

Systems Neuroscience

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Somatosensory system

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Organisation principles in sensory systems:

- Functional segregation
- Parallel pathways
- Relay in the thalamus (except olfaction)
- Faithful representation in early cortical stages
- Columnar organization in cortex

SOMATOSENSORY SYSTEM FUNCTIONS

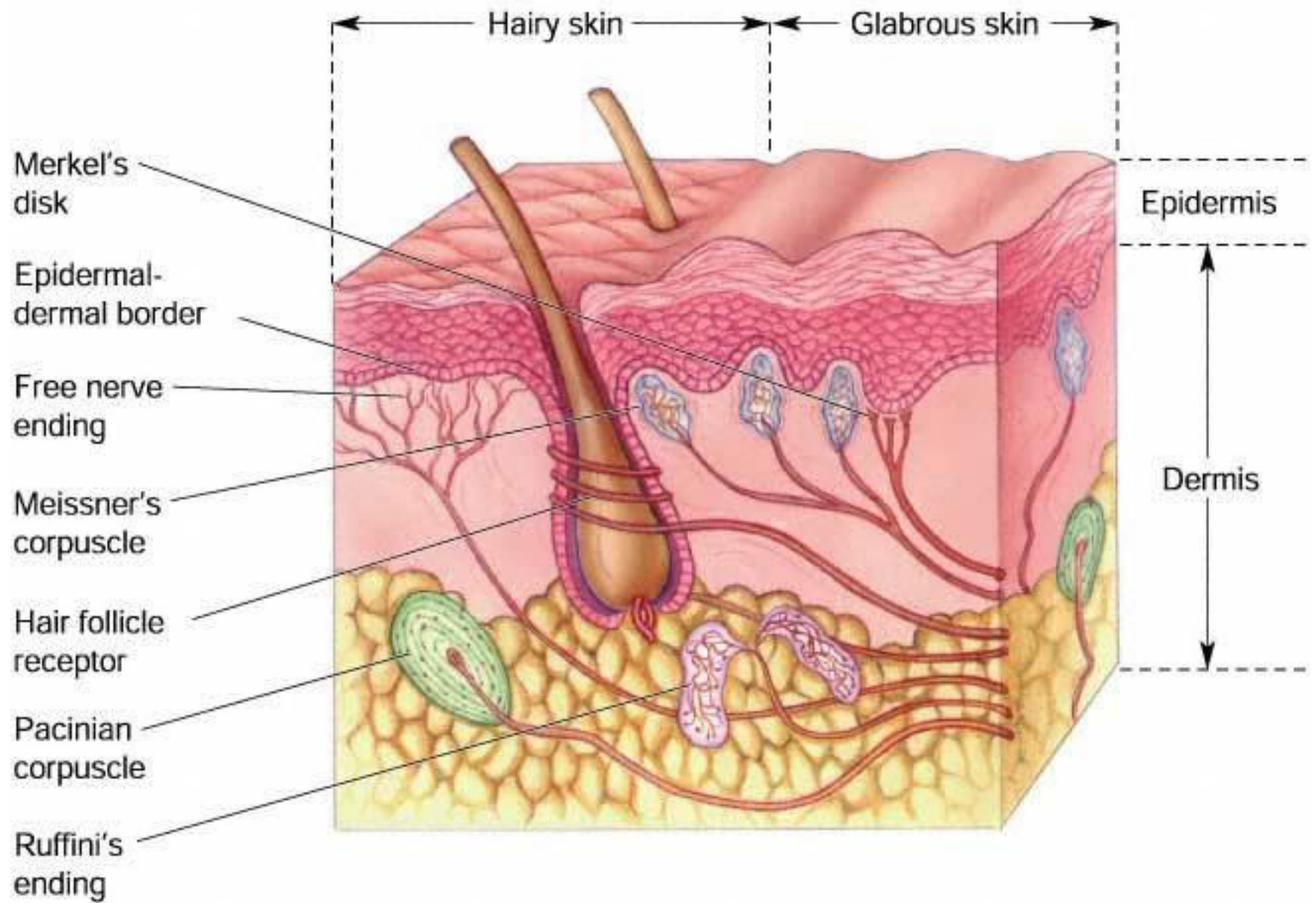
- **EXTEROCEPTIVE FUNCTIONS**
 - **MECHANORECEPTION** – pressure or touch (TACTILE sensitivity)
 - **THERMORECEPTION** - temperature (THERMAL sensitivity)
 - **NOCICEPTION** - noxious (damaging or potentially damaging) stimuli (NOXIOUS sensitivity)
- **PROPRIOCEPTIVE FUNCTIONS (KINAESTHESIS)** - information about position and movement of limbs and body in space
- **INTEROCEPTIVE FUNCTIONS** - information from internal organs

MECHANORECEPTION

- **FORM PERCEPTION**
 - e.g., identification of objects by touch alone; Braille reading; measured experimentally in terms of “two-point threshold”
 - note variation in sensitivity across skin surface
- **TEXTURE PERCEPTION**
- **VIBRATION PERCEPTION**
 - flutter (frequencies < 40 Hz)
 - vibration (frequencies 40 – 400 Hz)

SKIN AND SKIN RECEPTORS

- Size of skin as receptor surface
- **GLABROUS** (hairless) and hairy skin
- Distinctions between
 - **ENCAPSULATED** and **UNENCAPSULATED** receptors
 - **SUPERFICIAL (CUTANEOUS)** and **DEEP** receptors



SKIN AND SKIN RECEPTORS cont.

