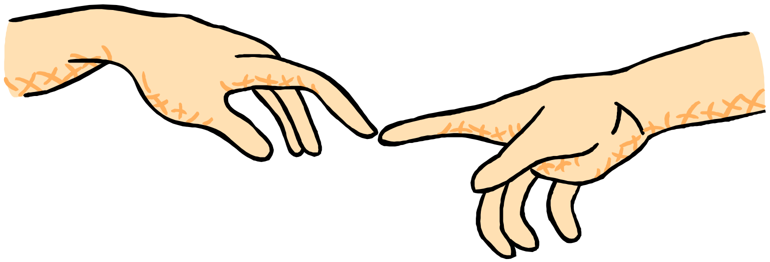
Touching



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

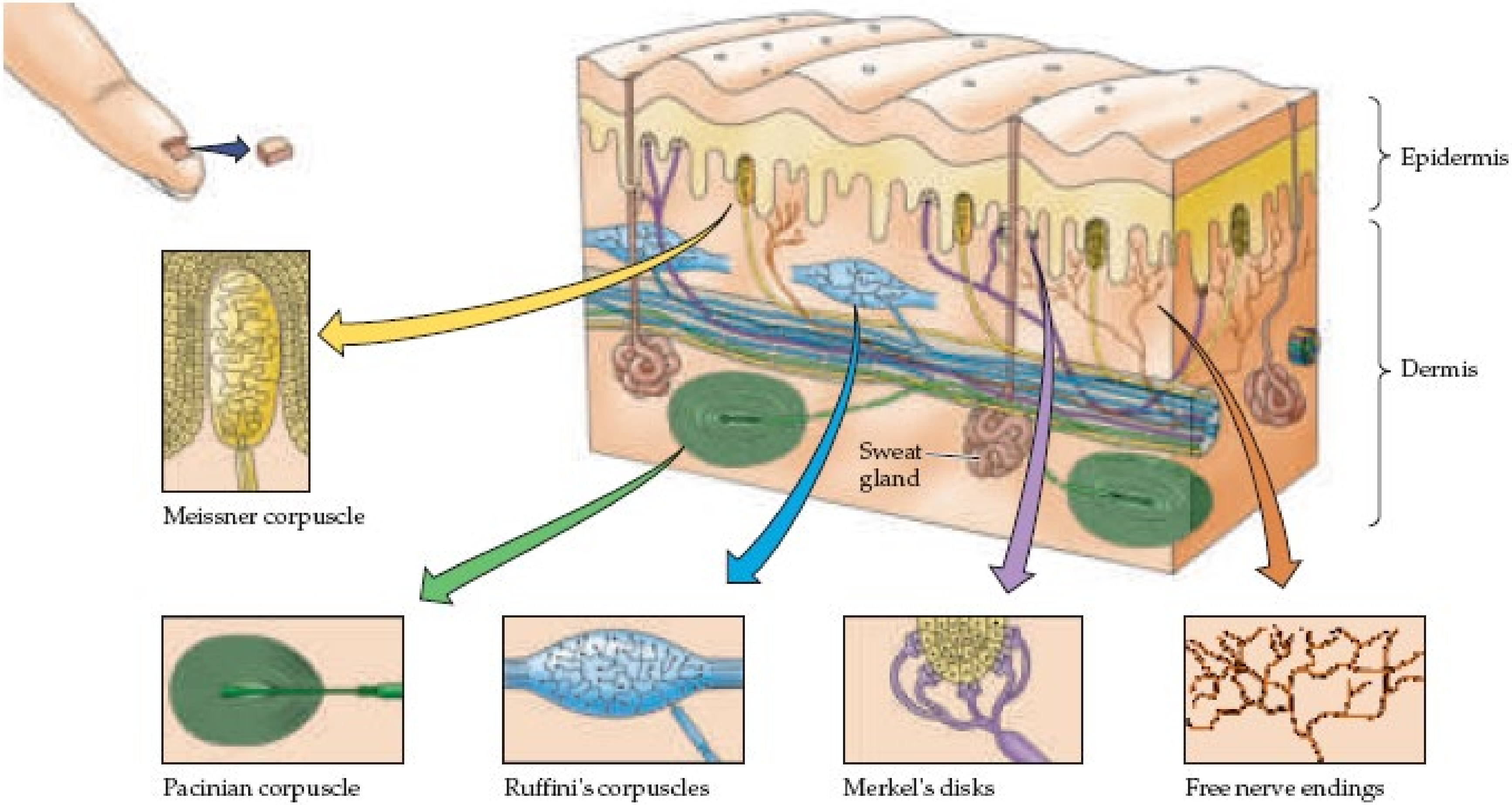
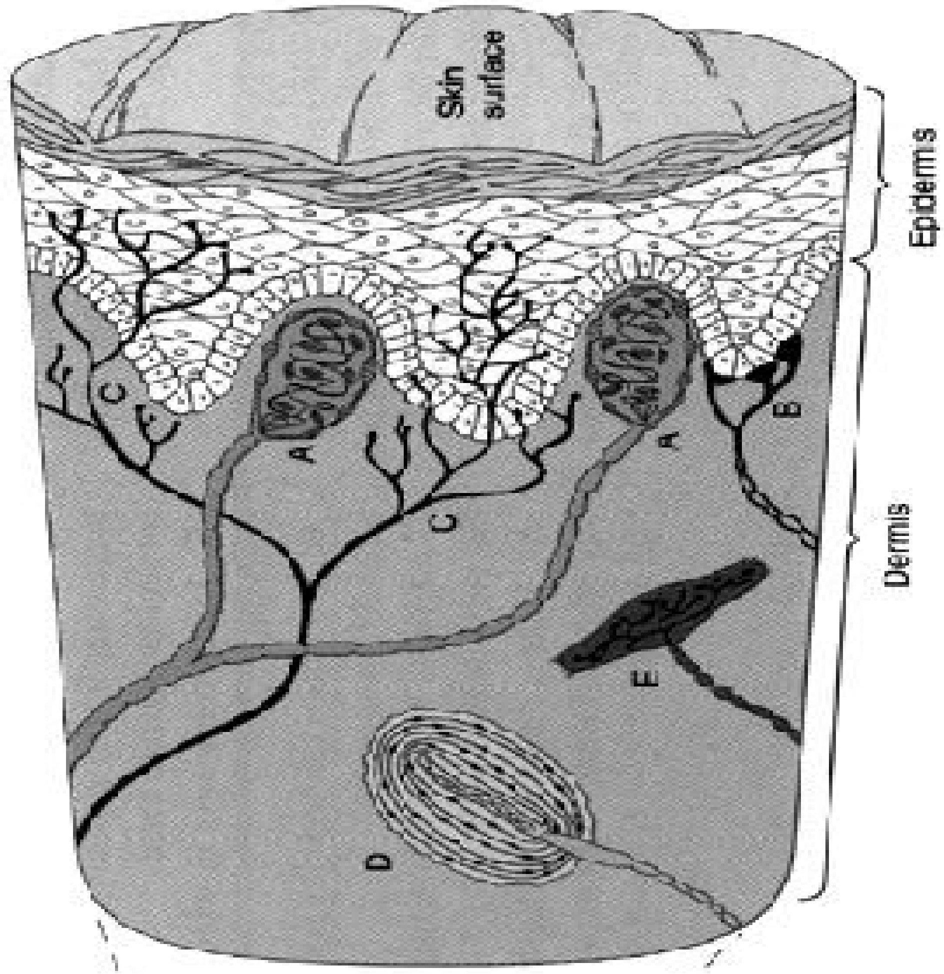


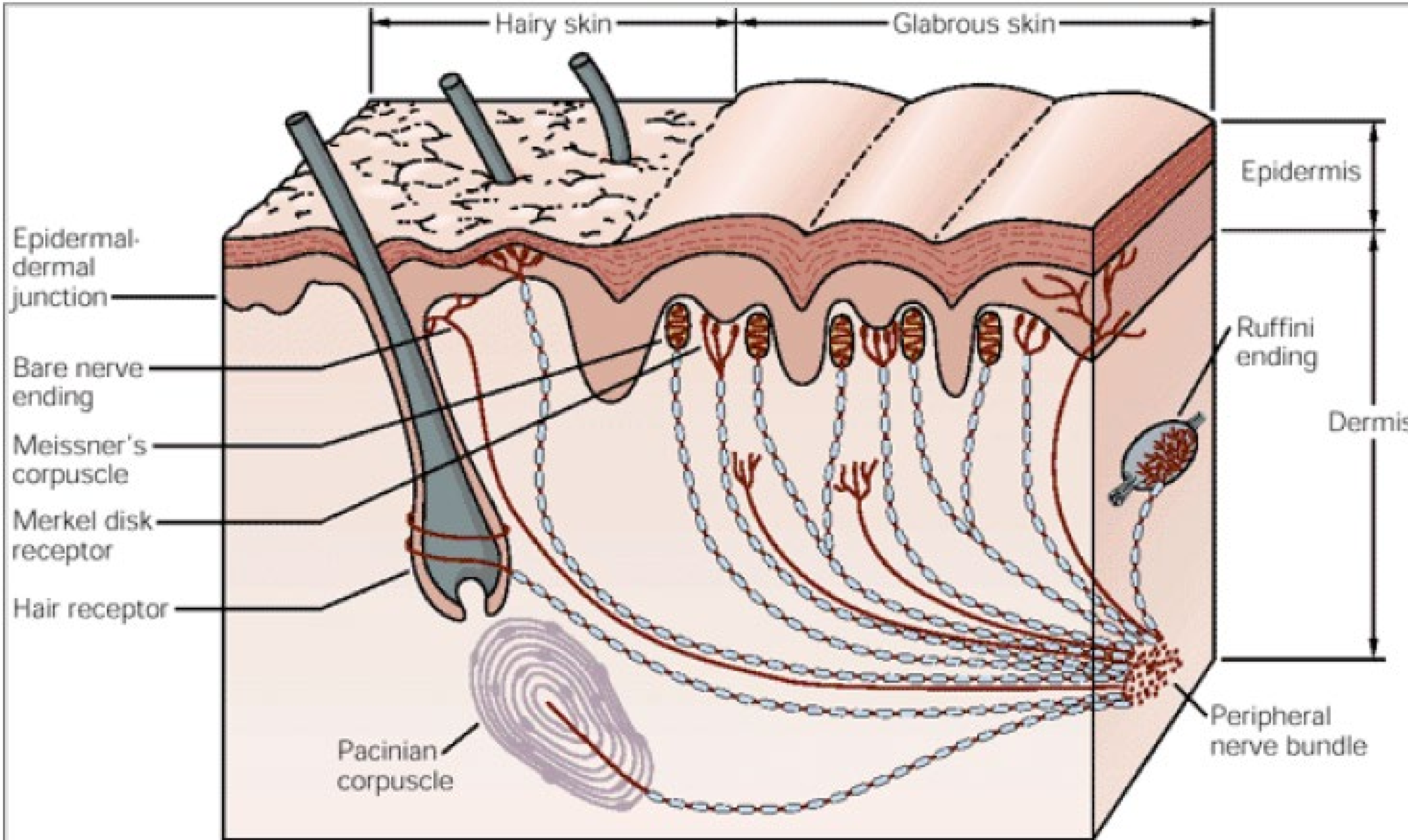
Figure 8.3 The skin harbors a variety of morphologically distinct mechanoreceptors. This diagram represents the smooth, hairless (also called glabrous) skin of the fingertip. The major characteristics of the various receptor types are summarized in Table 8.1. (After Darian-Smith, 1984.)

Mechanoreception underneath the skin



~200 µm

Mechanoreception underneath the skin



Body-world interface

Underneath the skin

TABLE 8.1
The Major Classes of Somatic Sensory Receptors

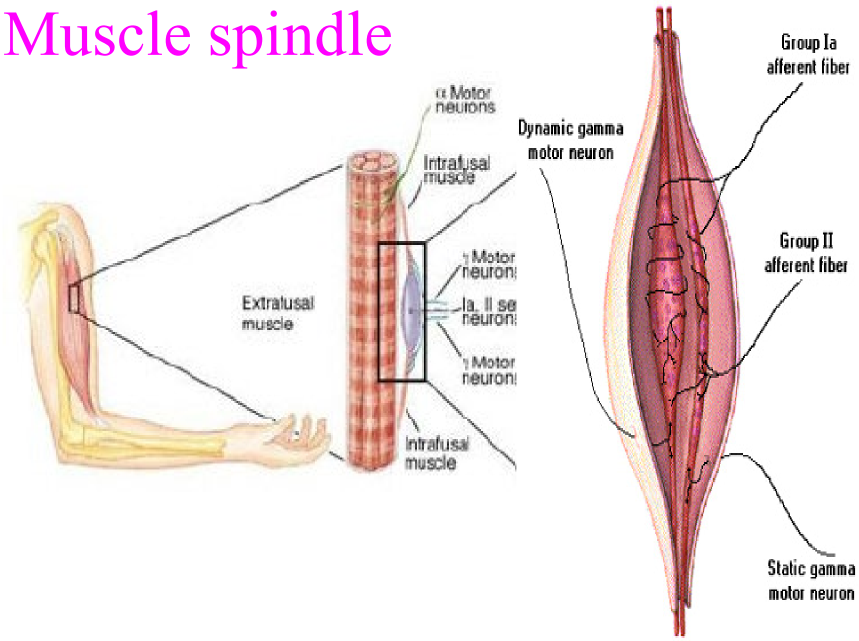
Receptor type	*Anatomical characteristics*	*Associated axons[a] (and diameters)*	*Axonal conduction velocities*	*Location*	*Function*	*Rate of adaptation*	*Threshold of activation*
Free nerve endings	Minimally specialized nerve endings	Aδ C	2–20 m/s .5 – 2 m/s	All skin	Pain, temperature, crude touch	Slow	High
Meissner's corpuscles	Encapsulated; between dermal papillae	Aβ 6–12 μm	30 – 70 m/s	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	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)

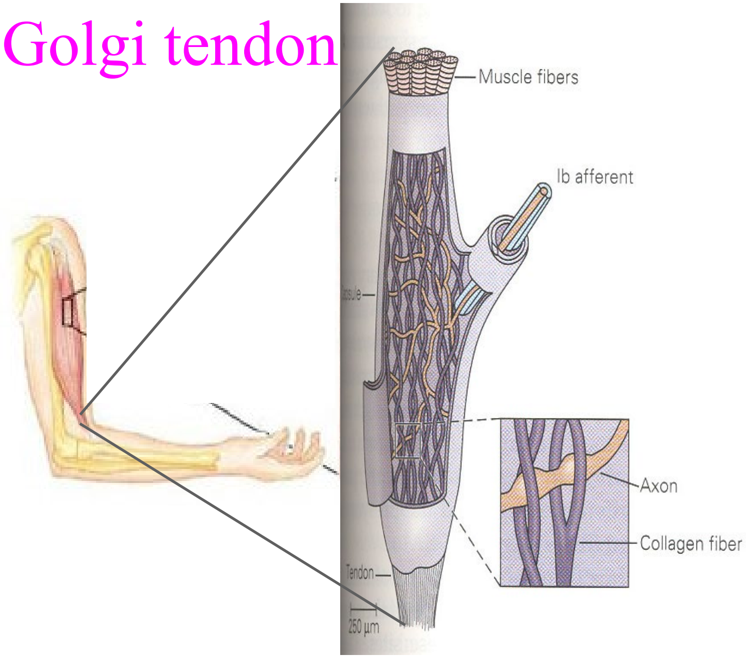
Proprio-(re)ceptors (re-afferents)

[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

Muscle spindle

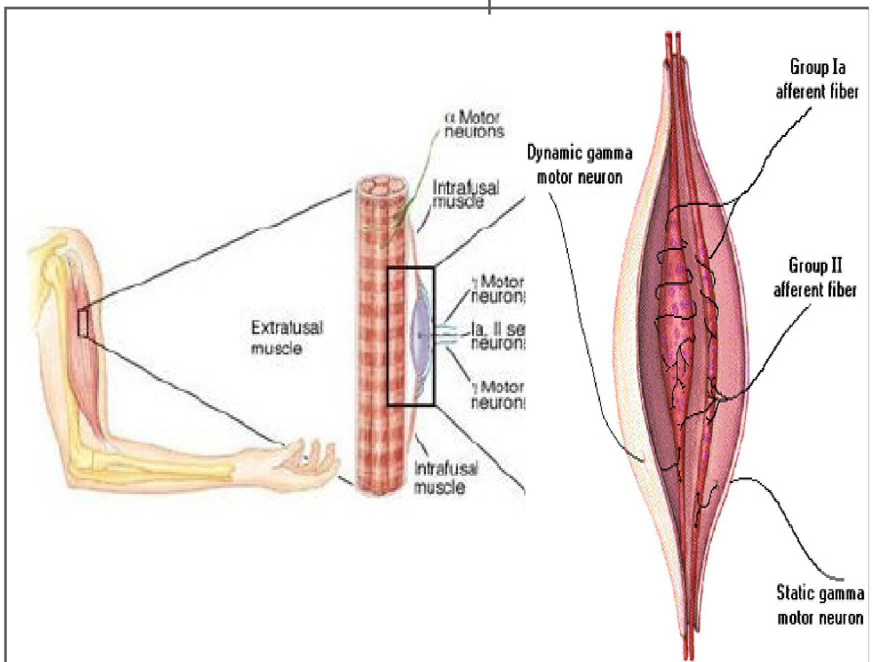


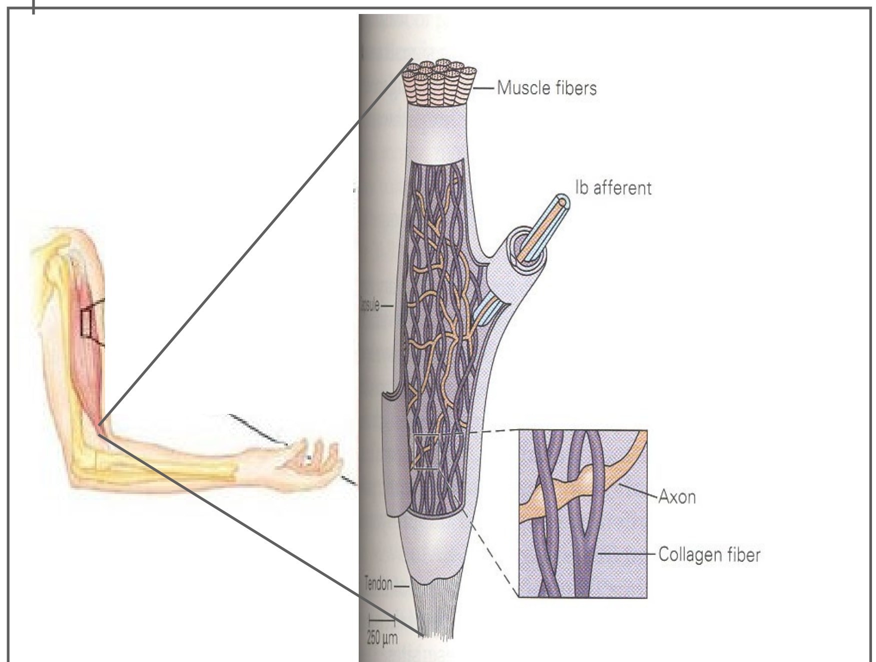
Golgi tendon



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
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Muscle spindles	Highly specialized (see Figure 8.5 and Chapter 15)					...w ...pid	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)

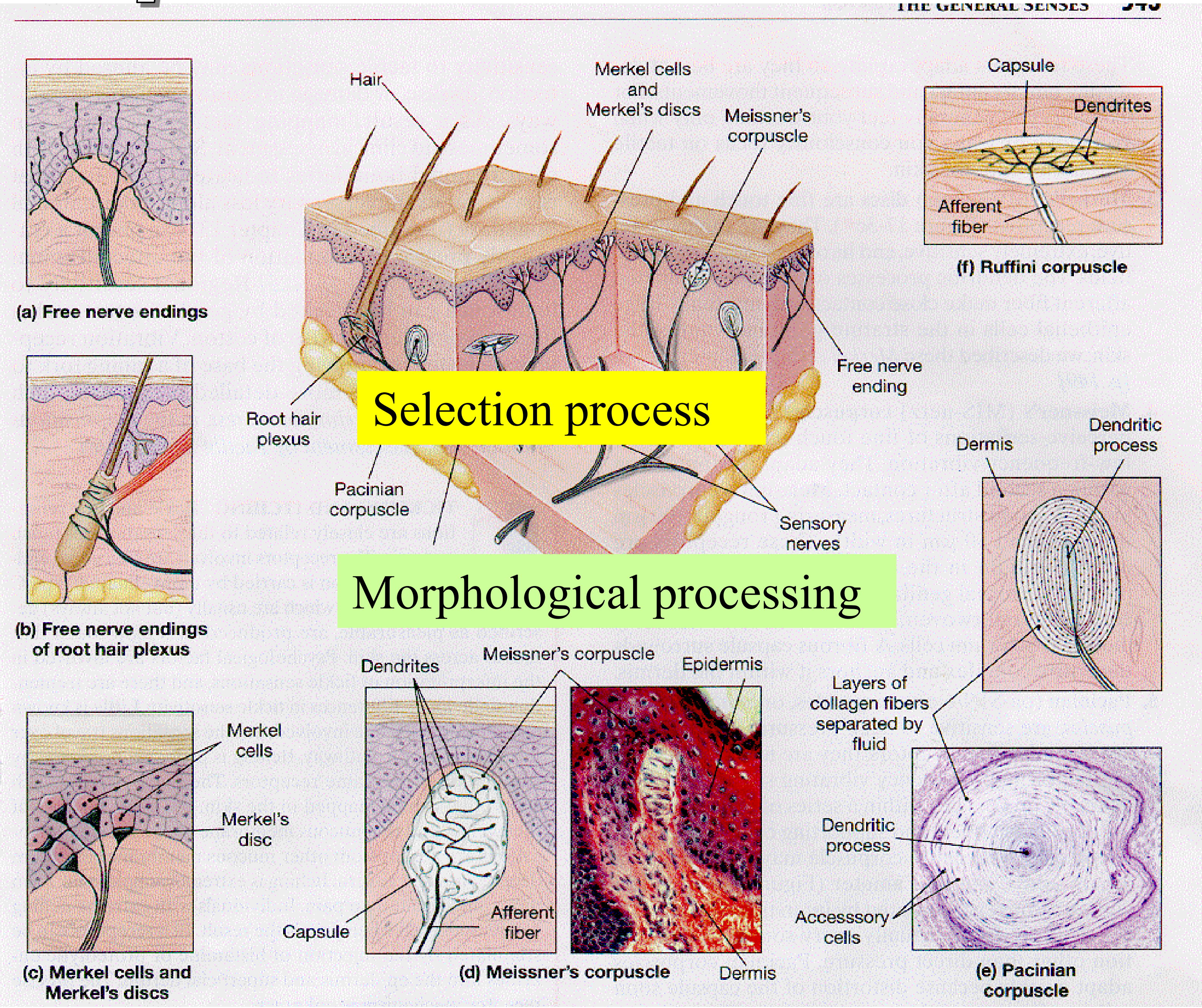
Why does the brain need re-afferents?

