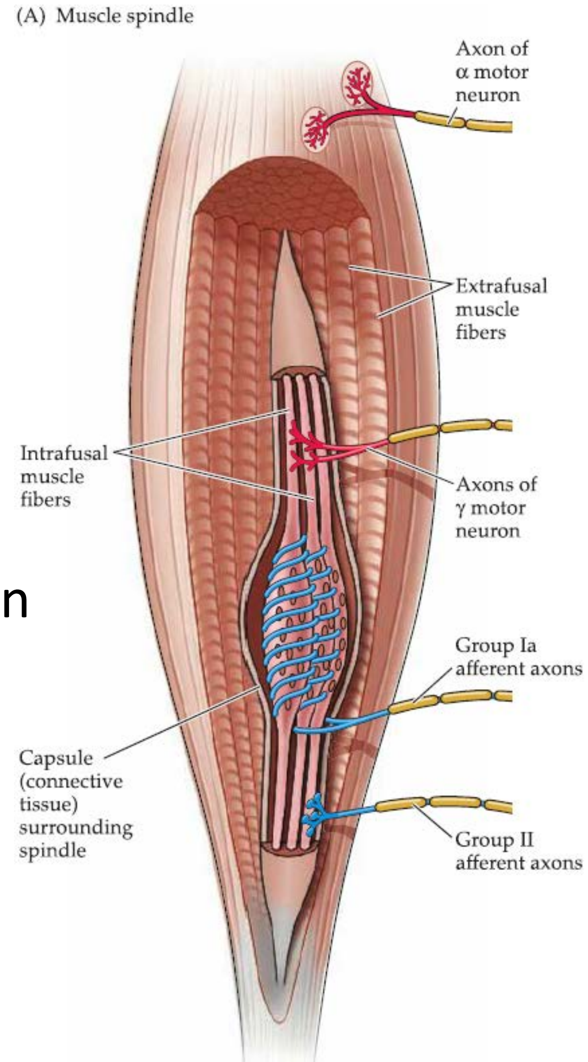
Mechanoreceptors for proprioception

- While cutaneous mechanoreceptors provide information derived from external stimuli, another major class of receptors provides information about mechanical forces arising within the body itself particularly from the musculoskeletal system.
- The purpose of these proprioceptors (“receptors for self”) is primarily to give detailed and continuous information about the position of the limbs and other body parts in space.
- The most detailed knowledge about proprioception derives from studies of **muscle spindles**, which are found in all but a few striated (skeletal) muscles.
- Muscle spindles consist of four to eight specialized **intrafusal muscle fibers** surrounded by a capsule of connective tissue.
- The intrafusal fibers are distributed among and in a parallel arrangement with the **extrafusal fibers** of skeletal muscle, which are the true force-producing fibers.



Mechanoreceptors for proprioception

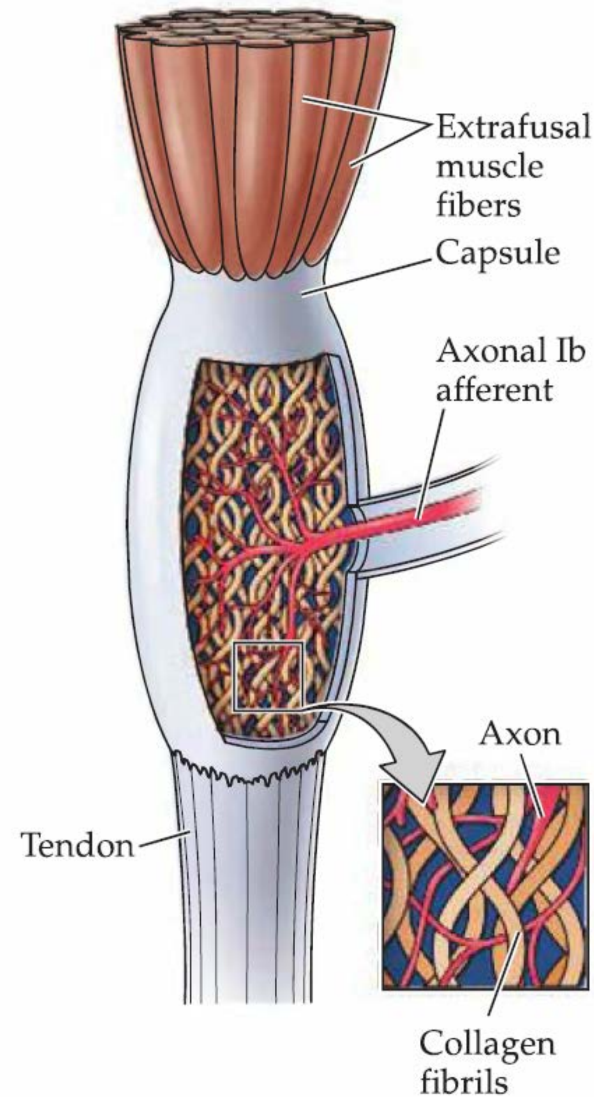
- Sensory afferents are coiled around the central part of the intrafusal spindle and, when the muscle is stretched, the tension on the intrafusal fibers activates mechanically gated ion channels in the nerve endings, triggering action potentials.
- Innervation of the muscle spindle arises from two classes of fibers: primary and secondary endings.
  - Primary endings arise from the largest myelinated sensory axons (**group Ia afferents**) and have rapidly adapting responses to changes in muscle length.
  - Secondary endings (**group II afferents**) produce sustained responses to constant muscle lengths.
- Primary endings are thought to transmit information about limb dynamics-the velocity and direction of movement whereas secondary endings provide information about the static position of limbs.



Mechanoreceptors for proprioception

- Whereas muscle spindles are specialized to signal changes in muscle length, low-threshold mechanoreceptors in tendons inform the central nervous system about changes in muscle tension.

