Obecná fyziologie smyslů

Table 10.1 Main types of sensory modalities

Sensory modality	Form of energy	Receptor organ	Receptor cell
Chemical			
common chemical	molecules	various	free nerve endings
arterial oxygen	O_2 tension	carotid body	cells and nerve endings
toxins (vomiting)	molecules	medulla	chemoreceptor cells
osmotic pressure	osmotic pressure	hypothalamus	osmoreceptors
glucose	glucose	hypothalamus	glucoreceptors
pH (cerebrospinal fluid)	ions	medulla	ventricle cells
Taste	ions and molecules	tongue and pharynx	taste bud cells
Smell	molecules	nose	olfactory receptors
Somatosensory			
touch	mechanical	skin	nerve terminals
pressure	mechanical	skin and deep tissue	encapsulated nerve endings
heat and cold	temperature	skin, hypothalamus	nerve terminals and central neurons
pain	various	skin and various organs	nerve terminals
Muscle			
vascular pressure	mechanical	blood vessels	nerve terminals
muscle stretch	mechanical	muscle spindle	nerve terminals
muscle tension	mechanical	tendon organs	nerve terminals
joint position	mechanical	joint capsule and ligaments	nerve terminals
Balance			
linear acceleration (gravity)	mechanical	vestibular organ	hair cells
angular acceleration	mechanical	vestibular organ	hair cells
Hearing	mechanical	inner ear (cochlea)	hair cells
Vision	electromagnetic (photons)	eye (retina)	photoreceptors

Modified from Ganong (1985)

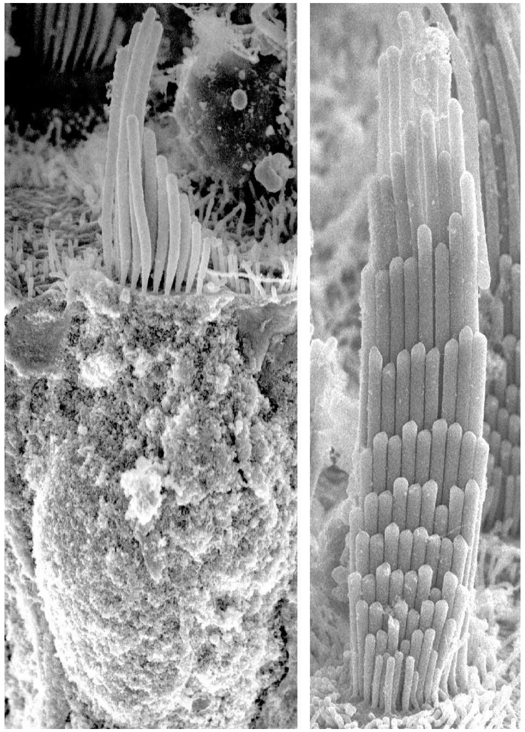
3 úrovně organizace sensorických systémů

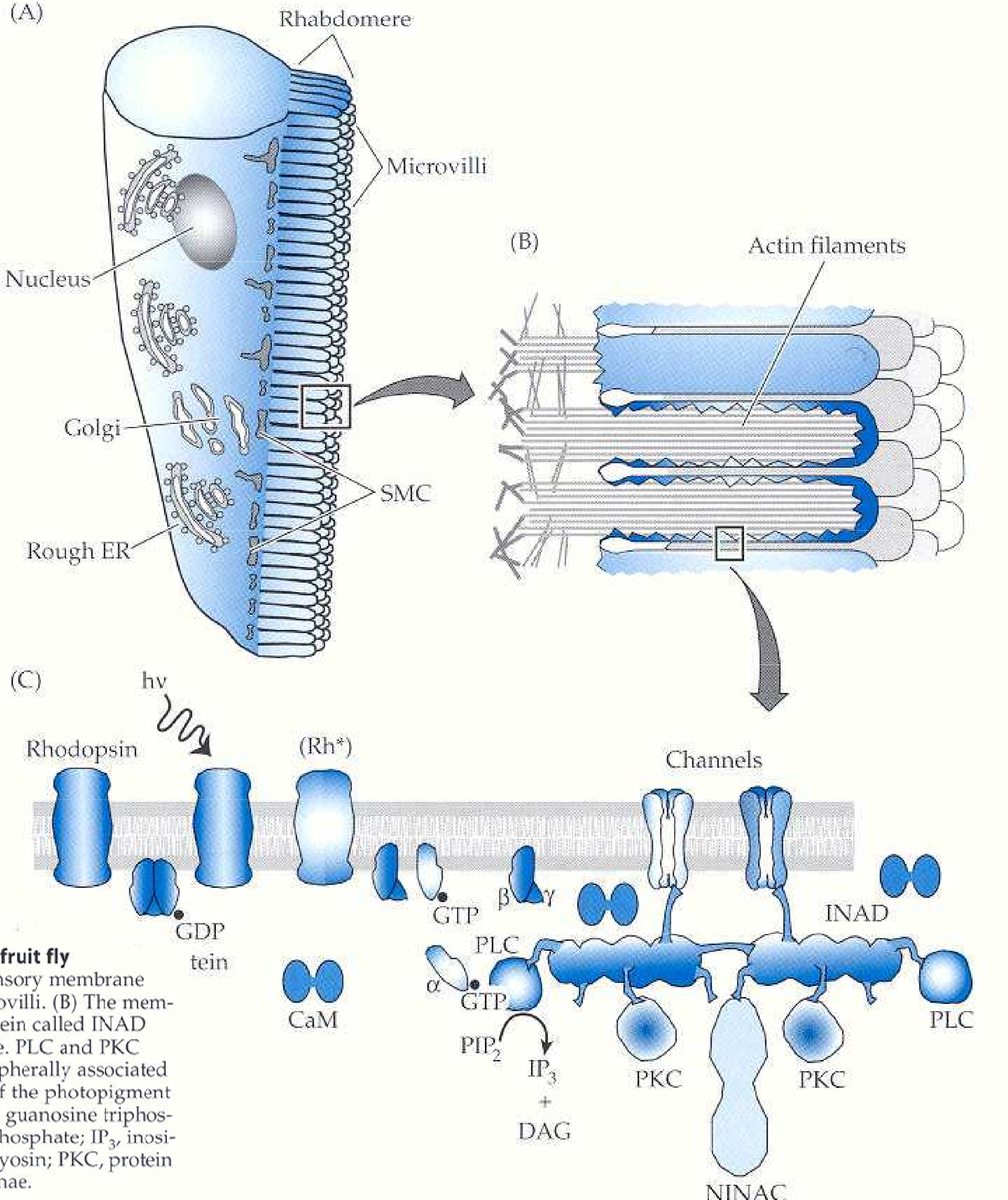
A) Receptory
B) Sensorické obvody a dráhy
C) Sensorická percepce

3 úrovně organizace sensorických systémů

A) Receptory
   sensorická membrána
   a) mikrovili (vláskové buňky, čich vom., foto. čl.)
   b) cilie (čich v nosní sl., foto. obr.)

Mikrovily





Organization of sensory membrane of a photoreceptor in the fruit fly *Drosophila* (A) Anatomy of a *Drosophila* photoreceptor. The sensory membrane forms a structure, called a rhabdomere, composed of 50,000 microvilli. (B) The membrane of the microvillus is highly organized by a scaffolding protein called INAD (C), which binds to proteins in the cytosol and plasma membrane. PLC and PKC proteins are shown as if cytosolic but are likely to be at least peripherally associated with the plasma membrane. Abbreviations: Rh^*, activated form of the photopigment rhodopsin; GDP, guanosine diphosphate; CaM, calmodulin; GTP, guanosine triphosphate; PLC, phospholipase C; PIP_2, phosphatidylinositol 4,5-bisphosphate; IP_3, inositol 1,4,5-triphosphate; DAG, diacylglycerol; NINAC, a form of myosin; PKC, protein kinase C; ER, endoplasmic reticulum; SMC, submicrovillar cisternae.

Cilie

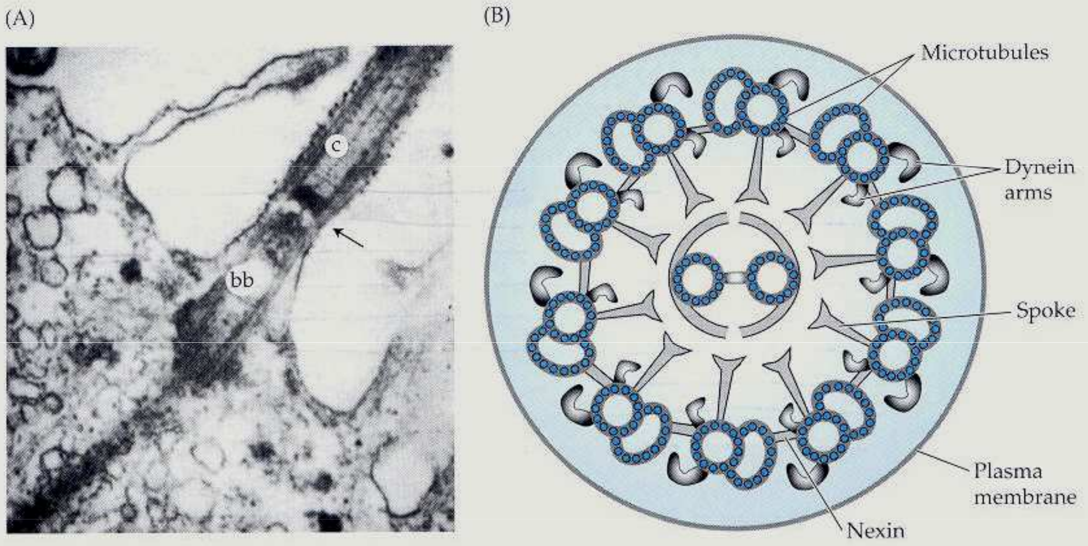


Figure 2.3
Cilium (A) Structure of a cilium from a sea urchin embryo. Note the basal body (bb) at the base of the cilium (c). Magnification 22,000×. (B) Schematic drawing of a cross section of cilium. (A from Chakrabarti et. al., 1998.)

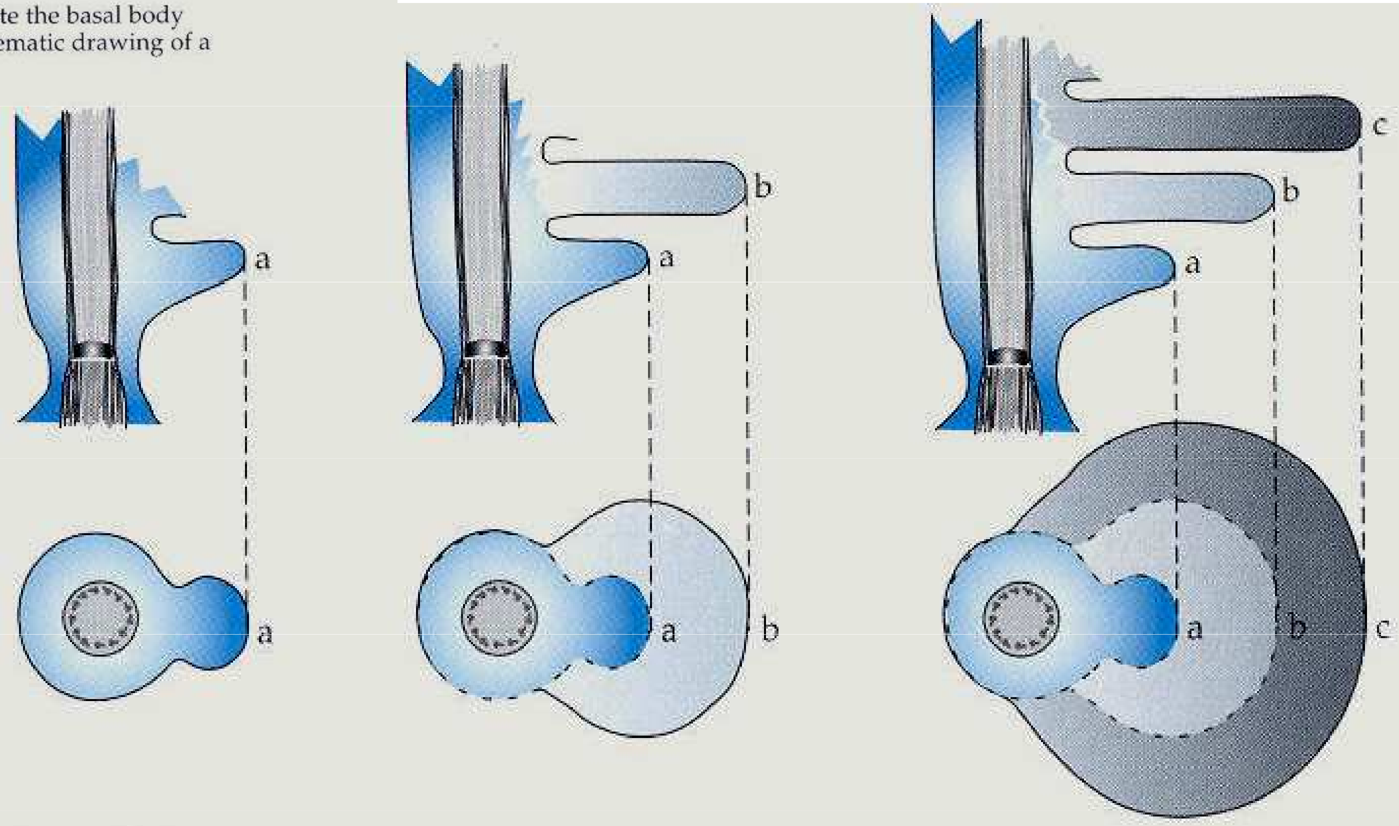
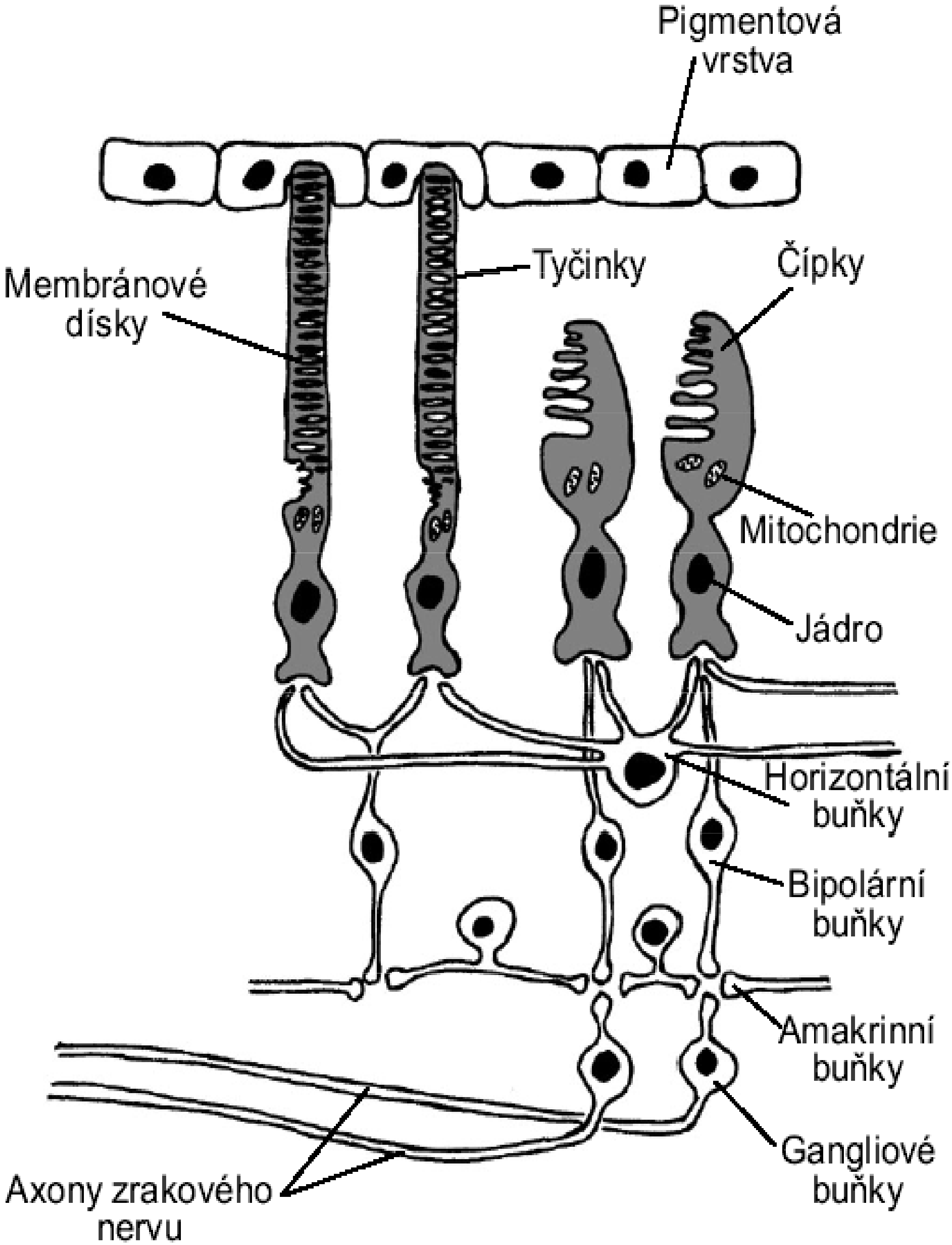
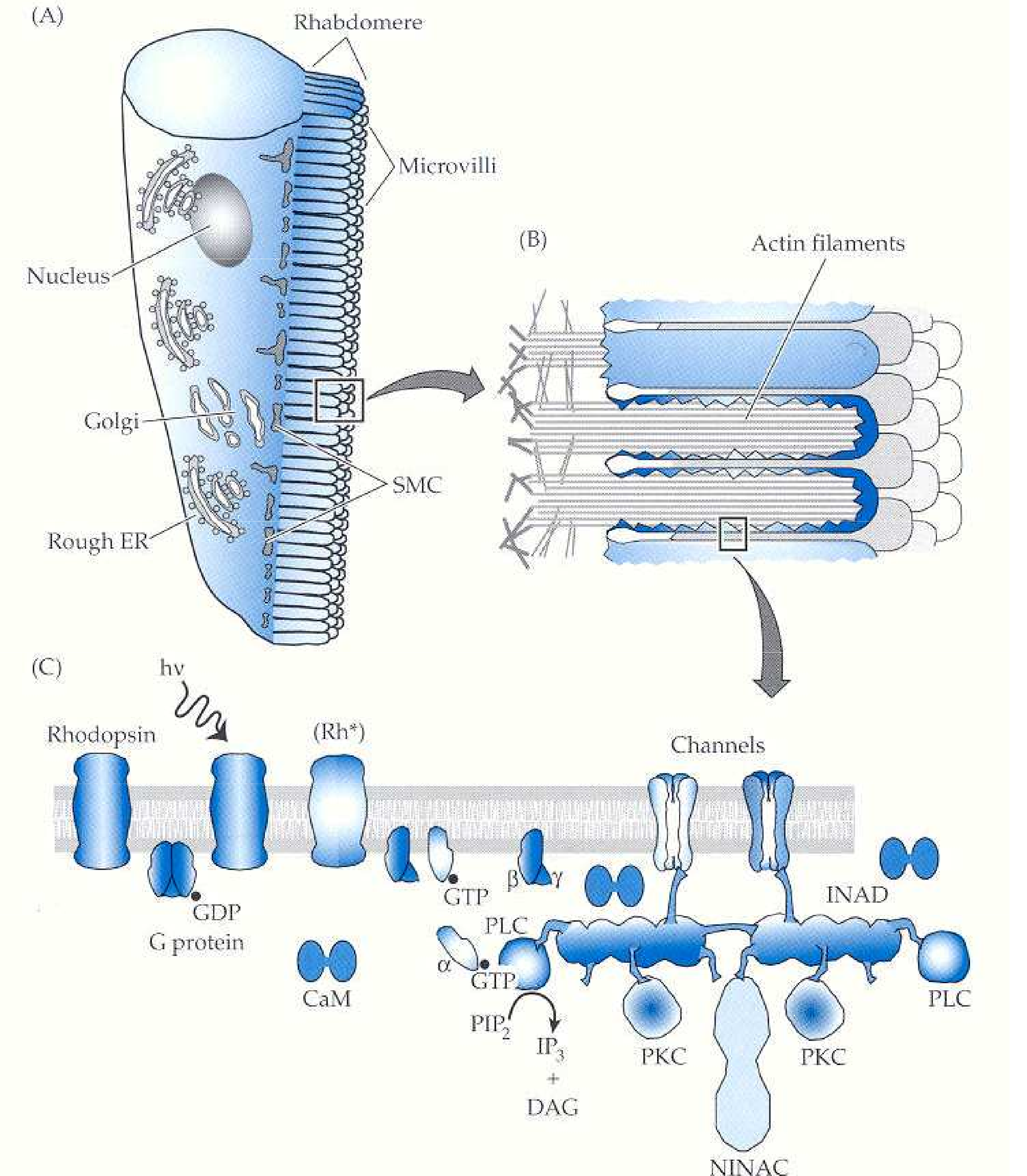


Figure 2.4
Formation of disks of a rod photoreceptor Disks are intiated at the base of the rod outer segment adjacent to a cilium. (After Steinberg, 1980.)


Pigmentová vrstva
Membránové dísky
Tyčinky
Čípky
Mitochondrie
Jádro
Horizontální buňky
Bipolární buňky
Amakrinní buňky
Gangliové buňky
Axony zrakového nervu

Signalplex



(A)
Rhabdomere
Microvilli
Nucleus
Golgi
SMC
Rough ER
(B)
Actin filaments
(C)
hν
Rhodopsin
(Rh*)
Channels
GDP
G protein
GTP
β
γ
INAD
PLC
α
GTP
CaM
PIP2
IP3
+
DAG
PKC
PKC
PLC
NINAC

Obnova membrány

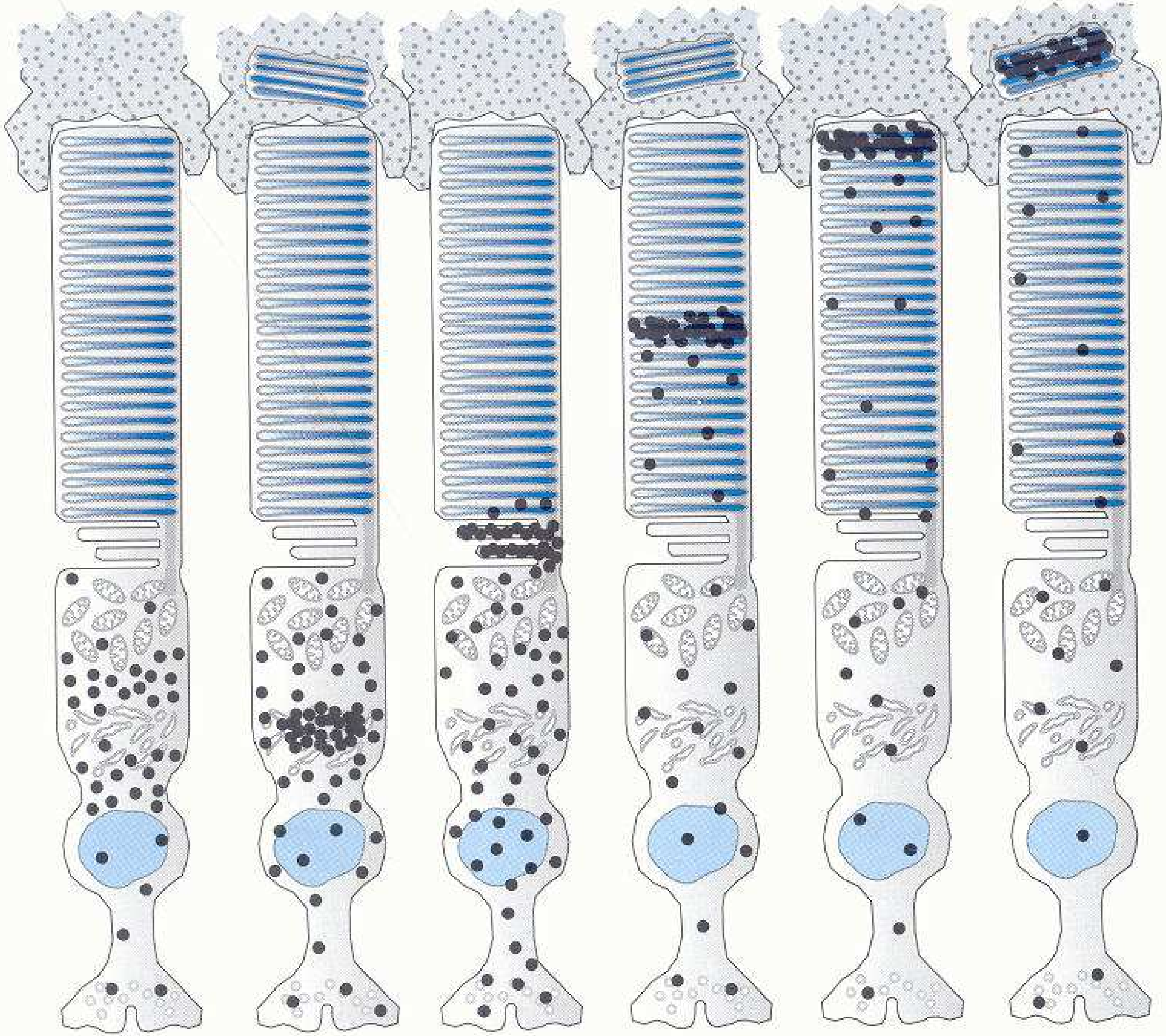
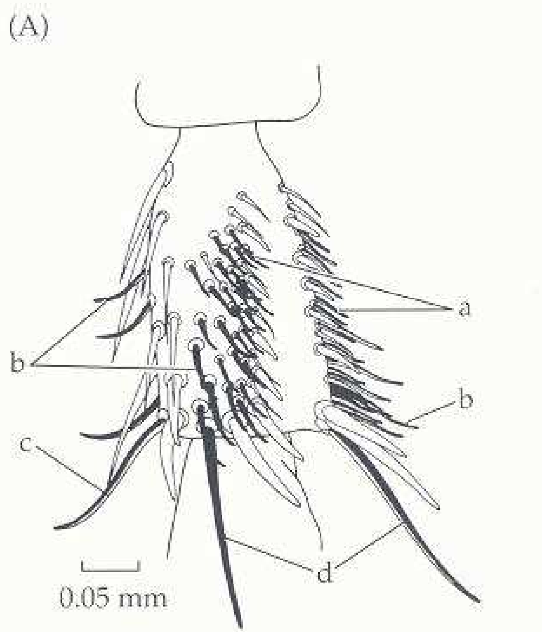


Figure 2.7
Renewal of sensory membrane in a vertebrate photoreceptor Renewal of membrane in the outer segment of rod photoreceptor. Black dots indicate labeled amino acid, first incorporated into protein in the inner segment, then transported to the outer segment as components of the disk (largely as rhodopsin). Synthesis of new disks pushes label upward until, after 10–14 days, it is shed by the outer segment and phagocytosed by the cells of an adjacent cell layer, called the retinal pigment epithelium. (After Young, 1976.)

