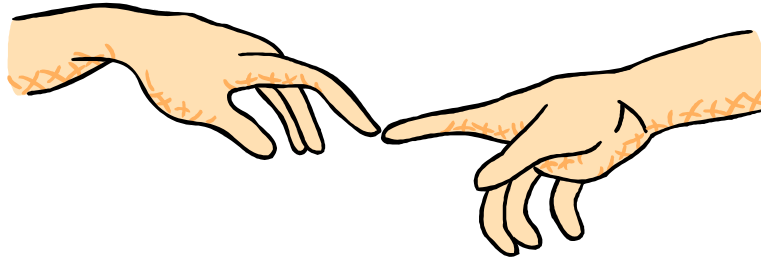


Touching



Ehud Ahissar

Touching

- Body-world interface
- Mechanisms of sensory processing (across senses)
- Motor-sensory coupling
- Passive vs active touch
- Neuronal coding
- Morphological coding

Body-world interface

Underneath the skin

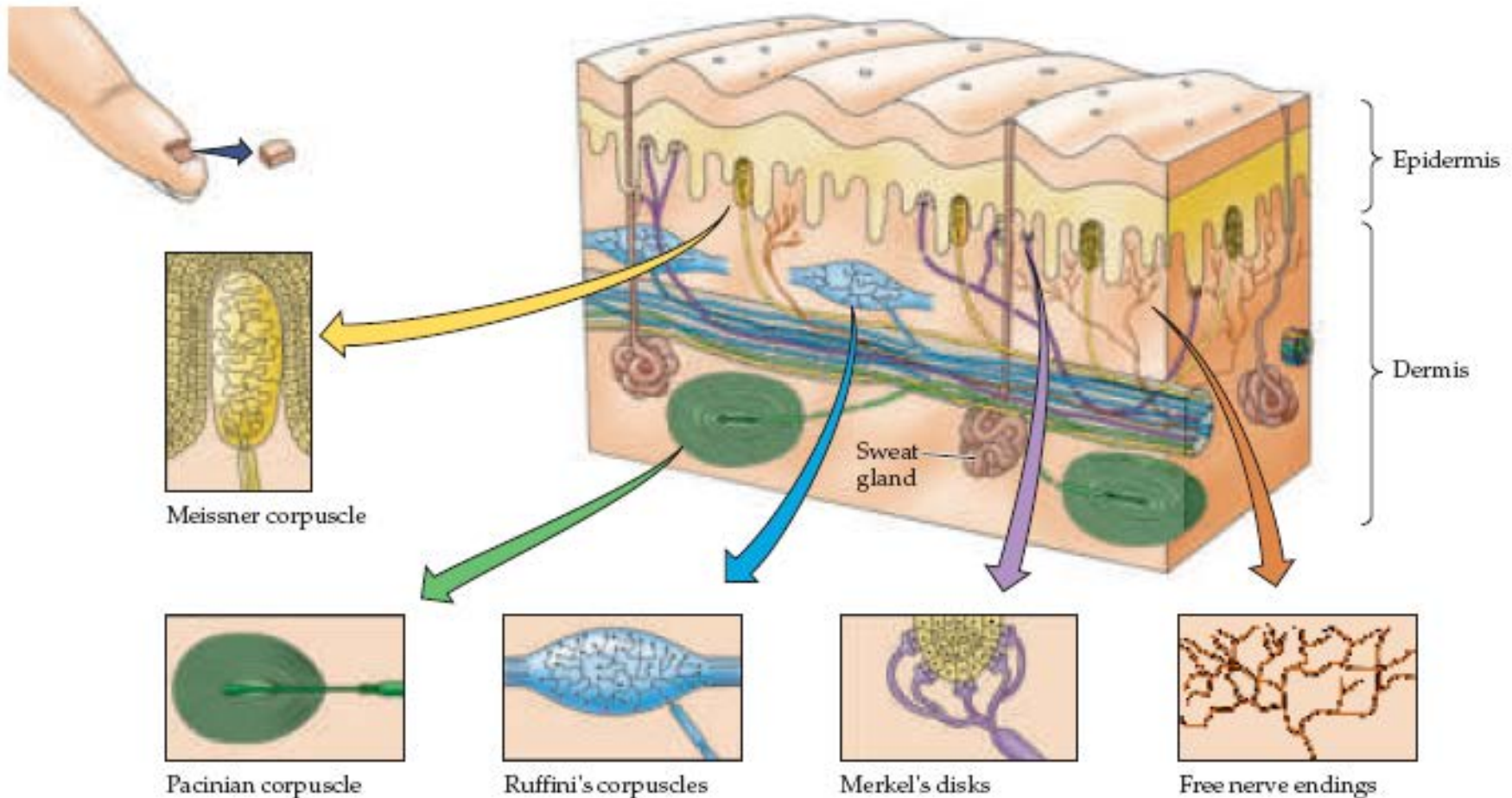
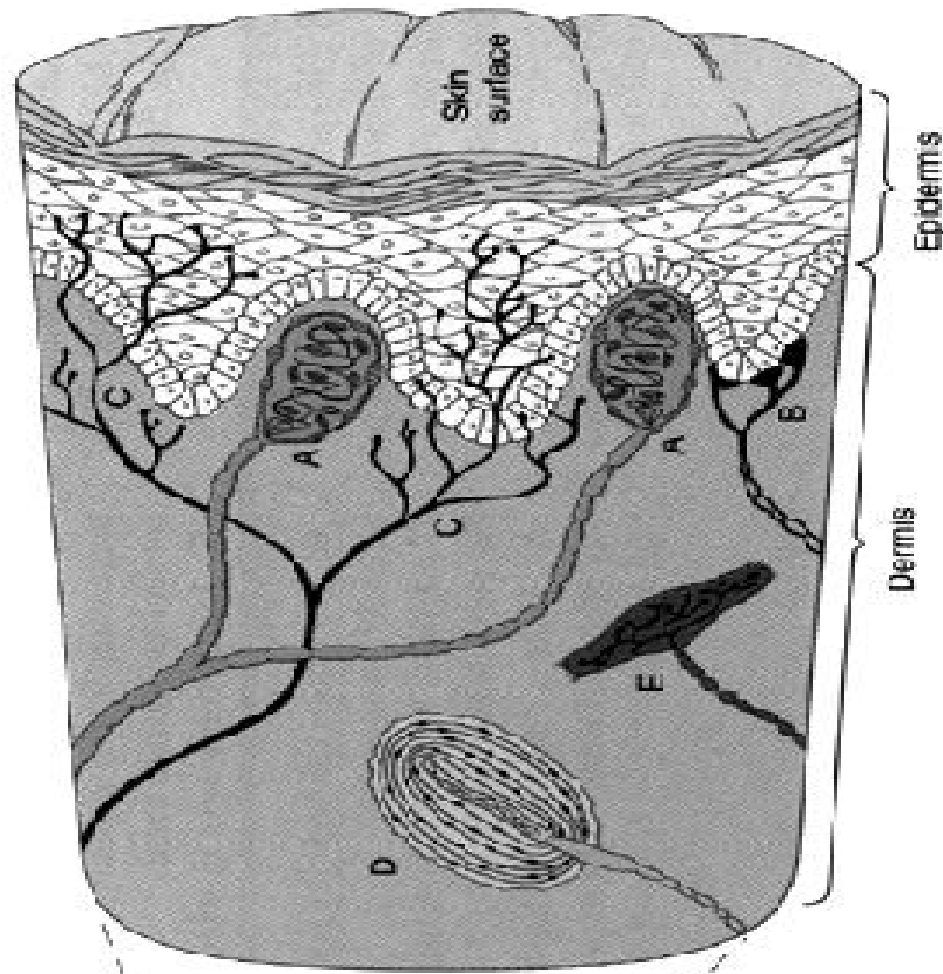


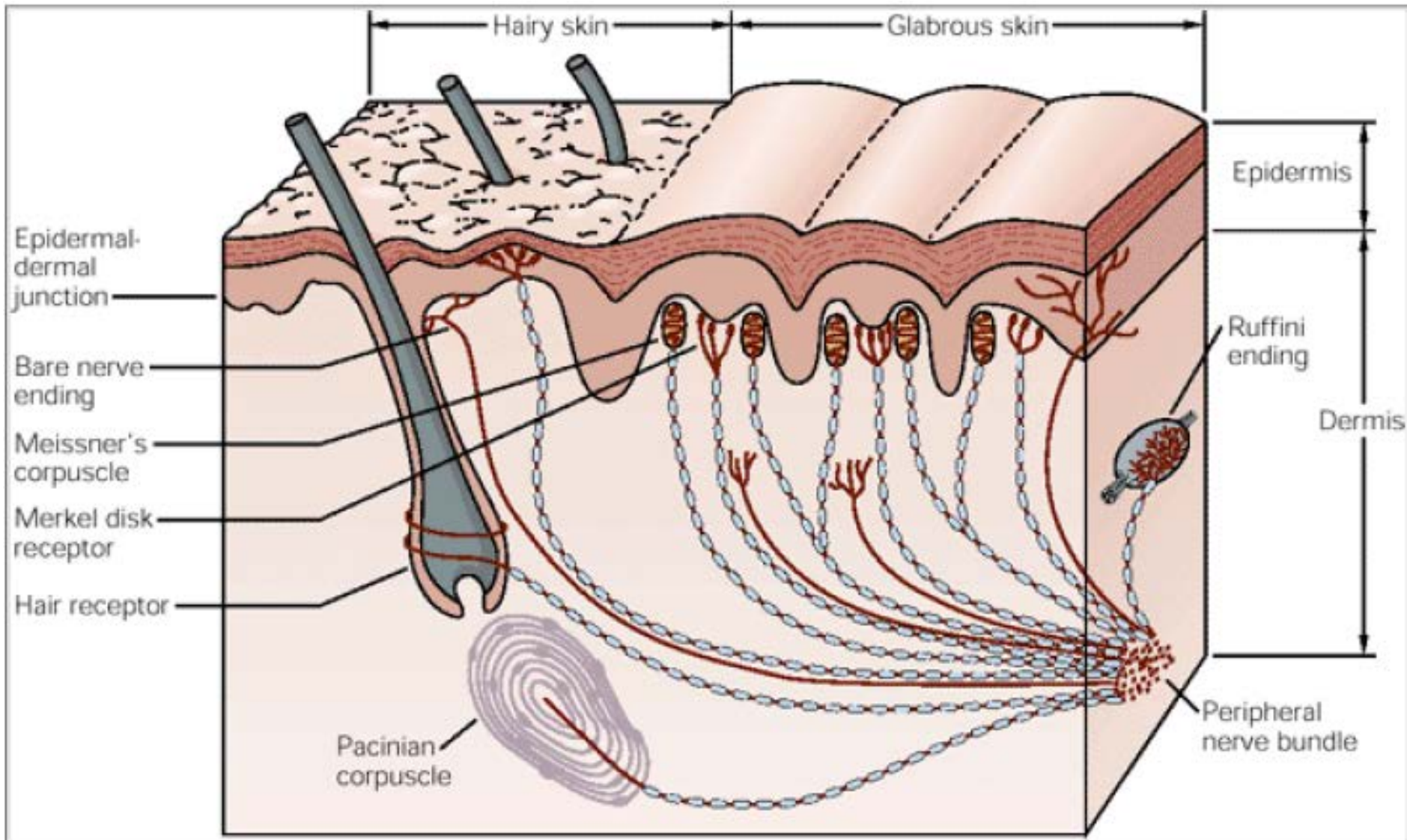
Figure 8.3 The skin harbors a variety of morphologically distinct mechanoreceptors. This diagram represents the smooth, hairless (also called glabrous) skin of the fingertip. The major characteristics of the various receptor types are summarized in Table 8.1. (After Darian-Smith, 1984.)

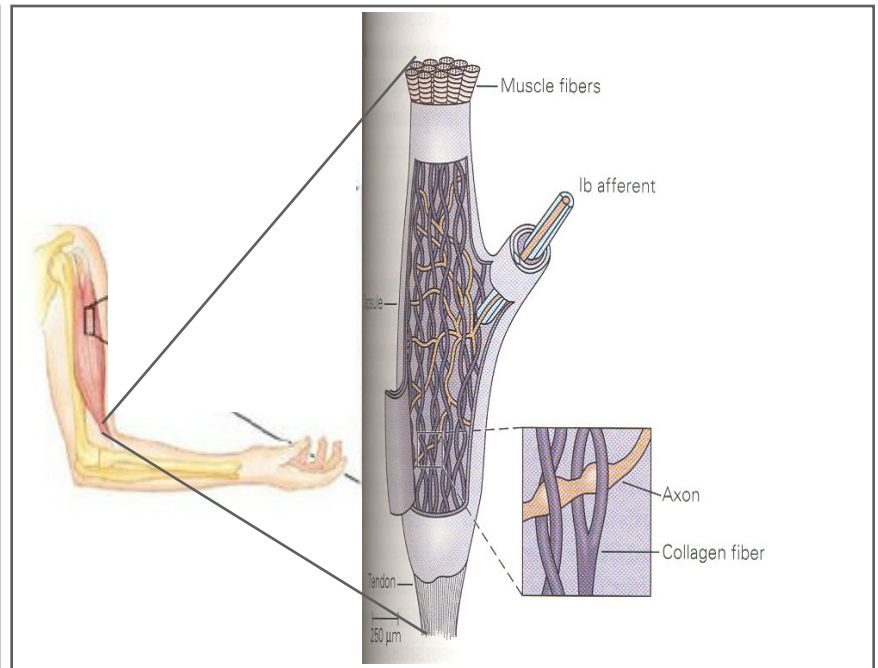
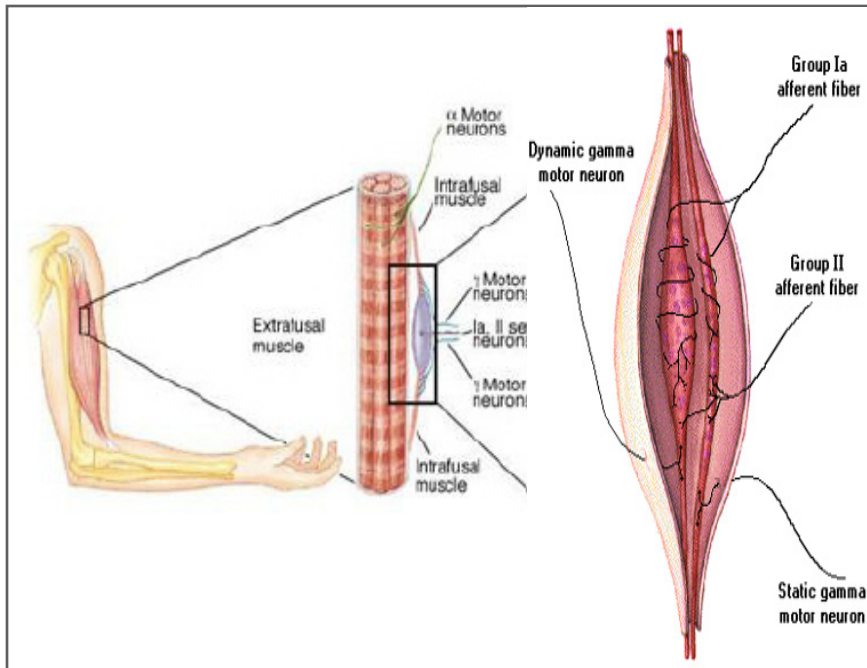
Mechanoreception underneath the skin



~200 μm

Mechanoreception underneath the skin





Proprioceptive receptor types

Name:

Muscle spindle receptors

Golgi tendon organs

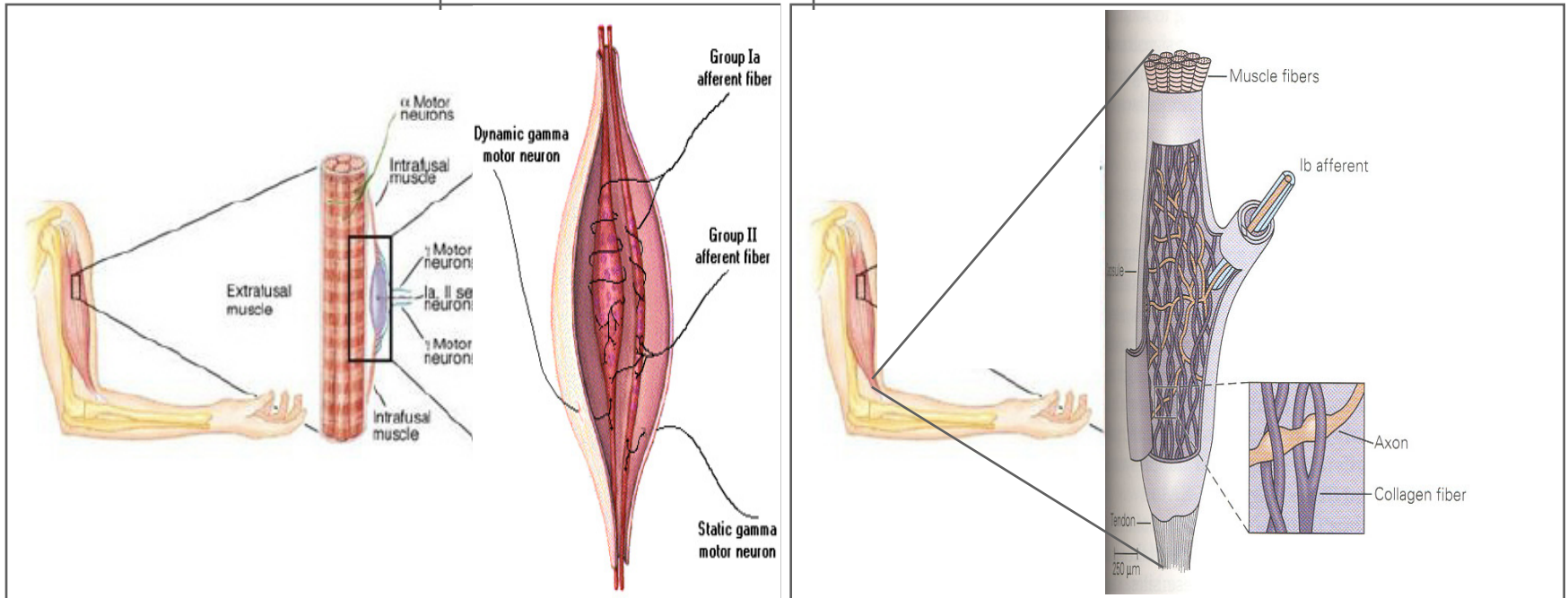
Joint receptors

Sensitive to:

muscle length change

muscle tension

Joint angle



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	A δ C	2–20 m/s .5 – 2 m/s	All skin	Pain, temperature, crude touch	Slow	High
Meissner's corpuscles	Encapsulated; between dermal papillae	A β 6–12 μ m	30 – 70 m/s	Principally glabrous skin	Touch, pressure (dynamic)	Rapid	Low
Pacinian corpuscles	Encapsulated; onionlike covering	A β 6–12 μ m		Subcutaneous tissue, interosseous nerves, viscera	Deep pressure, vibration (dynamic)	Rapid	Low
Merkel's disks	Encapsulated; associated with peptide-releasing cells	A β		All skin, hair follicles	Touch, pressure (static)	Slow	Low
Ruffini's corpuscles	Encapsulated; oriented along stretch lines	A β 6–12 μ m		All skin	Stretching of skin	Slow	Low
Muscle spindles	Highly specialized (see Figure 8.5 and Chapter 15)	Ia and II	80 – 120 m/s	Muscles	Muscle length	Both slow and rapid	Low
Golgi tendon organs	Highly specialized (see Chapter 15)	Ib	80 – 120 m/s	Tendons	Muscle tension	Slow	Low
Joint receptors	Minimally specialized	—		Joints	Joint position	Rapid	Low

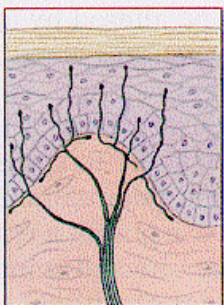
Mechano-receptors
(ex-afferents)

Proprio-(re)ceptors
(re-afferents)

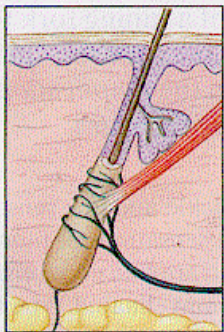
^aIn the 1920s and 1930s, there was a virtual cottage industry classifying axons according to their conduction velocity. Three main categories were discerned, called

Receptors

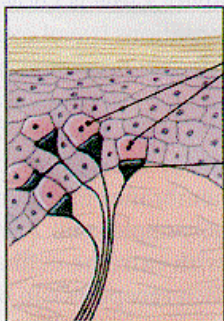
Evolutionary specialization



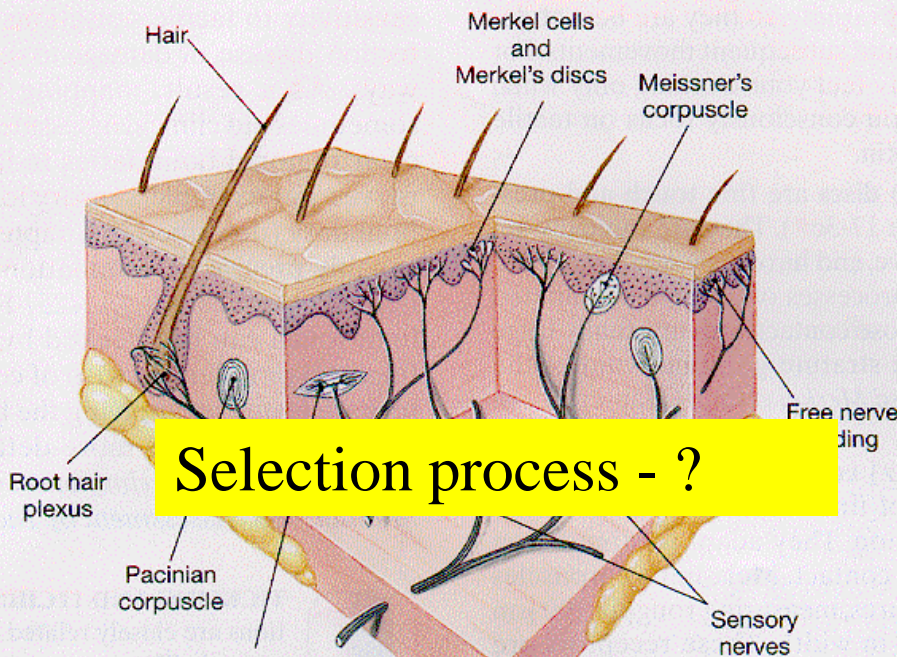
(a) Free nerve endings



(b) Free nerve endings of root hair plexus

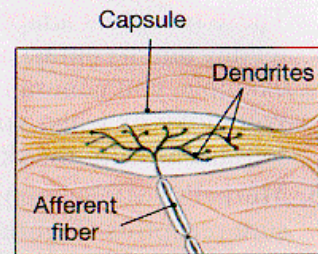


(c) Merkel cells and Merkel's discs

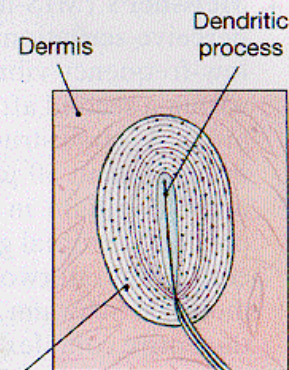


Selection process - ?

