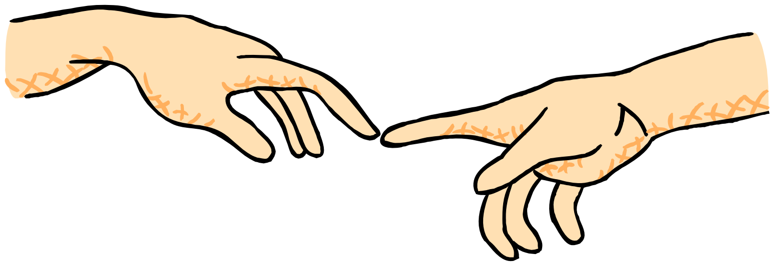
Touching



Ehud Ahissar

Touching

- Body-world interface
- Passive vs active touch
- Perceptual loops

Body-world interface

Underneath the skin

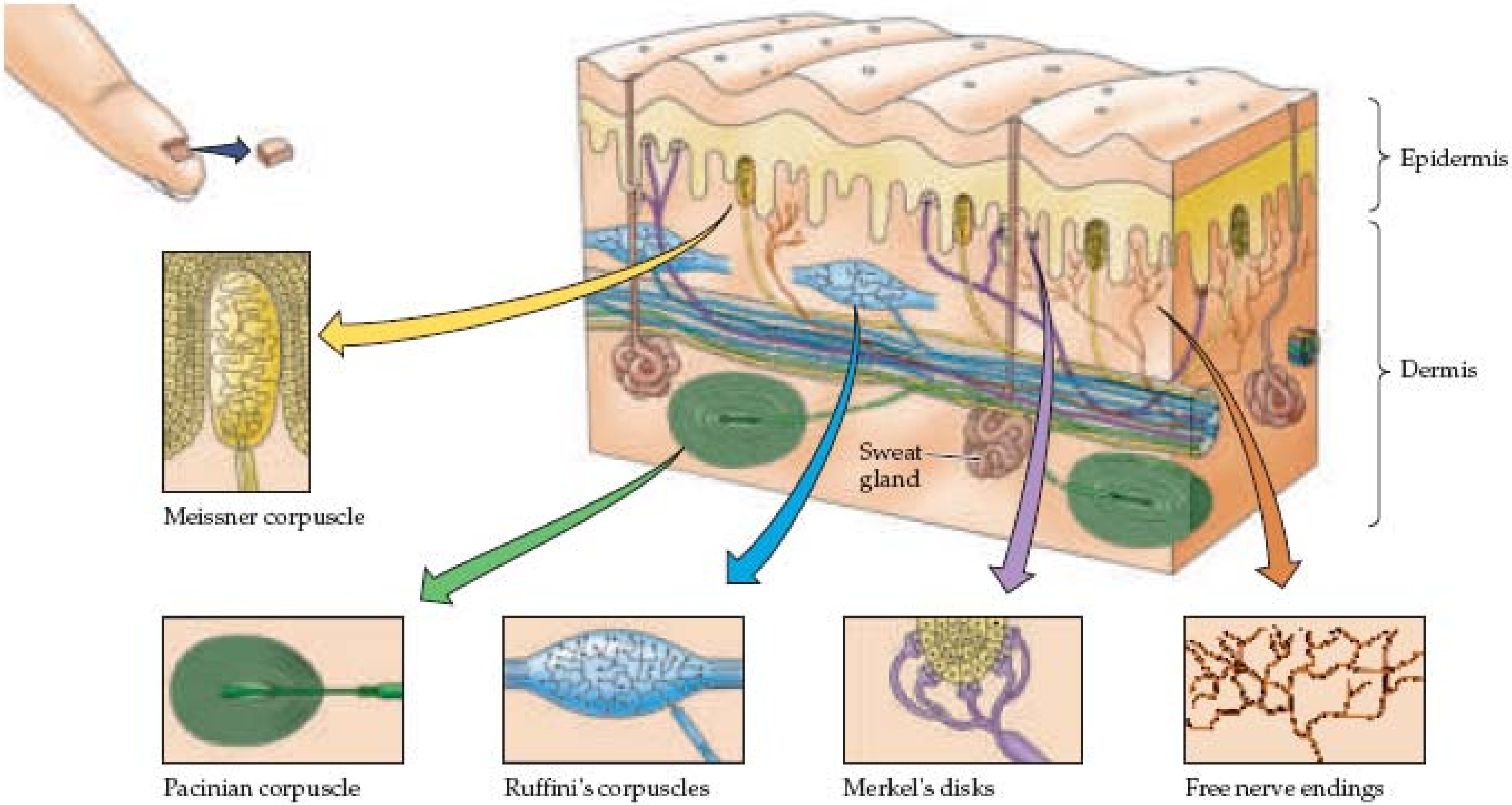
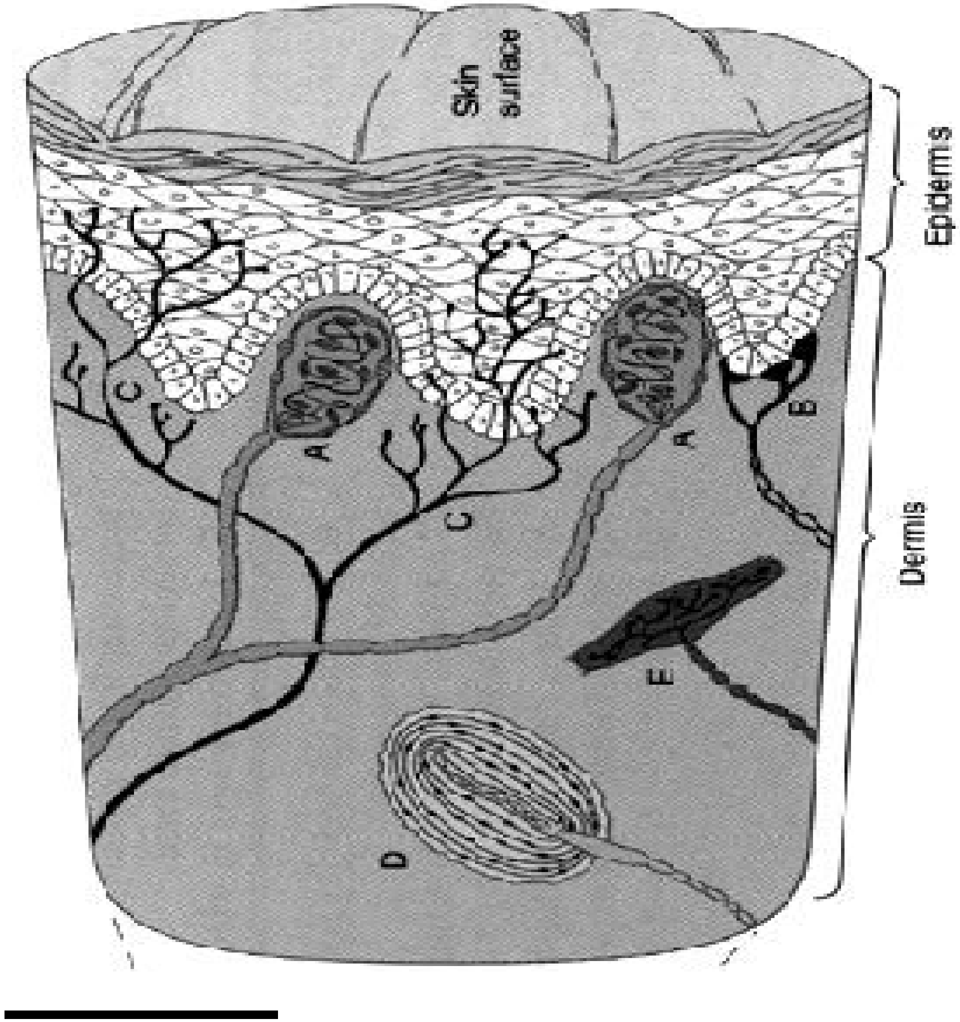


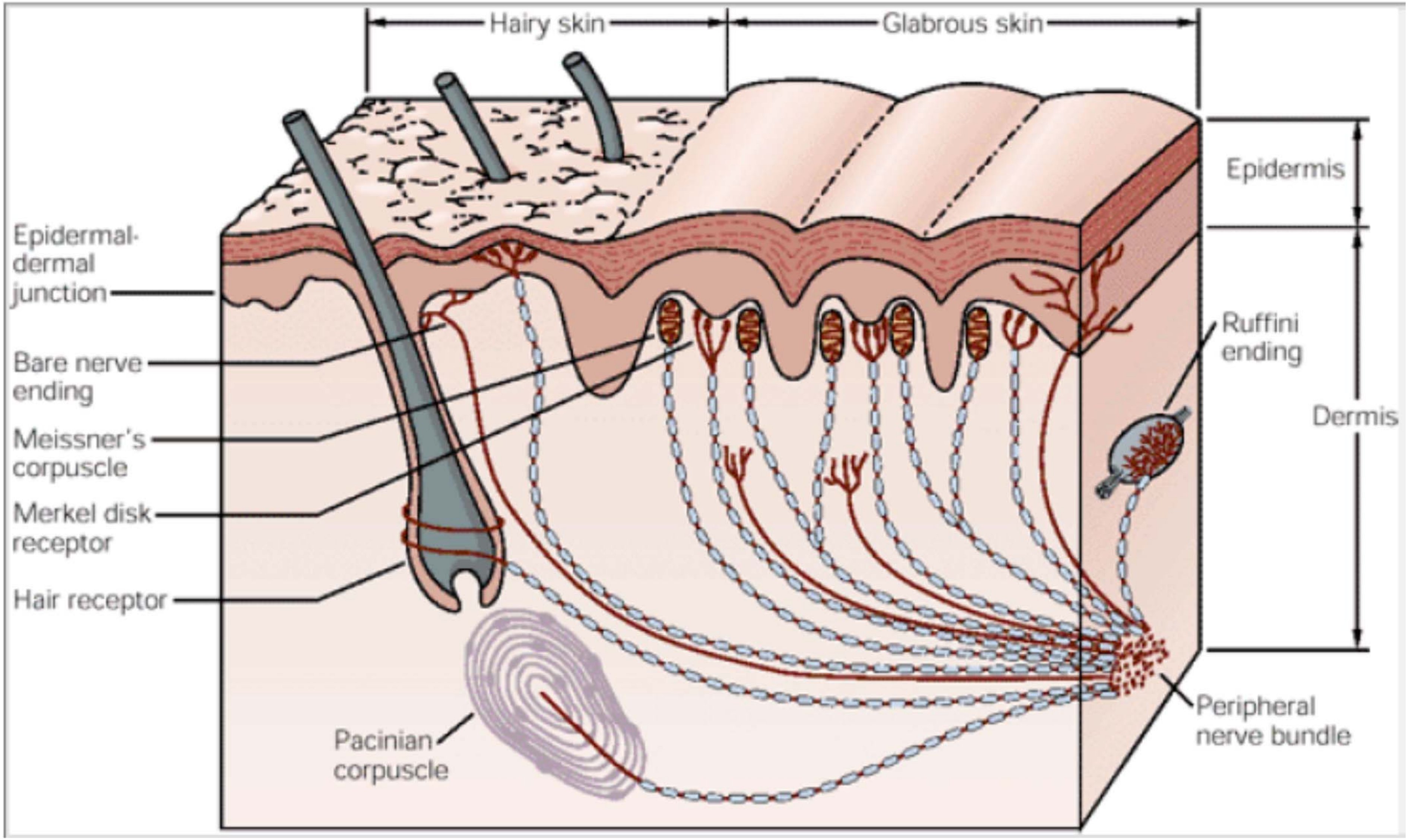
Figure 8.3 The skin harbors a variety of morphologically distinct mechanoreceptors. This diagram represents the smooth, hairless (also called glabrous) skin of the fingertip. The major characteristics of the various receptor types are summarized in Table 8.1. (After Darian-Smith, 1984.)

Mechanoreception underneath the skin



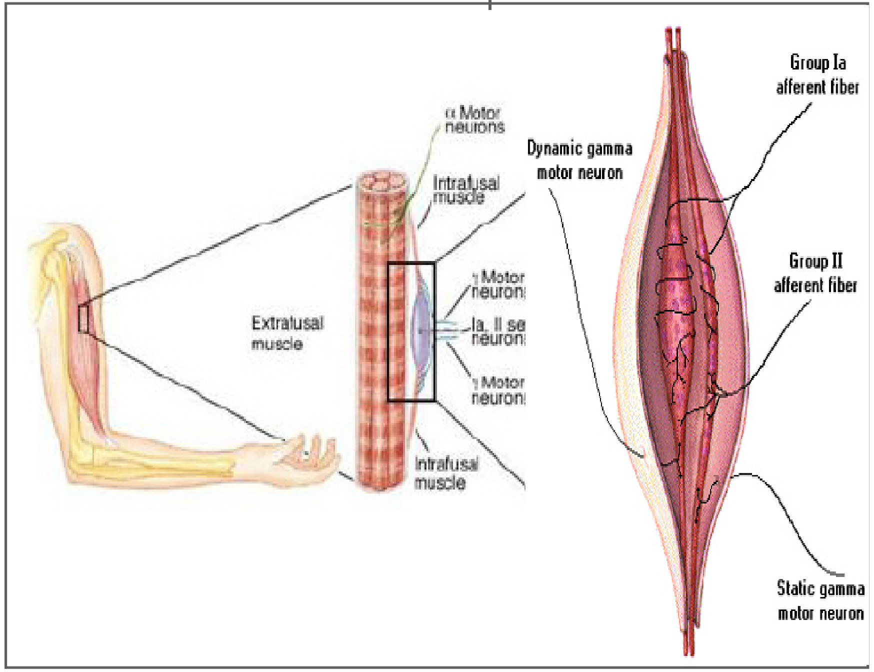
~200 μm

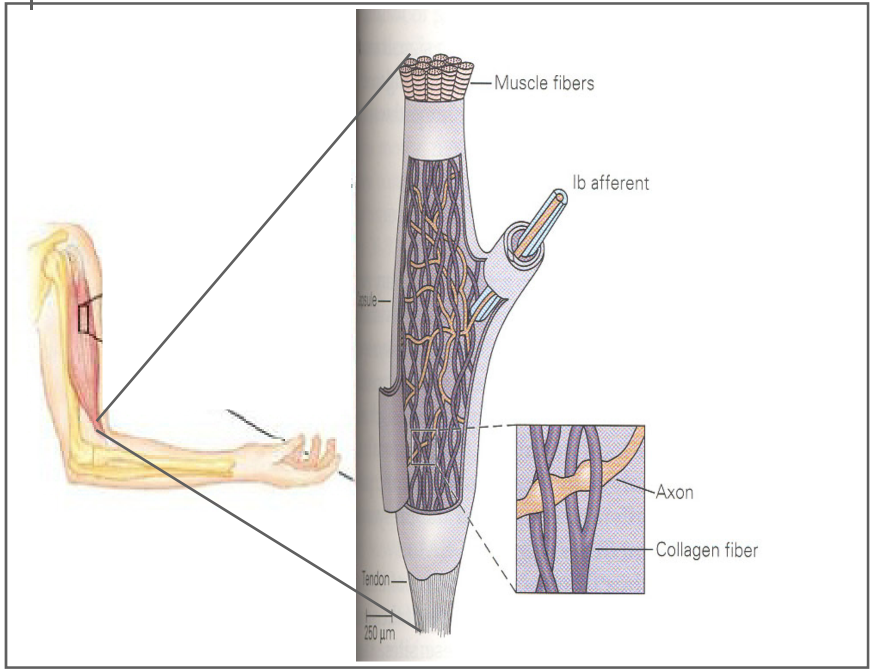
Mechanoreception underneath the skin



Proprioceptive receptor types

Name:	Muscle spindle receptors	Golgi tendon organs	Joint receptors
Sensitive to:	muscle length	muscle tension	Flexion, extension





Body-world interface

Underneath the skin

TABLE 8.1
The Major Classes of Somatic Sensory Receptors

Receptor type	*Anatomical characteristics*	*Associated axons[a] (and diameters)*	*Axonal conduction velocities*	*Location*	*Function*	*Rate of adaptation*	*Threshold of activation*
Free nerve endings	Minimally specialized nerve endings	C, Aδ	2–20 m/s	All skin	Pain, temperature, crude touch	Slow	High
Meissner's corpuscles	Encapsulated; between dermal papillae	Aβ 6–12 μm		Principally glabrous skin	Touch, pressure (dynamic)	Rapid	Low
Pacinian corpuscles	Encapsulated; onionlike covering	Aβ 6–12 μm		Subcutaneous tissue, interosseous membranes, viscera	Deep pressure, vibration (dynamic)	Rapid	Low
Merkel's disks	Encapsulated; associated with peptide-releasing cells	Aβ		All skin, hair follicles	Touch, pressure (static)	Slow	Low
Ruffini's corpuscles	Encapsulated; oriented along stretch lines	Aβ 6–12 μm		All skin	Stretching of skin	Slow	Low
Muscle spindles	Highly specialized (see Figure 8.5 and Chapter 15)	Ia and II		Muscles	Muscle length	Both slow and rapid	Low
Golgi tendon organs	Highly specialized (see Chapter 15)	Ib		Tendons	Muscle tension	Slow	Low
Joint receptors	Minimally specialized	—		Joints	Joint position	Rapid	Low

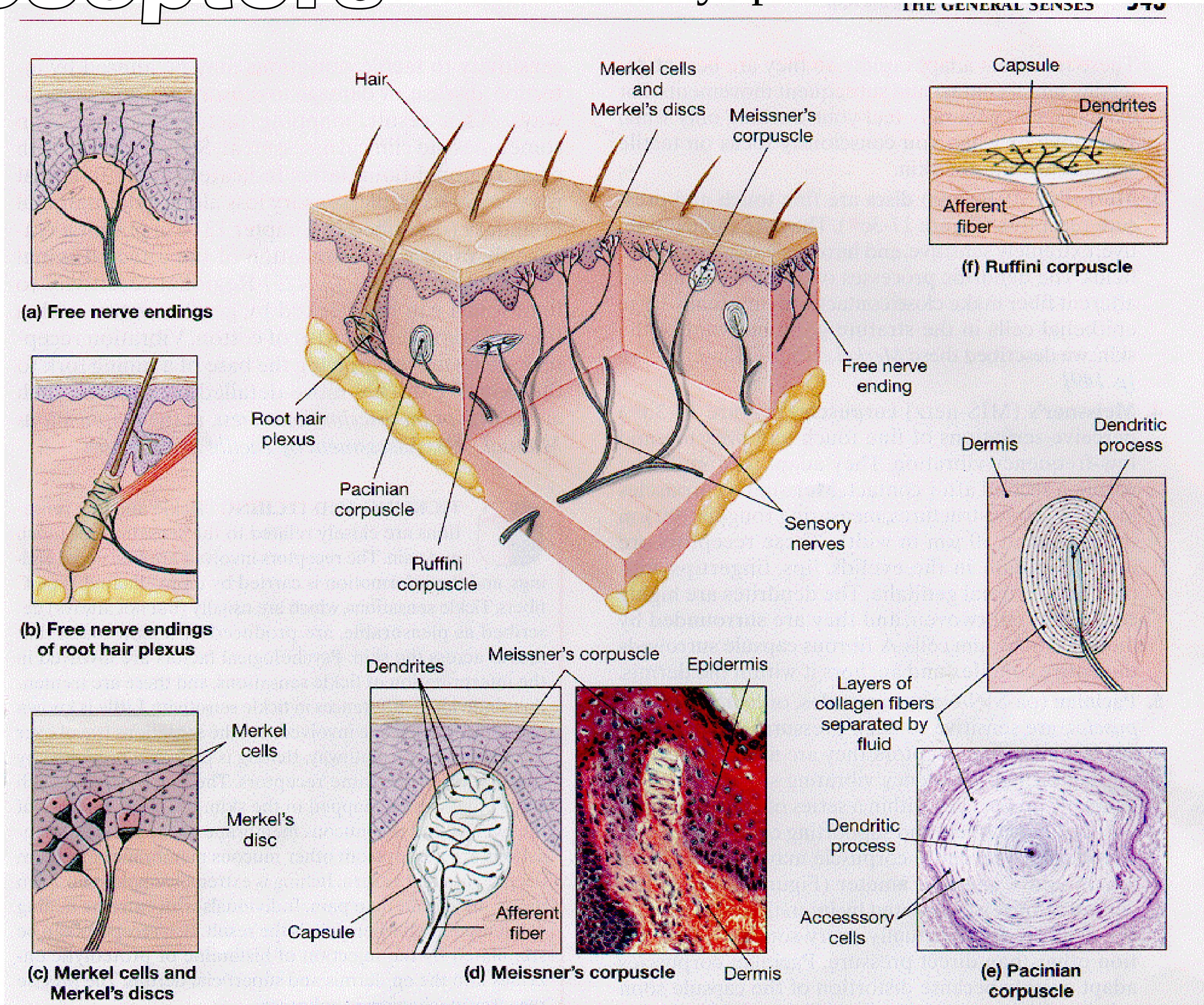
Mechano-receptors (ex-afferents)