(B) Golgi tendon organ

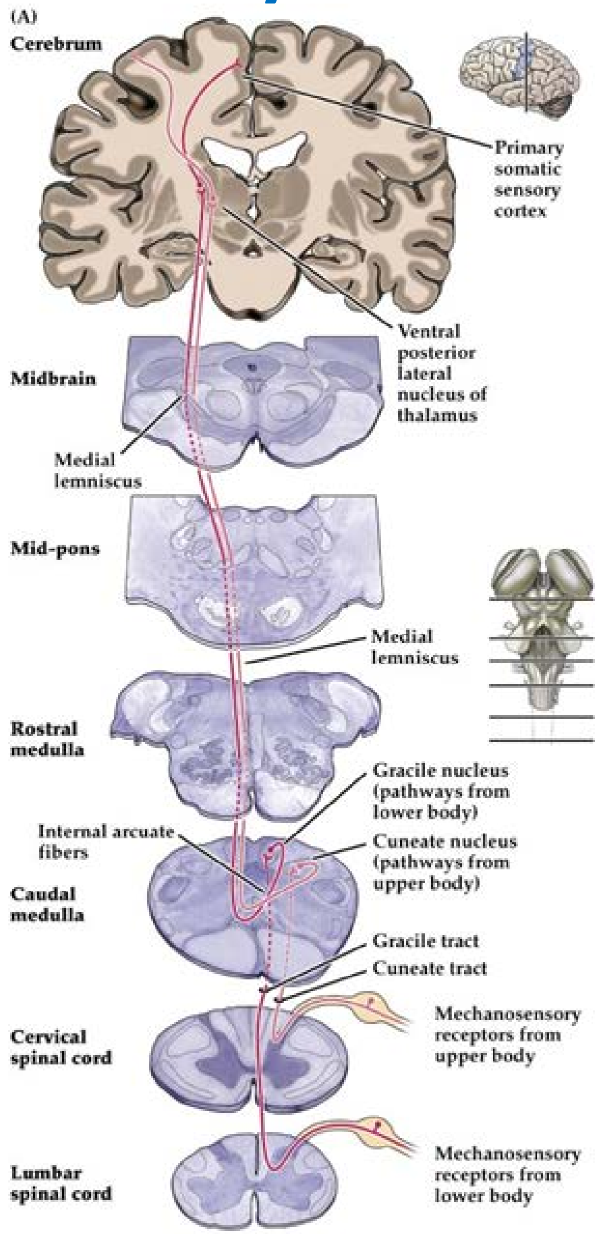


- These mechanoreceptors, called **Golgi tendon organs**, are formed by branches of **group Ib afferents** distributed among the collagen fibers that form the tendons.

- Each Golgi tendon organ is arranged in series with a small number (10-20) of extrafusal muscle fibers.

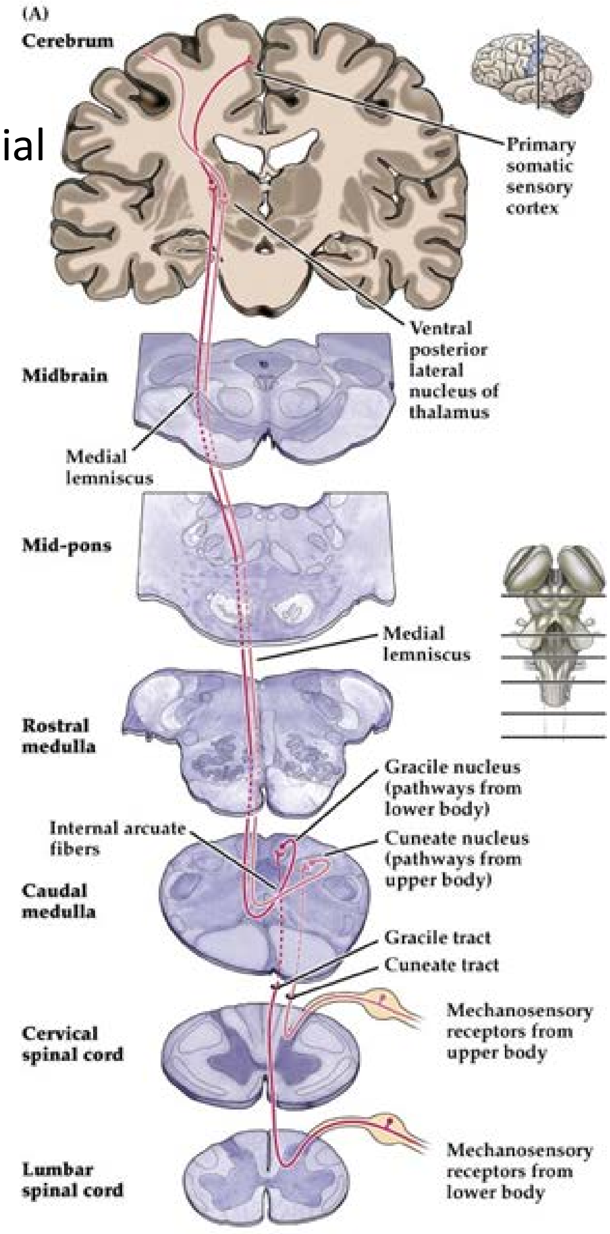
Central pathways conveying tactile information from the body: the dorsal column-medial lemniscal system

- The axons of cutaneous mechanosensory afferents enter the spinal cord through the dorsal roots.
- The majority ascend ipsilaterally through the **dorsal columns** (also called the **posterior funiculi**) of the cord to the lower medulla, where they synapse on neurons in the dorsal column nuclei.
  - The term "column" refers to the gross columnar appearance of these fibers as they run the length of the spinal cord.
- These *first-order neurons* in the pathway can have quite long axonal processes: neurons innervating the lower extremities, for example, have axons that extend through the entire length of the cord.



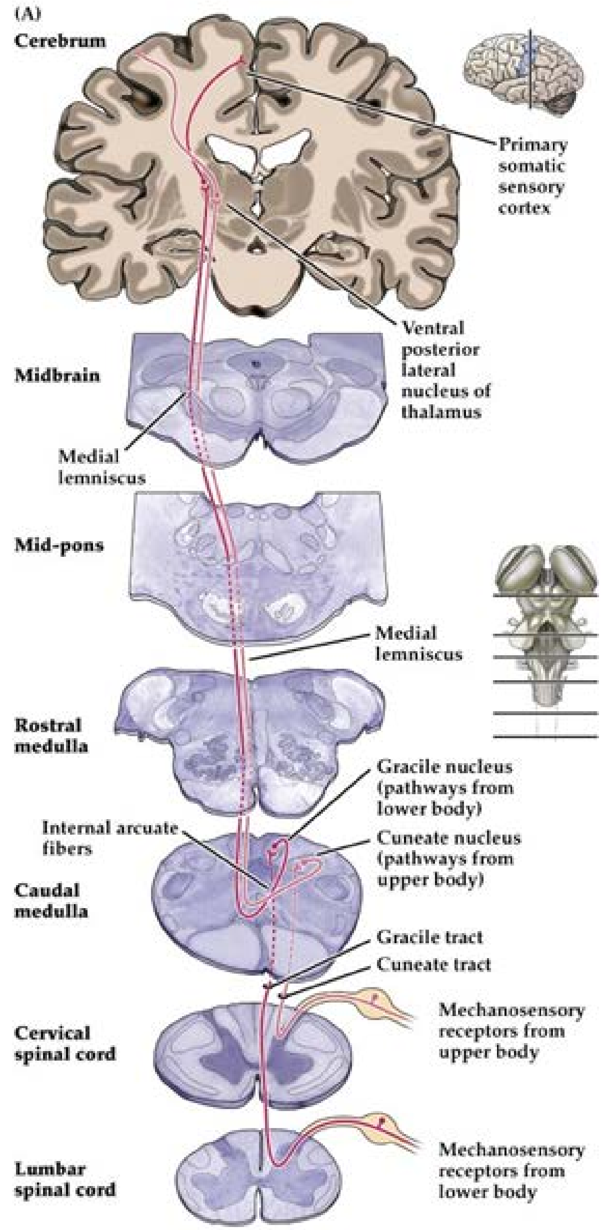
Central pathways conveying tactile information from the body

- The dorsal columns of the spinal cord are topographically organized:
  - Fibers conveying information from <u>lower</u> limbs lie most medial and travel in a circumscribed bundle known as **fasciculus gracilis** (Latin *fasciculus*, "bundle"; *gracilis*, "slender").
  - Fibers conveying information from <u>upper</u> limbs, trunk, and neck lie in a more lateral bundle known as the **fasciculus cuneatus** ("wedge-shaped bundle").
- The fibers in these two tracts innervate different subdivisions of the dorsal column nuclei: a medial subdivision, the **nucleus gracilis**; and a lateral subdivision, the **nucleus cuneatus**.
- These *second-order neurons* in the dorsal column nuclei send their axons to the somatic sensory portion of the thalamus.
- The axons exiting from dorsal column nuclei are identified as **the internal arcuate fibers**.
- The internal arcuate fibers subsequently cross the midline and then form a dorsoventrally elongated tract known as the **medial lemniscus**.