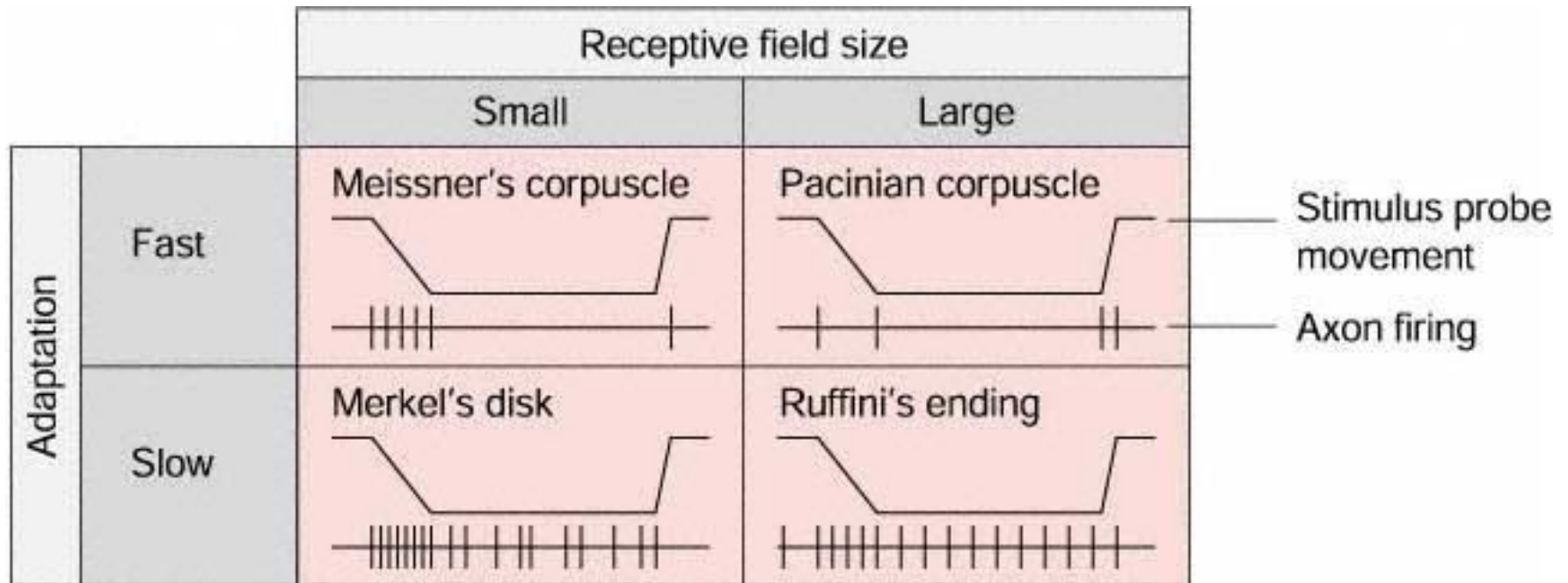
- SUPERFICIAL ENCAPSULATED RECEPTORS:
 - MERKEL RECEPTOR/DISK
 - MEISSNER CORPUSCLE
- DEEP ENCAPSULATED RECEPTORS
 - RUFFINI ENDING
 - PACINIAN CORPUSCLE
- UNENCAPSULATED RECEPTORS – free nerve endings

SKIN AND SKIN RECEPTORS cont.

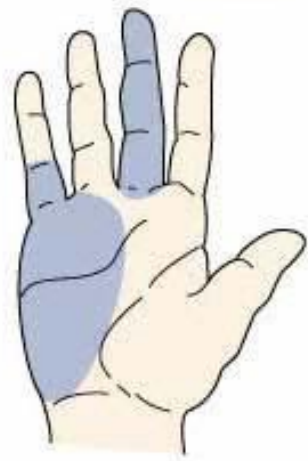
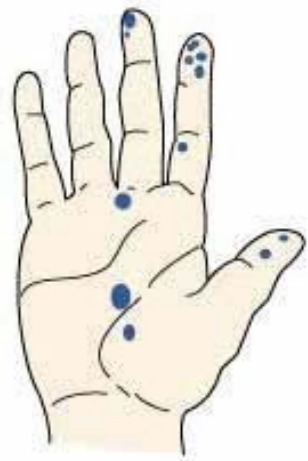
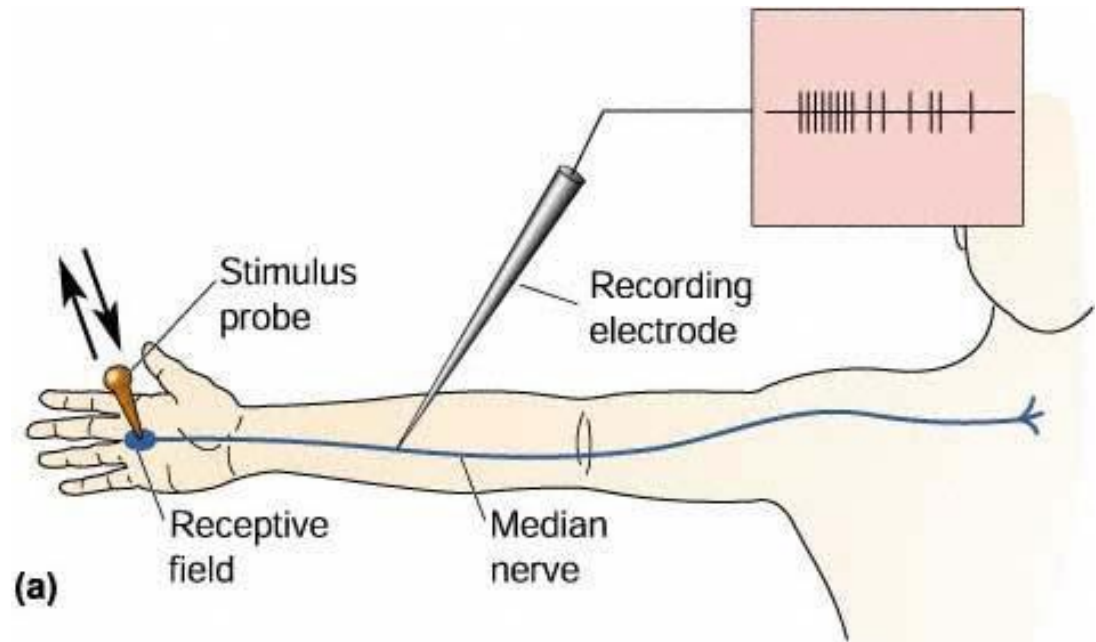
- Because of their location in the skin and the nature of their specialisations, different encapsulated receptor types have different forms of cutaneous sensitivity
- This was first discovered not by looking at receptors themselves but by recording from **single CUTANEOUS AFFERENT FIBRES** (can be done in humans and in animals)
- All of the mechanoreceptor afferent axons are medium diameter (6-12 μm), well-myelinated fibres with conduction velocities of 35-75 m/s. They are called **A β fibres**.

CUTANEOUS AFFERENTS

Fibres are classified as either **RAPIDLY ADAPTING (RAs)** or **SLOWLY ADAPTING (SAs)**, and in terms of the size of their **RECEPTIVE FIELD** (the size of the area on the skin from which they can be activated)



Schematic illustration of determination of receptive field

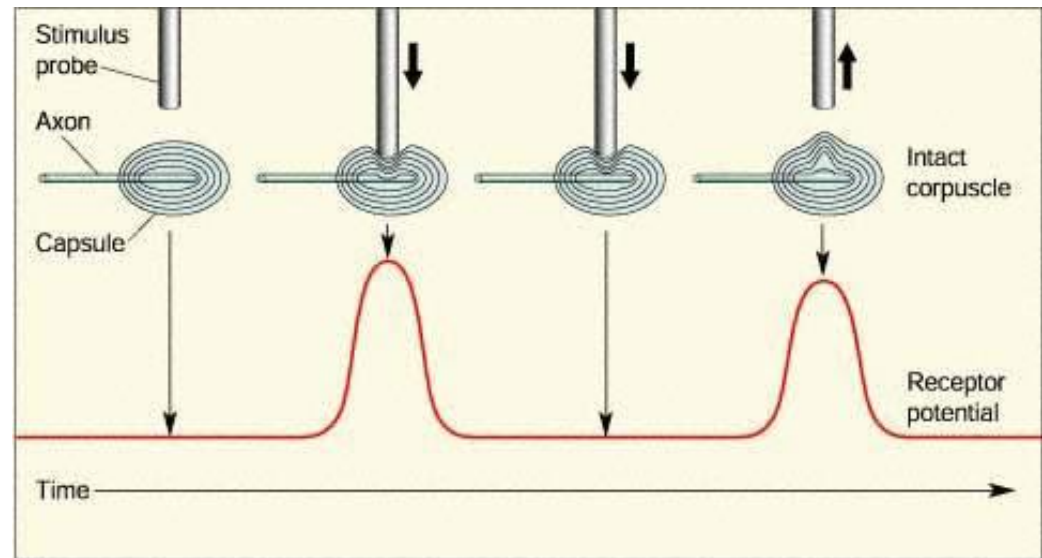


(b)