Proprio-(re)ceptors (re-afferents)

[a]In the 1920s and 1930s, there was a virtual cottage industry classifying axons according to their conduction velocity. Three main categories were discerned, called

Receptors

Evolutionary specialization

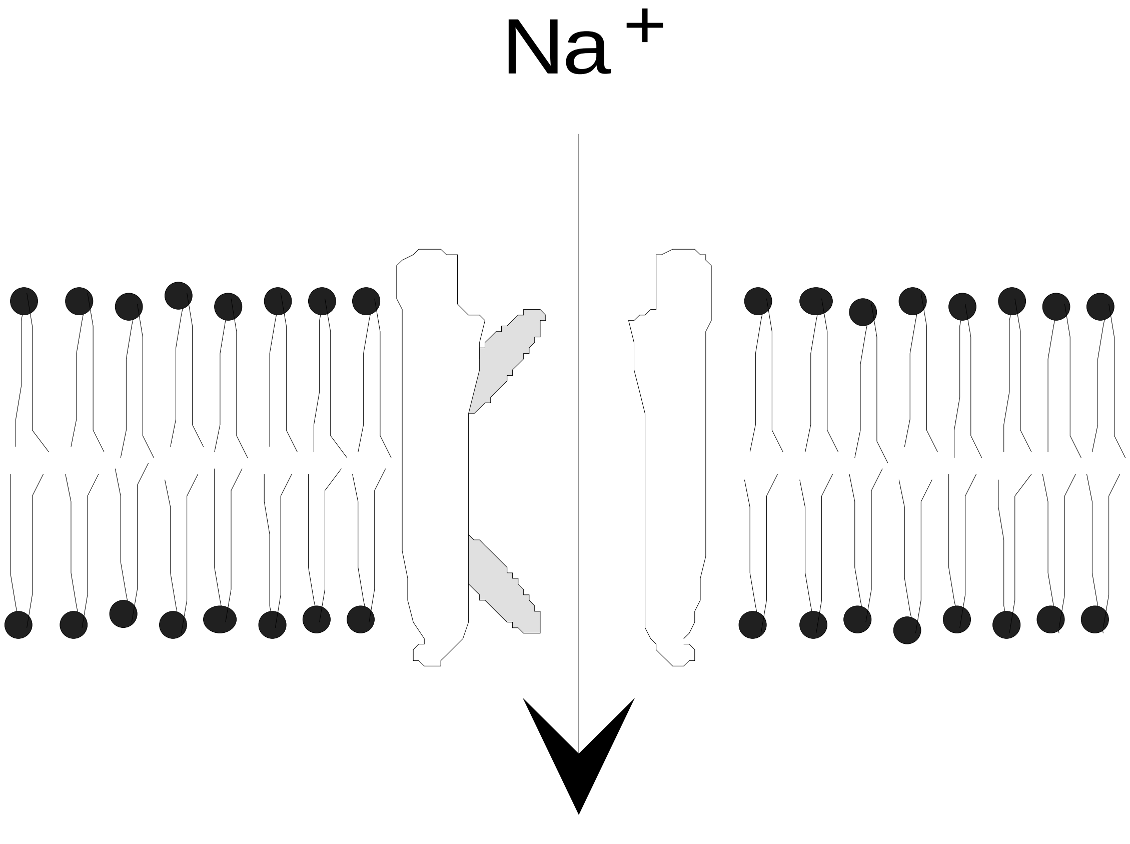


Signal transduction

Transduction

The receptor potential is produced by a **mechanically sensitive channel** that opens when the membrane is deformed

The channel is permeable to positive ions, primarily Na^+, K^+ and Ca^{2+}



Transduction

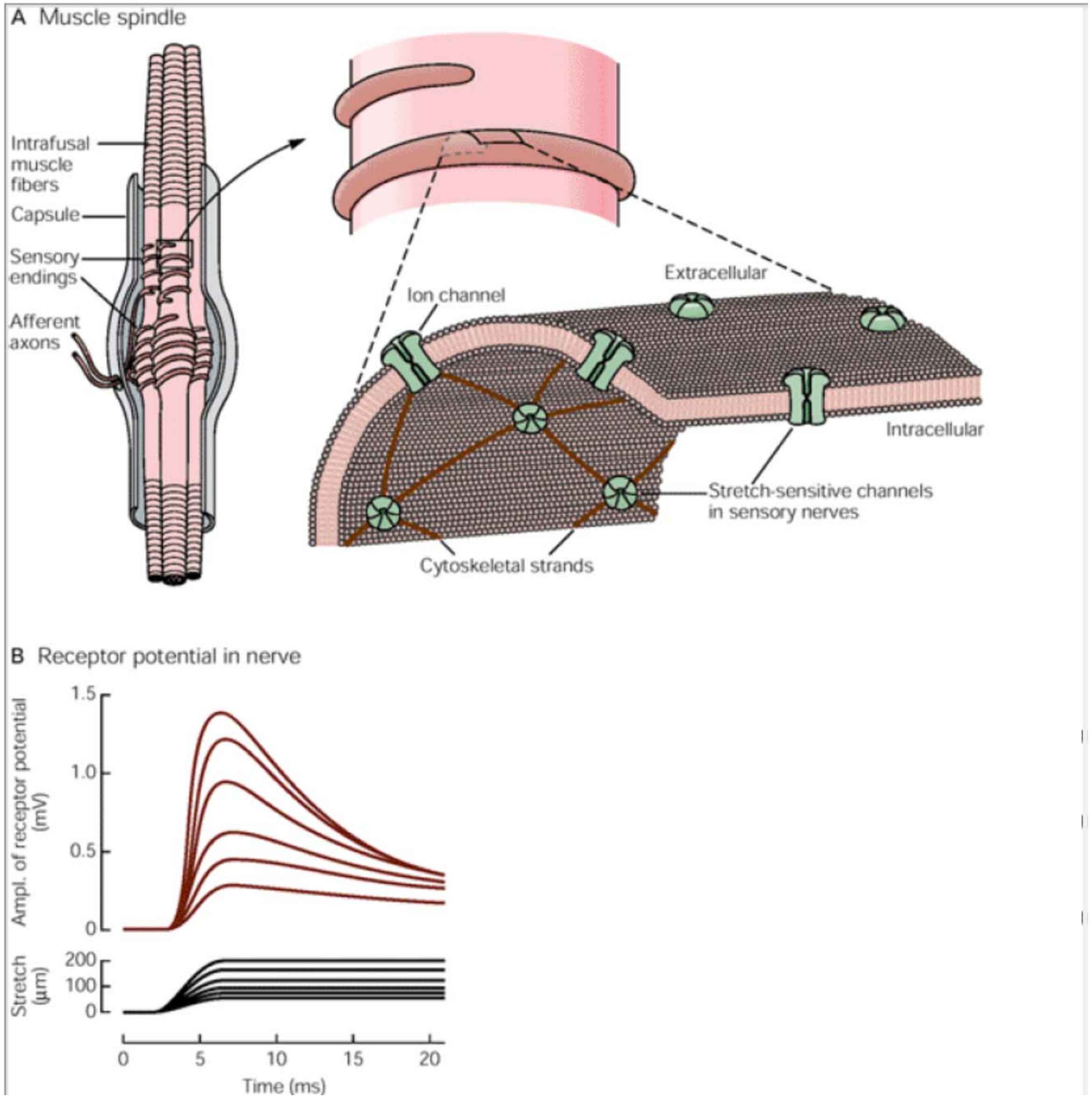
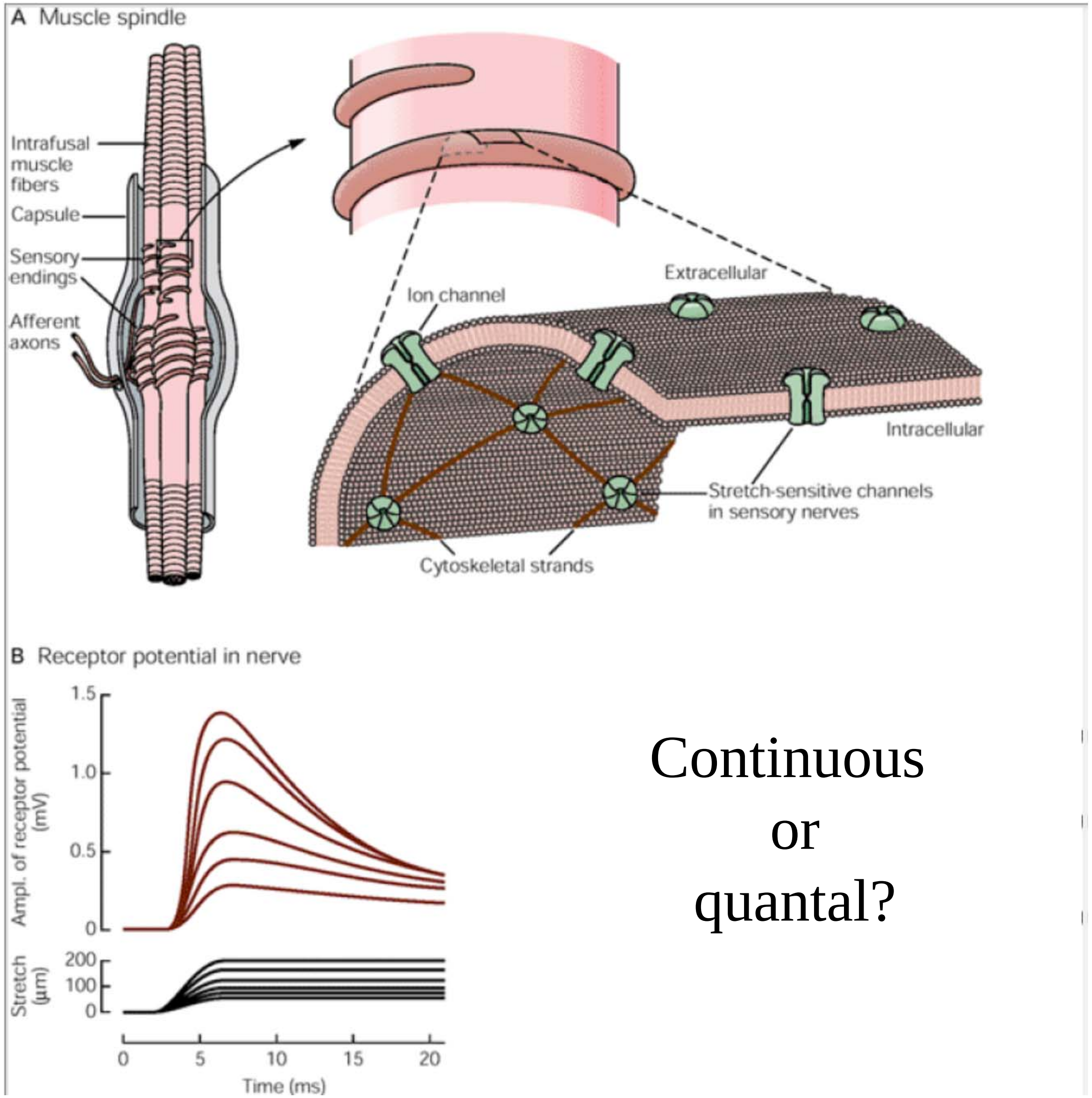


Figure 21-2 Mechanoreceptors are depolarized by stretch of the cell membrane and the depolarization is proportional to the stimulus amplitude.
A. The spindle organ in skeletal muscle mediates limb proprioception. These receptors signal muscle length and the speed at which the

Transduction



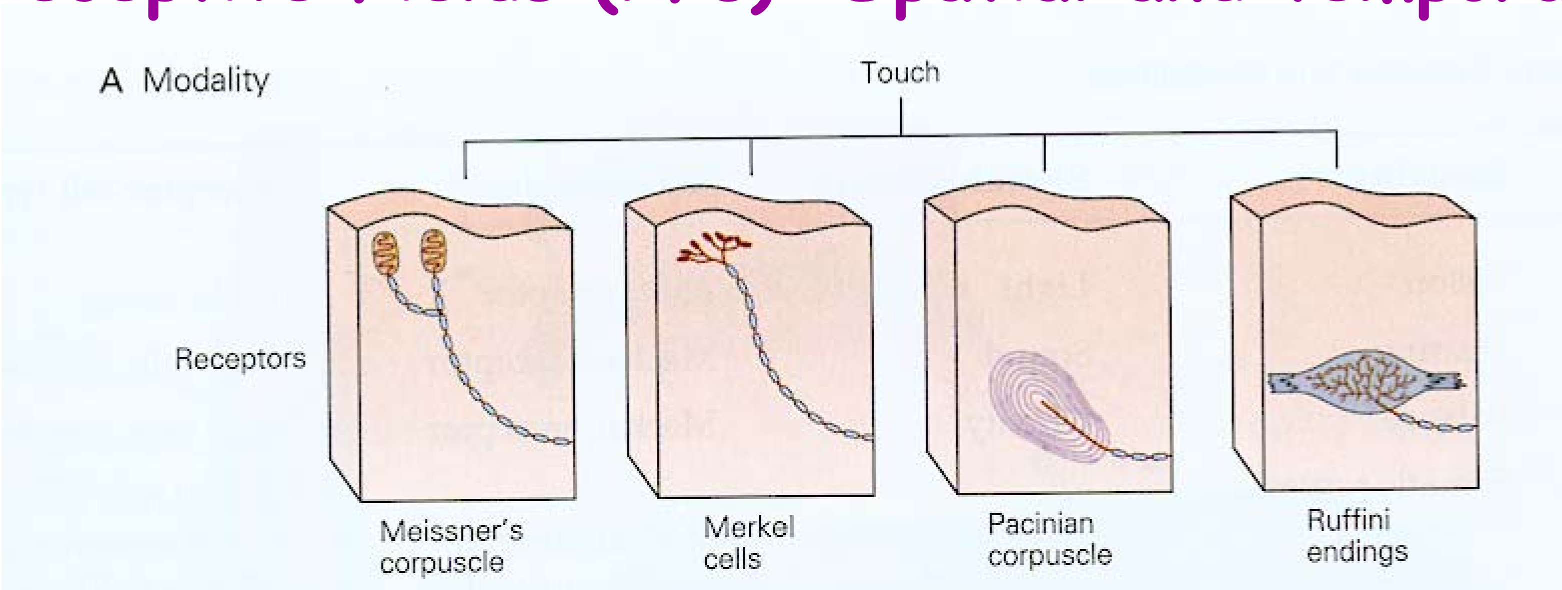
Continuous
or
quantal?

Figure 21-2 Mechanoreceptors are depolarized by stretch of the cell membrane and the depolarization is proportional to the stimulus amplitude.
A. The spindle organ in skeletal muscle mediates limb proprioception. These receptors signal muscle length and the speed at which the

Receptive Fields (RFs):