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



Selection process

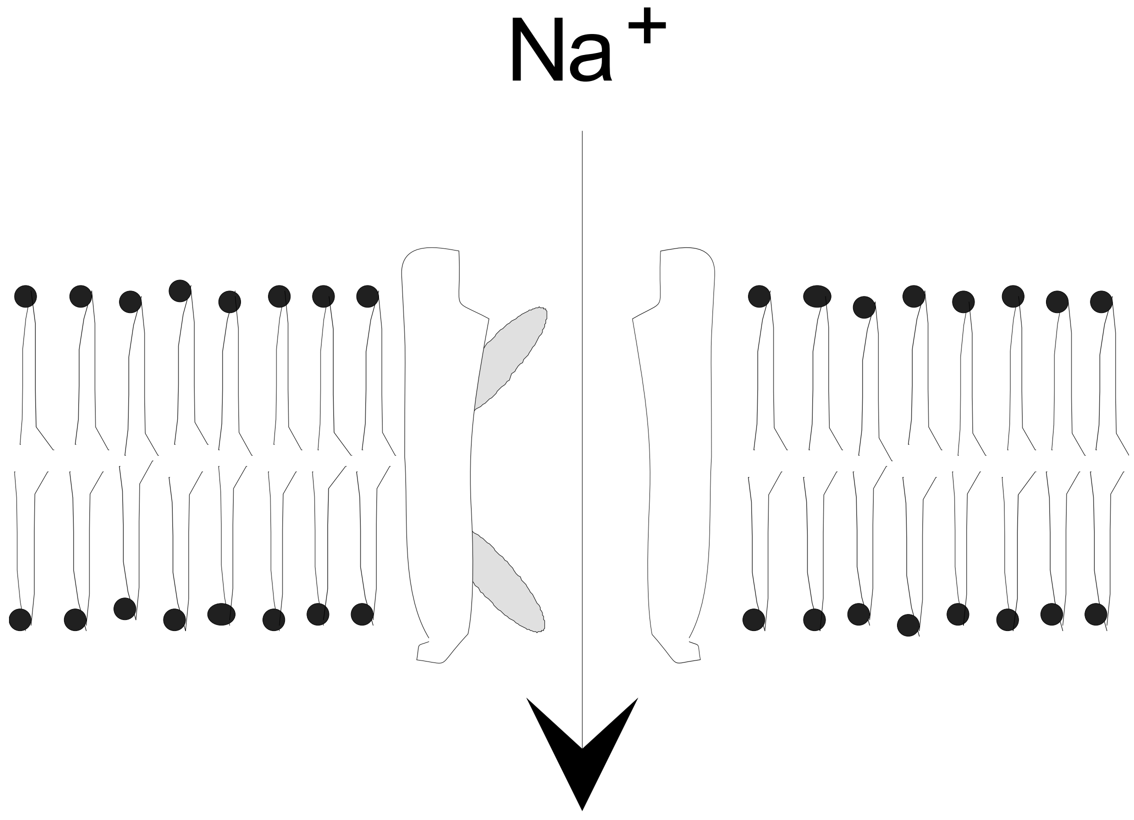
Morphological processing

Signal transduction

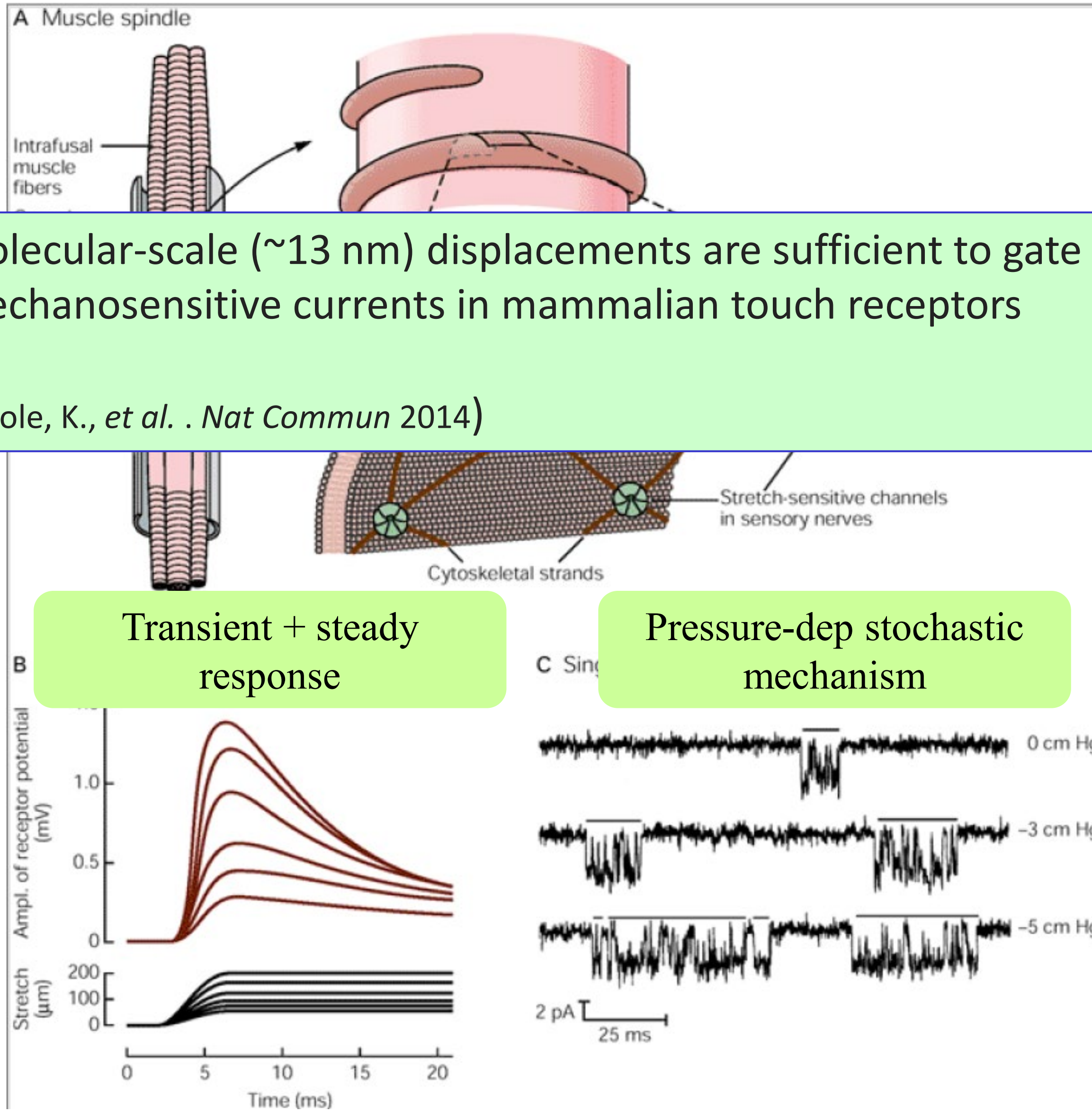
Transduction

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



molecular-scale (~13 nm) displacements are sufficient to gate mechanosensitive currents in mammalian touch receptors

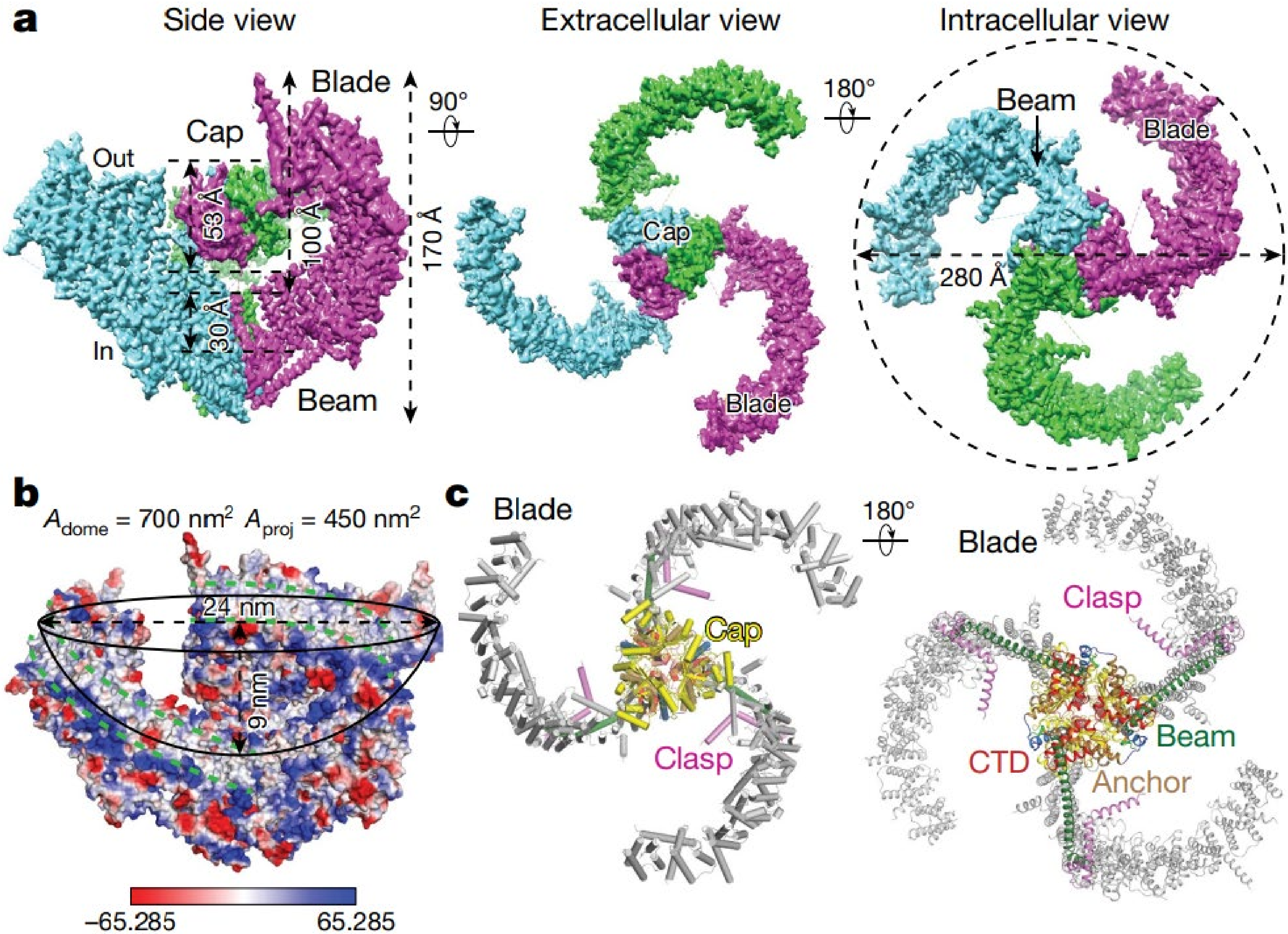
(Poole, K., *et al.* . *Nat Commun* 2014)

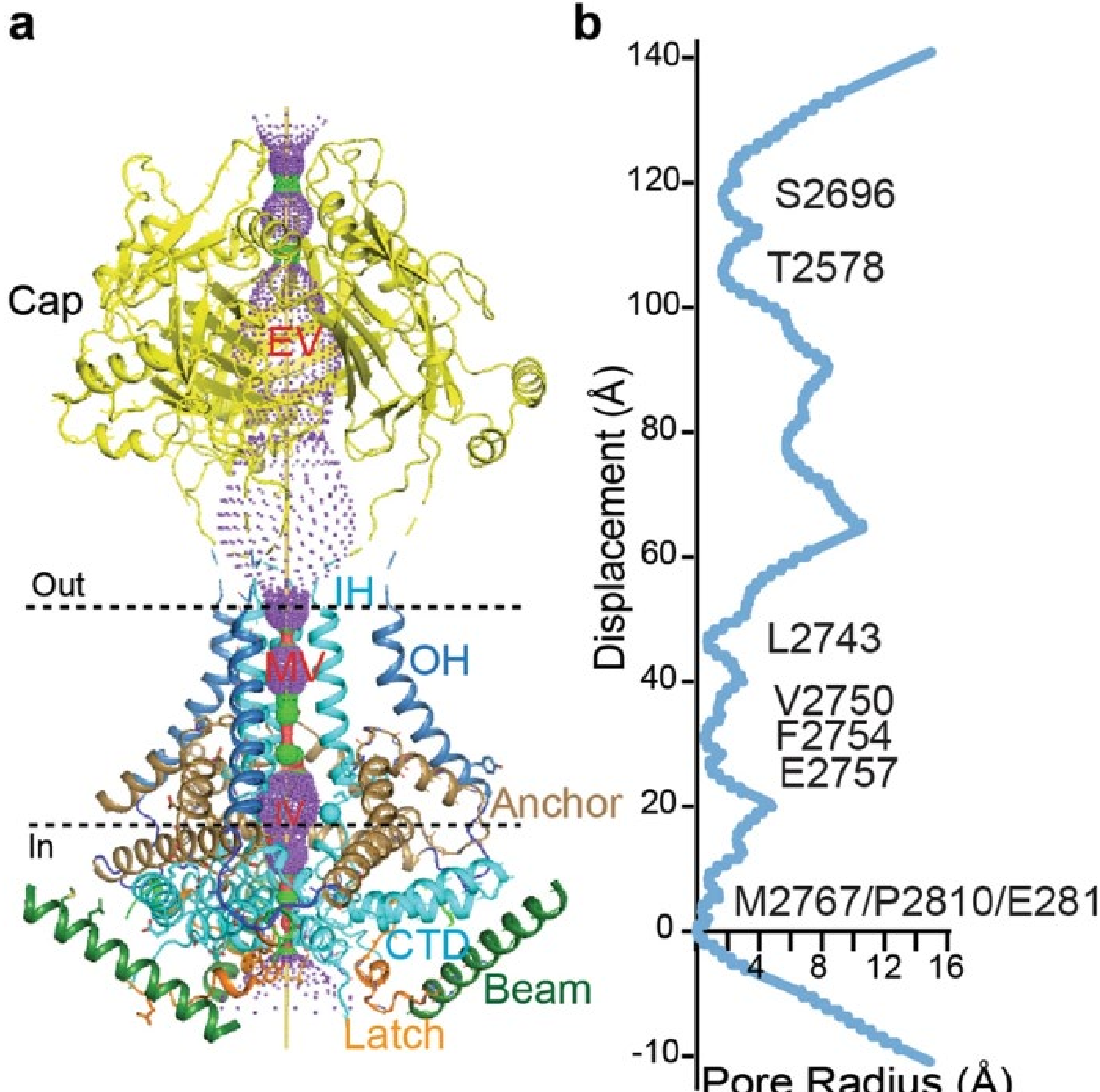
Transient + steady response

Pressure-dep stochastic mechanism

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

The PIEZO2 channel (Wang et al Nature 2019)



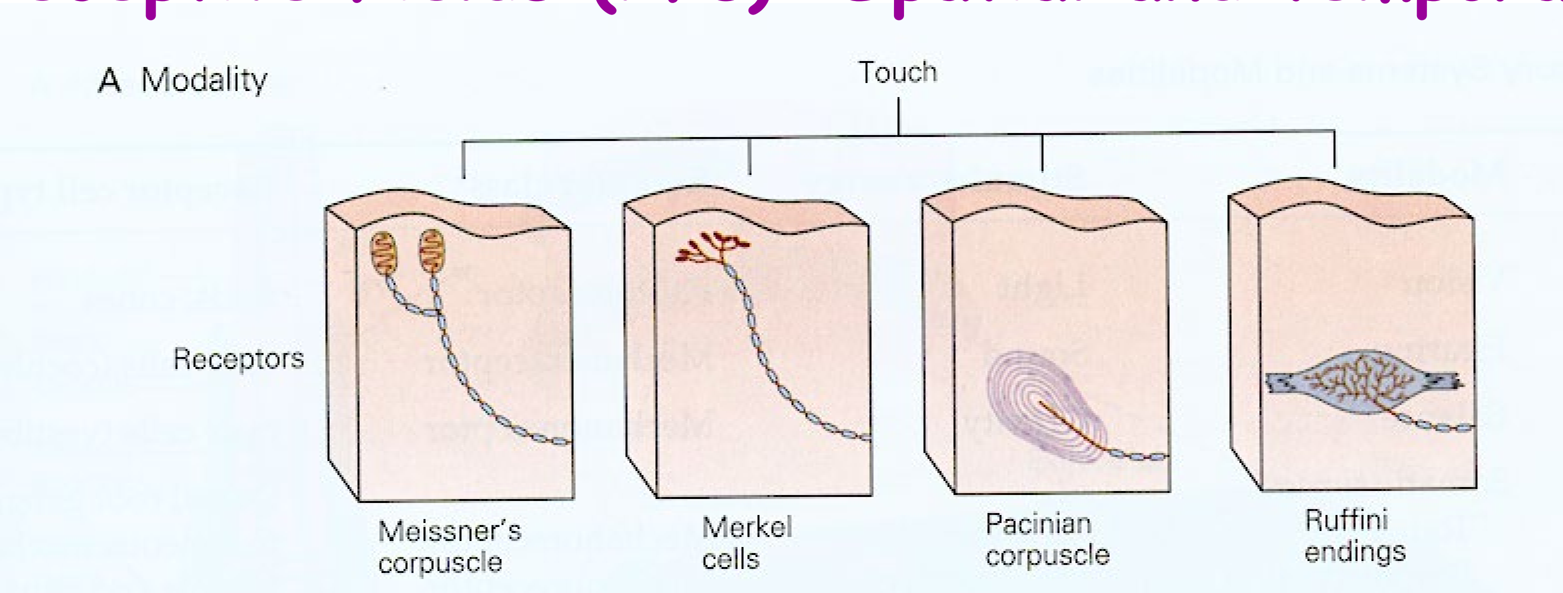


a
b
Cap
EV
Out
IH
MV
OH
IV
In
Anchor
CTD
Beam
Latch
140
120
100
80
60
40
20
0
-10
S2696
T2578
L2743
V2750
F2754
E2757
M2767/P2810/E281
4
8
12
16
Displacement (Å)
Pore Radius (Å)

Receptive Fields (RFs):

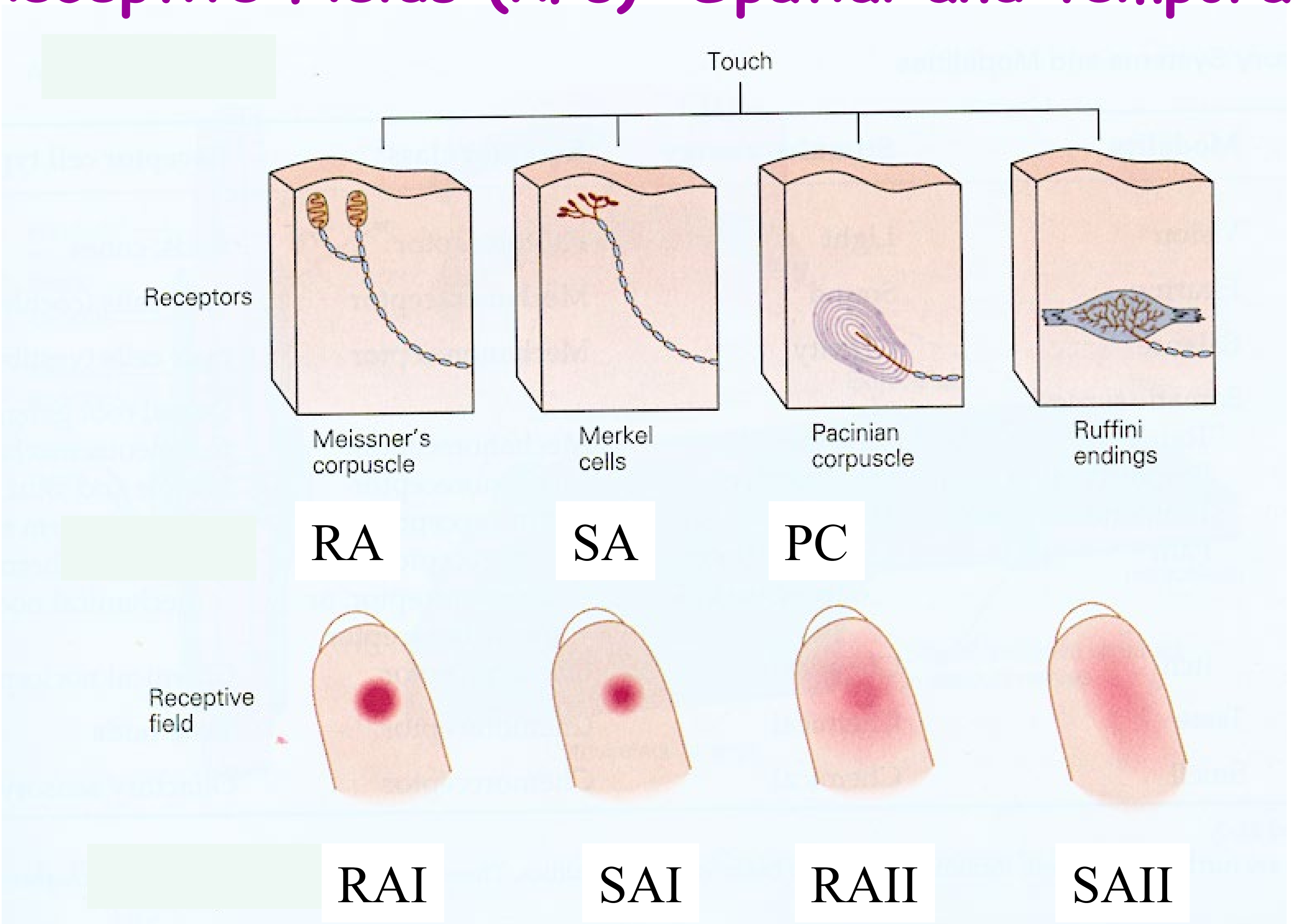
Spatial and temporal

Receptive Fields (RFs): Spatial and temporal



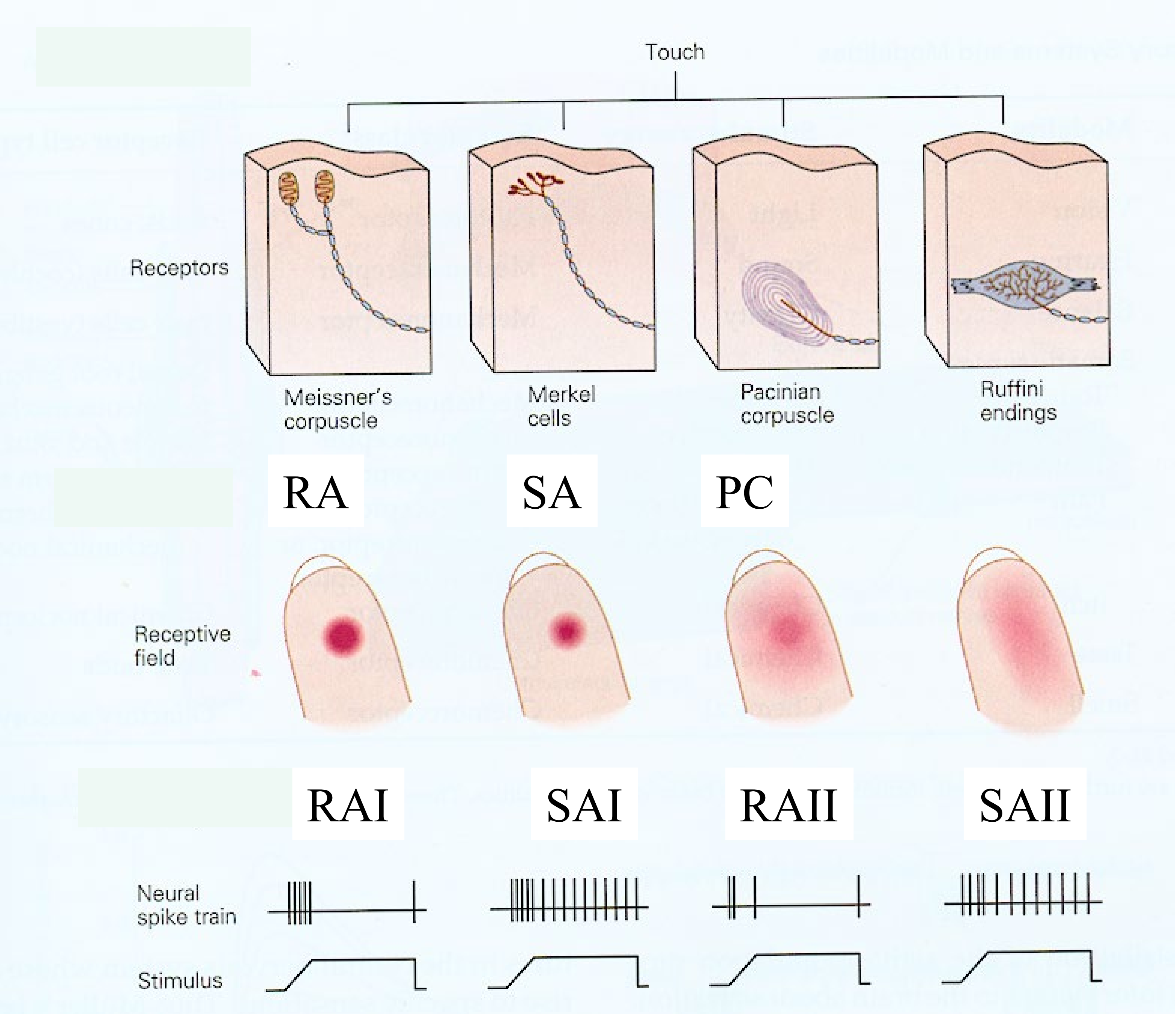
RF size?