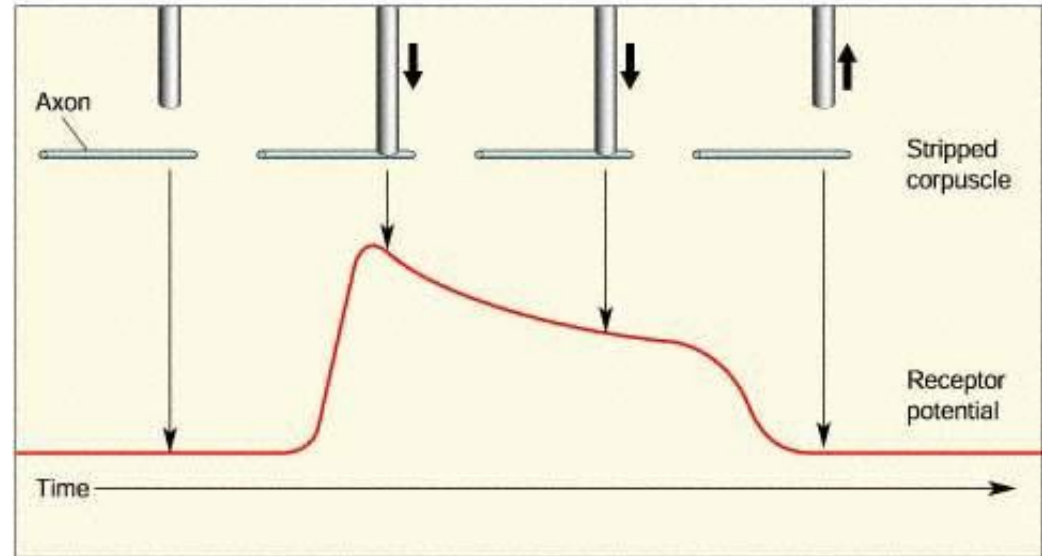
CUTANEOUS AFFERENTS

- **RAs** respond only at the beginning and end of sustained displacements (i.e., to transients) but respond well to higher frequency vibrations. Two types:
 - **RAI: MEISSNER CORPUSCLES** (10-200 Hz) small RF
 - **RAII: PACINIAN CORPUSCLES** (70-1000 Hz)
large RF
- **SAs** respond throughout sustained displacements of the skin, and are thus suited to coding the duration and magnitude of mechanical stimuli. Two types:
 - **SAI: MERKEL RECEPTORS/DISKS** - small RF
 - **SAII: RUFFINI ENDINGS** - large RF

The sensitivity characteristics of a particular afferent fibre reflects the specialized nature of the encapsulated ending (e.g., if you dissect away the onion-like layers of a PC, the fibre from that PC becomes sensitive to sustained displacement) and its position on the skin.



(a)



(b)

SUMMARY CLASSIFICATION TABLE

	SUPERFICIAL (small RF)	DEEP (large RF)
RA	MEISSNER CORPUSCLE (RAI)	PACINIAN CORPUSCLE (PC)
SA	MERKEL DISK (SAI)	RUFFINI ENDING (SAII)

HAIRY SKIN

- Merkel disks, Pacinian corpuscles, and free nerve endings as in glabrous skin
- Innervation of hair follicles (by free nerve endings or more specialized endings)
- A recent discovery – hairy skin has “soft touch” receptors that project to cortical regions associated with emotion and sexual arousal

NOCICEPTION





- Nociceptors respond to noxious mechanical and thermal stimuli (i.e. stimuli that produce or threaten to produce tissue damage) and also to chemicals released by damaged tissue (e.g., histamine, etc)
- Note distinction between noxiousness as a quality of the stimulus and pain as perceptual and emotional response.
- Two types of nociceptor:
 - **HIGH THRESHOLD MECHANORECEPTORS**
 - **POLYMODAL NOCICEPTORS**

NOCICEPTION cont.

- Receptors are **free nerve endings**
- Afferent axons are of different types:
 - HIGH THRESHOLD MECHANORECEPTORS : **A δ FIBRES**
 - POLYMODAL NOCICEPTORS: **C FIBRES**

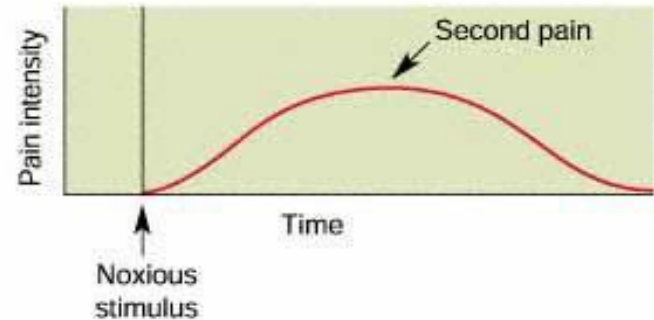
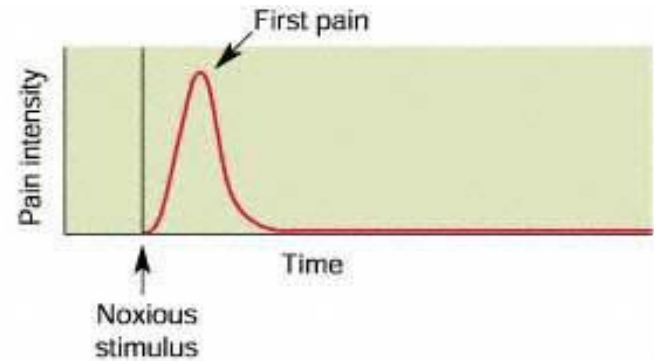
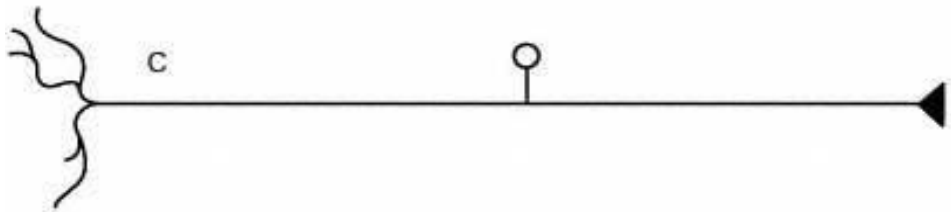
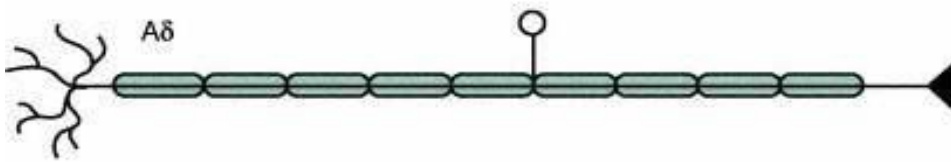
Axon types in nerves from skin and from muscles

(Note different terminologies associated with different origins)

Axons from skin	A α	A β	A δ	C
Axons from muscles	Group I	II	III	IV
				
Diameter (μm)	13–20	6–12	1–5	0.2–1.5
Speed (m/sec)	80–120	35–75	5–30	0.5–2
Sensory receptors	Proprioceptors of skeletal muscle	Mechanoreceptors of skin	Pain, temperature	Temperature, pain, itch

NOCICEPTION cont.