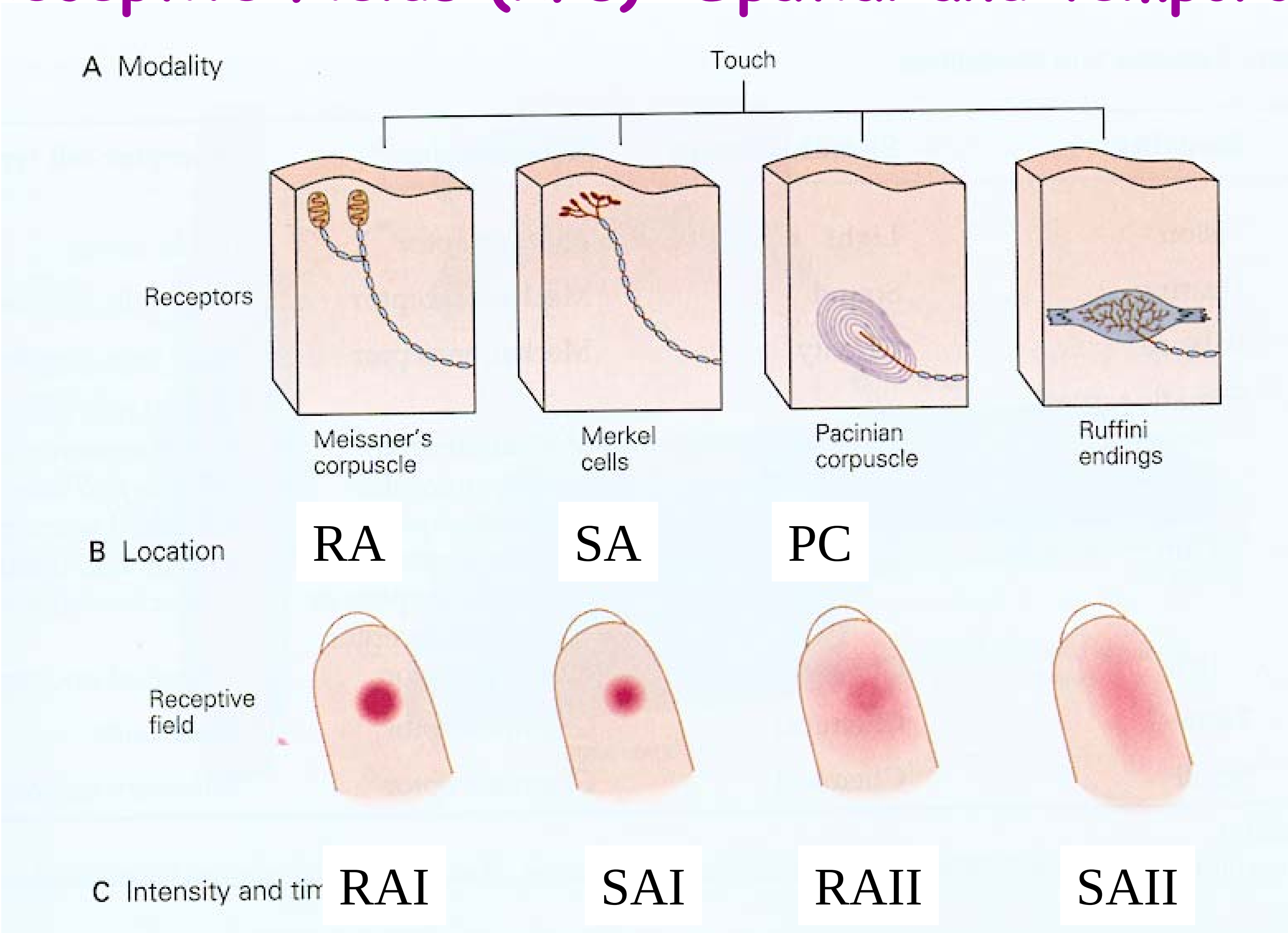
Spatial and temporal

Receptive Fields (RFs): Spatial and temporal



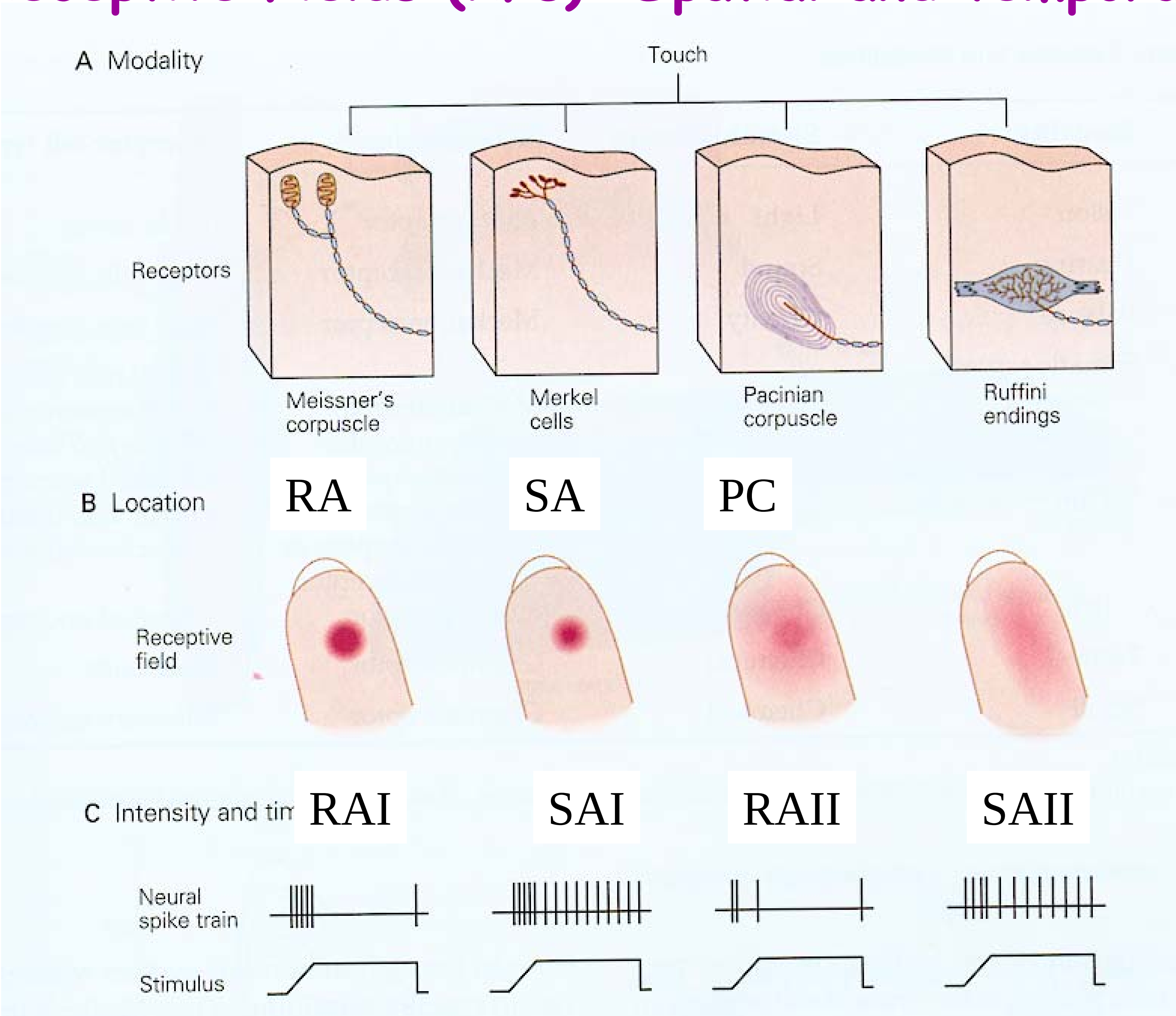
RF size?

Receptive Fields (RFs): Spatial and temporal



Response dynamics?

Receptive Fields (RFs): Spatial and temporal



Cutaneous Mechanoreceptor Channels

Receptive Field Size

Temporal adaptation

Rapidly Adapting (RA1)

These are a ssocaited with Meissner’s corpuscles.

Rapidly Adapting (RA2)

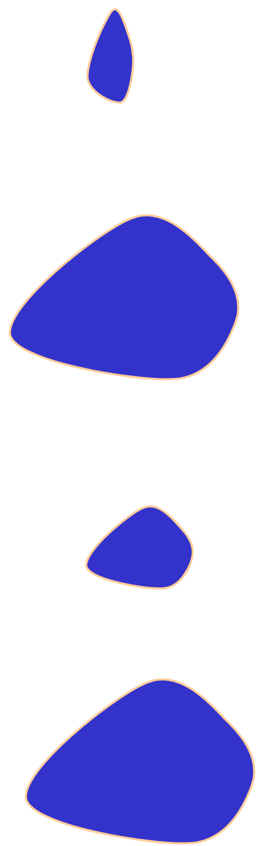
These are also called PC because they are associated with Pacinian corpuscles

Slowly Adapting (SA1)

Associated with Merkels cells

Slowly Adapting (SA2)

Associated with Ruffini’s endings



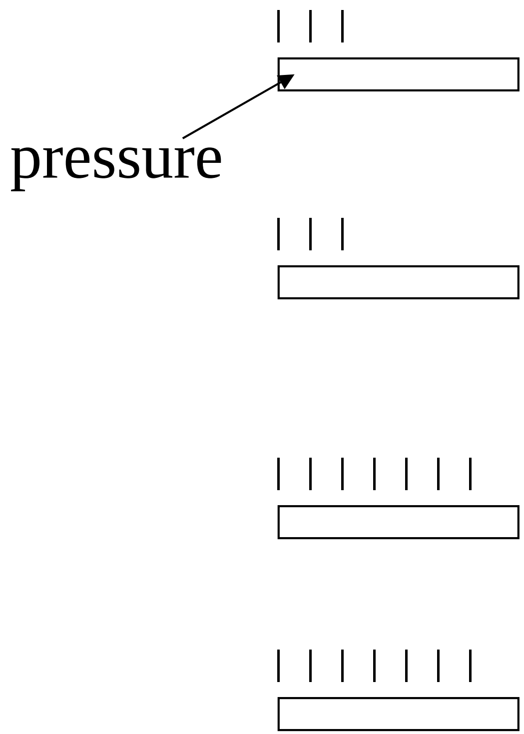


Table 22-1 Receptor Types Active in Somatic Sensation

Receptor type	Fiber groups[1]	Fiber name[1]	Modality
Cutaneous and subcutaneous mechanoreceptors			Touch
Meissner's corpuscle	Aα,β	RA	Stroking, fluttering
Merkel disk receptor	Aα,β	SAI	Pressure, texture
Pacinian corpuscle[2]	Aα,β	PC	Vibration
Ruffini ending	Aα,β	SAII	Skin stretch
Hair-tylotrich, hair-guard	Aα,β	G1, G2	Stroking, fluttering
Hair-down	Aδ	D	Light stroking
Field	Aα,β	F	Skin stretch
Thermal receptors			Temperature
Cool receptors	Aδ	III	Skin cooling (25°C)
Warm receptors	C	IV	Skin warming (41°C)
Heat nociceptors	Aδ	III	Hot temperatures (>45°C)
Cold nociceptors	C	IV	Cold temperatures (<5°C)
Nociceptors			Pain
Mechanical	Aδ	III	Sharp, pricking pain
Thermal-mechanical	Aδ	III	Burning pain
Thermal-mechanical	C	IV	Freezing pain
Polymodal	C	IV	Slow, burning pain
Muscle and skeletal mechanoreceptors			Limb proprioception
Muscle spindle primary	Aα	Ia	Muscle length and speed
Muscle spindle secondary	Aβ	II	Muscle stretch
Golgi tendon organ	Aα	Ib	Muscle contraction
Joint capsule mechanoreceptors	Aβ	II	Joint angle
Stretch-sensitive free endings	Aδ	III	Excess stretch or force

[1] See Table 22-2. [2] Pacinian corpuscles are also located in the mesentery, between layers of muscle, and on interosseous membranes.

Receptor density

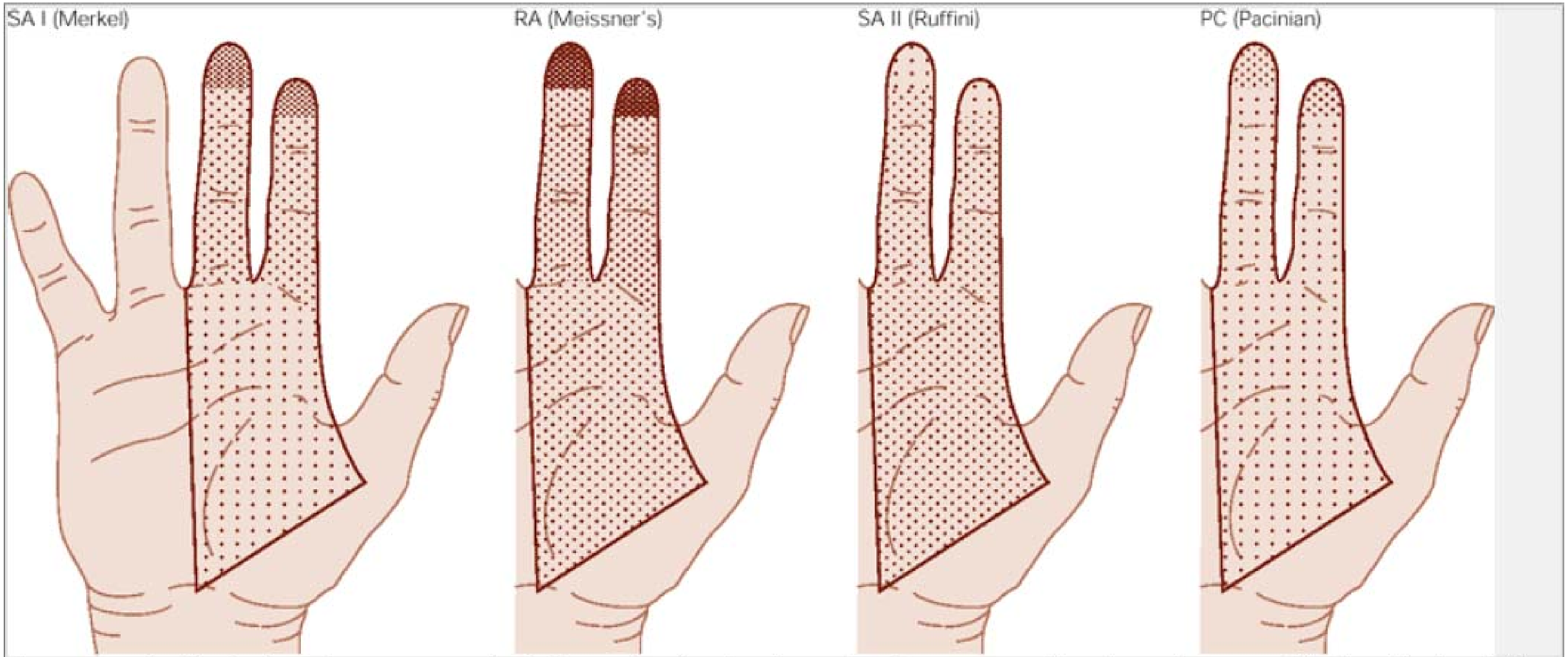
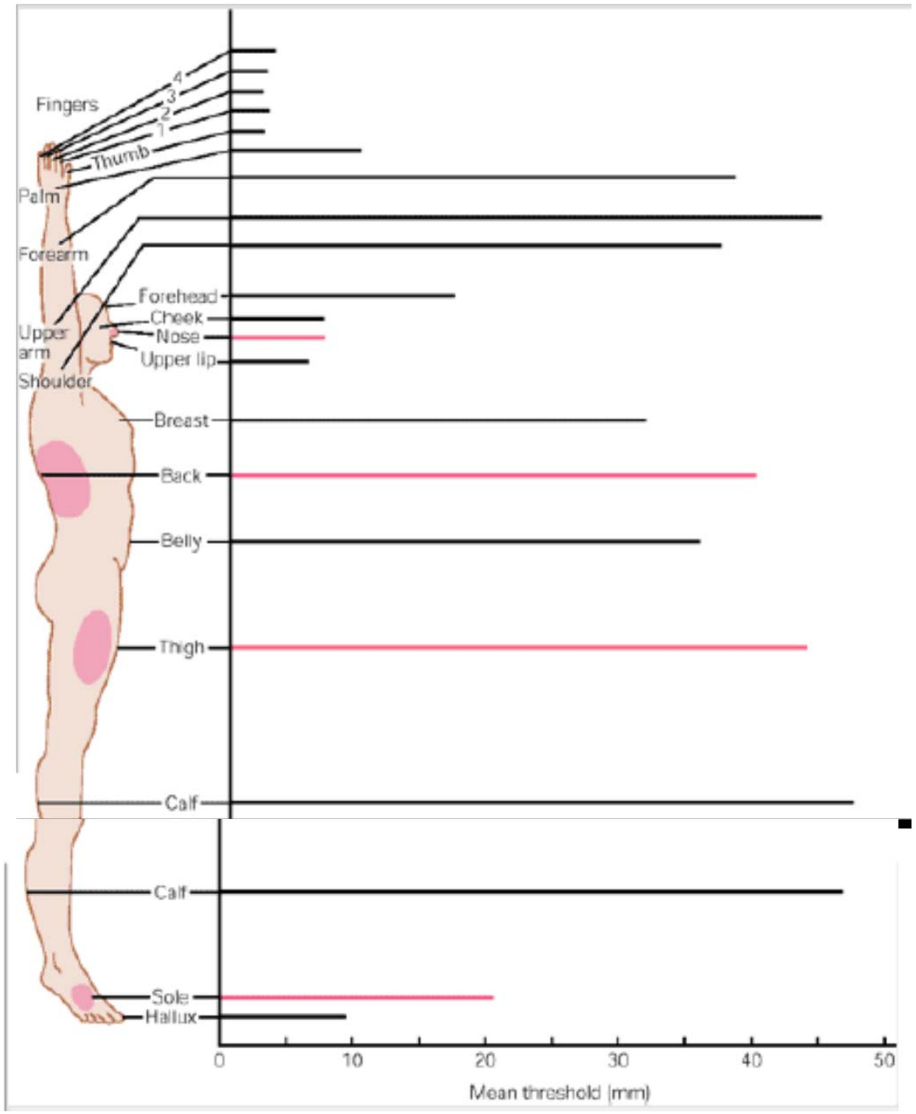


Figure 22-4 The distribution of receptor types in the human hand varies. The number of sensory nerve fibers innervating an area is indicated by the stippling density, with the highest density of receptors shown by the heaviest stippling. (**RA** = 5 rapidly adapting, **SA** = 5 slowly adapting.) Meissner's corpuscles (RA) and Merkel disk receptors (SA I) are the most numerous receptors; they are distributed preferentially on the distal half of the fingertip. Pacinian corpuscles (PC) and Ruffini endings (SA II) are much less common; they are distributed more uniformly on the hand, showing little differentiation of the distal and proximal regions. The fingertips are the most densely innervated region of skin in the human body, receiving approximately 300 mechanoreceptive nerve fibers per square centimeter. The number of mechanoreceptive fibers is reduced to $120/cm^2$ in the proximal phalanges, and to $50/cm^2$ in the palm. (Adapted from Vallbo and Johansson 1978.)