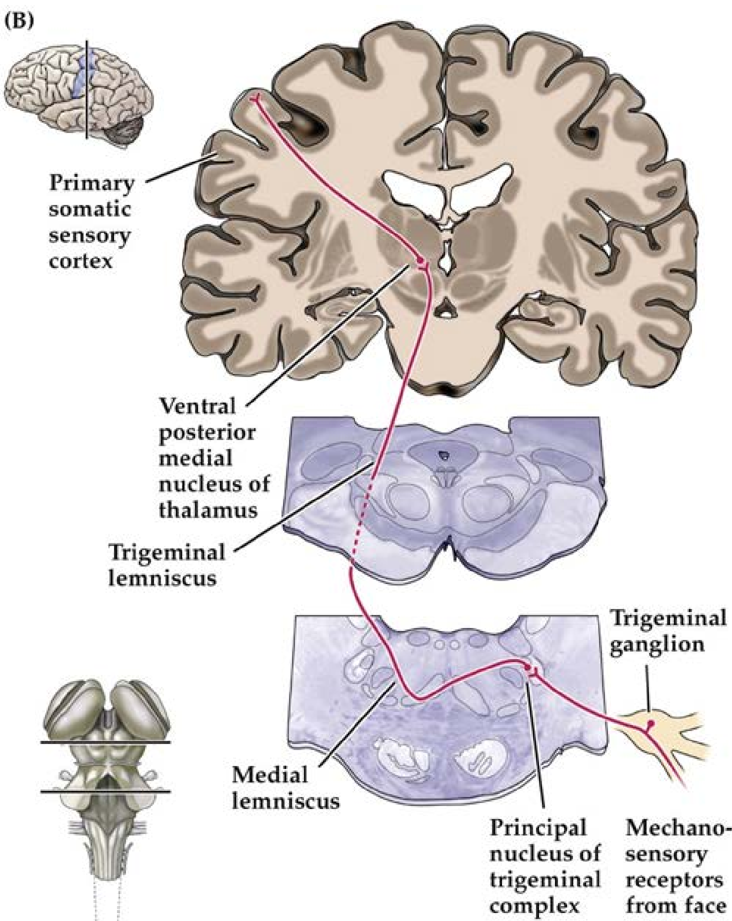
Central pathways conveying tactile information from the body

- In a cross section through the caudal medulla, the medial lemniscal axons carrying information from the lower limbs are located ventrally, whereas the axons related to the upper limbs are located dorsally.
- As the medial lemniscus ascends through the pons and midbrain, it rotates 90 degrees laterally, so that the fibers representing the upper body are eventually located in the medial portion of the tract and those representing the lower body are in the lateral portion.
- The axons of the medial lemniscus synapse with thalamic neurons located in the **ventral posterior lateral nucleus** (**VPL**).
- These *third-order neurons* in the VPL send their axons via the **internal capsule** to terminate in the **postcentral gyrus** of the cerebral cortex, a region known as the **primary somatosensory cortex**, or **SI**.
- Neurons in the VPL also send axons to the **secondary somatosensory cortex** (**SII**), a smaller region that lies in the upper bank of the lateral sulcus.

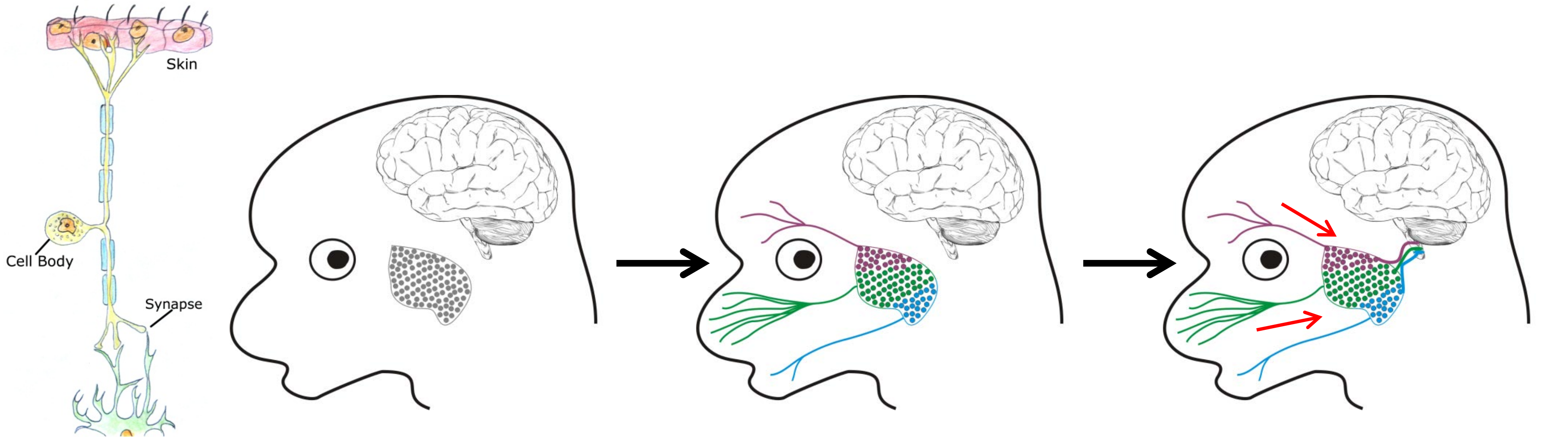


Central pathways conveying tactile information from the face: the trigeminothalamic system

- Cutaneous mechanoreceptor information from the face is conveyed centrally by a separate set of *first-order neurons* that are located in the trigeminal (cranial nerve V) ganglion.

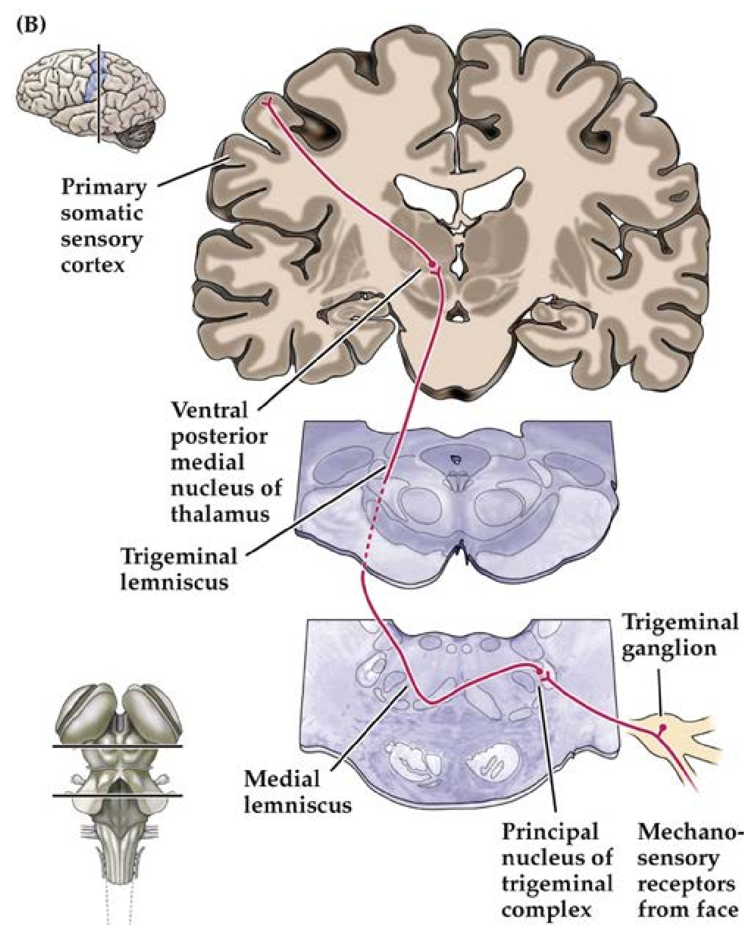


Trigeminal ganglion is the relay station in somatosensory system



Central pathways conveying tactile information from the face: the trigeminothalamic system