- Different fibre types give rise to different pain sensations:
 - “First” or “cutaneous pricking” pain – mediated by **A δ** fibres
 - “Second” or “burning” pain - mediated by **C** fibres



THERMORECEPTION

- Thermoreceptors: “**WARM**” fibres and “**COLD**” fibres
- They respond to increase or decrease in temperature, respectively, from steady state and to maintained temperature
- At intermediate skin temperatures (approx. 30-35 deg) there is ongoing discharge in both warm and cold fibres, and a change in skin temperature reciprocally modifies the discharge in the two fibre types. At a lower adapting temperature (e.g., 26 deg) only cold fibres are active, and an increase in temperature first decreases the discharge in cold fibres, and then – with larger increments – begins to engage the previously silent warm fibres.

THERMORECEPTION

- Large receptive fields, so temperature sensations are not well localized
- Note relativity of thermal sensations (i.e., change in temperature is what is felt as warm or cold) and similar relativity of neuronal responses.
- Receptors are free/bare nerve endings
- Afferent axons:
 - **Warm fibres:** C fibres
 - **Cold fibres:** A δ fibres

PROPRIOCEPTION (THE KINAESTHETIC SENSE)

- Provides information about the position and movement of the limbs and body in space (give examples: limb movement without vision; passive movement)
- Proprioceptive information supplements “efference copy” information from motor system
- Information is provided by three classes of receptors:
 - CUTANEOUS MECHANORECEPTORS
 - JOINT RECEPTORS
 - MUSCLE SPINDLES AND GOLGI TENDON ORGANS

CUTANEOUS MECHANORECEPTORS AND JOINT RECEPTORS

- **CUTANEOUS MECHANORECEPTORS**
 - Information about skin stretch from Ruffini/SAIL afferents
 - Of different importance in different regions (important around hands, mouth and feet)
- **JOINT RECEPTORS**
 - Ruffini-type endings and Pacinian corpuscles in joint capsule
 - But not essential, because anaesthesia or removal of joint capsules does not result in loss of limb position sense

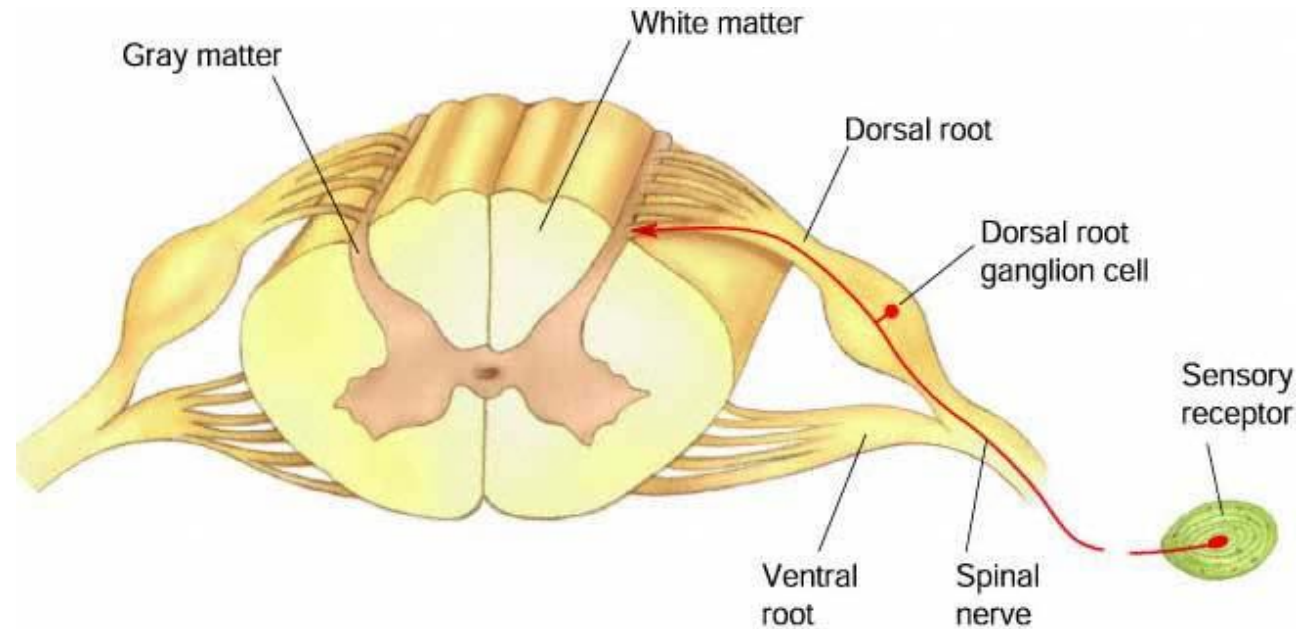
MUSCLE SPINDLES AND GOLGI TENDON ORGANS

- Golgi tendon organs (**Ib** fibres): respond to tendon stretch
- Muscle spindles (type **1a** and **II** axons) are coiled around intrafusal muscle fibres; respond to muscle stretch; type I axons constitute the sensory component of the knee-jerk reflex

DORSAL ROOT GANGLIA

All somatic fibres are the axons of dorsal root ganglion cells (or trigeminal ganglion cells in the case of the head and neck)