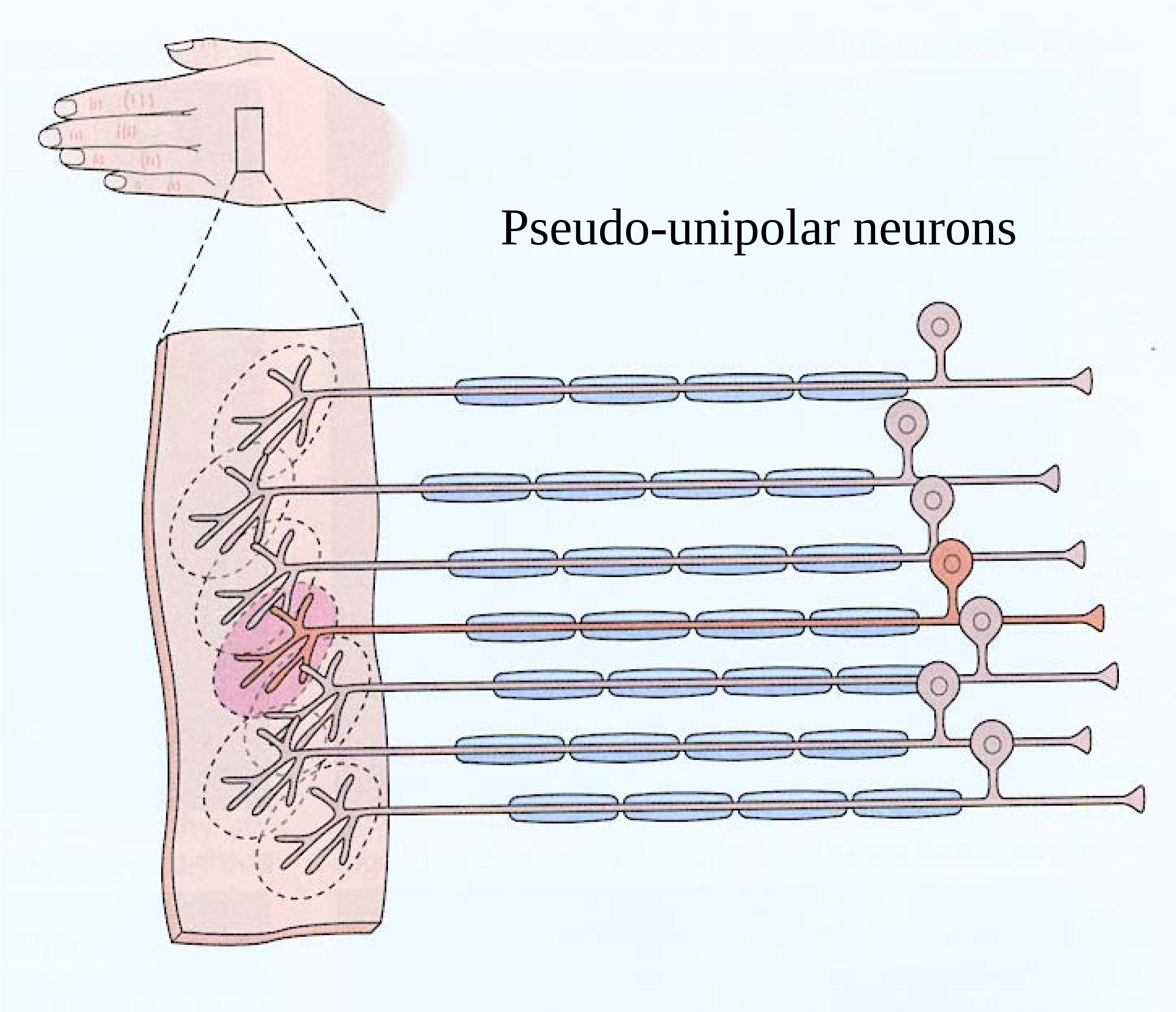
Neurometric – psychometric matching

Spatial resolution

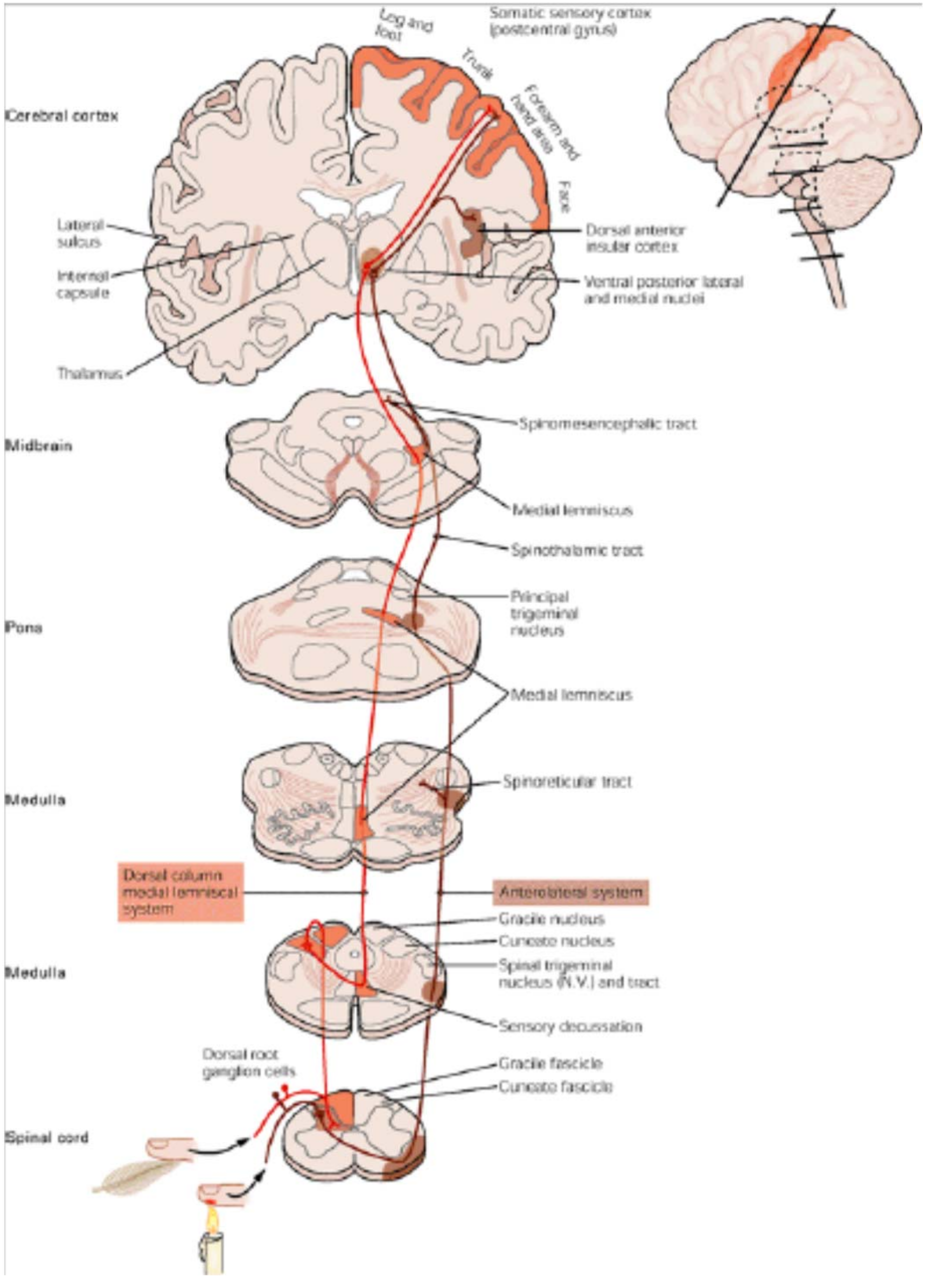


Signal conduction

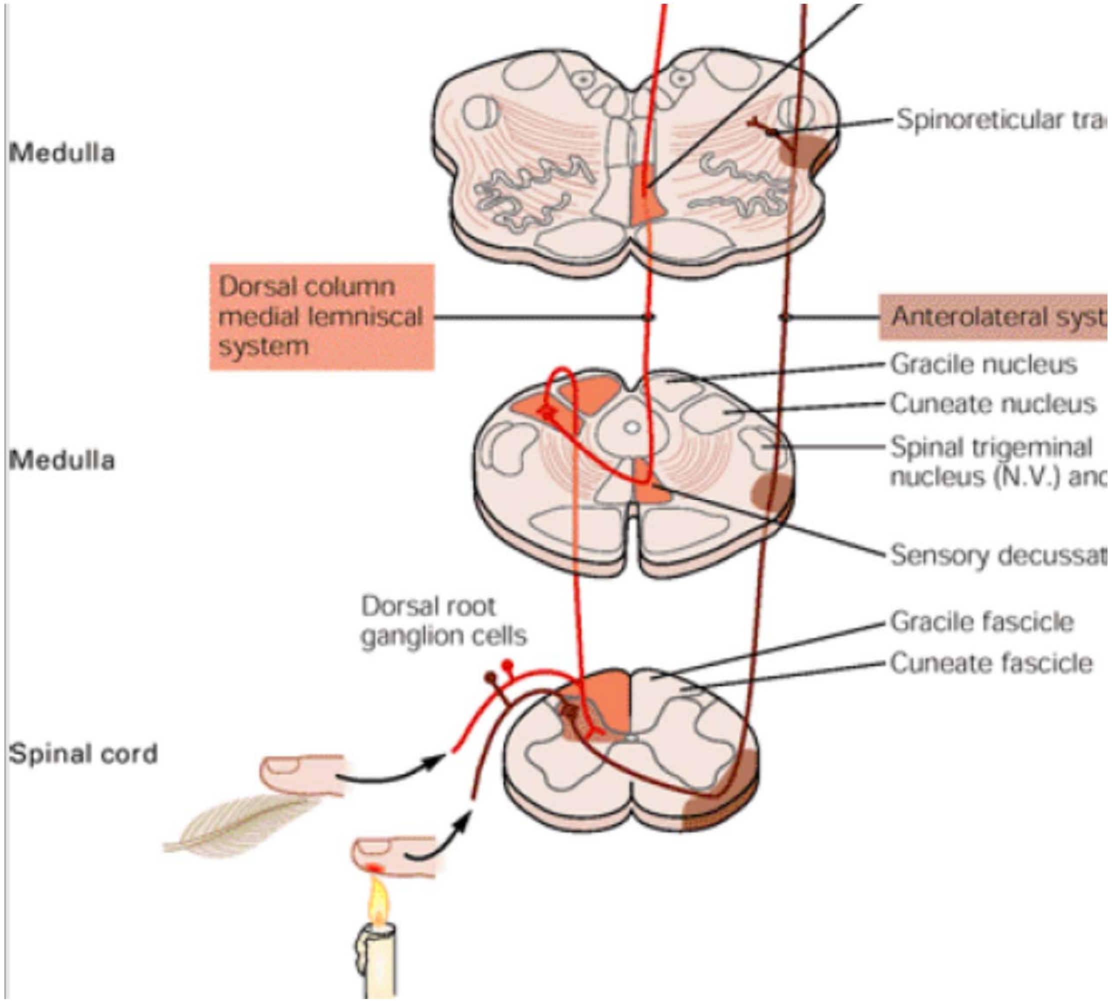
Sensory signal conduction



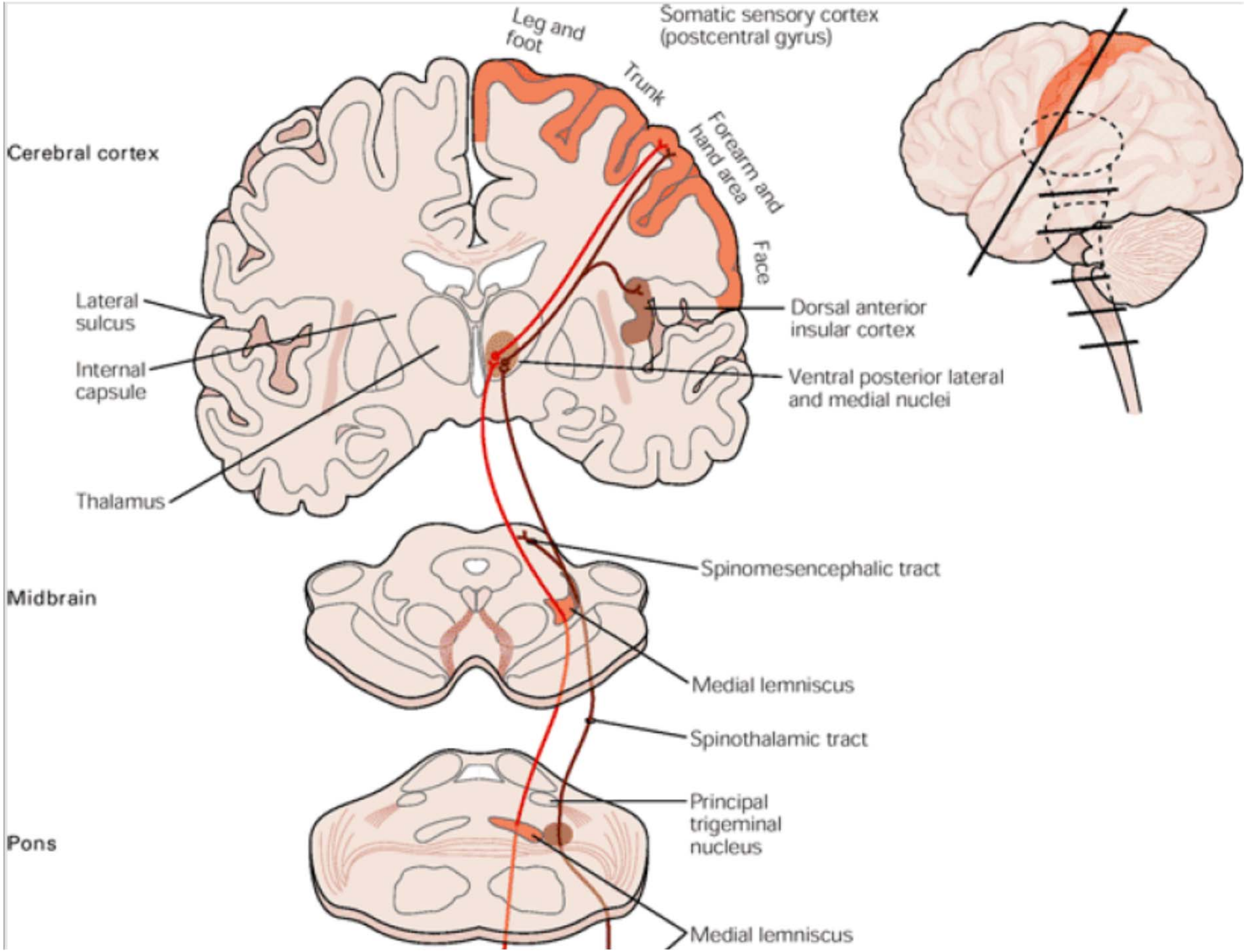
Sensory signal conduction



Sensory signal conduction



Sensory signal conduction



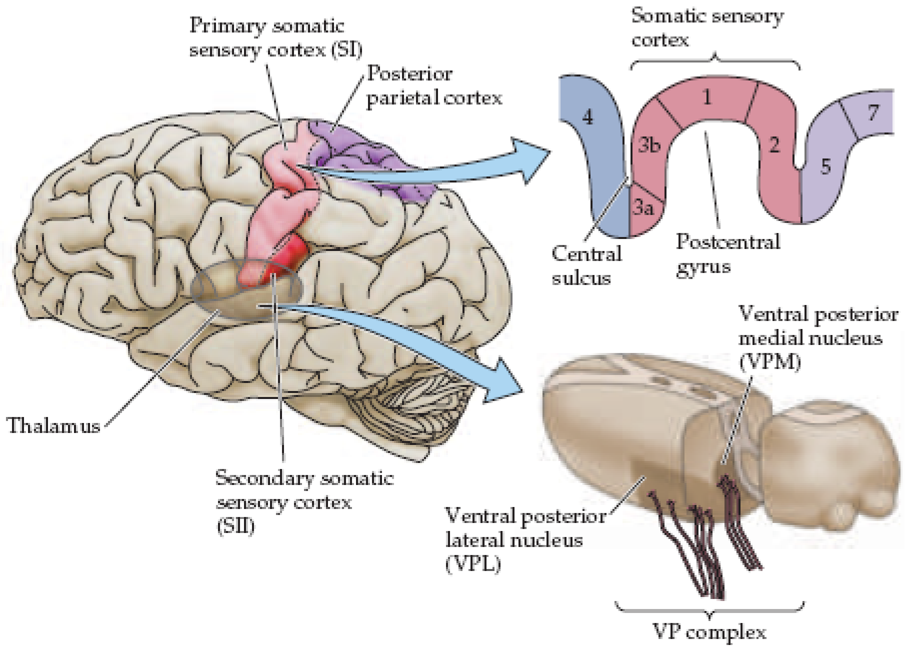
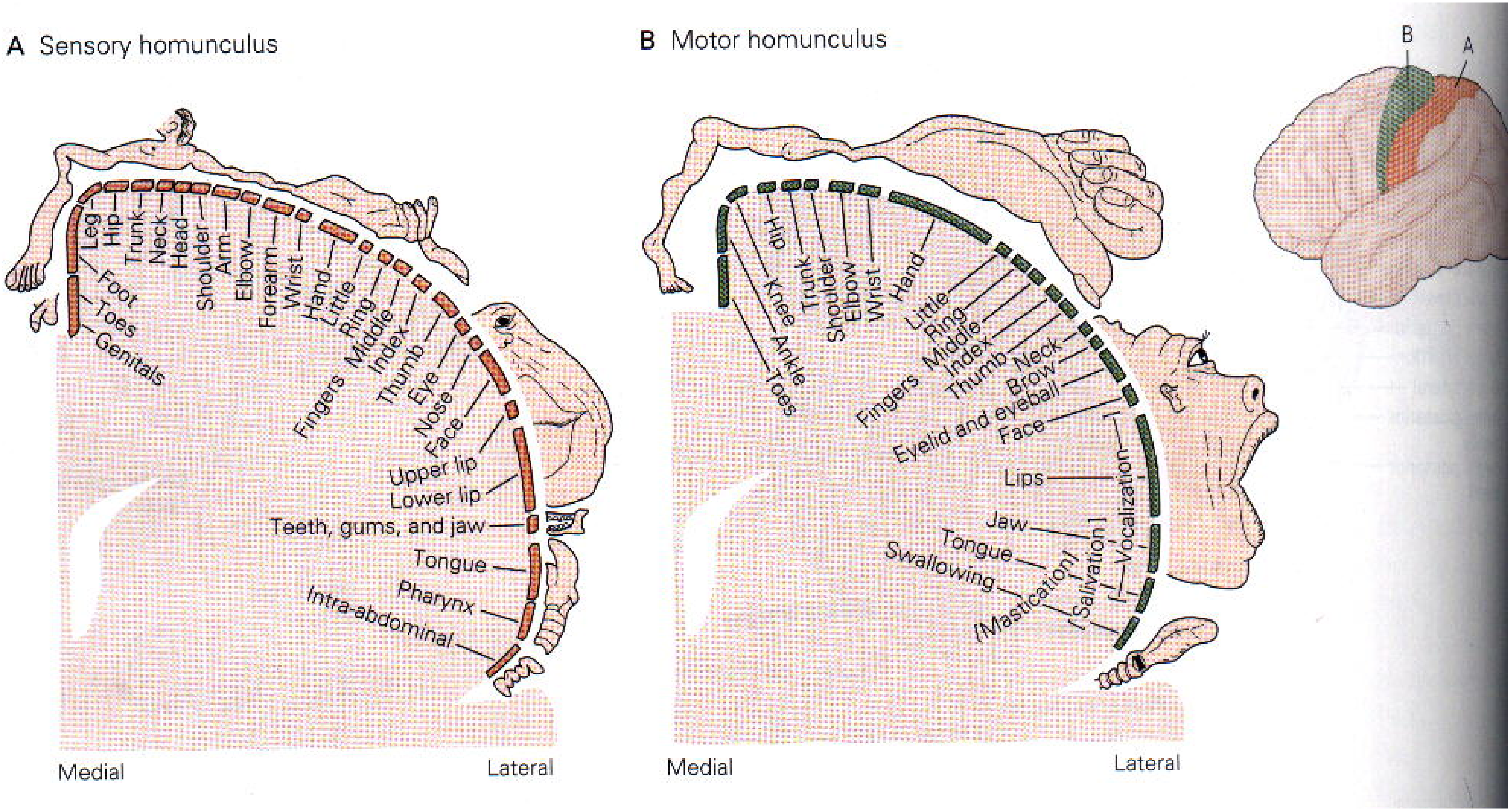


Figure 8.7 Diagram of the somatic sensory portions of the thalamus and their cortical targets in the postcentral gyrus. The ventral posterior nuclear complex comprises the VPM, which relays somatic sensory information carried by the trigeminal system from the face, and the VPL, which relays somatic sensory information from the rest of the body. Inset above shows organization of the primary somatosensory cortex in the postcentral gyrus, shown here in a section cutting across the gyrus from anterior to posterior. (After Brodal, 1992, and Jones et al., 1982.)

The Homunculi



The Homunculi

Relative size reflects innervation density

phylogenetically

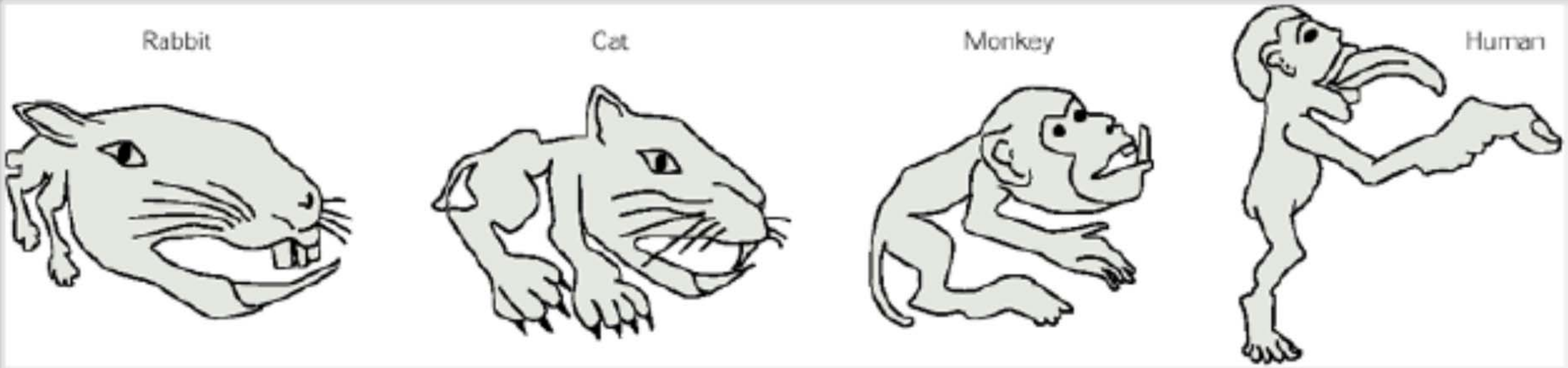


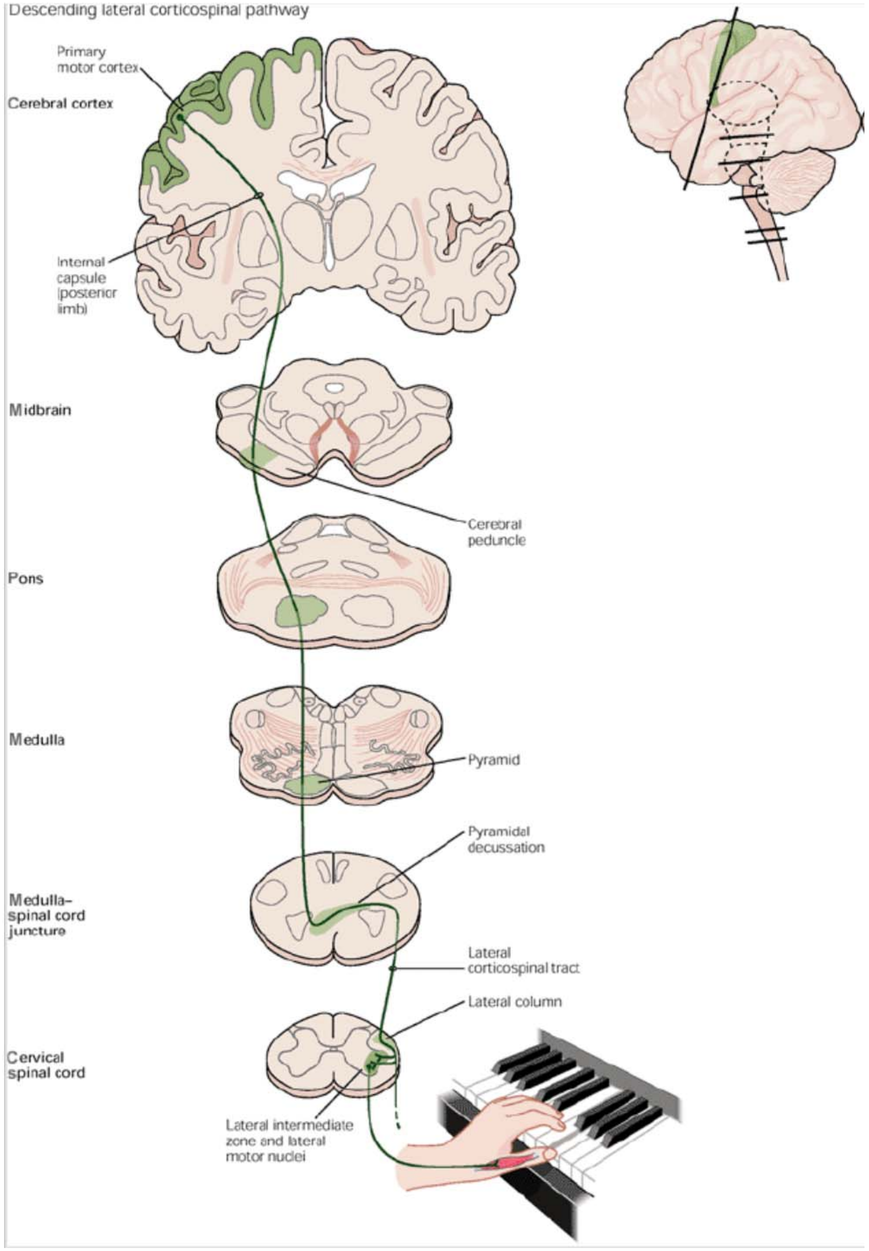
Figure 20-5 Different species rely on different parts of the body for adaptive somatosensory information. These drawings show the relative importance of body regions in the somatic sensibilities of four species, based on studies of evoked potentials in the thalamus and cortex.