- The *second-order neurons* of the trigeminal brainstem nuclei give off axons that cross the midline and ascend to the **ventral posterior medial** (**VPM**) nucleus of the thalamus by way of the **trigeminothalamic tract** (also called the **trigeminal lemniscus**).
- Neurons in the VPM send their axons to cortical areas SI and SII.

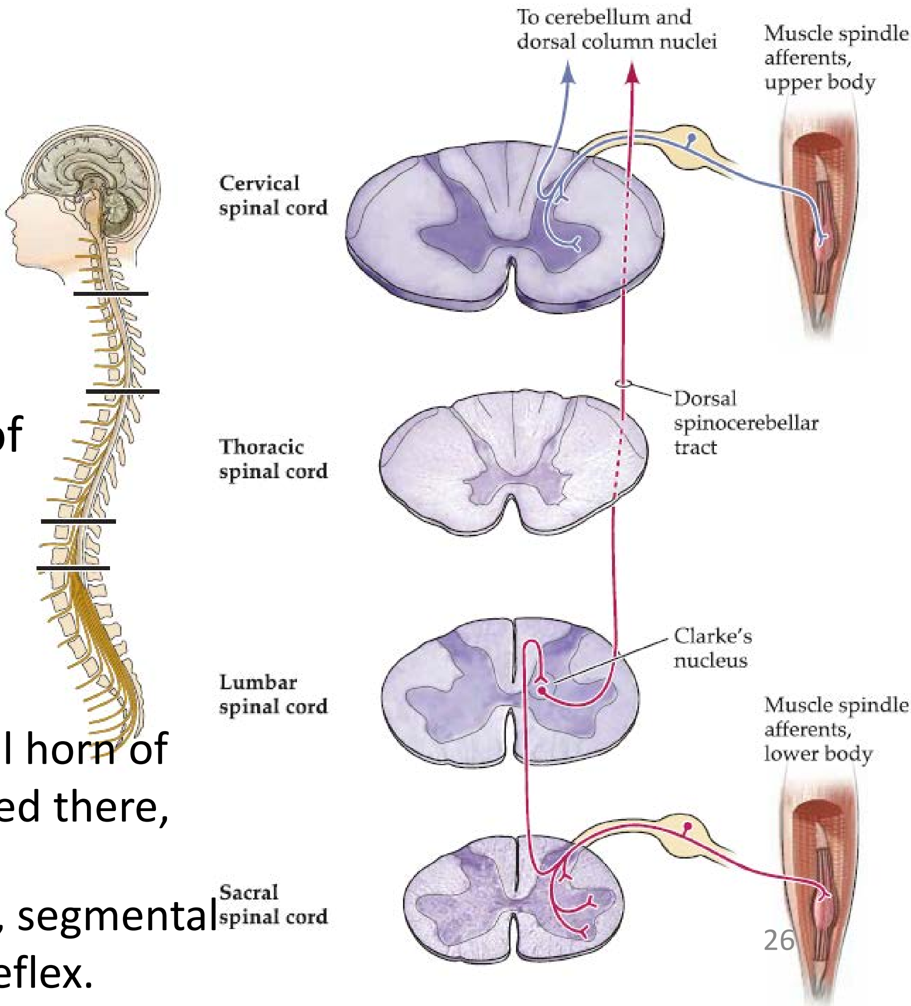


Central pathways conveying proprioceptive information from the body

- ❖ Like their counterparts for cutaneous sensation, axons of proprioceptive afferents enter the spinal cord through the dorsal roots and, for much of their course, travel with the axons conveying cutaneous information.
- ❖ Some differences in the spinal cord routes for proprioceptive pathways reflect the important role proprioceptive information plays in the reflex regulation of motor control as well as perception:

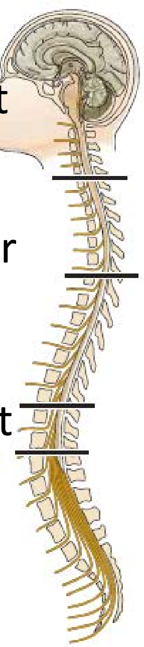
1. When they enter the spinal cord, many of the fibers from proprioceptive afferents bifurcate into ascending and descending branches, which in turn send collateral branches to several spinal segments.

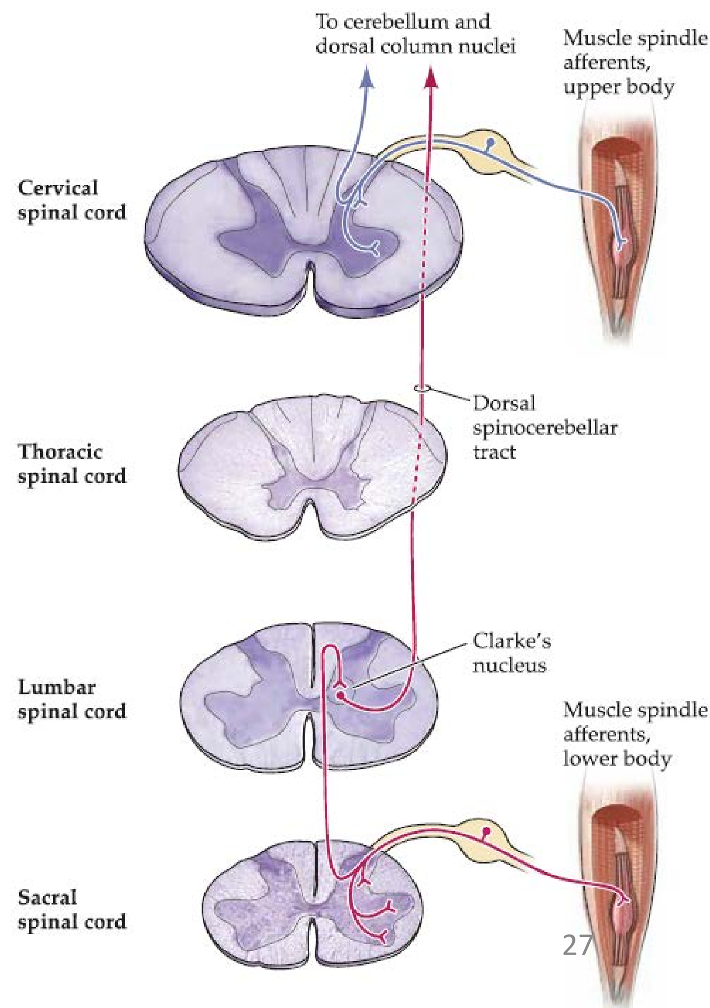
- Some collateral branches penetrate the dorsal horn of the spinal cord and synapse on neurons located there, as well as on neurons in the ventral horn.
- These synapses mediate, among other things, segmental reflexes such as the "knee-jerk" or myotatic reflex.