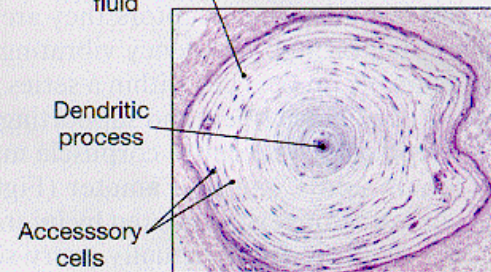
Morphological processing



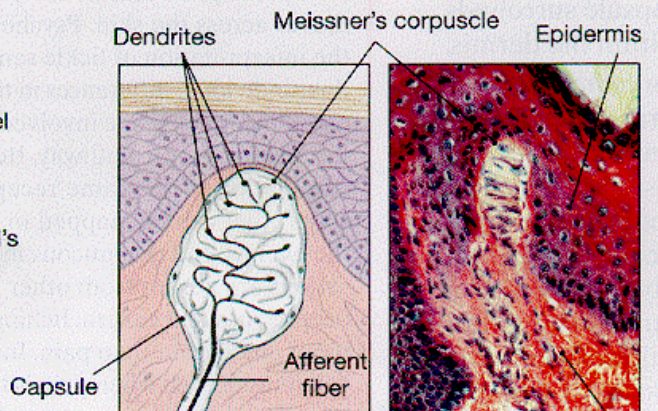
(f) Ruffini corpuscle



Layers of collagen fibers separated by fluid



(e) Pacinian corpuscle



(d) Meissner's corpuscle

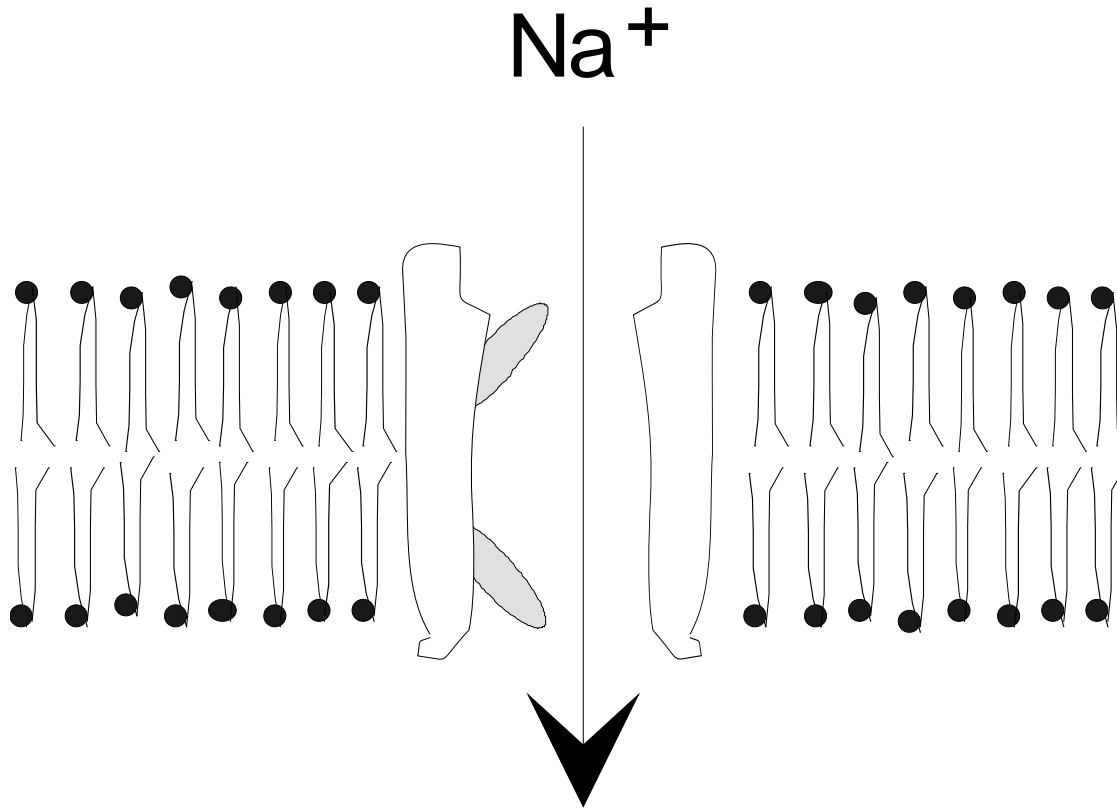
Dermis

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

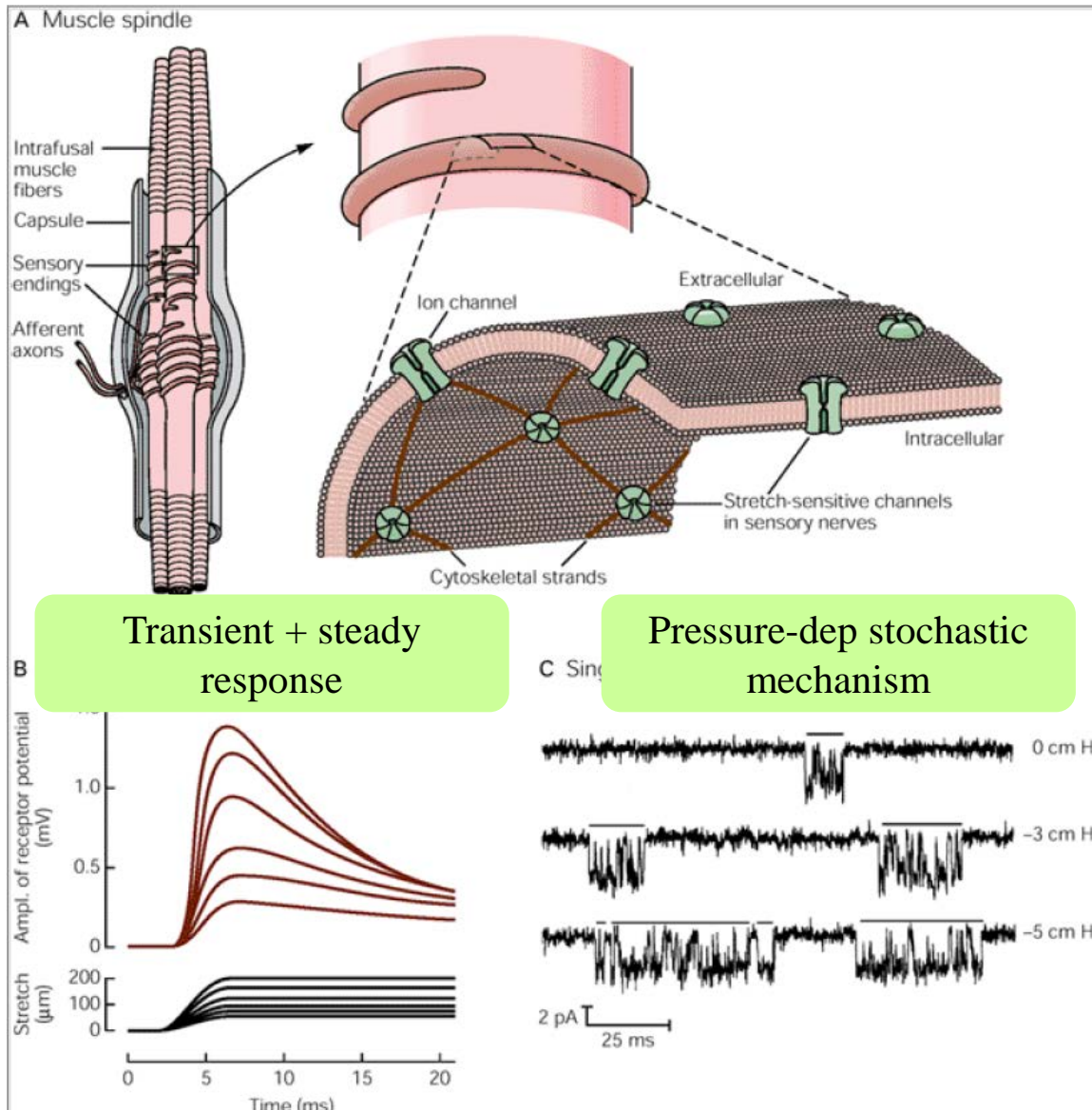


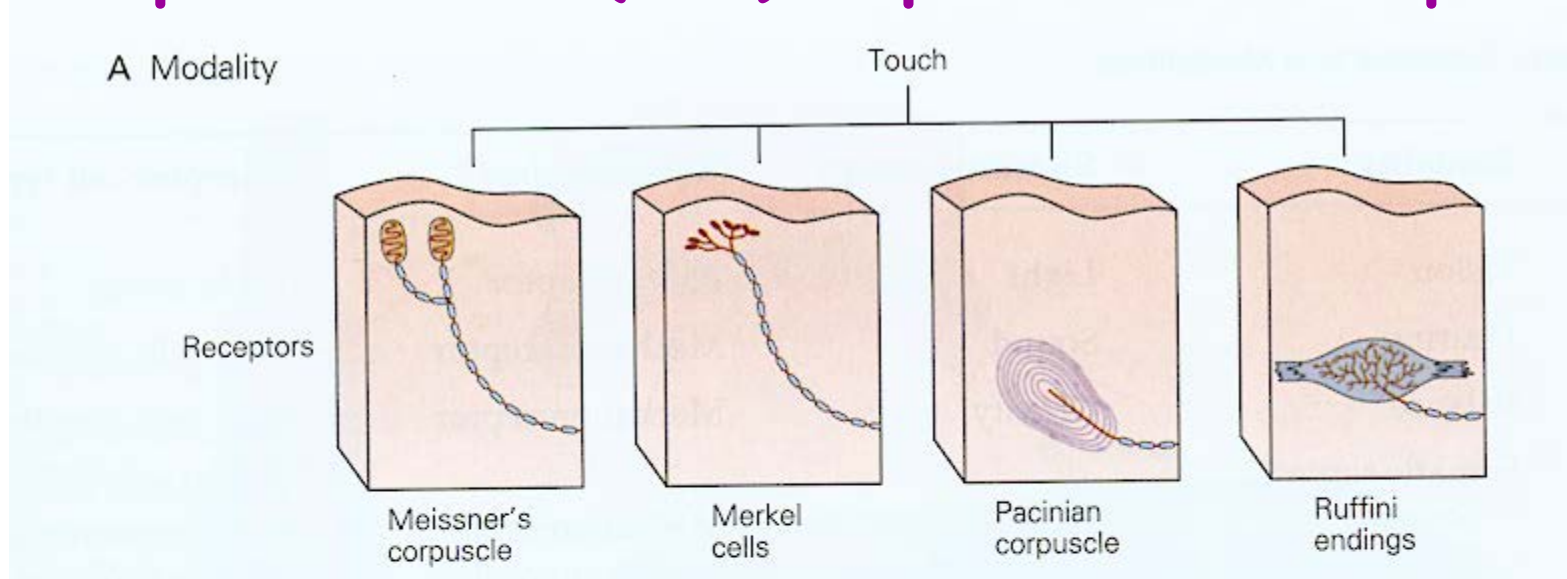
Figure 21-2 Mechanoreceptors are depolarized by stretch of the cell membrane and the depolarization is proportional to the stimulus amplitude.

A. The spindle organ in skeletal muscle mediates limb proprioception. These receptors signal muscle length and the speed at which the

Receptive Fields (RFs):

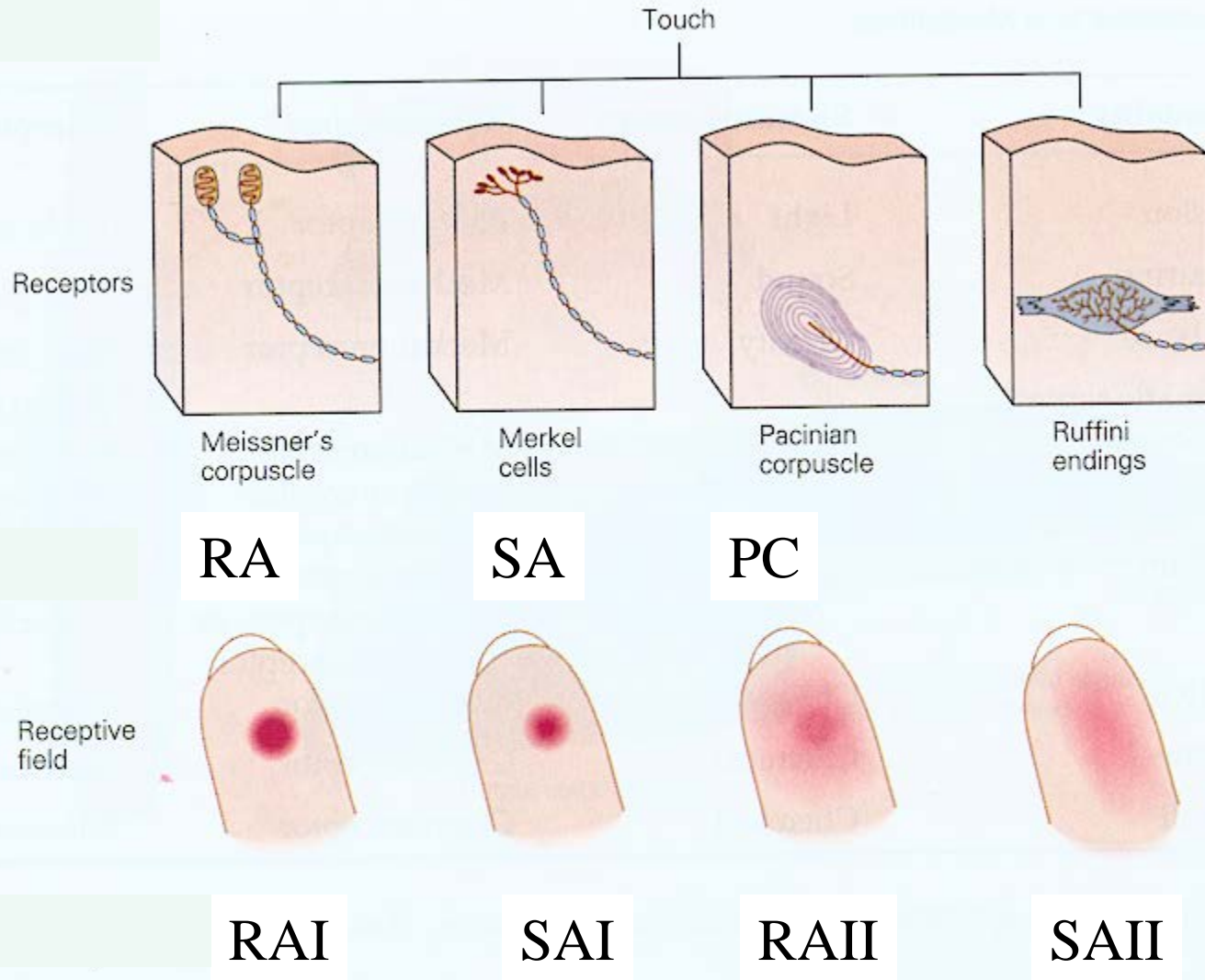
Spatial and temporal

Receptive Fields (RFs): Spatial and temporal



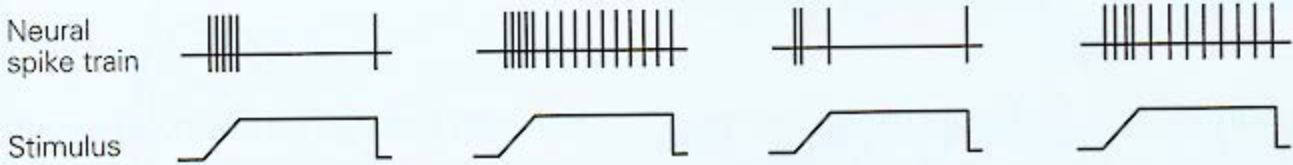
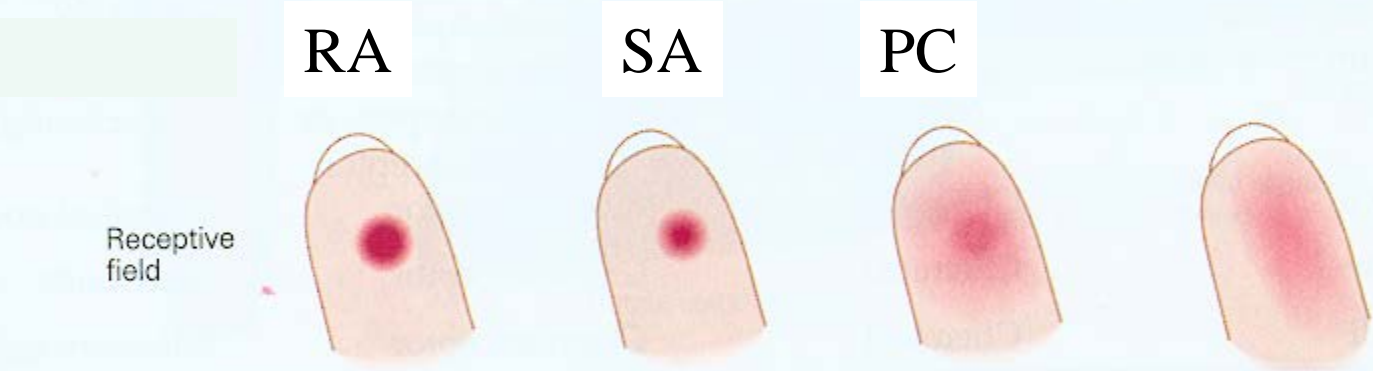
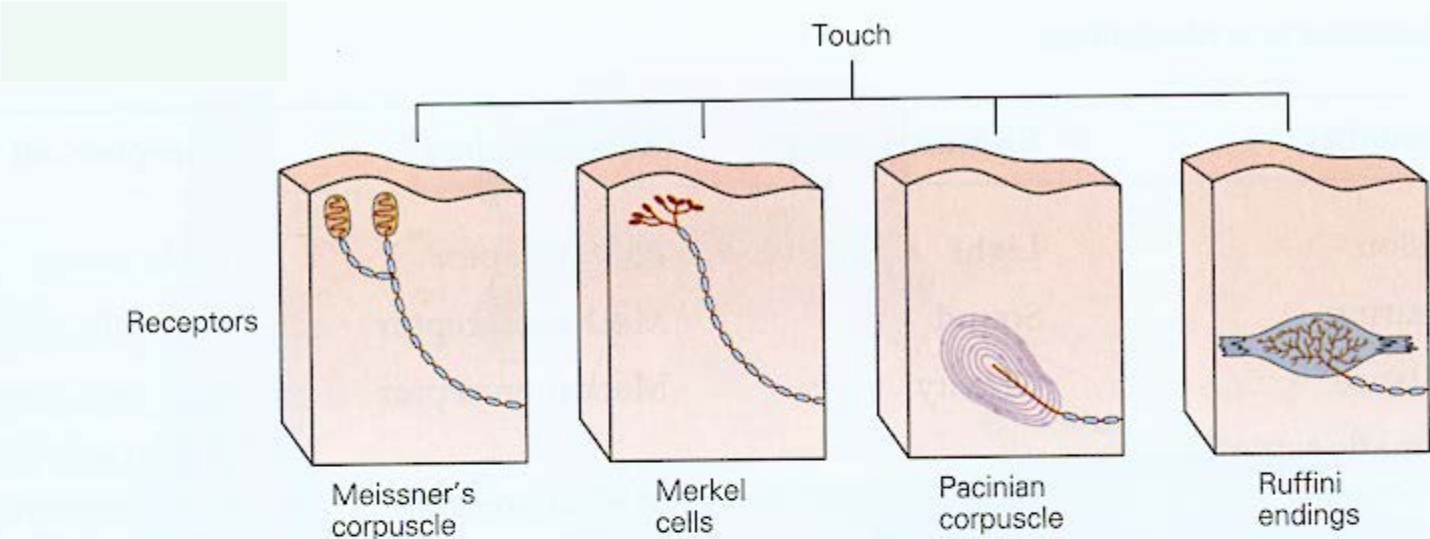
RF size?