The Homunculi

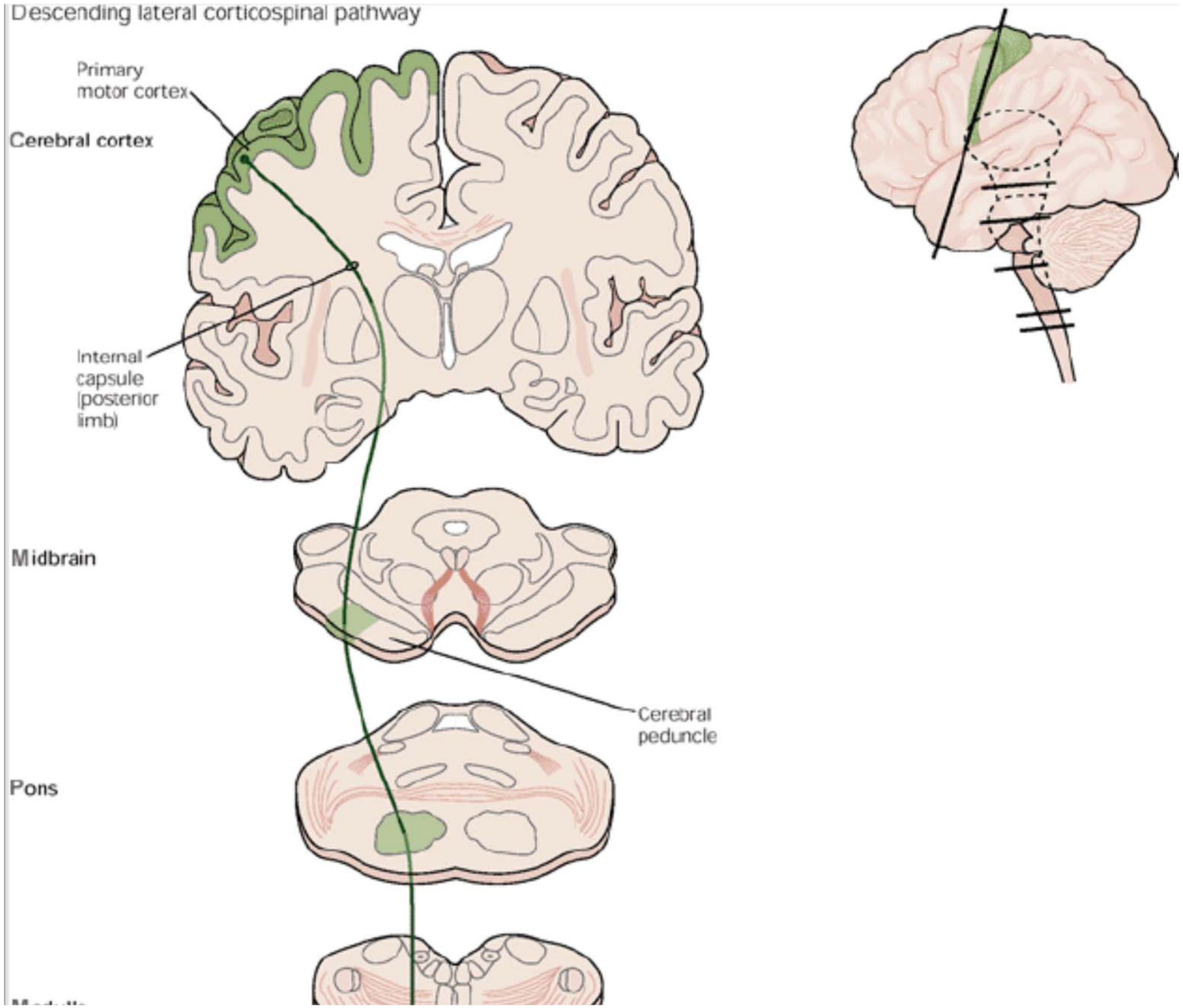
Relative size reflects innervation density

ontogenetically

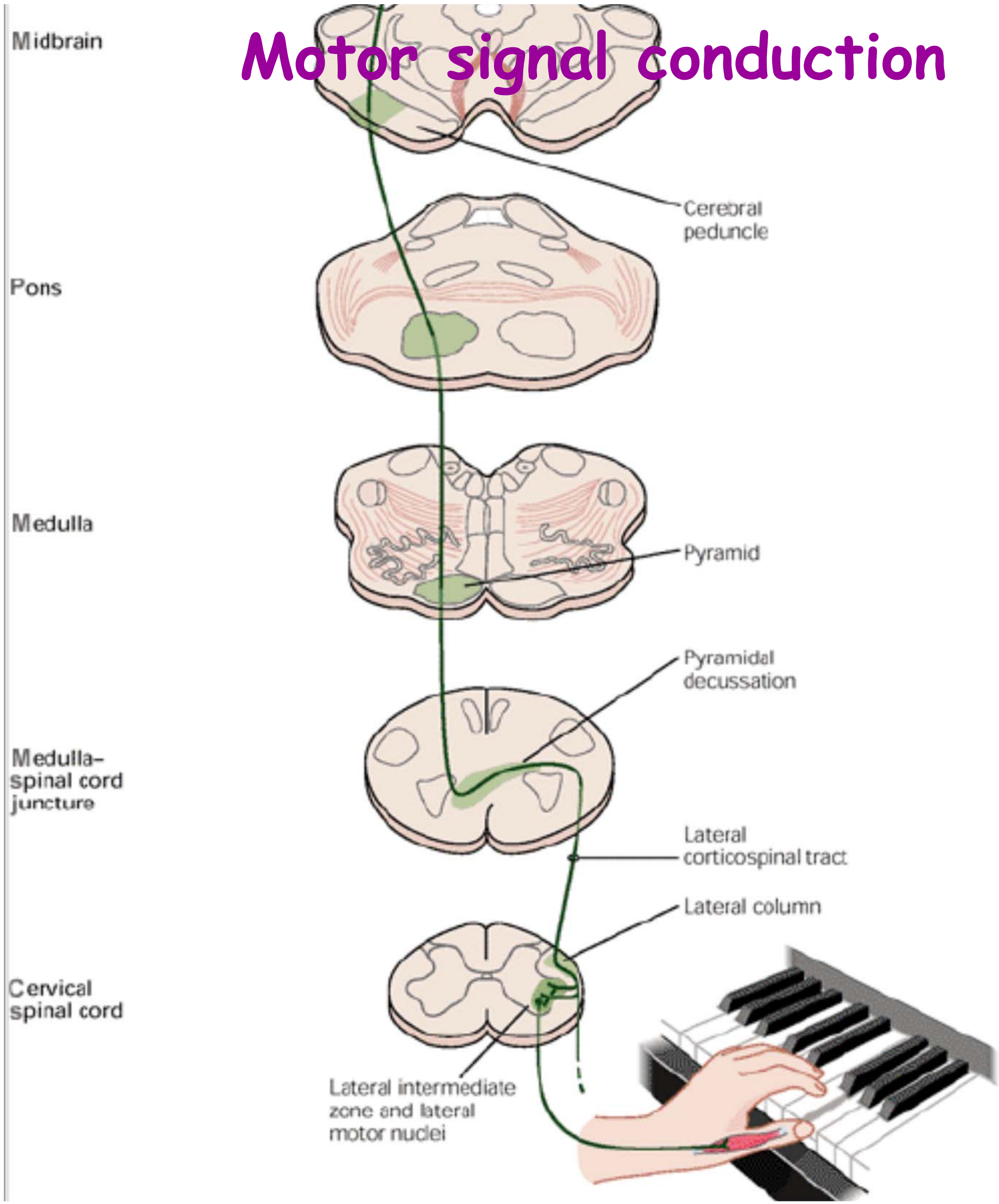
Motor signal conduction



Motor signal conduction



Motor signal conduction



The Homunculi

Accurate spatial organization

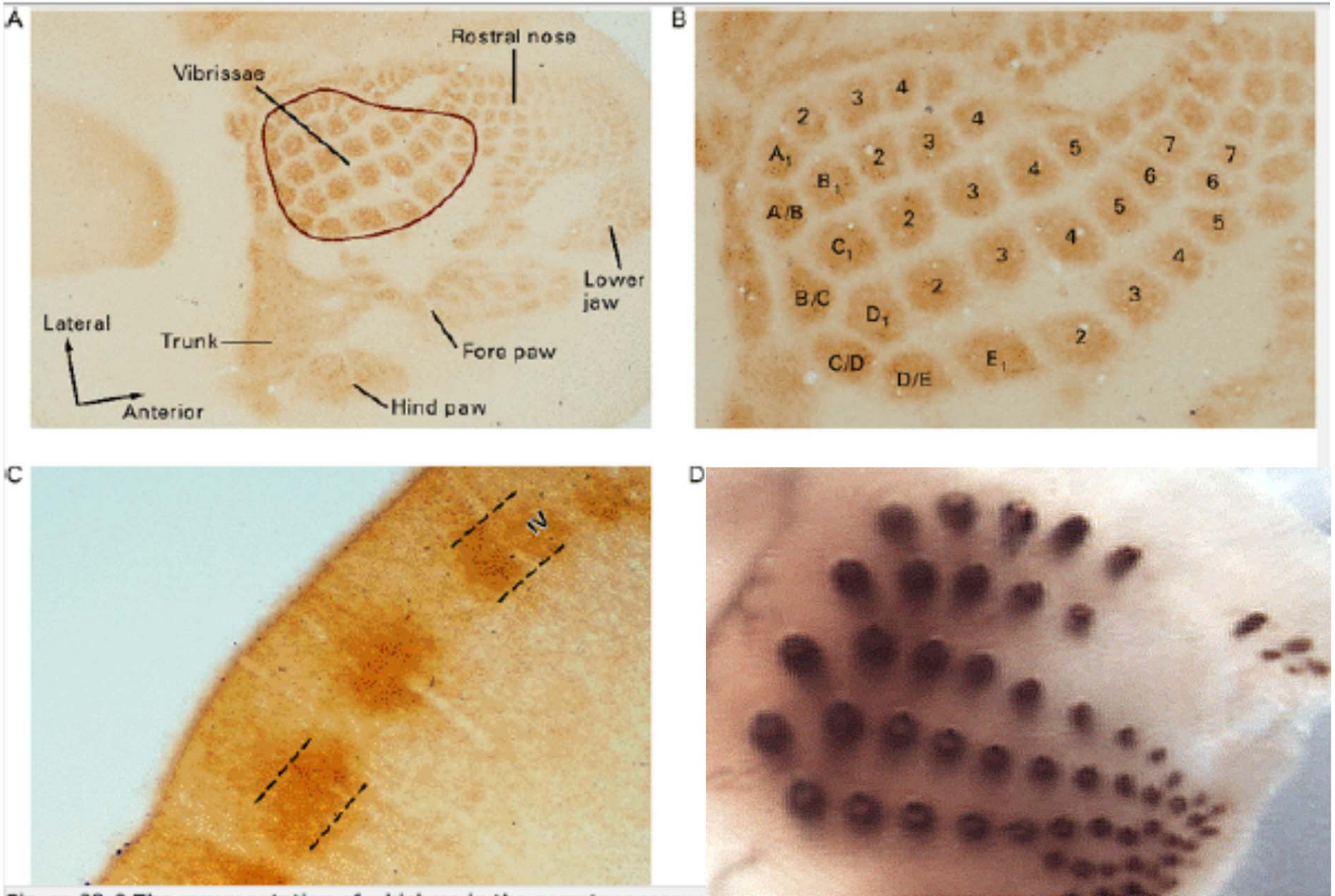
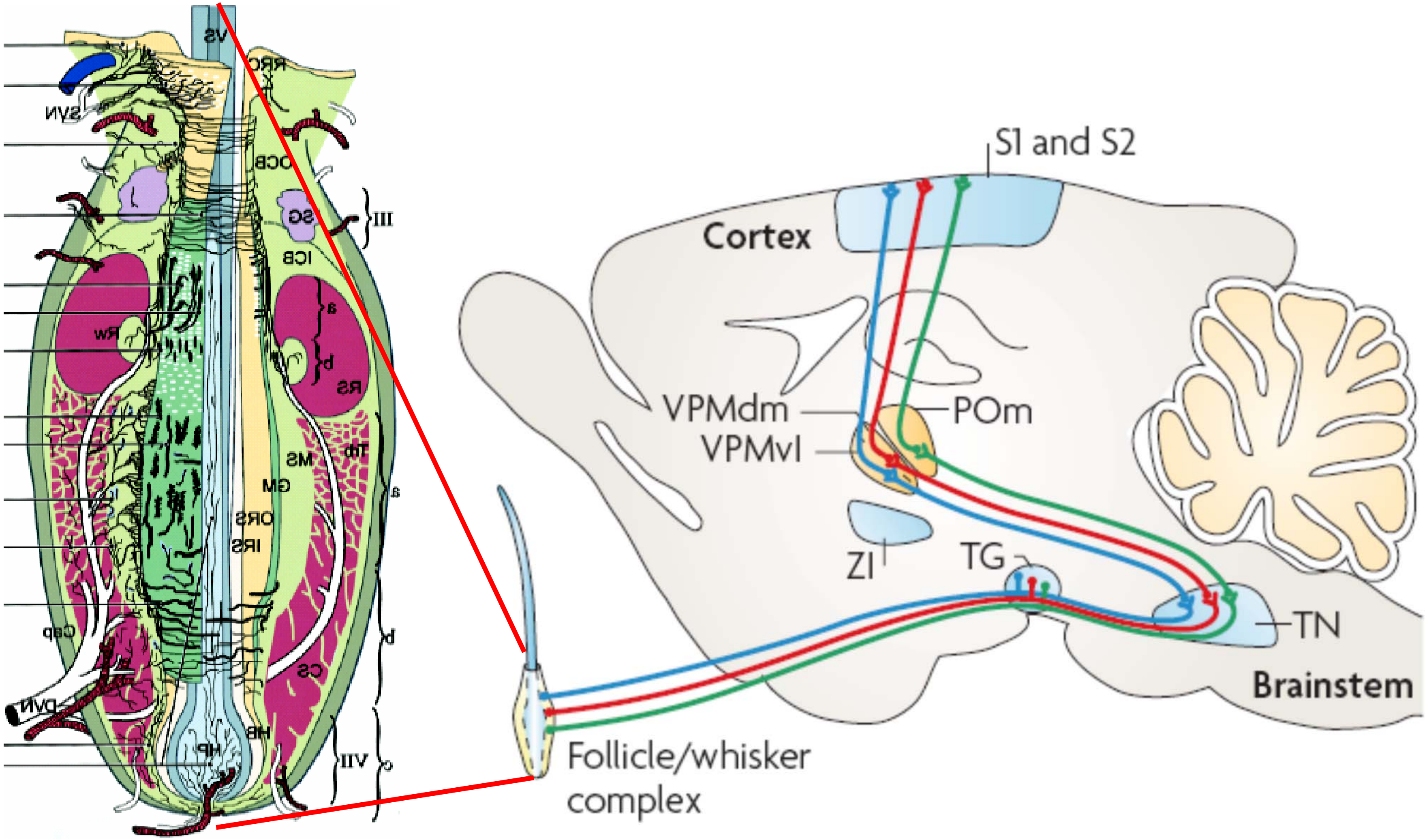


Figure 23-9 The representation of whiskers in the somatosensory cortex of the rat. (Adapted from Bennett-Clarke et al. 1997).