Central pathways conveying proprioceptive information from the body

2. The information supplied by proprioceptive afferents is important not only for our ability to sense limb position; it is also essential for the functions of the cerebellum, a structure that regulates the timing of muscle contractions necessary for the performance of voluntary movements.
    - The association with cerebellar pathways is especially clear for the route that conveys proprioceptive information for the lower part of the body to the dorsal column nuclei.
    - *First-order* proprioceptive afferents that enter the spinal cord between the mid-lumbar and thoracic levels (L2-T1) synapse on neurons in **Clarke's nucleus**, located in the medial aspect of the dorsal horn.
    - *Second-order neurons* in Clarke's nucleus send their axons into the ipsilateral posterior lateral column of the spinal cord, where they travel up to the level of the medulla in the dorsal spinocerebellar tract.



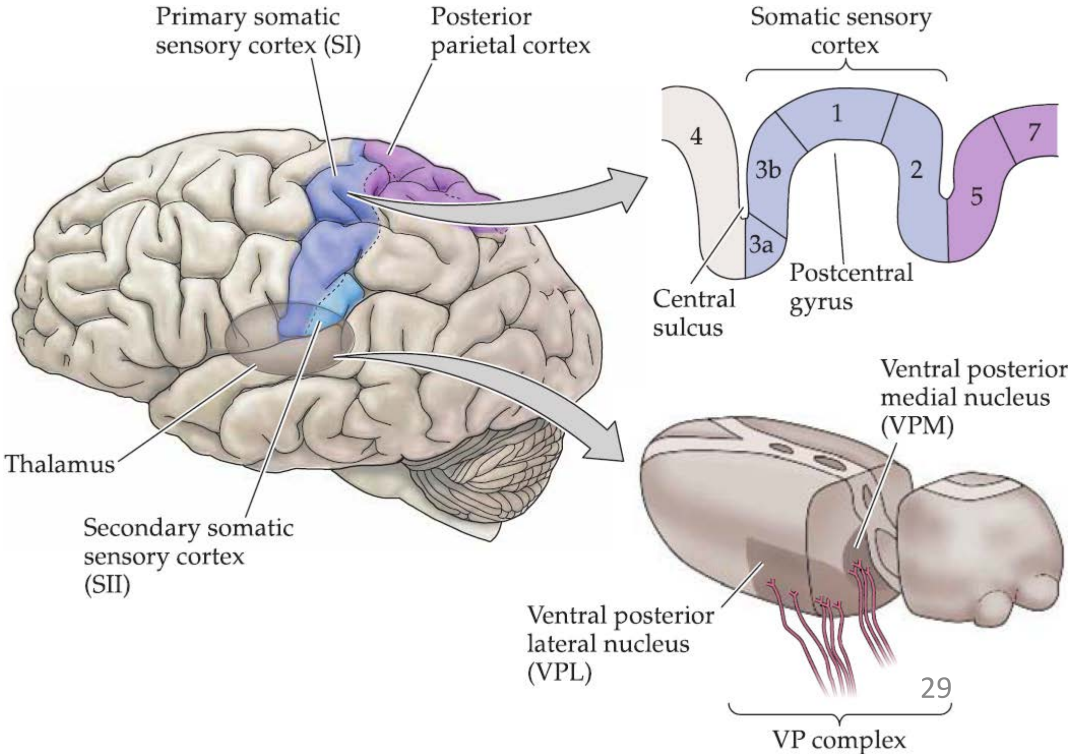


Central pathways conveying proprioceptive information from the face

- The cell bodies of the first-order proprioceptive neurons for the face have an unusual location: instead of residing in the trigeminal ganglia, they are found within the central nervous system, in the **mesencephalic trigeminal nucleus**.
- This cluster of neurons lies at the lateral extent of the central gray region of the midbrain.
- Like their counterparts in the trigeminal and dorsal root ganglia, these pseudounipolar neurons have:
  1. peripheral processes that innervate muscle spindles and Golgi tendon organs associated with facial musculature (especially the jaw muscles).
  2. central processes that include projections to brainstem nuclei responsible for reflex control of facial muscles.
- Although the exact route is not clear, information from proprioceptive afferents in the mesencephalic trigeminal nucleus also reaches the thalamus and is represented in somatic sensory cortex.

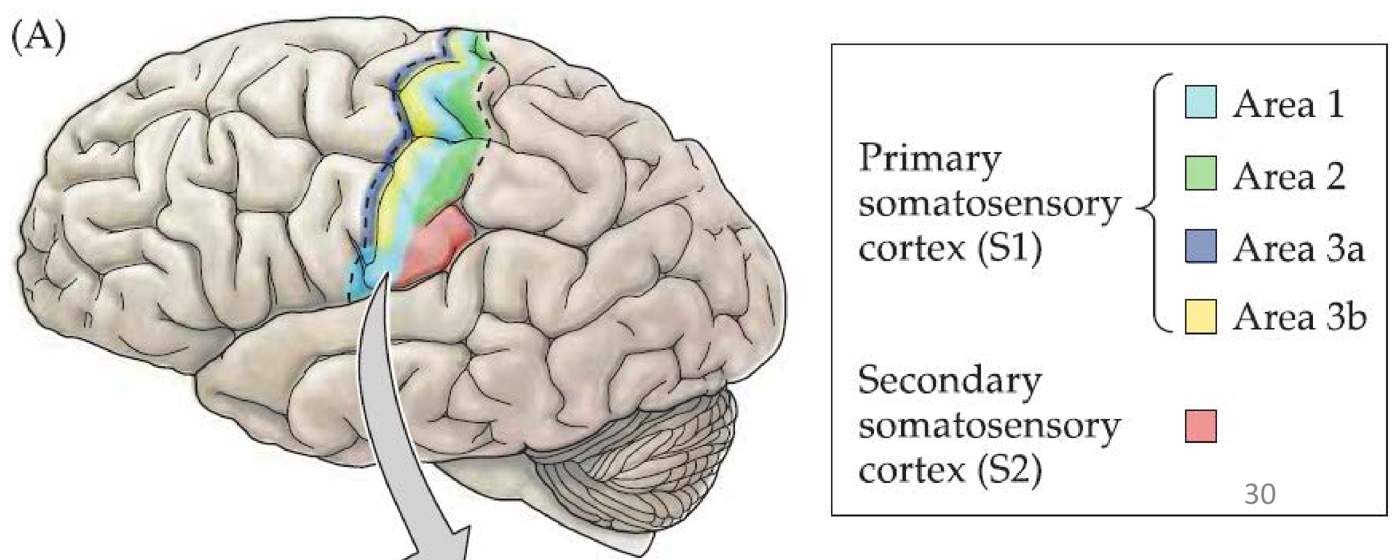
The somatic sensory components of thalamus

- Each of the several ascending somatic sensory pathways originating in the spinal cord and brainstem converge on the **ventral posterior complex** of the thalamus and terminate in an organized fashion.
  - the more laterally located ventral posterior lateral nucleus (VPL) receives projections from the medial lemniscus carrying somatosensory information from the body and posterior head.
  - the more medially located ventral posterior medial nucleus (VPM) receives axons from the trigeminal lemniscus conveying somatosensory information from the face.
- Inputs carrying different types of somatosensory terminate on separate populations of relay cells within the ventral posterior complex.