Receptive Fields (RFs): Spatial and temporal

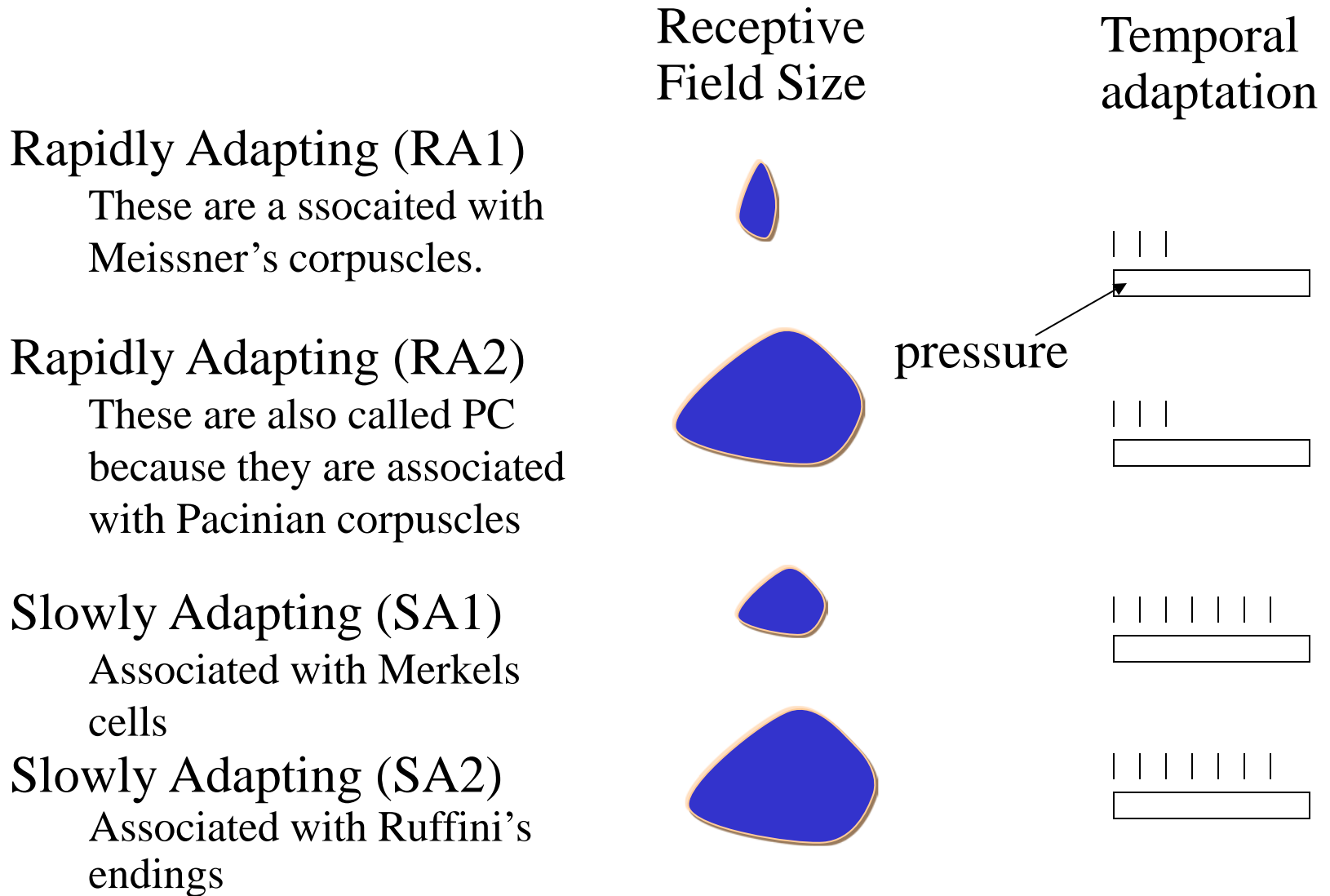


Response dynamics?

Receptive Fields (RFs): Spatial and temporal



Cutaneous Mechanoreceptor Channels



Receptor density

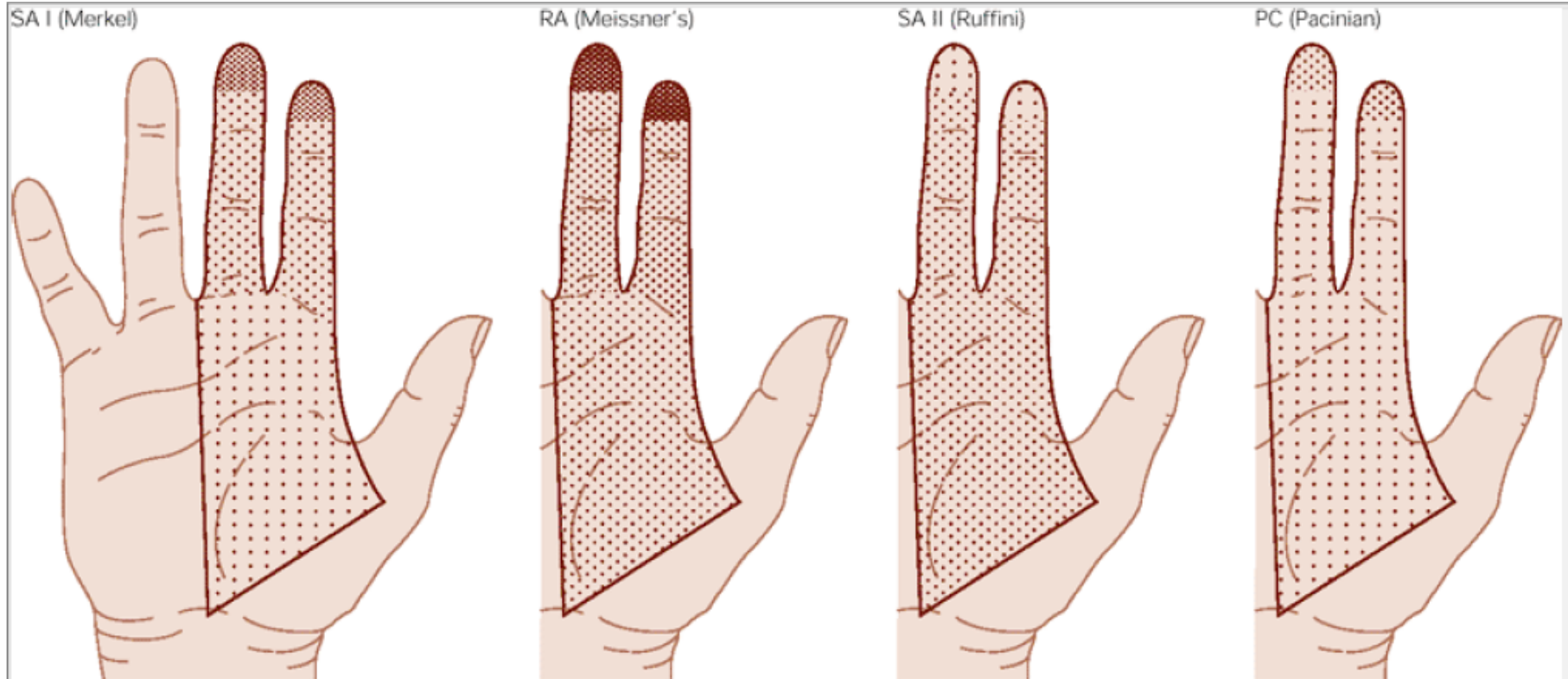
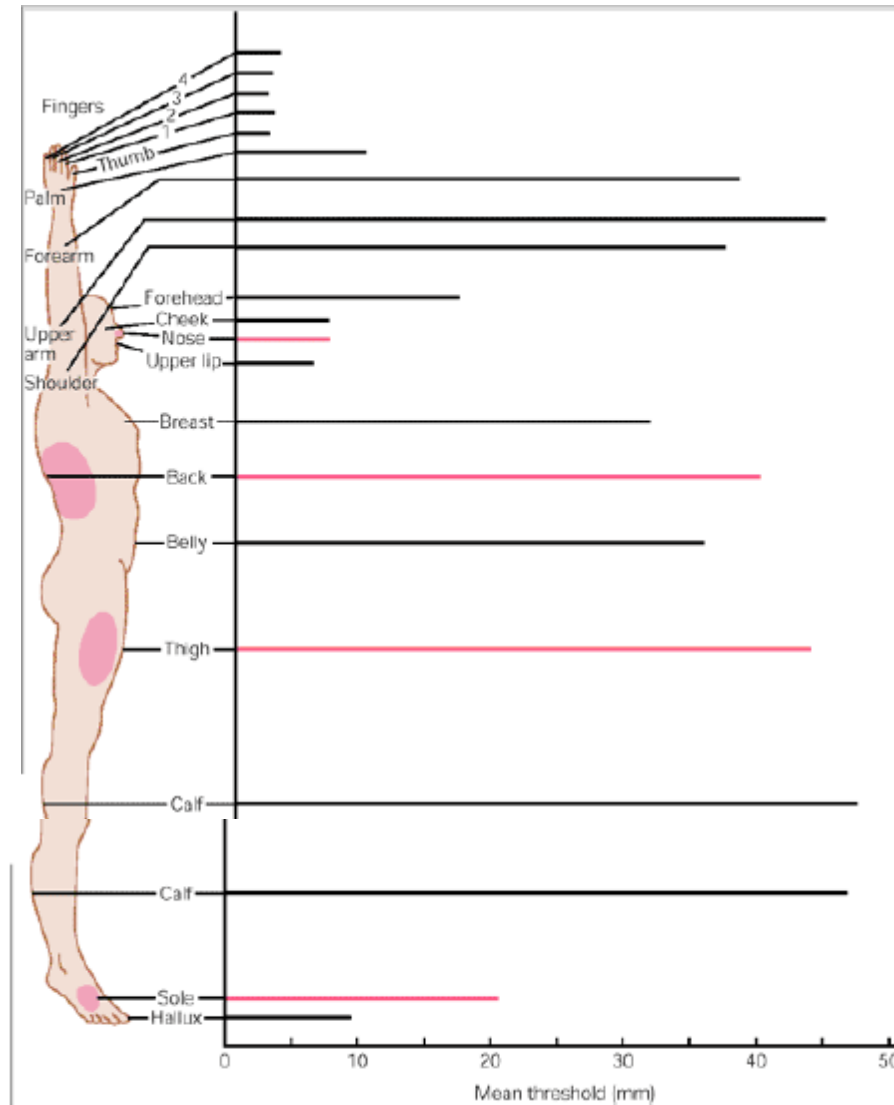


Figure 22-4 The distribution of receptor types in the human hand varies. The number of sensory nerve fibers innervating an area is indicated by the stippling density, with the highest density of receptors shown by the heaviest stippling. (**RA** = 5 rapidly adapting, **SA** = 5 slowly adapting.) Meissner's 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/cm² in the proximal phalanges, and to 50/cm² in the palm. (Adapted from Vallbo and Johansson 1978.)

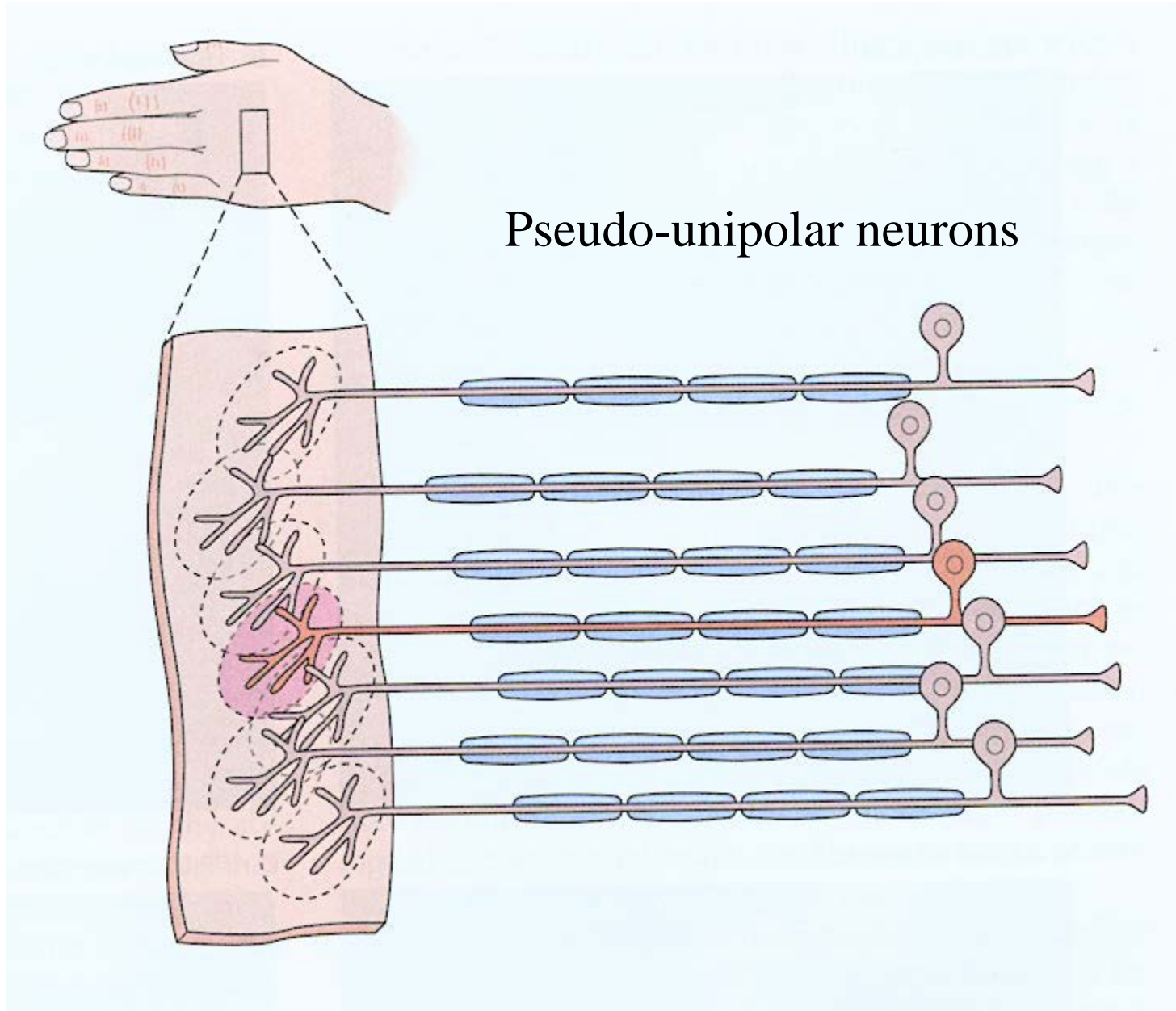
Neurometric - psychometric matching

Spatial resolution (by JND)