Externí specializace



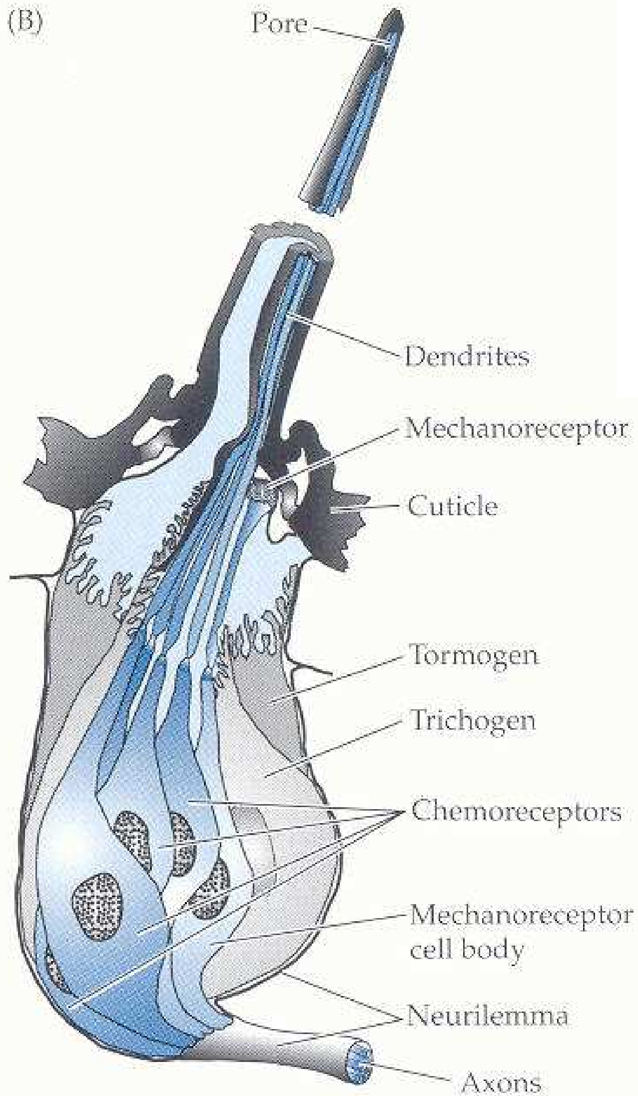
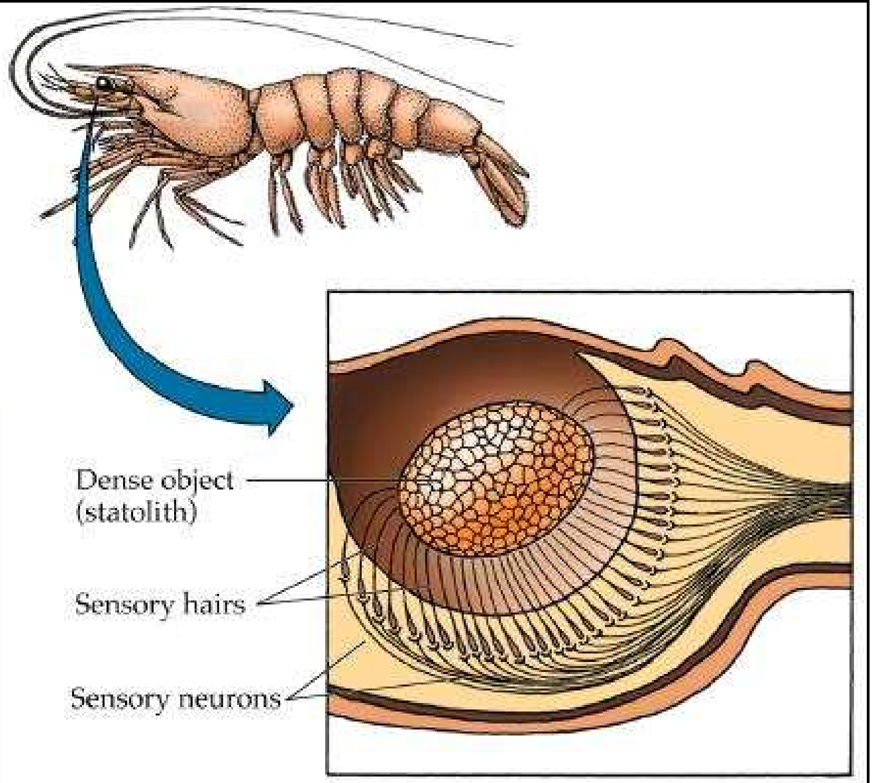


Figure 2.8
Taste receptors of the housefly
(A) Chemosensory bristles (hairs) on the tarsus of the housefly. Letters indicate different anatomical classes of hairs (type a, type b, etc; see discussion in Chapter 8). (B) Structure of a chemosensory bristle. In addition to two to four chemoreceptors, the bristle also contains a single mechanoreceptor. Trichogen and tormogen cells are accessory cells that secrete the hair and bristle socket.



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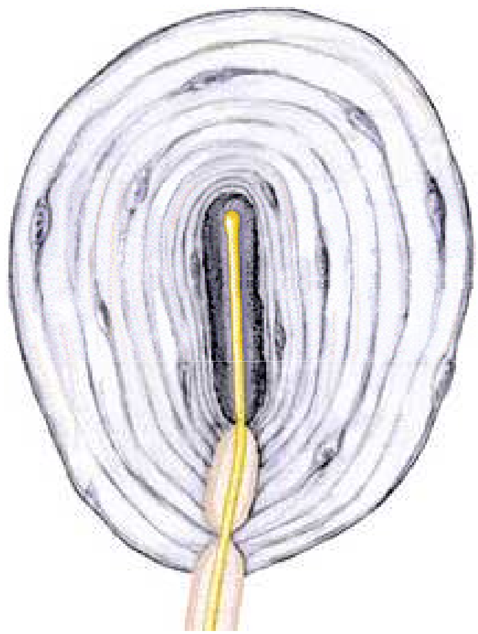
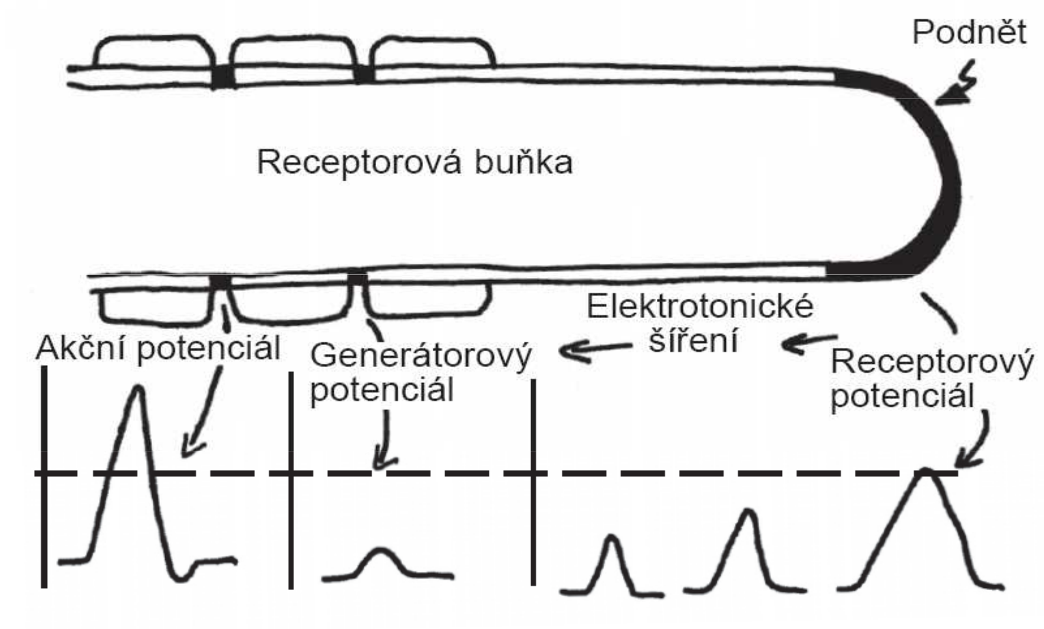
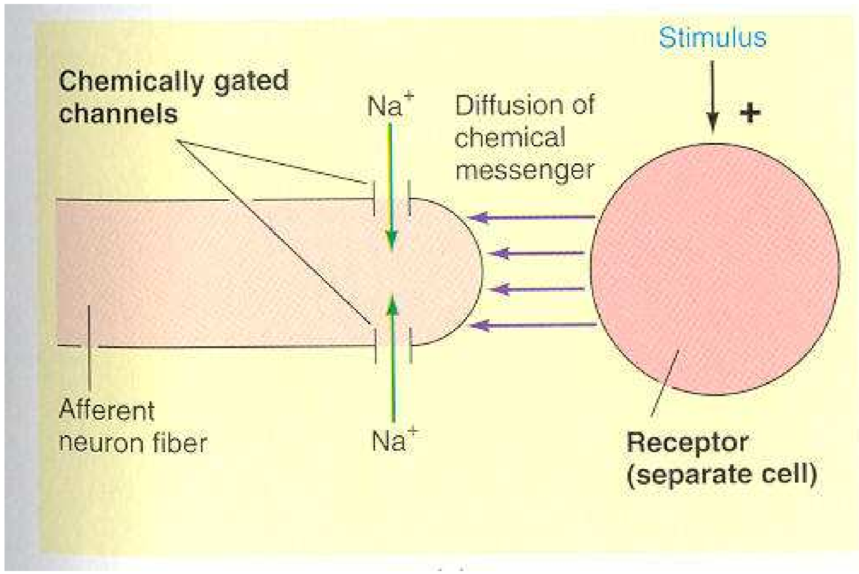


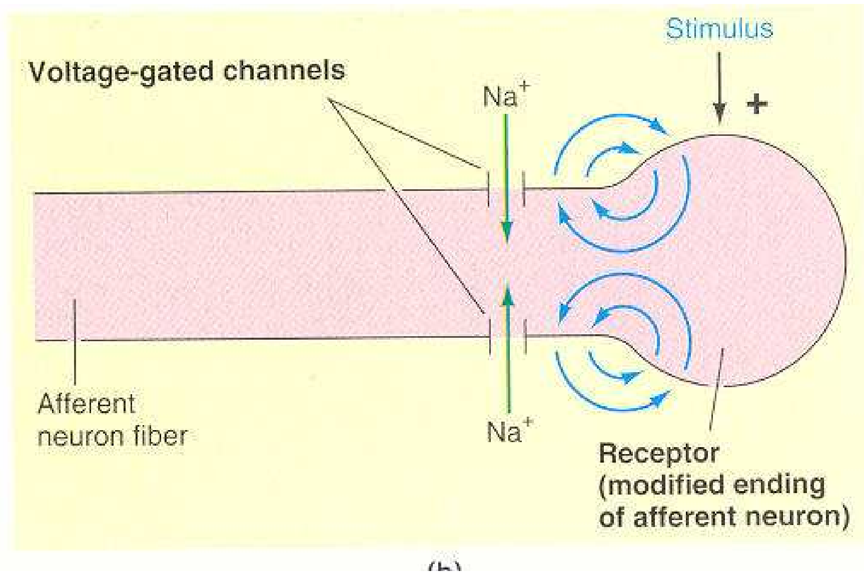
Kódování signálu



Sekundární receptor



Primární receptor



Kódování signálu

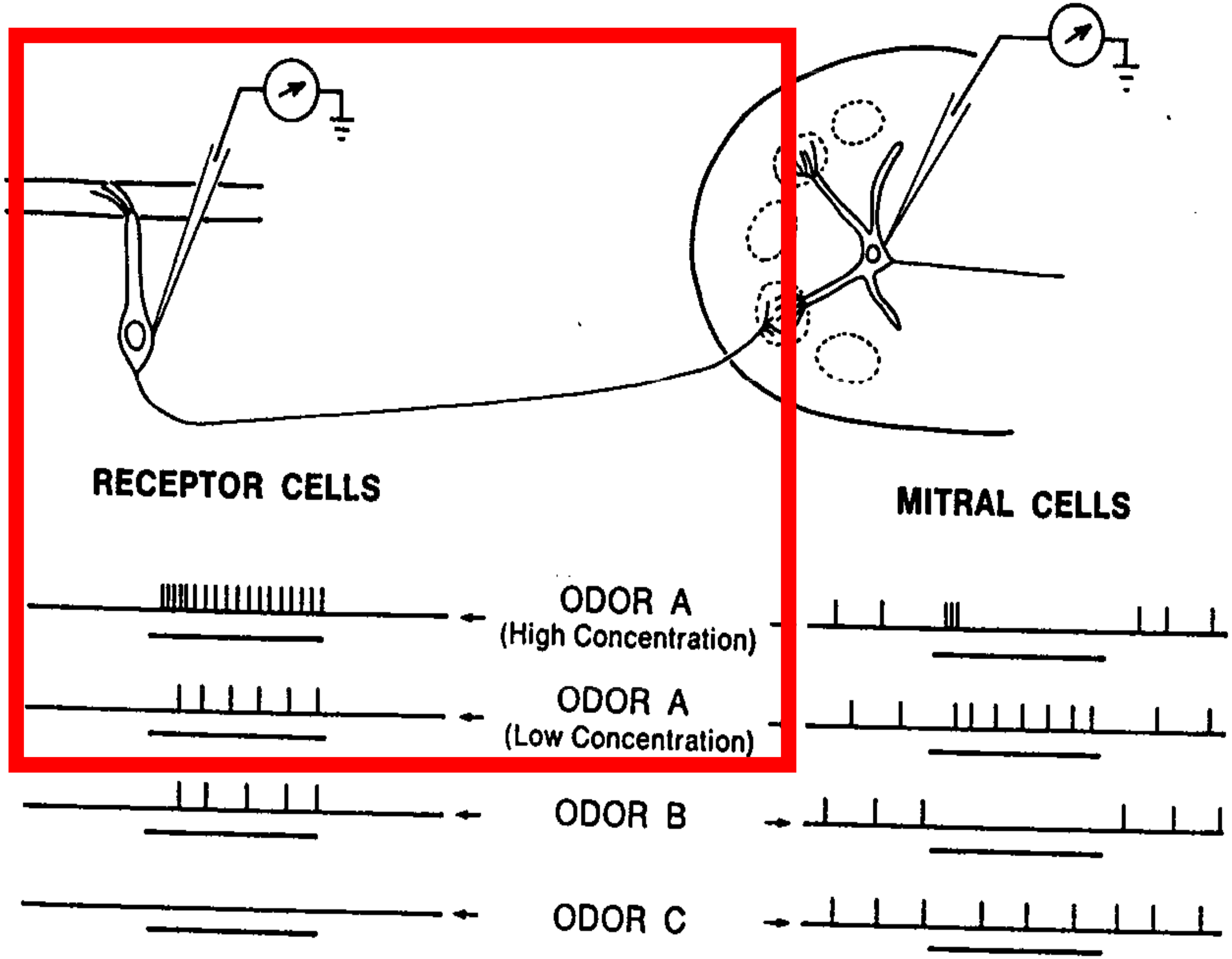


Fig. 11.11 Extracellular single-unit recordings of responses to odors of receptor cells *(left)* and mitral cells *(right)* in the salamander, showing different types of responses and different temporal patterns of activity. (After Kauer, 1974, and Getchell and Shepherd, 1978)

Spontánní aktivita a centrifugální řízení

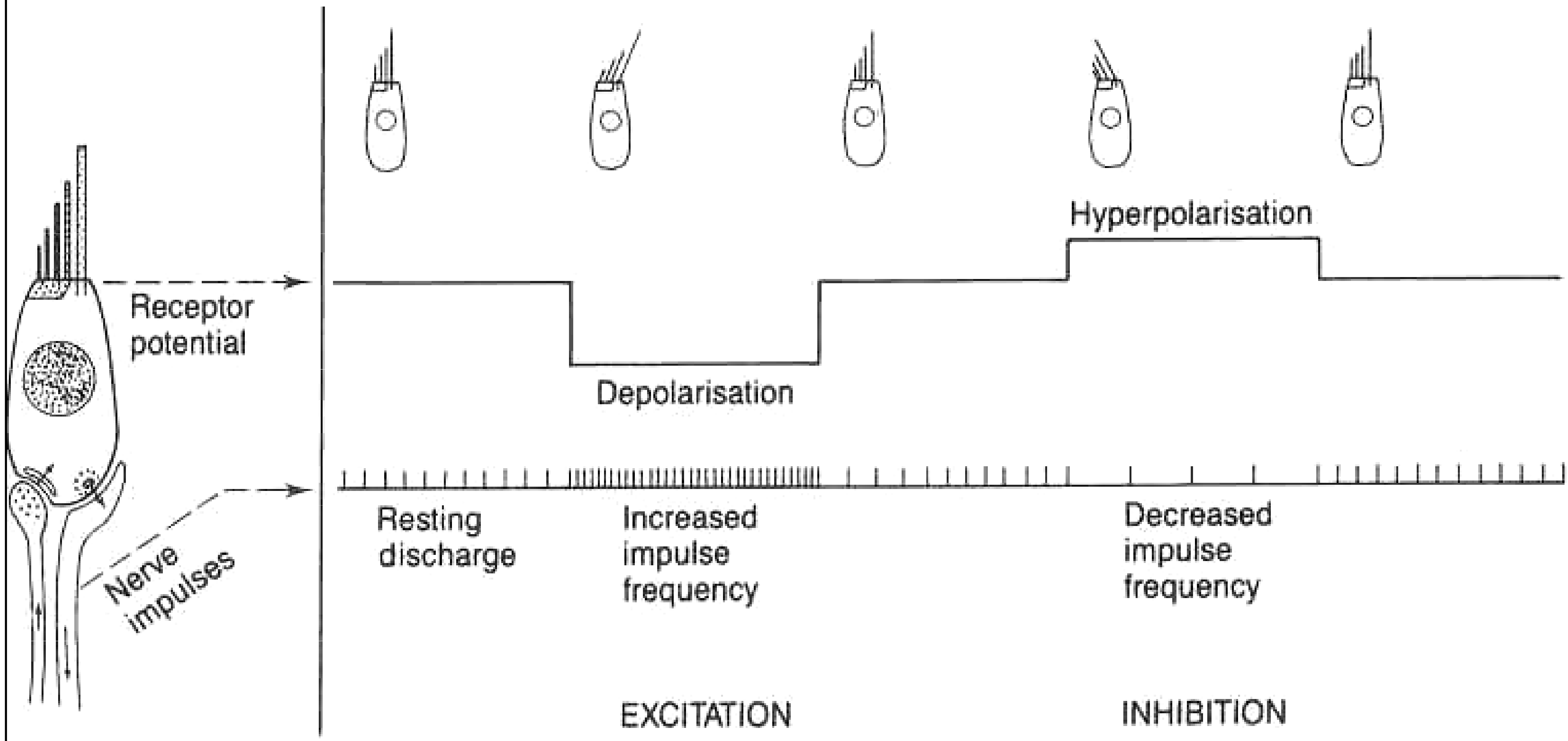


Table 10.3 Common operations in sensory transduction

Transduction operations	Operations in single sensory cells	Operations in cell populations
Detection	Perireceptor mechanisms: filters: carriers: tuning; inactivation Sensitivity Rapidity	Perireceptor mechanisms: filters; carriers; tuning; inactivation Different thresholds
Amplification	Positive feedback Active processes Signal/noise enhancement	Positive feedback Signal/noise enhancement
Encoding/ discrimination	Intensity coding Quality coding Temporal differentiation	Different dynamic ranges Quality independent of intensity Center–surround antagonisms Opponent mechanisms Construction of maps
Adaptation and termination	Desensitization Negative feedback Temporal discrimination Repetitive responses	Temporal discrimination
Sensory channel gating	Open or close conductance gating	
Electrical response	Depolarization or hyperpolarization	
Transmission to brain	Electrotonic spread Active properties Synaptic output or impulse discharges	Spatial patterns: maps and image formation Temporal patterns: directional selectivity, etc.

From Shepherd (1991b)

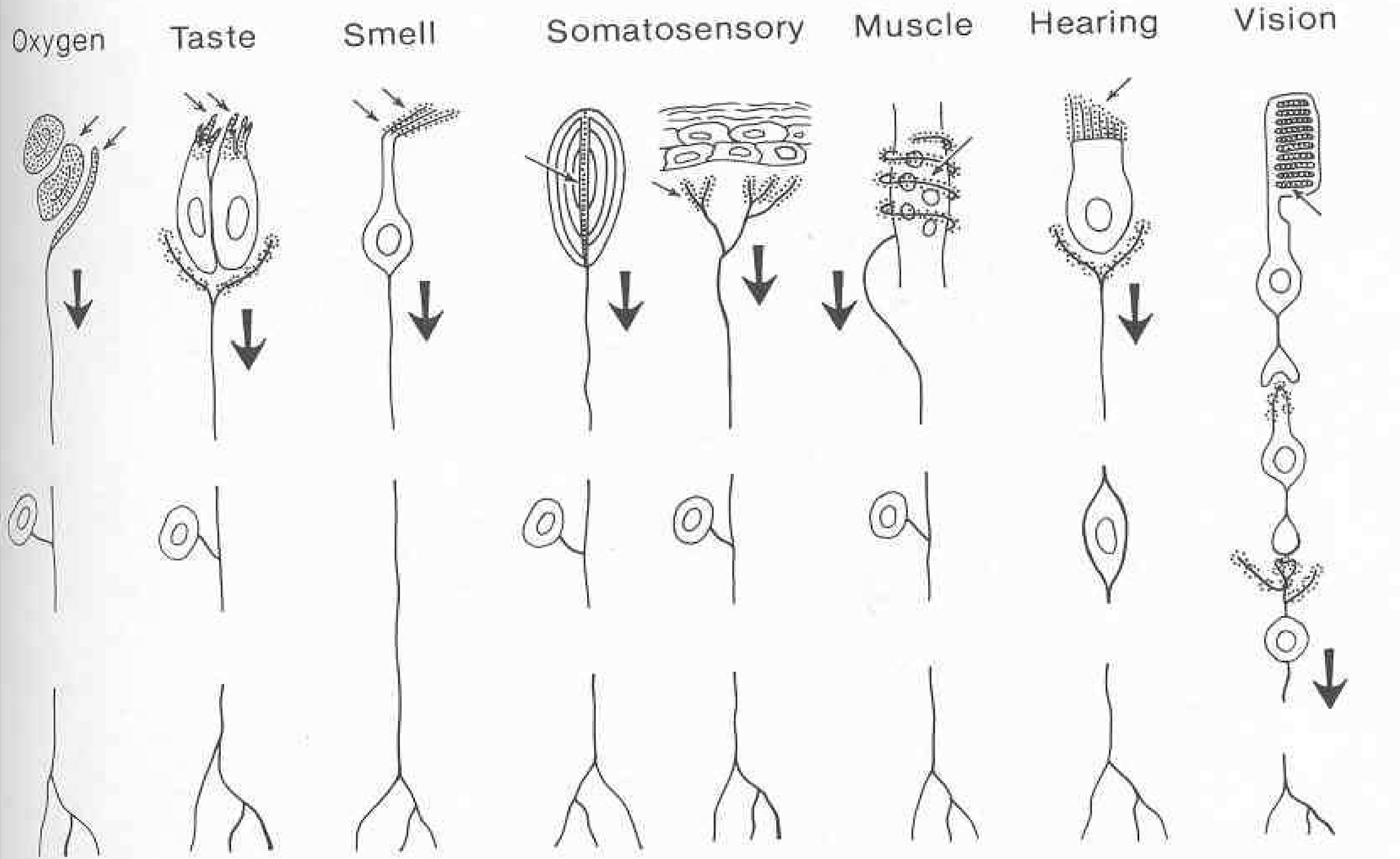


Fig. 10.1 Different types of sensory receptor cells in vertebrates. Small arrows indicate sites where sensory stimuli act. Stippling indicates sites for transduction of the sensory stimuli, and also for synaptic transmission; both of these sites mediate graded signal transmission. Heavy arrows indicate sites of impulse initiation. (Adapted from Bodian, 1967)

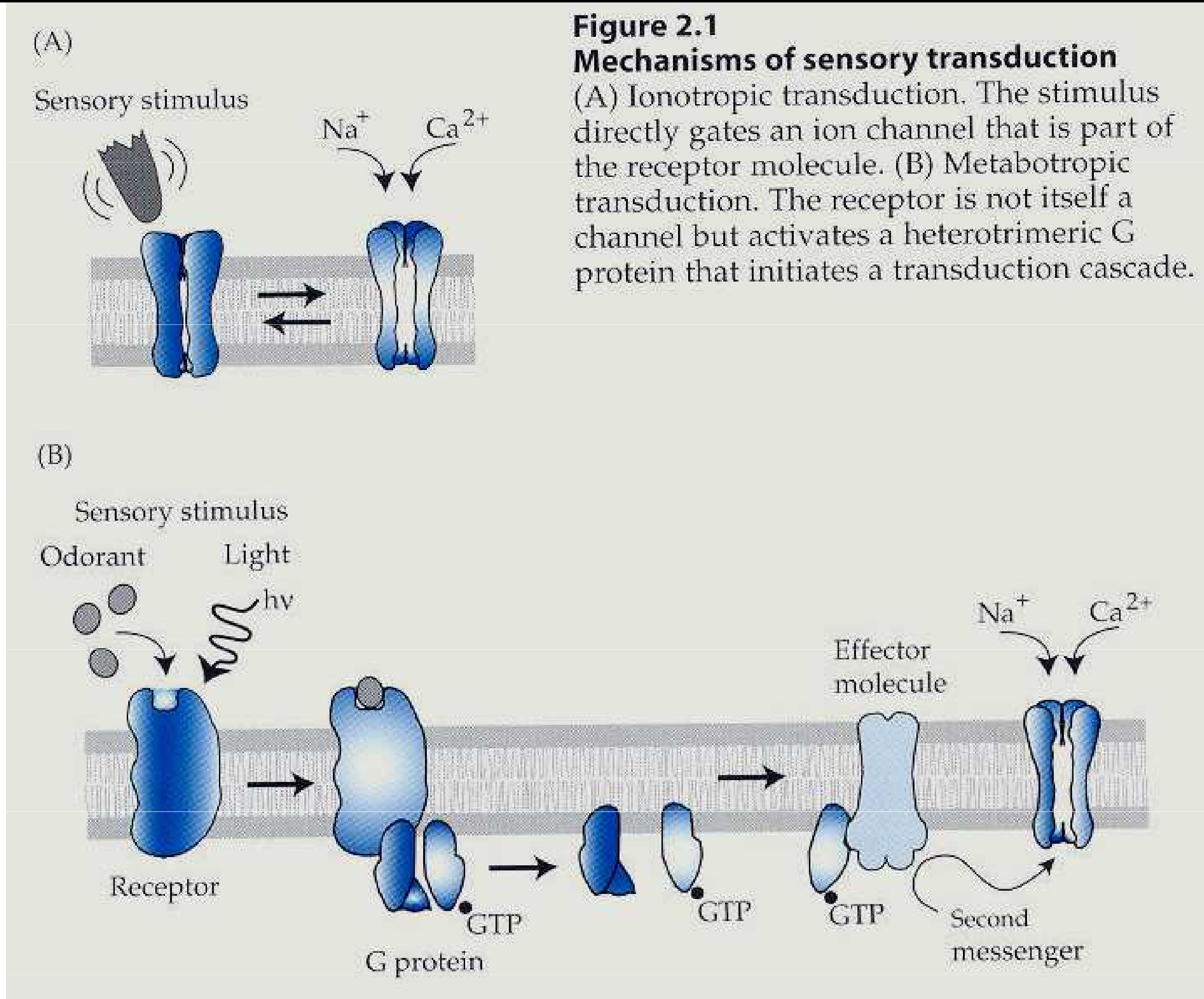


Figure 2.1
Mechanisms of sensory transduction
(A) Ionotropic transduction. The stimulus directly gates an ion channel that is part of the receptor molecule. (B) Metabotropic transduction. The receptor is not itself a channel but activates a heterotrimeric G protein that initiates a transduction cascade.