Receptive Fields (RFs): Spatial and temporal



Response dynamics?

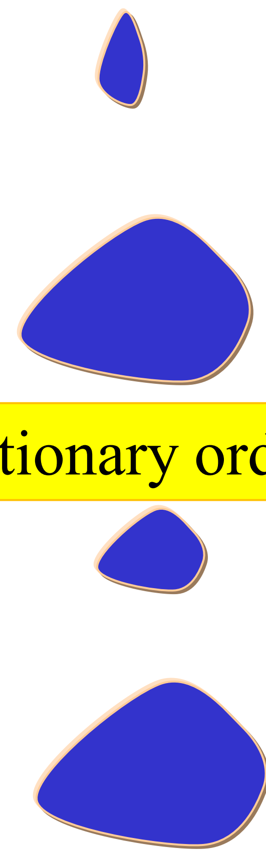
Receptive Fields (RFs): Spatial and temporal

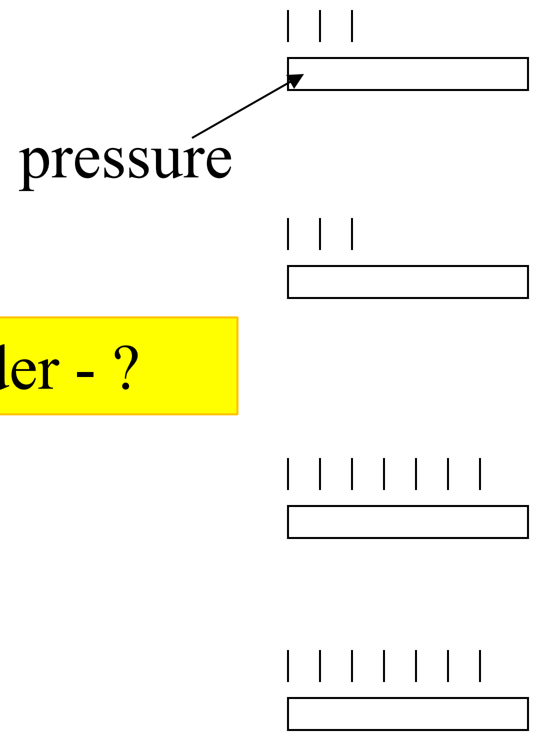


Cutaneous Mechanoreceptor Channels

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** corpuscle

Evolutionary order - ?

Slowly Adapting (SA1)

Associated with **Merkel** cells

Slowly Adapting (SA2)

Associated with **Ruffini**'s endings

Receptor density

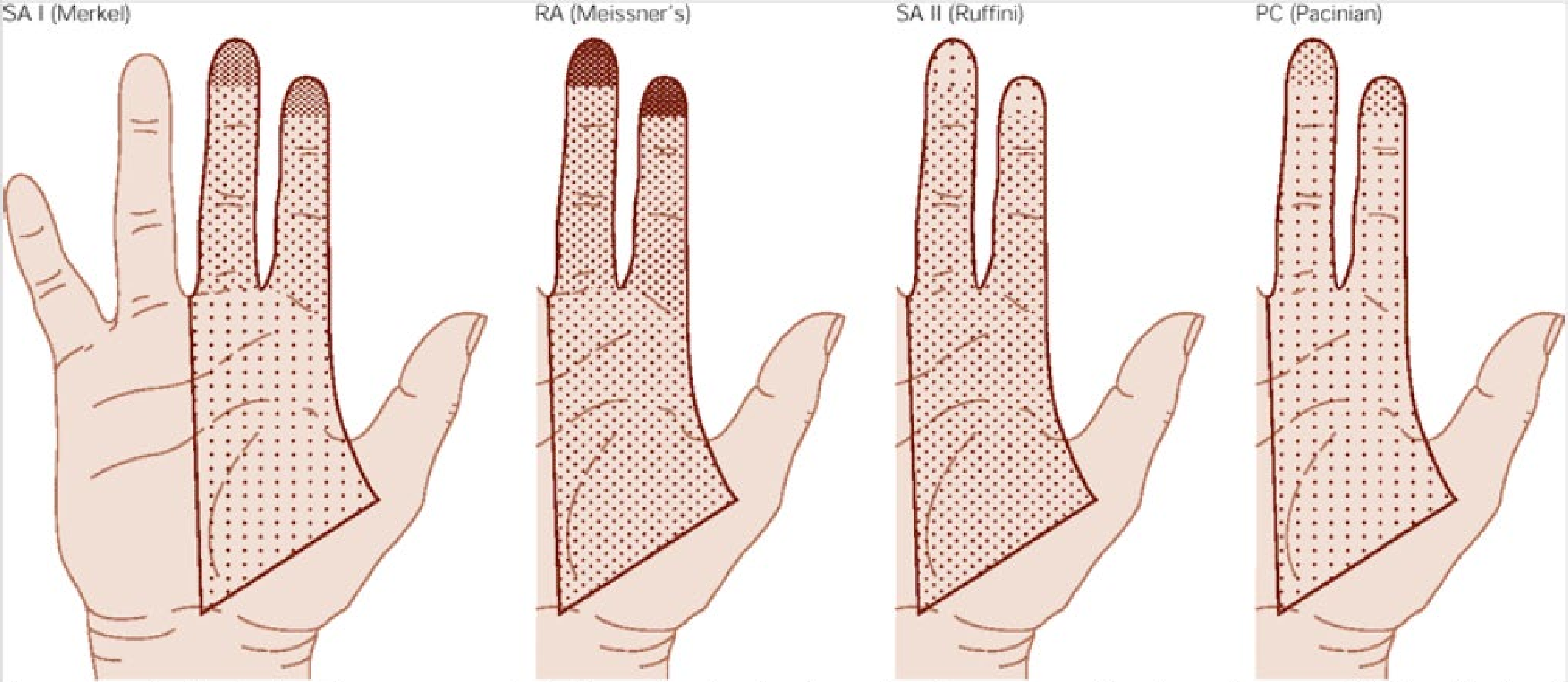
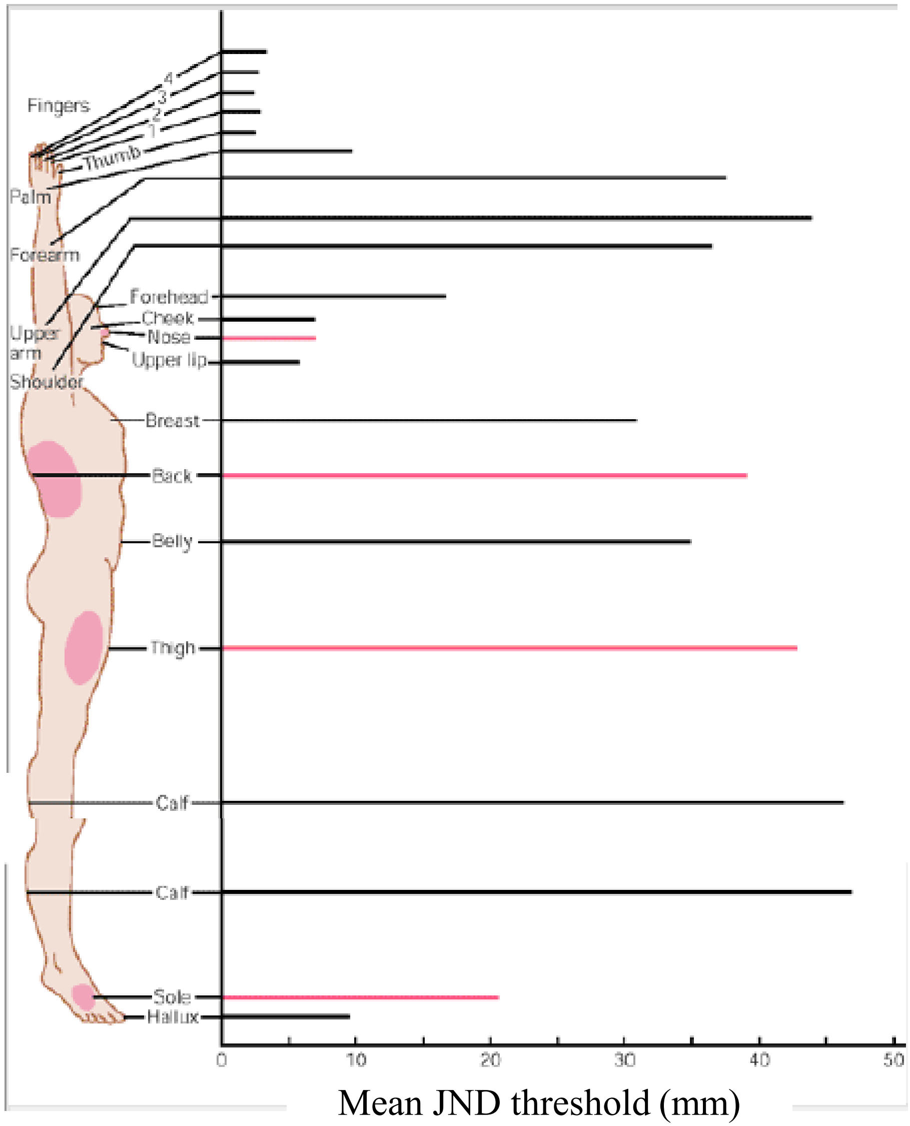


Figure 22-4 The distribution of receptor types in the human hand varies. The number of sensory nerve fibers innervating an area is indicated by the stippling density, with the highest density of receptors shown by the heaviest stippling. (**RA** = 5 rapidly adapting, **SA** = 5 slowly adapting.) Meissner's 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

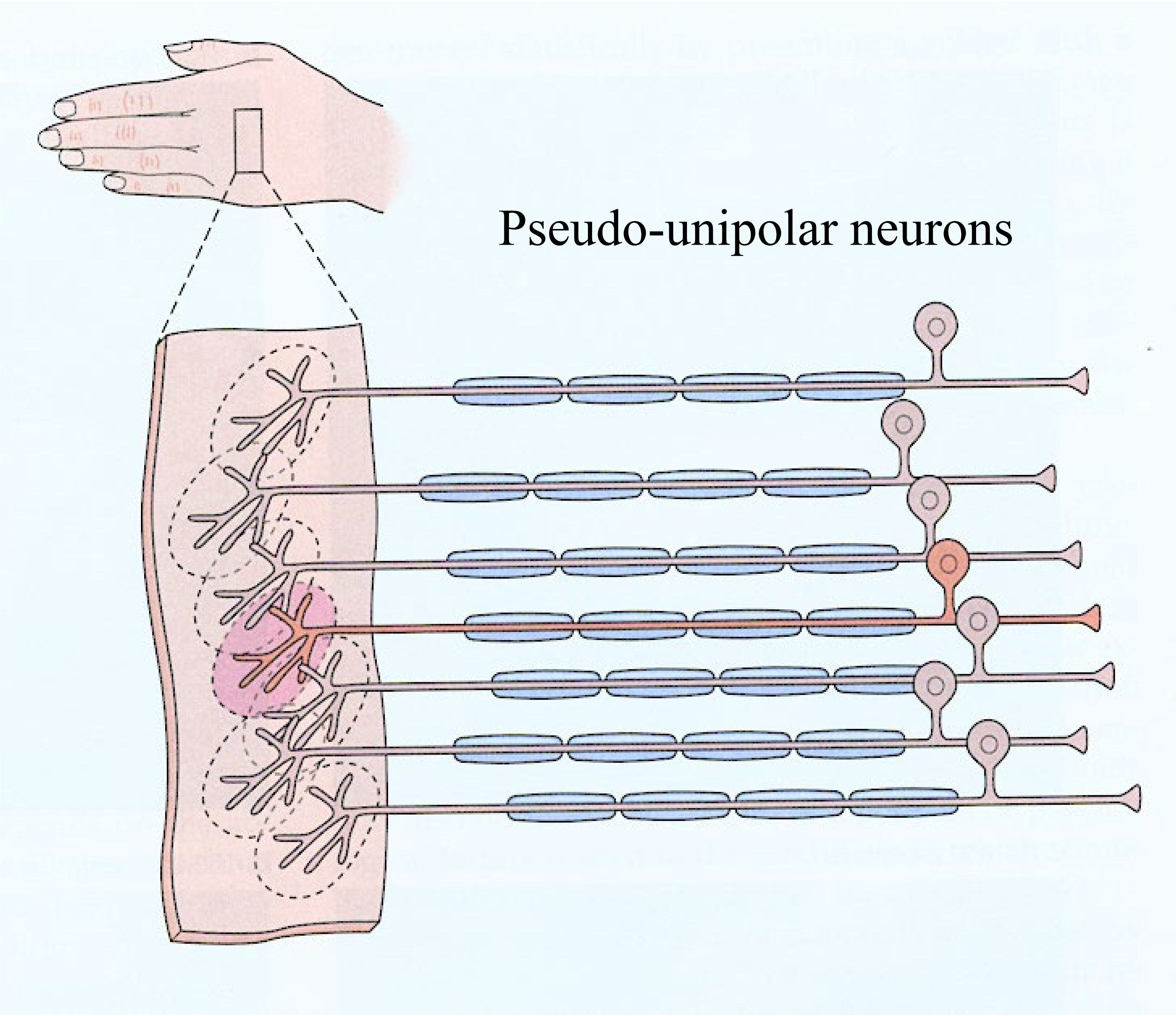
Spatial resolution (by JND)



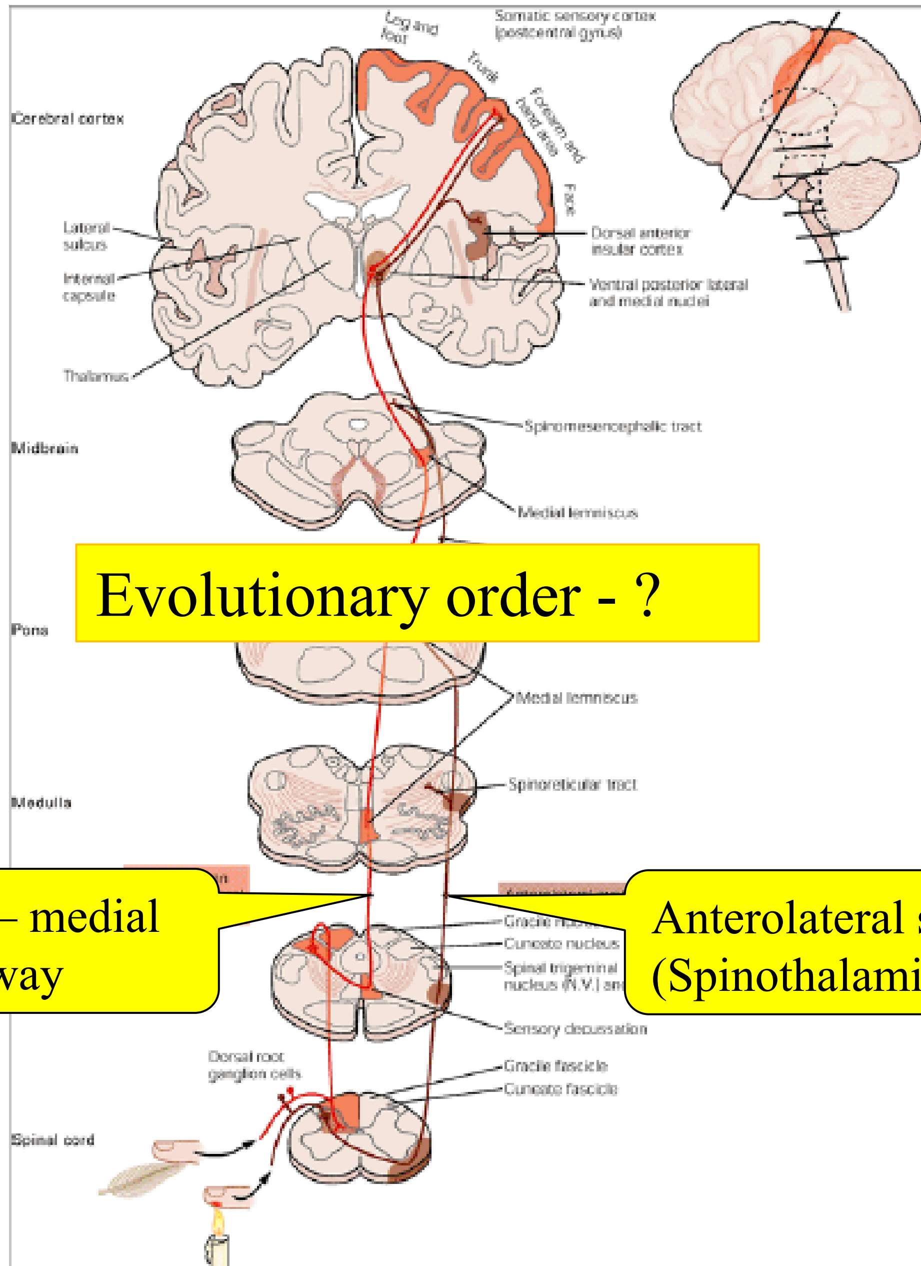
- Break ?

Signal conduction

Sensory signal conduction



Sensory signal conduction



Evolutionary order - ?

Dorsal column – medial lemniscus pathway

Anterolateral system pathway (Spinothalamic tracts)

Sensory signal conduction

Evolutionary order - ?

TABLE 8.1
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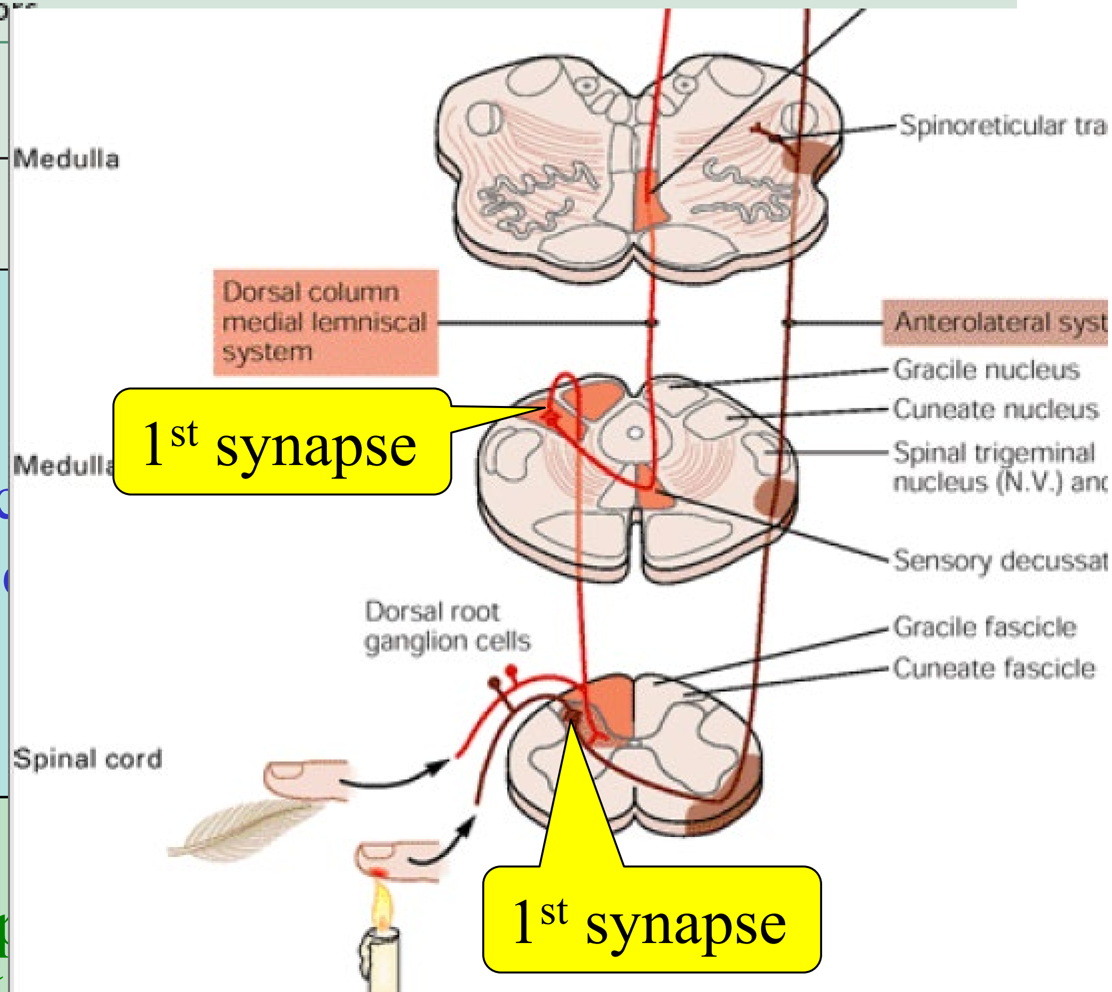
Merkel's disks	Encapsulated; associated with peptide-releasing cells	Aβ				
Ruffini's corpuscles	Encapsulated; oriented along stretch lines	Aβ 6–12 μm				
Muscle spindles	Highly specialized (see Figure 8.5 and Chapter 15)	Ia and II				
Golgi tendon organs	Highly specialized (see Chapter 15)	Ib				
Joint receptors	Minimally specialized	—	Joints	Joint position	Rapid	Low