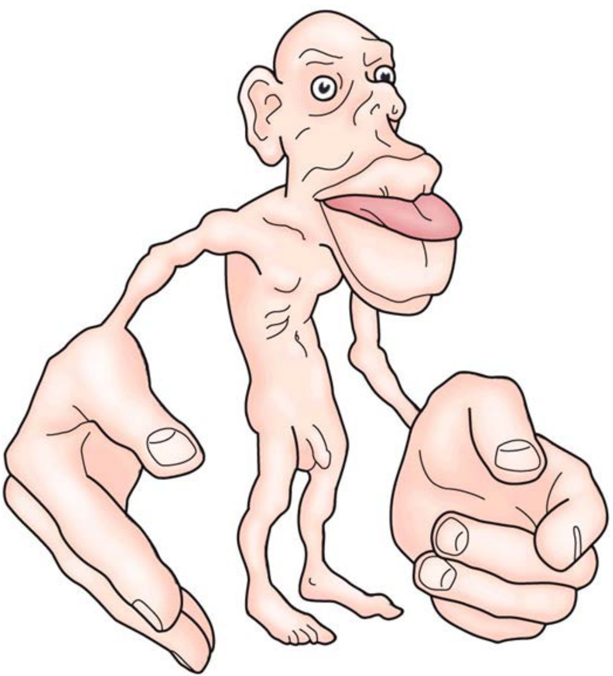
Primary somatic sensory cortex

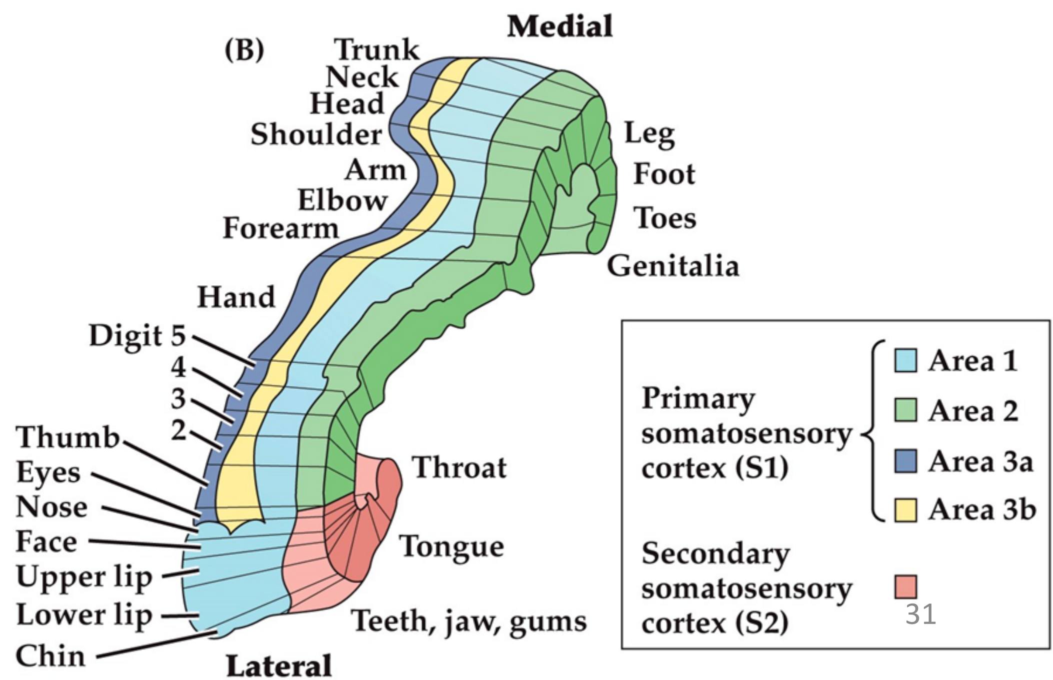
- The majority of the axons arising from neurons in the ventral posterior complex of the thalamus project to cortical neurons located in layer 4 of the primary somatic sensory cortex.
- The **primary somatic sensory cortex** in humans (also called **SI**) is located in the postcentral gyrus of the parietal lobe and comprises four distinct regions, or fields, known as Brodmann's areas 3a, 3b, 1, and 2.
- Mapping studies in humans and other primates show further that each of these four cortical areas contains a separate and complete representation of the body.



Primary somatic sensory cortex

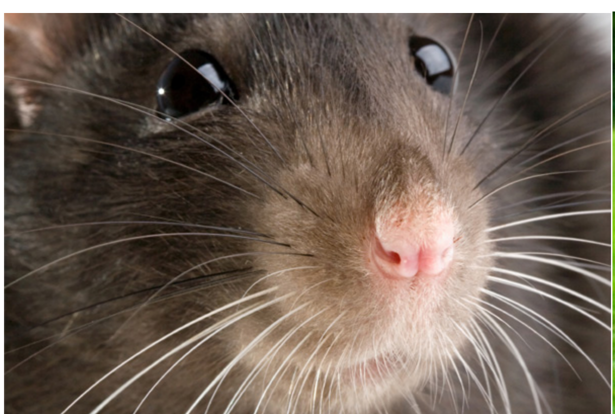
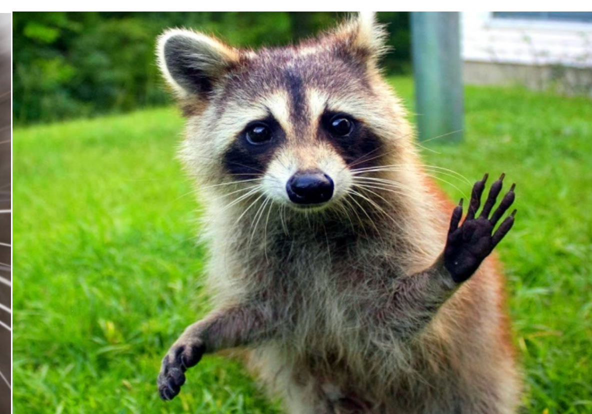
- In these **somatotopic maps**, the foot, leg, trunk, forelimbs, and face are represented in a medial to lateral arrangement.
- When neurosurgeons determined the representation of the human body in the primary sensory (and motor) cortex, the homunculus ("little man") defined by such mapping procedures had a grossly enlarged face and hands compared to the torso and proximal limbs.
- These anomalies arise because manipulation, facial expression, and speech are extraordinarily important for humans and require a great deal of circuitry, both central and peripheral to govern them.





Primary somatic sensory cortex

- In humans, the cervical spinal cord is enlarged to accommodate the extra circuitry related to the hand and upper limb and, as stated earlier, the density of receptors is greater in regions such as the hands and lips.
- Such distortions are also apparent when topographical maps are compared across species:
  - In the rat brain, an inordinate amount of the somatic sensory cortex is devoted to representing the large facial whiskers that are key components of the somatic sensory input for rats and mice.
  - Raccoons overrepresent their paws and the platypus its bill.
- The sensory input (or motor output) that is particularly significant to a given species gets relatively more cortical representation.