Ionotropní – přímá stimulace kanálu

Metabotropní – stejně jako hormony, transmitery…

Receptor ne vždy nutný – slano, MGP

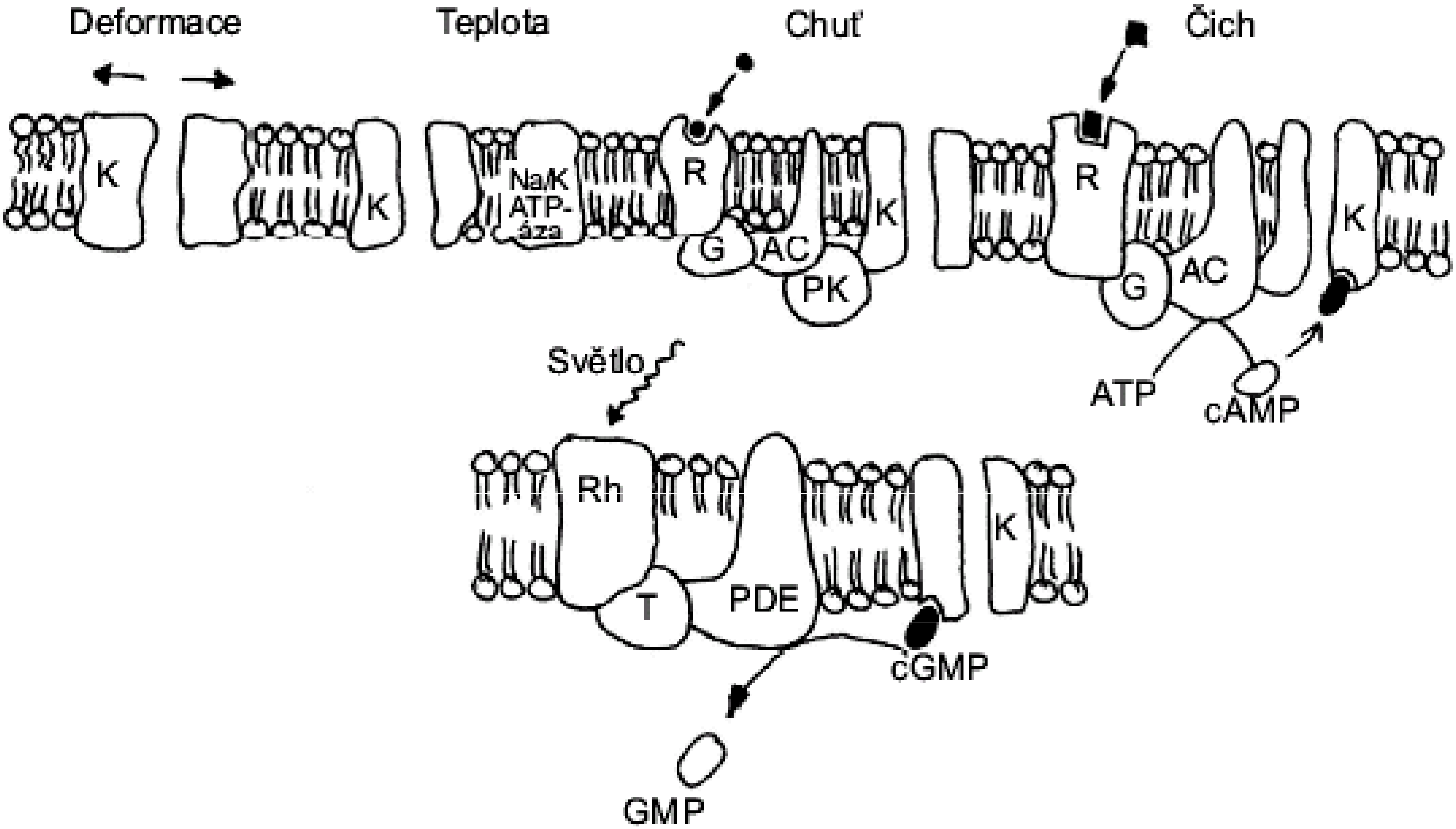

Deformace
Teplota
Chuť
Čich
K
K
Na/K
ATP-
áza
R
G
AC
PK
K
R
G
AC
K
ATP
cAMP
Světlo
Rh
T
PDE
K
cGMP
GMP

Table 10.2 Steps in sensory transduction

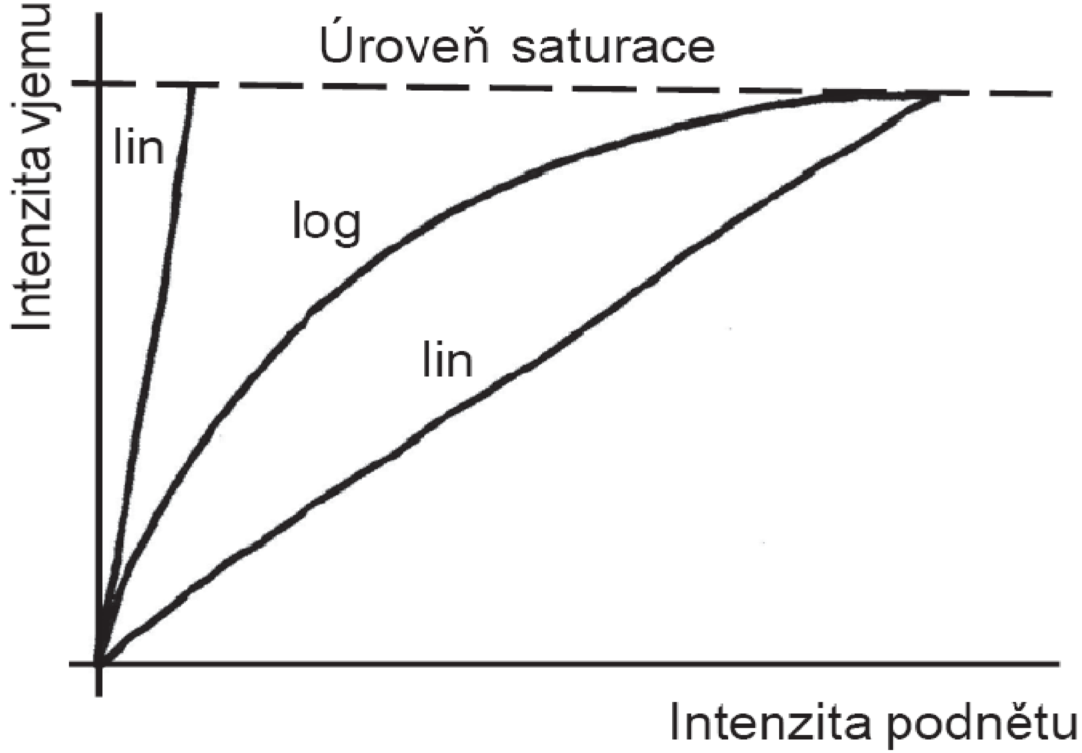
Transduction step	Vision	Olfaction	Taste: Sweet/bitter amino acids	Taste: Salt/sour	Mechanoreception (hair cells)
Energy	Photons ↓	Molecules ↓	Molecules ↓	Na^+, H^+ ↓	Displacement ↓
Membrane receptor	7TD family: rhodopsin ↓	7TD family: olfactory ↓	7TD family: gustatory ↓		
G protein	Transducin ↓	G_{olf} ↓	G_{gust} ↓		
G-protein target	Phosphodiesterase ↓	Adenylate cyclase III; phospholipase C ↓	AC; PLC ↓		
Second messenger	cGMP ↓	cAMP; IP_3 ↓	cAMP; IP_3 ↓		
Protein kinase			Protein kinase A? ↓		
Membrane channel	Cationic; inward ↓	Cationic; inward Anionic; inward ↓	K^+ ↓	Na^+; K^+ ↓	Cationic; inward ↓
Sensory response	Close channel ↓	Open channel ↓	Close channel ↓	Open; close ↓	Open channel ↓
Adaptation mechanism	Ca^{2+}; phosphorylation?; arrestin ↓	Ca^{2+}; protein kinases ? ↓	? ↓	? ↓	Myosin/actin motor; Ca^{2+}? ↓
Cell body output	Synapses	Impulses	Synapses	Synapses	Synapses

7TD family: 7 transmembrane domain receptor family.

From Shepherd (1991b)

Weber-Fechnerův zákon

$S = a \log I/I_0 + b$



Obr. 4.15. Intenzita vjemu roste s intenzitou podnětu logaritmicky – ne lineárně. Tento kompromis mezi rozlišovací schopností a saturačním prahem (nasycením) receptorů umožňuje zachovat odstupňovanou reakci na velmi široký rozsah intenzit současně s velkou citlivostí pro slabé podněty.

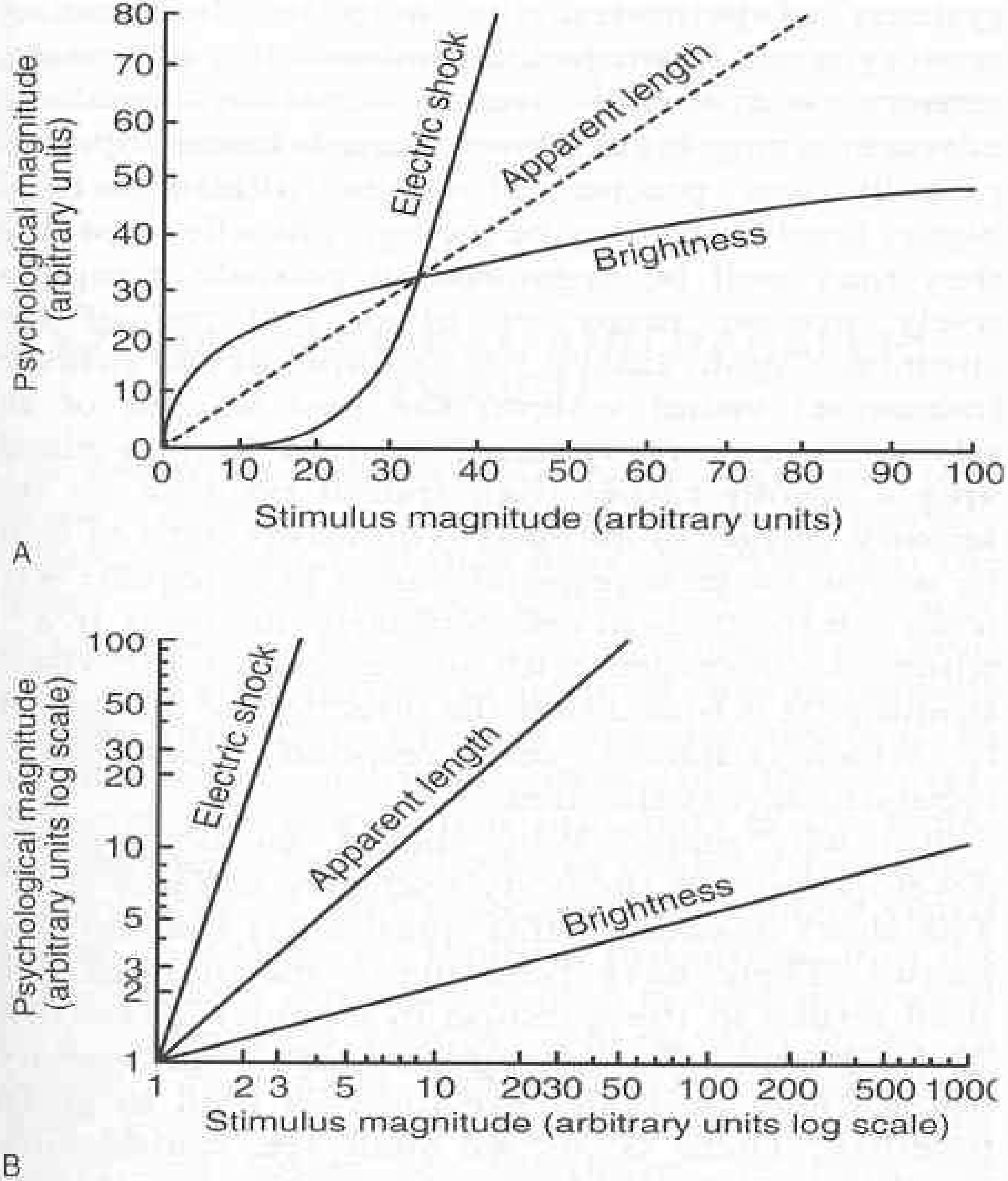
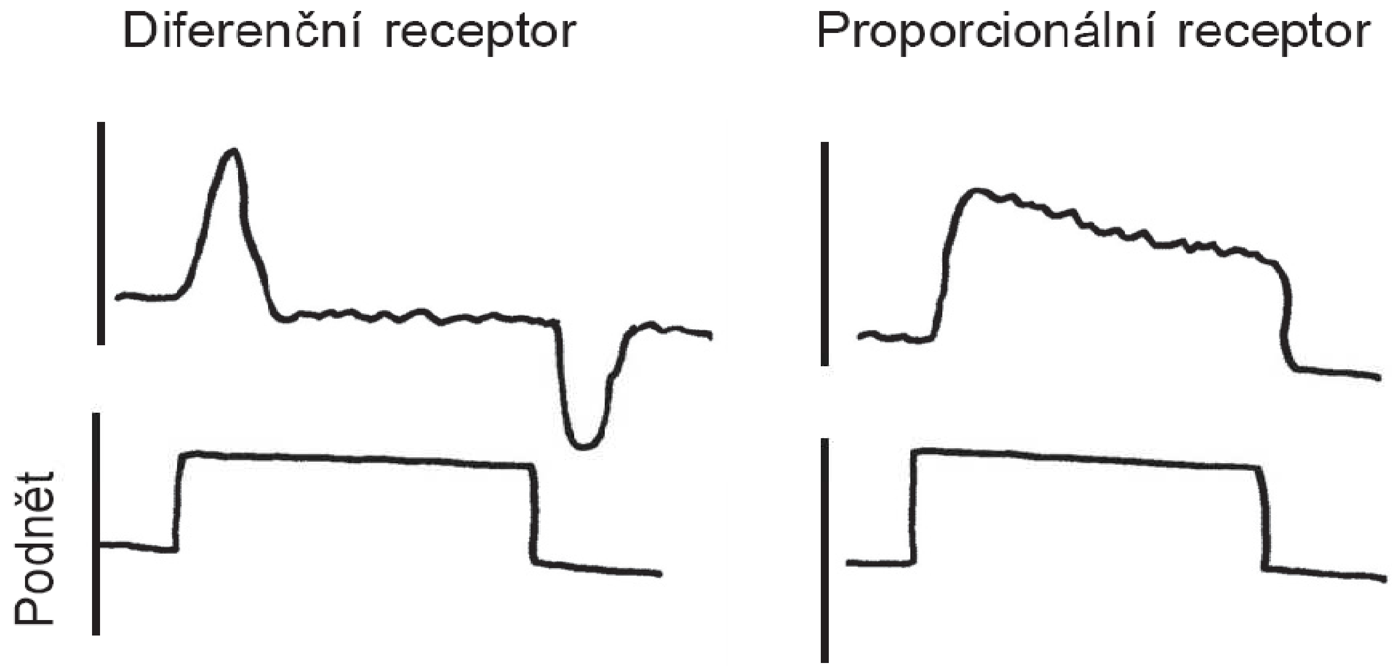


Figure 3.2 Psychophysical correlations. (a) When subjective magnitude is graphed against stimulus magnitude on linear coordinates the lines are frequently curved upwards or downwards. (b) When graphed against log–log coordinates straight lines are obtained whose gradients depend on the value of the exponent, '*n*'. From Stevens, 1961

Sensorická adaptace



Obr. 4.16. Rozdíl v adaptaci D- (diferenčních) a P- (proporcionálních) receptorů. D-receptory reagují jen na časovou změnu podnětu. Odpověď P-receptorů trvá po celou dobu působení podnětu.

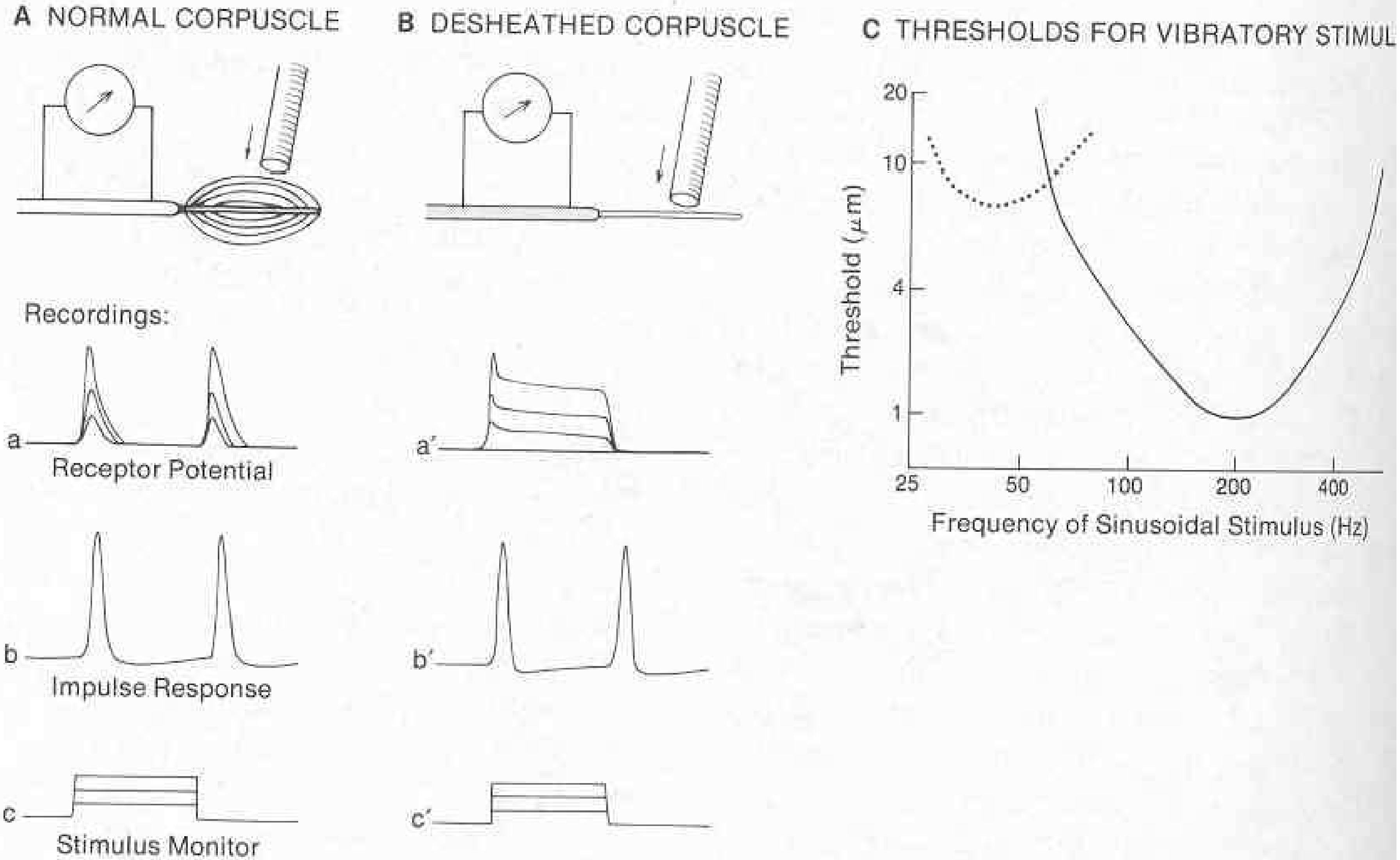


Fig. 12.5 Experimental analysis of transduction in the Pacinian corpuscle. **A.** Diagram showing probe for stimulating the intact corpuscle, and recording from the nerve. *(Below)* recordings of the receptor potential and impulse discharge. **B.** Repeat of experiment after removal of lamellae. C. Sensitivity of Pacinian corpuscle to vibratory stimulation at different frequencies. Sensitivity of Meissner's corpuscle is shown by dotted line. (A, B based on Loewenstein, 1971; C modified from Schmidt, 1978)

Smyslový práh zesílení

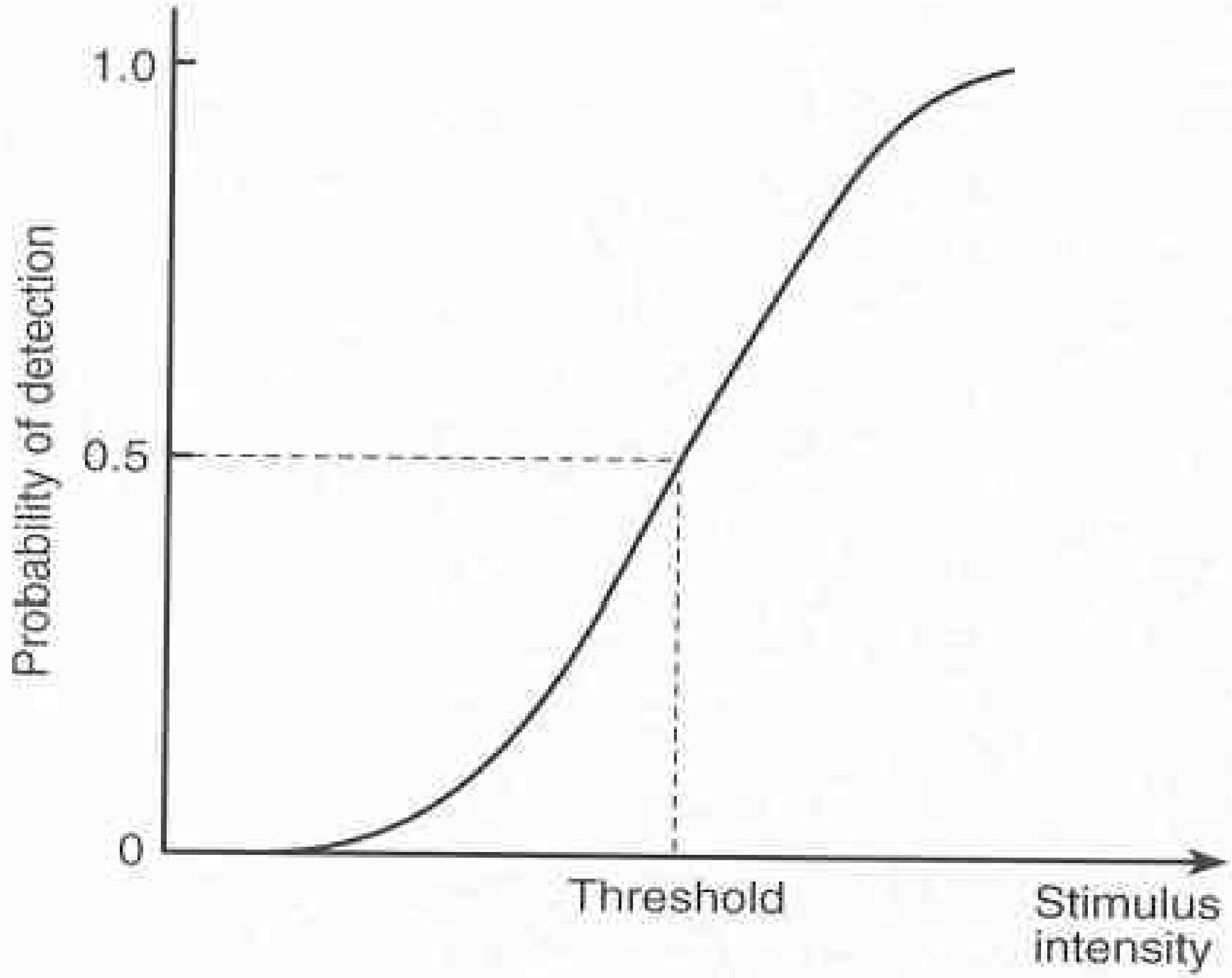
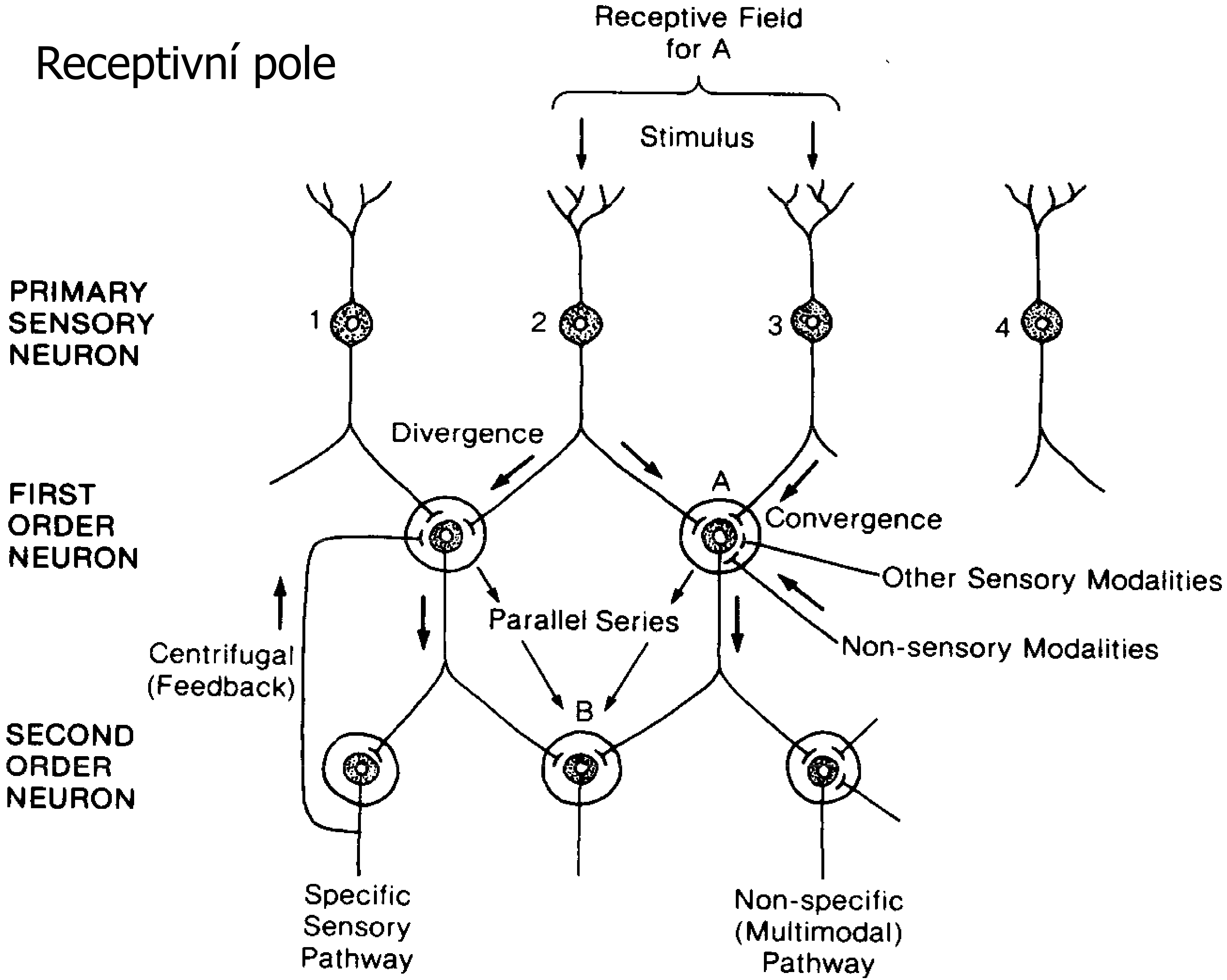


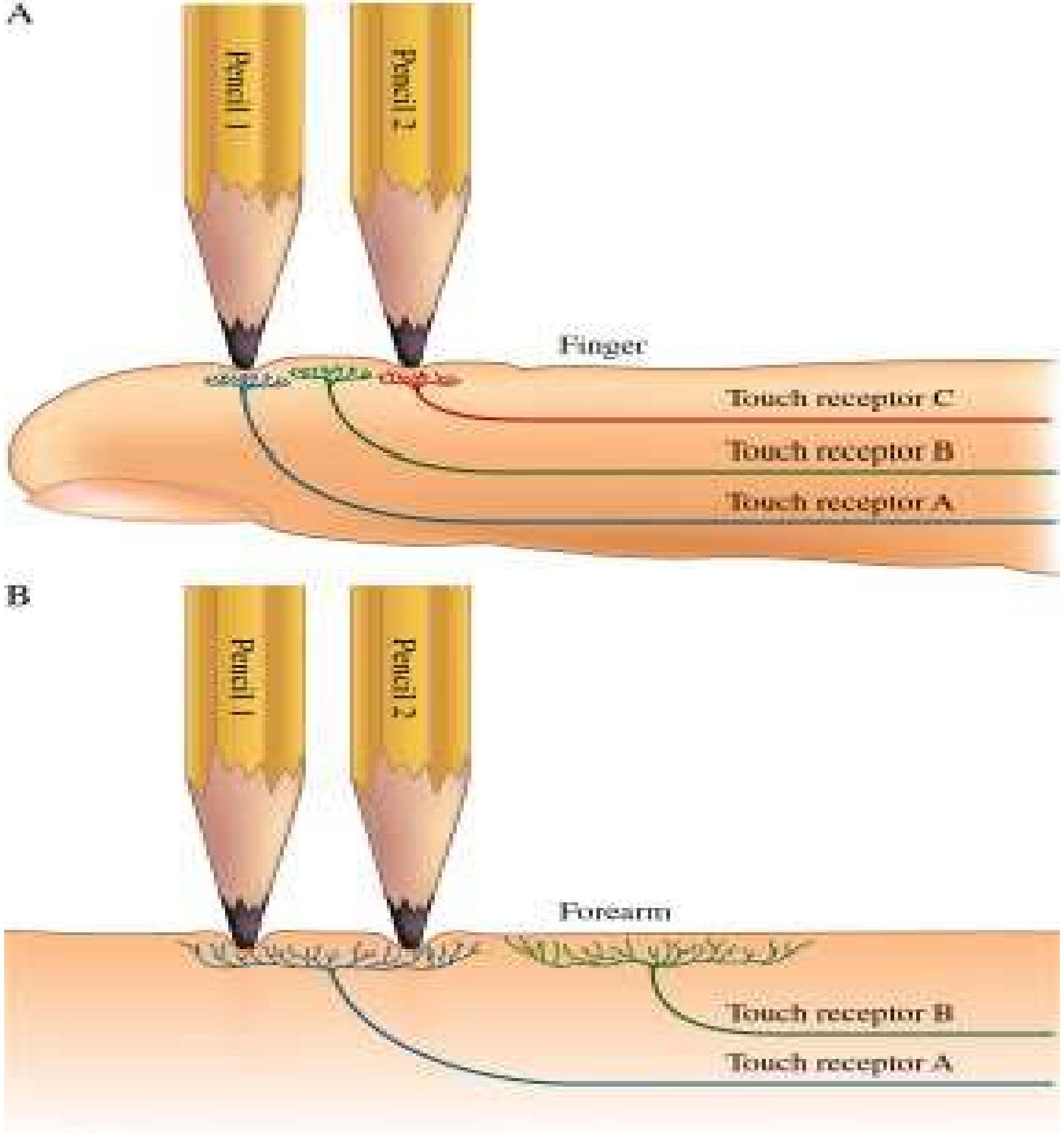
Figure 3.1 Psychometric curve. The threshold is defined as the intensity when half the responses are correct. The position of the curve on the ordinate is arbitrary. It will shift to the right or left according to circumstances

3 úrovně organizace sensorických systémů

A) Receptory
B) Sensorické obvody a dráhy
C) Sensorická percepce

Receptivní pole





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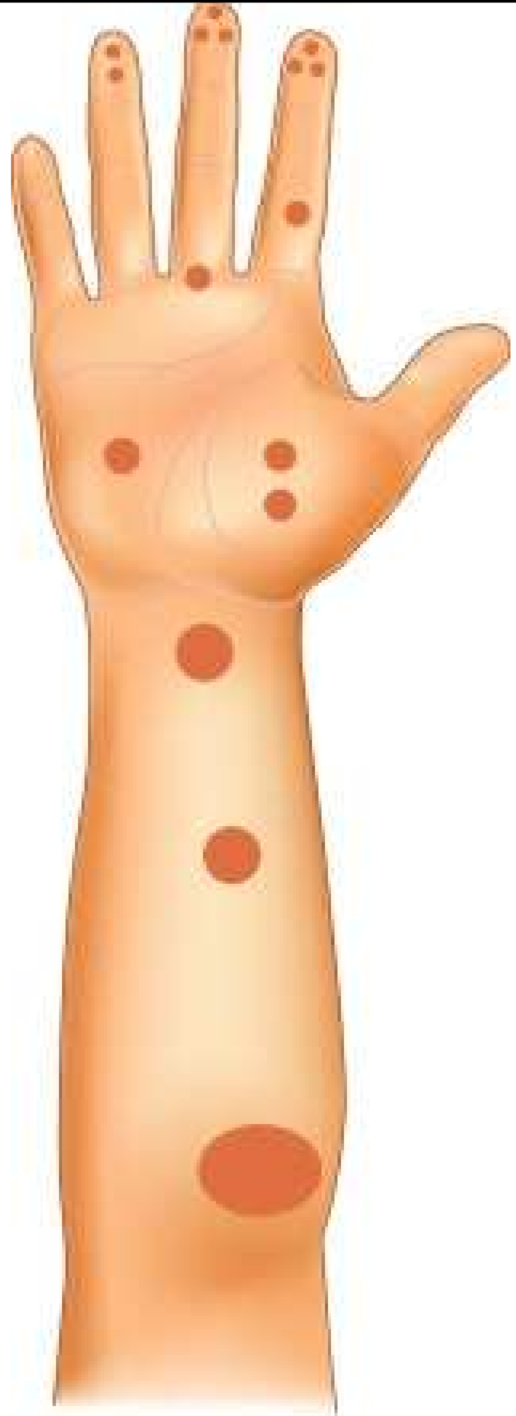