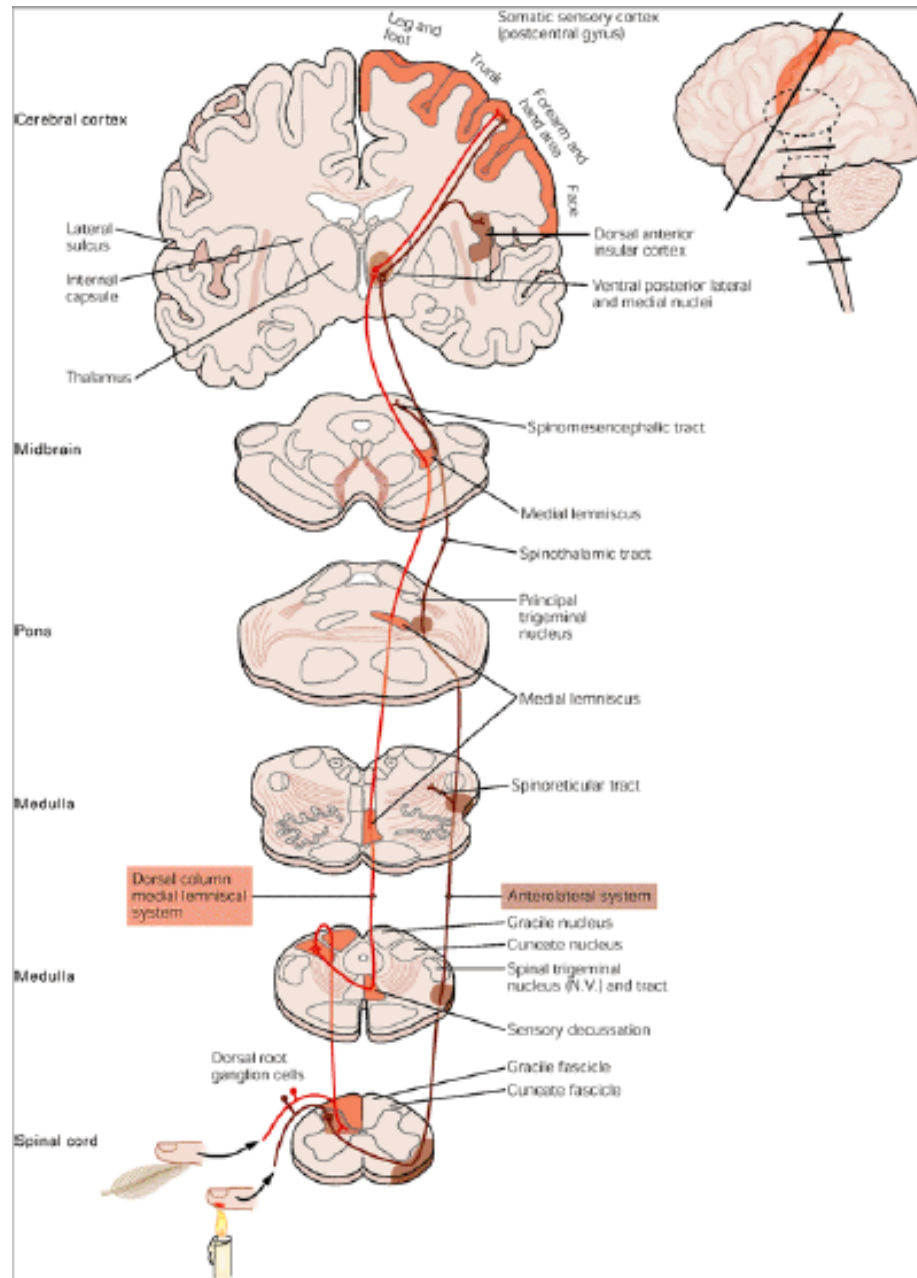


Signal conduction

Sensory signal conduction



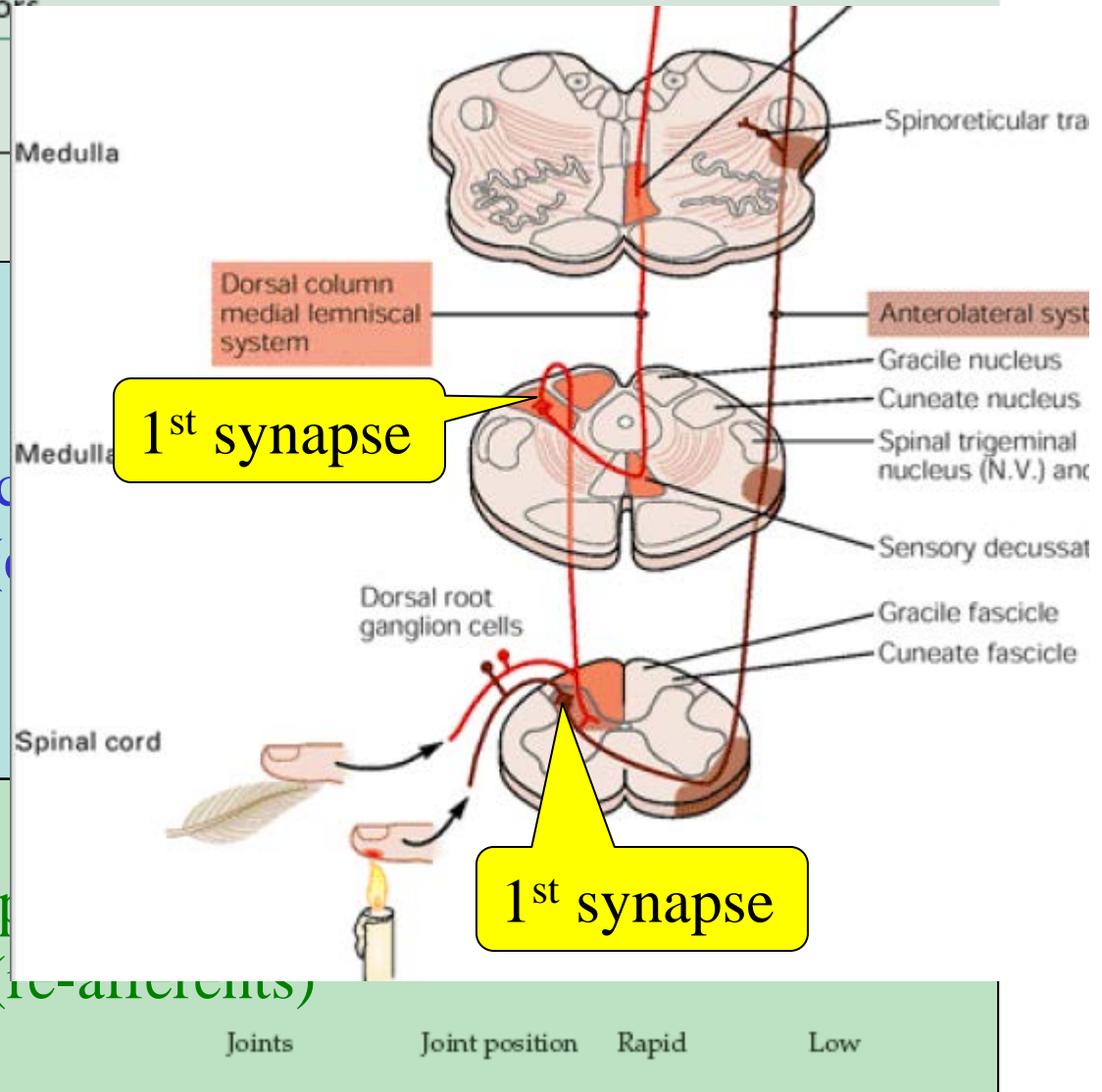
Sensory signal conduction



Sensory signal conduction

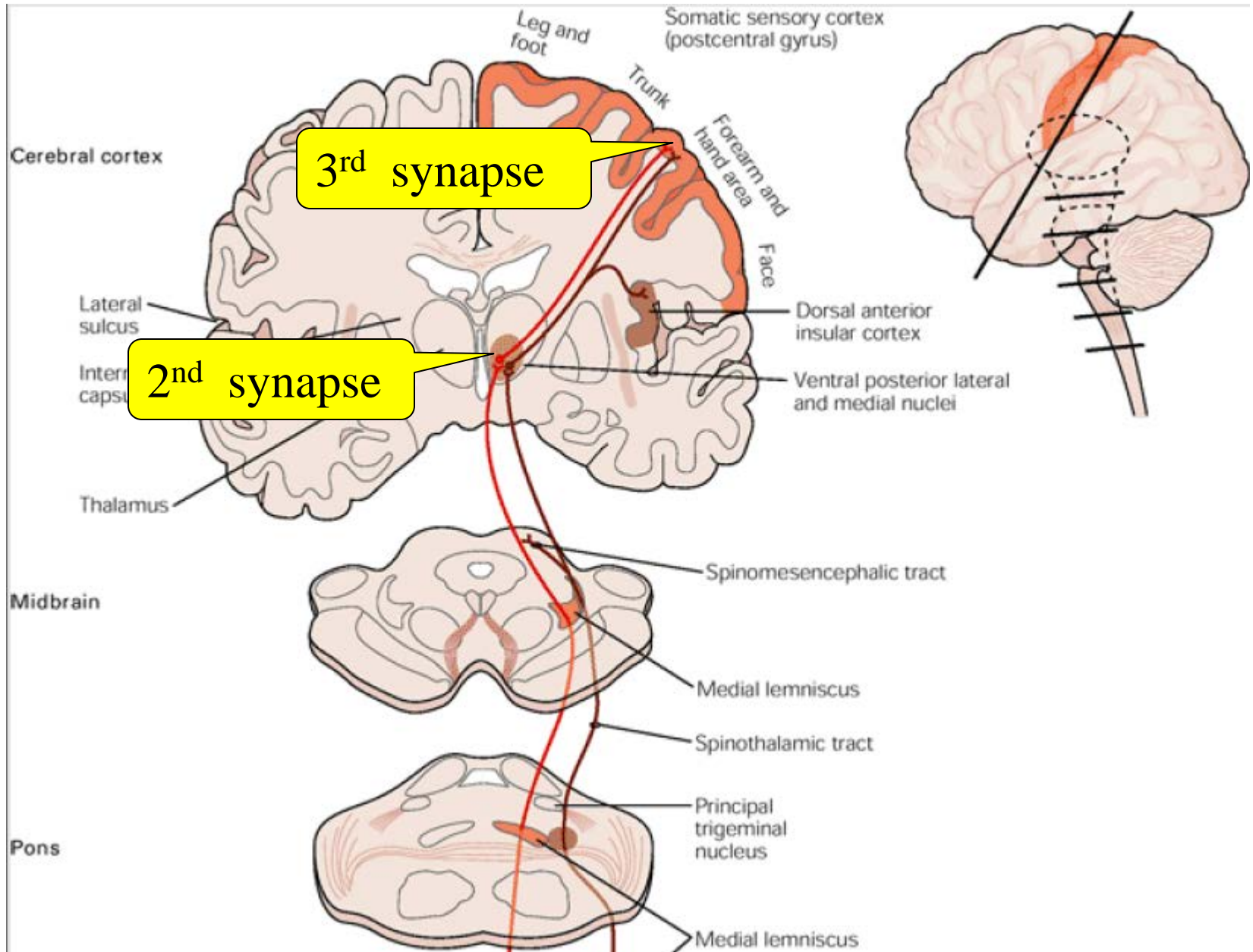
TABLE 8.1
The Major Classes of Somatic Sensory Receptors

Receptor type	Anatomical characteristics	Associated axons ^a (and diameters)
Free nerve endings	Minimally specialized nerve endings	C, A δ , A β
Meissner's corpuscles	Encapsulated; between dermal papillae	A β 6–12 μ m
Pacinian corpuscles	Encapsulated; onionlike covering	A β 6–12 μ m
Merkel's disks	Encapsulated; associated with peptide-releasing cells	A β
Ruffini's corpuscles	Encapsulated; oriented along stretch lines	A β 6–12 μ m
Muscle spindles	Highly specialized (see Figure 8.5 and Chapter 15)	Ia and II
Golgi tendon organs	Highly specialized (see Chapter 15)	Ib
Joint receptors	Minimally specialized	—



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

Sensory signal conduction



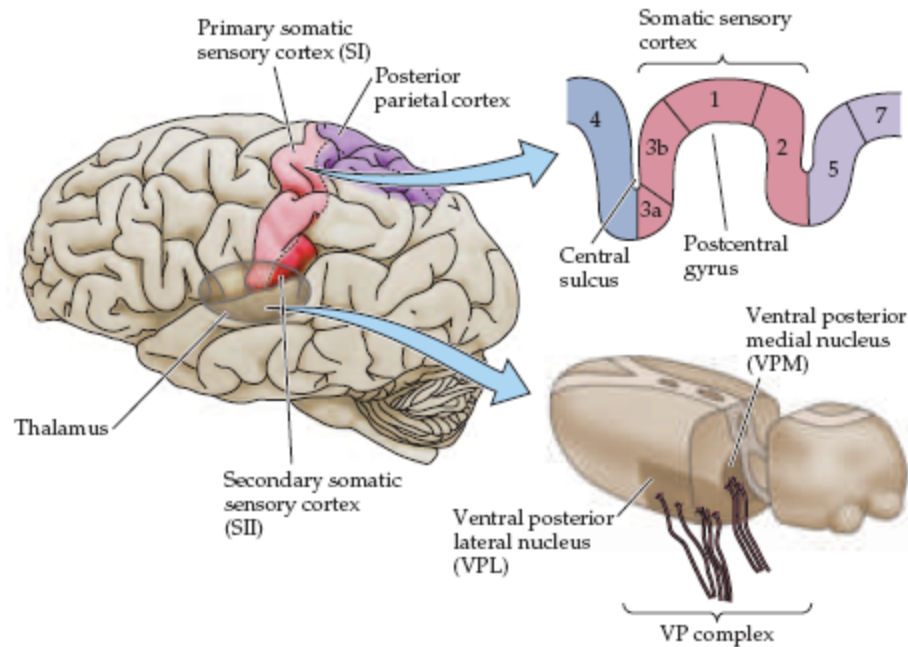
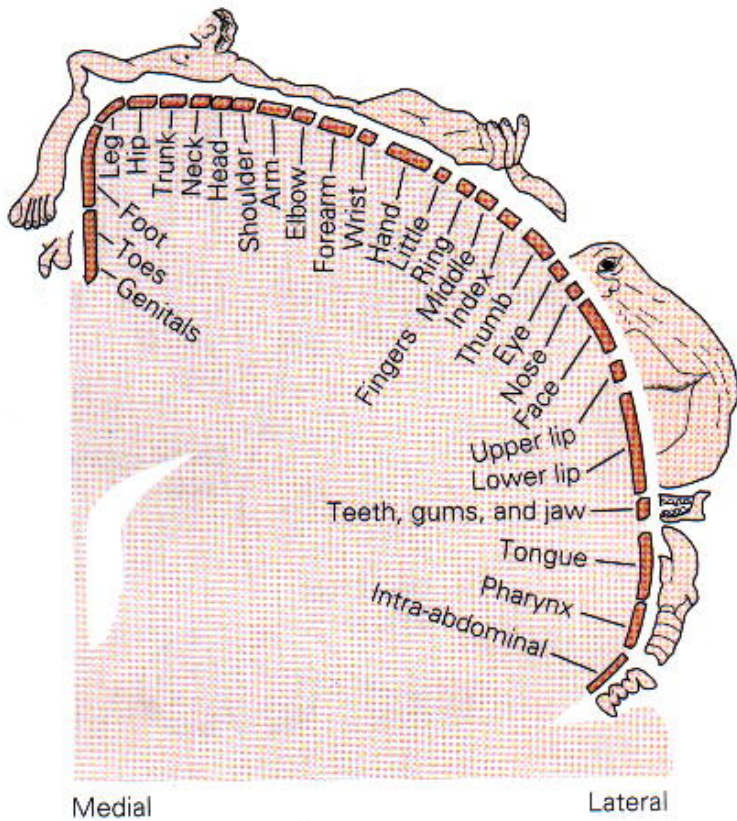


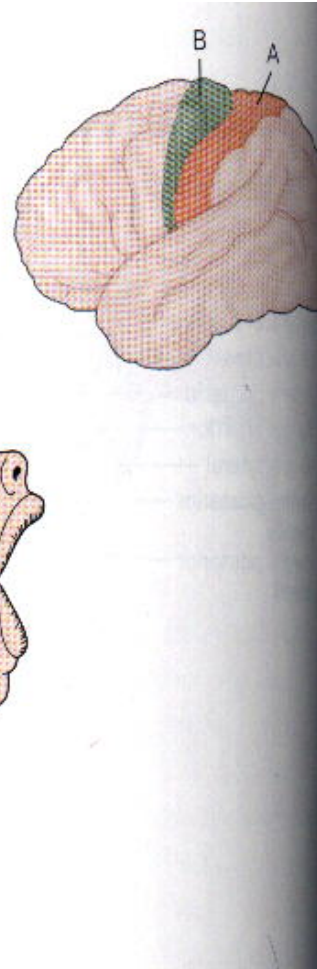
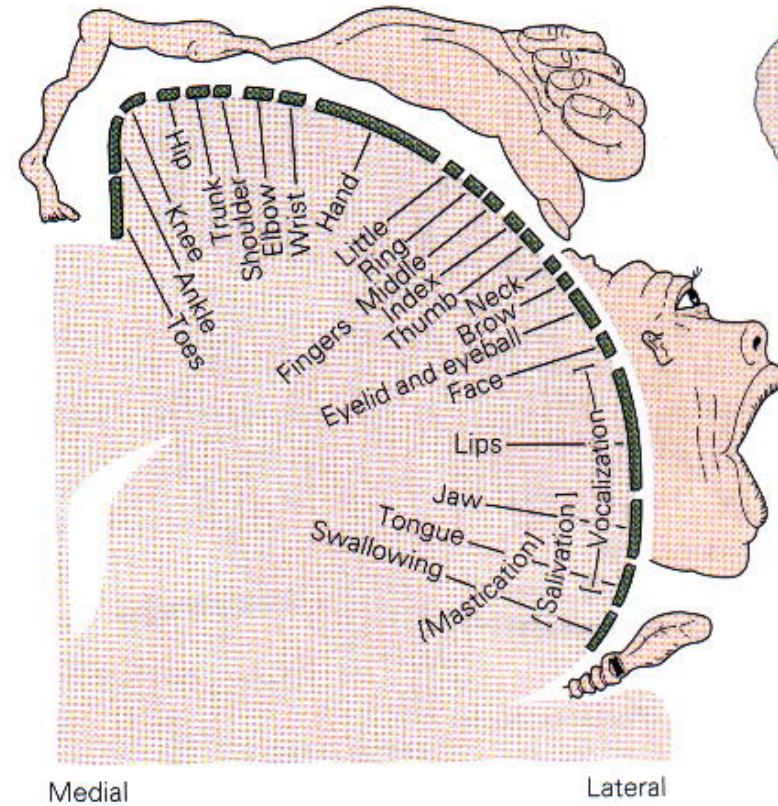
Figure 8.7 Diagram of the somatic sensory portions of the thalamus and their cortical targets in the postcentral gyrus. The ventral posterior nuclear complex comprises the VPM, which relays somatic sensory information carried by the trigeminal system from the face, and the VPL, which relays somatic sensory 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

A Sensory homunculus



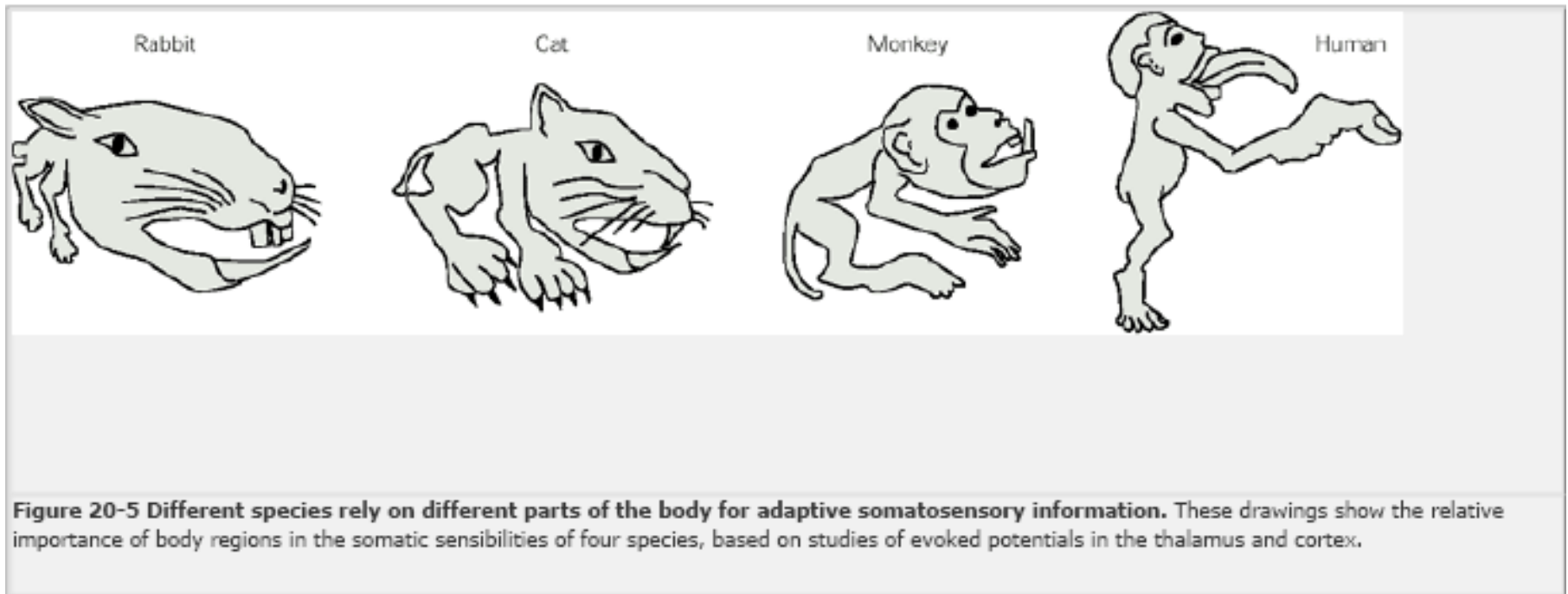
B Motor homunculus



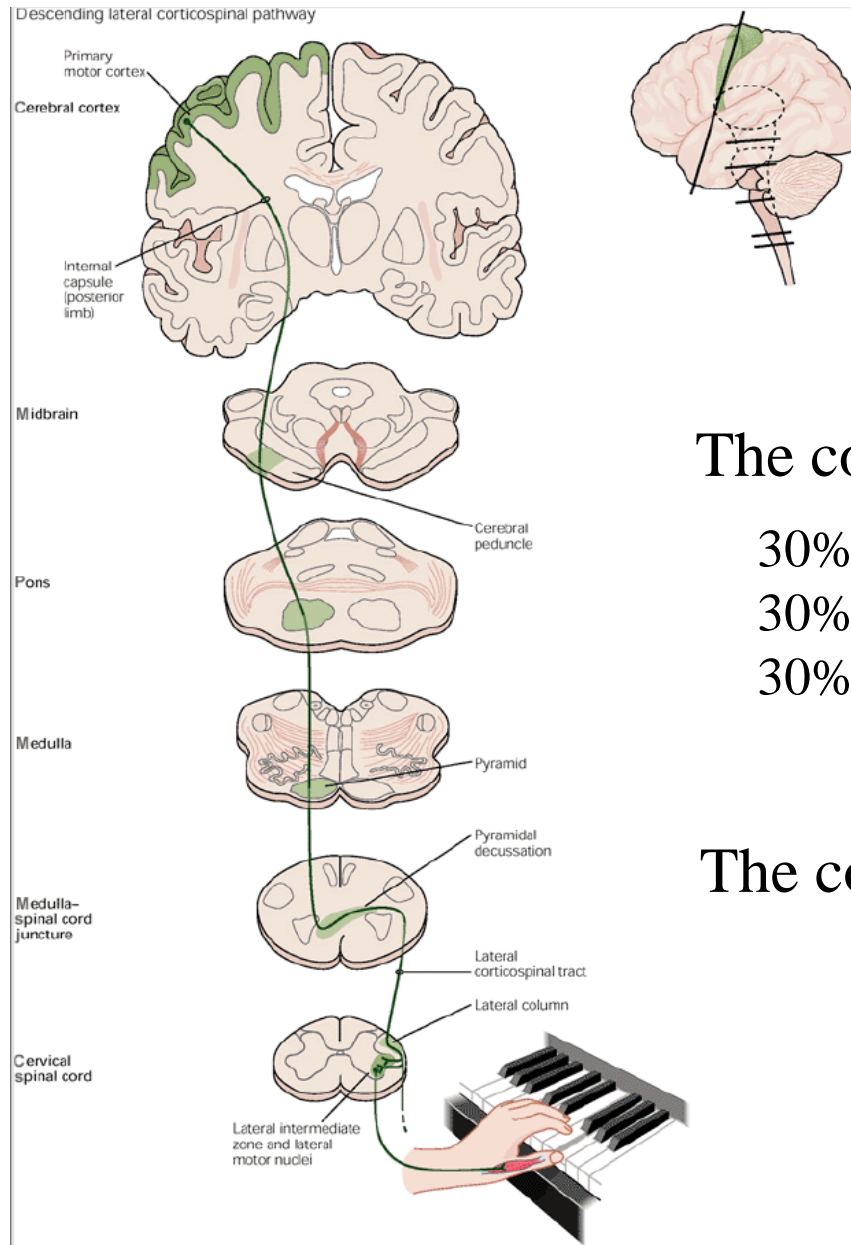
The Homunculi

Relative size reflects innervation density

phylogenetically



Motor signal conduction



The cortico-spinal tract

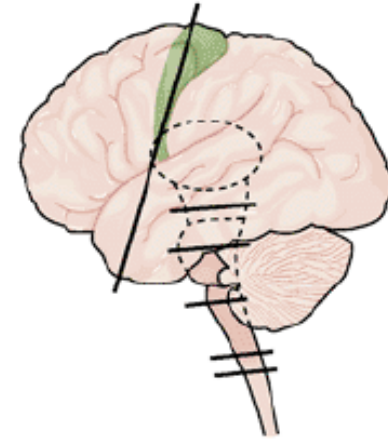
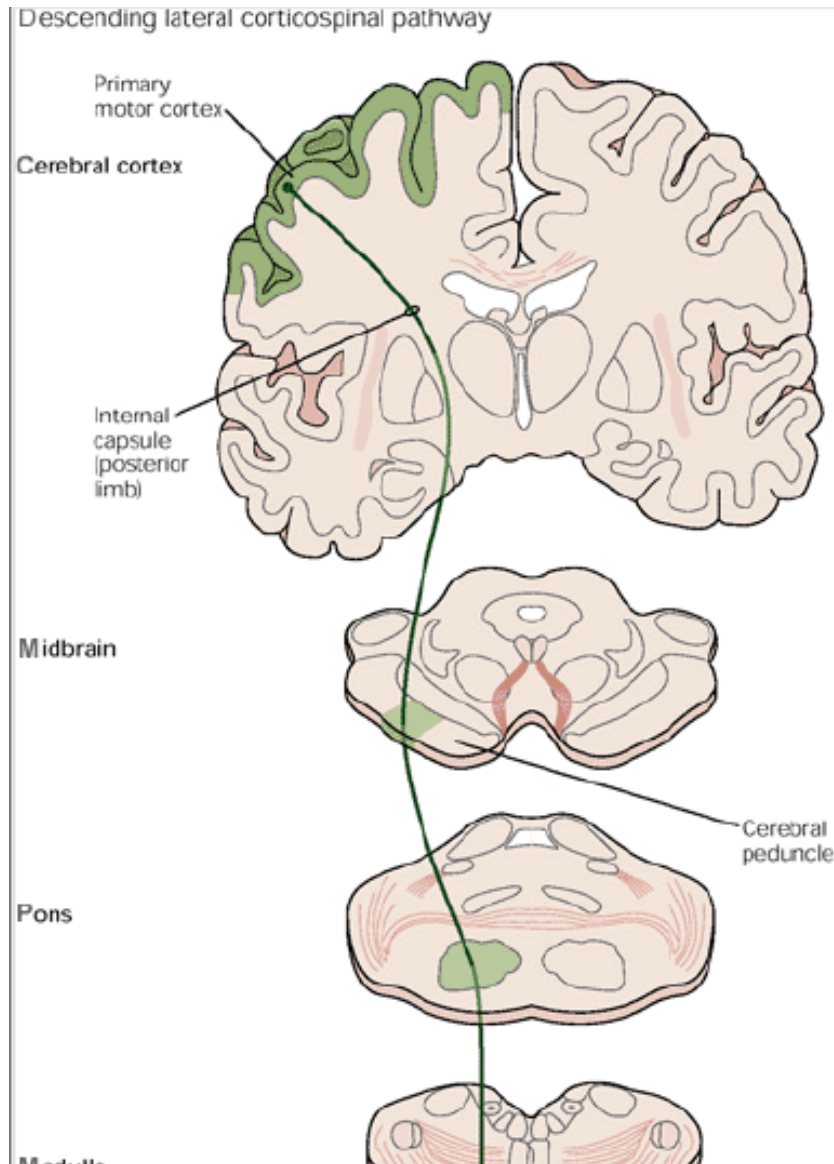
30% - M1