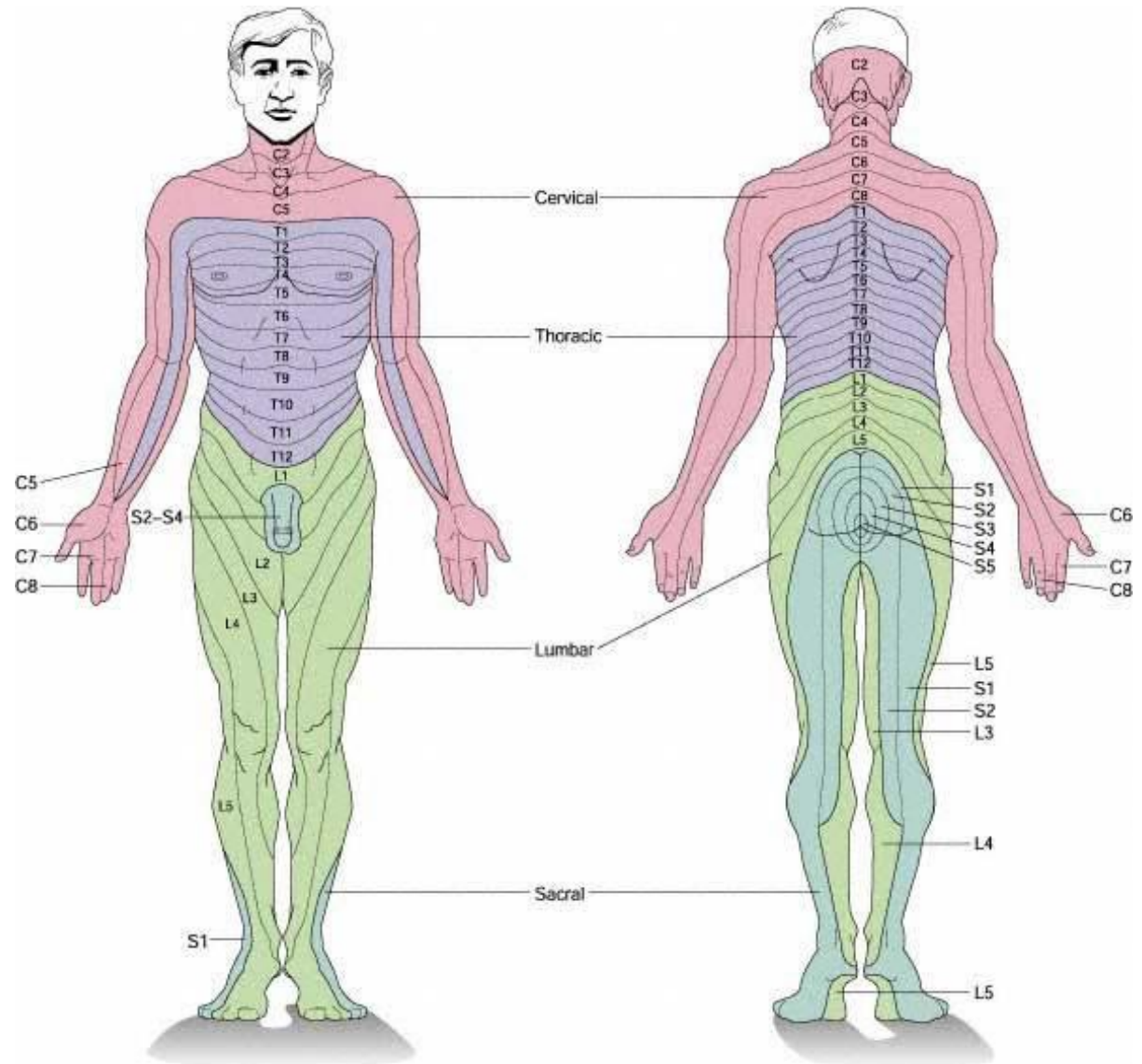
DRG cells have no dendrite, but a single bifurcating axon - sends one process to the periphery and another to the CNS



DERMATOMES

The axons of an individual dorsal root innervate a restricted region of skin that is the same in everyone –
DERMATOME

DERMATOMAL MAP:
Stereotyped pattern of dermatomes allows diagnosis of location of injury or infection of dorsal roots on basis of skin distribution of sensitivity (e.g., in shingles)



MODALITY SEGREGATION

- ...is the basic principle of organization of the somatosensory system
- Information from each class of receptors reaches a different group of neurons in the CNS and these neurons project to higher levels along segregated “parallel” pathways
- This segregation begins with the place of termination of different classes of afferent axon in the spinal cord
- It continues with two major ascending pathways:
 - **The dorsal column - medial lemniscal pathway**
 - **The spino-thalamic pathway**

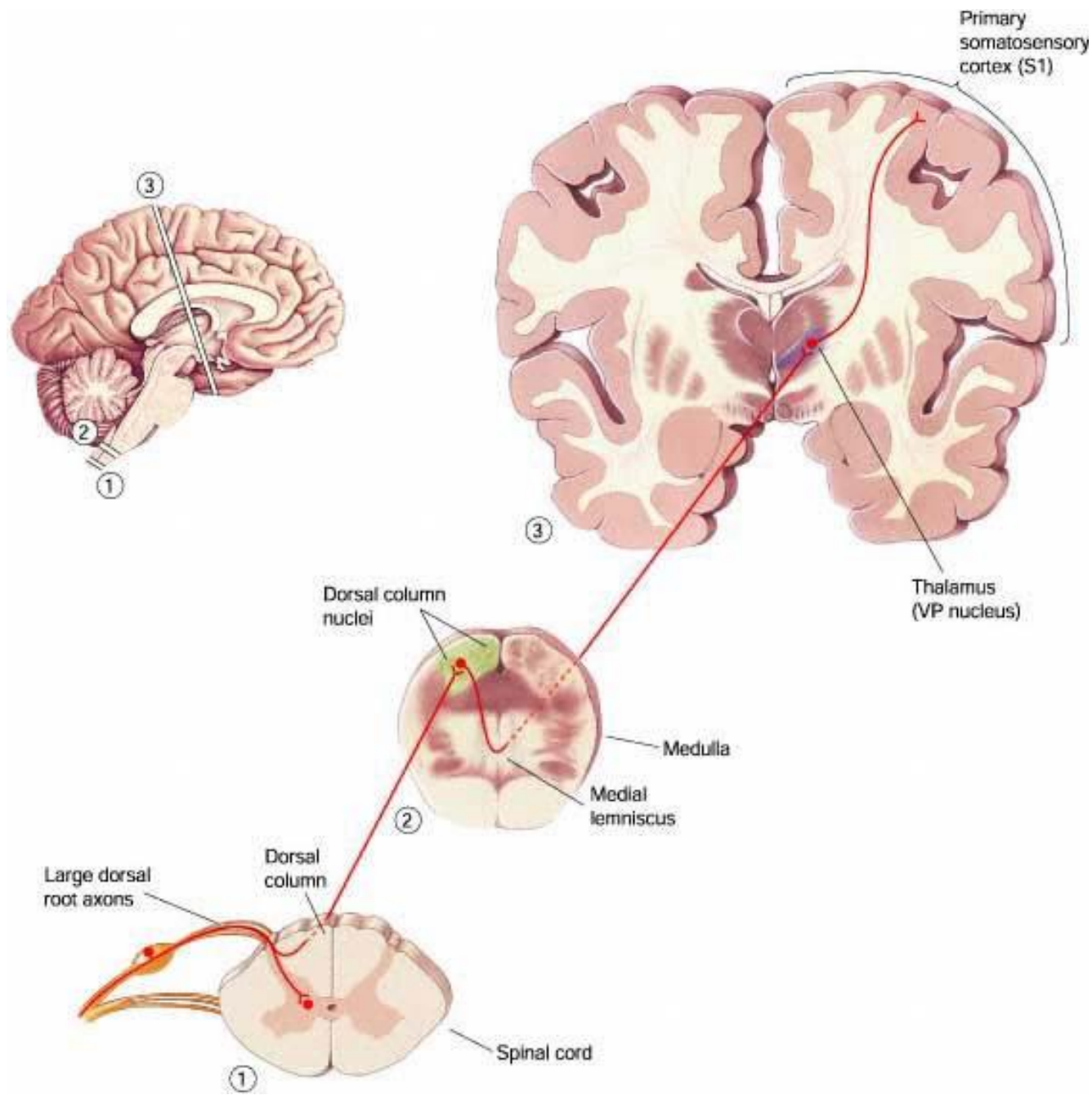
SEGREGATION IN SPINAL CORD

- The spinal grey matter is divided into a number of layers (laminae); laminae I – VI comprise the dorsal horn
- A δ and C fibers terminate predominantly in layer I (the marginal layer) and layer II (the substantia gelatinosa)
- A β axons bifurcate, one branch ascending in the dorsal columns, the other terminating on cells in the deeper dorsal laminae