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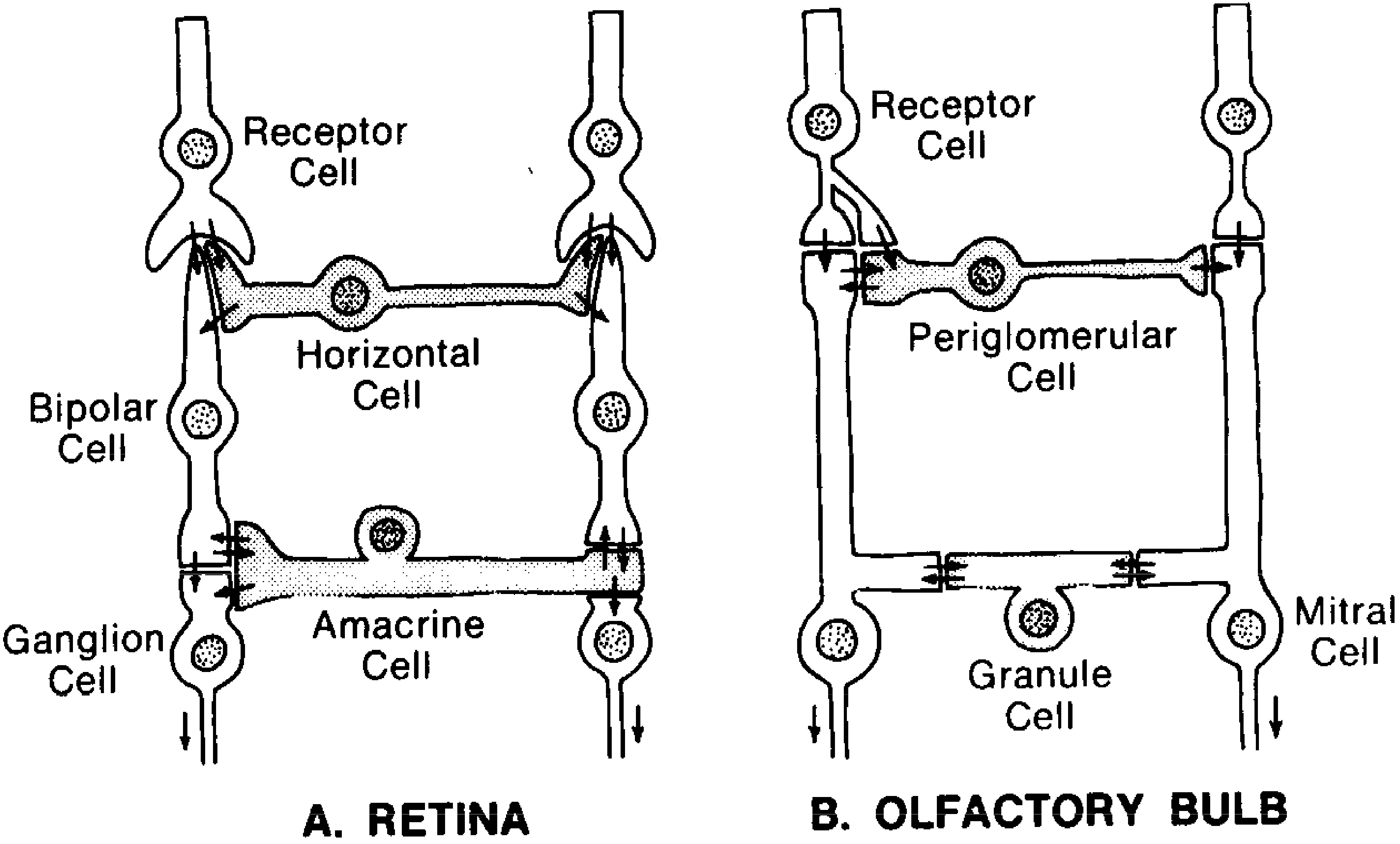
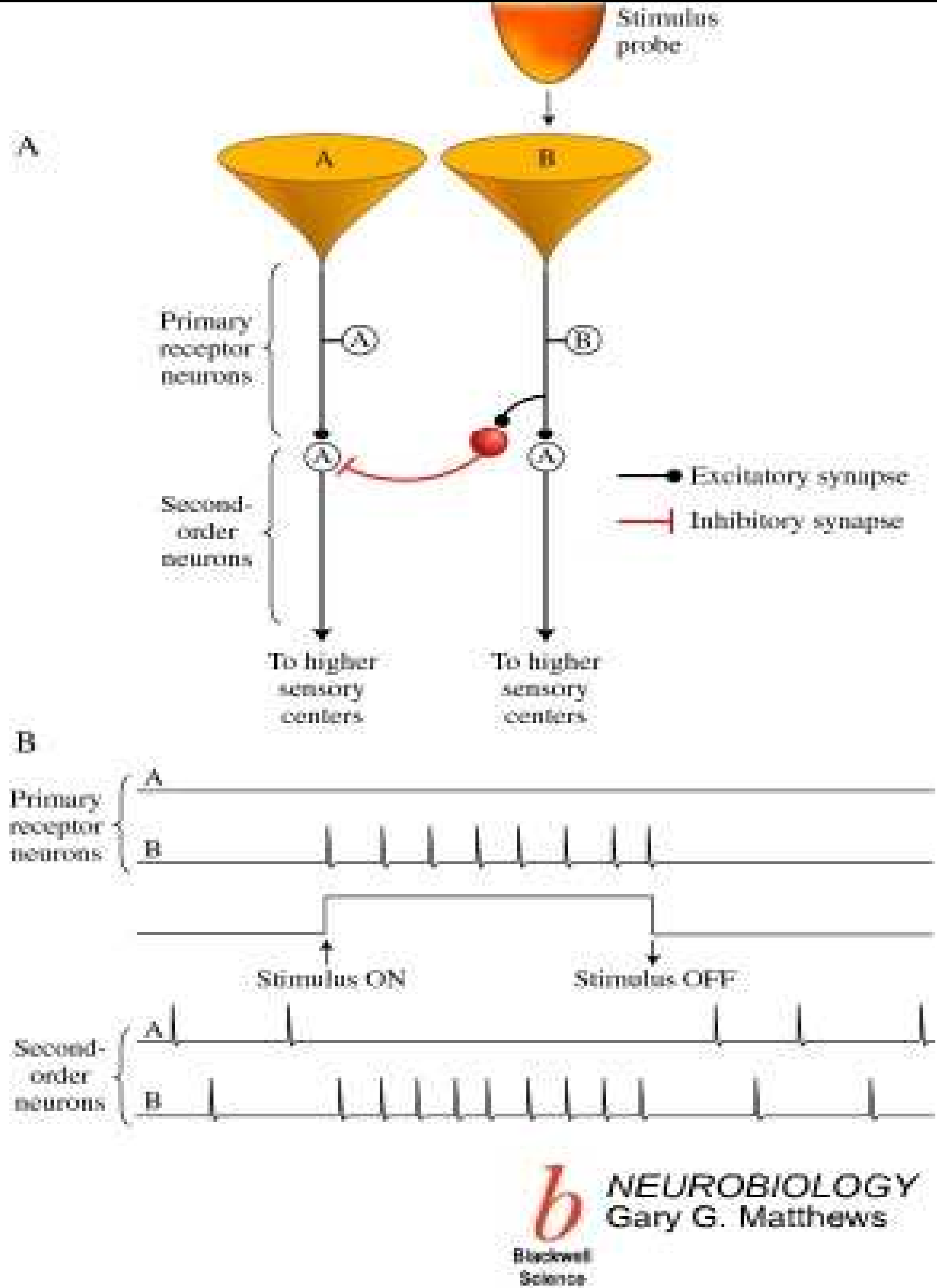
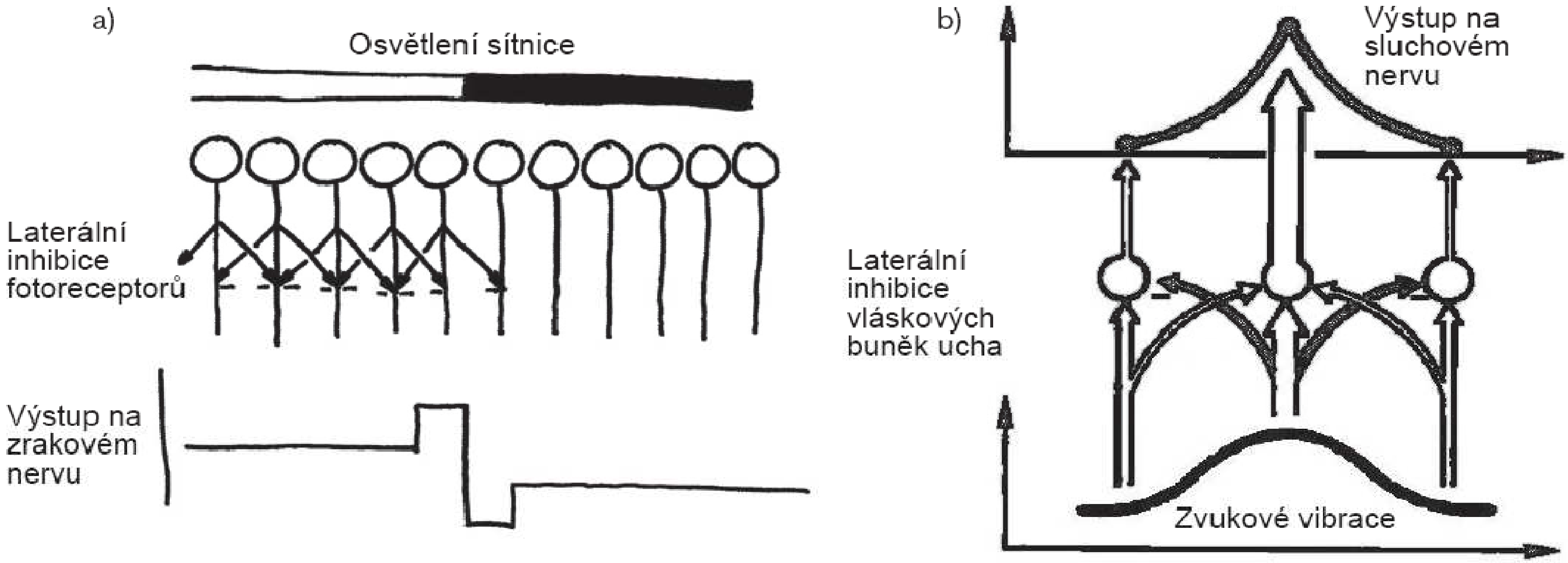


Comparison between simplified basic circuit diagrams of the vertebrate r
bulb. (After Shepherd, 1978)

Laterální inhibice

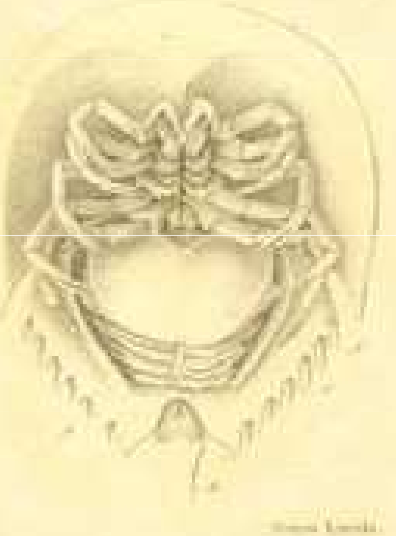




Obr. 4.17. Význam laterální inhibice při zpracování smyslových vstupů. a) Kontrastní přechod mezi osvětlenou a neosvětlenou sítnicí je ještě více zvýrazněn. b) Místo sluchového aparátu (hlemýždě), kde jsou zvukové vibrace maximální, je zvýrazněno proti méně vibrujícímu okolí – kontrast je ještě ostřejší.

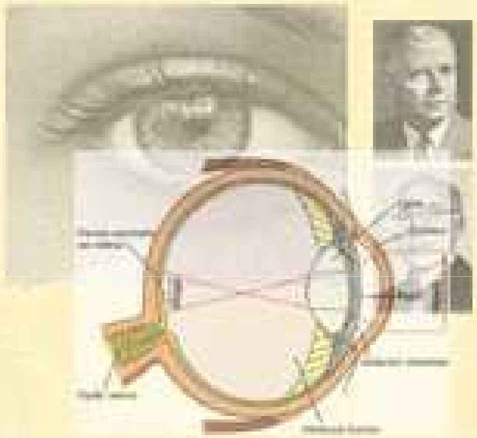
The Horseshoe Crab
Limulus polyphemus

MBL Home



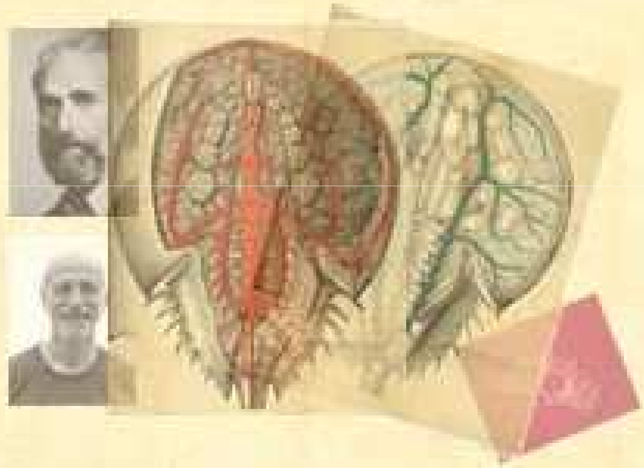
the animal

La Limule



the science

the issues



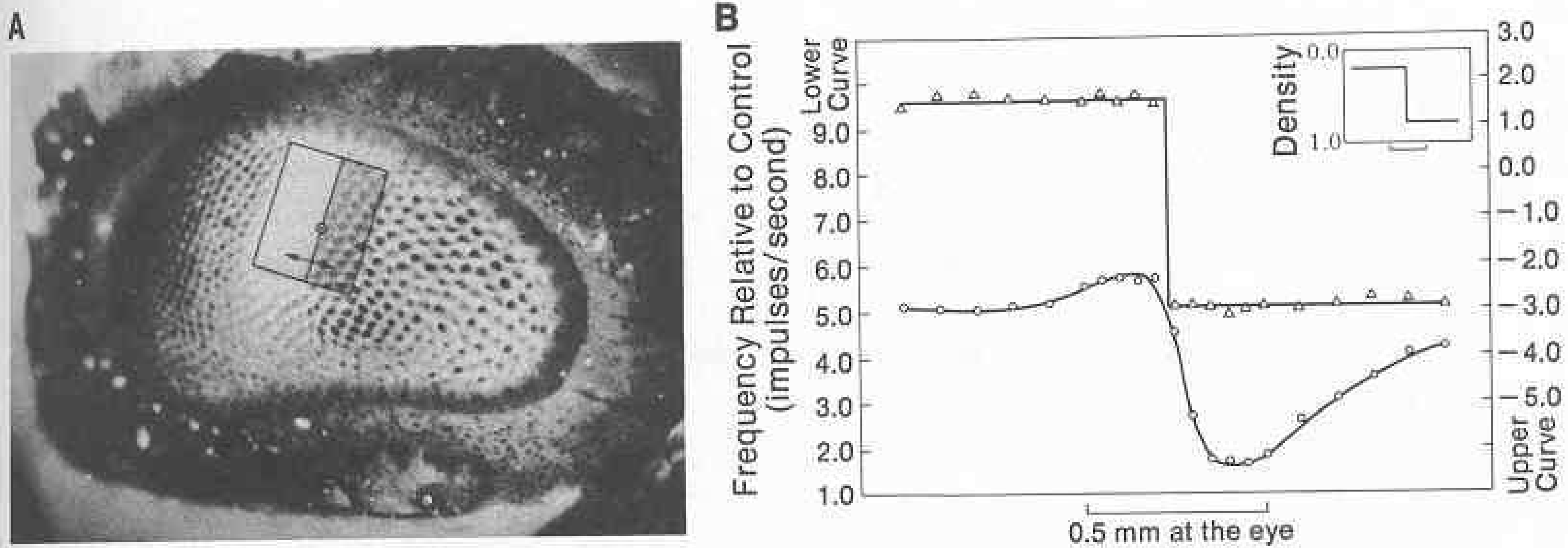
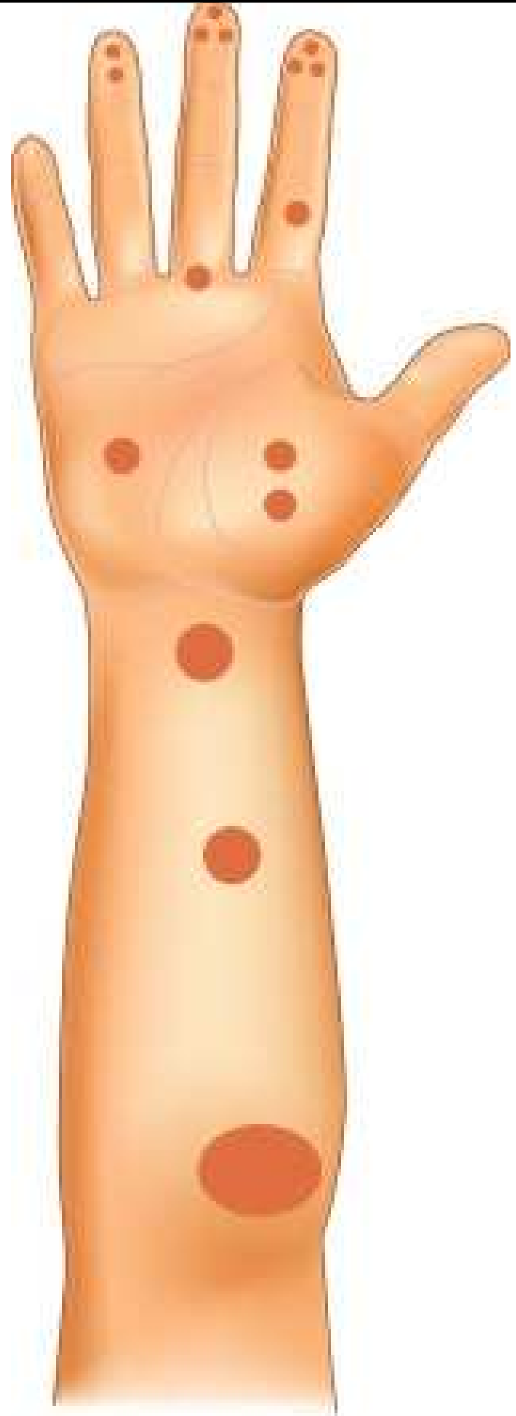


Fig. 10.6 Enhancement of spatial contrast in *Limulus* eye. **A.** Surface of *Limulus* eye, with superimposed rectangular stimulus pattern; pattern is divided into lighter (left) and darker (right) regions. Pattern is centered on test ommatidium (×). Arrows show directions in which the test pattern was displaced, to produce lower curve in graph in B. **B.** Recordings of spike frequency in axon from test ommatidium in A. *Lower curve:* responses to rectangular test pattern in A. *Upper curve:* responses to small spot of light, at high and low intensities corresponding to those of test pattern (see insert). The differences between the two curves illustrate that lateral inhibition enhances the response on the light side of an edge (because there is less inhibition from the more darkly lit neighbors to the right) and depresses the response on the dark side of an edge (because there is more inhibition from the brightly lit neighbors to the left). (From Ratliff, 1965)



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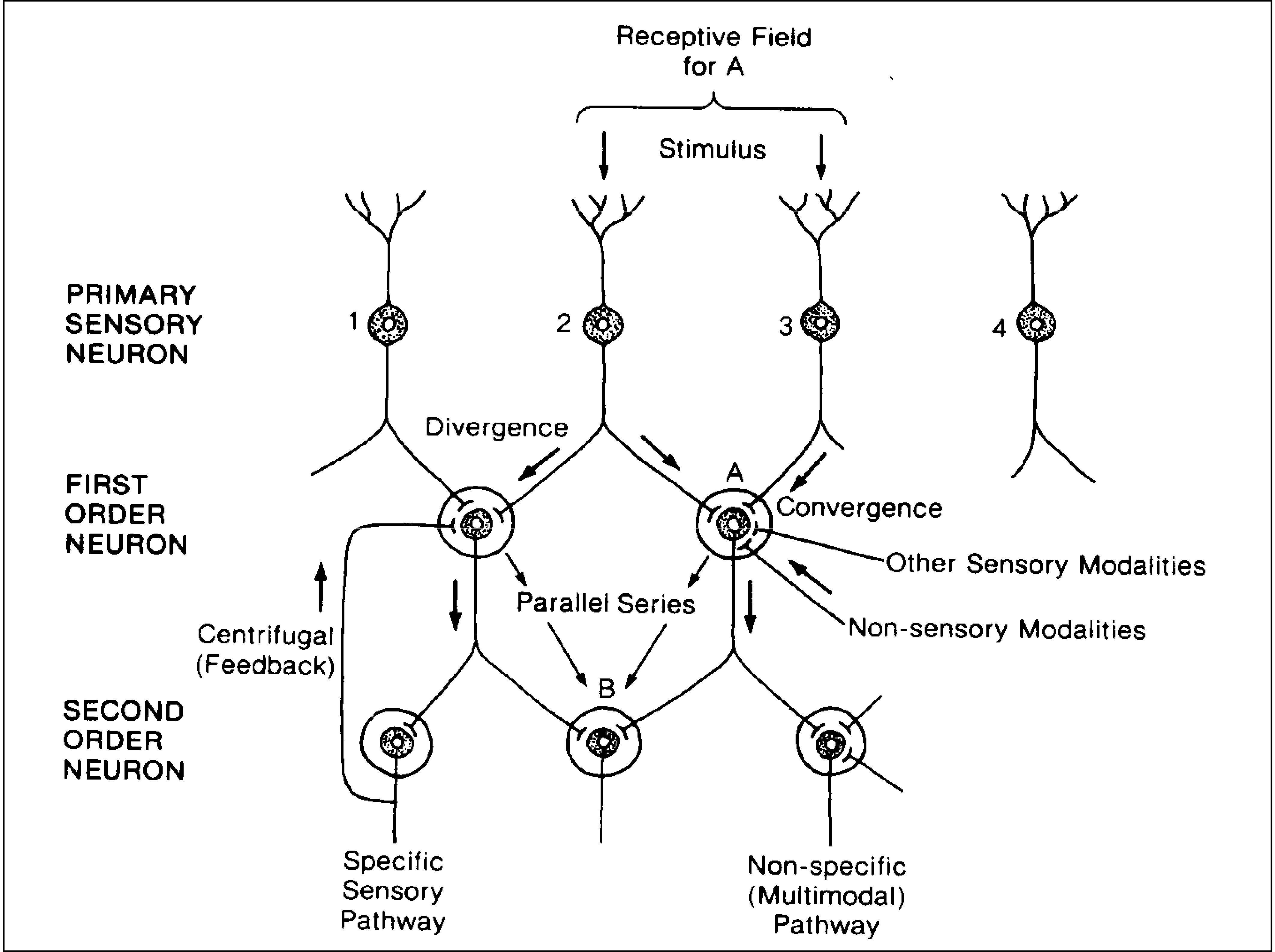
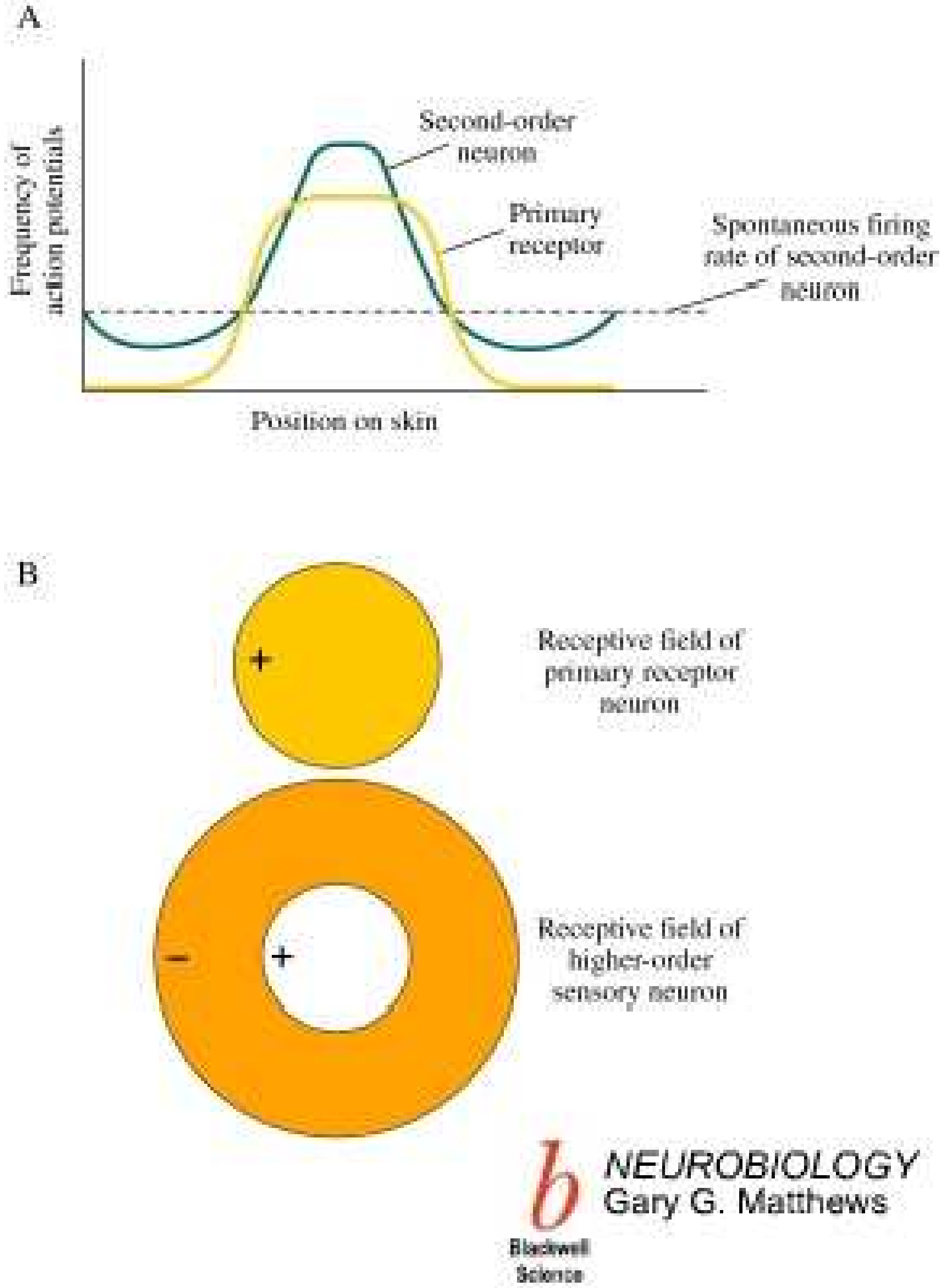
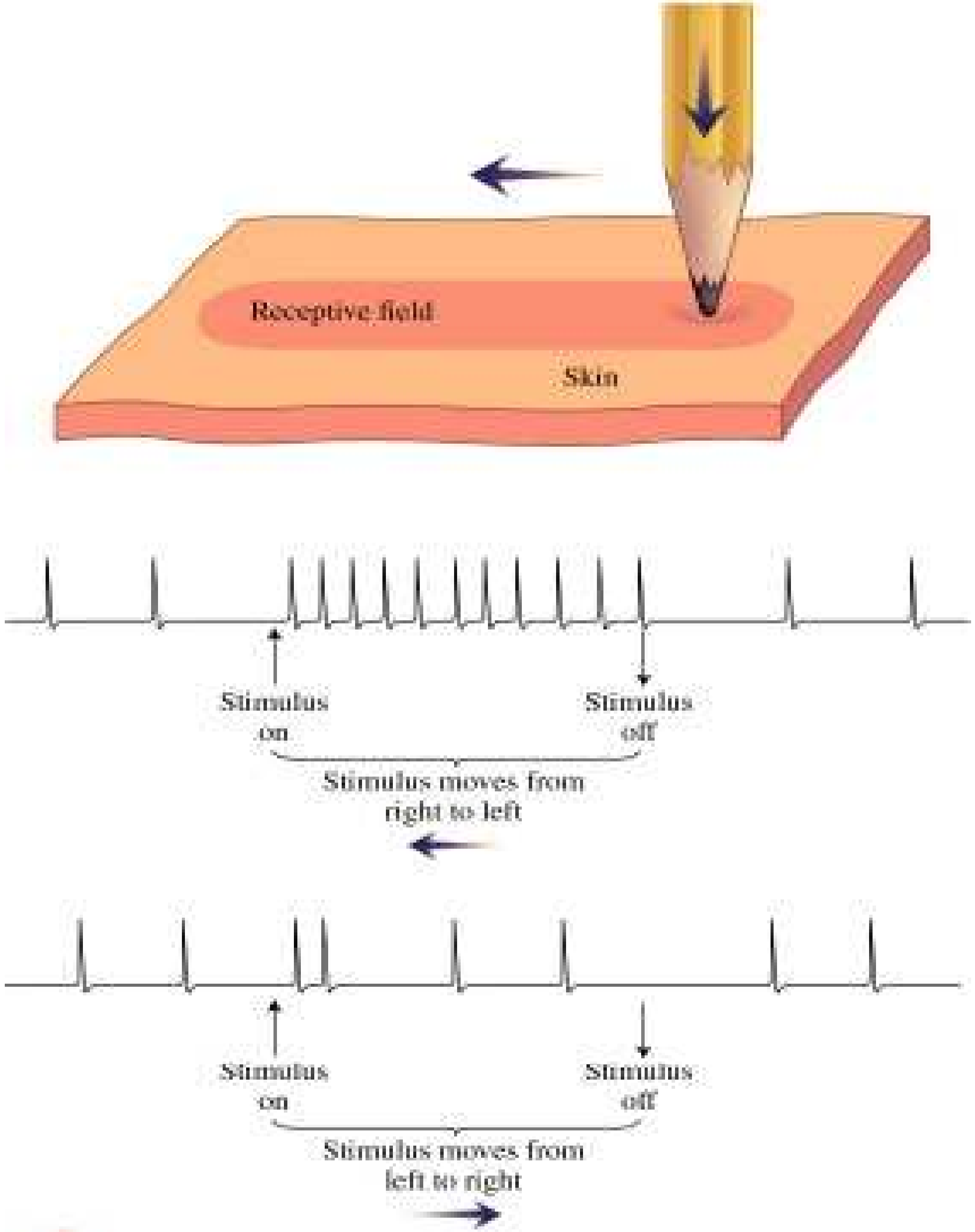