Sensory signal conduction

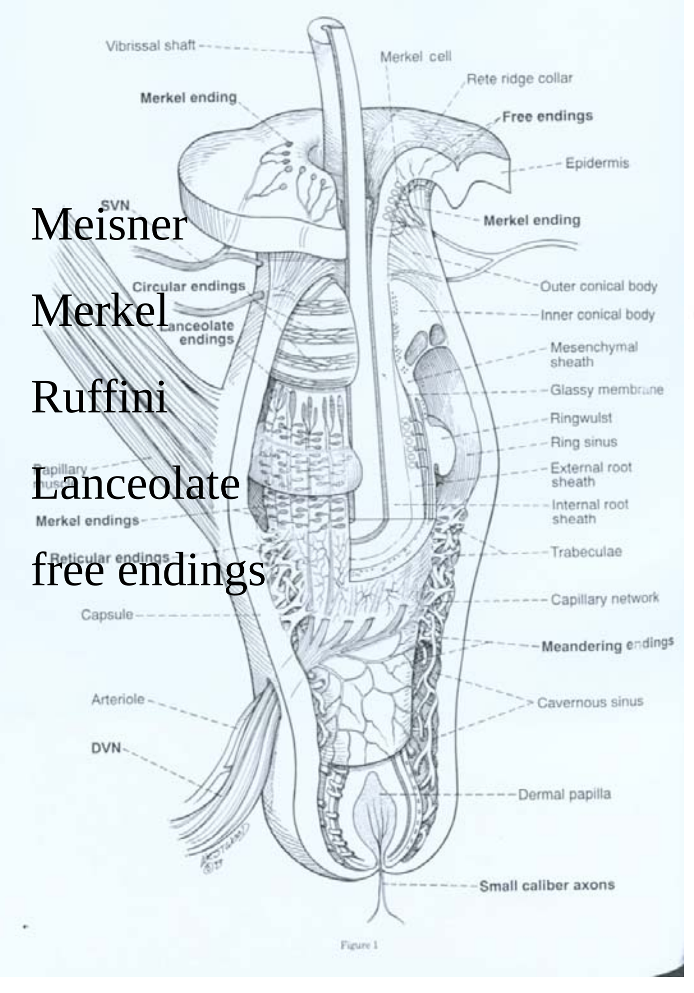
The vibrissal system

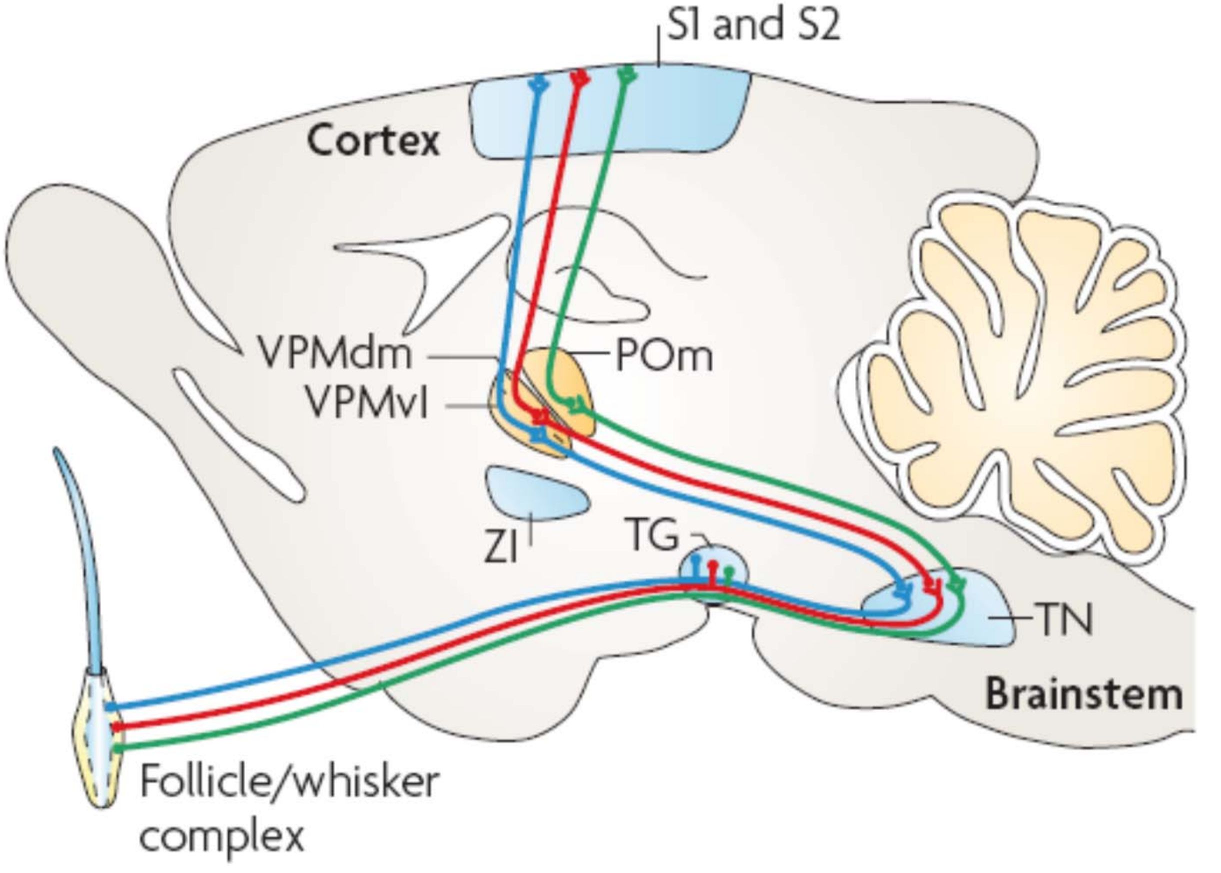


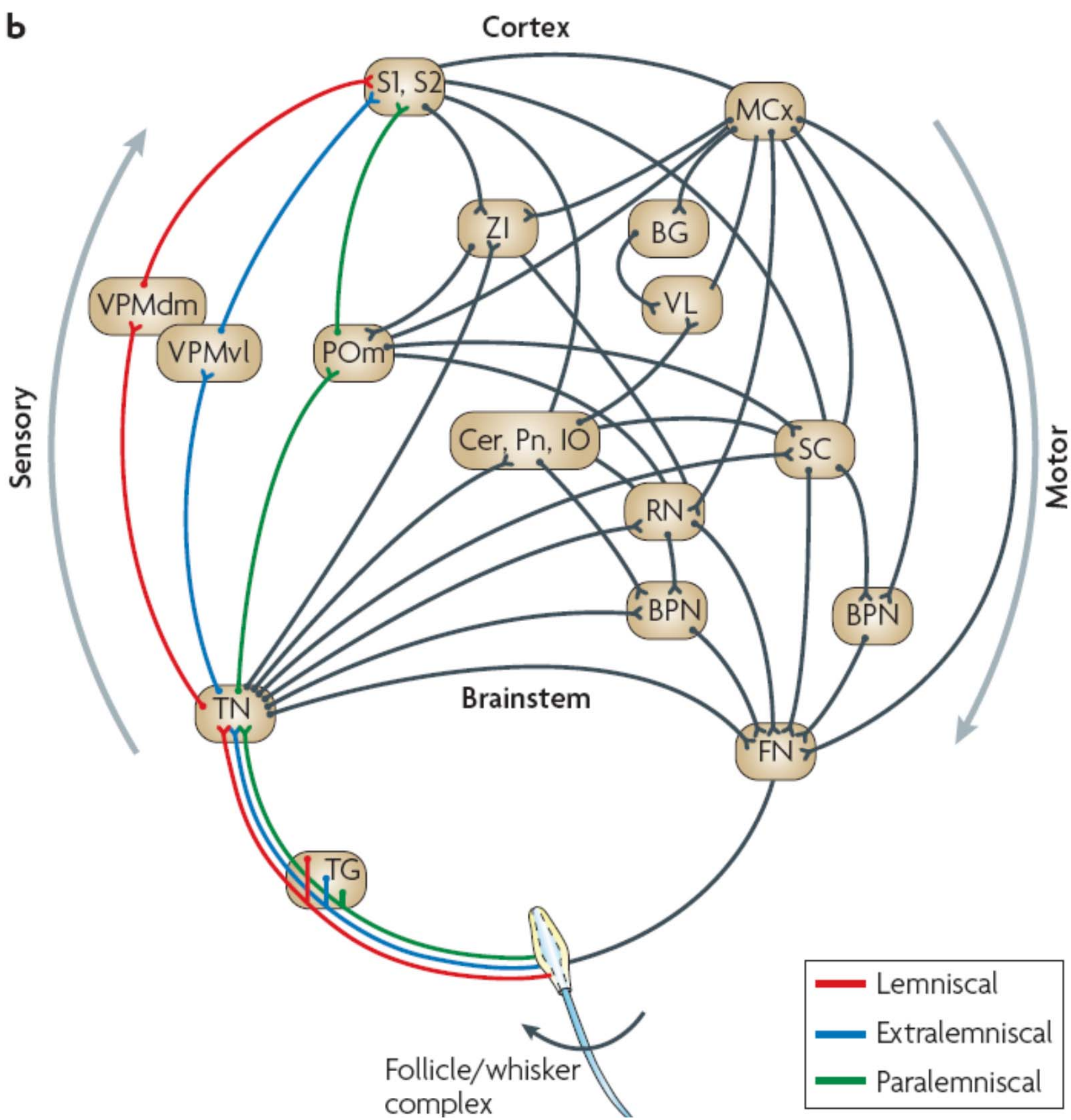
Sensory signal conduction

The vibrissal system

whisker

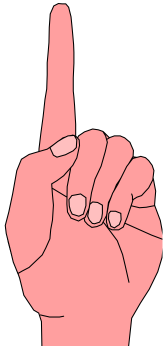


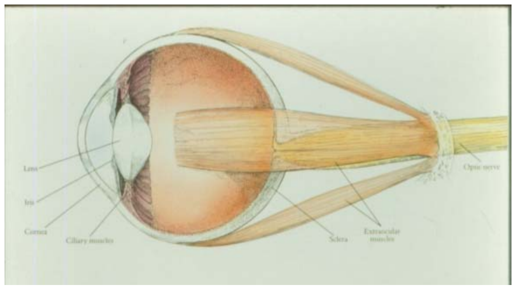


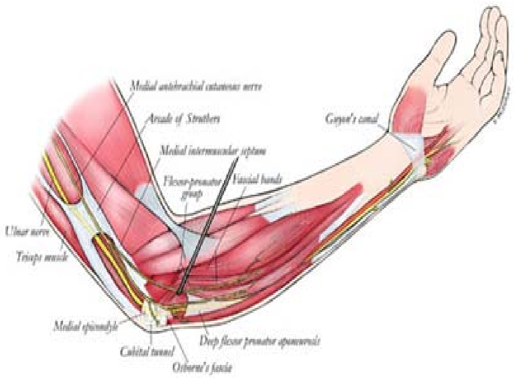

b
Cortex
S1, S2
MCx
ZI
BG
VL
VPMdm
VPMvl
POm
Cer, Pn, IO
SC
RN
BPN
BPN
TN
FN
TG
Sensory
Motor
Brainstem
Follicle/whisker complex
Lemniscal
Extralemniscal
Paralemniscal