THE DORSAL COLUMN - MEDIAL LEMNISCAL PATHWAY

- The ascending branches of $A\beta$ axons (conveying discriminative touch information) ascend in the dorsal columns (the **gracile and cuneate fasciculi**), and synapse on cells in the **dorsal column nuclei (DCN)** in the medulla (the **gracile and cuneate nuclei**, respectively)
- The axons of DCN cells cross the midline and ascend in the **medial lemniscus** to the **lateral division of the ventro-posterior nucleus (VPL)** of the thalamus
- **VPL** cells in turn project to the primary somatosensory cortex (**SI**)

The dorsal column system



THINGS TO NOTE ABOUT DORSAL COLUMN – MEDIAL LEMNISCAL PATHWAY

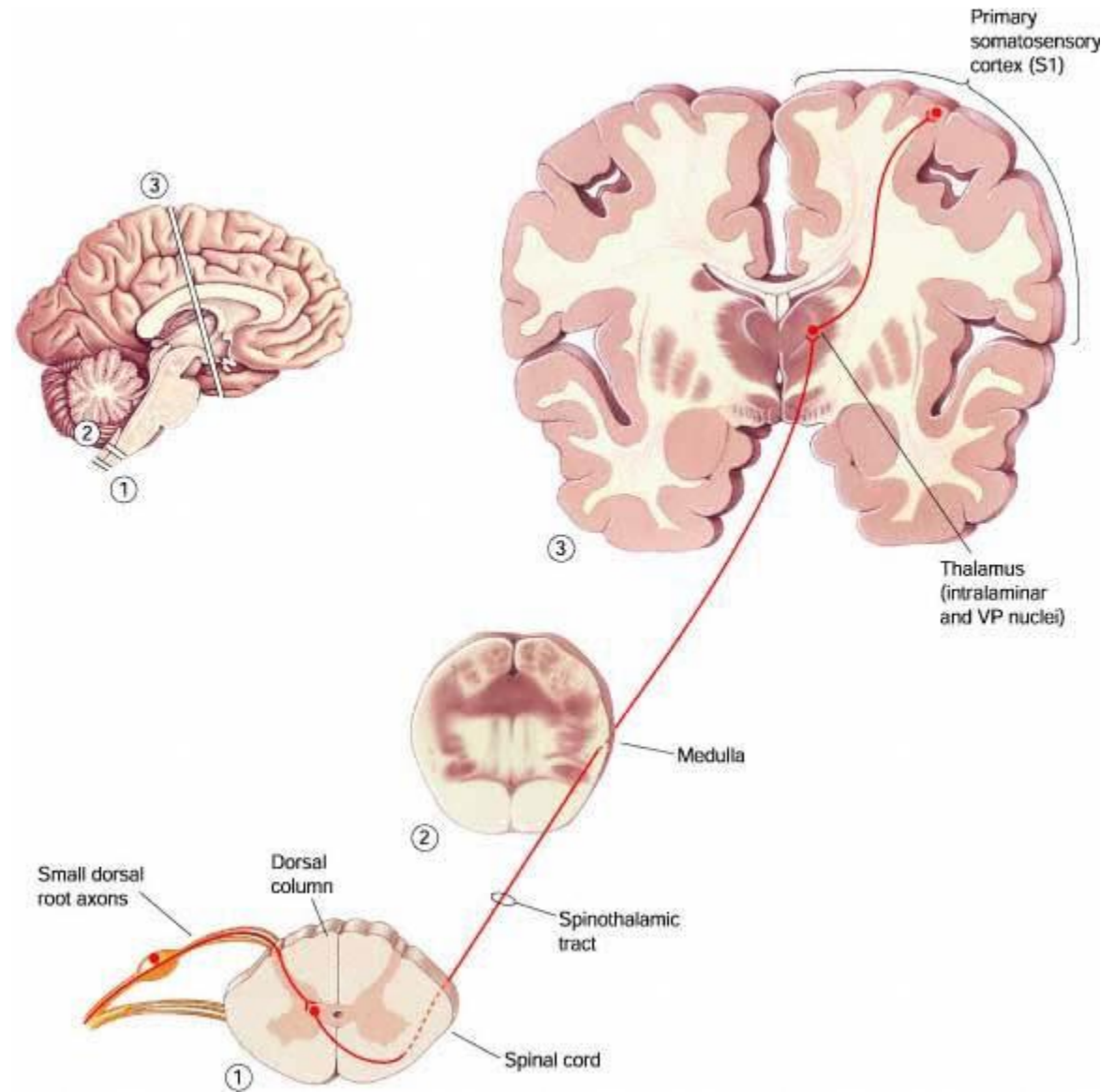
- The **gracile fasciculus** extends the entire length of the spinal cord; it and the **gracile nucleus** contain a representation of the feet, legs, and lower trunk
- The **cuneate fasciculus** begins at the cervical level; it and the **cuneate nucleus** contain a representation of the hands, arms, and upper trunk
- The entire system is topographically organized (i.e., adjacent parts of the body surface are represented by adjacent neurons - **SOMATOTOPY**)
- The decussation (crossing over) of the medial lemnisci results in a representation of the **contralateral** body surface on each side of the brain at levels above the DCN