Receptive Field
for A
Stimulus
PRIMARY
SENSORY
NEURON
1
2
3
4
Divergence
FIRST
ORDER
NEURON
A
Convergence
Other Sensory Modalities
Parallel Series
Non-sensory Modalities
Centrifugal
(Feedback)
B
SECOND
ORDER
NEURON
Specific
Sensory
Pathway
Non-specific
(Multimodal)
Pathway



[Video receptivní pole]



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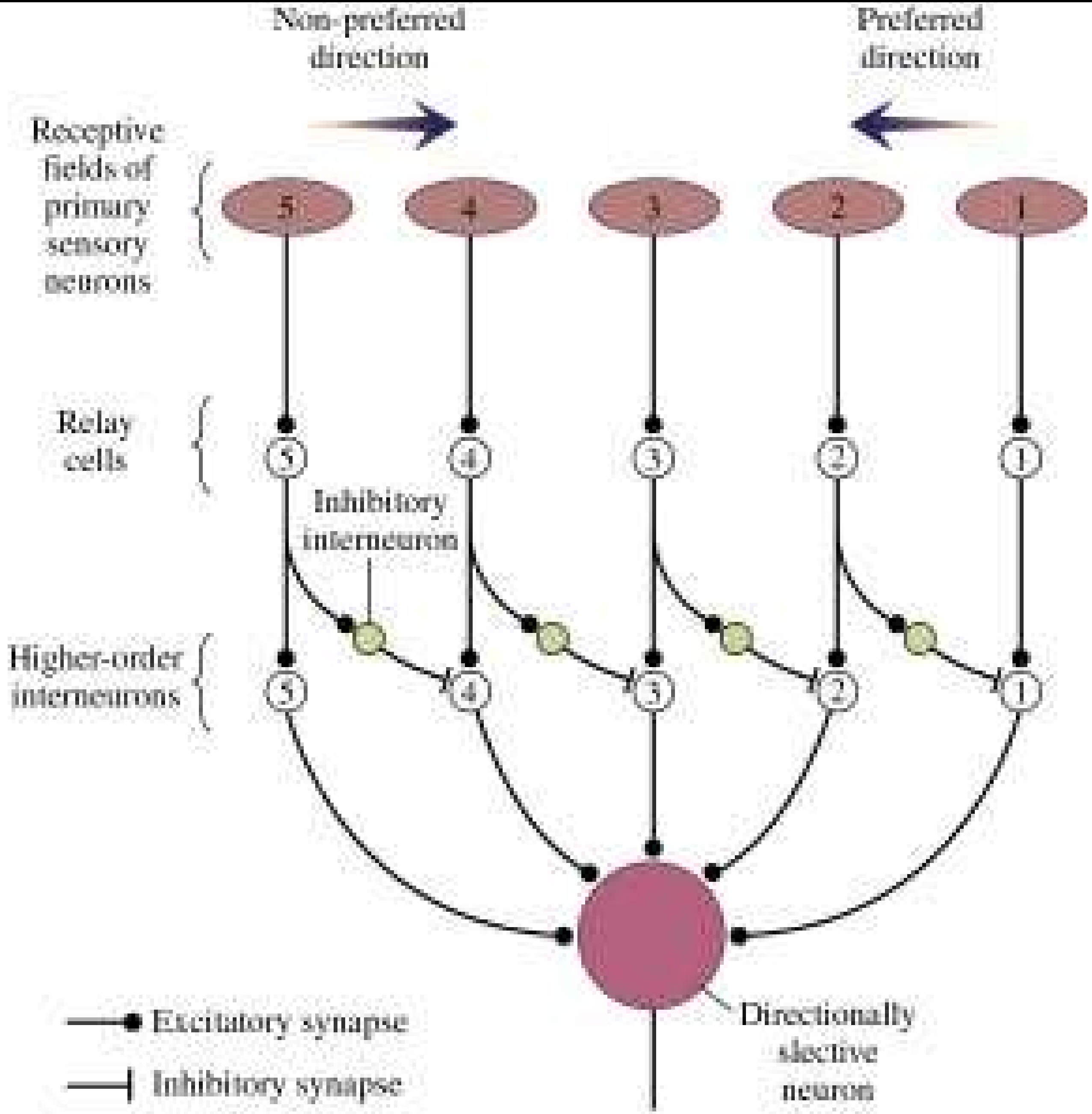

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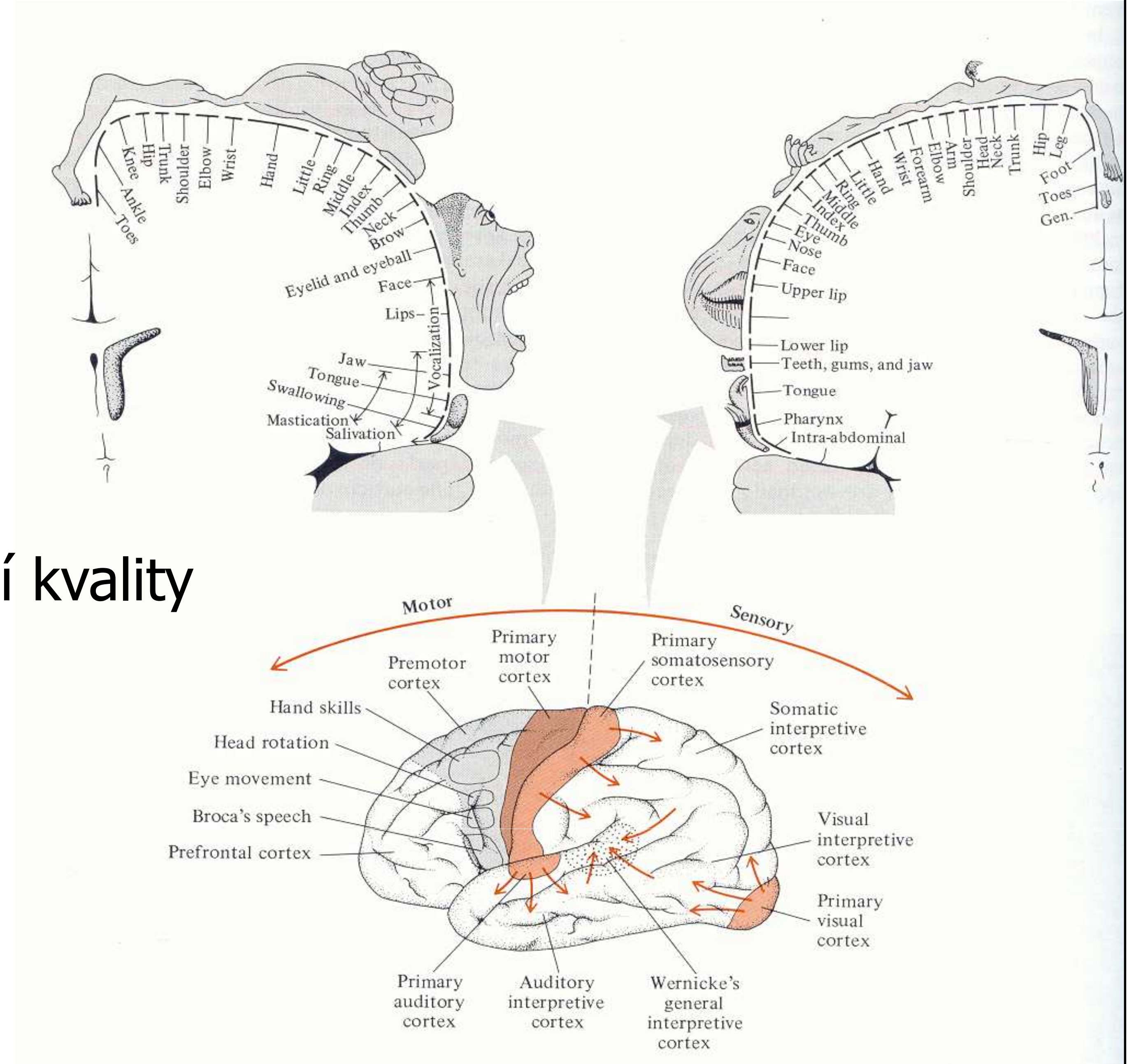
Sensorické mapy
- somatotopie
- retinotopie
- tonotopie
- chemotopie

- specializace na další kvality



3 úrovně organizace sensorických systémů

A) Receptory
B) Sensorické obvody a dráhy
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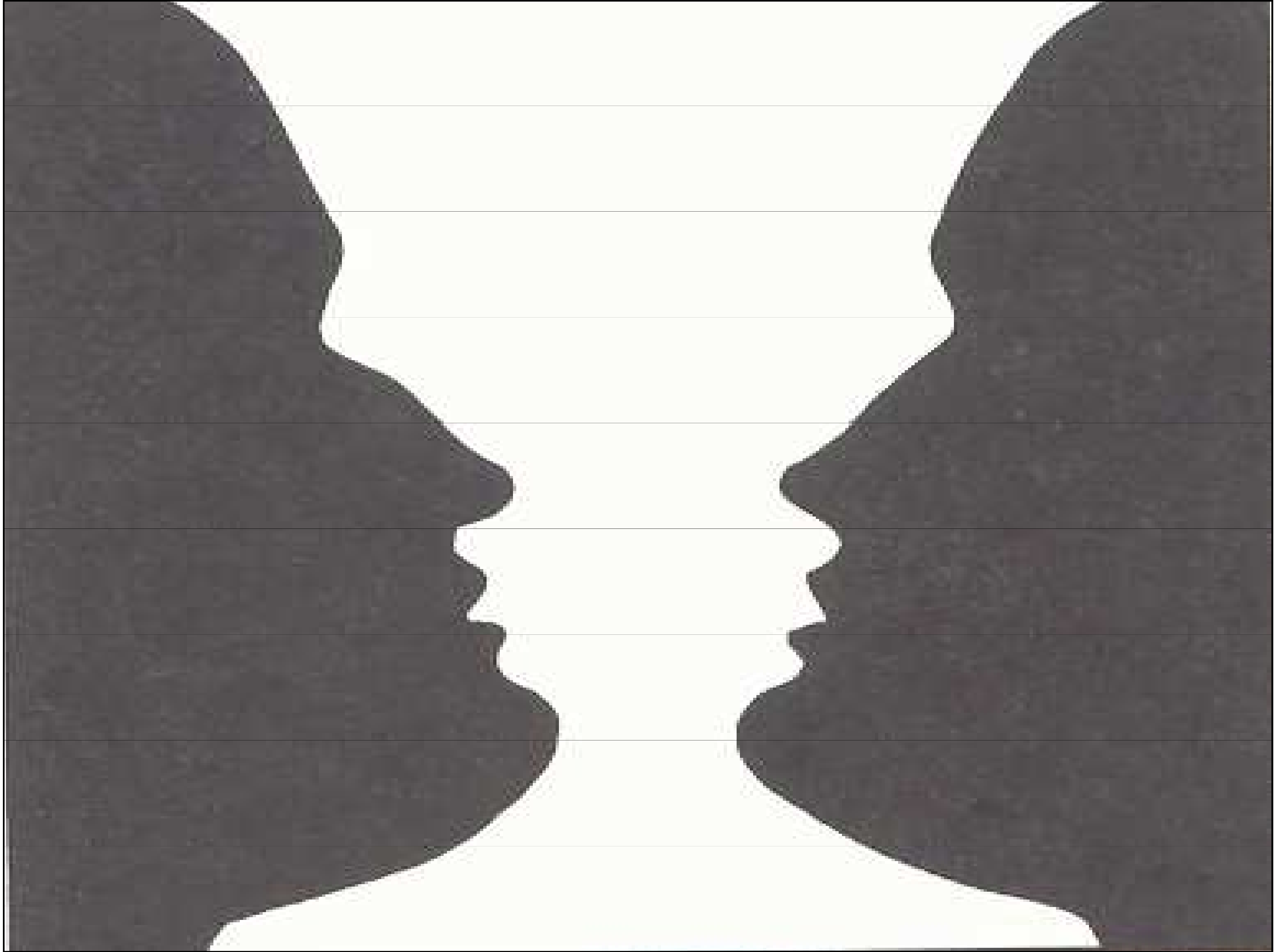
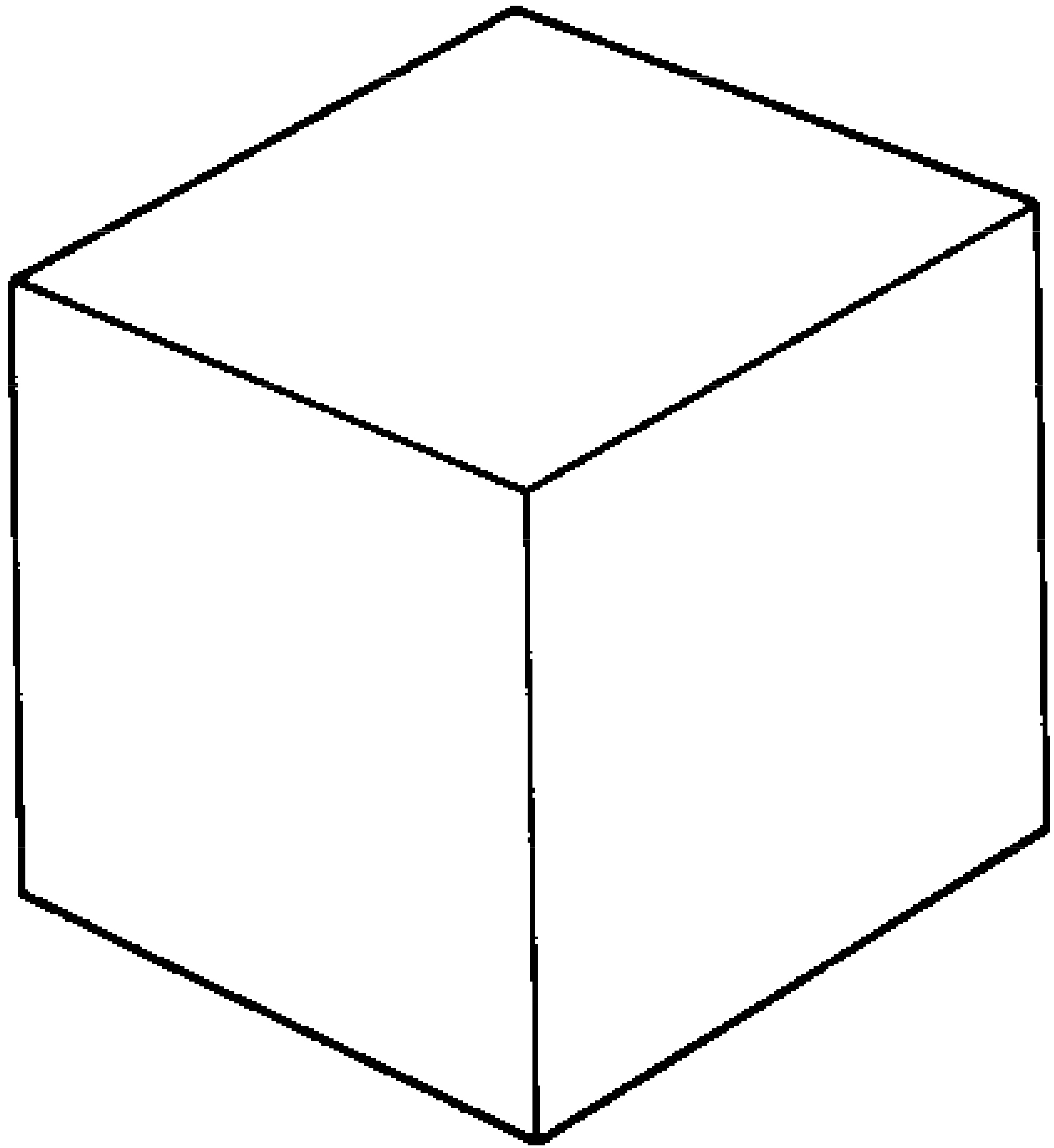




Mechanorecepce

E. coli

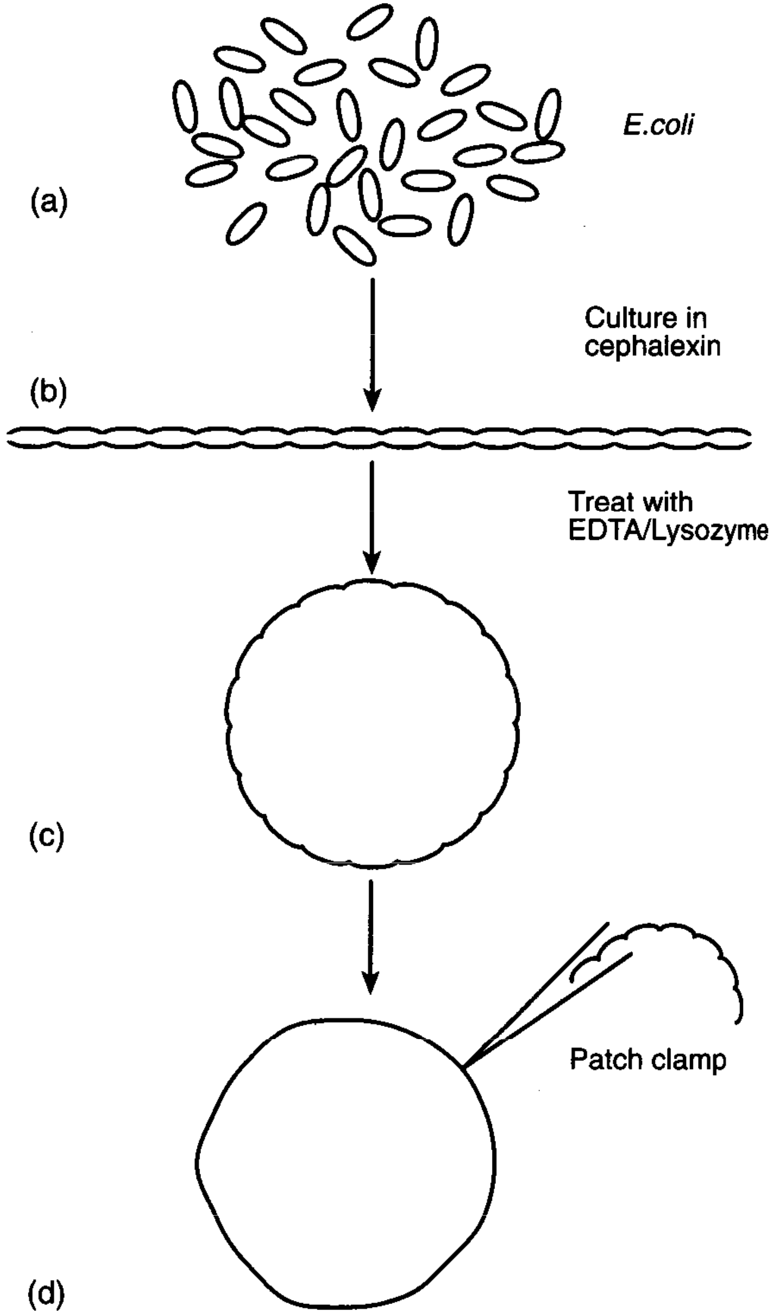
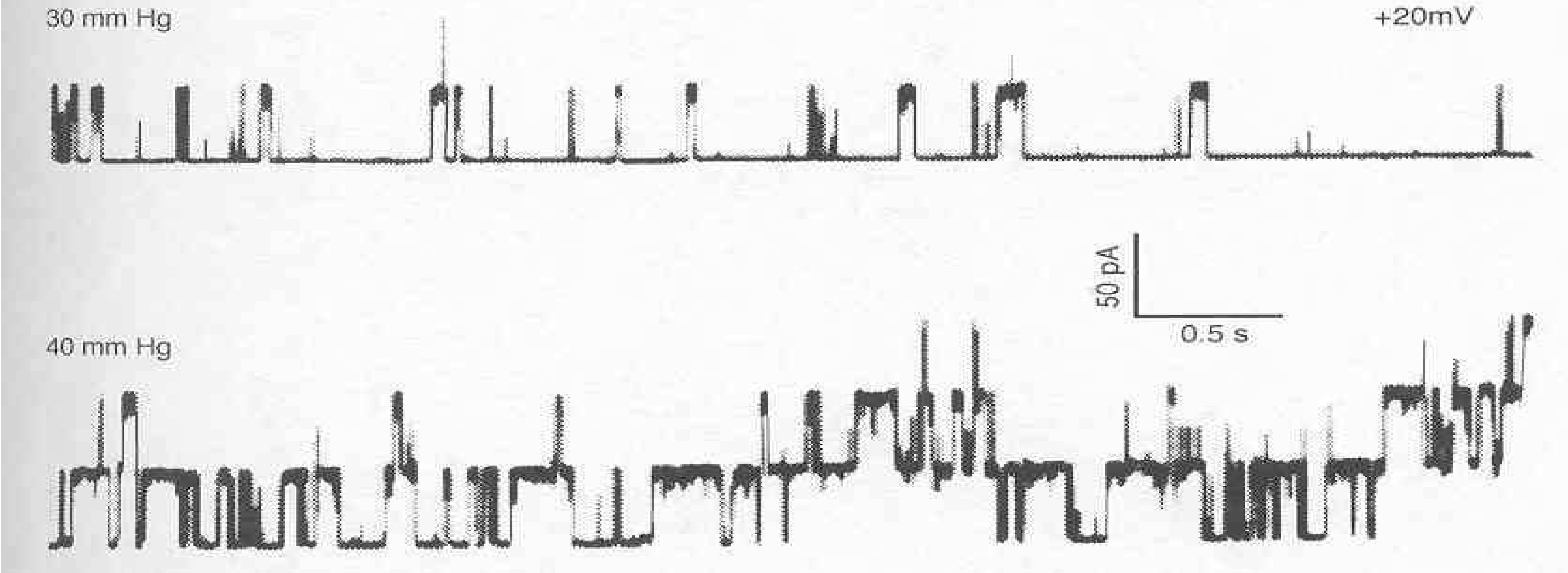
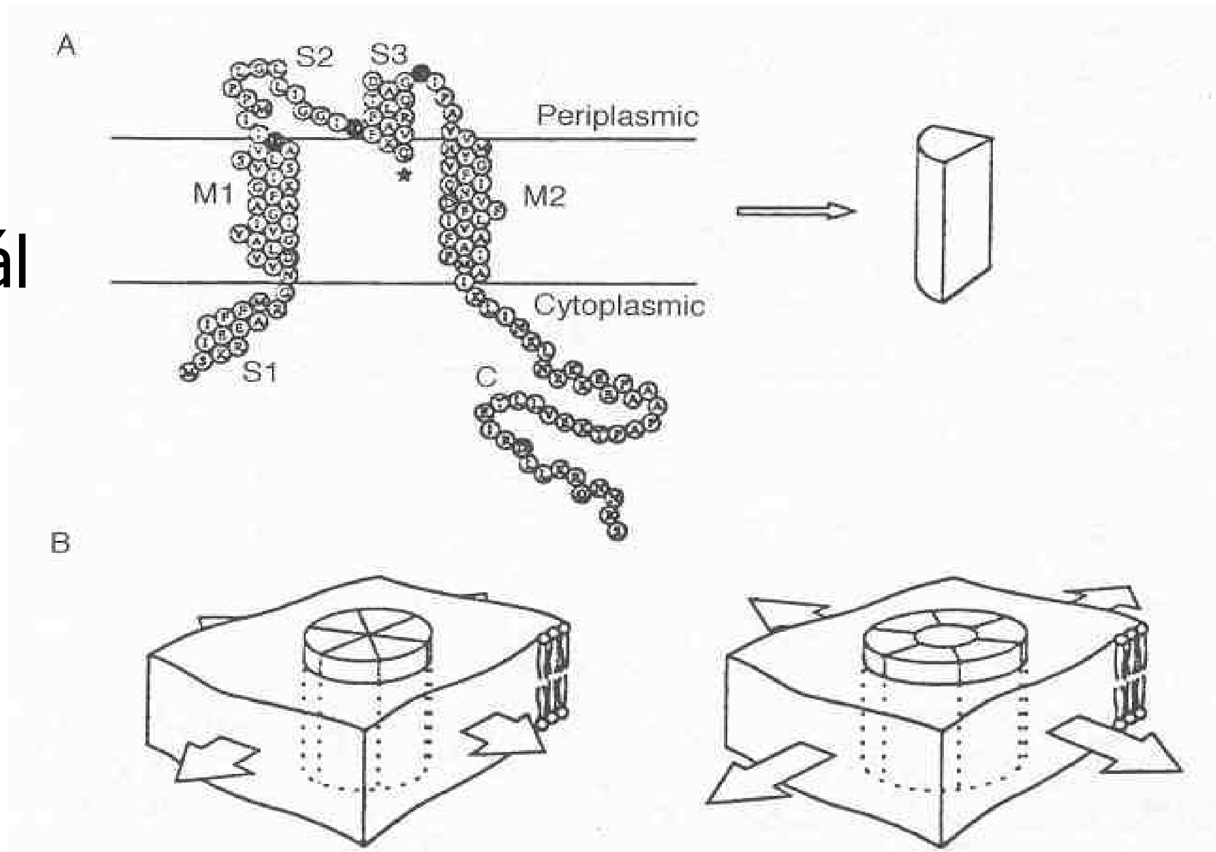


Figure 5.1 Patch-clamping *E coli*. (a) *E. coli* cell. (b) Cultured in medium containing cephalexin and forms lengthy filaments. (c) Filament treated with EDTA/lysozyme and rounds-up to form large spheroplast. (d) Microelectrode (tip diameter about 0.5 mm) inserted to form a patch-clamp. Further explanation in text