Mec

(c

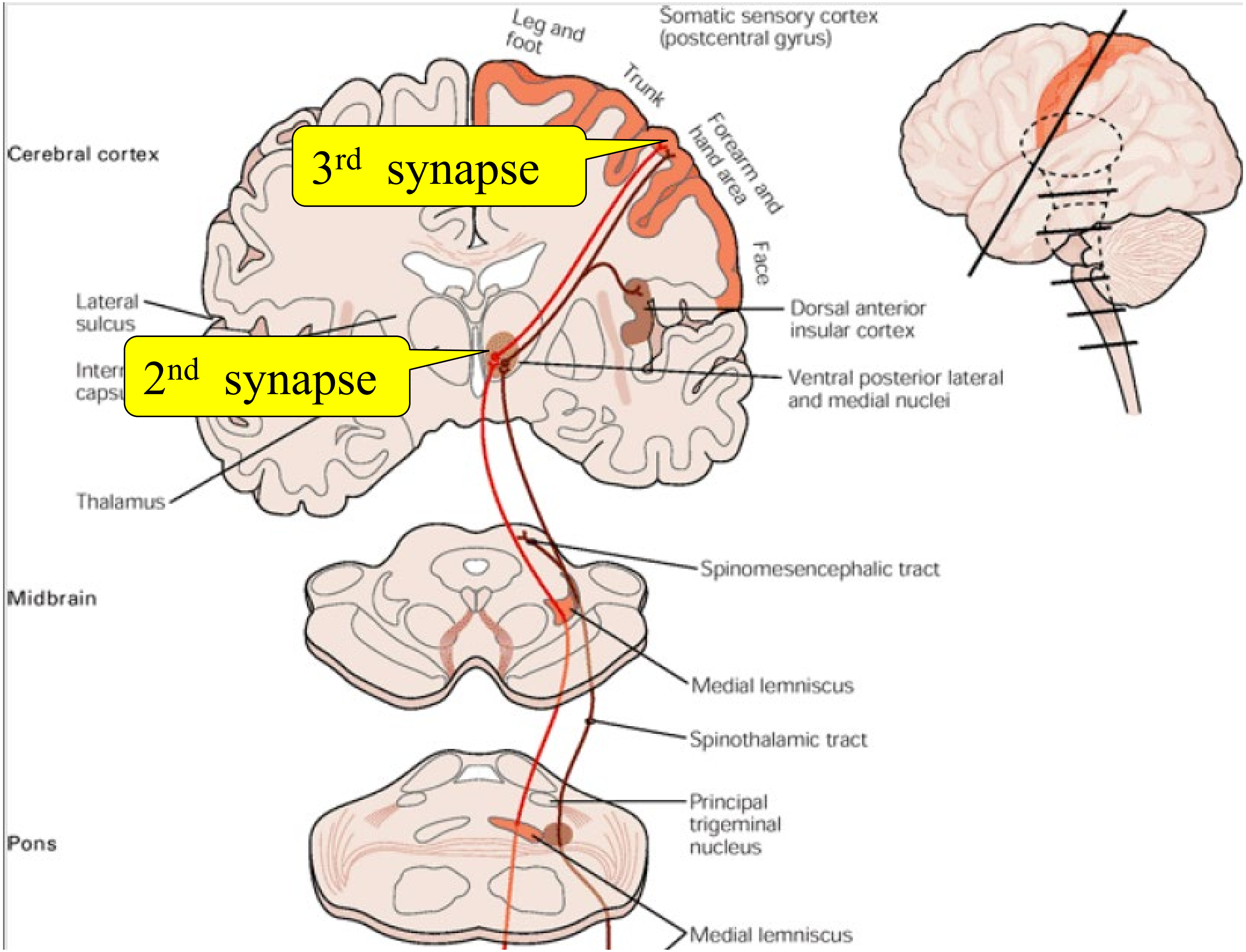
Prop

(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

Sensory signal conduction



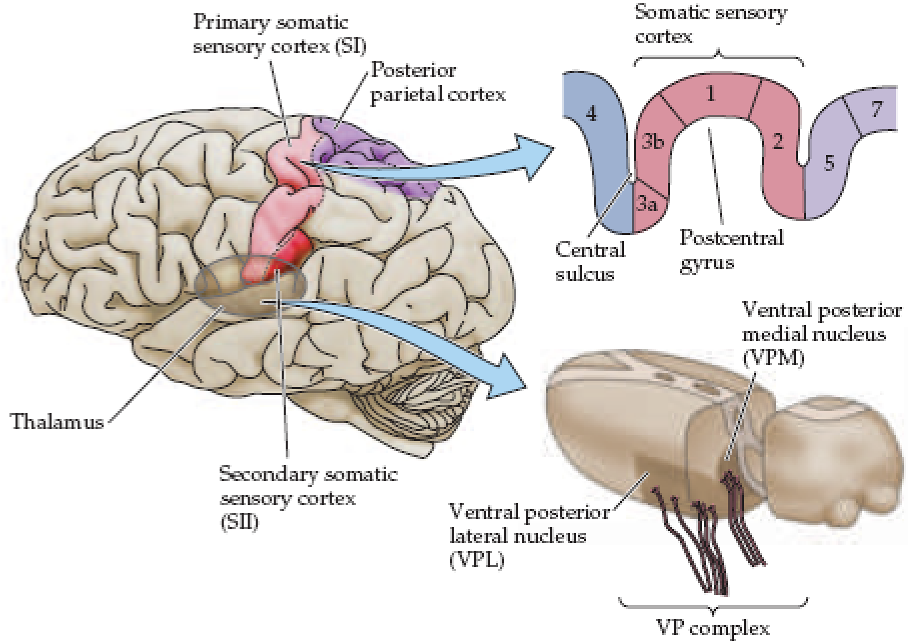
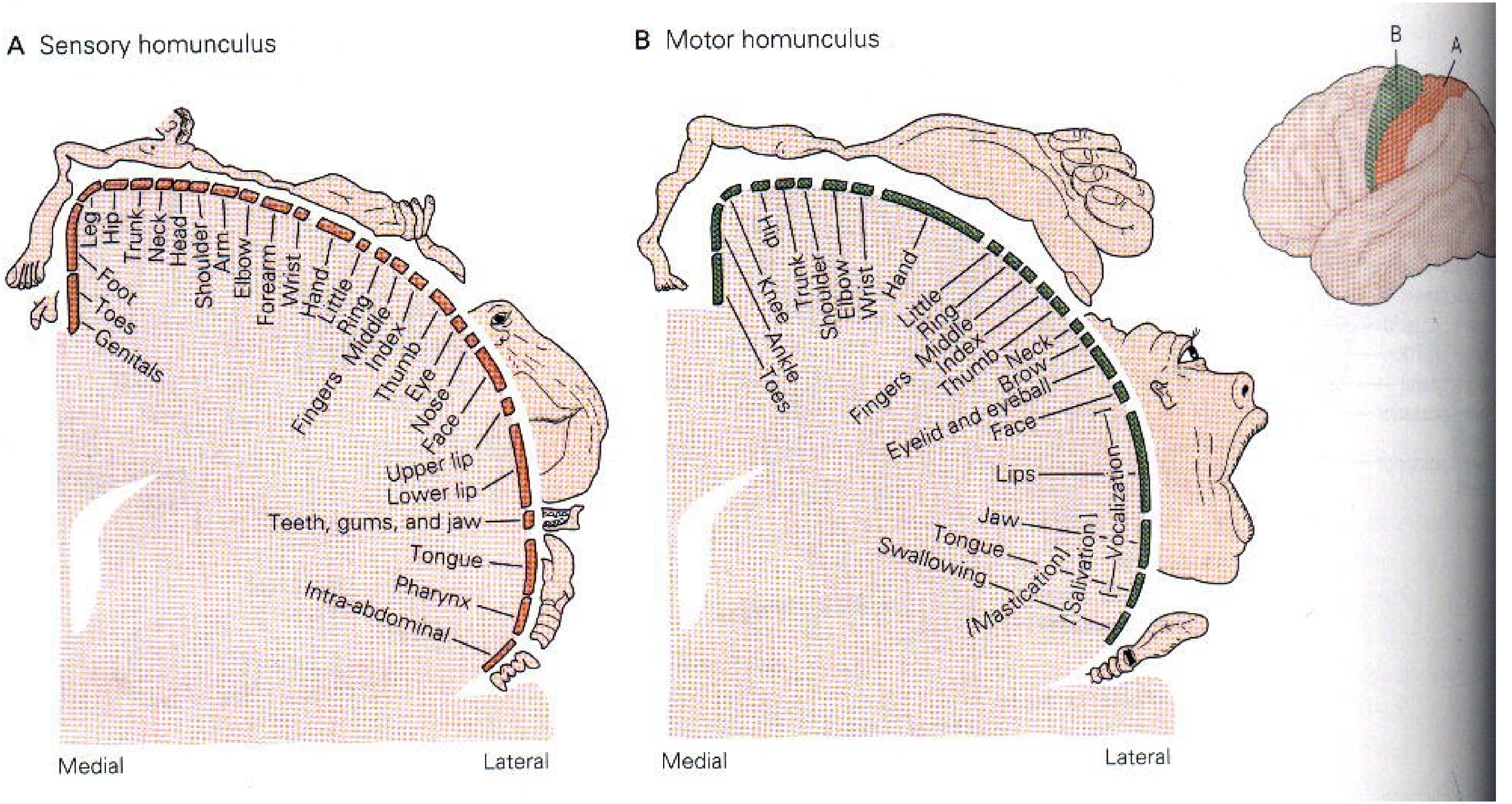


Figure 8.7 Diagram of the somatic sensory portions of the thalamus and their cortical targets in the postcentral gyrus. The ventral posterior nuclear complex comprises the VPM, which relays somatic sensory information carried by the trigeminal system from the face, and the VPL, which relays somatic sensory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

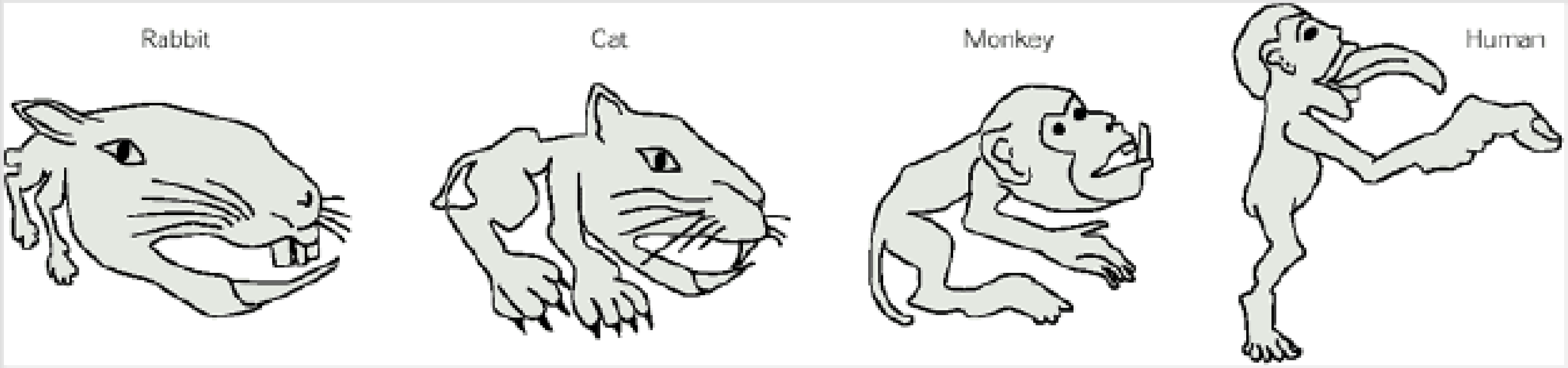


Figure 20-5 Different species rely on different parts of the body for adaptive somatosensory information. These drawings show the relative importance of body regions in the somatic sensibilities of four species, based on studies of evoked potentials in the thalamus and cortex.

The Homunculi

Accurate spatial organization

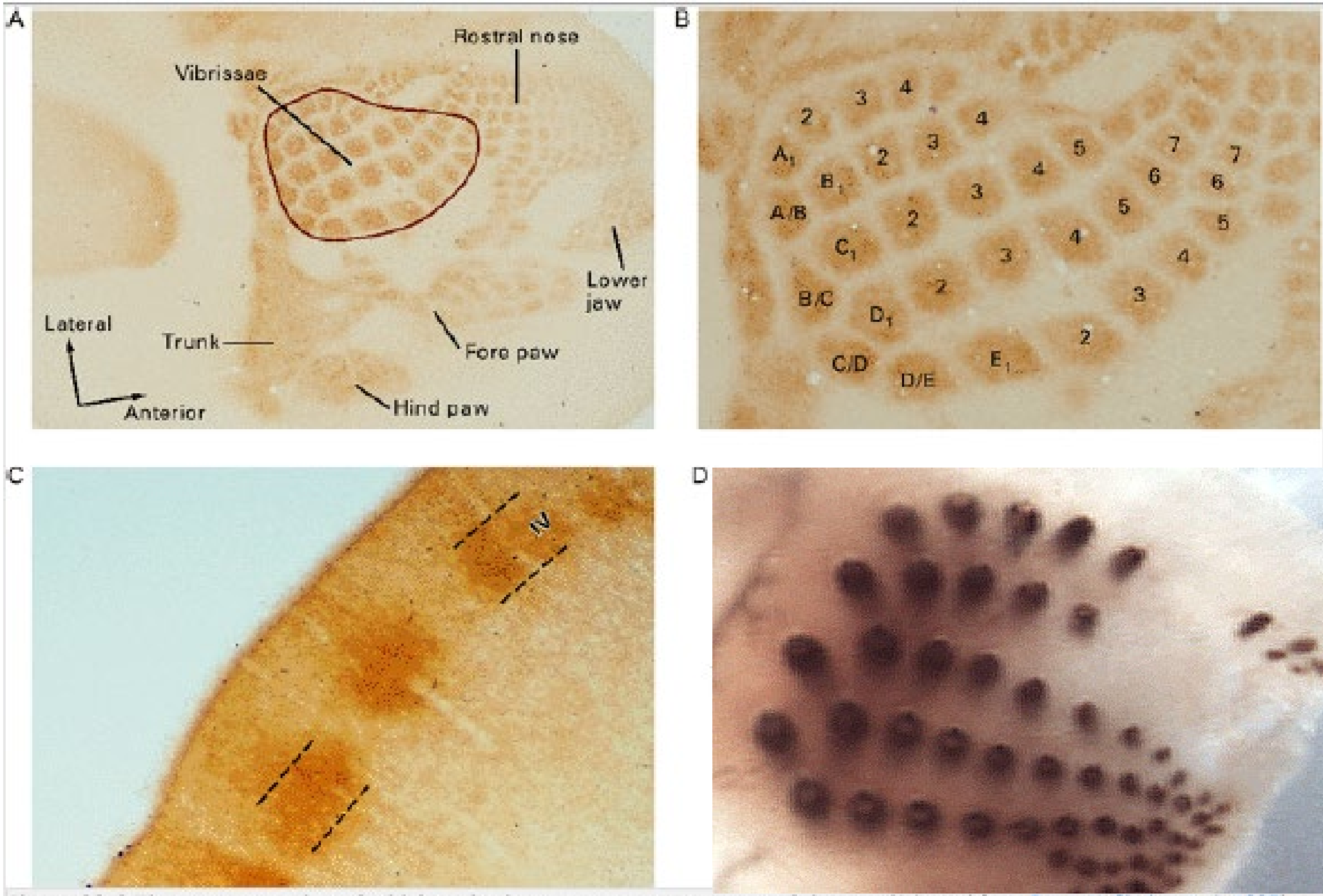
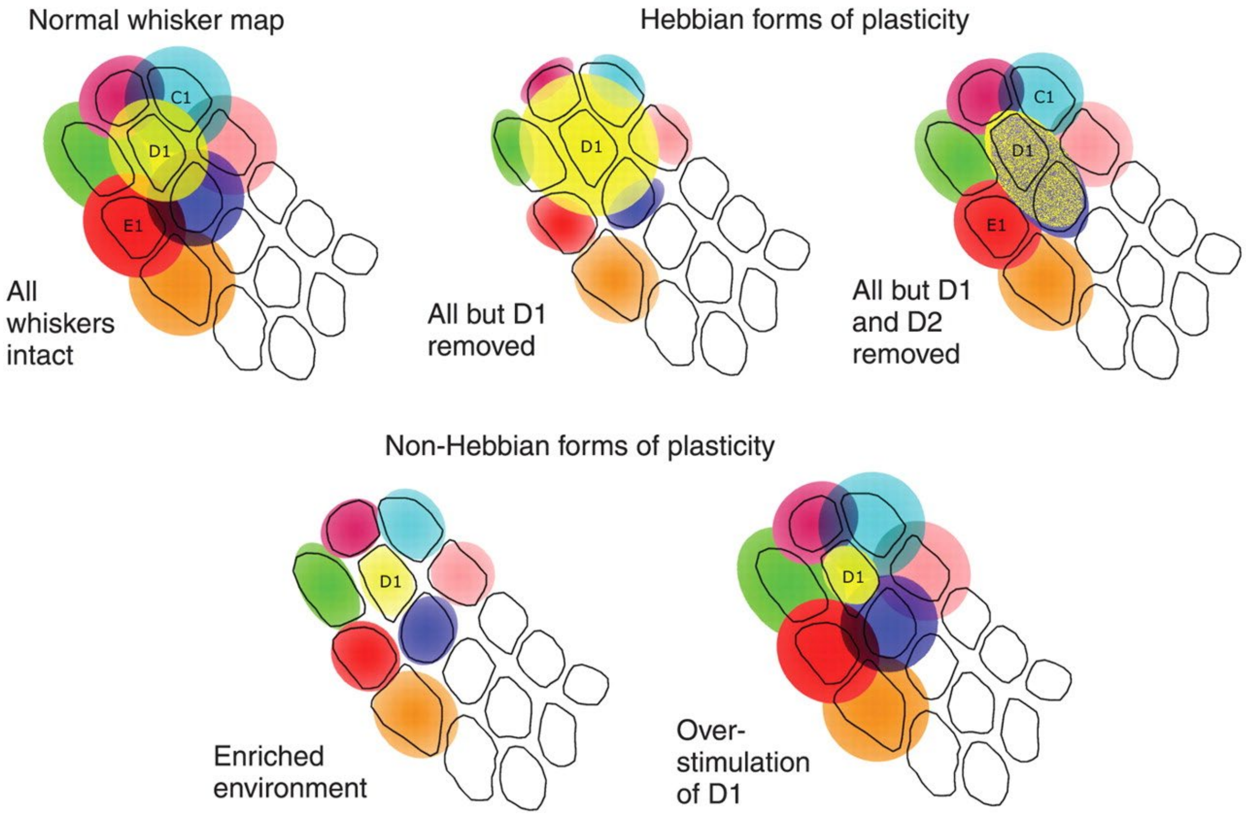


Figure 23-9 The representation of whiskers in the somatosensory cortex of the rat. (Adapted from Bennett-Clarke et al. 1997).

The Homunculi

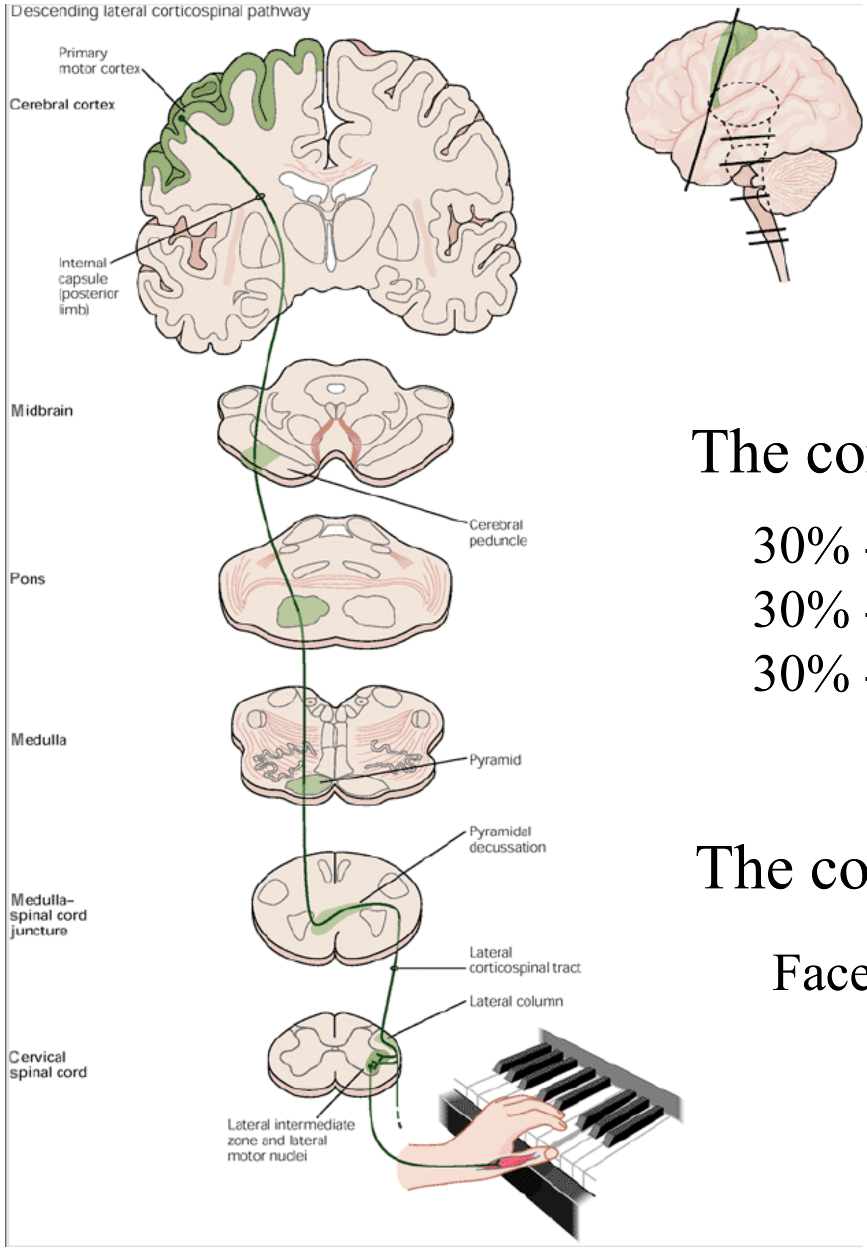
Relative size reflects innervation density

ontogenetically



Daniel E. Feldman, and Michael Brecht Science 2005;310:810-815

Motor signal conduction



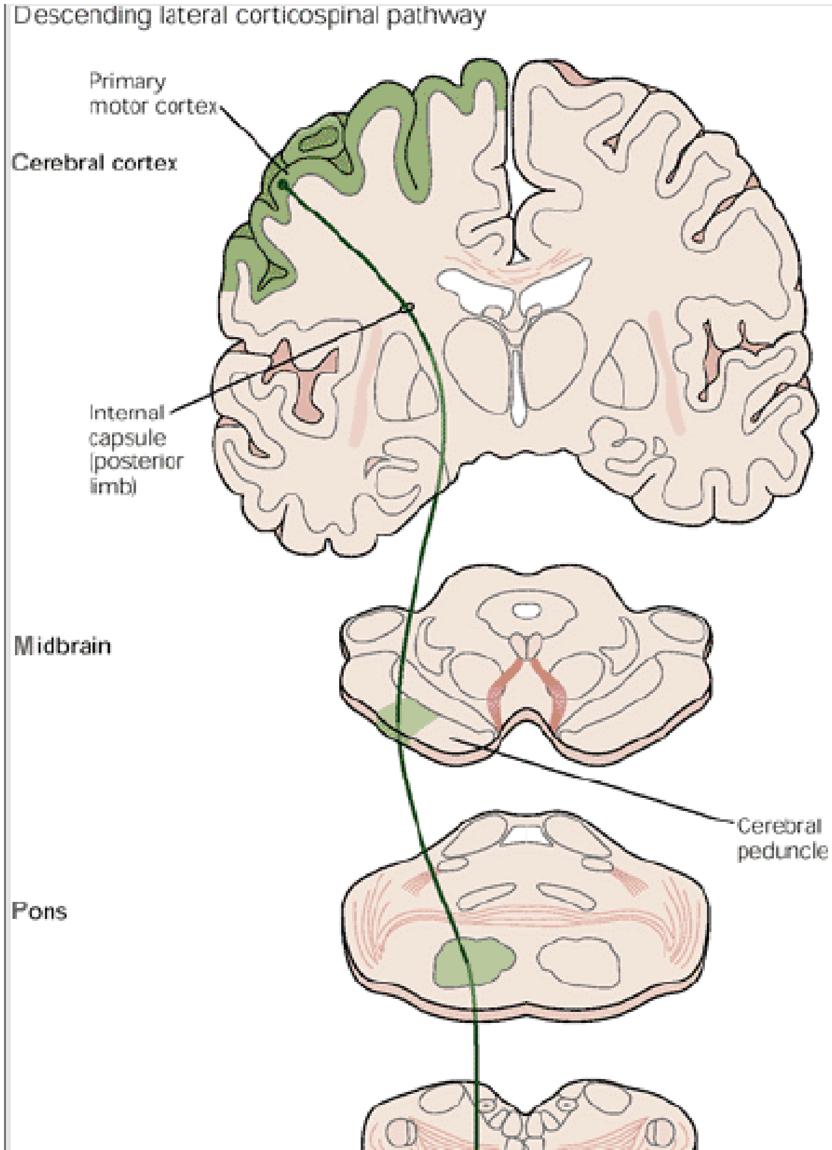
The cortico-spinal tract

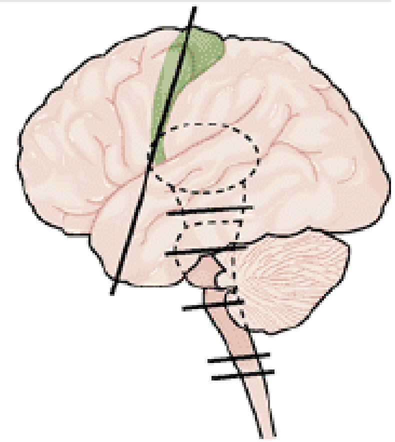
30% - M1
30% - premotor
30% - somatosensory, parietal