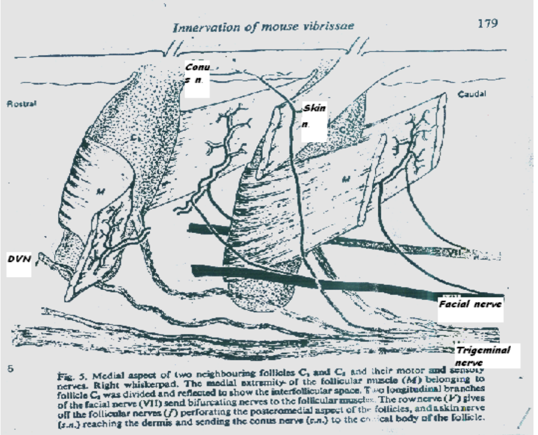
Common mechanisms of sensory processing

Rich muscular system



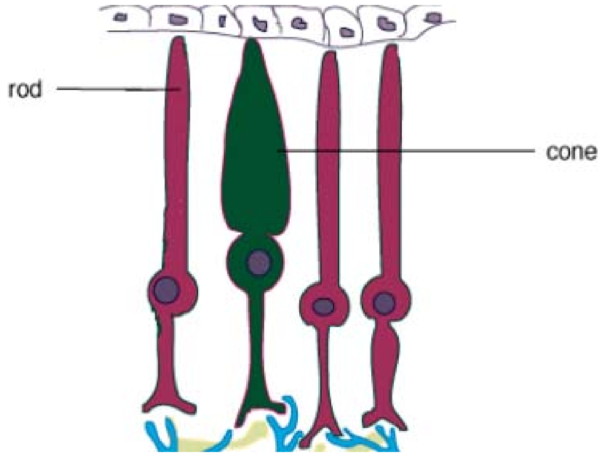






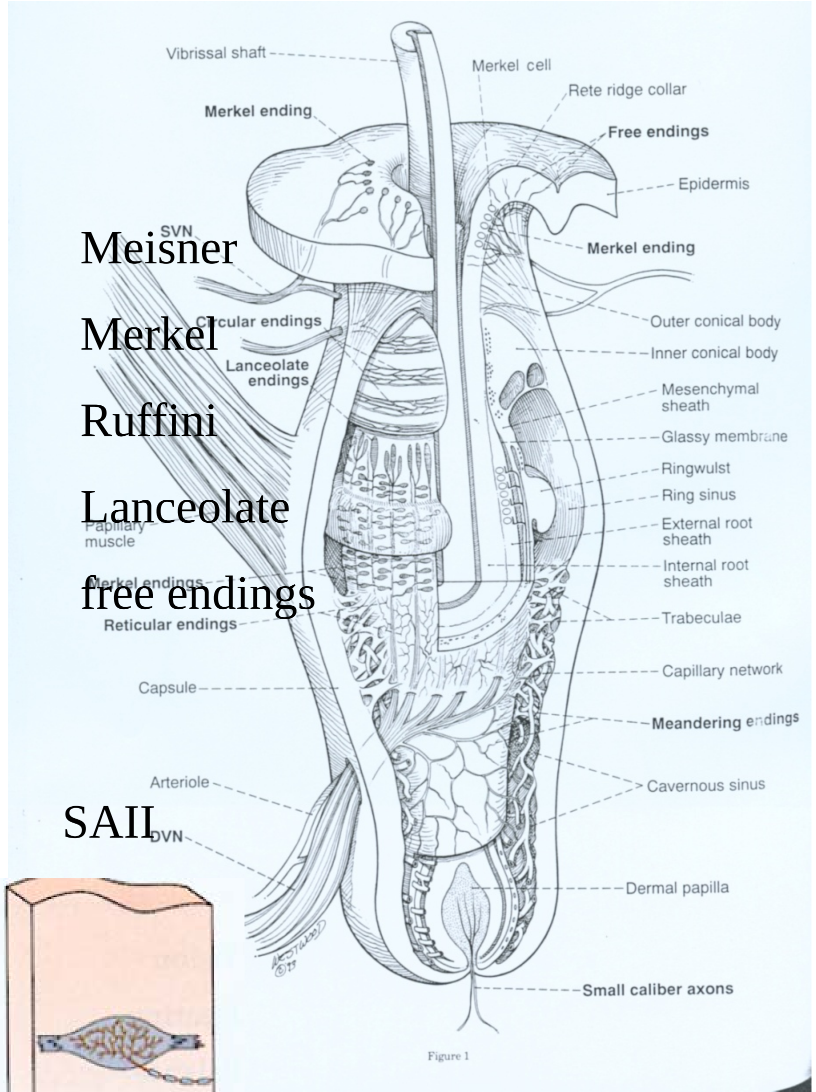
Receptor types

eye



R G B

whisker



Meisner

Merkel

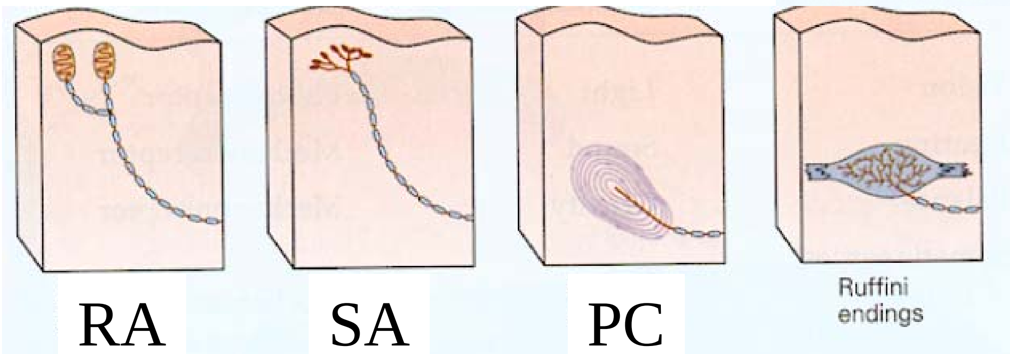
Ruffini

Lanceolate

free endings

finger

RAI SAI RAII SAII

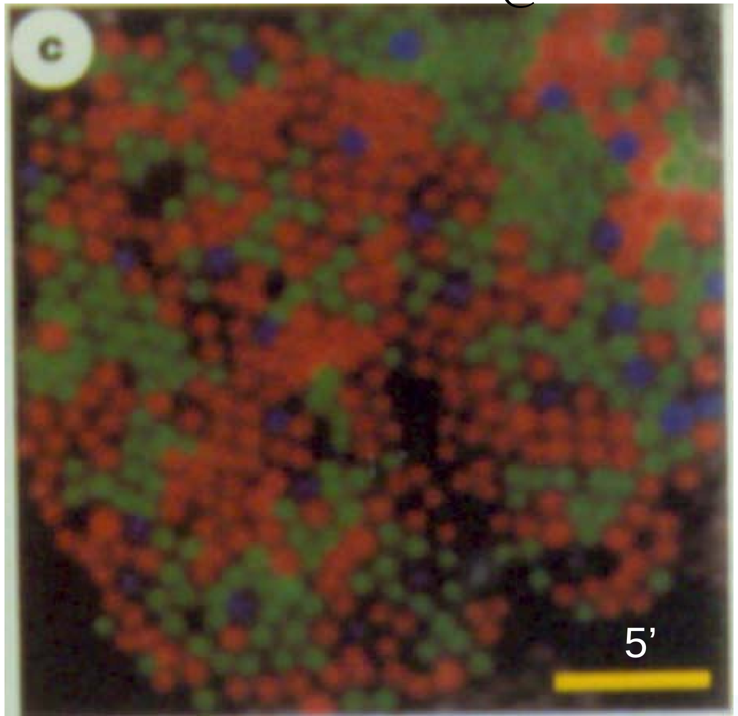


RA SA PC

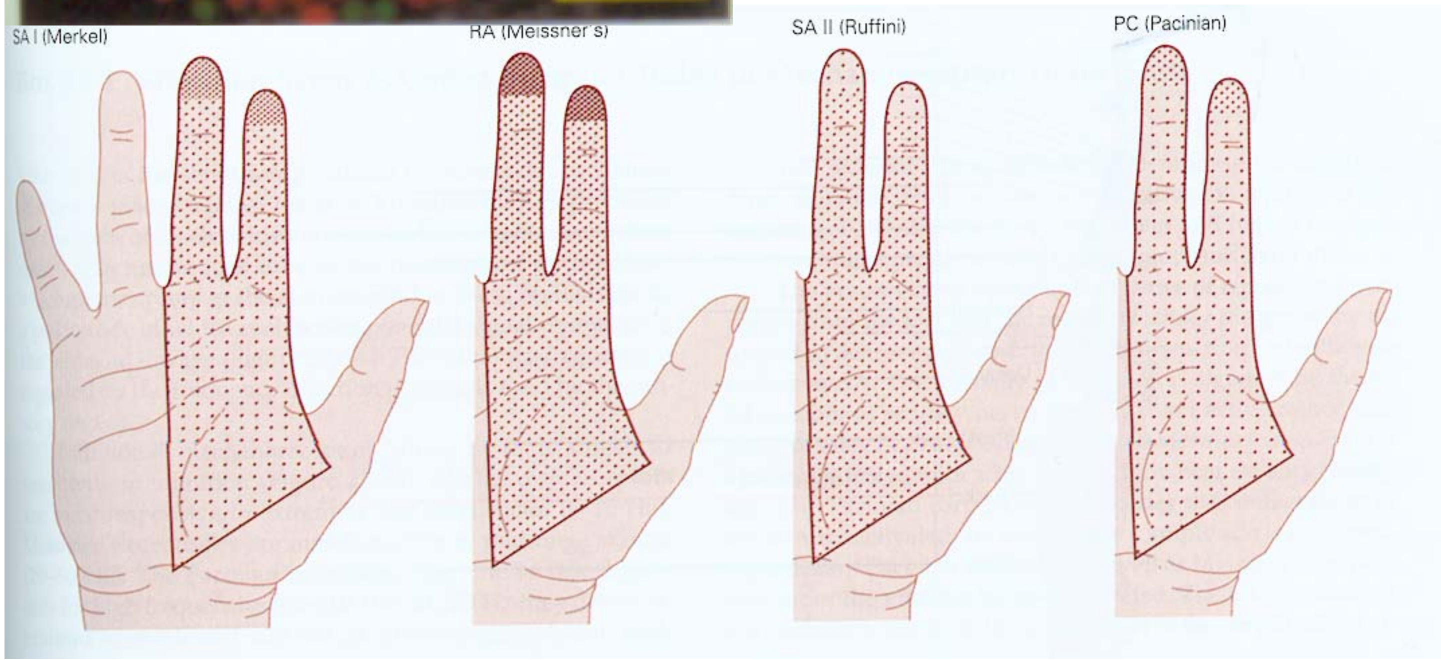
Receptors mix in clusters

eye

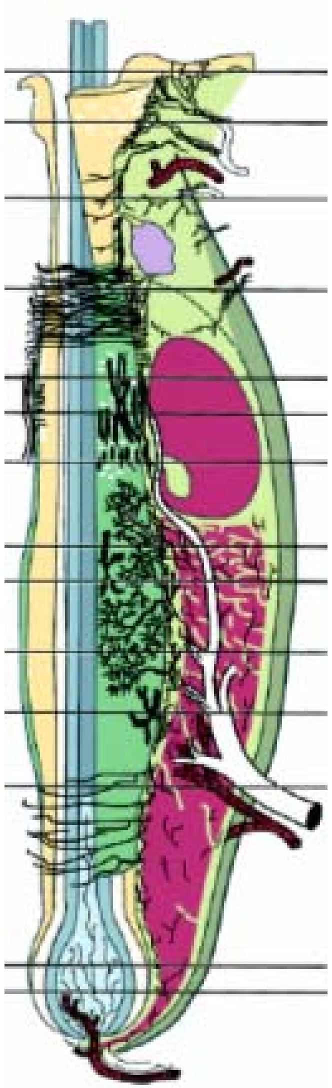
@ 1°



finger



whisker



Receptor convergence / divergence

Human eye: 5M cones (+ 120M rods) --> 1M fibers

Human skin: 2,500 receptors/cm^2 --> 300 fibers / cm^2

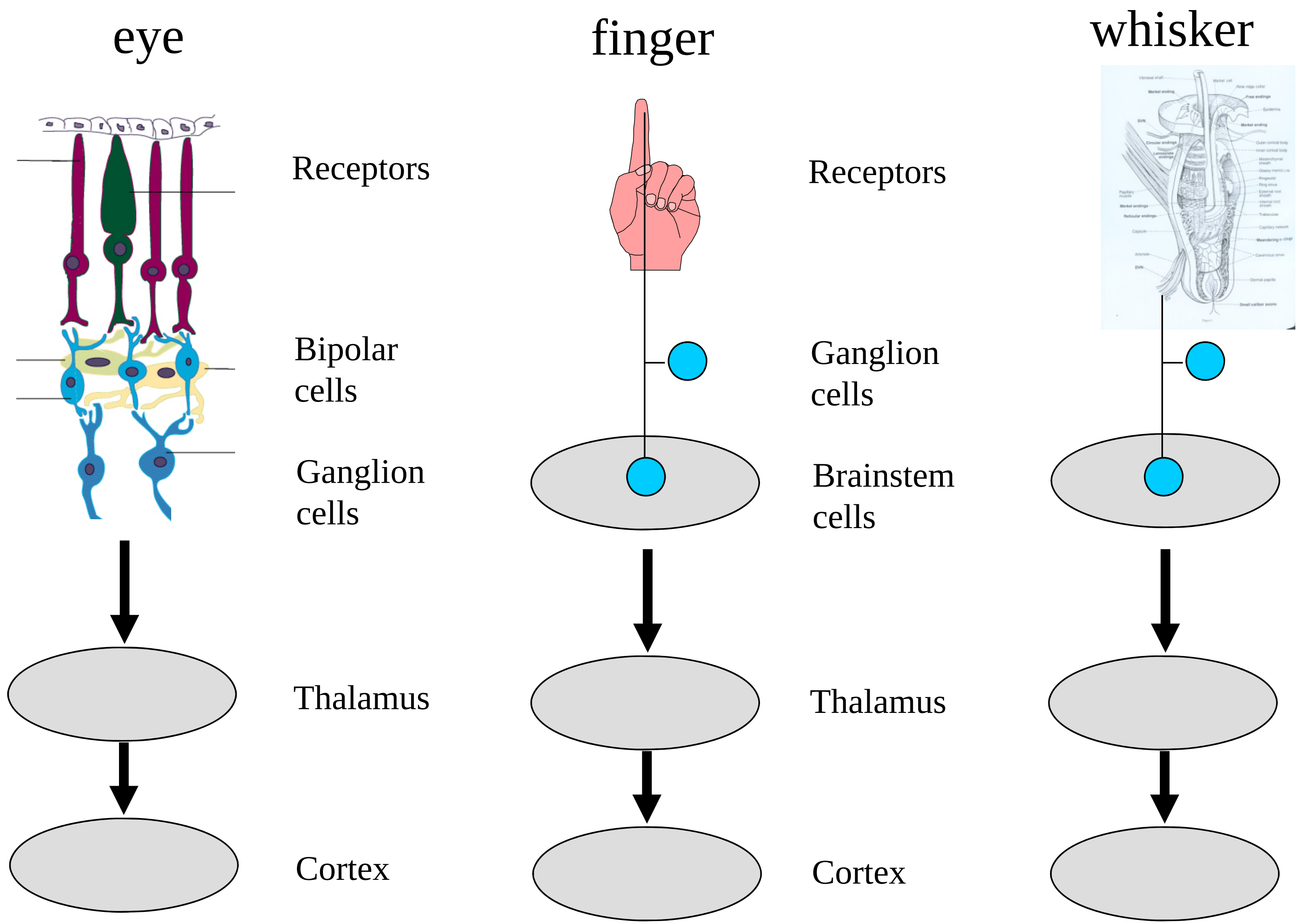
Rat whisker: 2,000 receptors --> 300 fibers

~ 10 -> 1 convergence

Human ear: 3,000 hair cells --> 30,000 fibers

~ 1 -> 10 divergence

Processing stations



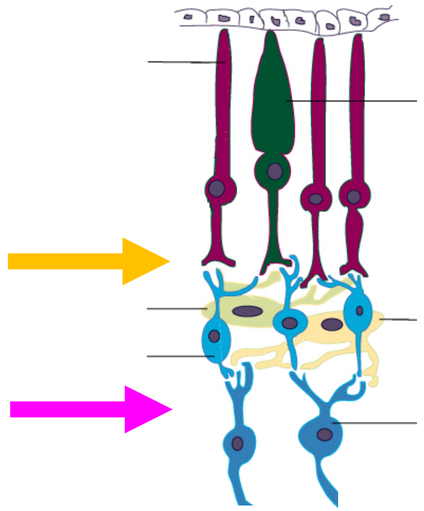
Spatial processing (by Lateral inhibition)

eye

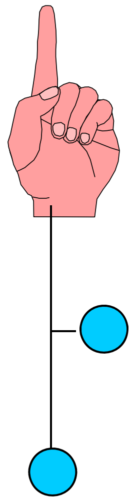
finger

?

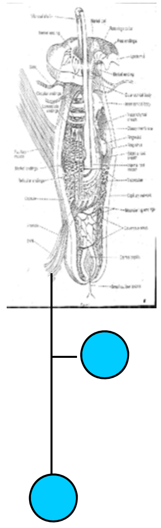
whisker



Receptors



Receptors

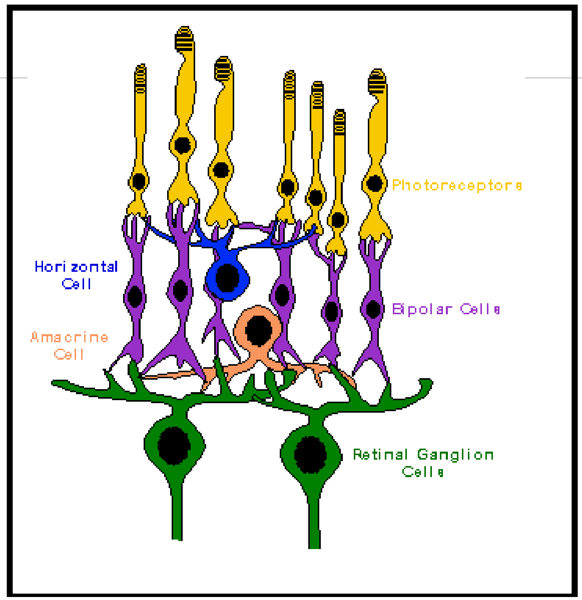


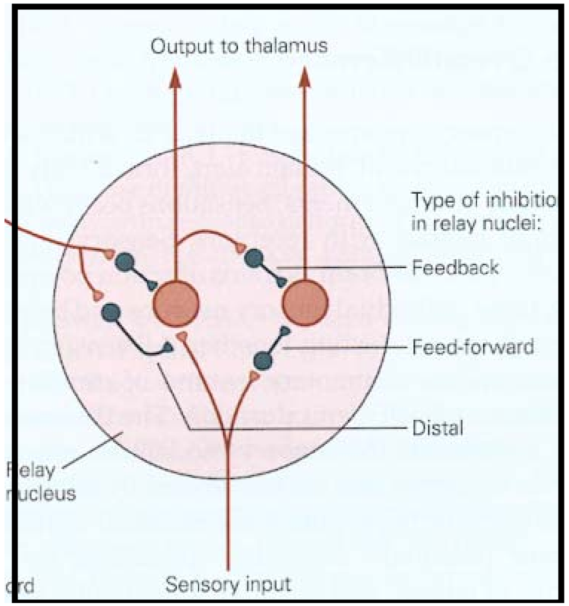
Bipolar cells

Ganglion cells

Ganglion cells

Brainstem cells





Efficient coding

(by only coding changes)

Changes in time:

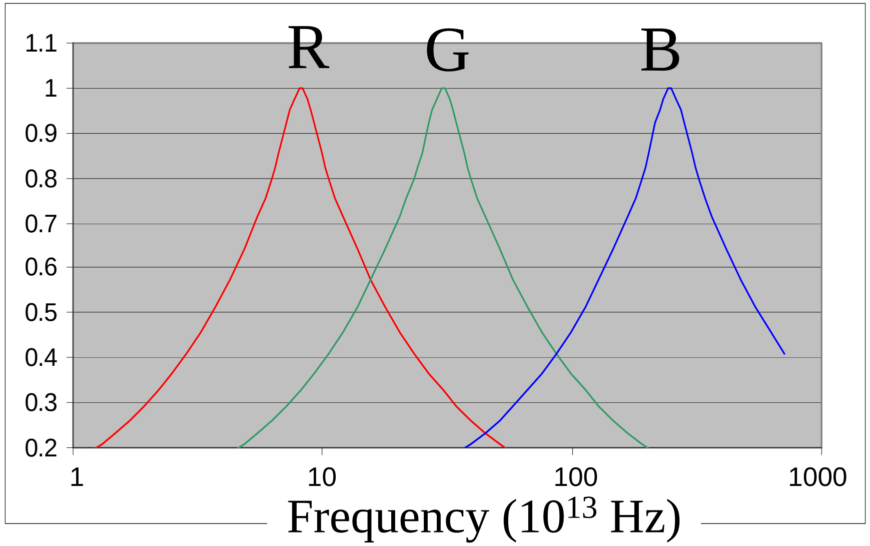
- Intrinsic in individual neurons
- Starting at the receptor level

Changes in space:

- Circuits of neurons
- Starting after lateral inhibition

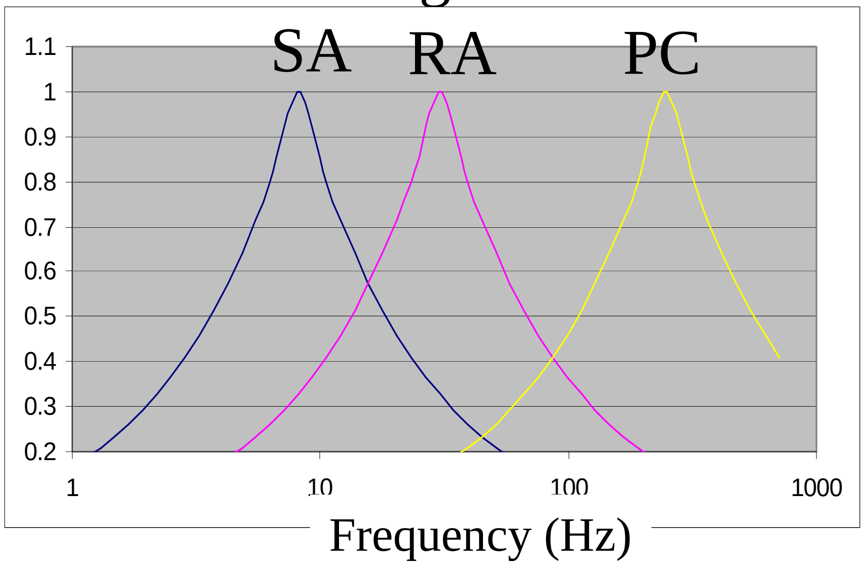
Temporal filtering (by intrinsic factors)

eye



whisker

finger



Neurometric – psychometric matching

sensitivity

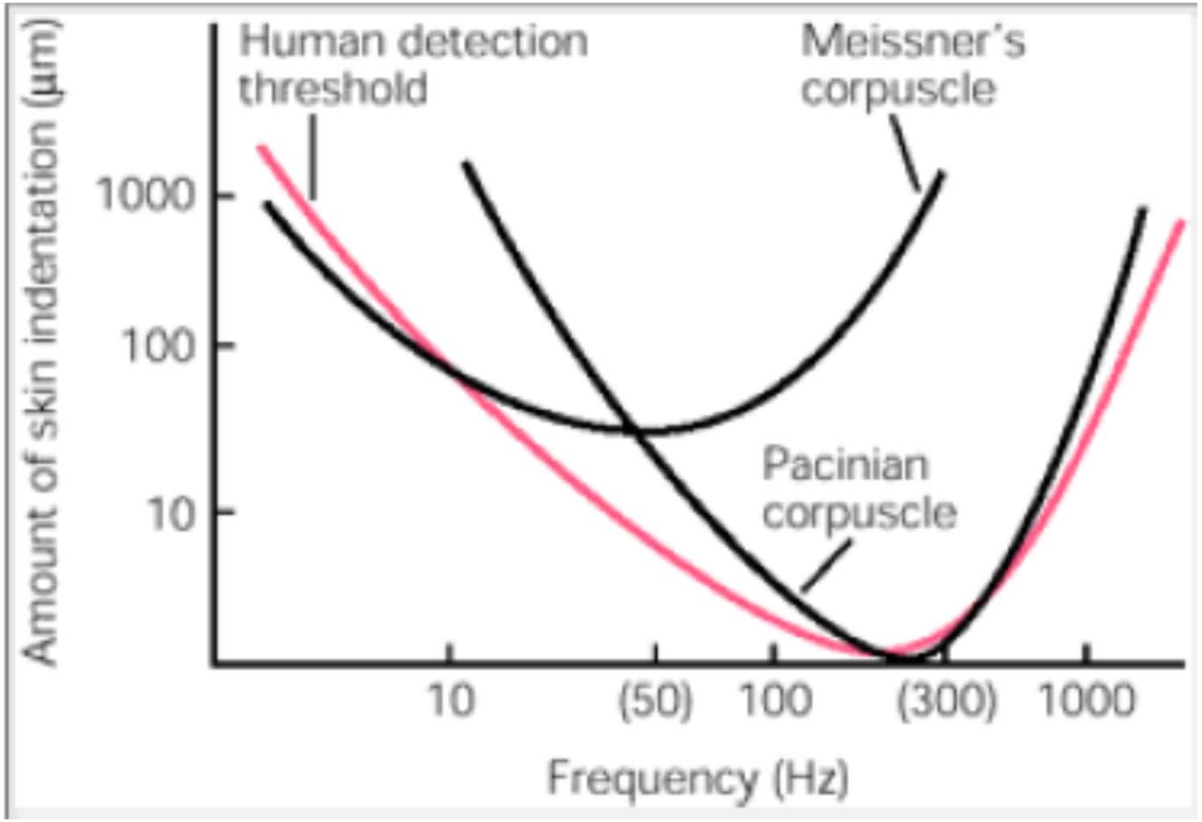


Figure 22-6B The threshold for detecting vibration corresponds to the tuning threshold of the mechanoreceptor. The sensitivity threshold for Meissner's corpuscles is lowest for frequencies of 20-50 Hz. Pacinian corpuscles sense higher frequencies. (Adapted from Mountcastle et al. 1972.)

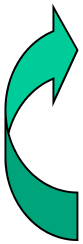
Passive and active touch

Passive touch

- Perceptual processing follows sensory events

Active touch

- Perceptual processing surrounds sensory events:



o The brain probes the world

o Compares sensory data with internal expectations

o Updates internal expectations

Active touch is done in a loop:

- Change of expectations => probing the world
- probing the world => Change of expectations

Passive and active touch

Passive touch

- low thresholds
- poor accuracy

Active touch

- higher thresholds
- high accuracy

Passive and active touch

Passive touch

- low thresholds
- poor accuracy

⇓

Detection

Active touch

- higher thresholds
- high accuracy

⇓

Exploration
Object localization
Object identification

Passive and active touch

Passive touch	Active touch
▪ low thresholds	▪ higher thresholds
▪ poor accuracy	▪ high accuracy

Potential underlying mechanism: "Gating"

- Arousal, preparatory, or motor commands "gate out" sensory signals
- Example: Thalamic gating (Sherman & Guillery, JNP. 1996)

Thalamic neurons have 2 modes:

- in drowsiness: hyperpolarized, bursting, low threshold
- in alertness: depolarized, single spikes, high threshold

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Underlying mechanisms:

- Additional information
  - expectations
  - accumulation of sensory data over time
  - more coding dimensions
  - increased resolution due to scanning
- close-loop operation

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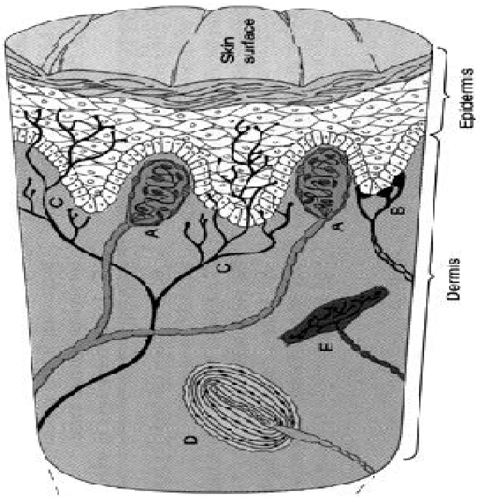
Sensory encoding: *What receptors tell the brain*

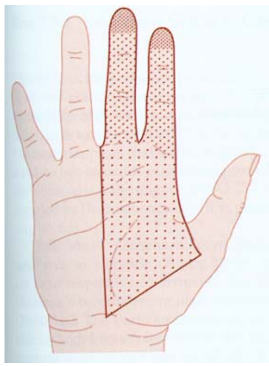
Sensory organs consist of **receptor arrays**:

somatosensation



~200 µm

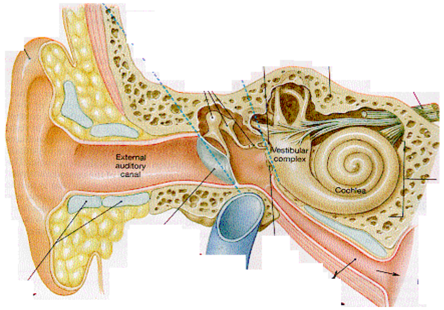
Finger pad



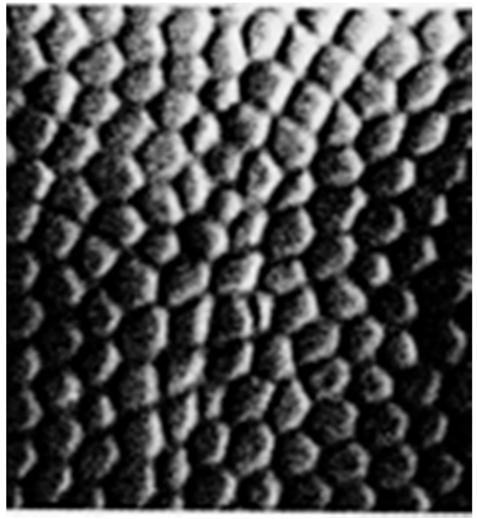
audition

10 µm

cochlea

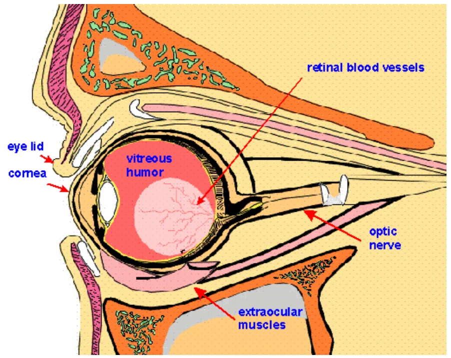


vision



10 µm

retina



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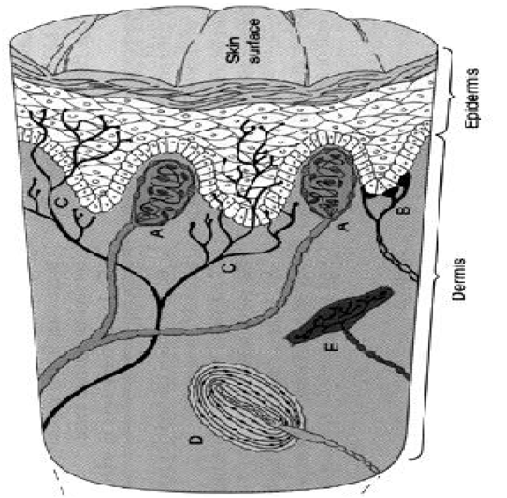

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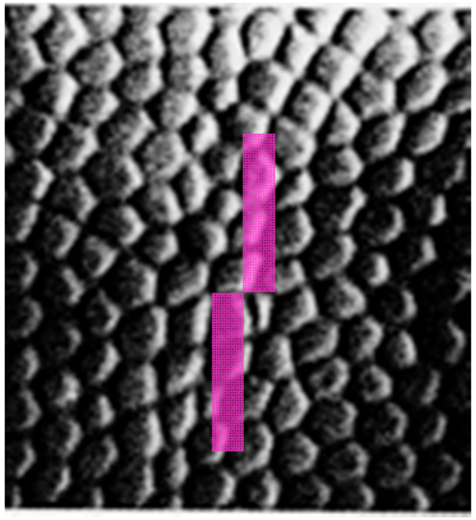


10 µm

retina

Spatial organization => Spatial coding (“*which* receptors are activated”)

Spatial coding metaphors

one could think of:

*the **eye** as a **camera***

*the **skin** as a **carbon paper***

light is

Imprinted on the retina via photo-receptors

Pressure is

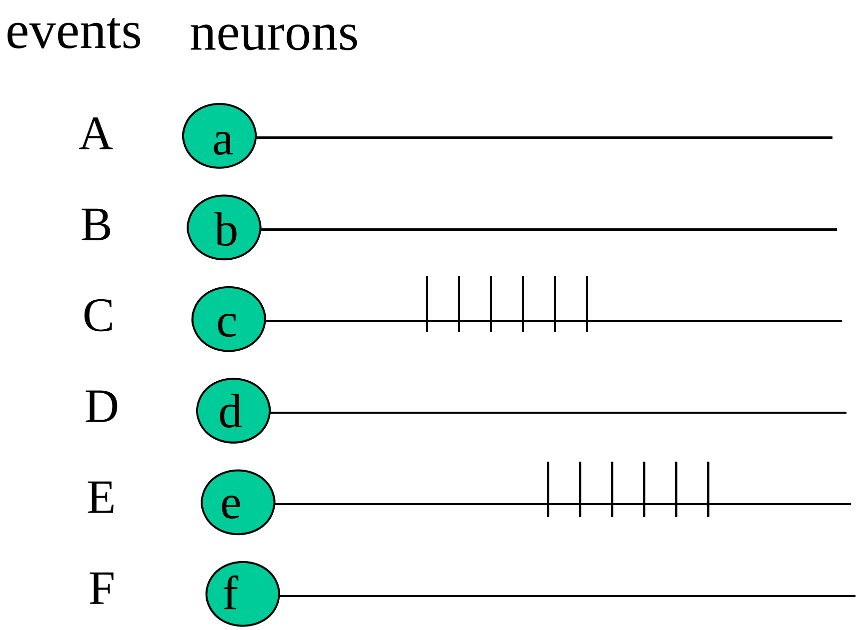
Imprinted on the skin via mechano-receptors

Imprinted on paper via carbon particles

How neurons encode external events in space?