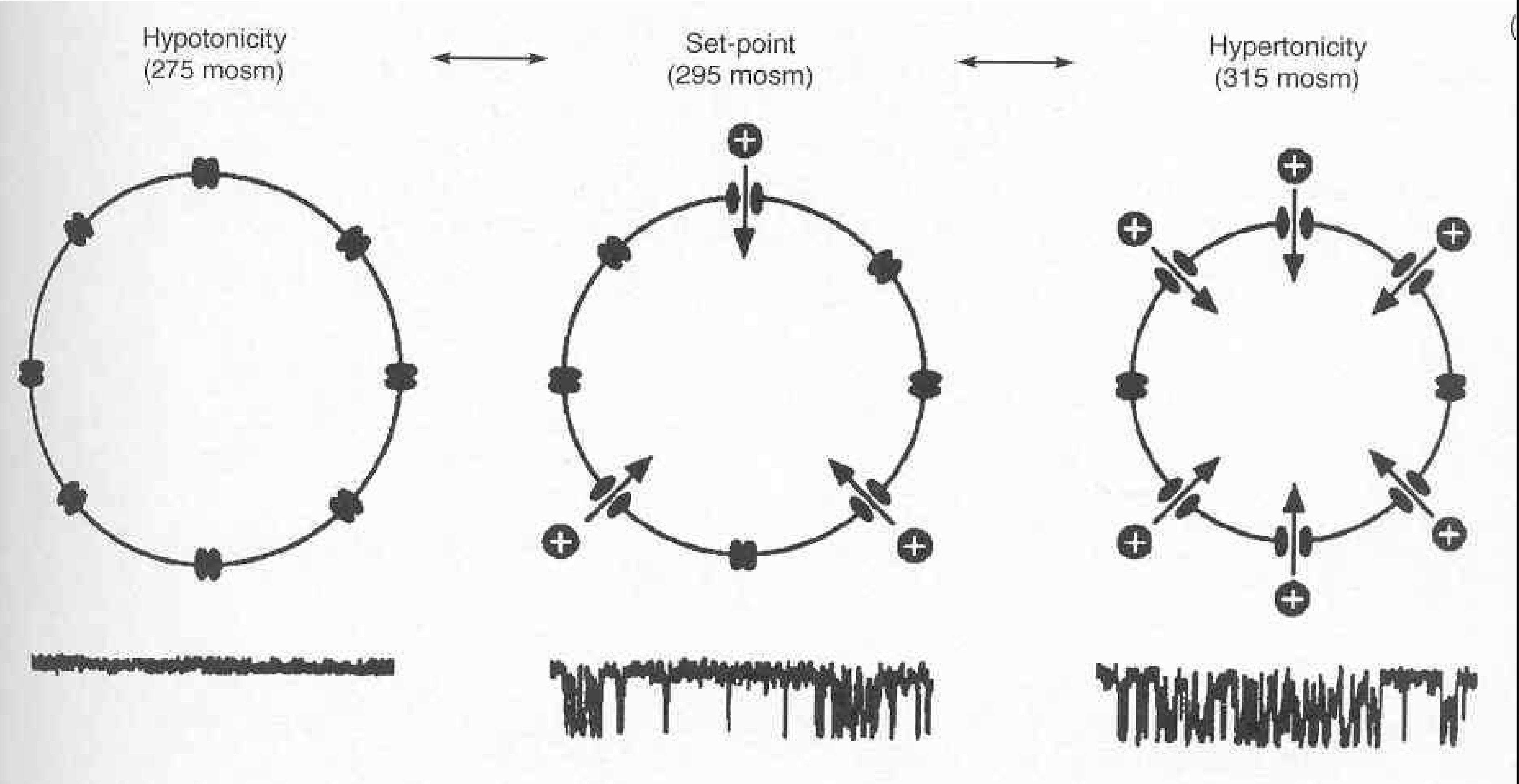
30 mm Hg
+20mV
50 pA
0.5 s
40 mm Hg

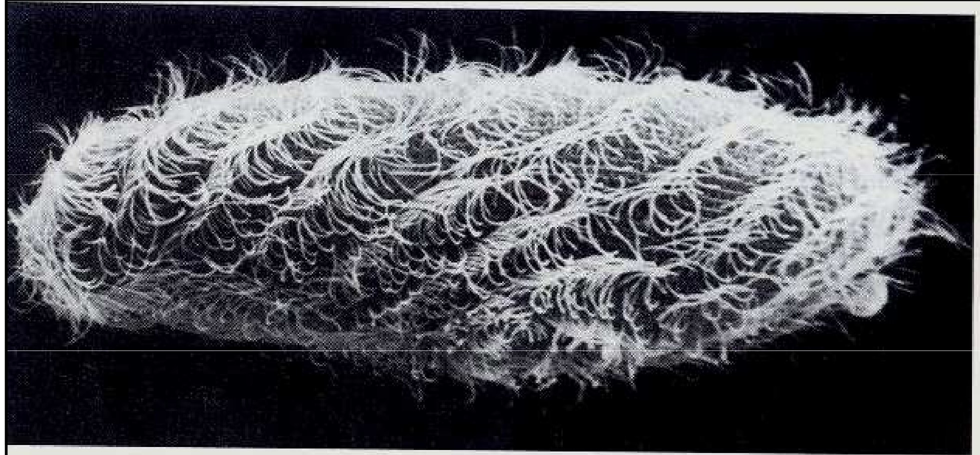
MscL kanál

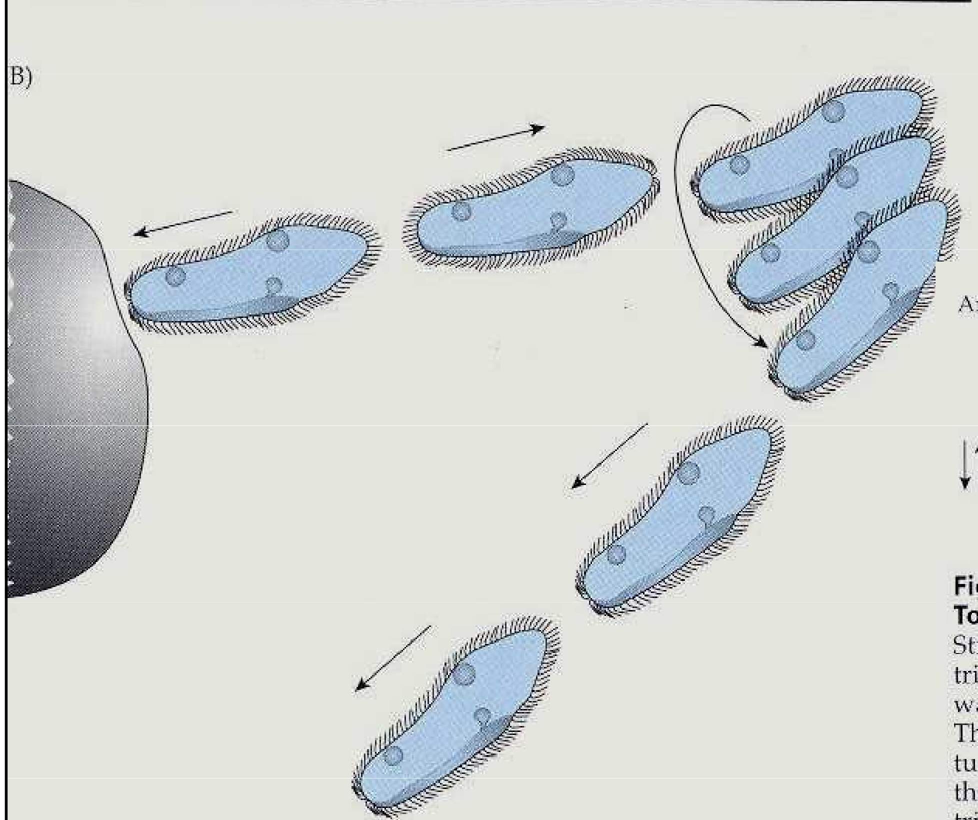


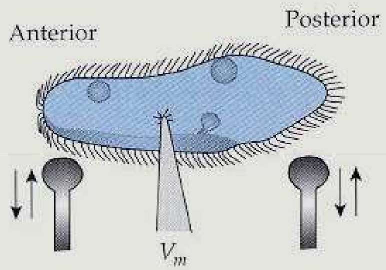
A
S2
S3
Periplasmic
M1
M2
Cytoplasmic
S1
C
B

Savčí osmosensitivní buňka









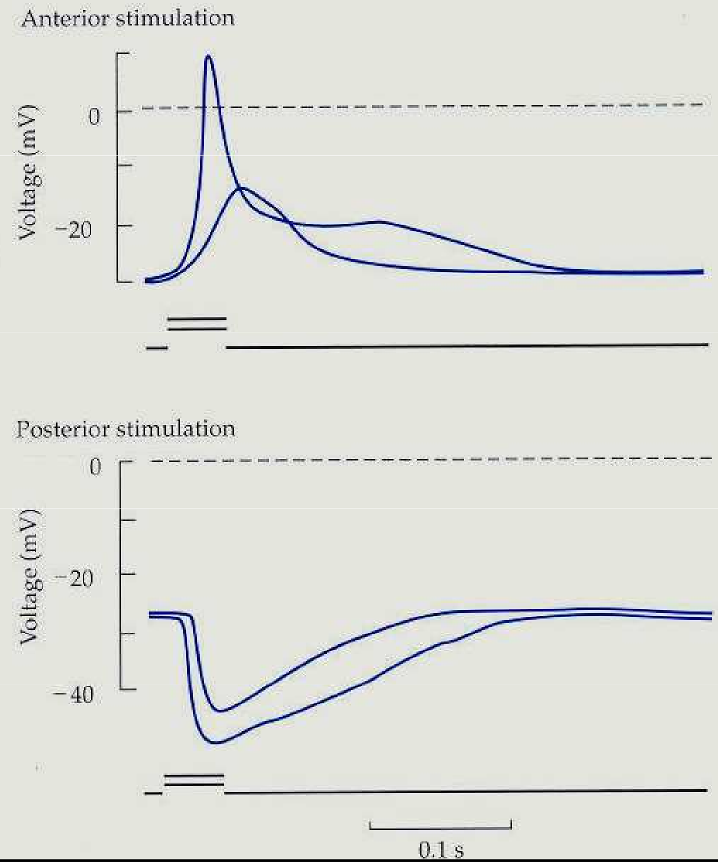


Figure 5.2
Touch responses of *Paramecium*
Stimuli were produced by an electrically driven microstylus that was pressed up against the cell. The timing and relative amplitude of the stimuli are shown in the traces below each of the electrical recordings. Two amplitudes of pressure were applied at each location. (From Eckert, 1972.)

Paramecium

Caenorhabditis elegans – háďátko

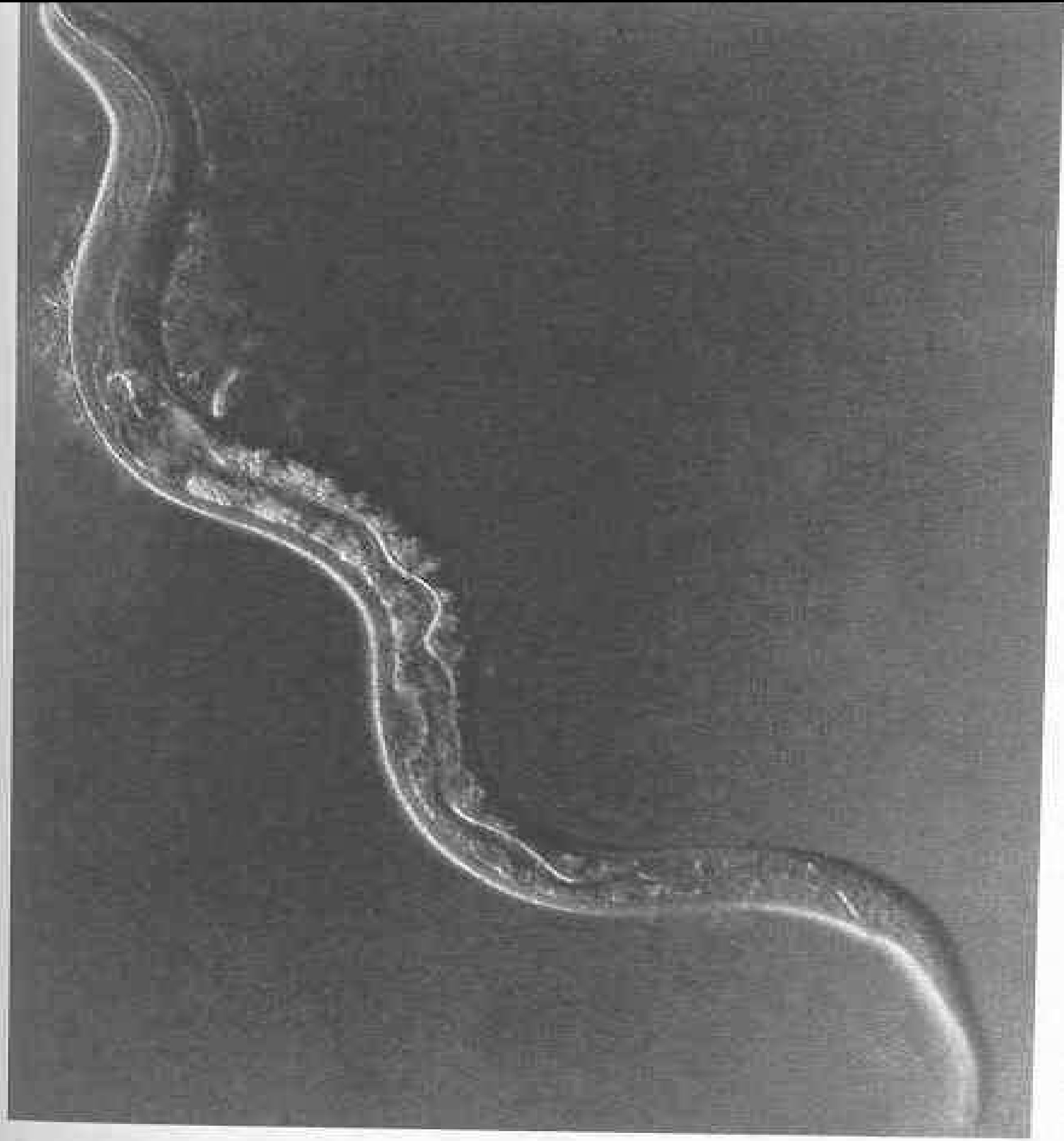
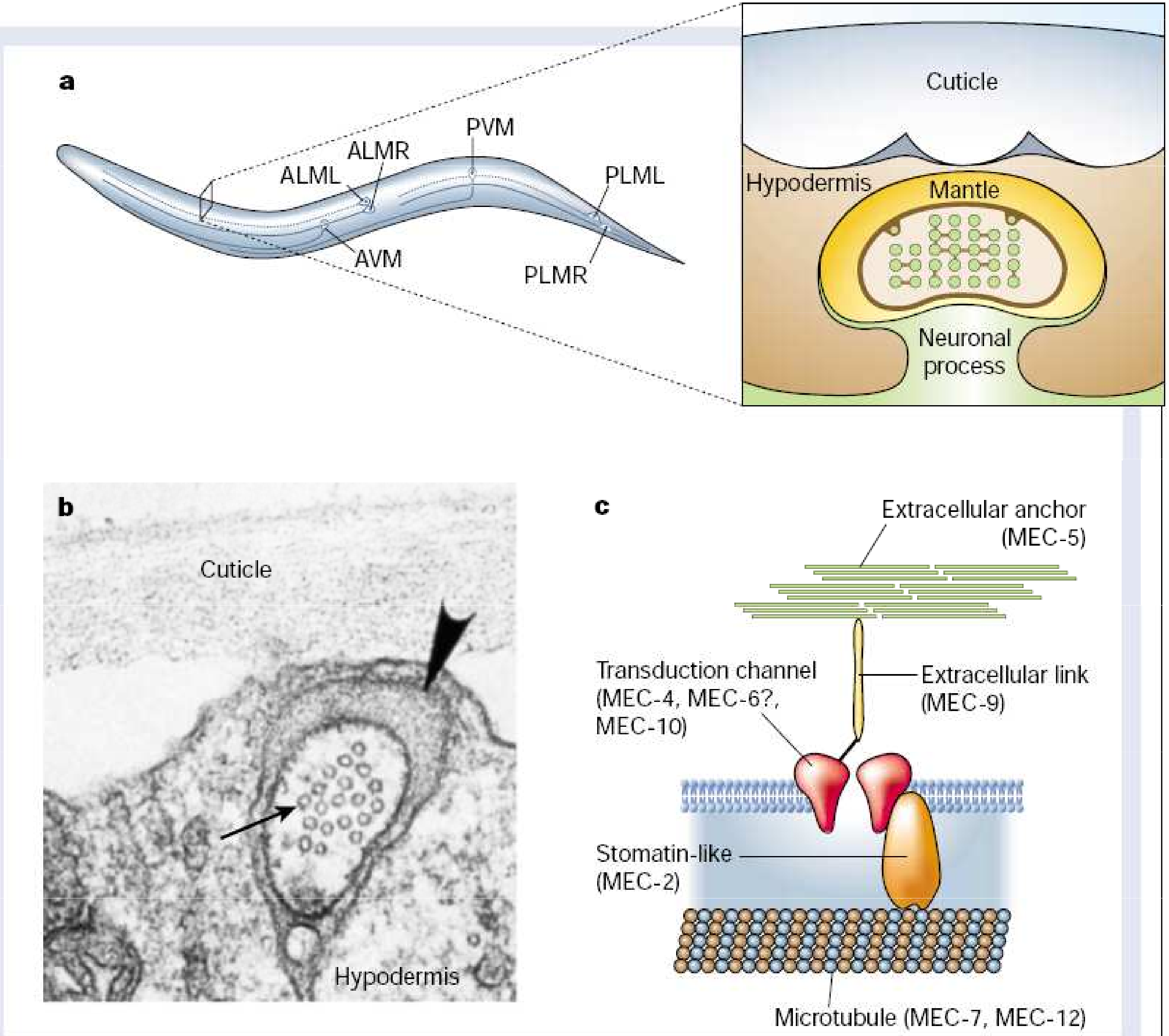


Figure 7.1 *Caenorhabditis elegans.* This worm is about 200 mm in length. *C. elegans* consists of 959 somatic cells of which 302 constitute the nervous system. The body is translucent and many of its cells can be distinguished in the living animal. Reprinted from J. G. White, 1985, 'Neuronal connectivity in Caenorhabditis elegans', *Trends in Neurosciences* 8, 277 with permission from Elsevier Science

6 hmatových neuronů

Figure 2 *C. elegans* touch-receptor structure and transduction model. **a**, View of *C. elegans* showing positions of mechanoreceptors. AVM, anterior ventral microtubule cell; ALML/R, anterior lateral microtubule cell left/right; PVM, posterior ventral microtubule cell; PLML/R, posterior lateral microtubule cell left/right. **b**, Electron micrograph of a touch-receptor neuron process. Mechanotransduction may ensue with a net deflection of the microtubule array relative to the mantle, a deflection detected by the transduction channel. Arrow, 15-protofilament microtubules; arrowhead, mantle. Modified from ref. 3. **c**, Proposed molecular model for touch receptor. Hypothetical locations of *mec* proteins are indicated.



Bohaté na mikrotubuly

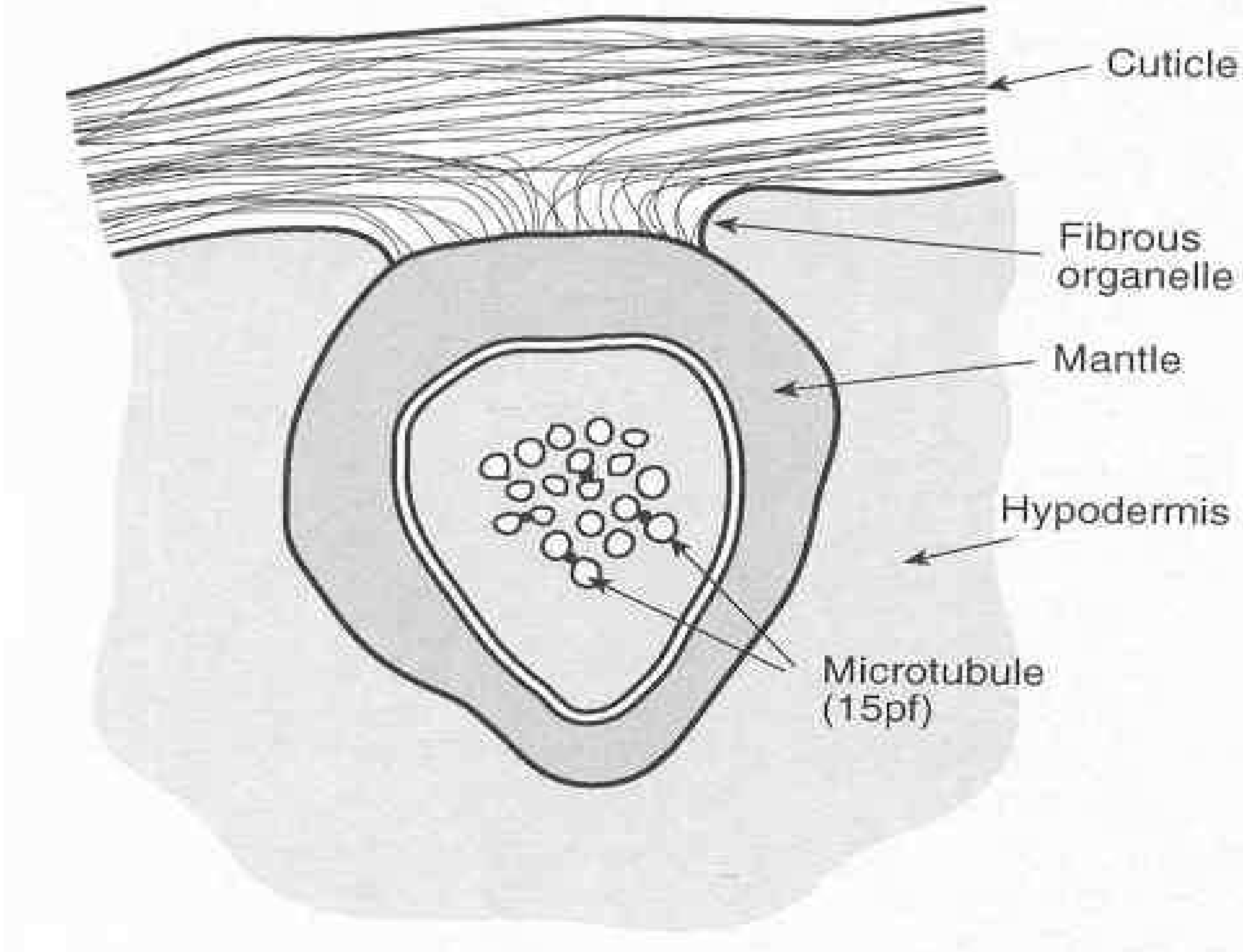


Figure 7.3 Ultrastructure of *C. elegans* touch receptor neuron in transverse section. The neuron is surrounded by a connective tissue mantle and is attached to the cuticle by a 'fibrous organelle'. It contains a bundle of microtubles (each composed of 15 protofilaments (pf)). After Tavernarakis and Driscoll, 1997

MEC-4 protein

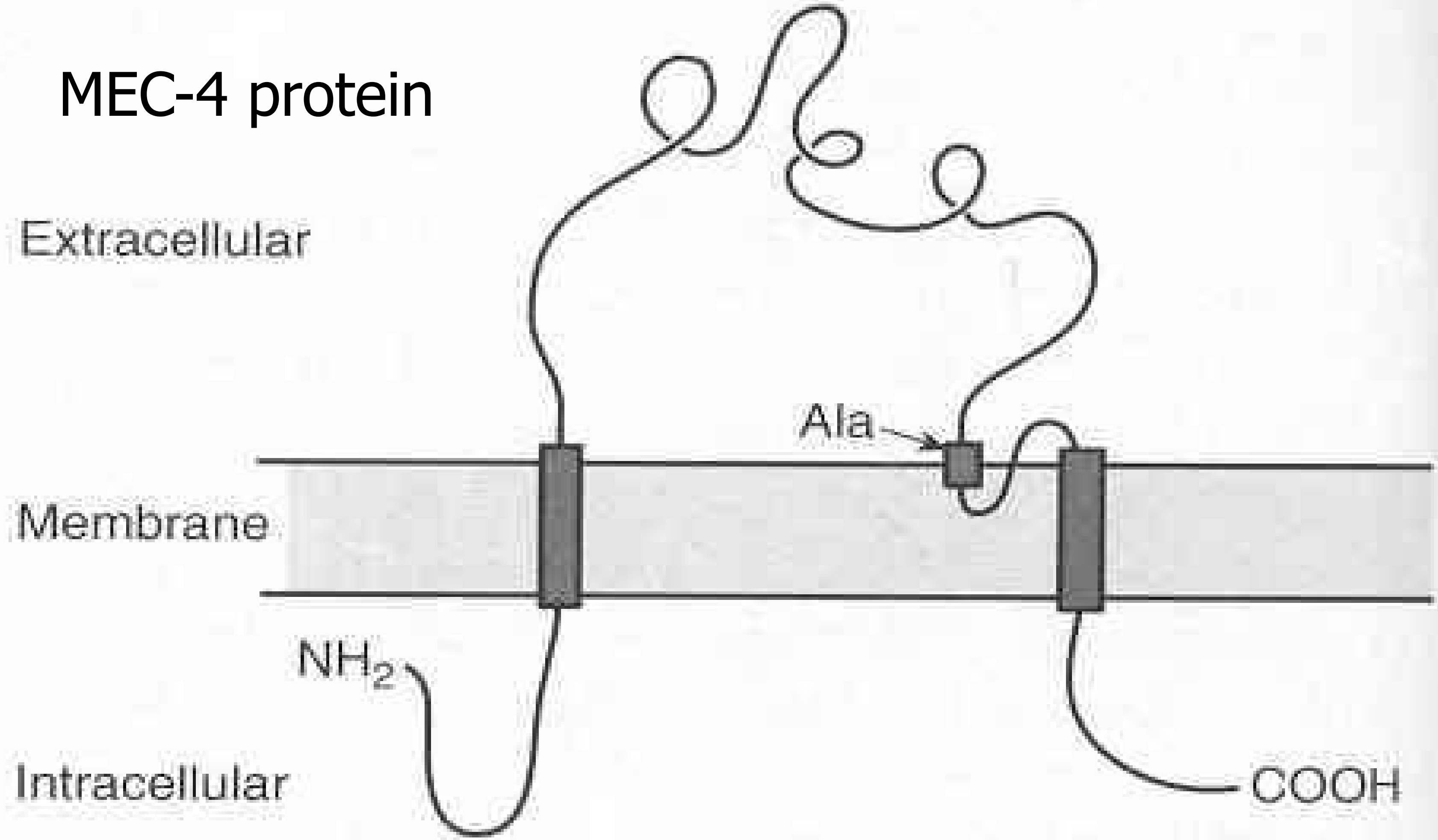


Figure 7.4 Transmembrane topology of the MEC-4 protein. There are two transmembrane domains and a small membrane insertion just before the second transmembrane helix. The bulk of the 768 residue protein is, as indicated, in the extracellular space. When Alanine_{713} (Ala) is replaced by a bulkier amino acid cell death ensues. After Tavernarakis and Driscoll, 1997