The cortico-bulbar tract

Face, head, neck

Motor signal conduction





The cortico-spinal tract

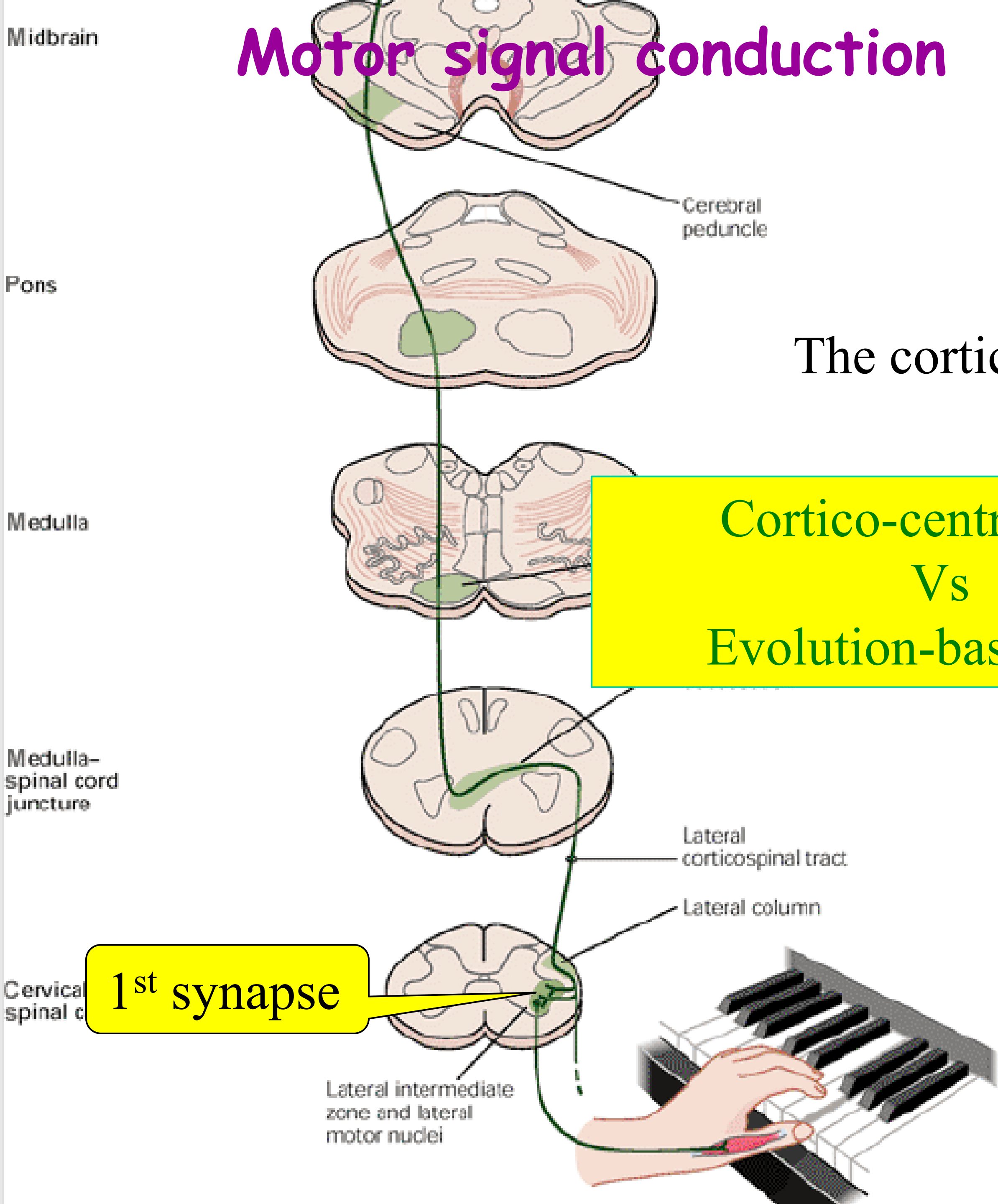
(not reversal of the afferent pathway)

Motor signal conduction

The cortico-spinal tract

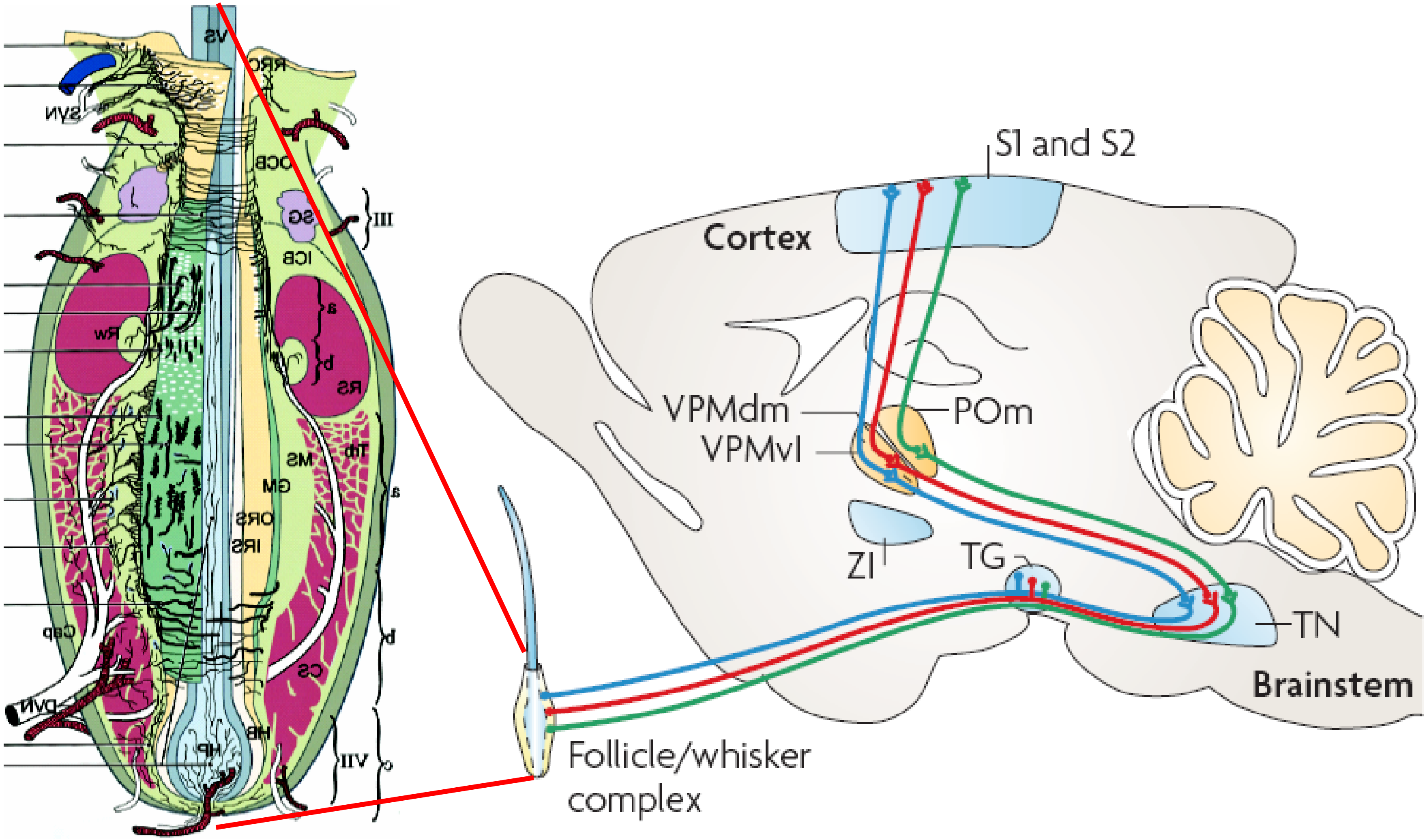
Cortico-centric view
Vs
Evolution-based view

1st synapse



Sensory signal conduction

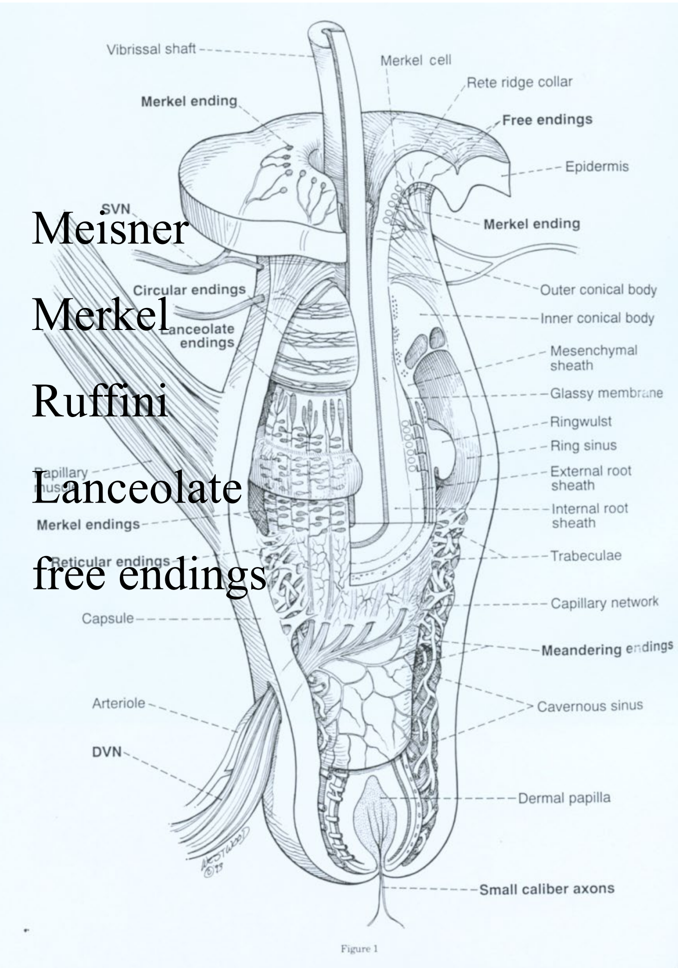
The vibrissal system

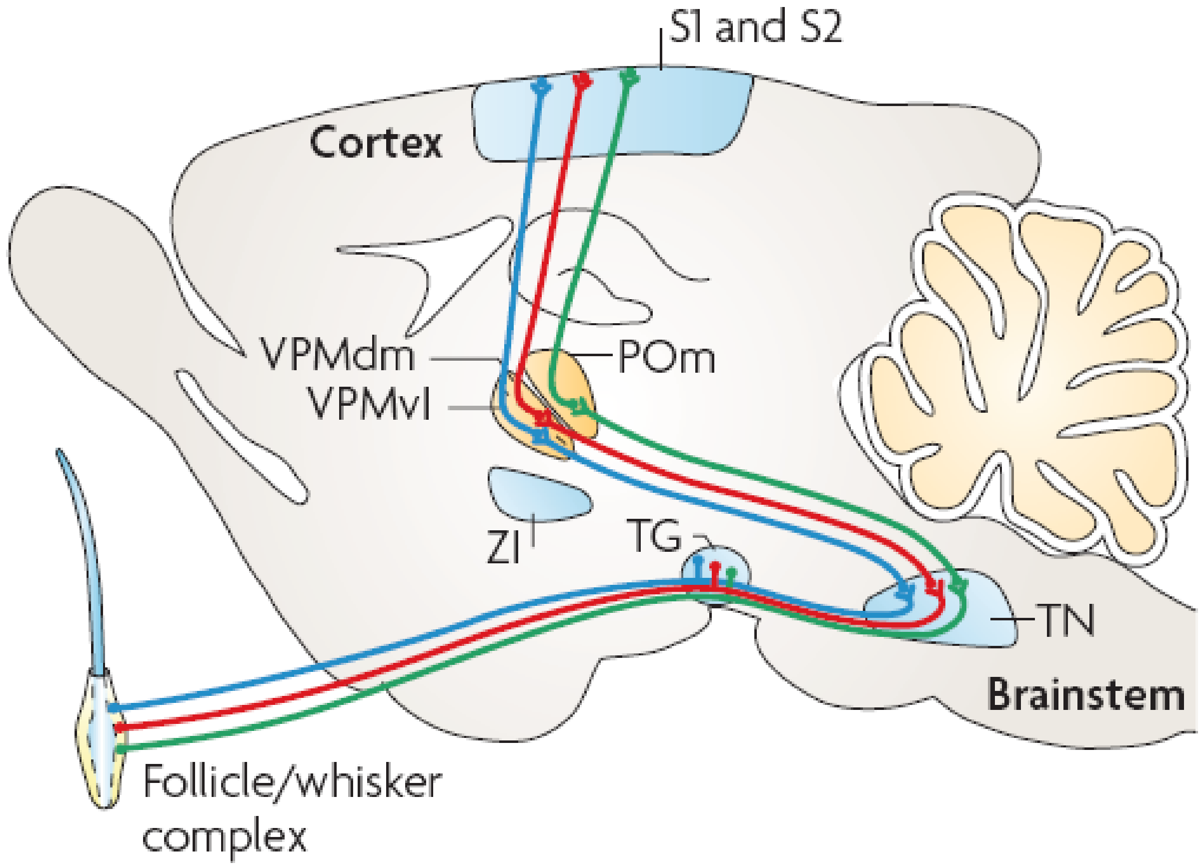


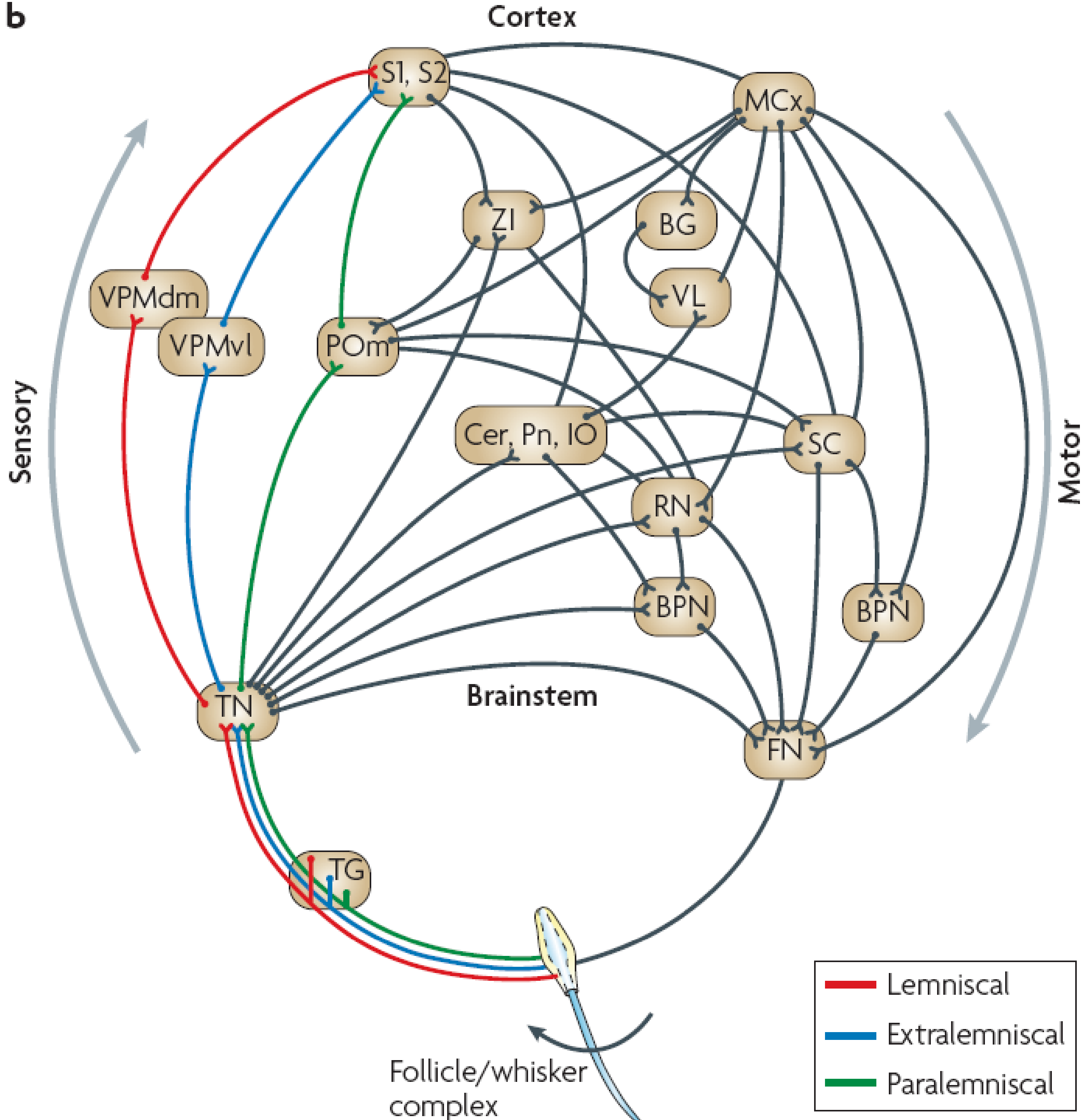
Sensory signal conduction

The vibrissal system

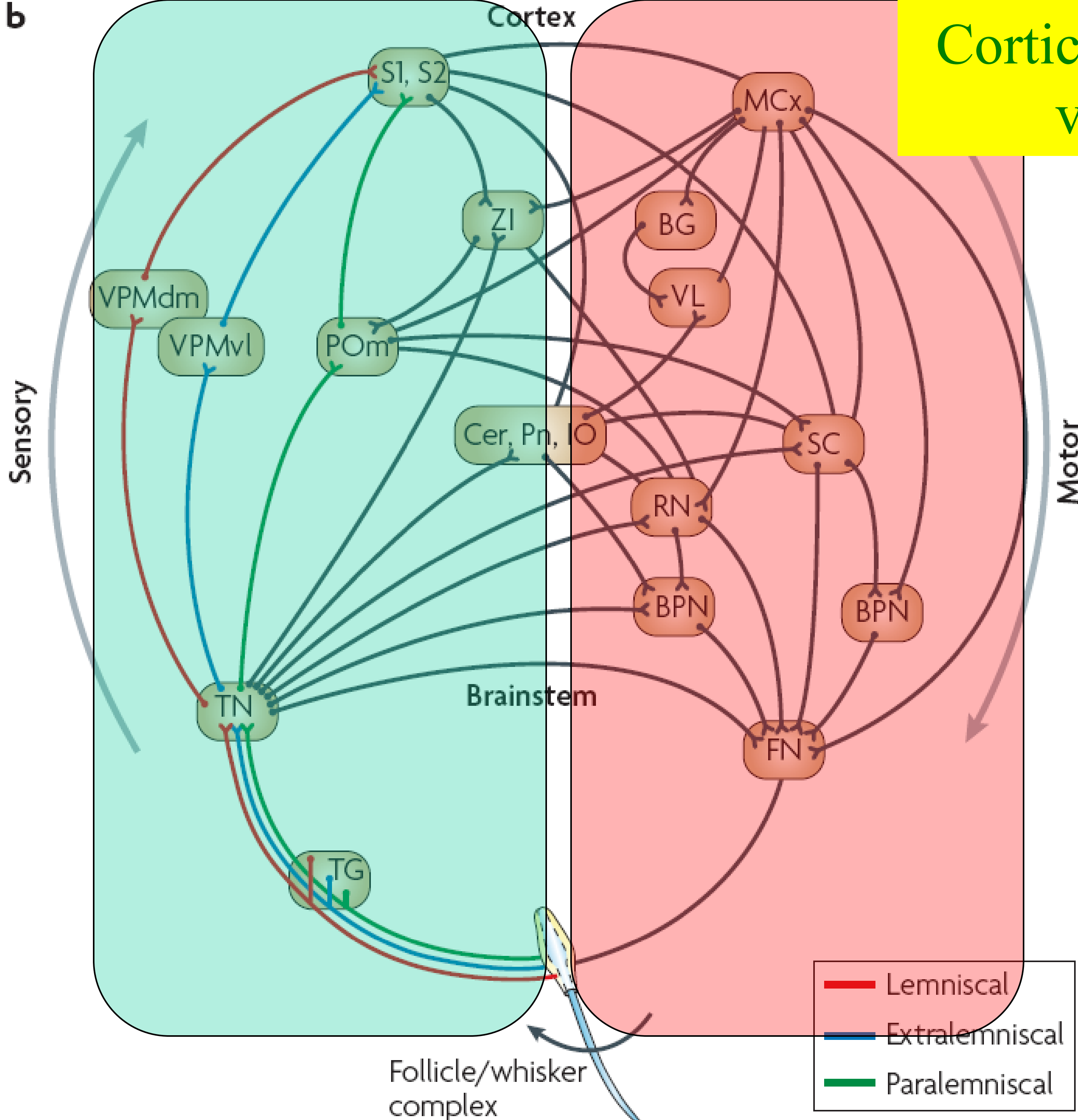
whisker

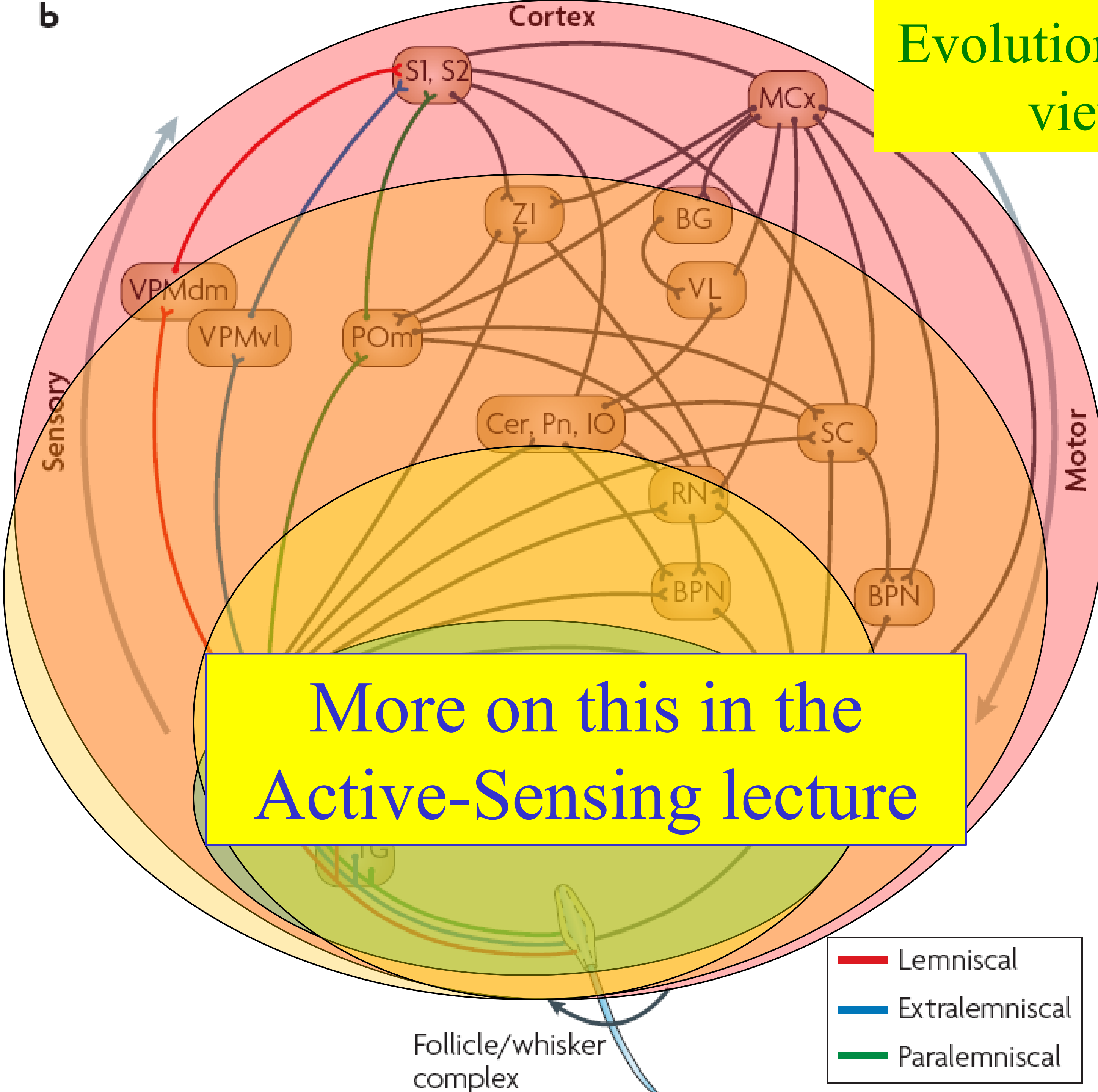





b
Cortex
S1, S2
MCx
ZI
BG
VL
VPMdm
VPMvl
POm
Cer, Pn, IO
SC
RN
BPN
BPN
Sensory
Motor
TN
Brainstem
FN
TG
Follicle/whisker complex
Lemniscal
Extralemniscal
Paralemniscal