30% - premotor

30% - somatosensory, parietal

The cortico-bulbar tract

Motor signal conduction



The cortico-spinal tract

(not reversal of the afferent pathway)

Motor signal conduction

Midbrain

Pons

Medulla

Medulla-spinal cord junction

Cervical spinal cord

Cerebral peduncle

Pyramid

Pyramidal decussation

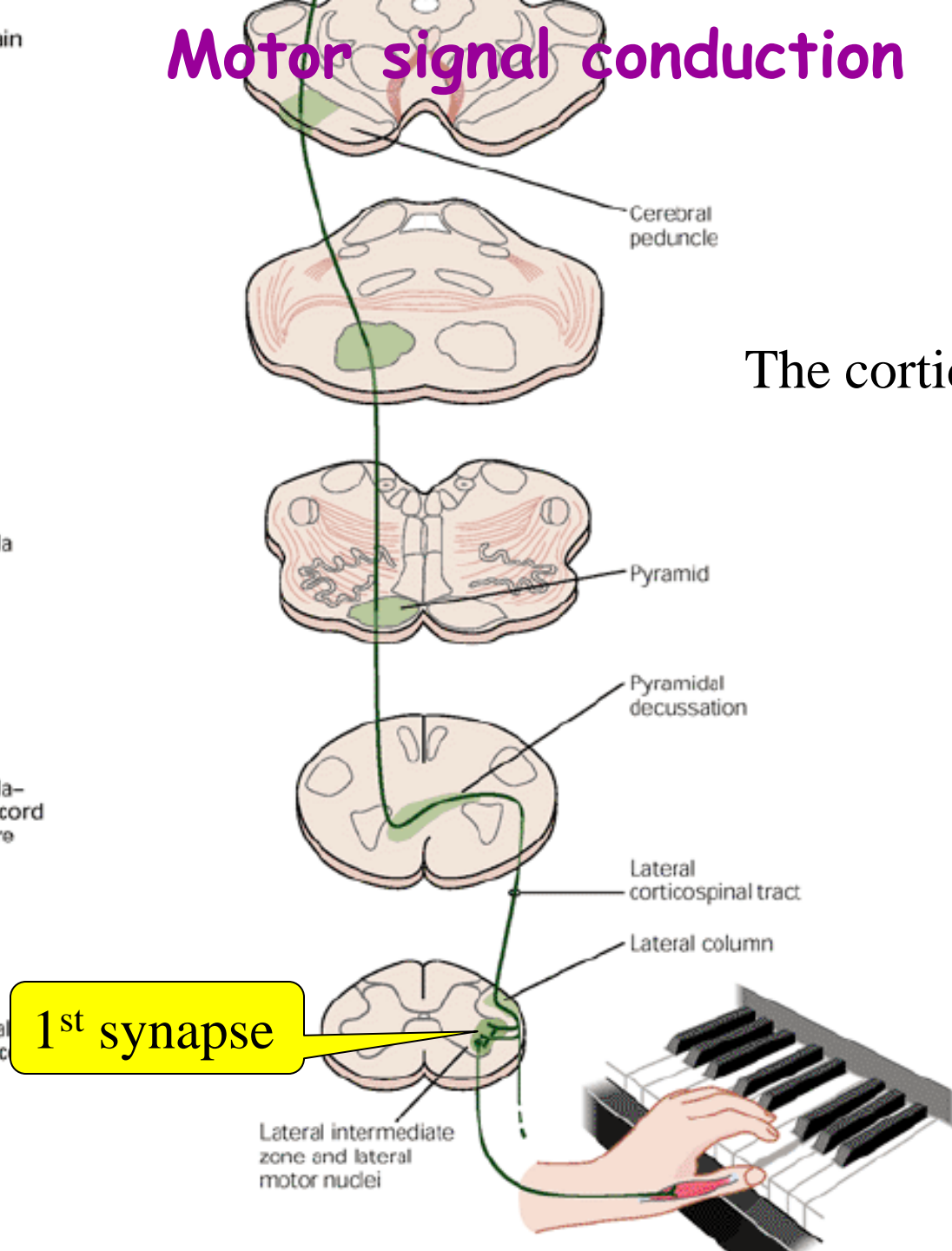
Lateral corticospinal tract

Lateral column

1st synapse

Lateral intermediate zone and lateral motor nuclei

The cortico-spinal tract



The Homunculi

Accurate spatial organization

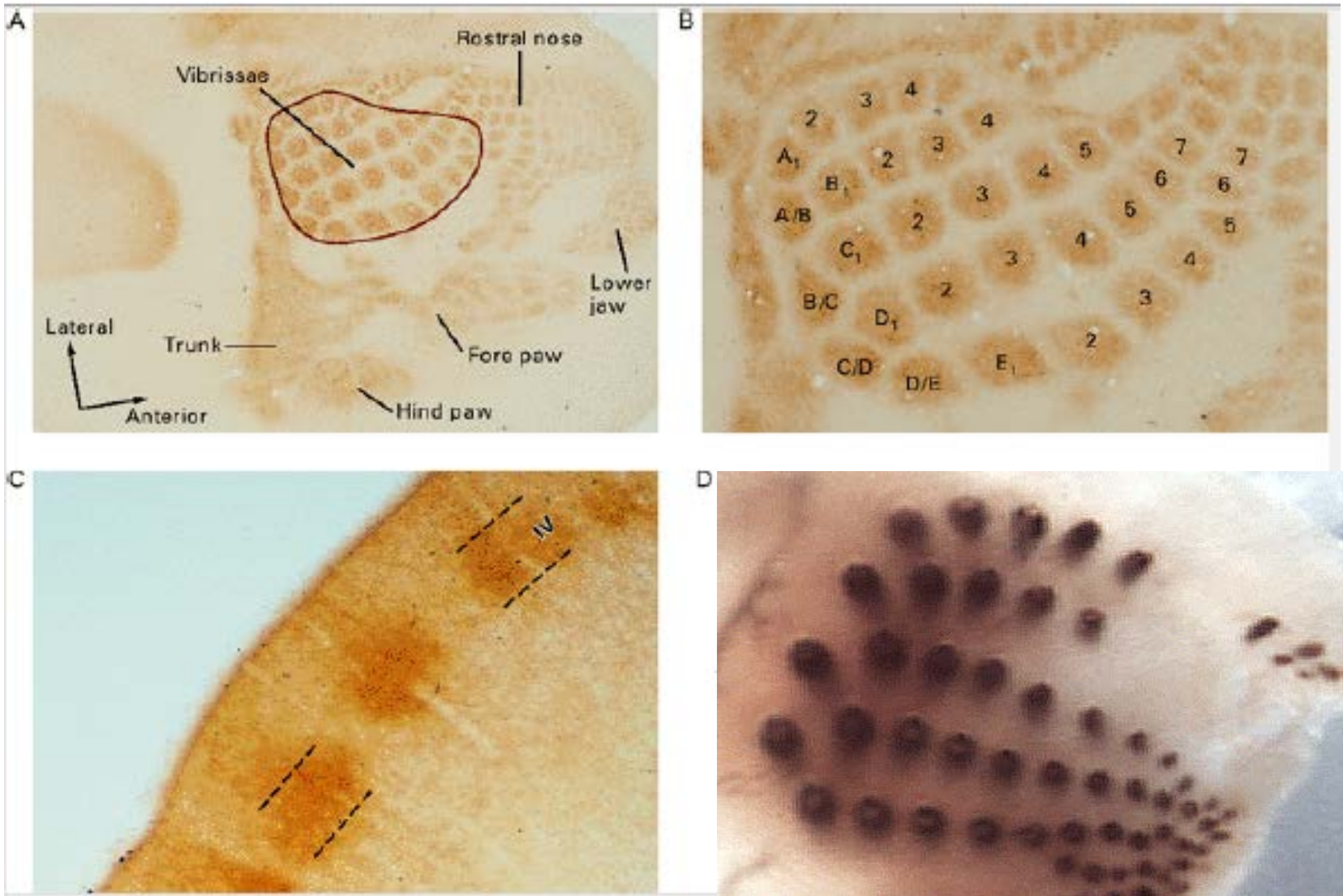
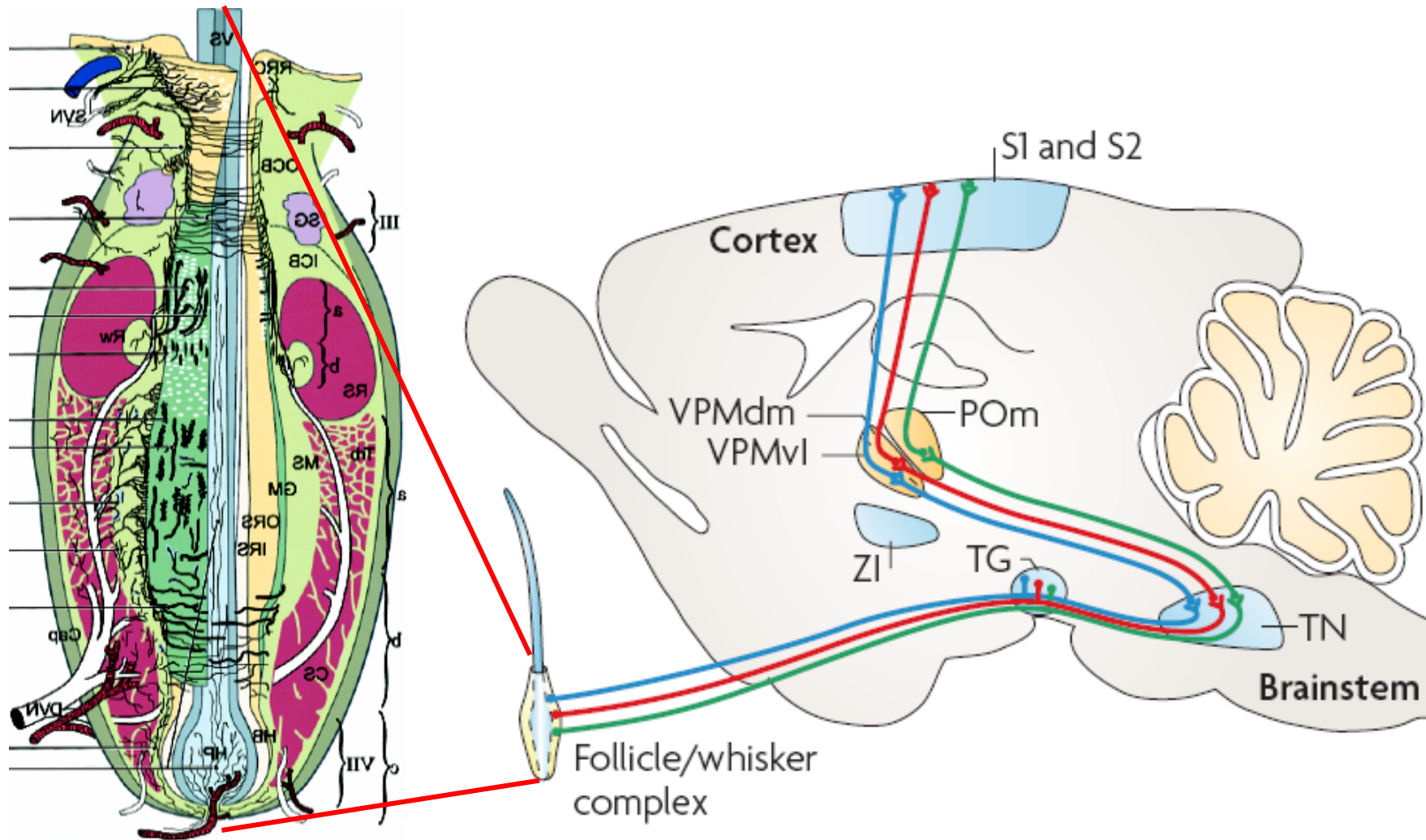


Figure 23-9 The representation of whiskers in the somatosensory cortex of the rat. (Adapted from [Bennett-Clarke et al. 1997](#)).

Sensory signal conduction

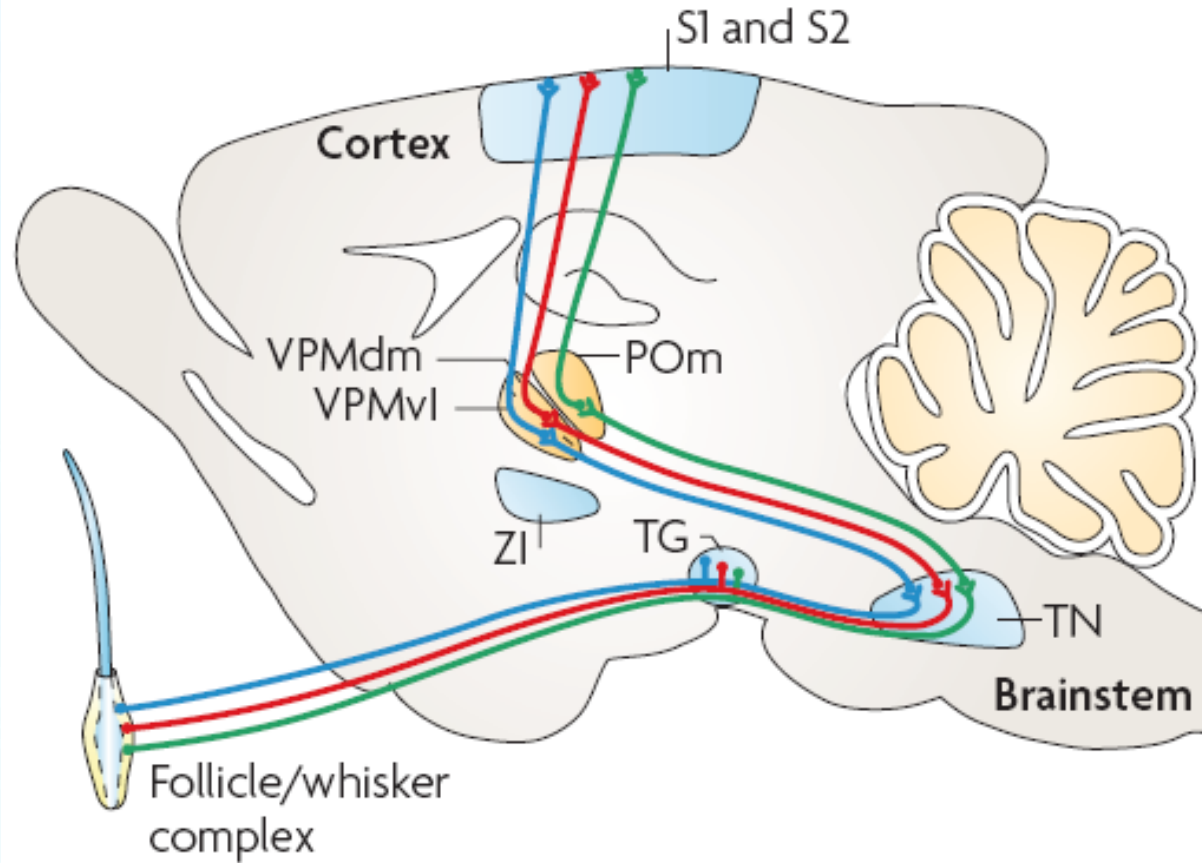
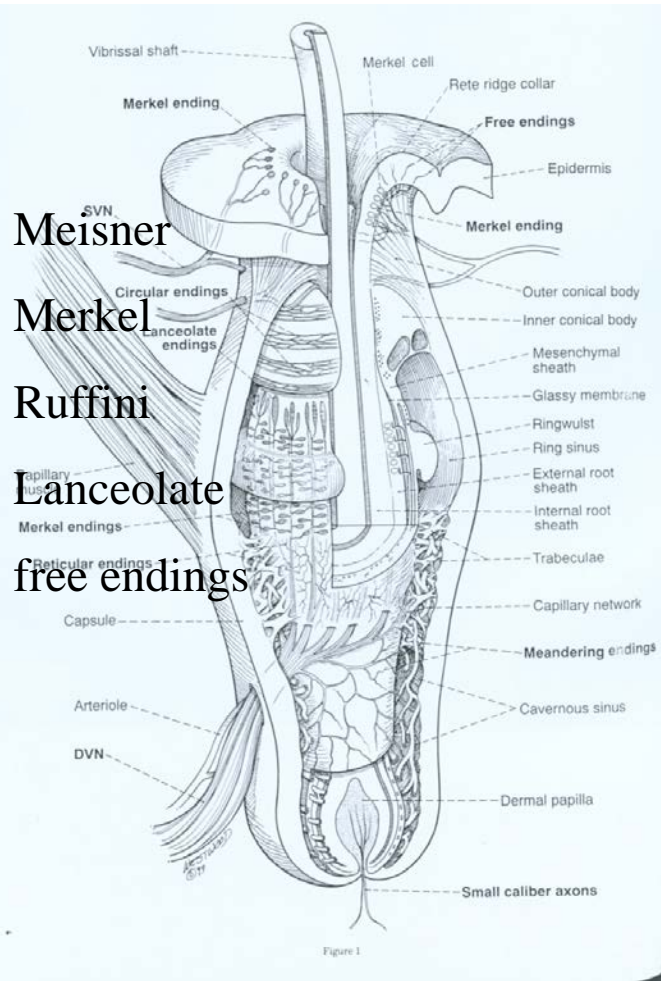
The vibrissal system