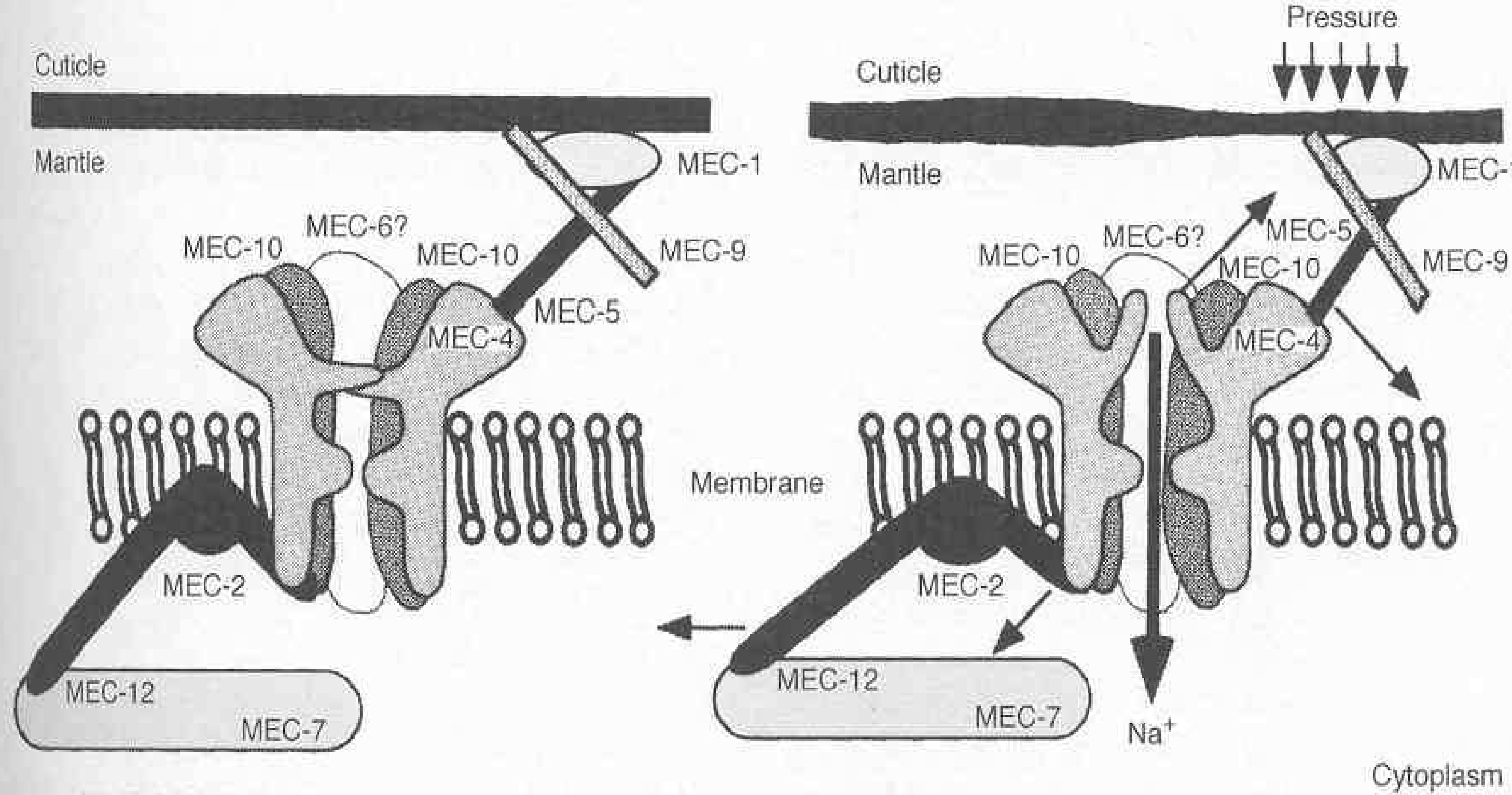
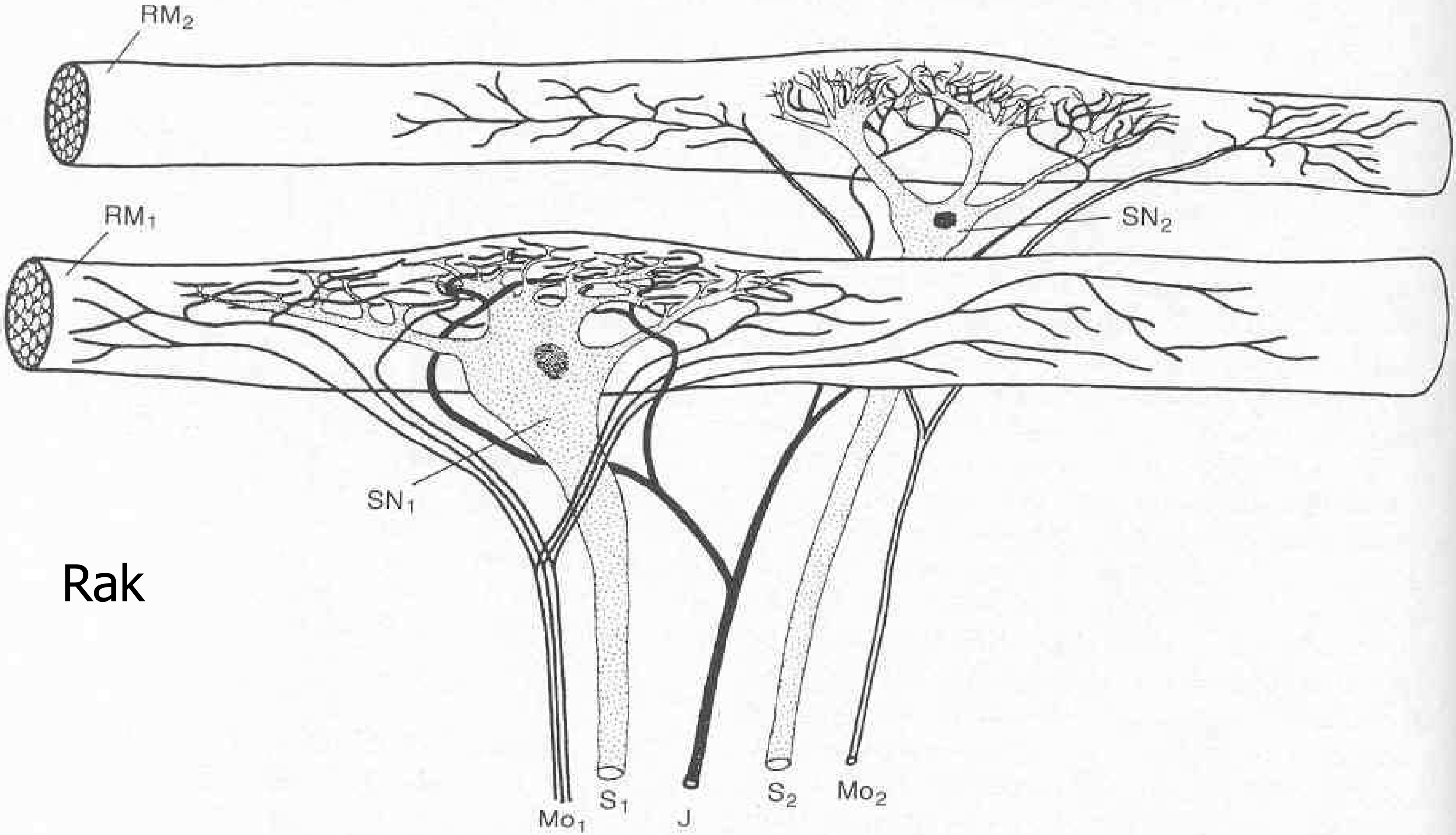


Figure 7.6 Conceptual model of *C. elegans* touch receptor. Explanation and nomenclature in text. From N. Tavernarakis and M. Driscoll, 1997, 'Molecular modelling of mechanotransduction in the nematode *Caenorhabditis elegans*', *Annual Review of Physiology*, **59**, 679. With permission, from the *Annual Review of Physiology*, Volume 59, ©1997, by Annual Reviews www.annualreviews.org



Rak

Figure 6.1 Schematic drawing of the stretch receptors in the abdominal segments of the crayfish, *Astacus fluviatilis*. RM1, RM2 = receptor muscles 1 and 2. SN1 = slow adapting sensory neuron; SN = fast adapting sensory neuron; S1, S2 = sensory fibres; Mo1 = three thin motor fibres to RM1; Mo2 = thick motor fibre to RM2; J = inhibitory fibre. From *Handbook of Physiology*, Section 1, Volume 1, *Neurophysiology* (1959), p. 378. Reproduced by permission of The American Physiological Society

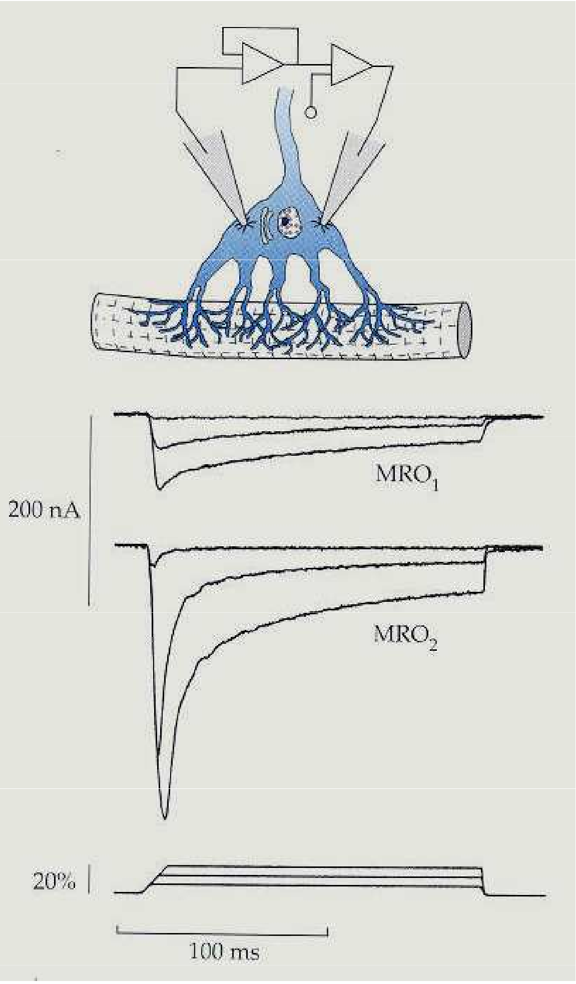
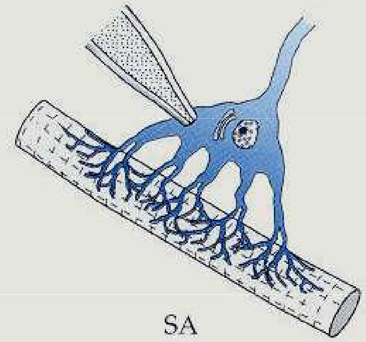
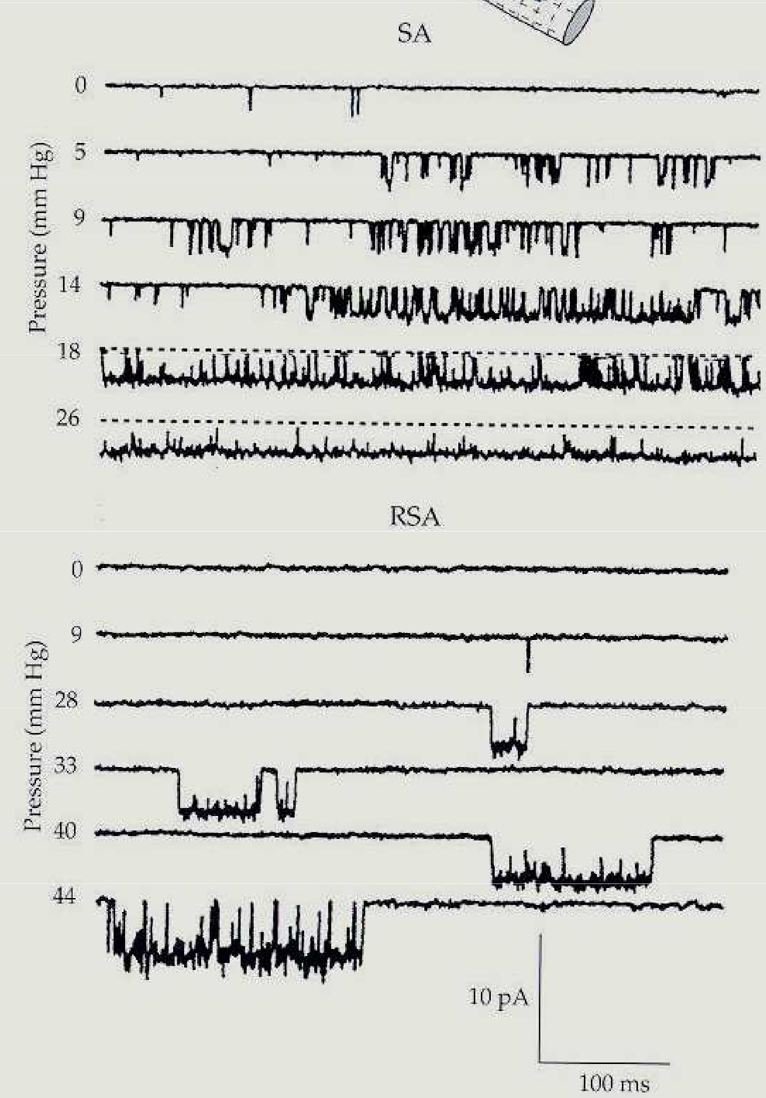
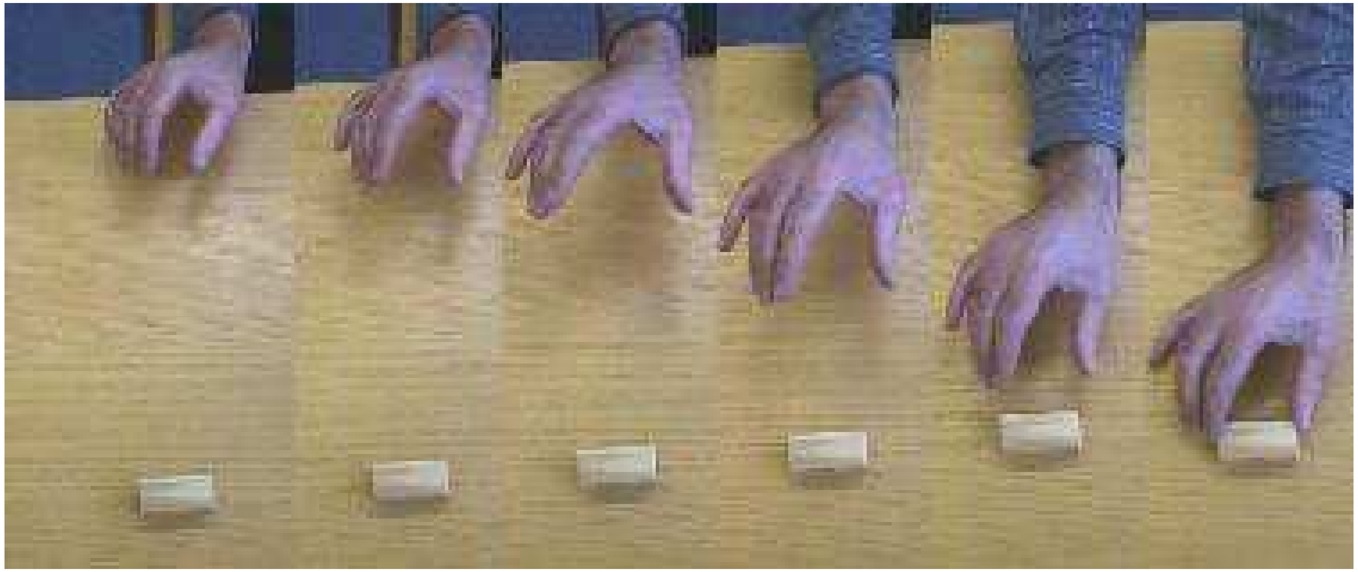


Figure 5.10
Single-channel recordings from crayfish stretch receptors On-cell patch recordings made from the cell body and main dendrites of stretch receptors. Channel openings were produced as in Figure 3.4 by the direct application to the patch pipette of suction from a calibrated pressure transducer. The amplitude of suction is given to the left in units of millimeters of mercury (Hg). Pressure was applied continuously for the duration of each record. Patches were voltage-clamped at the resting membrane potential (for SA) and 50 mV negative to the resting membrane potential (for RSA). (From Erxleben, 1989.)





Propriorecepce



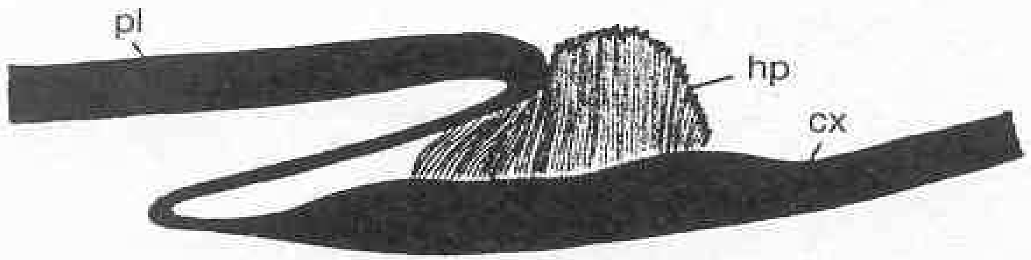


Figure 6.3 (a) The figure shows the brushwork of sensilla at the articulation of the second leg of the cockroach, *Periplaneta americana*. The thick cuticle of the pleuron (pl) thins to a delicate articular membrane and then thickens again to form the cuticle surrounding the coxa (cx), the first segment of the leg. The brush of sensilla forms a hairplate (hp). From Pringle, 1938

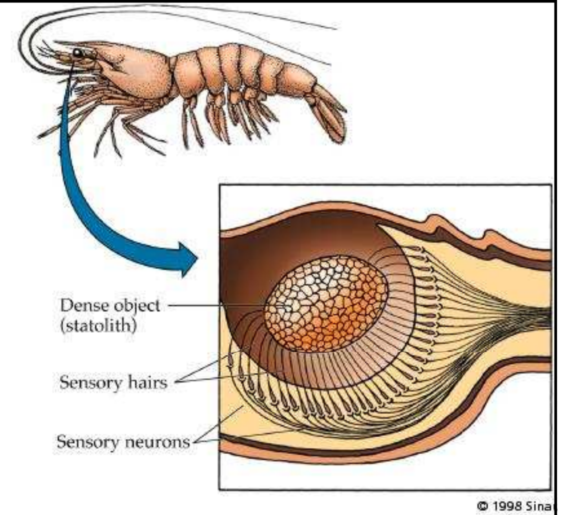
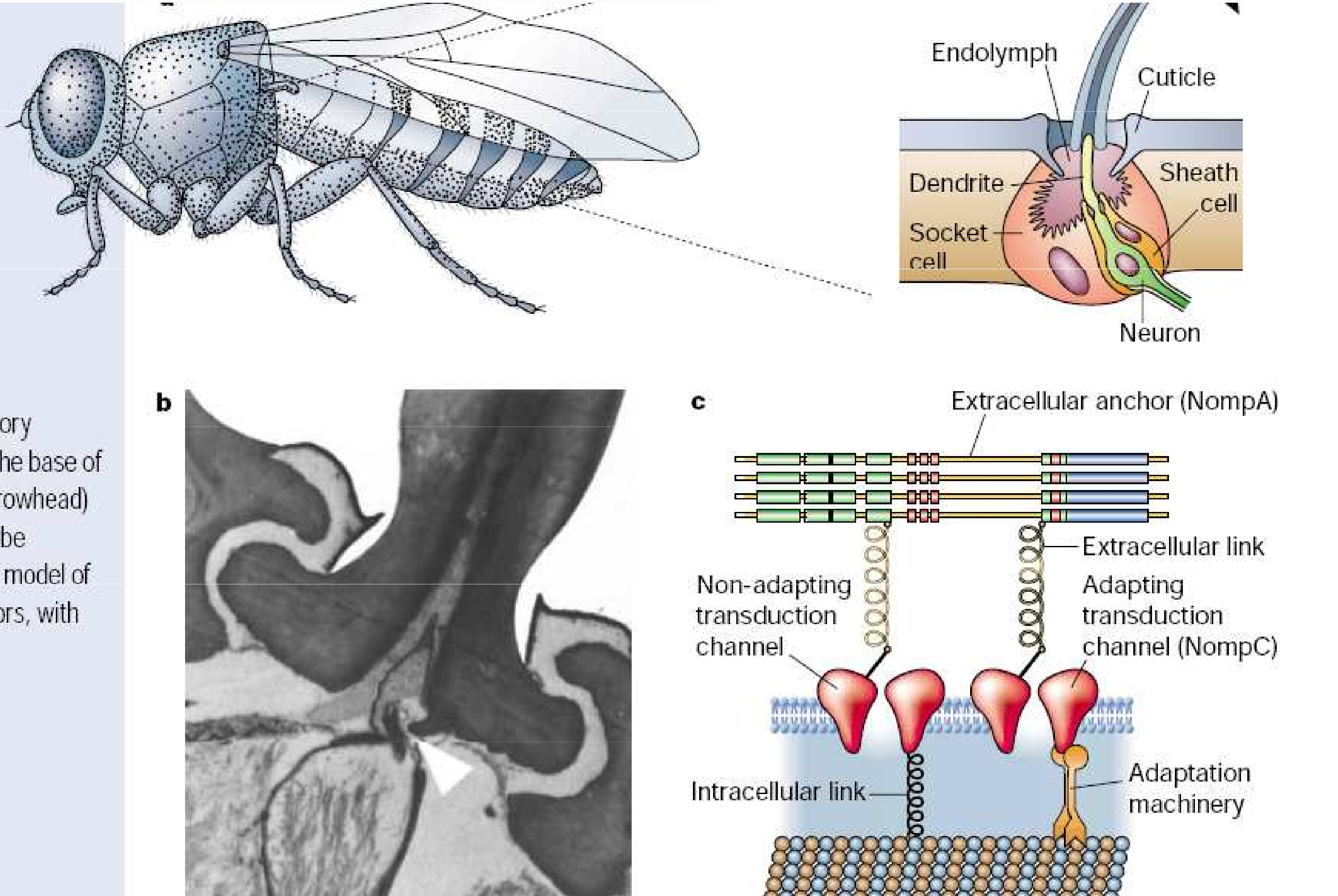
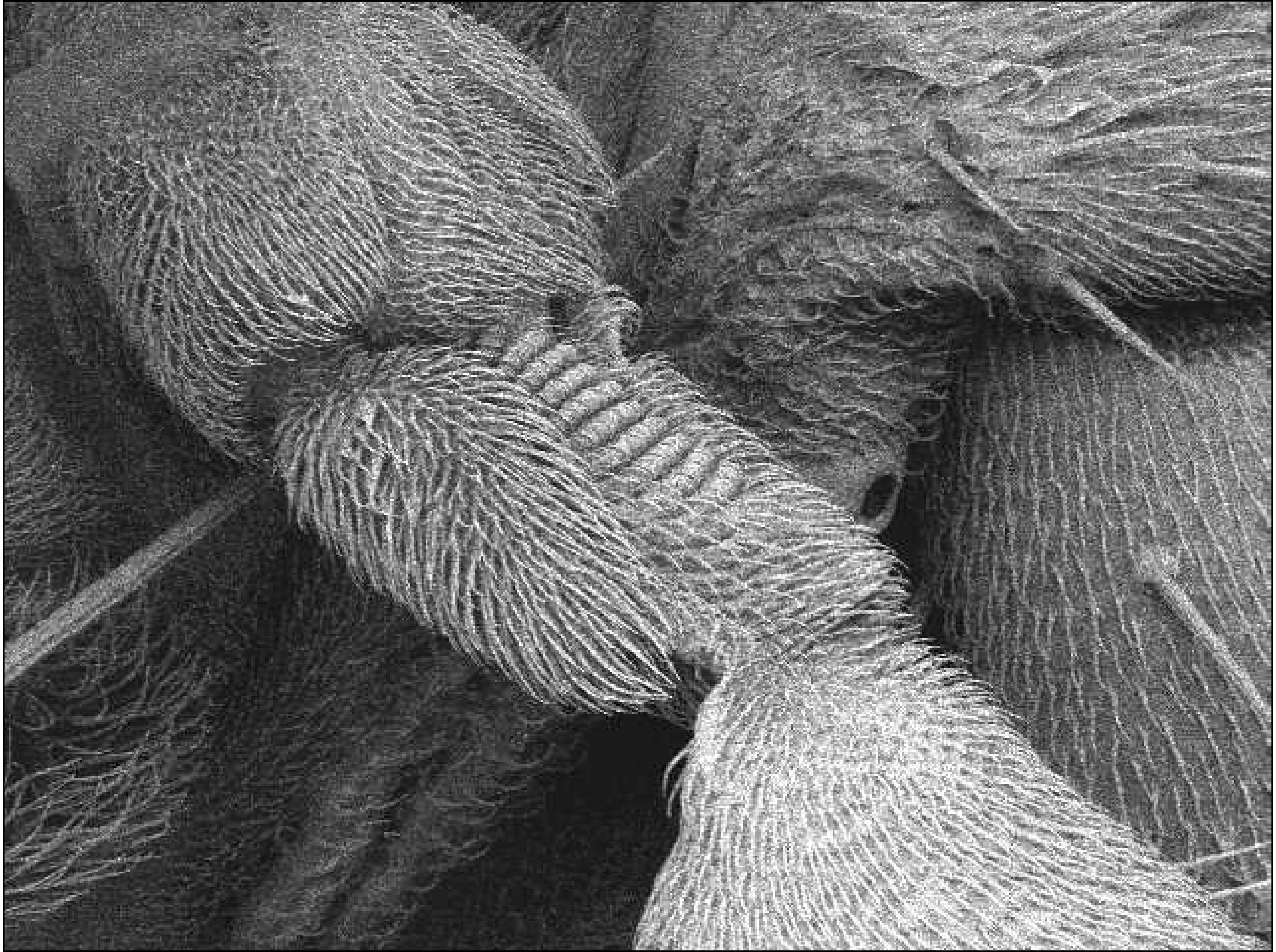


Figure 3 *Drosophila* bristle-receptor model. **a**, Lateral view of *D. melanogaster* showing the hundreds of bristles that cover the fly's cuticle. The expanded view of a single bristle indicates the locations of the stereotypical set of cells and structures associated with each mechanosensory organ. Movement of the bristle towards the cuticle of the fly (arrow) displaces the dendrite and elicits an excitatory response in the mechanosensory neuron. **b**, Transmission electron micrograph of an insect mechanosensory bristle showing the insertion of the dendrite at the base of the bristle. The bristle contacts the dendrite (arrowhead) so that movement of the shaft of the bristle will be detected by the neuron. **c**, Proposed molecular model of transduction for ciliated insect mechanoreceptors, with the locations of NompC and NompA indicated.





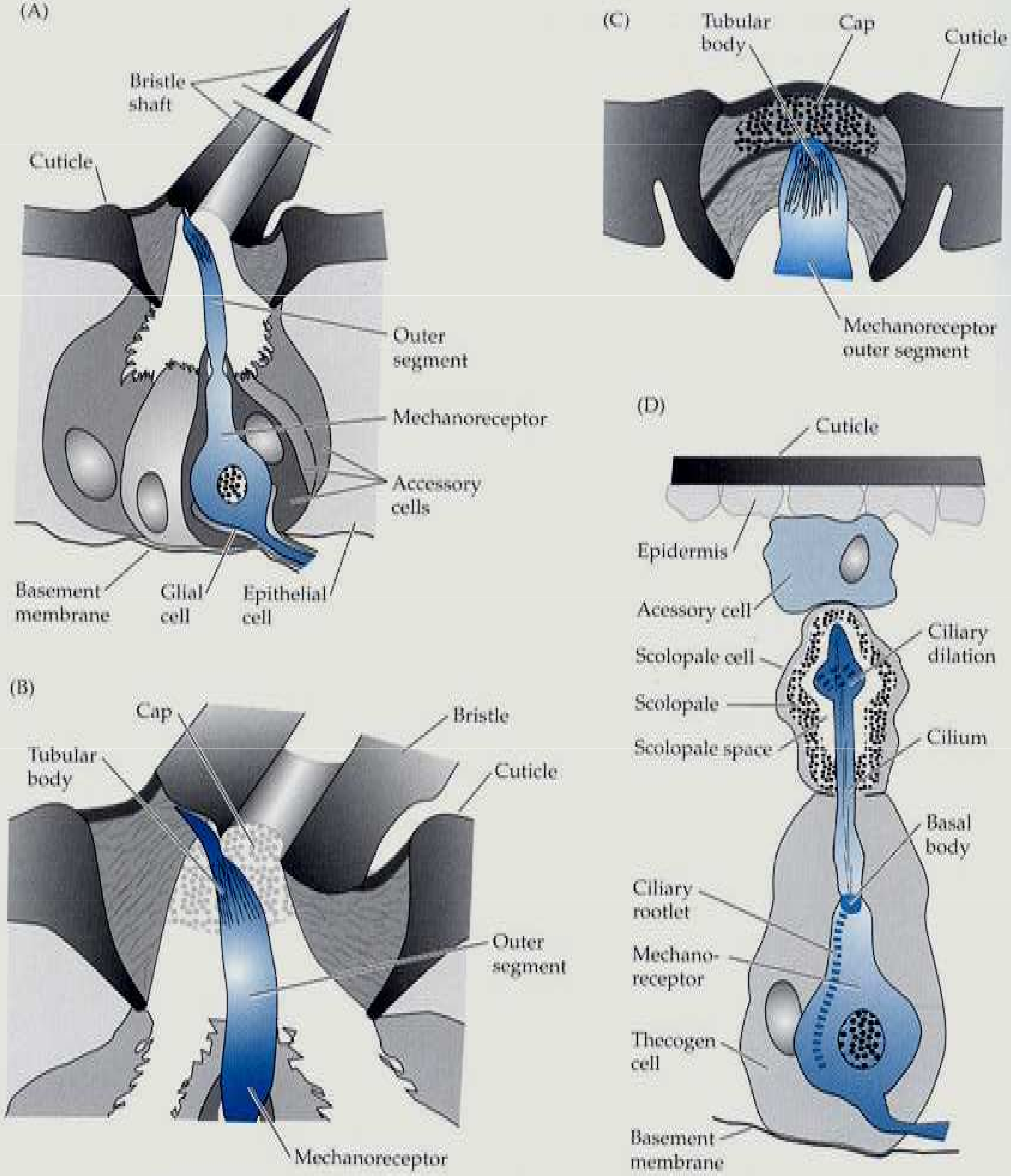
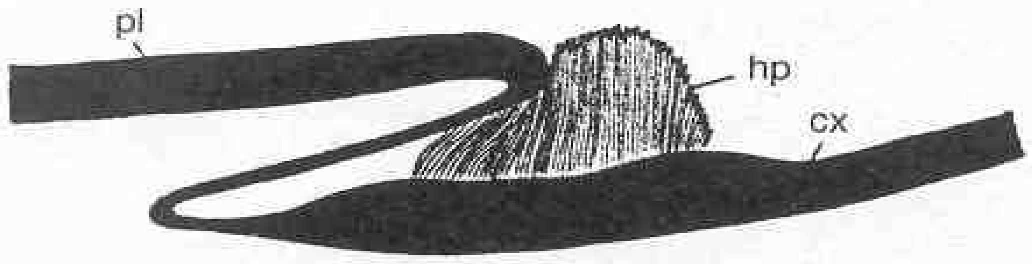


Figure 5.11
Anatomy of insect mechanoreceptive organs Schematic drawings of major morphological classes of touch sensilla. (A) Hair plate (bristle) sensillum. (B) Magnified view of hair plate sensillum. (C) Campaniform sensillum. (D) Scolopidial organ. The thecogen cell is a type of supporting cell. (After Thurm, 1964; Bullock and Horridge, 1965; Keil, 1997.)