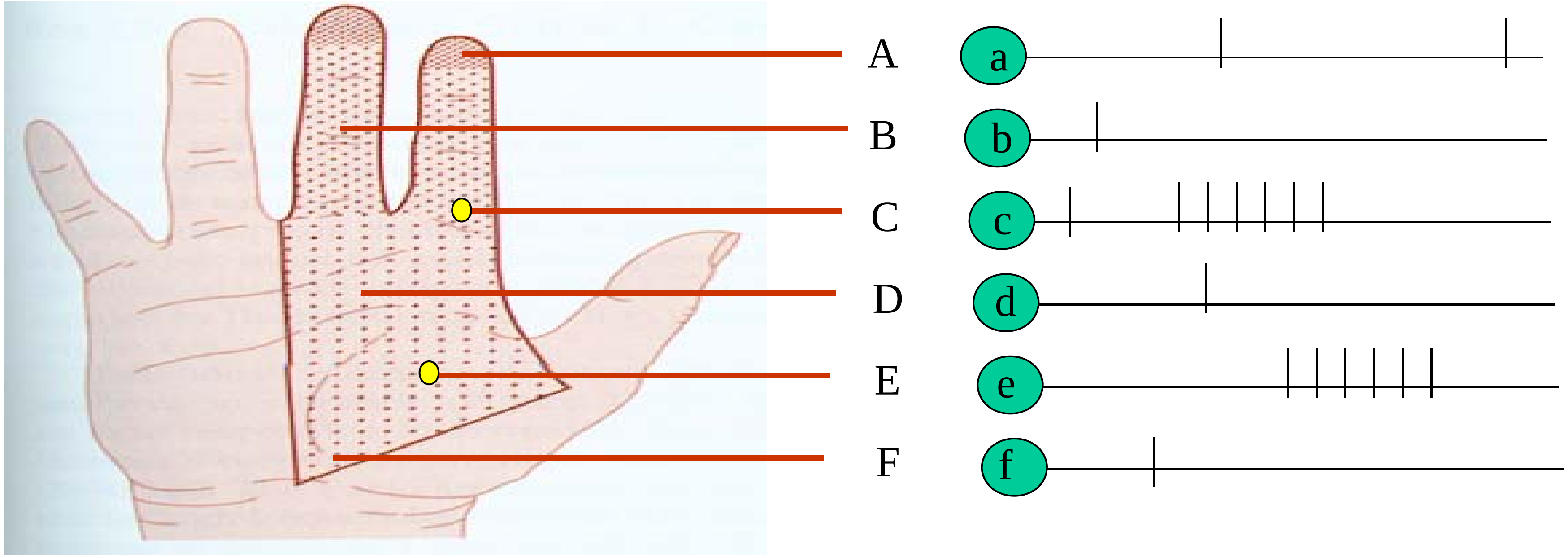
The “labeled-line code”.

a binary code, reporting yes/no **about the occurrence of a given event.**



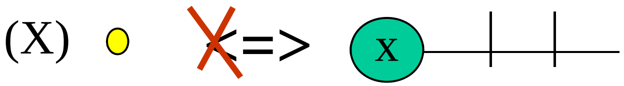
Every neuron has a “label”

Reading out the labeled line code



reading algorithm: a location X is pressed if neuron x fires spikes

On what condition will this algorithm be valid?



Neuron x fires *if ~~and only~~ if* X is pressed

Is this assumption valid?

1. The problem of background activity

2. The “problem” of sensor movements

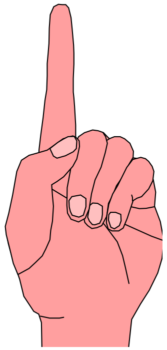
receptors are sensitive to changes

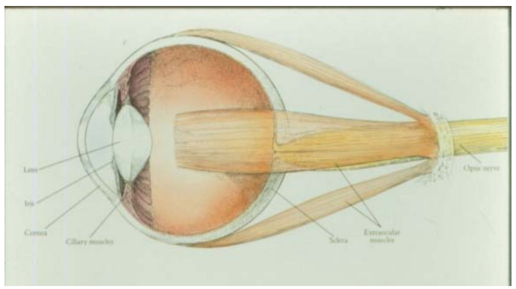
Thus

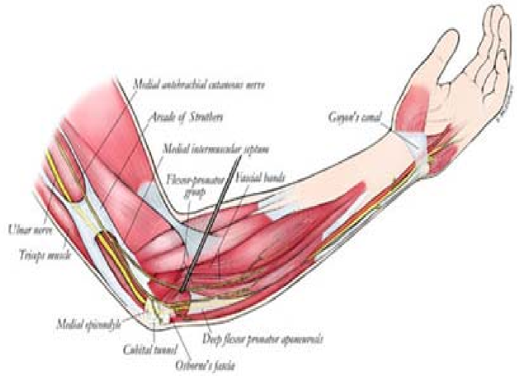
If both objects and sensors are passive (stationary), nothing will be sensed

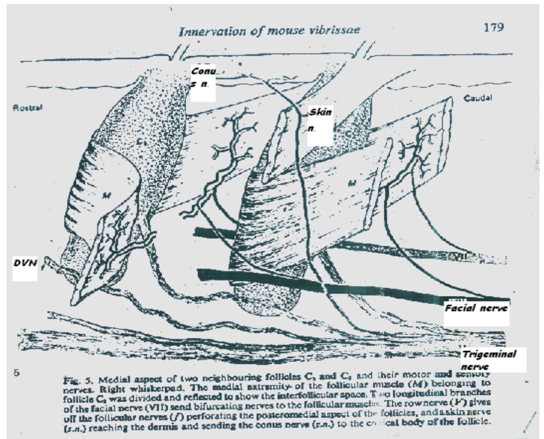
<u>Active Sensing</u> is a strategy that induces changes in sensed signals

In mammals, active sensing is typically implemented by sensor movements:









Drives for sensor movements

1. The world is not flashing

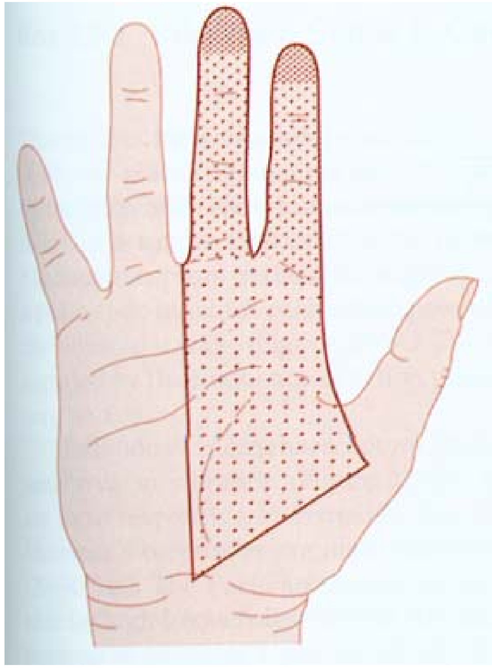
2. sensory sheets are not uniform

Fovea

eye

finger

whisker



Fovea => macro movements of the sensory organ

receptor sensitivity => micro movements of the sensory organ

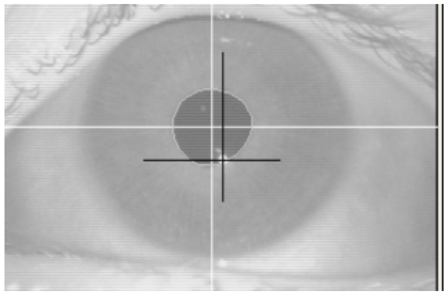
Sensor motion is required for

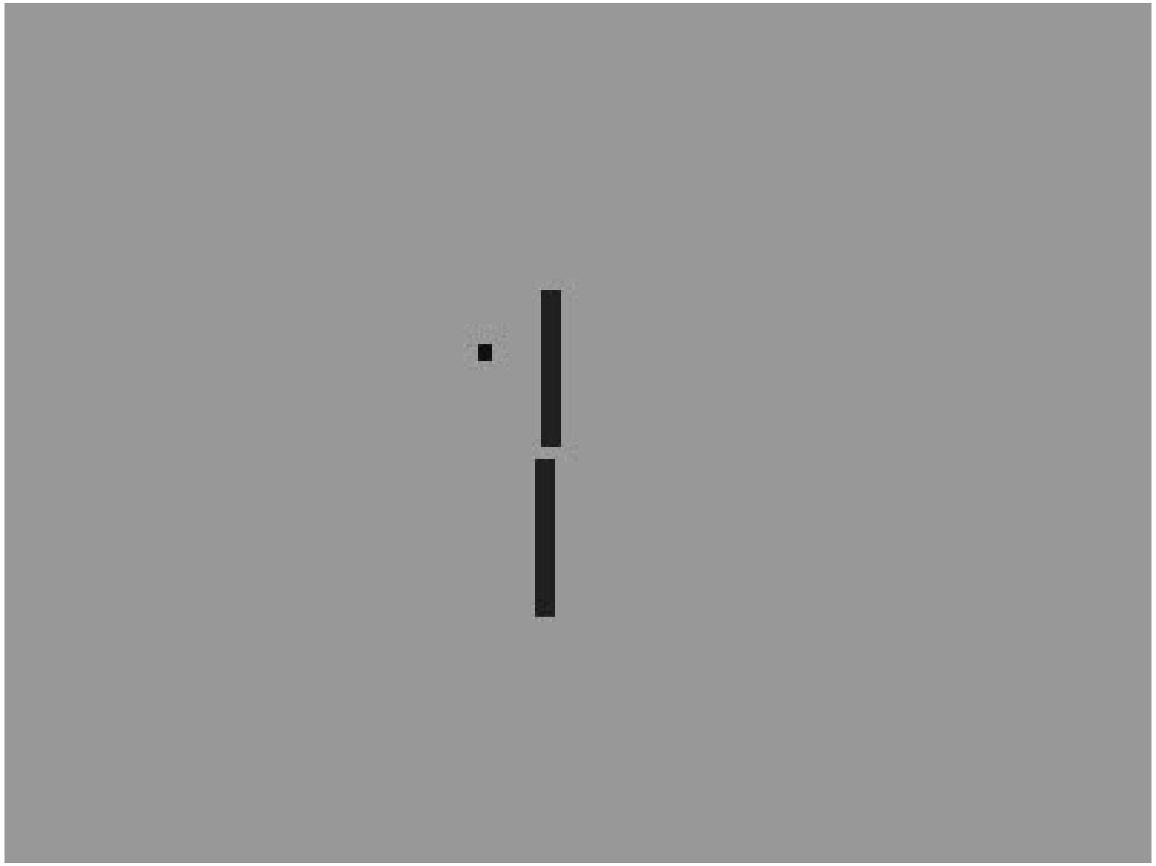
- Foveation
- Sensing stationary environment

- Without sensor motion sensation is limited to moving or flashing objects

How sensor motion constrains sensory coding?

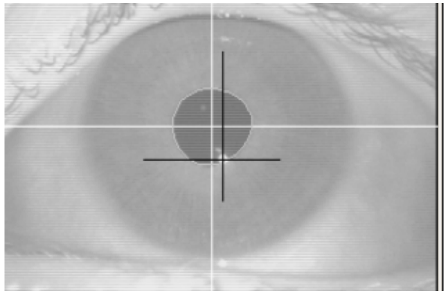
<u>Eye movements during fixation</u>

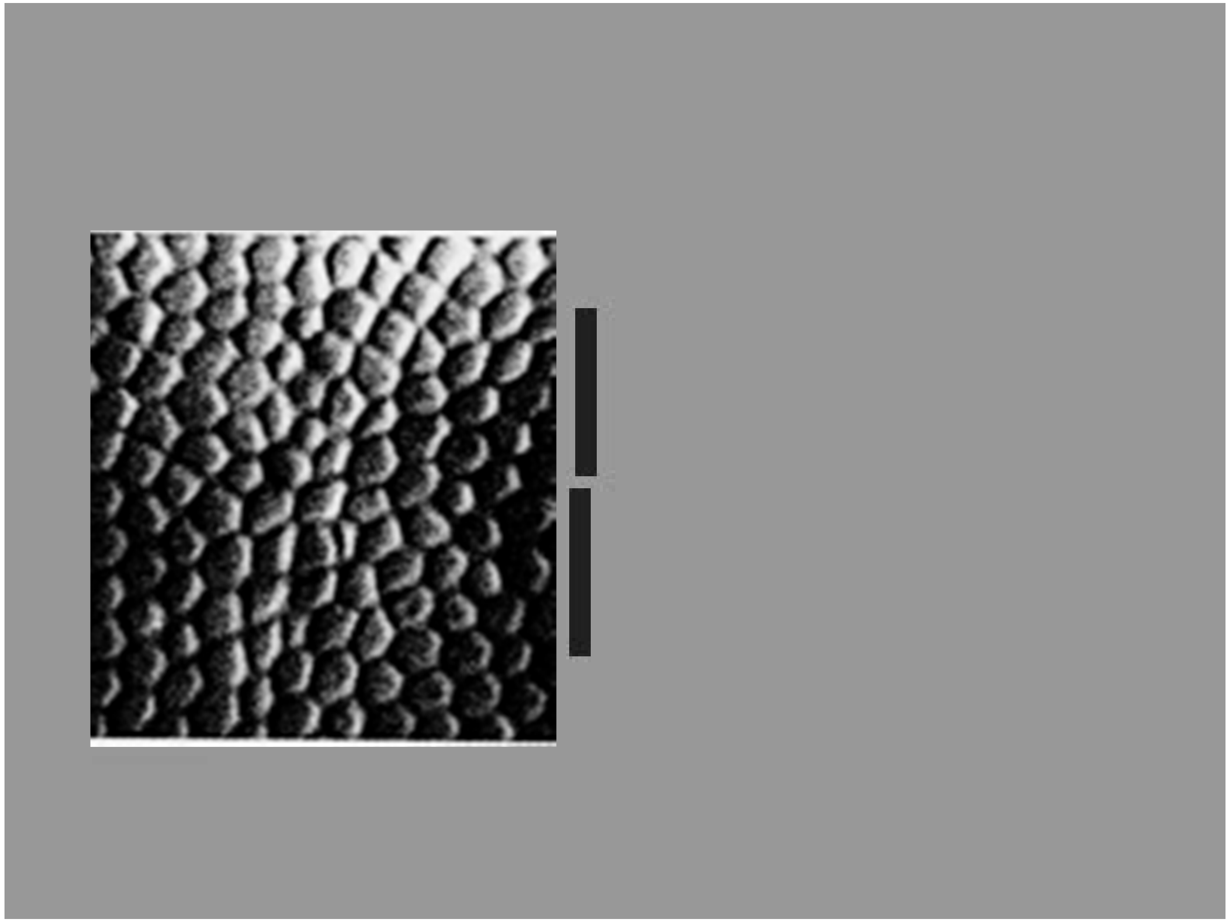




backward!

Eye movements during fixation





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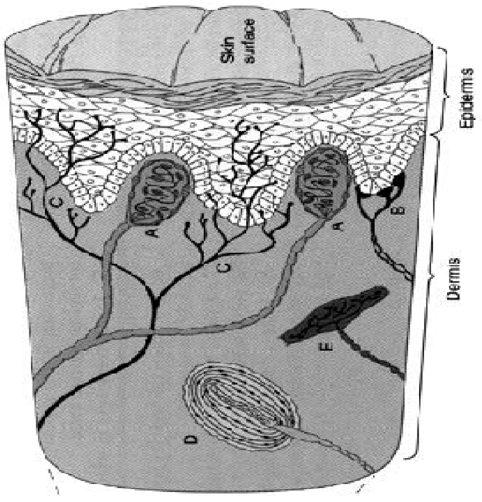
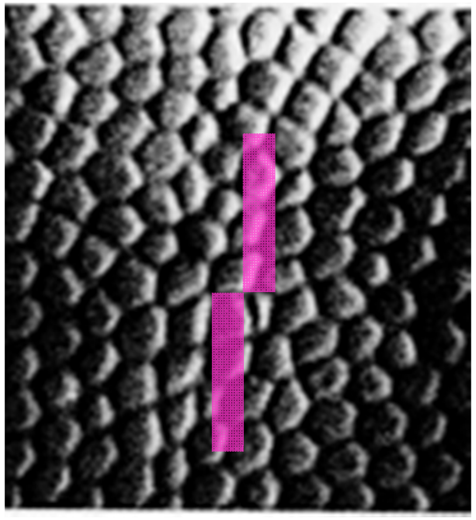
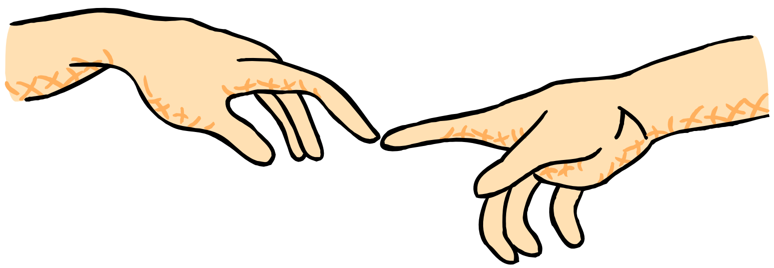
		
~200 μm	10 μm	10 μm
Finger pad	*cochlea*	*retina*

Spatial organization => Spatial coding (“*which* receptors are activated”)

Movements => Temporal coding (“*when* are receptors activated”)

Touching



The End