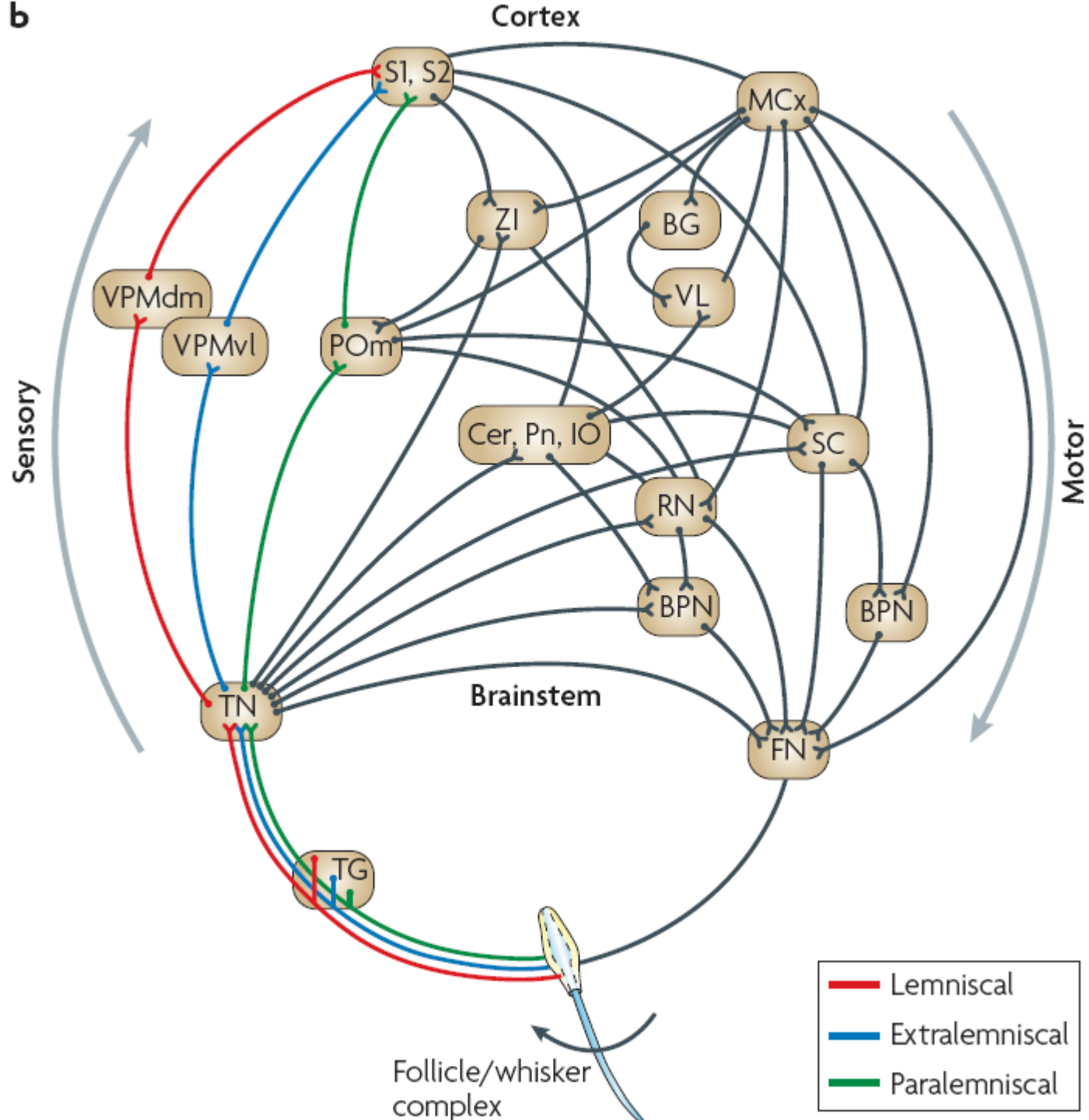


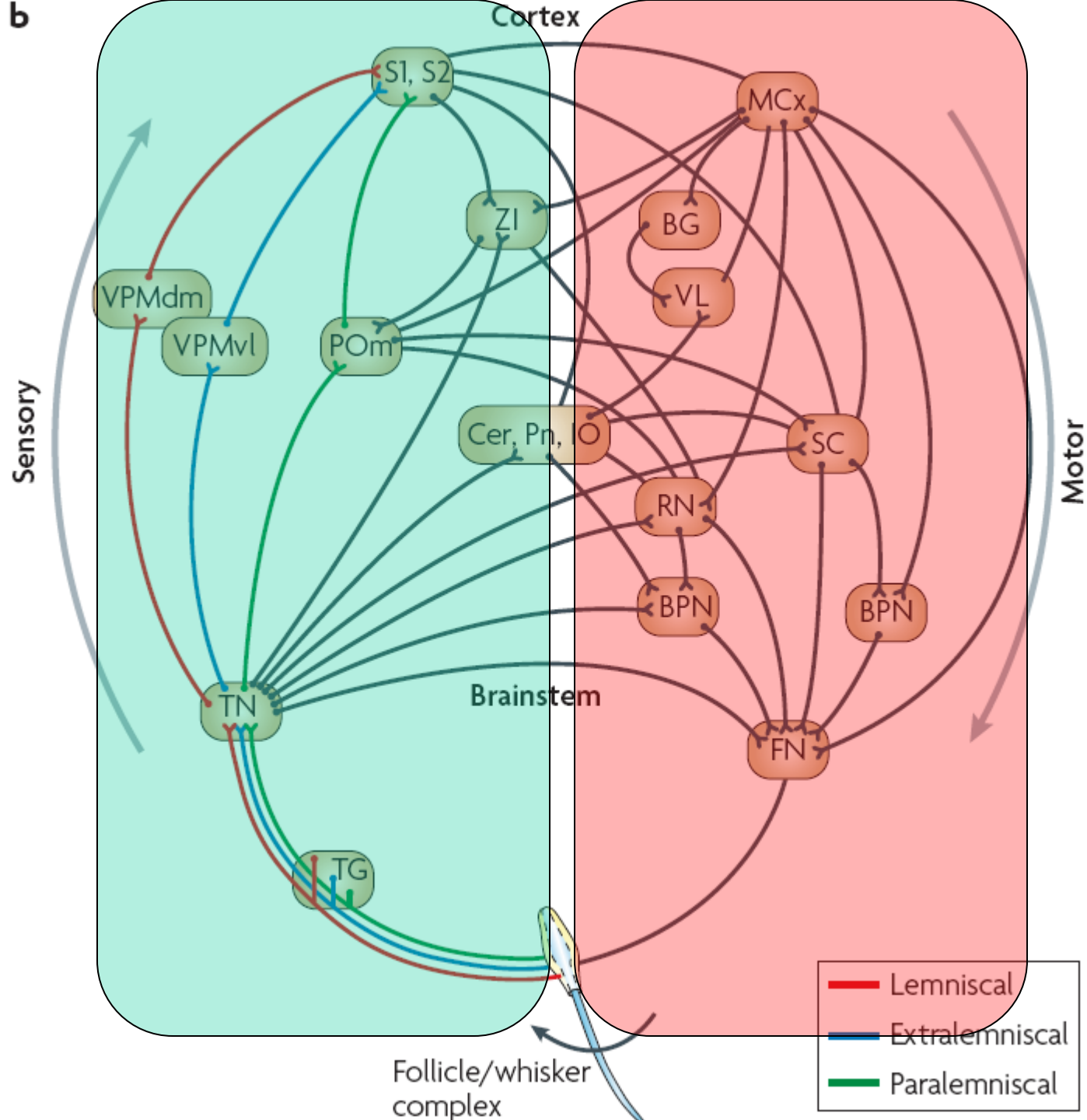
Sensory signal conduction

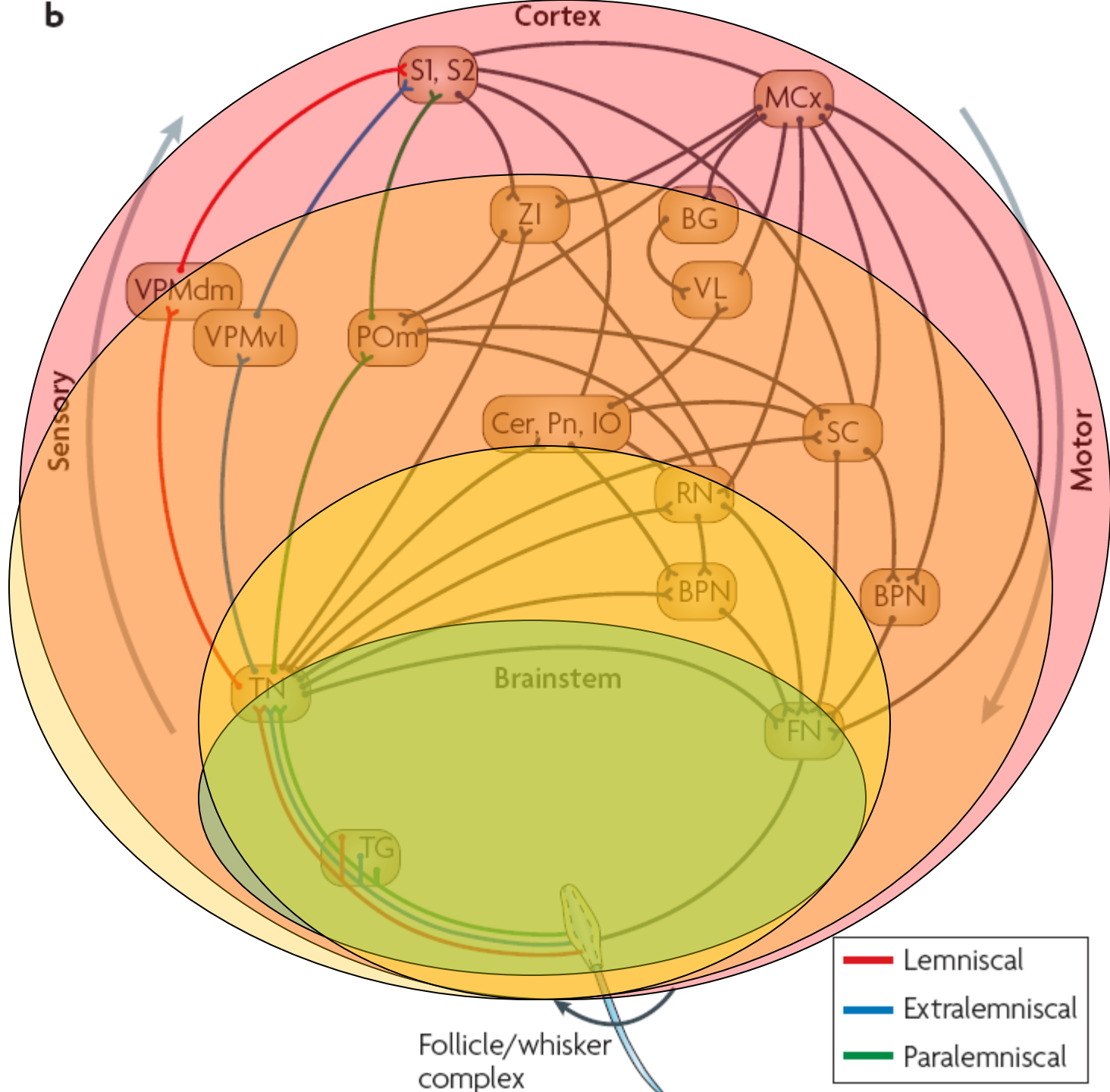
The vibrissal system

whisker



b





Common mechanisms of sensory processing

Rich muscular system

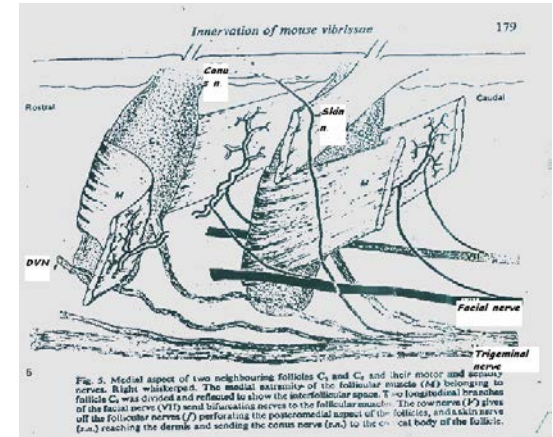
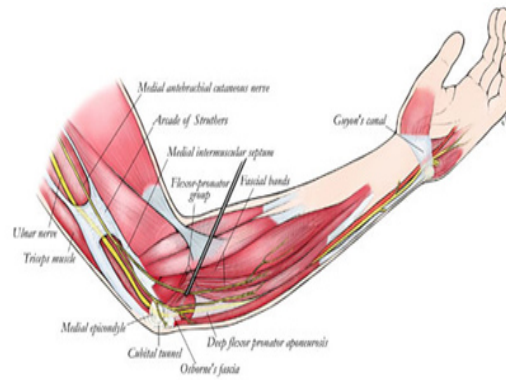
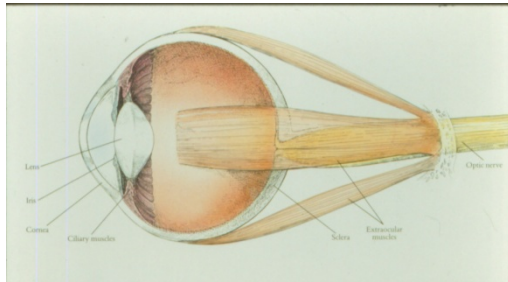
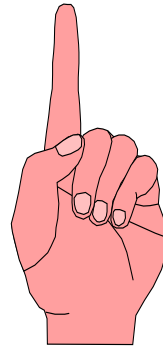
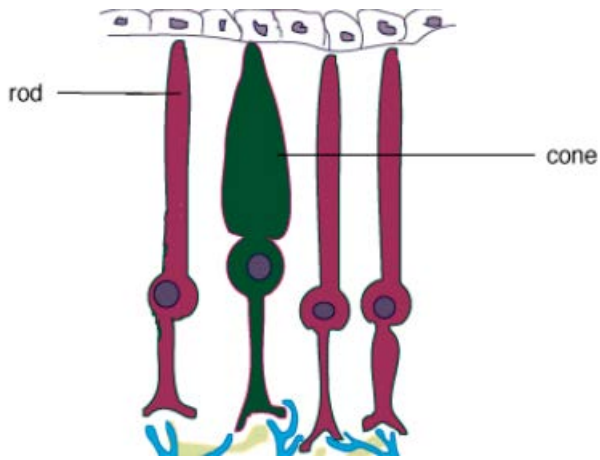


Fig. 5. Medial aspect of two neighbouring follicles C₁ and C₂ and their motor and sensory nerves. Right whiskerpost. The medial sacculus of the follicular muscle (M) belonging to follicle C₂ was divided and reflected to allow the interfollicular space. Two longitudinal branches of the facial nerve (V7) send bifurcating nerves to the follicular muscle. The row nerve (P3) gives off the follicular nerves (F) perforating the postmedial aspect of the follicles, and skin nerves (S) reaching the dermis and sending the coin nerve (S.A.) to the central body of the follicle.

Receptor types

eye



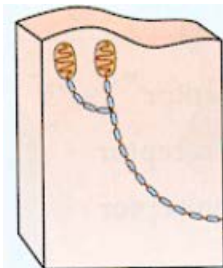
R G B

finger

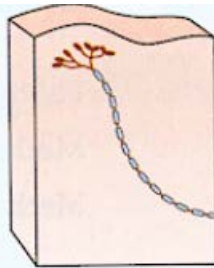
RAI

SAI

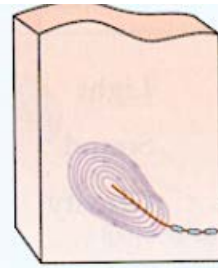
RAII



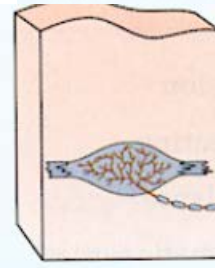
RA



SA



PC



Ruffini endings

whisker

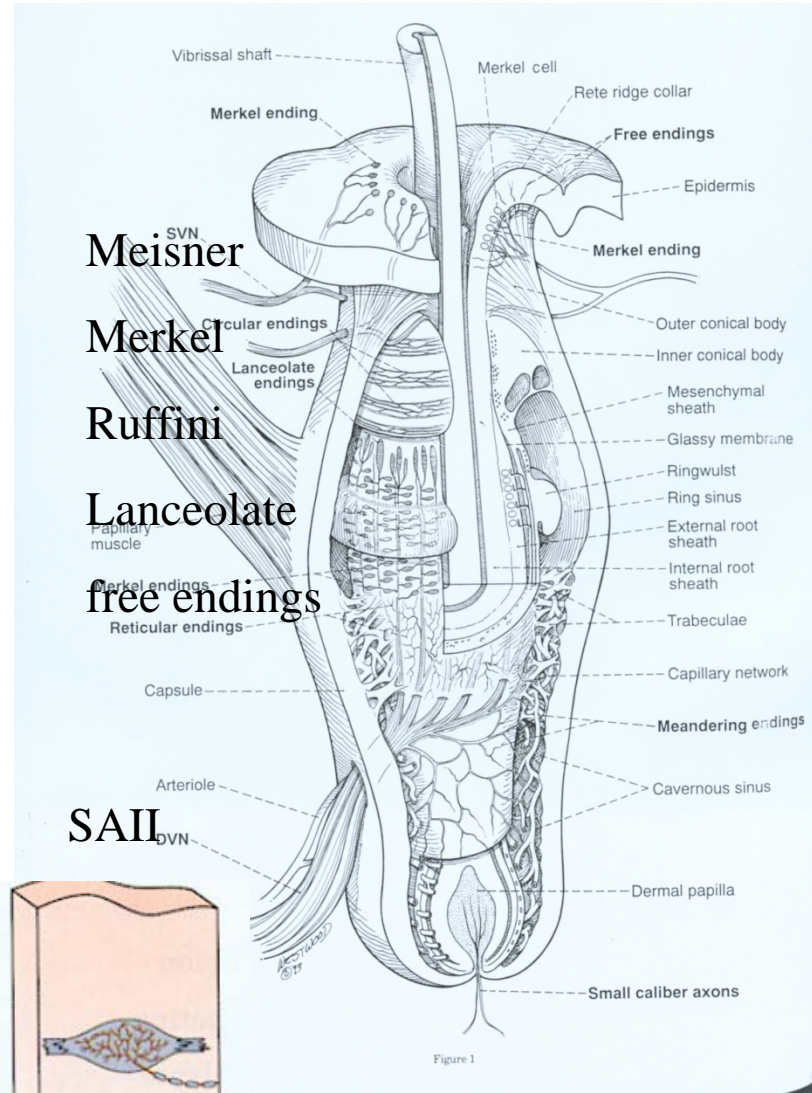
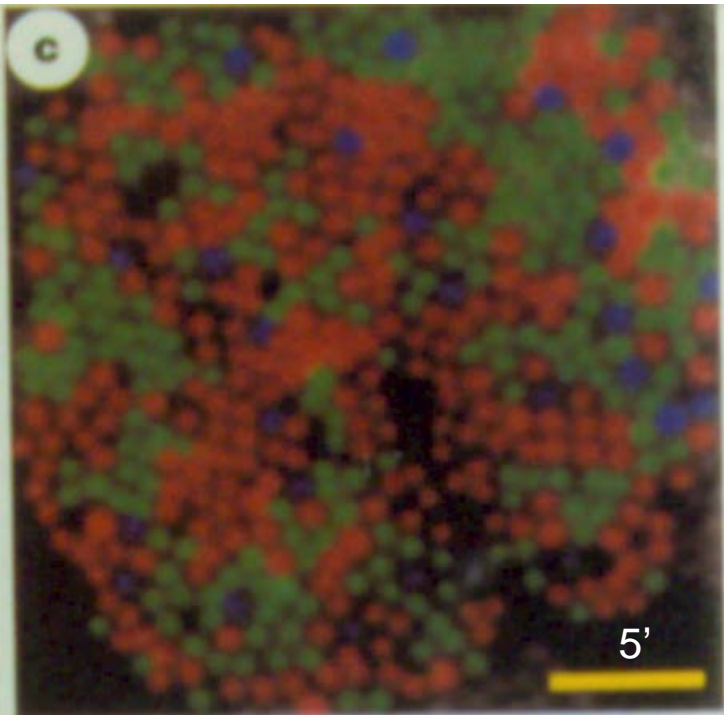


Figure 1

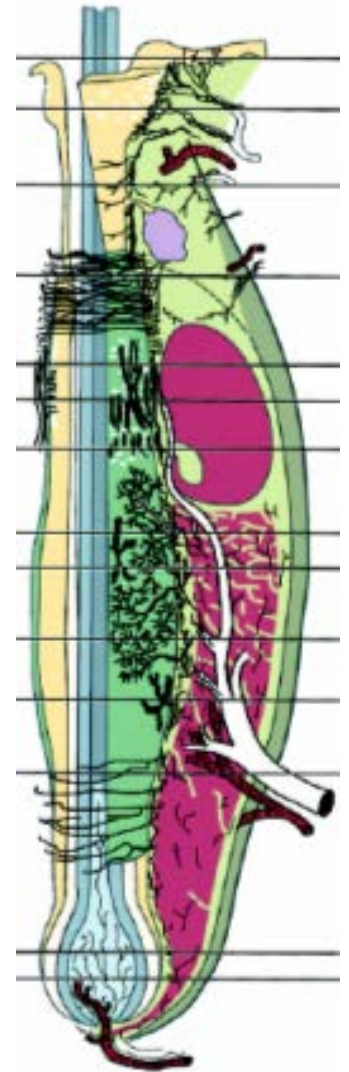
eye

@ 1°

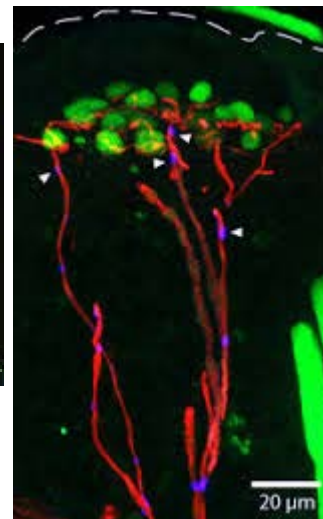
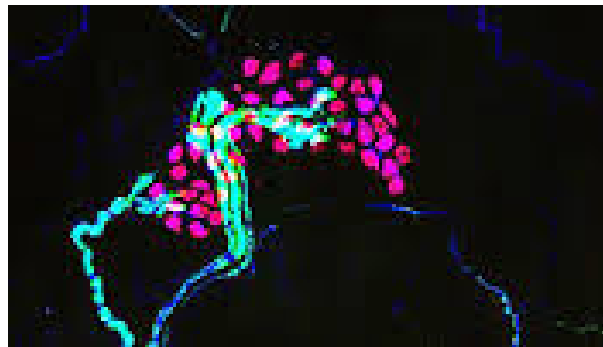
Receptors mix in clusters



whisker



finger



Merkel cells

Receptor convergence / divergence

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

Human skin: 2,500 receptors/cm² --> 300 fibers / cm²

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

~ 10 -> 1 convergence

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

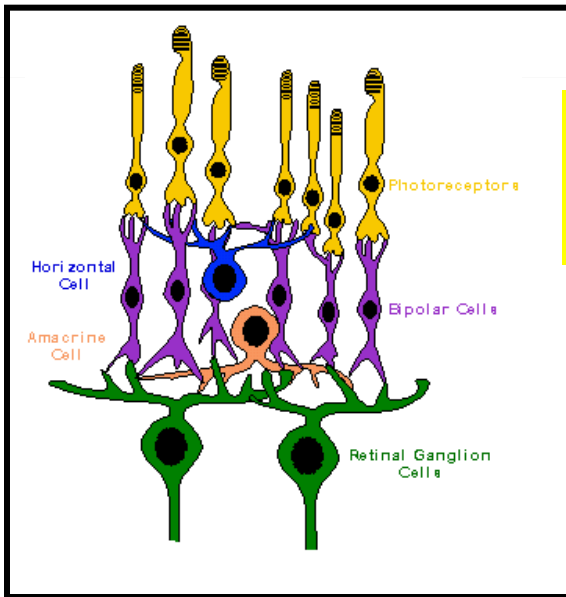
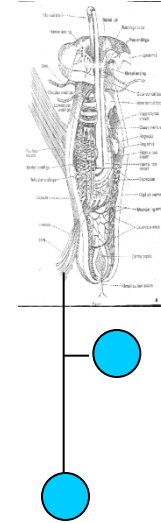
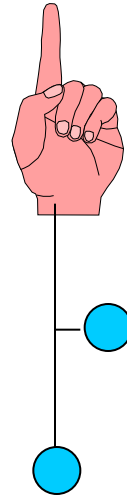
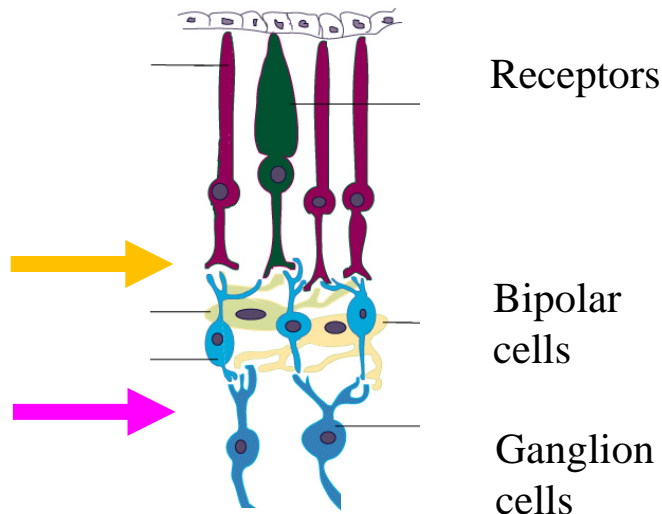
~ 1 -> 10 divergence