Cortico-centric view



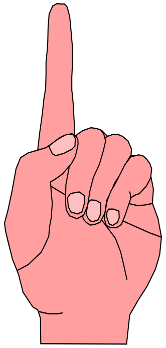


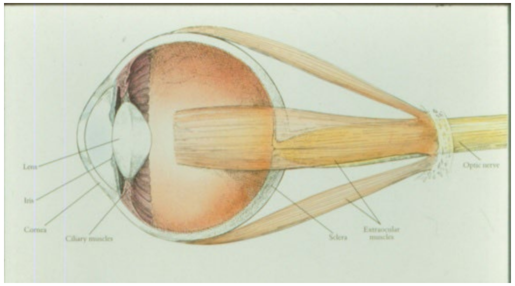
Evolution-based view

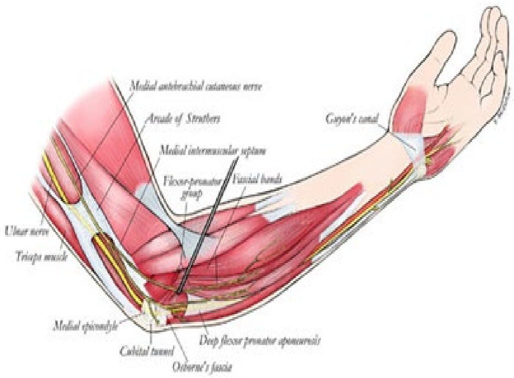
More on this in the Active-Sensing lecture

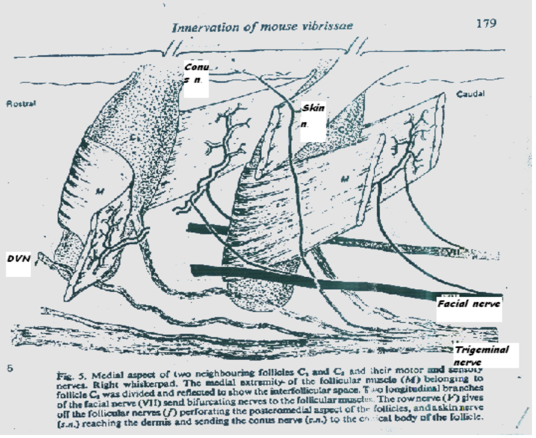
Common mechanisms of sensory processing

Rich muscular system



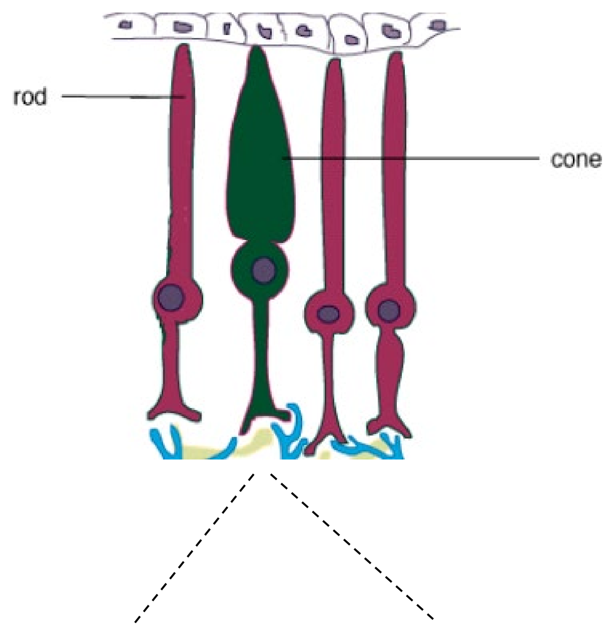






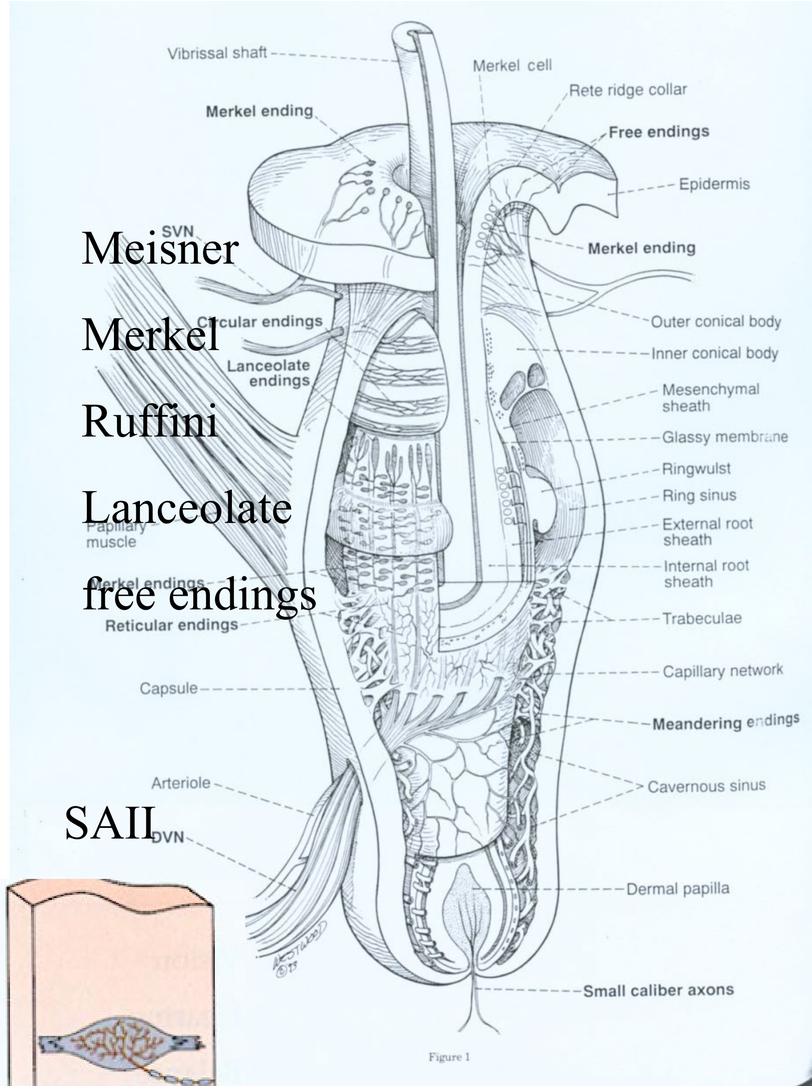
Receptor types

eye



R G B

whisker



Meisner

Merkel

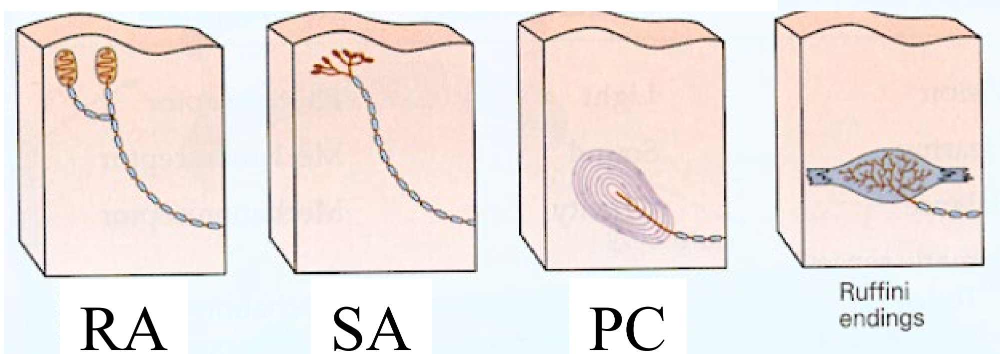
Ruffini

Lanceolate

free endings

finger

RAI SAI RAII SAII

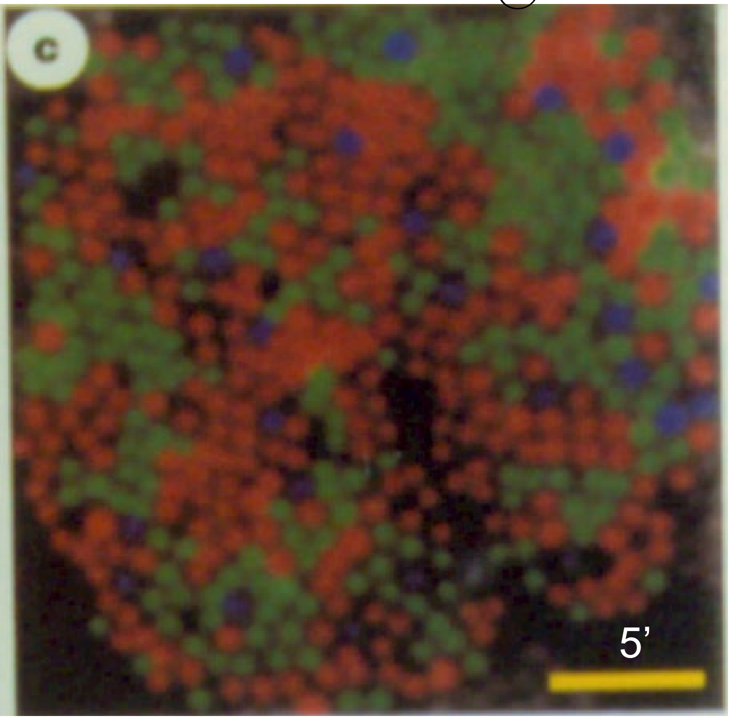


RA SA PC

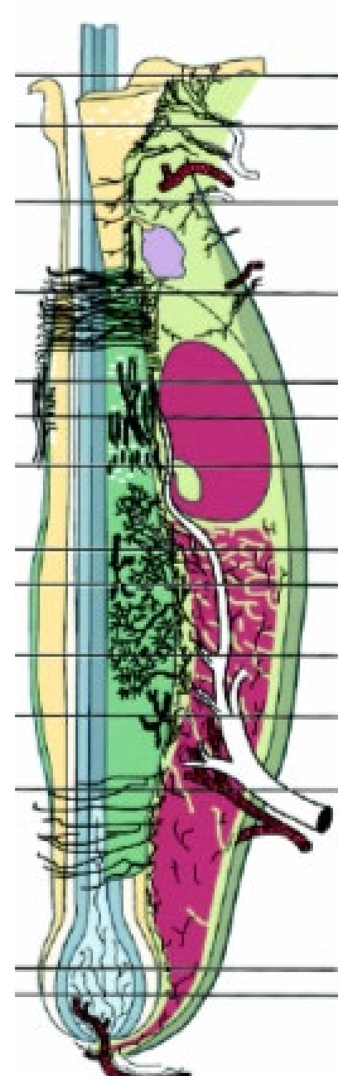
Receptors mix in clusters

eye

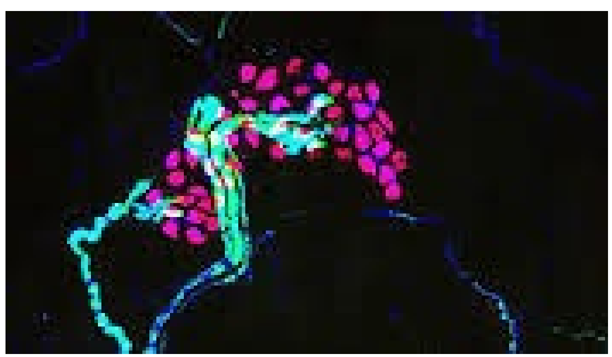
@ 1°

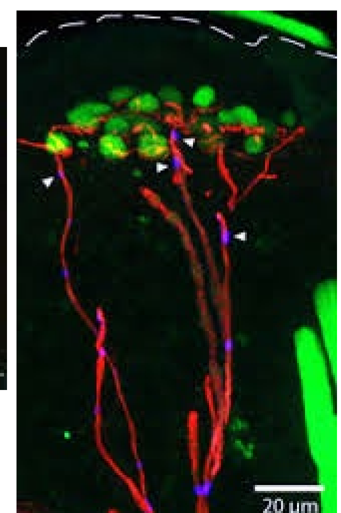


whisker



finger

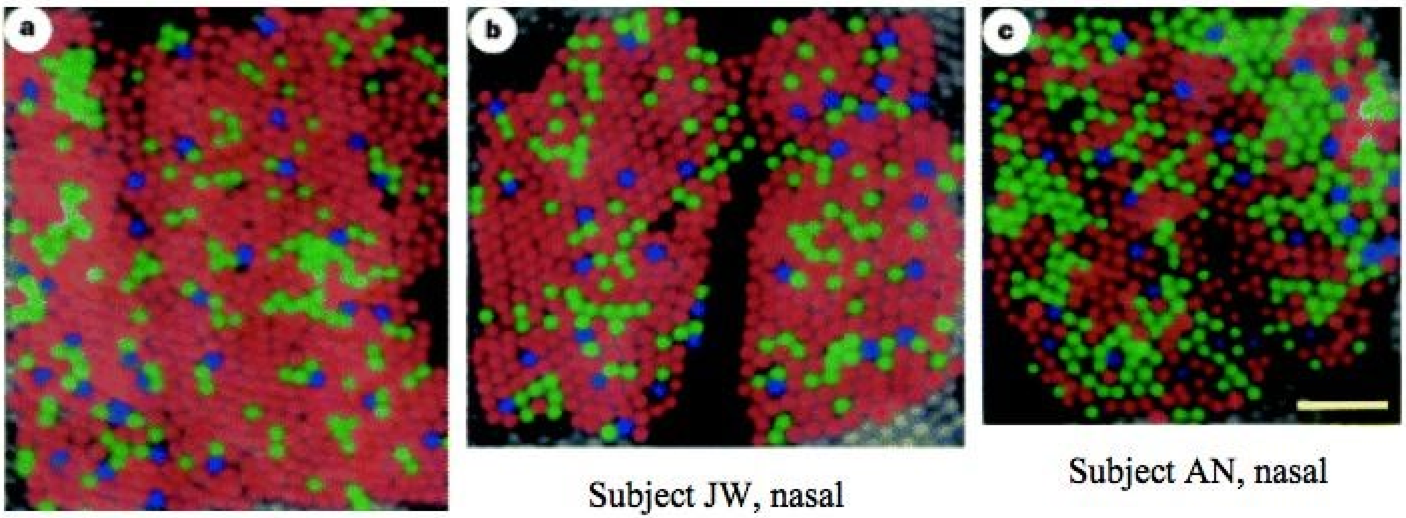




Merkel cells

Idiosyncratic clustering

Human cone mosaic



Subject JW, temporal

Subject JW, nasal

Subject AN, nasal

one degree eccentricity

Do they see the same world?

http://www.cns.nyu.edu/~david/courses/perception/lecturenotes/retina/retina.html

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

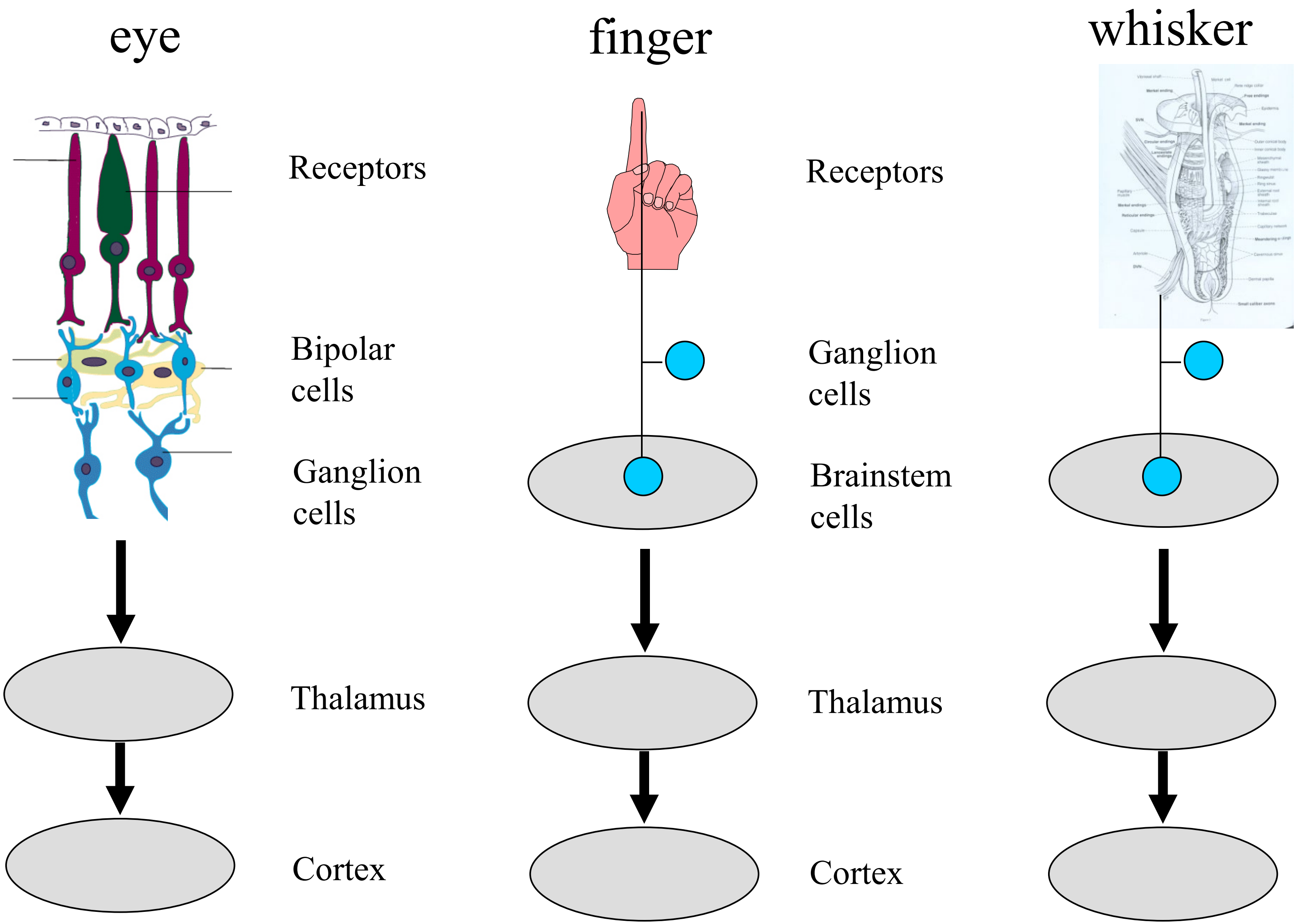
~ 10 -> 1 convergence

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

~ 1 -> 10 divergence

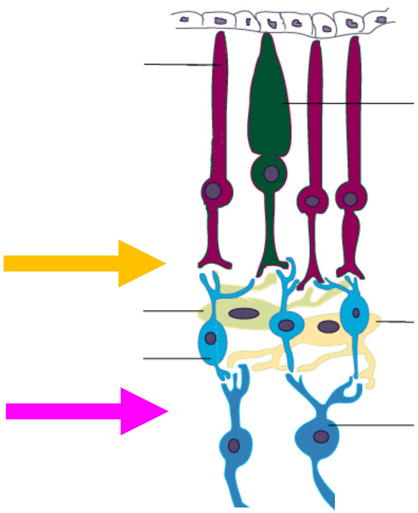
why?
Speculate at home…

Processing stations



Spatial processing (by Lateral inhibition)

eye

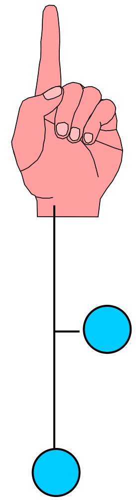


Receptors

Bipolar cells

Ganglion cells

finger



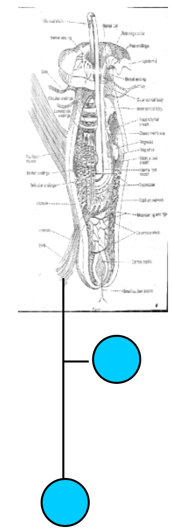
?

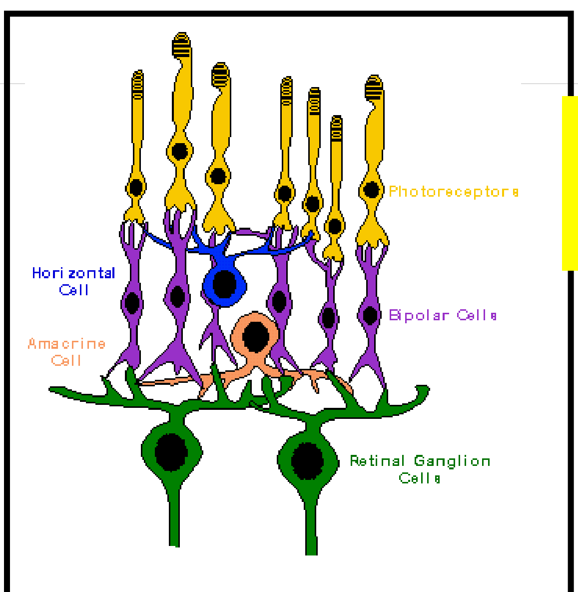
Receptors

Ganglion cells

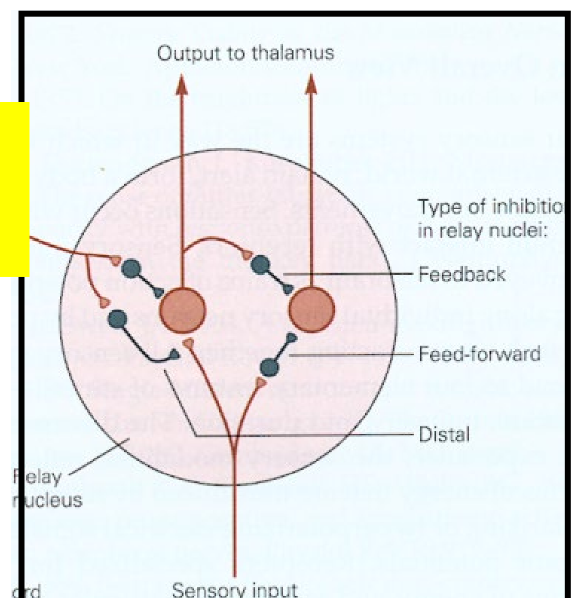
Brainstem cells

whisker





Drive for clustering?