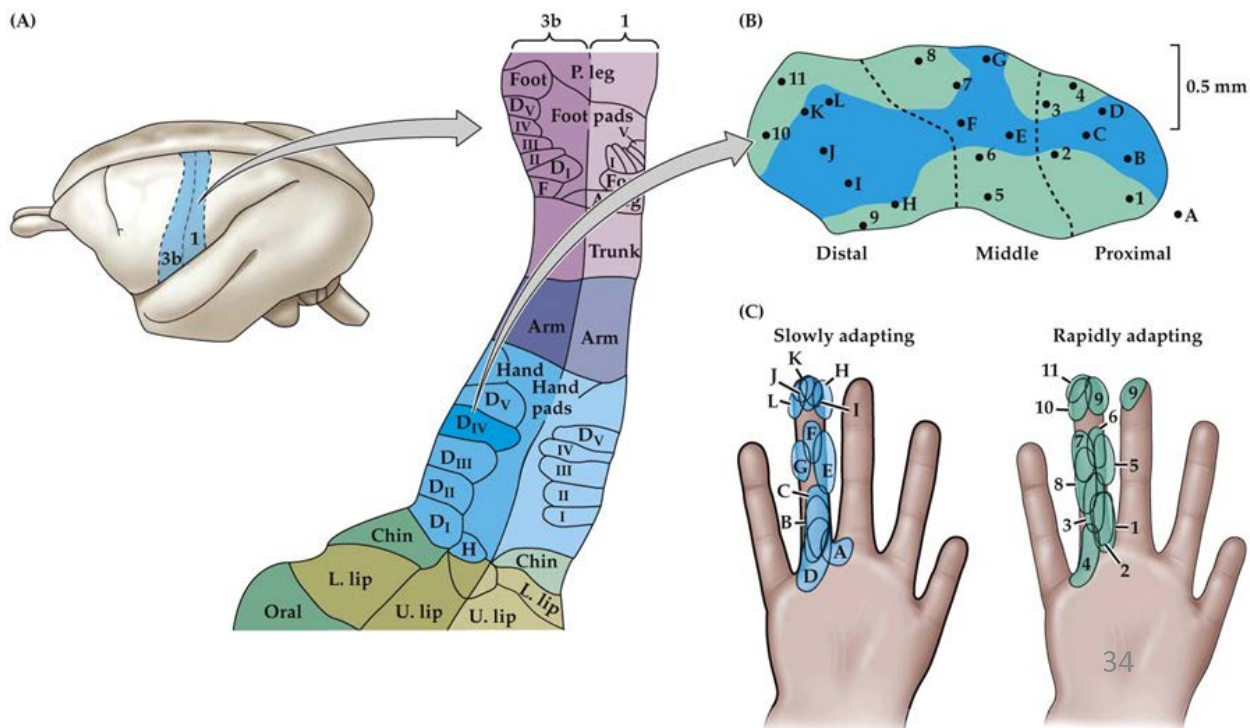




Primary somatic sensory cortex

- Although the topographic organization of the several somatic sensory areas is similar, the functional properties of the neurons in each region are distinct:
  - Experiments carried out in non-human primates indicate that neurons in areas 3b and 1 respond primarily to cutaneous stimuli.
  - Neurons in 3a respond mainly to stimulation of proprioceptors.
  - Area 2 neurons process both tactile and proprioceptive stimuli.
- Even finer parcellations of functionally distinct neuronal populations exist within single cortical areas.
- Based on his analysis of electrode penetrations in primary somatosensory cortex, **Vernon Mountcastle** was the first to suggest that neurons with similar response properties might be clustered together into functionally distinct "columns" that traverse the depth of the cortex.

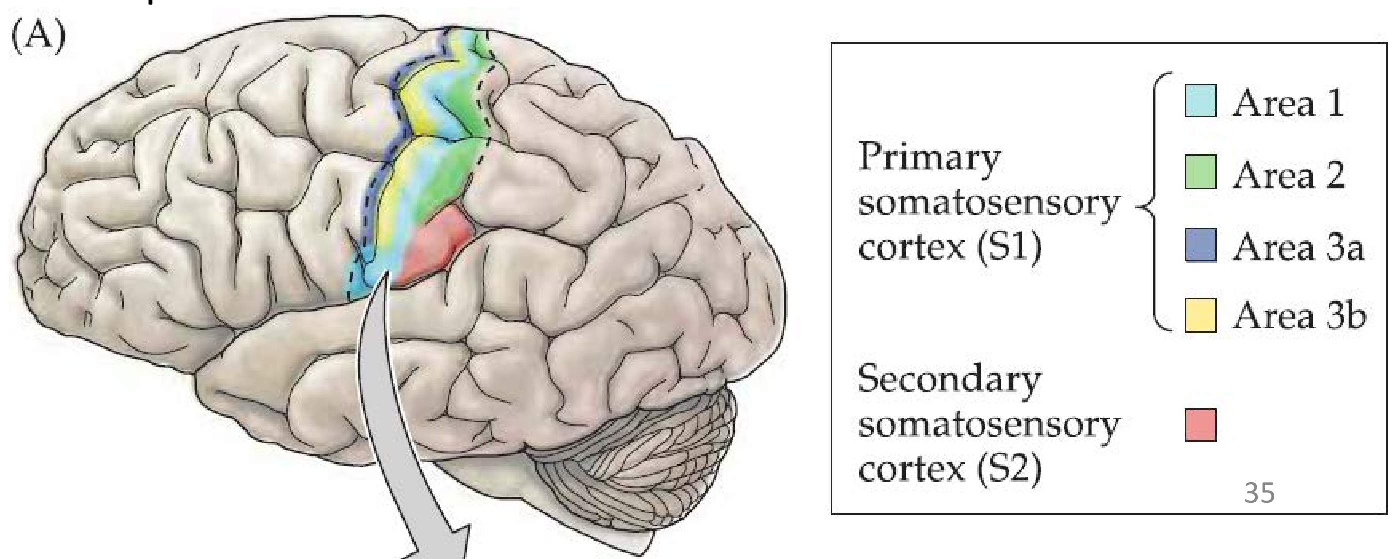
Primary somatic sensory cortex

- Subsequent studies of finely spaced electrode penetrations in area 3b provided strong evidence in support of this idea, demonstrating that neurons with responses to rapidly and slowly adapting mechanoreceptors were clustered into separate zones within the representation of a single digit.
- Although these patterns reflect specificity in the underling patterns of thalamocortical and corticocortical connections, the functional significance of columns remains unclear.



Beyond SI: corticocortical and descending pathways

- Somatic sensory information is distributed from the primary somatic sensory cortex to "higher order" cortical fields.
  - One of these higher order cortical centers, the **secondary somatosensory cortex** (**SII**), lies in the upper bank of the lateral sulcus.
    - SII receives convergent projections from all subdivisions of SI, and these inputs are necessary for the function of SII; lesions of SI eliminate the somatosensory responses of SII neurons.
    - Area SII sends projections in turn to limbic structures such as amygdala and hippocampus.
  - Neurons in SI also project to parietal areas posterior to area 2, especially areas 5a and 7b.
    - These areas receive direct projections from area 2 and, in turn, supply inputs to neurons in motor and premotor areas of the frontal lobe.