Spatial processing (by Lateral inhibition)

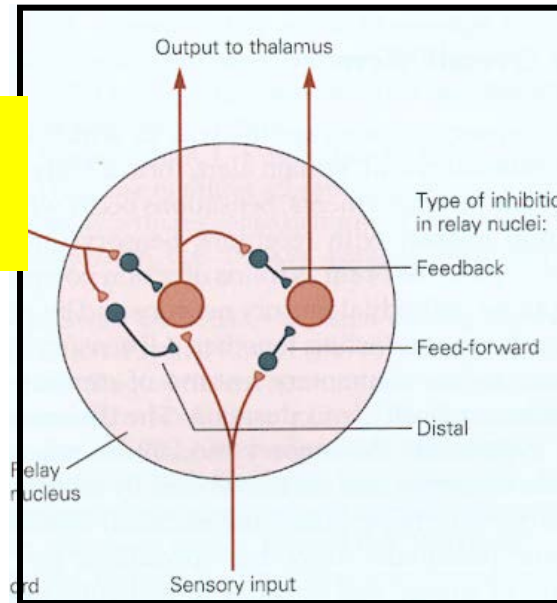
eye

finger

whisker



Drive for clustering?



Efficient coding

(by coding changes only)

Changes in time:

- Intrinsic in individual neurons
- Starting at the receptor level

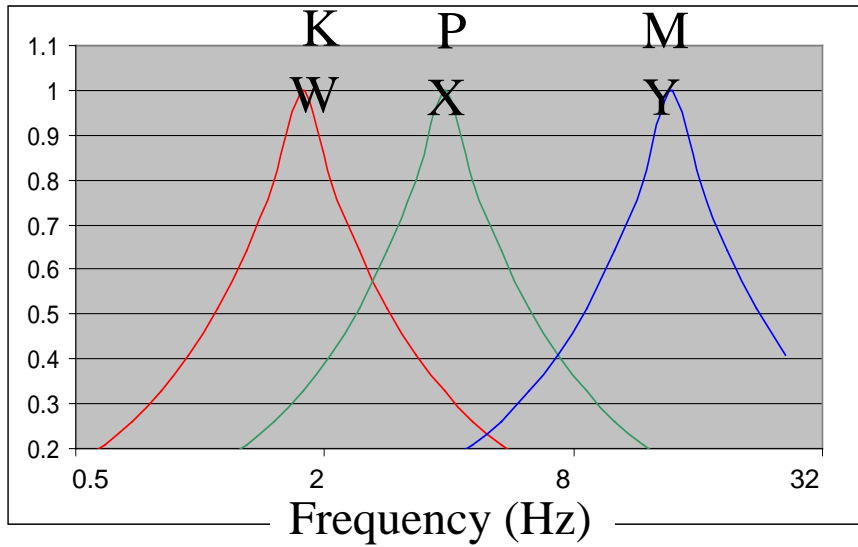
Changes in space:

- Circuits of neurons
- Starting after lateral inhibition

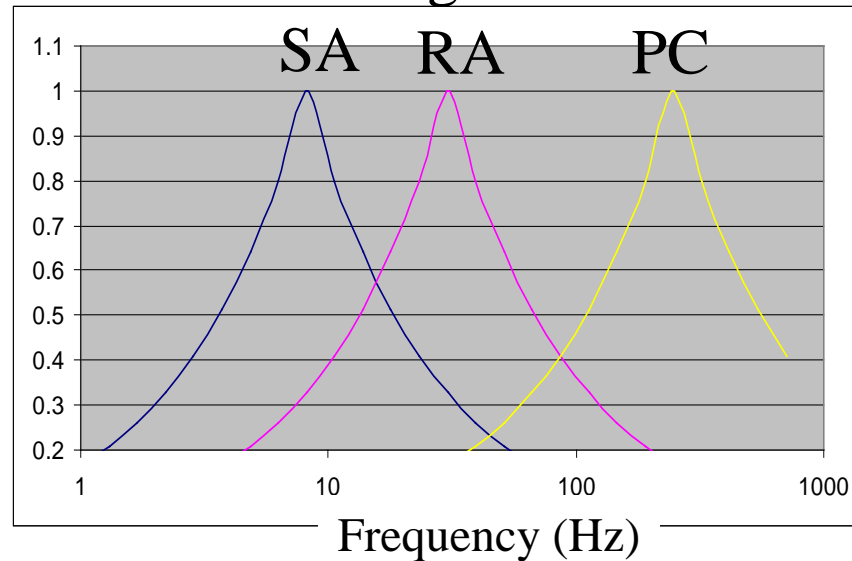
Temporal filtering (by intrinsic factors)

eye

whisker



finger



Neurometric - psychometric matching

sensitivity

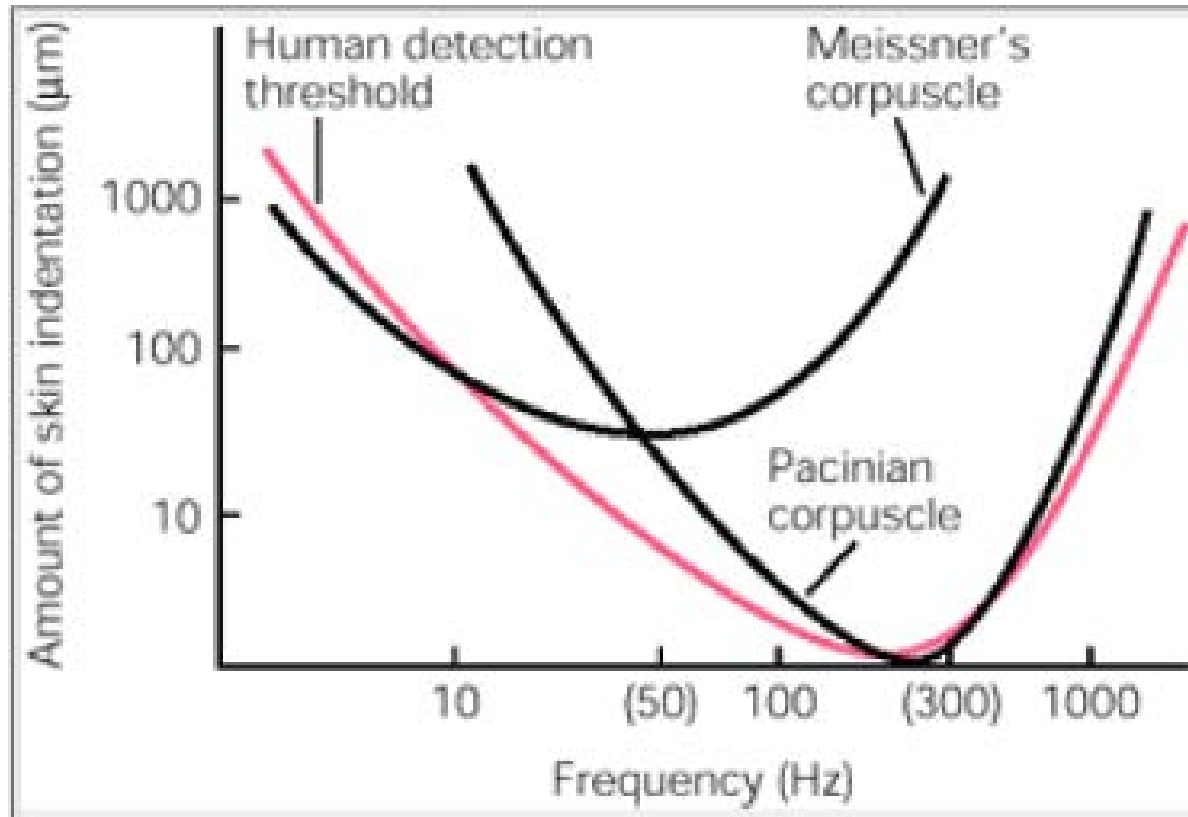


Figure 22-6B The threshold for detecting vibration corresponds to the tuning threshold of the mechanoreceptor. The sensitivity threshold for Meissner's corpuscles is lowest for frequencies of 20-50 Hz. Pacinian corpuscles sense higher frequencies. (Adapted from Mountcastle et al. 1972.)

Passive and active touch

Passive touch

- Perceptual processing follows sensory events

Active touch

- Perceptual processing surrounds sensory events:
 - The brain probes the world
 - Compares sensory data with internal expectations
 - 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

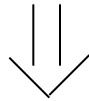
Active touch

- higher thresholds
- high accuracy

Passive and active touch

Passive touch

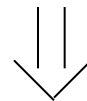
- low thresholds
- poor accuracy



Detection

Active touch

- higher thresholds
- high accuracy



Exploration

Object localization

Object identification

Passive and active touch

Passive touch

- low thresholds
- poor accuracy

Active touch

- higher thresholds
- 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

Passive and active touch

Passive touch

- low thresholds
- poor accuracy

Active touch

- higher thresholds
- high accuracy

Underlying mechanisms:

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

Passive and active touch

Passive touch

- low thresholds
- poor accuracy

Active touch

- higher thresholds
- high accuracy

Underlying active mechanisms:

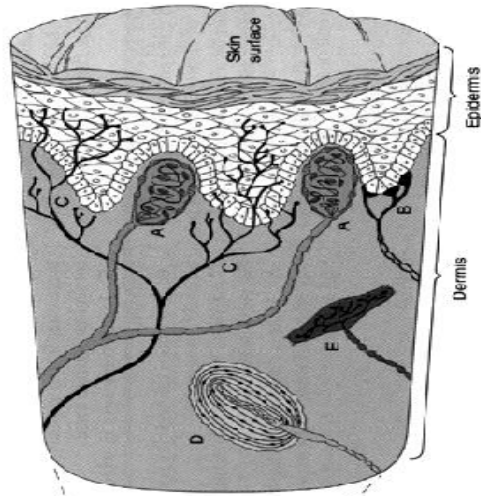
- Additional information
 - expectations
 - accumulation of sensory data over time
 - more coding dimensions
 - increased resolution due to scanning
- close-loop operation

Sensory encoding:

What receptors tell the brain

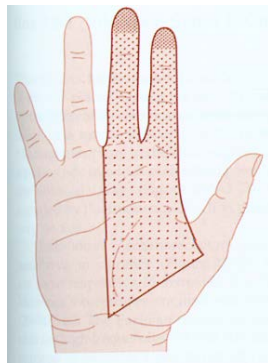
Sensory organs consist of **receptor arrays**:

somatosensation



~200 μm

Finger pad

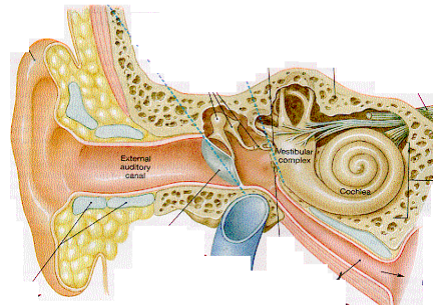


audition

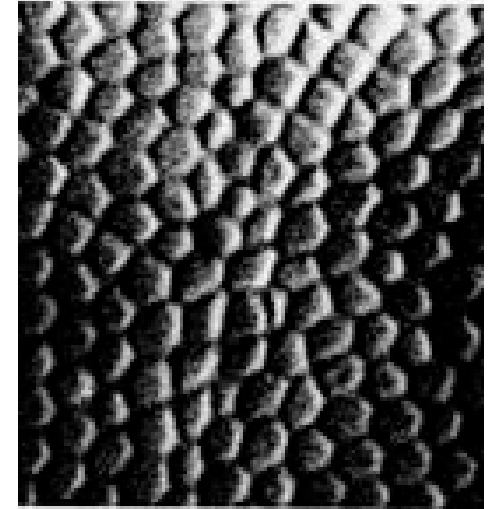


10 μm

cochlea

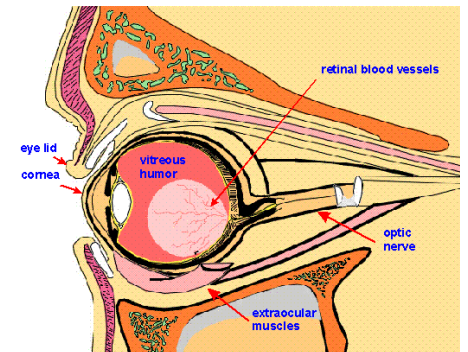


vision



10 μm

retina

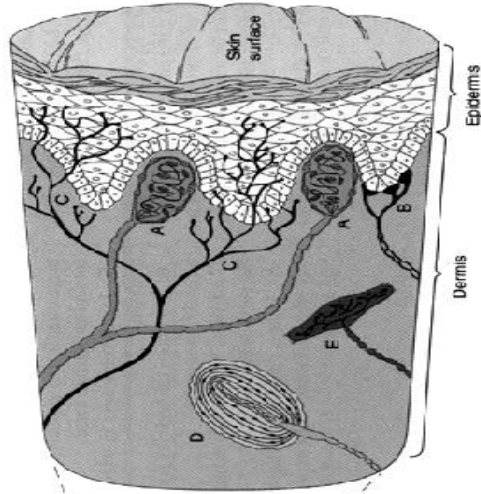


Sensory encoding:

What receptors tell the brain

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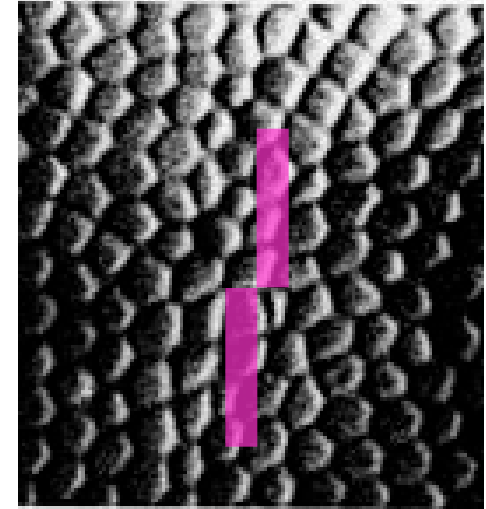
audition



10 μm

cochlea

vision



10 μm

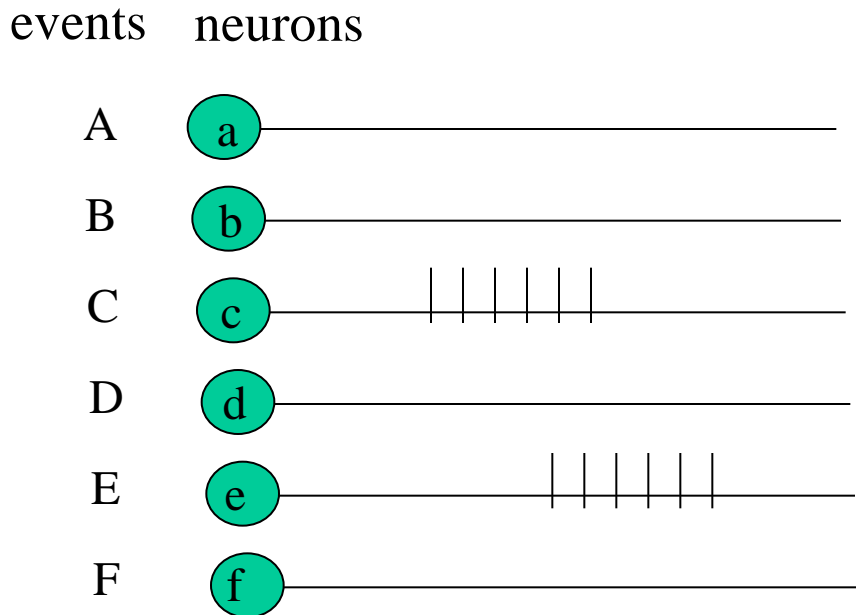
retina

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

How neurons encode external events in space?

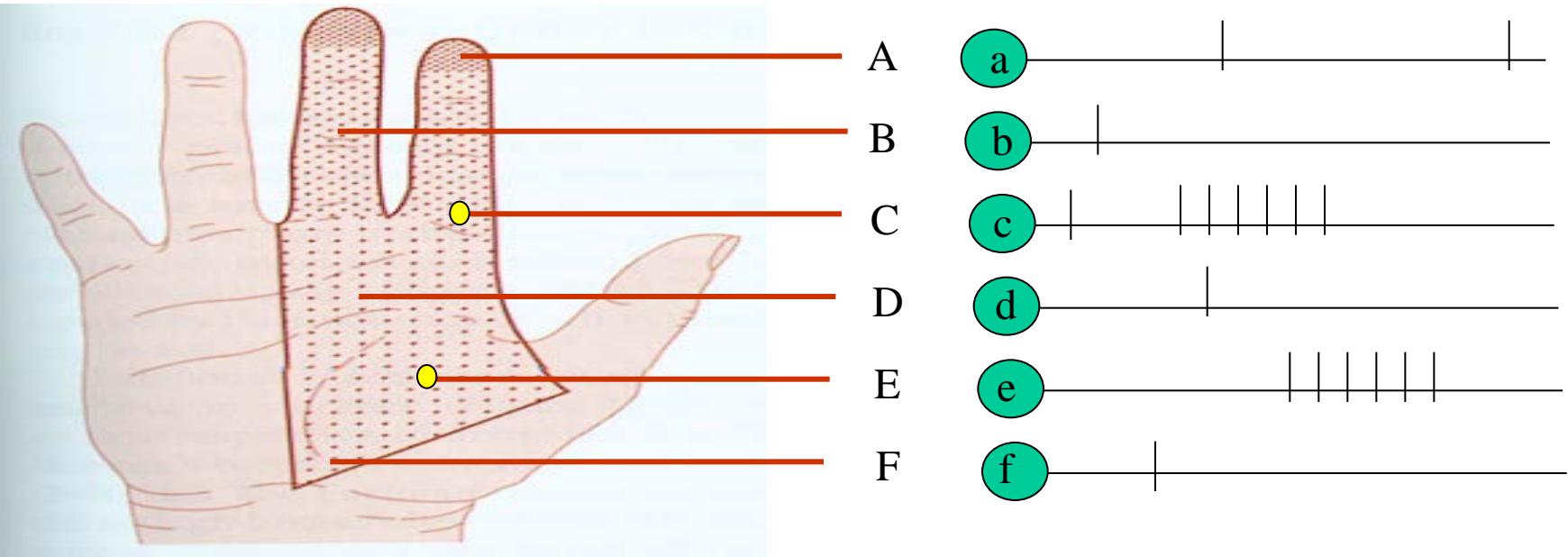
The “labeled-line code”.

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 and only if neuron x fires

On what condition will this algorithm be valid?