THE SPINO-THALAMIC PATHWAY

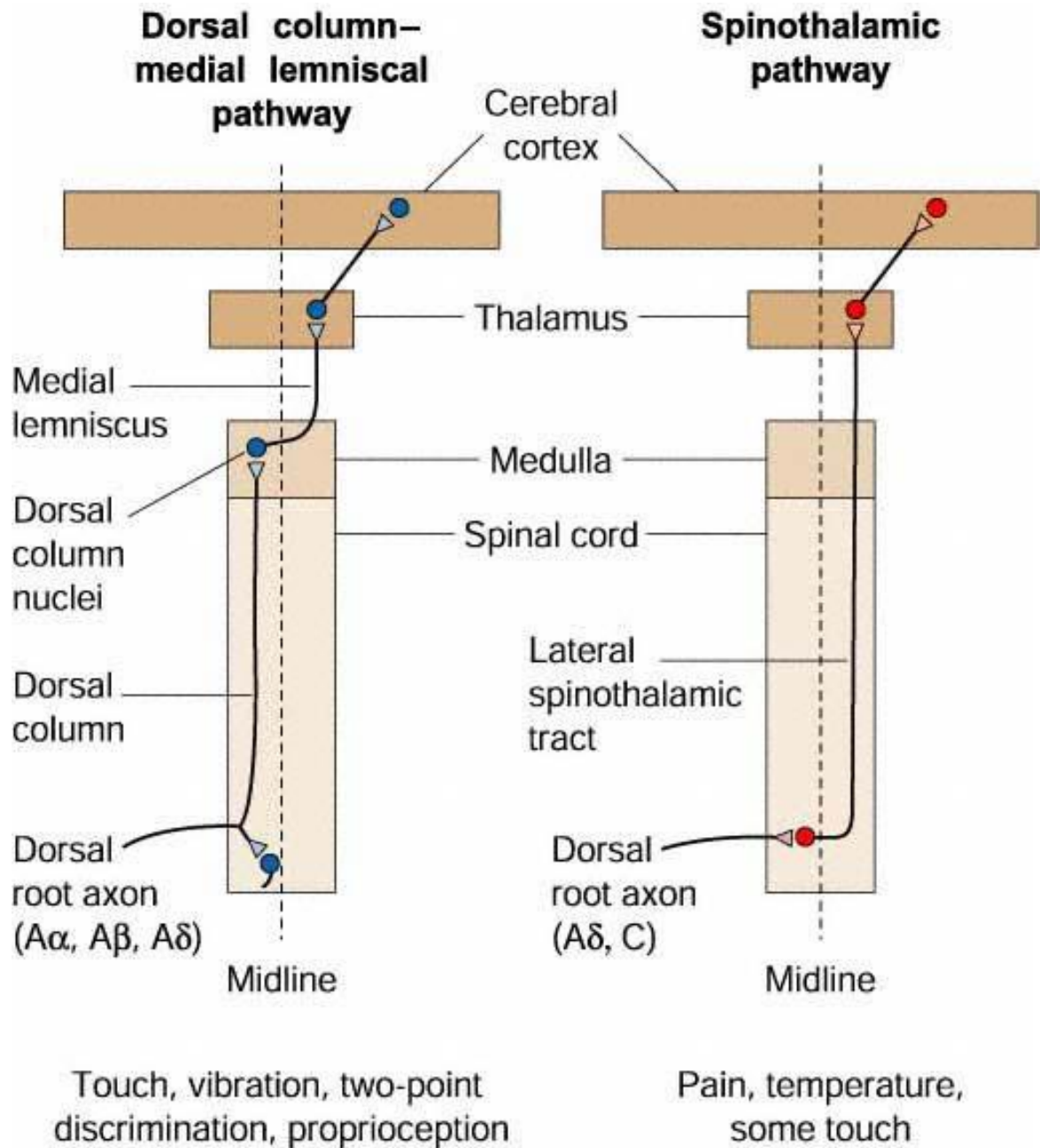
- Small-diameter myelinated and unmyelinated axons (**A δ** and **C** fibres serving temperature sensitivity and nociception) terminate in the spinal cord itself
- The axons of the spinal neurons then cross the midline and ascend as **the anterolateral system**
- Most of these fibres (constituting the **spino-thalamic system**) terminate in VPL and in the intralaminar and posterior groups of thalamic nuclei
- Other ascending fibres terminate in the reticular formation (the **spino-reticular system**) and in the midbrain
- The VPL neurons receiving spino-thalamic input are segregated from those receiving medial lemniscal input and project to both primary and secondary somatosensory cortex (**SI** and **SII**)

The spino-thalamic system

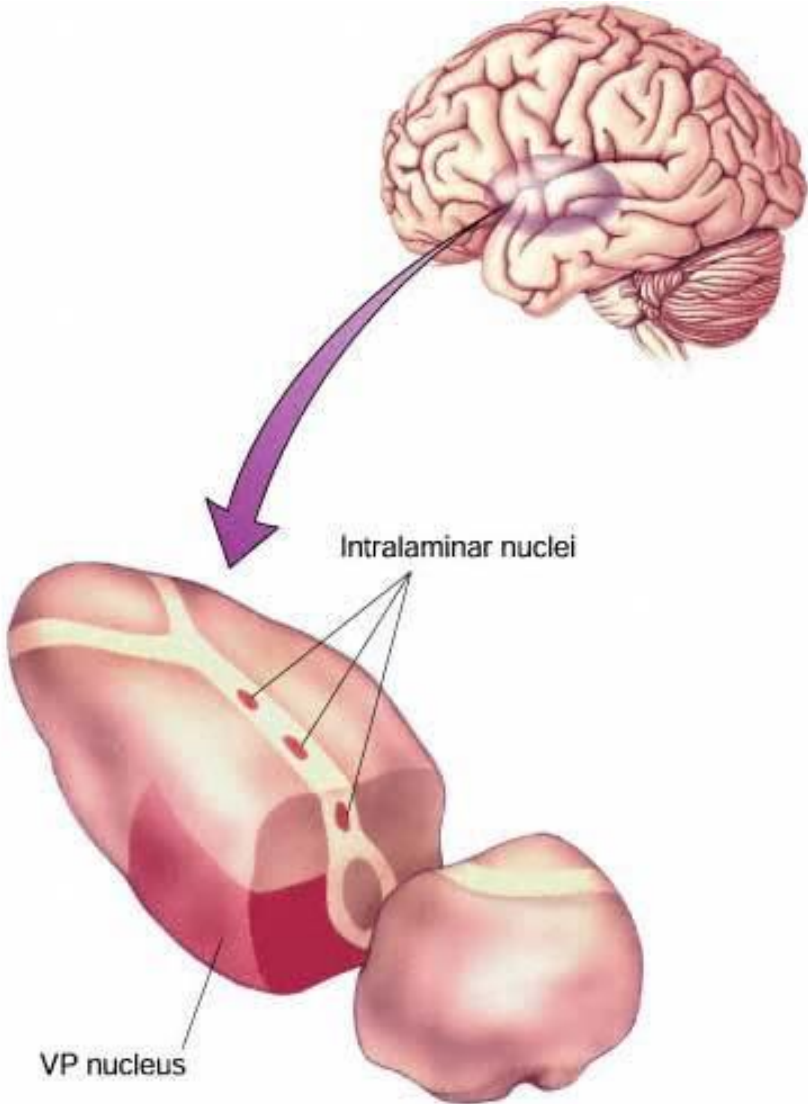
(note that the drawing is inaccurate with respect to the location of the cell body in the cord – it should be in lamina I or II)



Schematic representation of dorsal column – medial lemniscal and spino-thalamic pathways



Schematic illustration of the locations of the major thalamic nuclei involved in the processing of somatosensory information



THE TRIGEMINAL SYSTEM

- Conveys somatosensory input from the face
- Large-diameter myelinated axons of the trigeminal ganglion conveying discriminative touch information terminate in the principal trigeminal nucleus
- The axons of these cells then cross the midline, join the medial lemniscus, and terminate in the **medial division of the ventro-posterior nucleus (VPM)**

THE TRIGEMINAL SYSTEM cont.