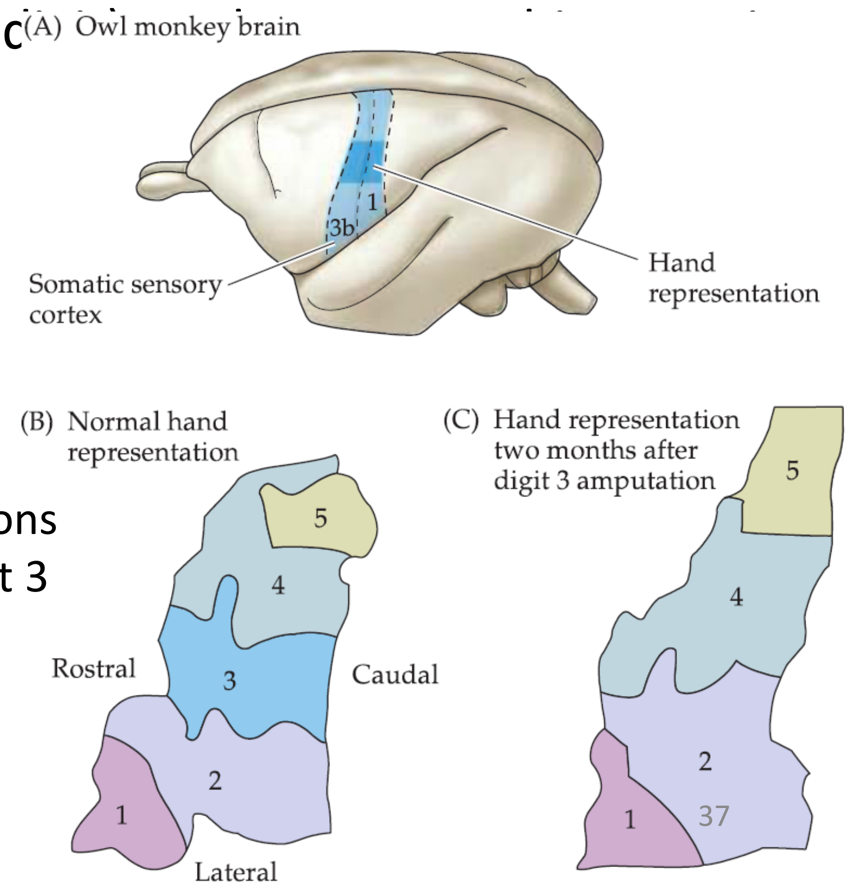


Beyond SI: corticocortical and descending pathways

- Finally, a fundamental but often neglected feature of the somatic sensory system is the presence of massive descending projections.
  - These pathways originate in sensory cortical fields and run to the thalamus, brainstem, and spinal cord.
  - Although their physiological role is not well understood, it is generally assumed (with some experimental support) that descending projections modulate the ascending flow of sensory information at the level of the thalamus and brainstem.

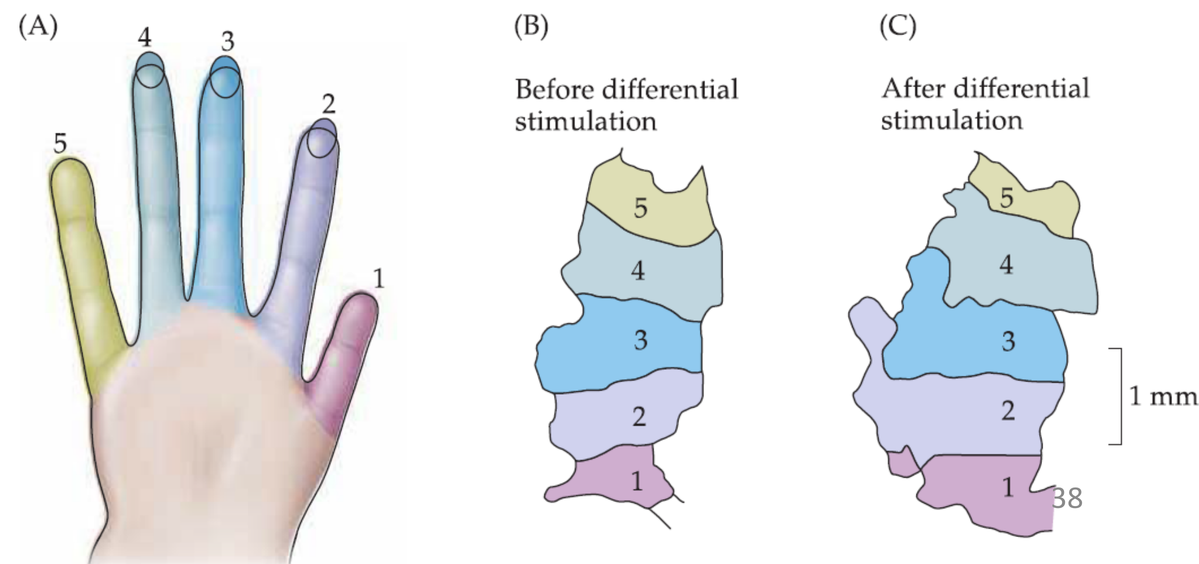
Plasticity in the adult cerebral cortex

- The analysis of maps of the body surface in primary somatic sensory cortex and the responses to altered patterns of activity in peripheral afferents has been instrumental in understanding the potential for the reorganization of cortical circuits in adults.
- Jon Kaas and Michael Merzenich were the first to explore this issue, by examining the impact of peripheral lesions (e.g., cutting a nerve that innervates the hand, or amputation of a c
somatosensory cortex.
    - Immediately after the lesion, the corresponding region of the cortex was found to be unresponsive.
    - After a few weeks, however, the unresponsive area became responsive to stimulation of neighboring regions of the skin.
    - If the third digit was amputated, cortical neurons that formerly responded to stimulation of digit 3 now responded to stimulation of digits 2 or 4.
    - The central representation of the remaining digits had expanded to take over the cortical territory that had lost its main input.



Plasticity in the adult cerebral cortex

- Appreciable changes in cortical representation also can occur in response to physiological changes in sensory or motor experience.
- If a monkey is trained to use a specific digit for a particular task that is repeated many times, the functional representation of that digit, determined by electrophysiological mapping, can expand at the expense of the other digits.



Summary

- The components of the somatic sensory system process information conveyed by mechanical stimuli that either impinge on the body surface (cutaneous mechanoreception) or are generated within the body itself (proprioception).
- Transmission of afferent mechanosensory information from the periphery to the brain begins with a variety of receptor types that initiate action potentials.
- This activity is conveyed centrally via a chain of nerve cells, referred to as the first-, second-, and third-order neurons.
  - First-order neurons are located in the dorsal root and cranial nerve ganglia.
  - Second-order neurons are located in brainstem nuclei.
  - Third-order neurons are found in the thalamus, from whence they project to the cerebral cortex.
- These pathways are topographically arranged throughout the system, the amount of cortical and subcortical space allocated to various body parts being proportional to the density of peripheral receptors.

Summary

- Studies of non-human primates show that specific cortical regions correspond to each functional submodality:
  - area 3b processes information from low-threshold cutaneous receptors.
  - area 3a processes inputs from proprioceptors.
- At least two broad criteria operate in the organization of the somatic sensory system: modality and somatotopy.