(X) ~~$\bullet \Rightarrow$~~ \bullet_x ~~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

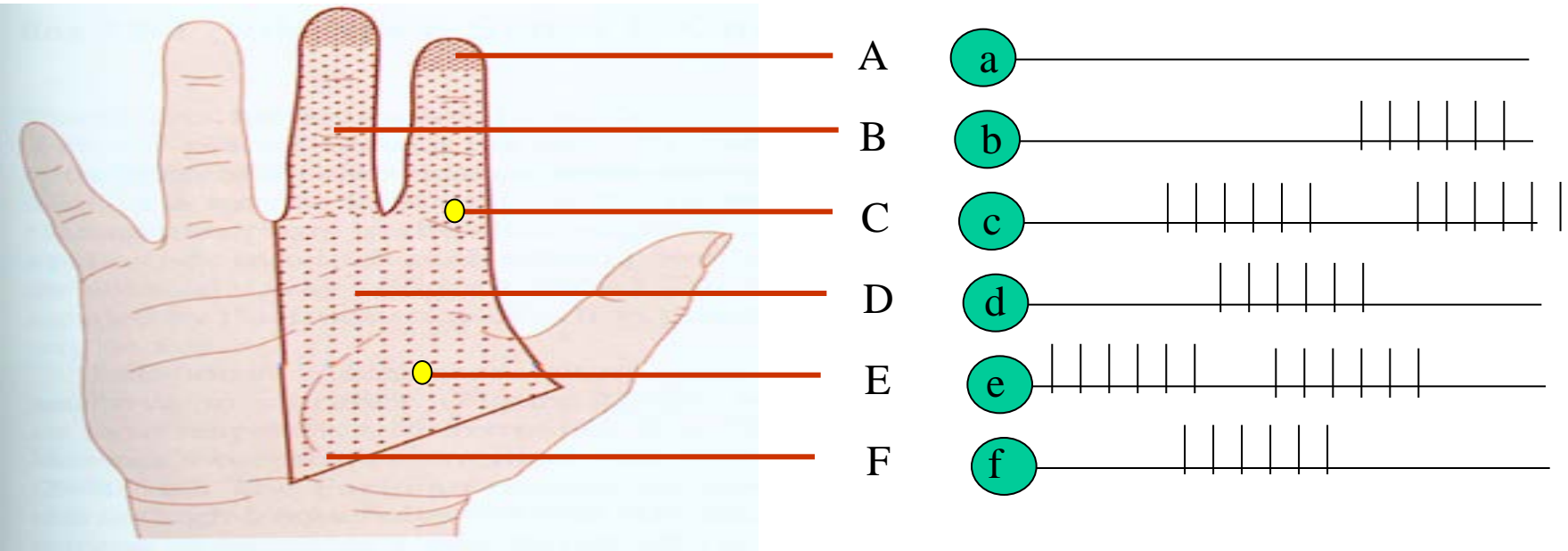
receptors are sensitive to changes

Thus

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

How sensor motion constrains sensory coding?

Reading out the labeled line code



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

On what condition will this algorithm be valid?

(X) ~~$\bullet \Rightarrow$~~ \bullet_x —|—|—| Neuron x fires ~~if and only if~~ X is pressed

Is this assumption valid?

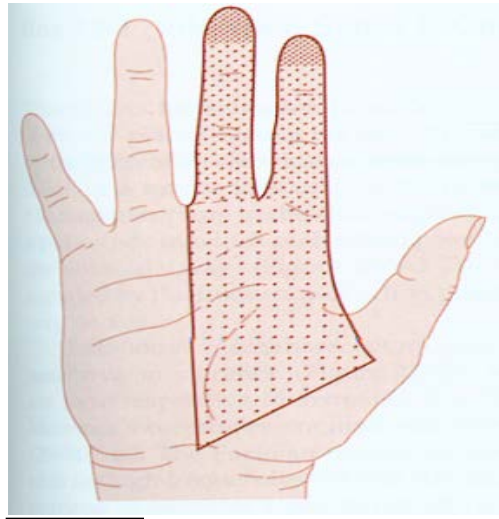
2. The “problem” of sensor motion

sensory encoding:

What receptors tell the brain

Sensory organs consist of **receptor arrays**:

somatosensation



~50 μm

Finger pad

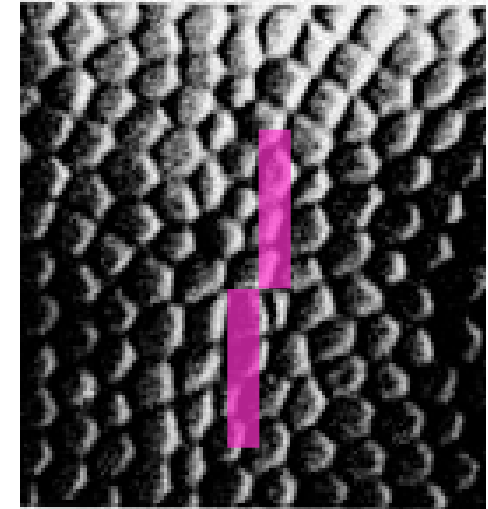
audition



10 μm

cochlea

vision



10 μm

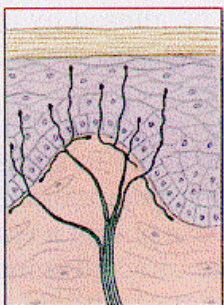
retina

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

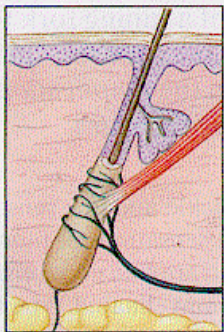
Movements => **Temporal coding** (“*when* receptors are activated”)

Receptors

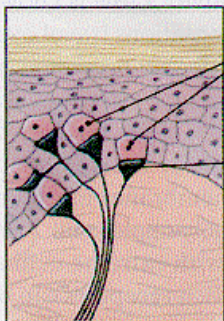
Evolutionary specialization



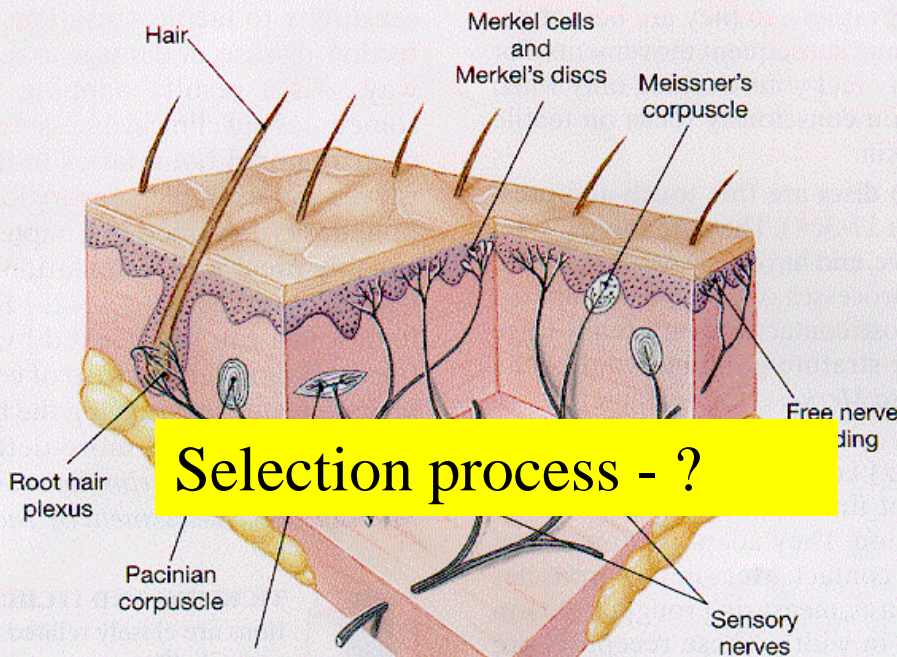
(a) Free nerve endings



(b) Free nerve endings of root hair plexus

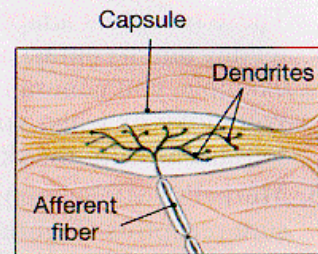


(c) Merkel cells and Merkel's discs

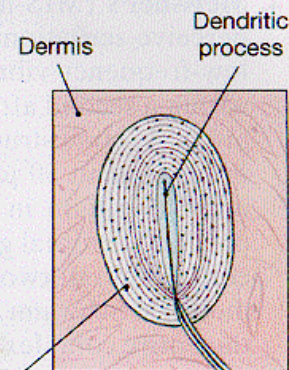


Selection process - ?

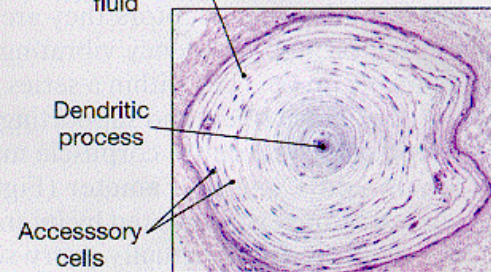
Morphological processing



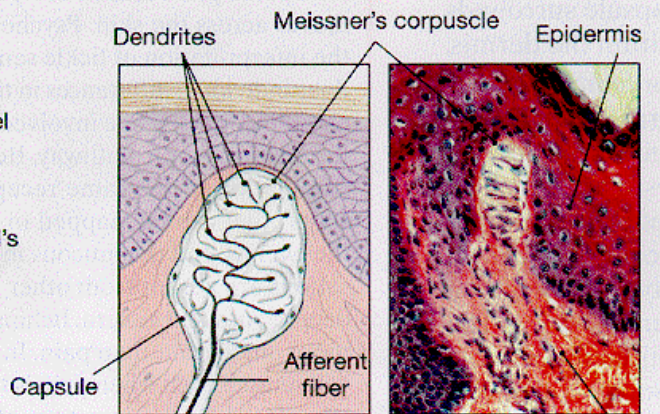
(f) Ruffini corpuscle



Layers of collagen fibers separated by fluid



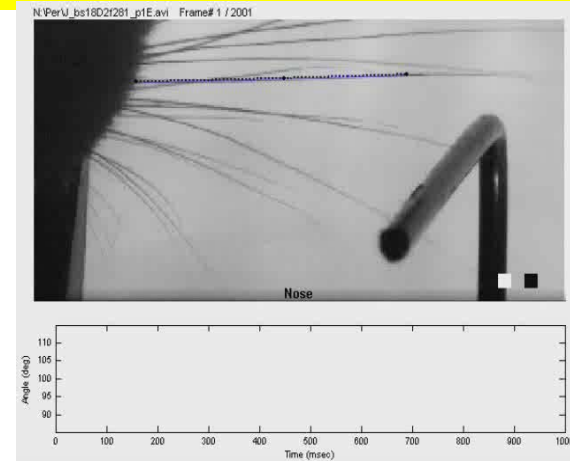
(e) Pacinian corpuscle



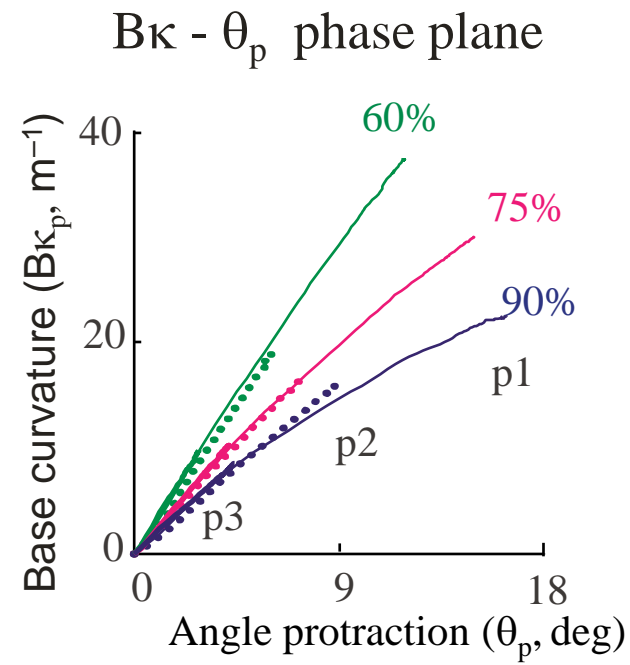
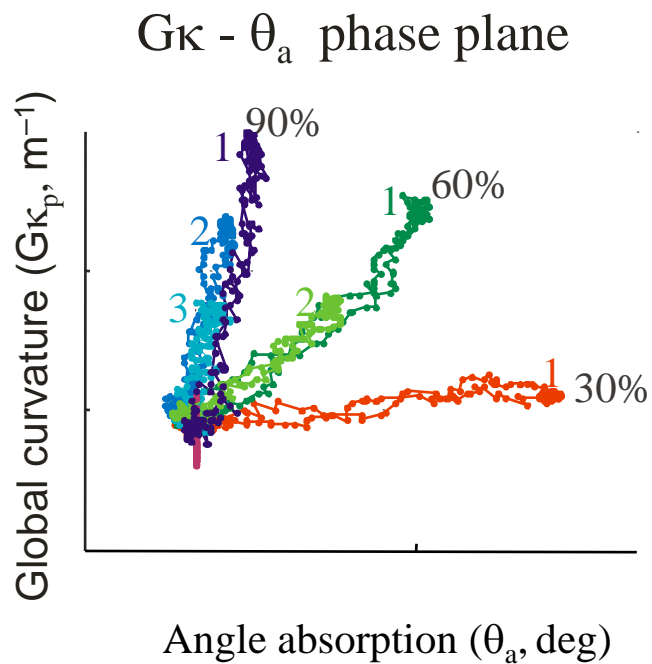
(d) Meissner's corpuscle

Dermis

Morphological processing

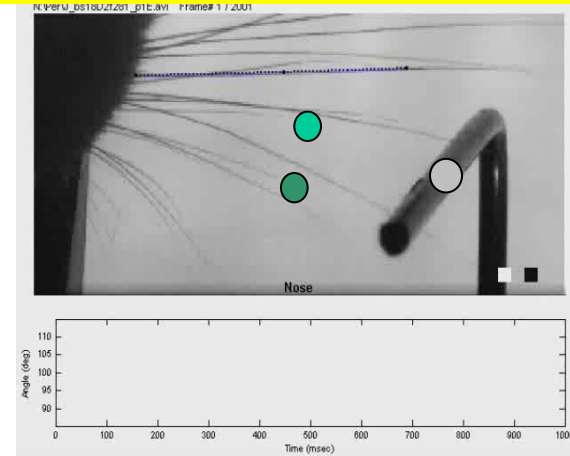


Morphological phase plane

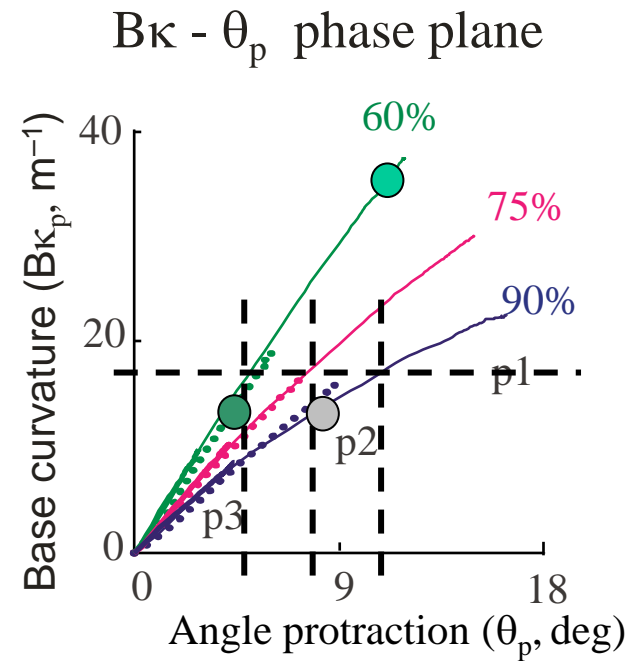
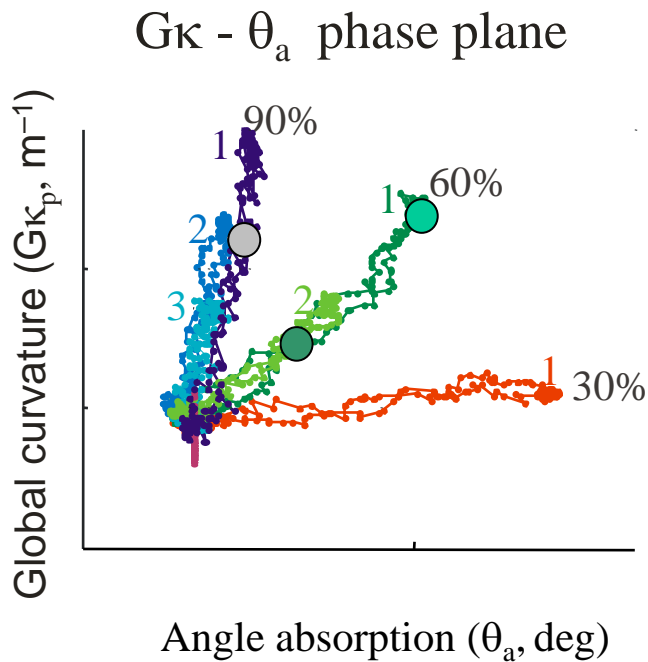


Morphological processing

Motor-sensory phase plane
Morphological phase plane

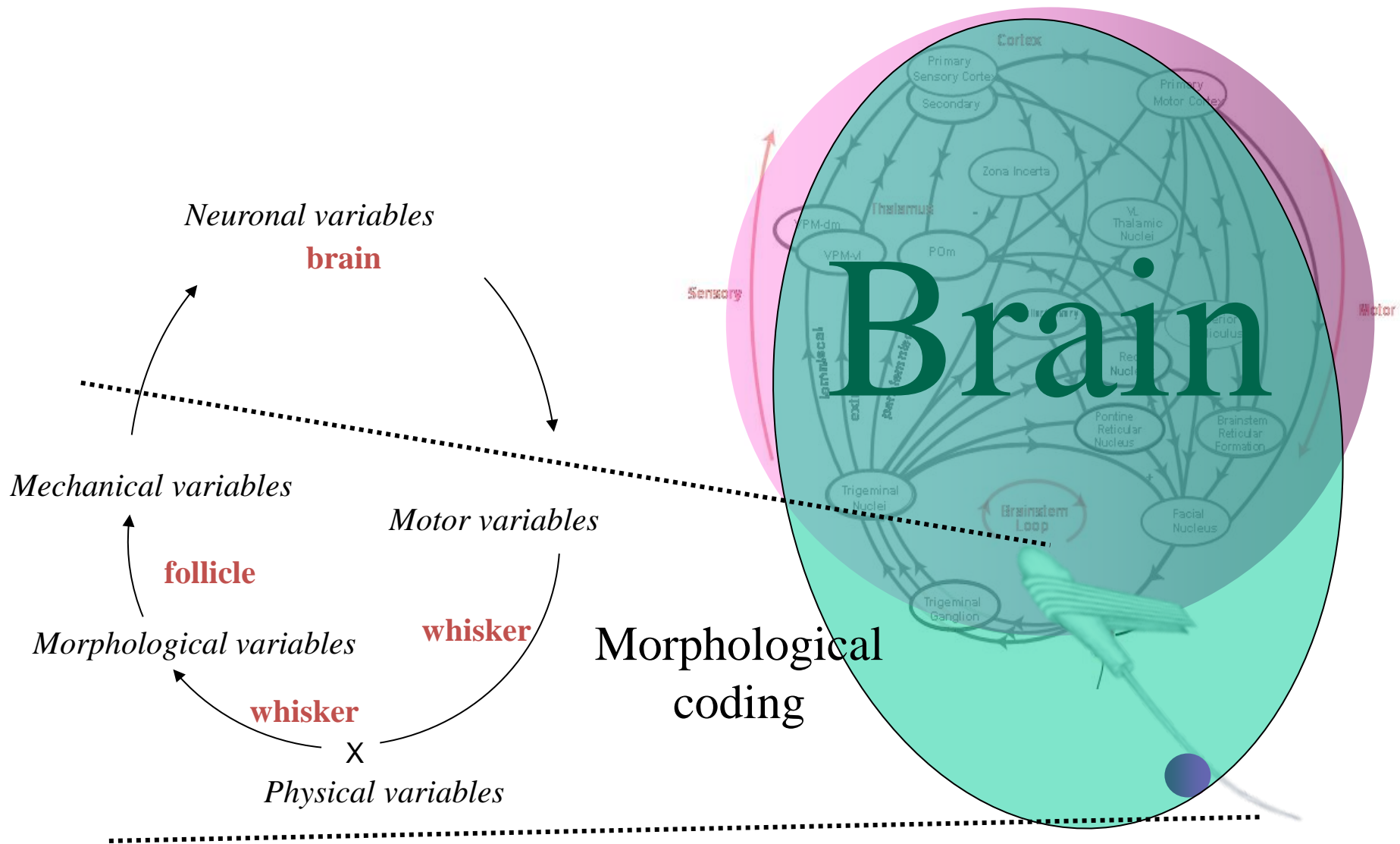


Sensory



Motor

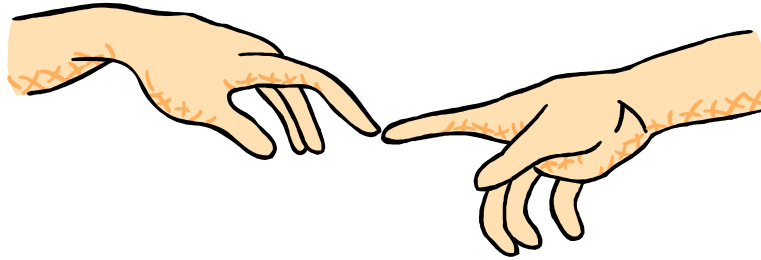
Organism-environment attractors



Touching

- Body-world interface
- Mechanisms of sensory processing (across senses)
- Motor-sensory coupling
- Passive vs active touch
- Neuronal coding
- Morphological coding

Touching



The End