- Small diameter lightly- myelinated and unmyelinated axons of the trigeminal ganglion conveying thermal and nociceptor information descend in the spinal trigeminal tract and terminate in the spinal trigeminal nucleus
- The axons of these cells then project to VPM and to the posterior and intralaminar thalamic nuclei (i.e., rather like the anterolateral system)

THE SOMATOSENSORY THALAMUS

(brief summary only)

- The **ventrobasal** complex of the thalamus has the two major divisions previously described:
 - **VPL** (somatosensory information from the body)
 - **VPM** (somatosensory information from the face)
- Both are somatotopically organized
- Thalamic neurons have adaptation properties (SA vs. RA) like those of peripheral neurons, but the RFs are larger than those of dorsal root ganglion cells and are commonly concentric, with a central excitatory area and a surrounding inhibitory area

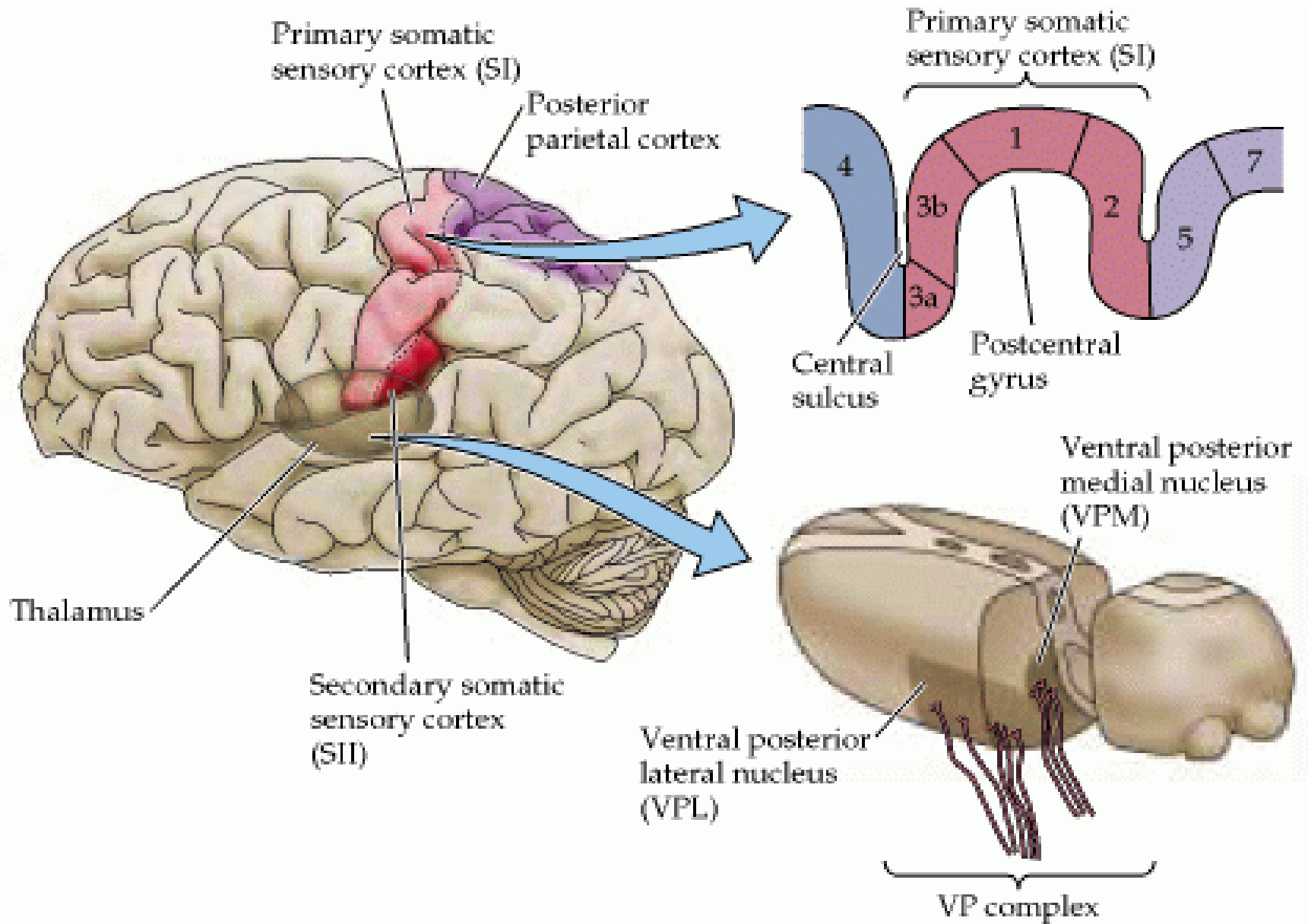
SOMATOSENSORY CORTEX

- Two major areas in primates
 - **SI** – on posterior bank of central sulcus and crown of post-central gyrus
 - **SII** – on lip and upper bank of lateral fissure
- SI contains 4 distinct areas (**3a, 3b, 1, and 2**) with different characteristics and functions:
 - Areas 3a and 3b receive most of the direct projections from the thalamus and in turn project to areas 1 and 2
 - Areas 3b and 1 receive input from skin receptors
 - Areas 3a and 2 receive input from joint and muscle receptors

SOMATOSENSORY CORTEX cont.

➤ Effects of cortical lesions:

- Large lesions of all of SI produce deficits in position sense and in discrimination of size, texture and shape. They also produce motor deficits in hand function
- Area 3b lesions result in severe deficits in tactile discrimination of texture, size, and shape
- Area 1 lesions affect texture but not size discrimination
- Area 2 lesions affect size and shape but not texture discrimination



CORTICAL RECEPTIVE FIELDS

- Receptive fields in area 3b, like those in the thalamus, are larger than those of DRG neurons and typically have excitatory centre – inhibitory surround structure
- Receptive fields in “higher” cortical areas are larger than those in 3b, and many are much more complex (e.g., sensitive to the orientation of an edge (cf. visual cortex), the direction of movement across the skin, or the surface curvature of objects)
- Some neurons in area 2 are selective for the 3-dimensional shape of objects

CORTICAL SOMATOTOPY

- Human somatotopy – classic map (“homunculus”) based on cortical stimulation (produced by Penfield)
- Distorted nature of homunculus
- Differences between species (enlarged representation of face and facial vibrissae in rodents (the “musunculus”))
- Neurophysiological evidence in monkeys indicates that each of the 4 areas comprising SI is somatotopically organized
- Note that multiple representations of the receptor surface are a common feature of all sensory cortices
- Note that representations are commonly “mirror-reversed” across field boundaries

COLUMNAR ORGANIZATION

- Neurons in a “column” running orthogonal to the cortical surface and through the cortical layers have very similar RFs and modality properties (including adaptation rate)
- A cortical column is ~300-600 μm in diameter
- Columnar organization was first described in detail by Mountcastle and his colleagues in somatosensory cortex and is now recognized as one of the fundamental principles of the organization of sensory cortex

Schematic illustration of columns defined by receptive field location and adaptation properties