Efficient, event-based, coding

(coding of changes)

Changes in time:

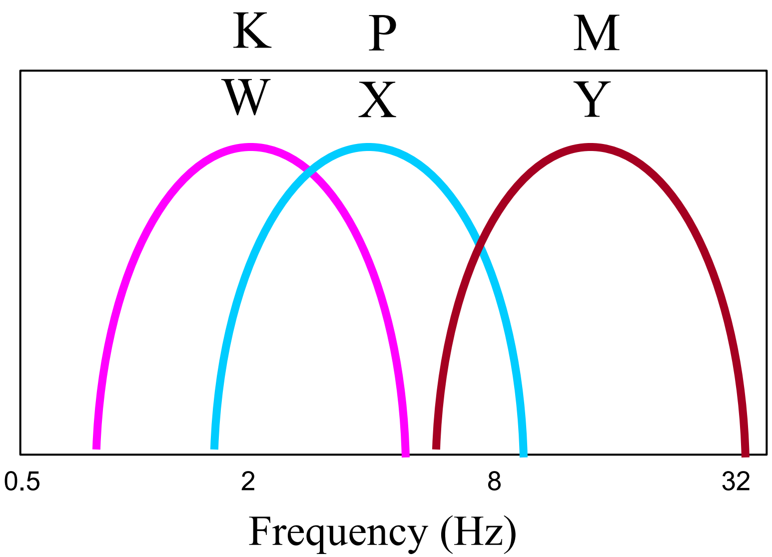
- Intrinsic in individual neurons
- Starting at the receptor level

Changes in space:

- Circuits of neurons
- Starting after lateral inhibition

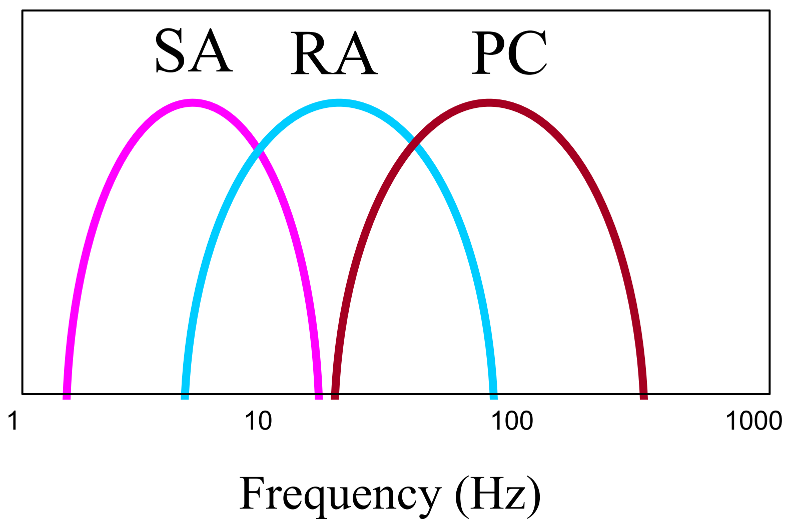
Temporal filtering (by intrinsic factors)

eye



whisker

finger



Neurometric – psychometric matching

sensitivity

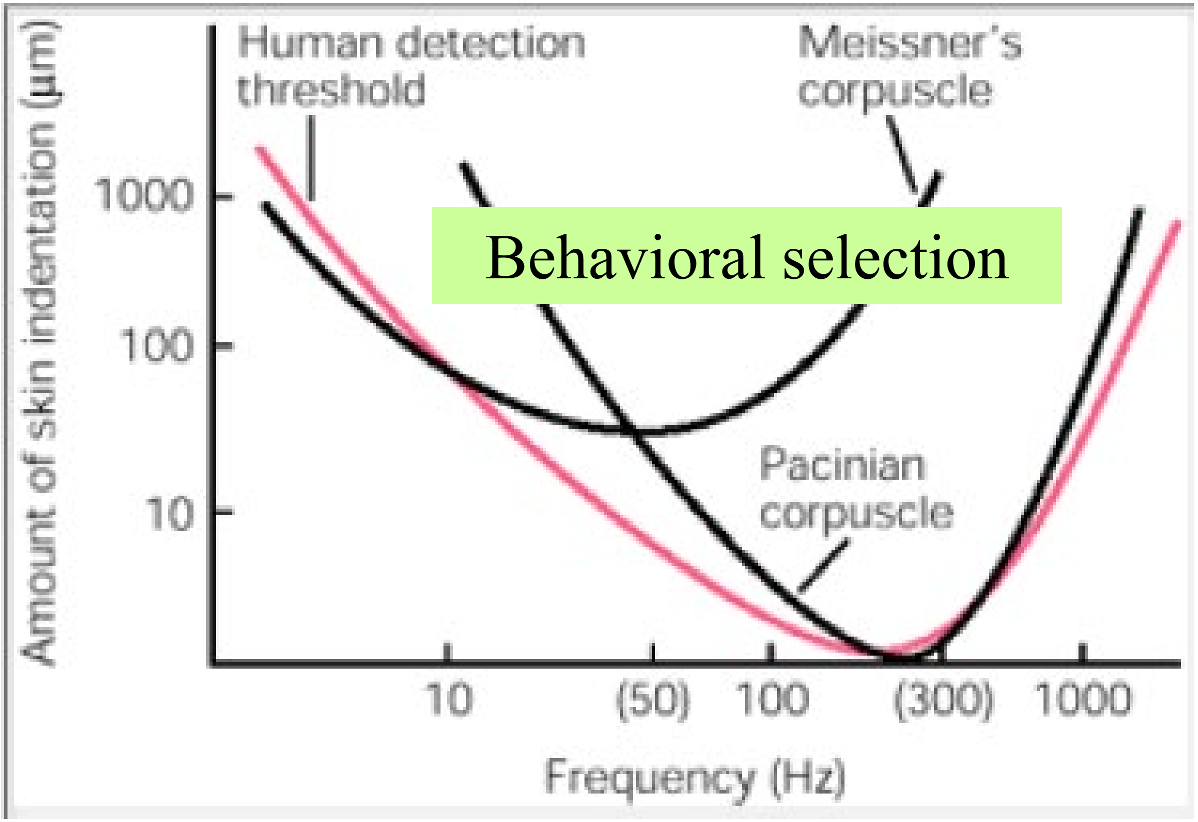


Figure 22-6B The threshold for detecting vibration corresponds to the tuning threshold of the mechanoreceptor. The sensitivity threshold for Meissner's corpuscles is lowest for frequencies of 20-50 Hz. Pacinian corpuscles sense higher frequencies. (Adapted from Mountcastle et al. 1972.)

- Break ?

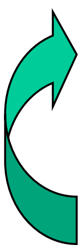
Passive and active touch

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

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

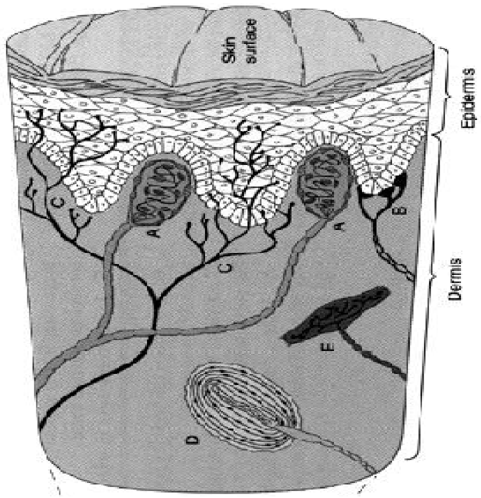
Underlying active mechanisms:

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

<u>*Sensory encoding:*</u> <u>*What receptors tell the brain*</u>

Sensory organs consist of **receptor arrays**:

somatosensation **audition** **vision**

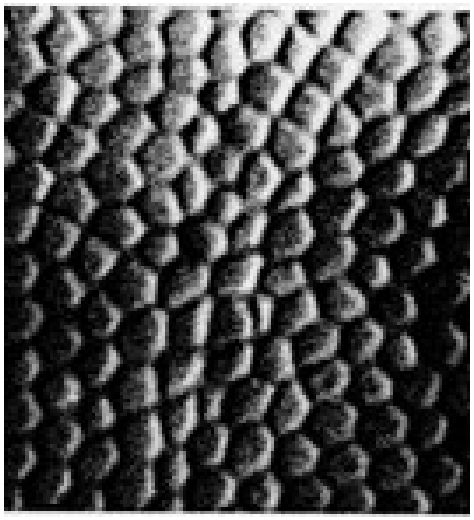


~200 μm

Finger pad

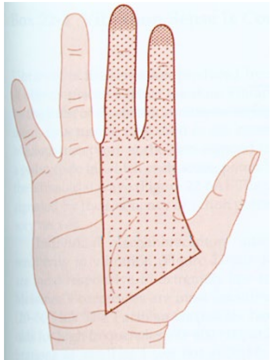
10 μm

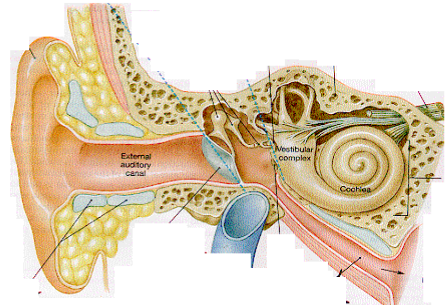
cochlea

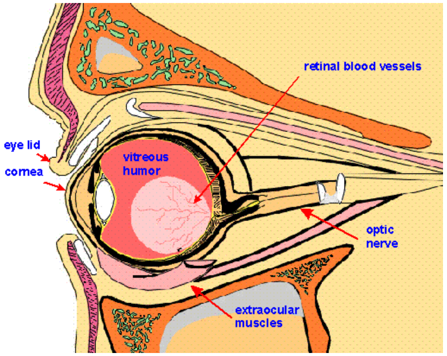


10 μm

retina



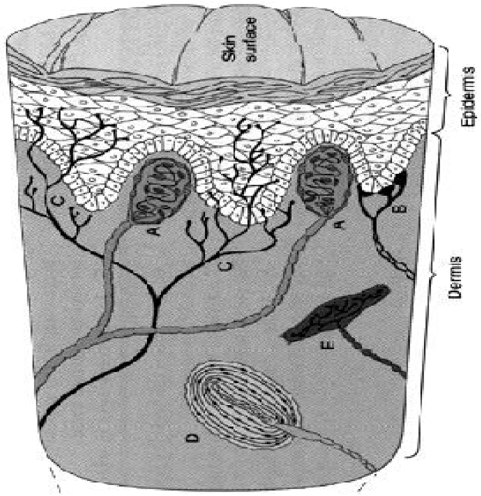




Sensory encoding: What receptors tell the brain

Sensory organs consist of **receptor arrays**:

somatosensation



~200 μm

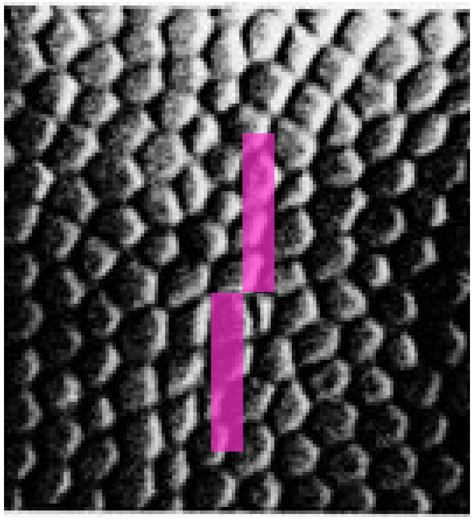
Finger pad

audition

10 μm

cochlea

vision



10 μm

retina

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

Spatial coding metaphors

one could think of:

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

light is

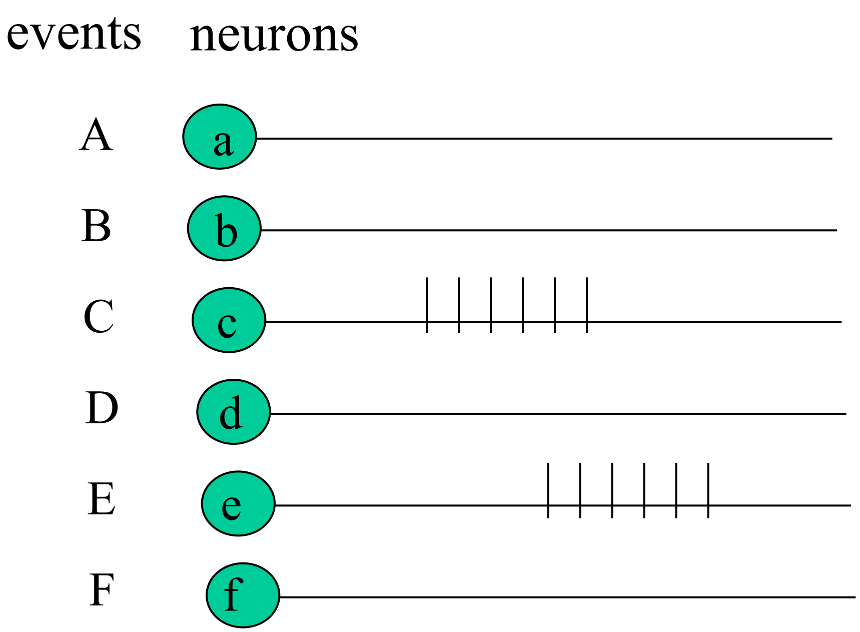
Imprinted on the retina via photo-receptors

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

How neurons encode external events in space?

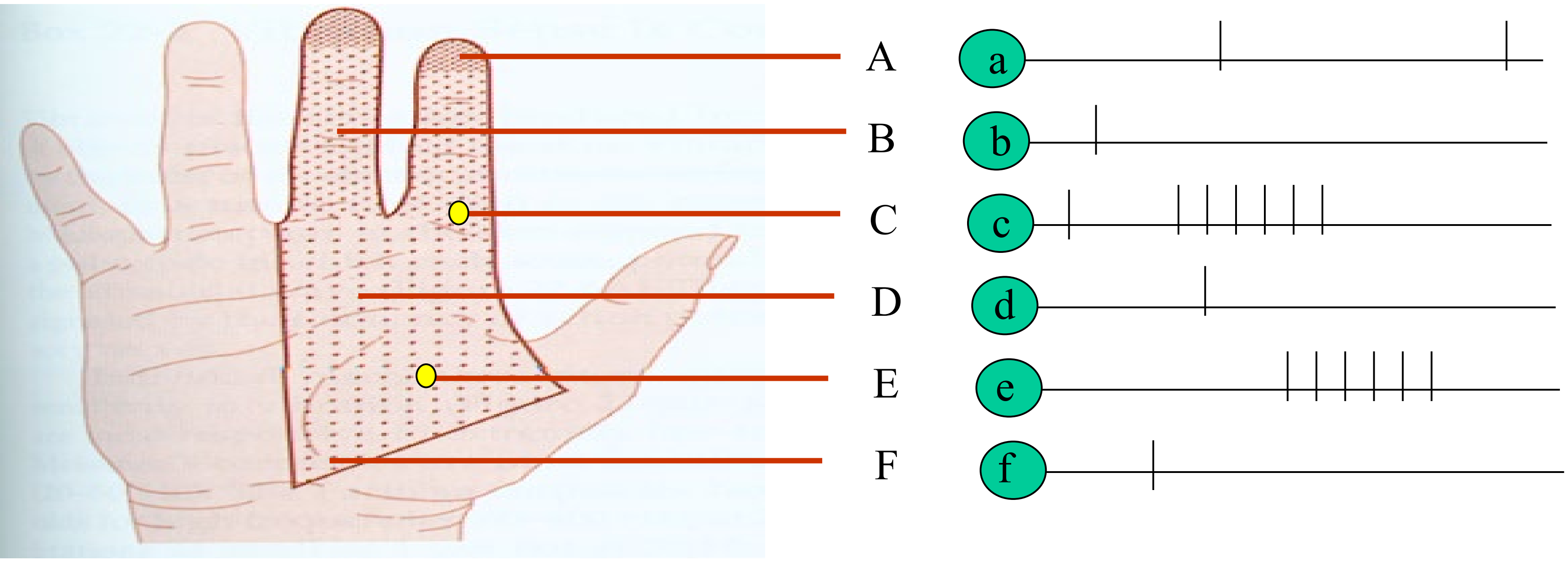
The “labeled-line code”.

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



Every neuron has a “label”

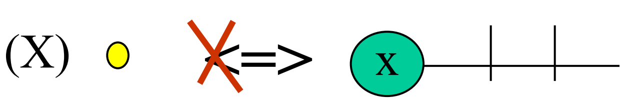
Reading out the labeled line code



reading algorithm:

if x fires, then a location X is pressed

if x does not fire, then a location X is not pressed



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 <u>changes</u>

Thus

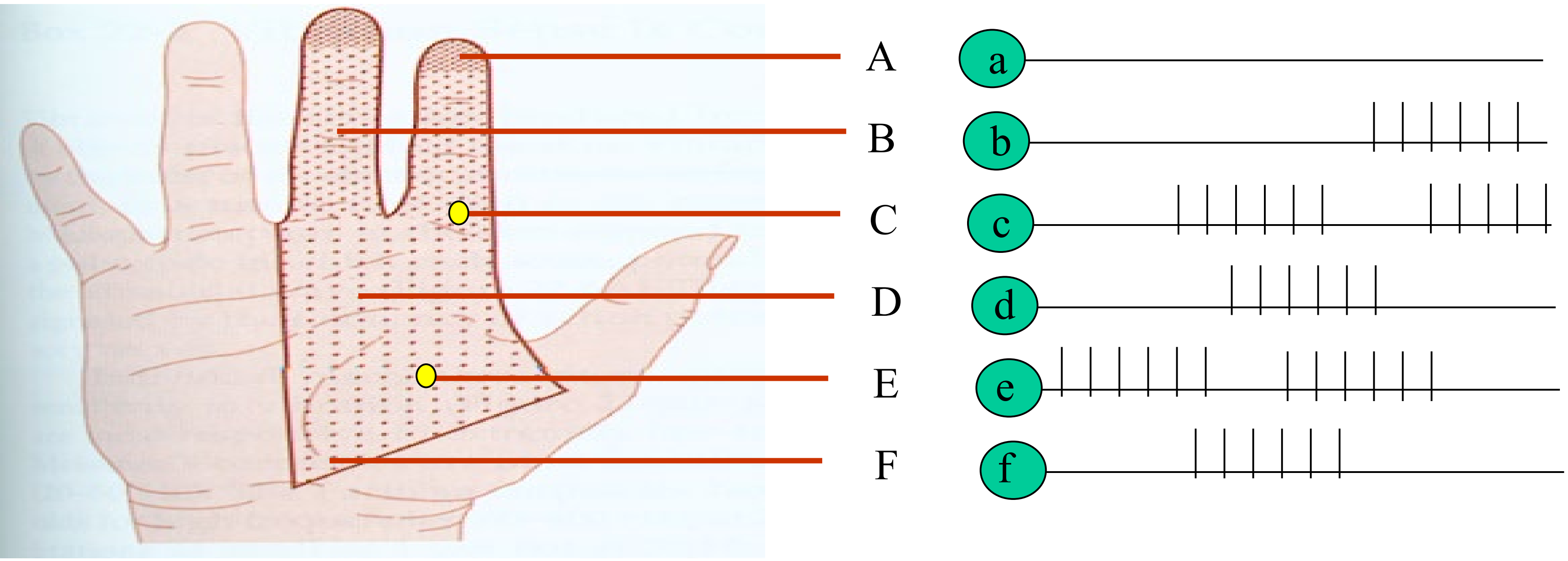
If both objects and sensors are passive (stationary), nothing will be sensed

Thus

Sensors must move in order to sense stationary objects

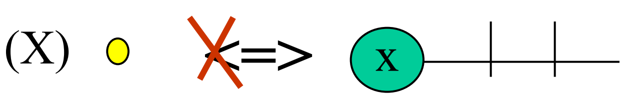
How sensor motion constrains sensory coding?

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?



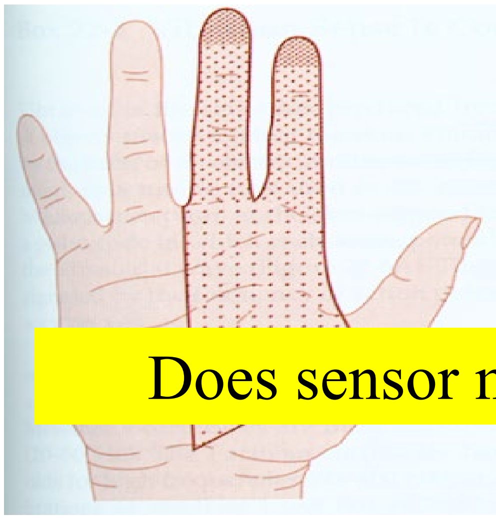
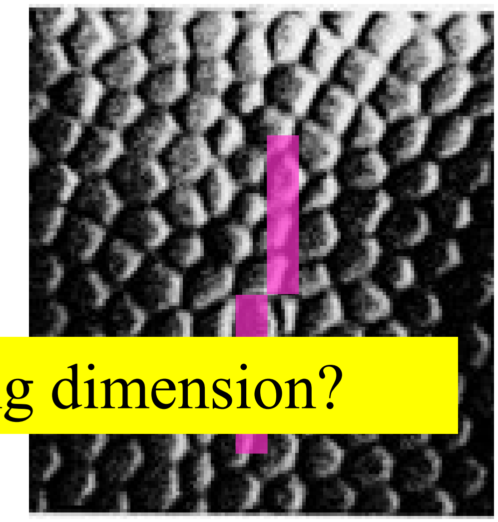
Neuron x fires ~~*if and only*~~ *if* X is pressed

Is this assumption valid?

2. The "problem" of sensor motion

sensory encoding: *What receptors tell the brain*

Sensory organs consist of **receptor arrays**:

somatosensation	**audition**	**vision**
		
~50 µm	10 µm	10 µm
Finger pad	*cochlea*	*retina*

Does sensor motion add additional coding dimension?

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

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

Passive and active touch

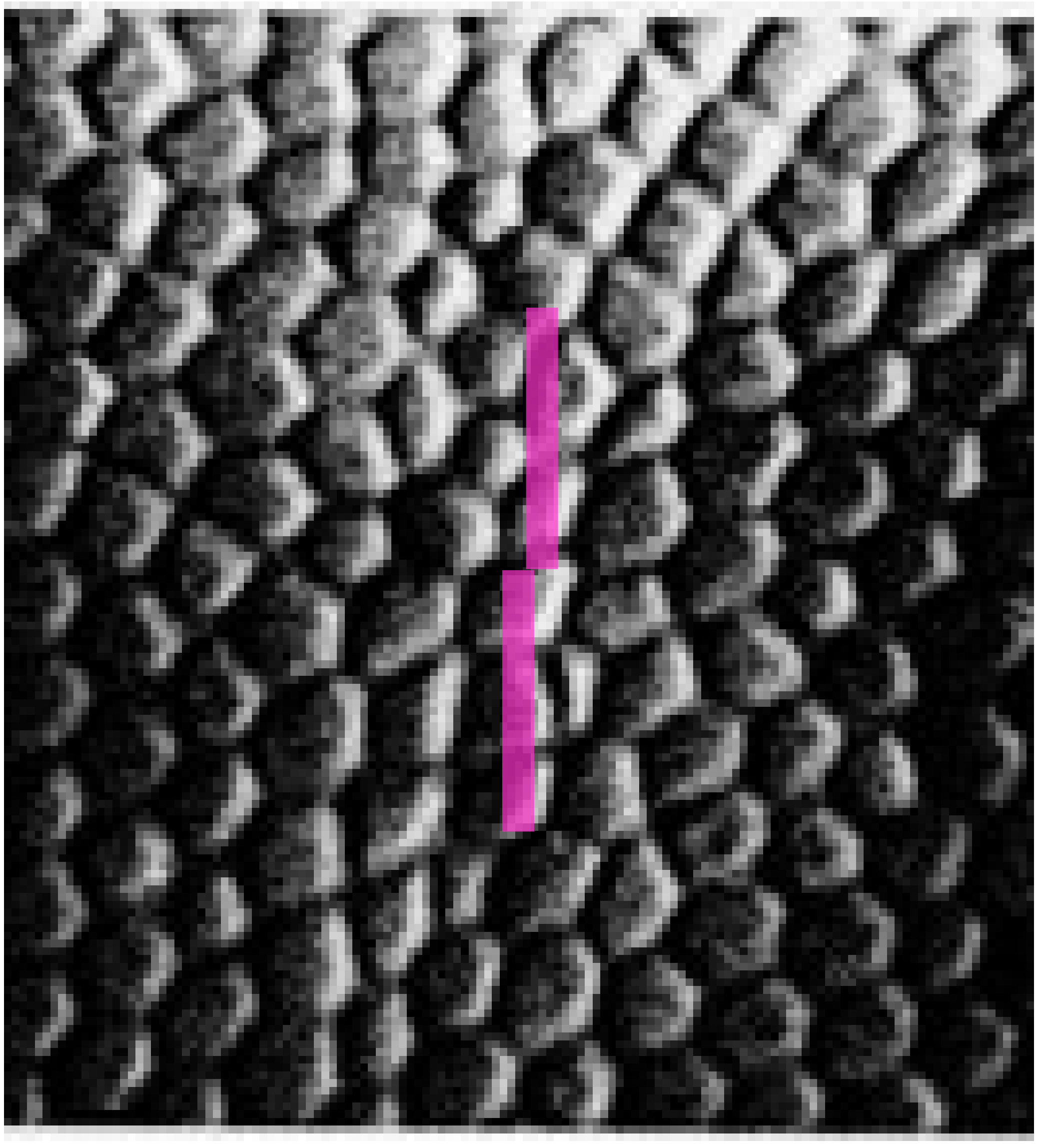
Passive touch	Active touch
▪ low thresholds	▪ higher thresholds
▪ poor accuracy	▪ high accuracy

Underlying active mechanisms:

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

Spatial coding	Spatio-temporal coding

<u>*sensory encoding:*</u> **Increased resolution due to scanning**



retina

Passive and active touch

Passive touch
- low thresholds
- poor accuracy

Active touch
- higher thresholds
- high accuracy

Coding dimensions

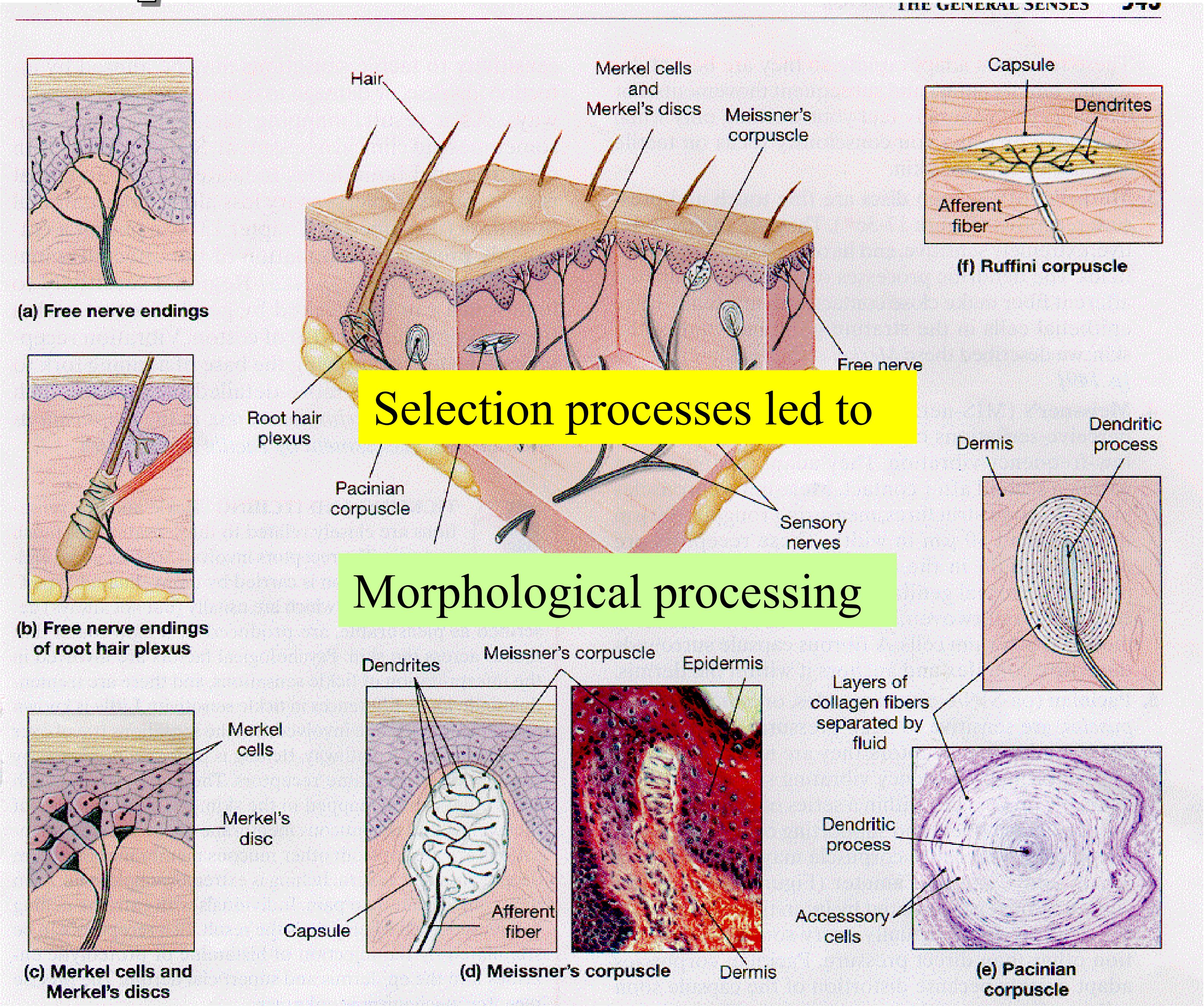
Spatial coding

Spatio-temporal coding

Interactive (morphological) coding

Receptors

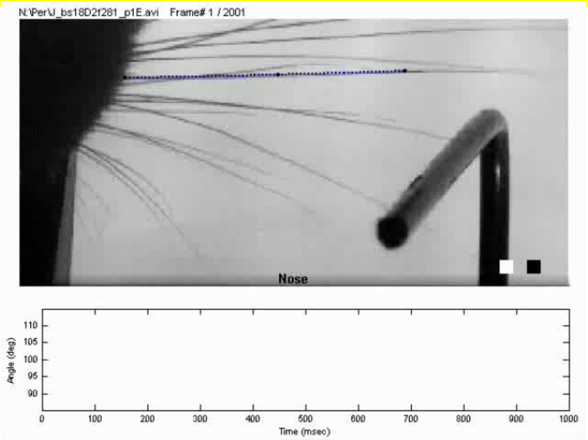
Evolutionary specialization



Selection processes led to

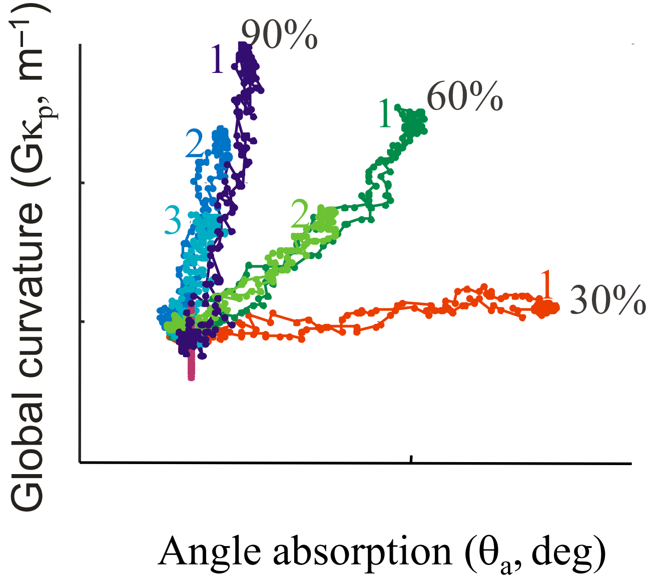
Morphological processing

Morphological processing

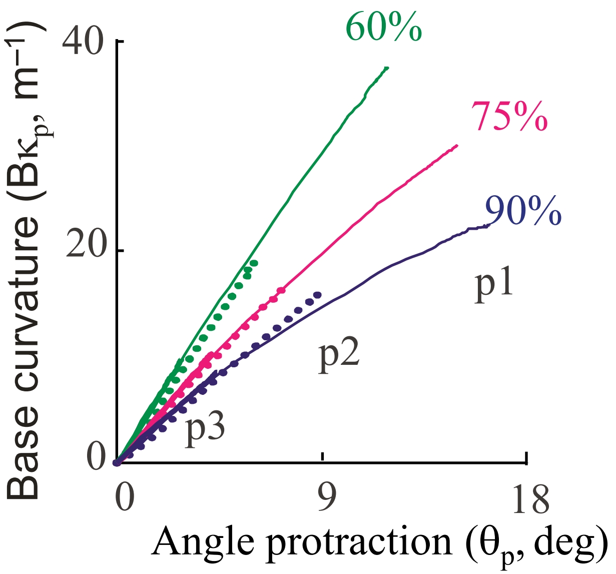


Morphological phase plane

Gκ - θ_a phase plane

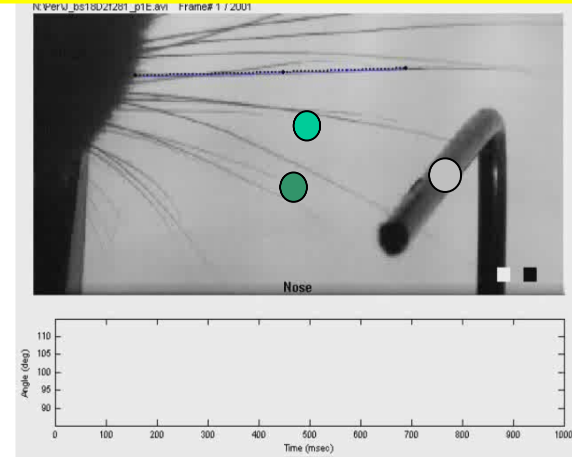


Bκ - θ_p phase plane



Bagdasarian et al. *Nat Neurosci* (2013)

Morphological processing



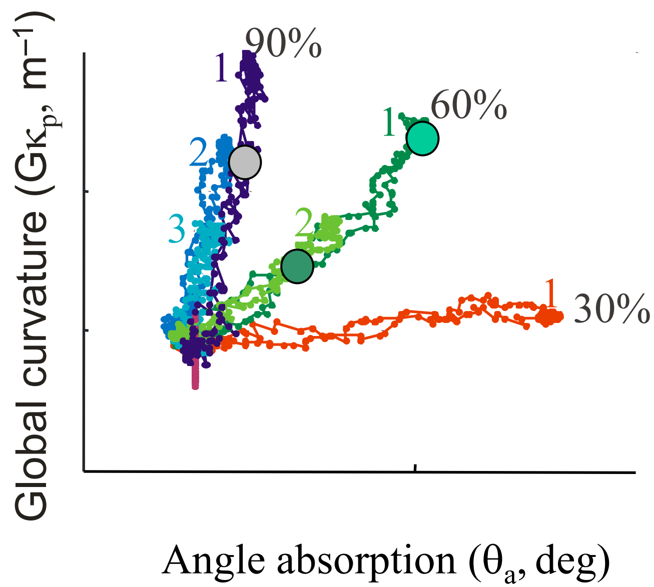
Motor-sensory phase plane

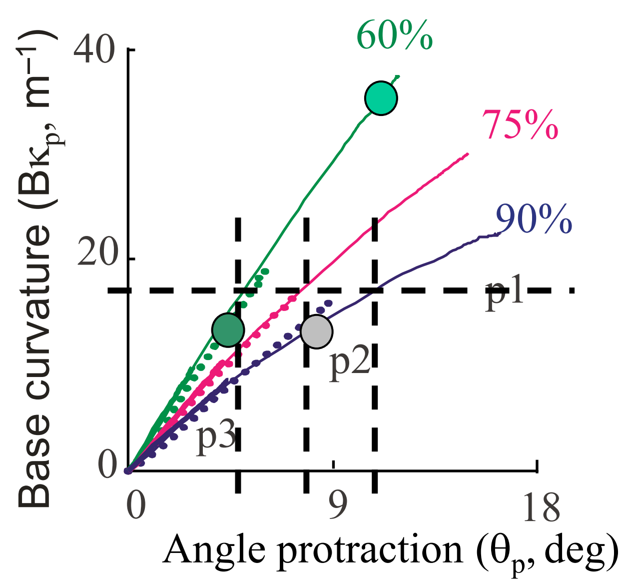
Morphological phase plane

Gκ - θ_a phase plane

Bκ - θ_p phase plane

Sensory



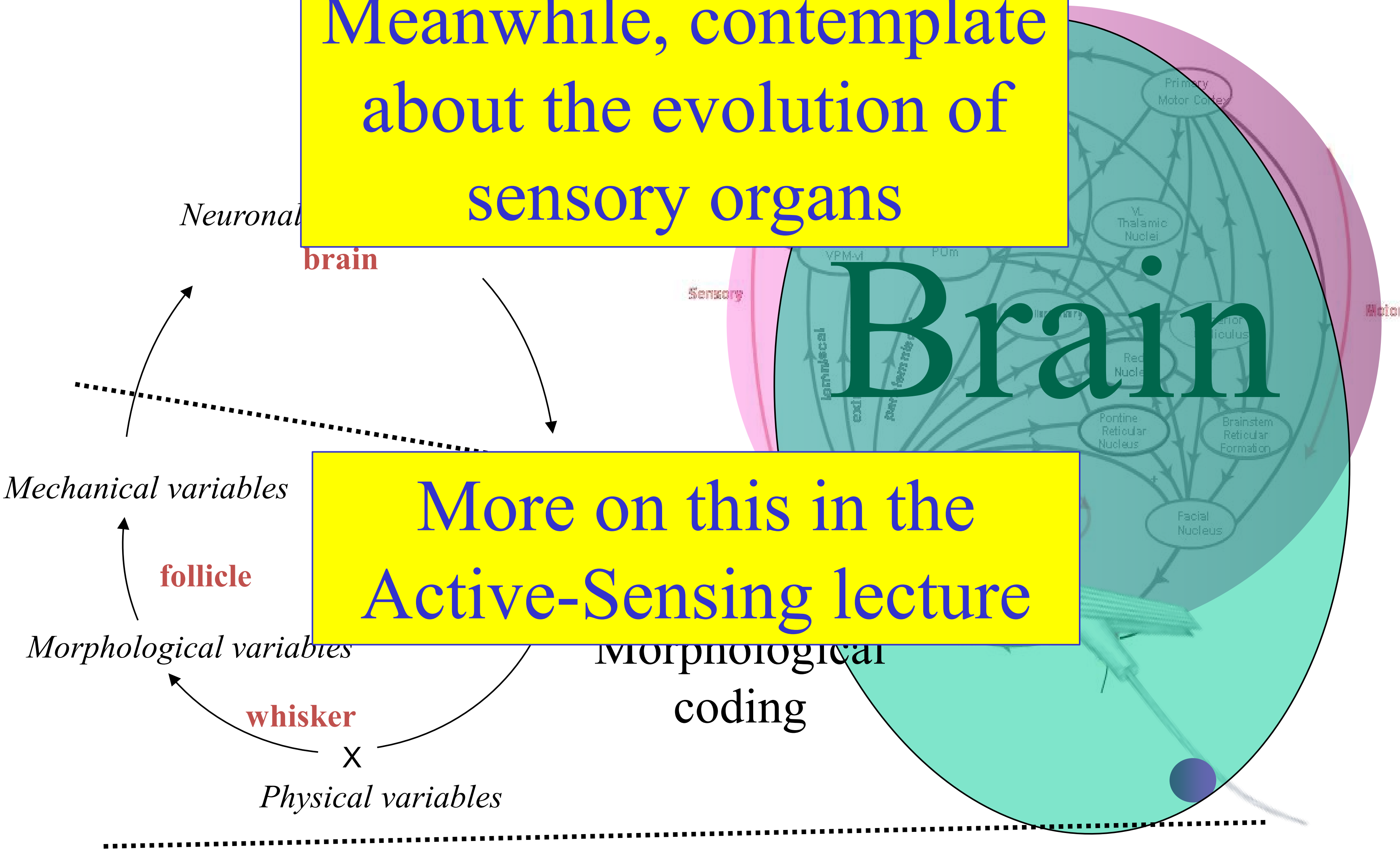


Motor

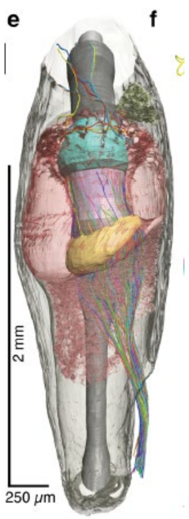
Bagdasarian et al. *Nat Neurosci* (2013)

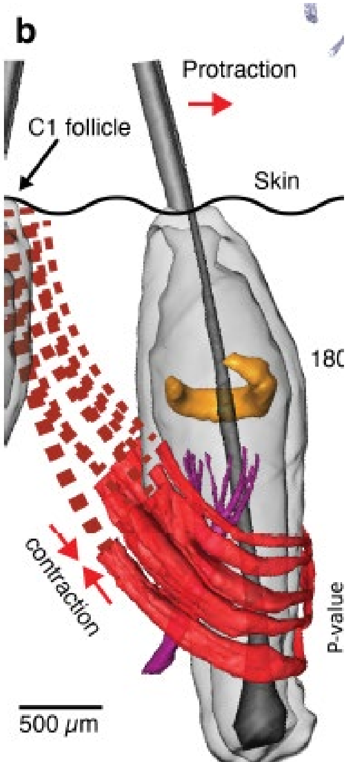
Organism-environment attractors

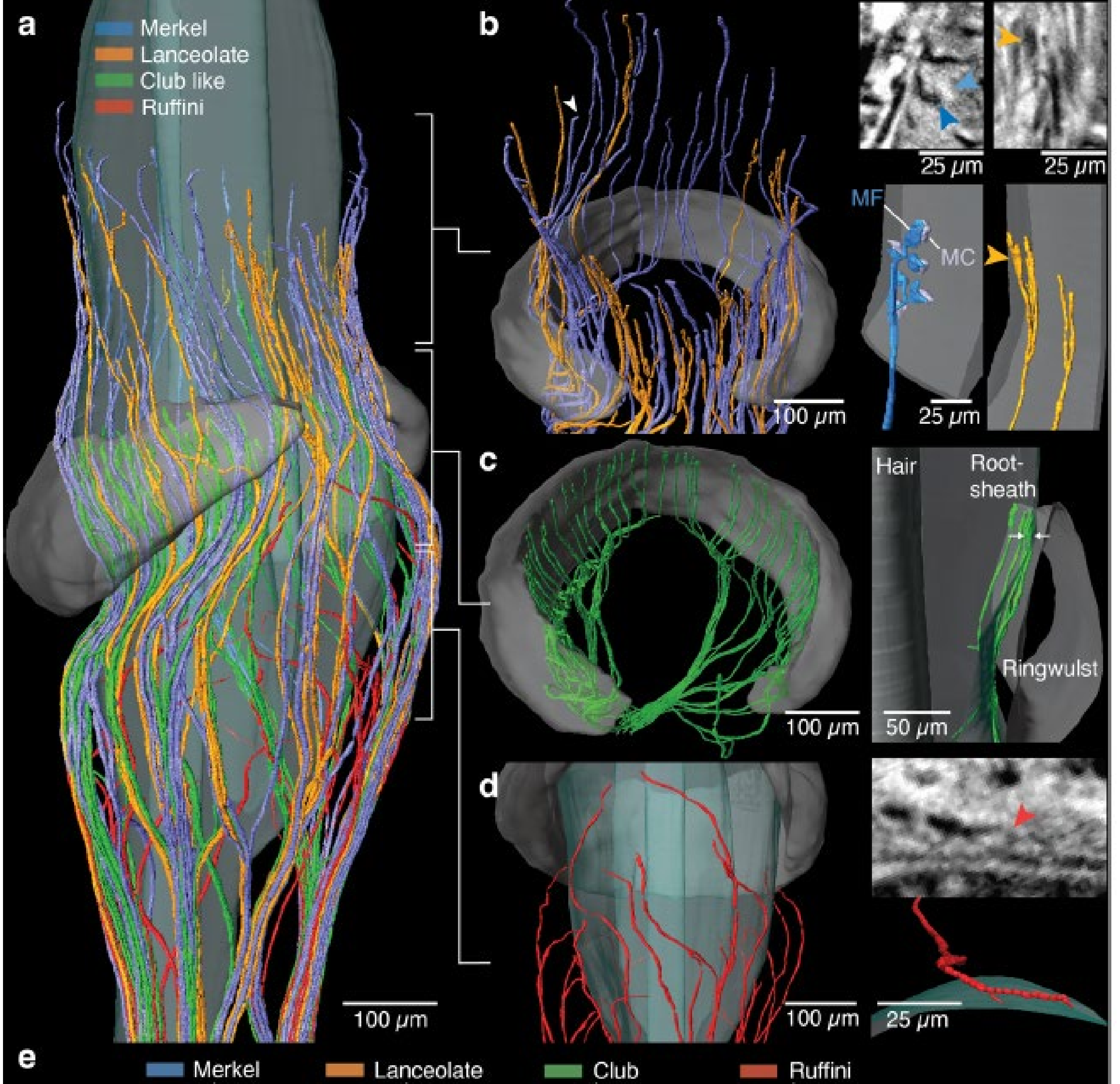
Meanwhile, contemplate about the evolution of sensory organs



More on this in the Active-Sensing lecture


e
f
2 mm
250 μm

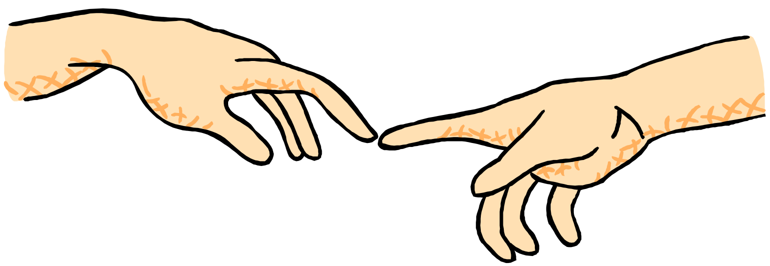

b
Protraction
C1 follicle
Skin
180
contraction
P-value
500 μm


a
Merkel
Lanceolate
Club like
Ruffini
100 μm
b
25 μm
25 μm
MF
MC
100 μm
25 μm
c
Hair
Root-sheath
Ringwulst
100 μm
50 μm
d
100 μm
25 μm
e
Merkel
Lanceolate
Club
Ruffini

Touching

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

Touching



The End