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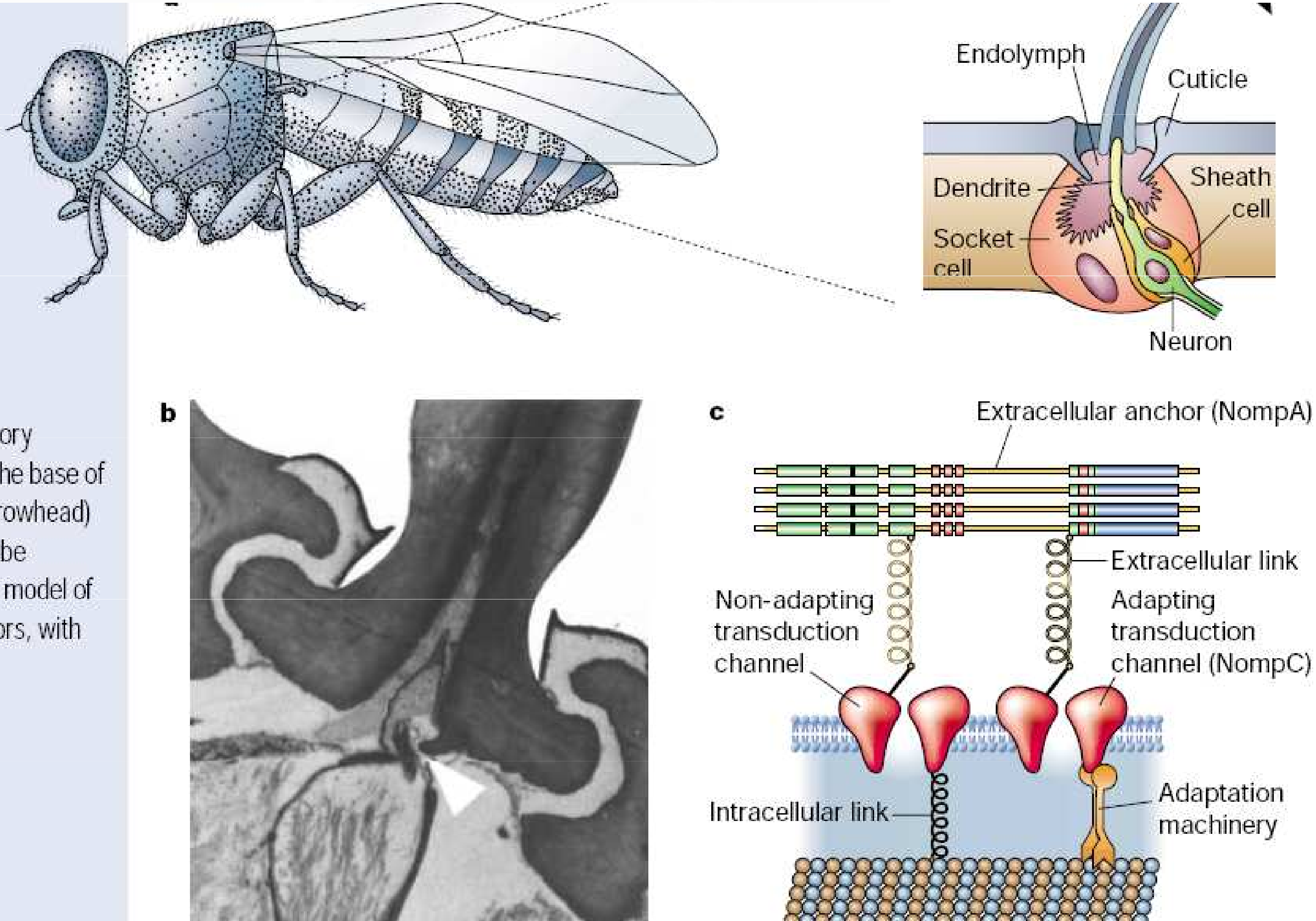


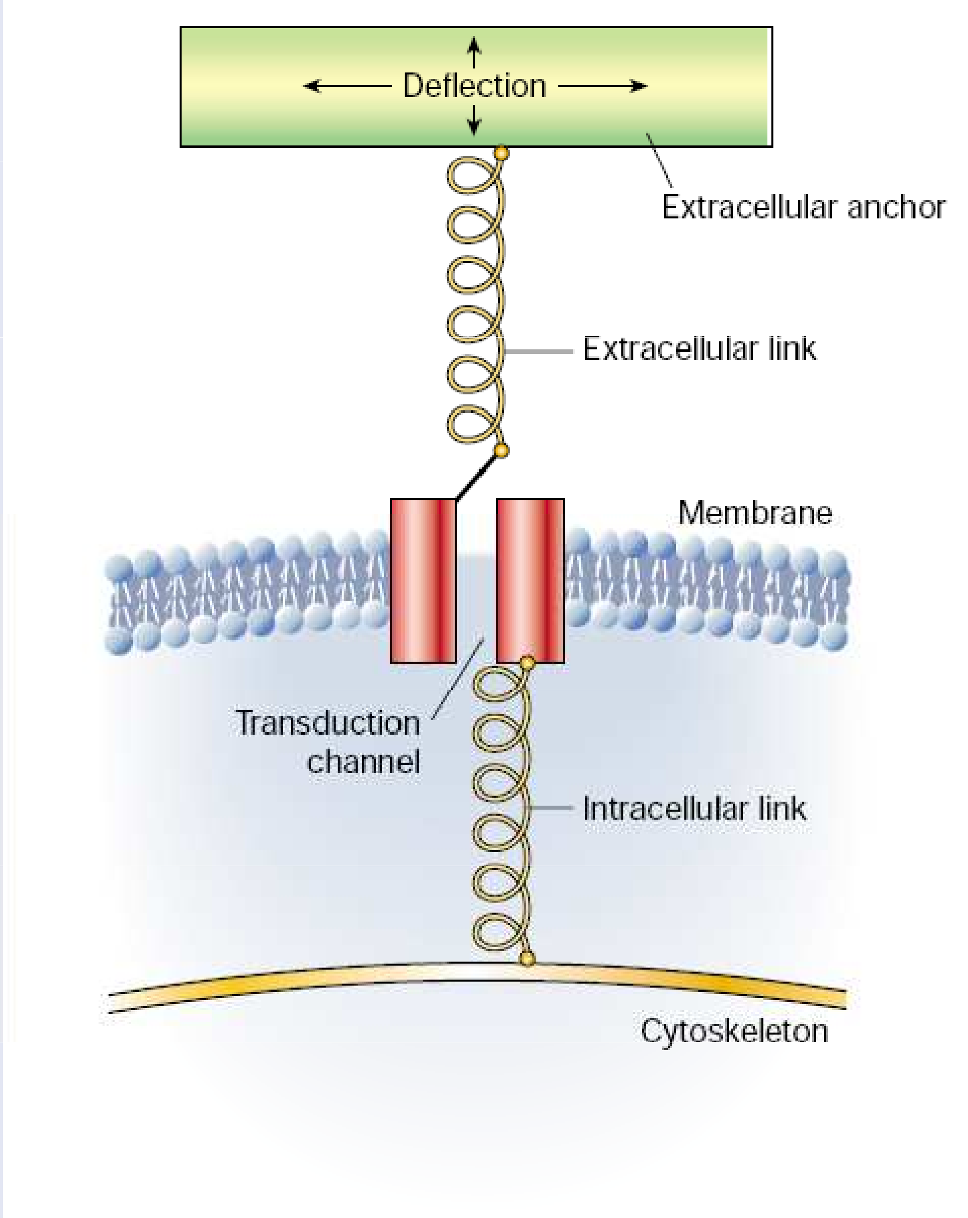
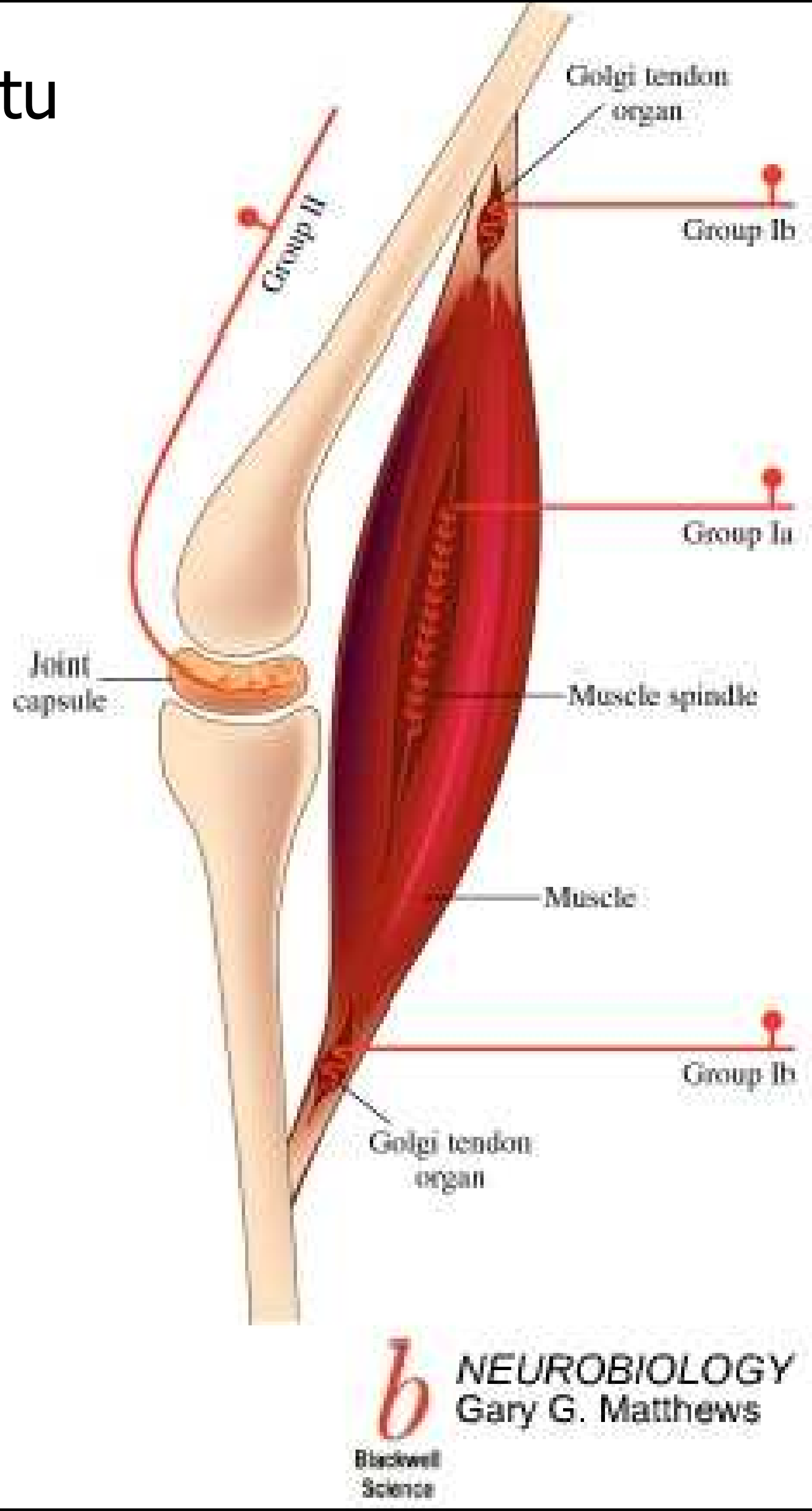
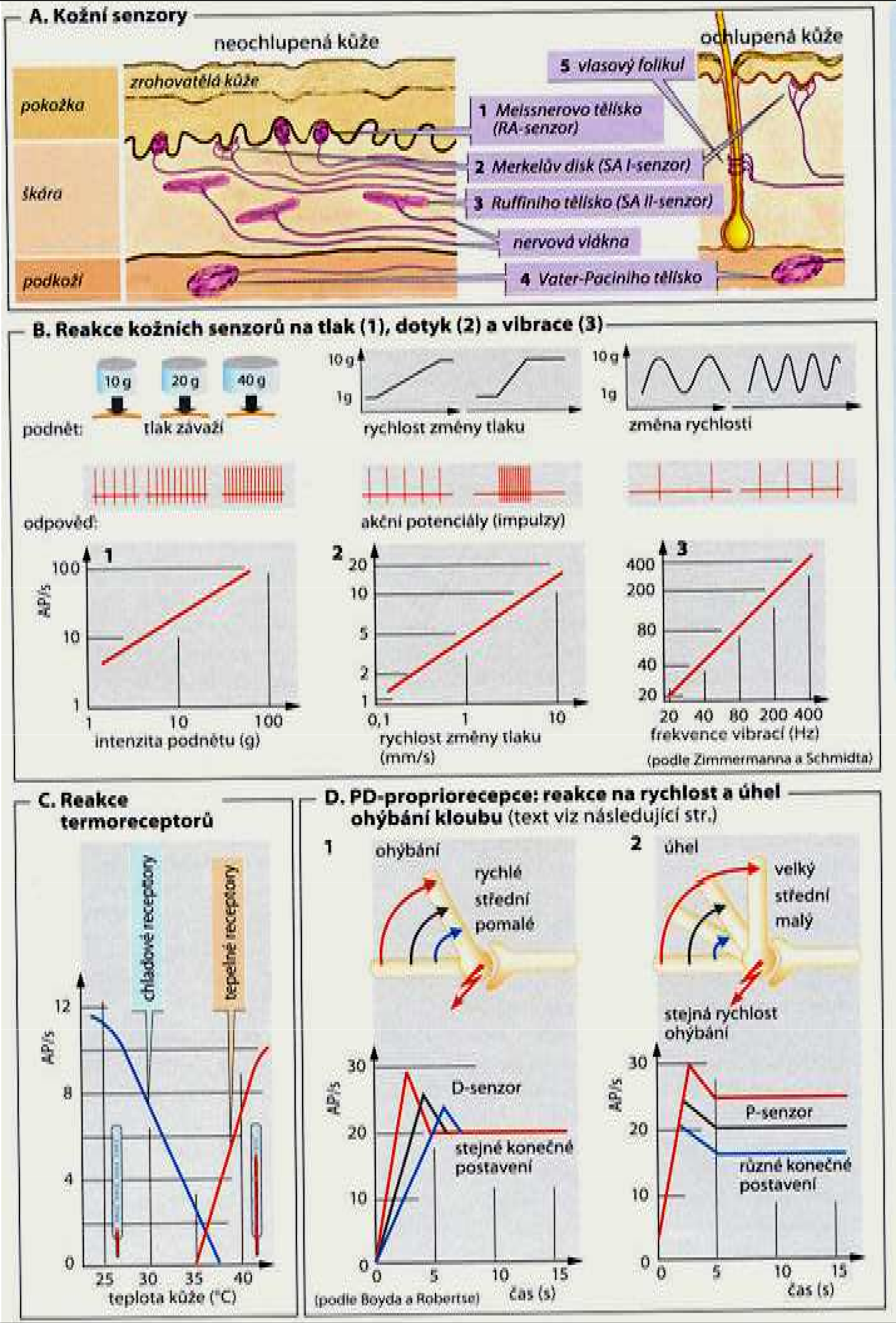
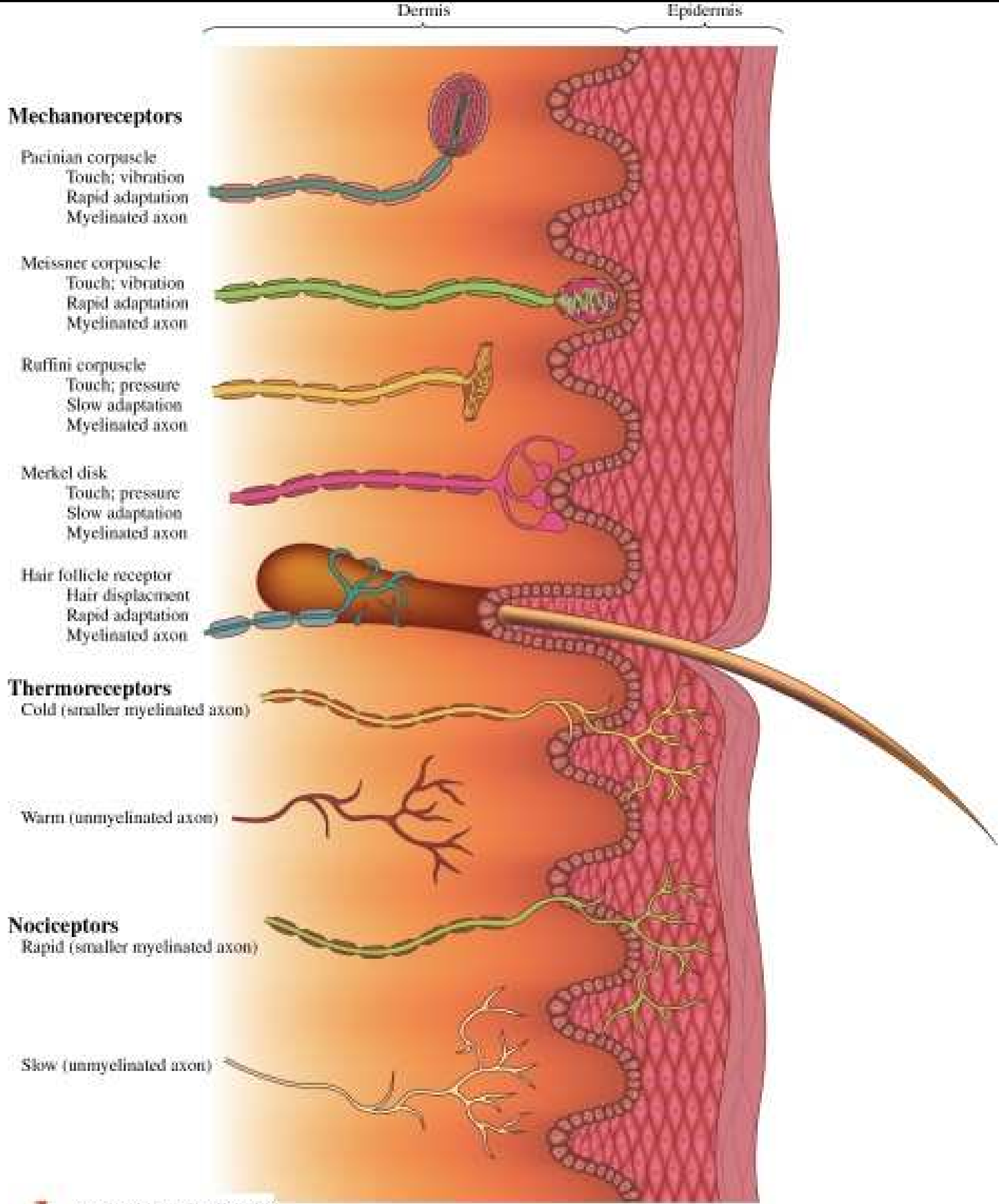


Figure 1 General features of mechanosensory transduction. A transduction channel is anchored by intracellular and extracellular anchors to the cytoskeleton and to an extracellular structure to which forces are applied. The transduction channel responds to tension in the system, which is increased by net displacements between intracellular and extracellular structures.

Propriorecepce u endoskelertu
Svalová vřeténka
Šlachová tělíska




A. Kožní senzory
neochlupená kůže
ochlupená kůže
zrohovatělá kůže
pokožka
škára
podkoží
5 vlasový folikul
1 Meissnerovo tělísko (RA-senzor)
2 Merkelův disk (SA I-senzor)
3 Ruffiniho tělísko (SA II-senzor)
nervová vlákna
4 Vater-Paciniho tělísko
B. Reakce kožních senzorů na tlak (1), dotyk (2) a vibrace (3)
10 g
20 g
40 g
podnět:
tlak závaží
rychlost změny tlaku
změna rychlostí
1g
odpověď:
akční potenciály (impulzy)
AP/s
1
100
10
1
intenzita podnětu (g)
2
20
5
0,1
rychlost změny tlaku (mm/s)
3
400
200
80
40
frekvence vibrací (Hz)
(podle Zimmermanna a Schmidta)
C. Reakce termoreceptorů
chladové receptory
tepelné receptory
12
8
4
0
25
30
35
40
teplota kůže (°C)
D. PD-propriorecepce: reakce na rychlost a úhel ohýbání kloubu (text viz následující str.)
1
ohýbání
rychlé
střední
pomalé
D-senzor
stejné konečné postavení
2
úhel
velký
střední
malý
stejná rychlost ohýbání
P-senzor
různé konečné postavení
30
15
čas (s)
(podle Boyda a Robertse)



NEUROBIOLOGY
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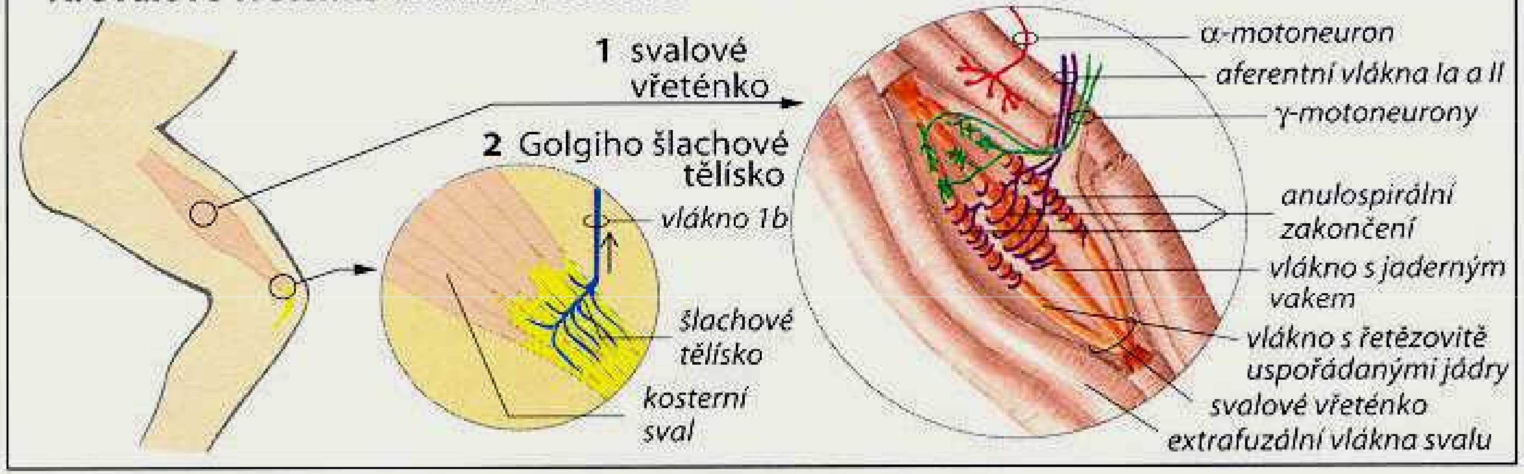
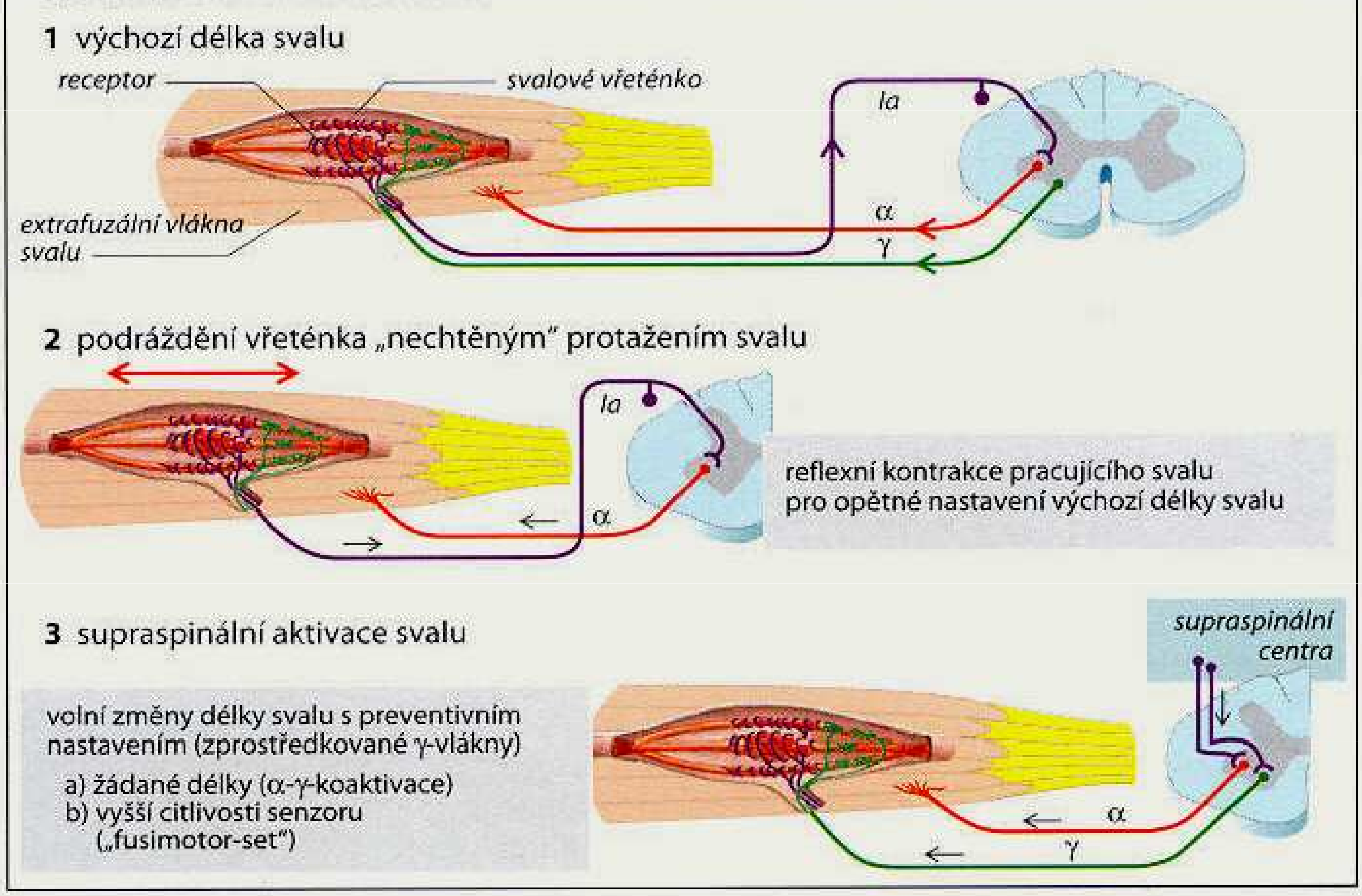
A. Svalové vřeténko a šlachové tělísko



B. Funkce svalového vřeténka



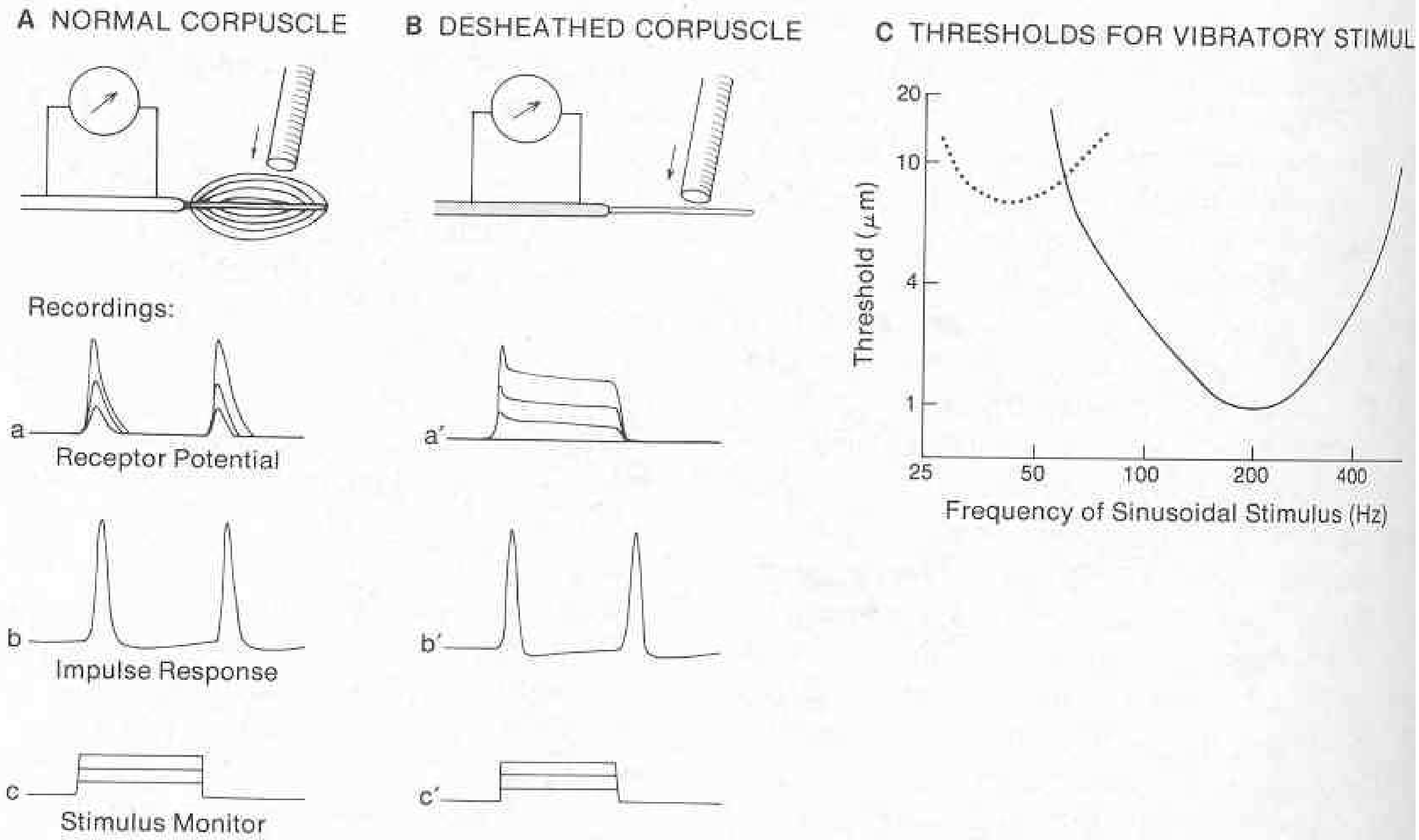
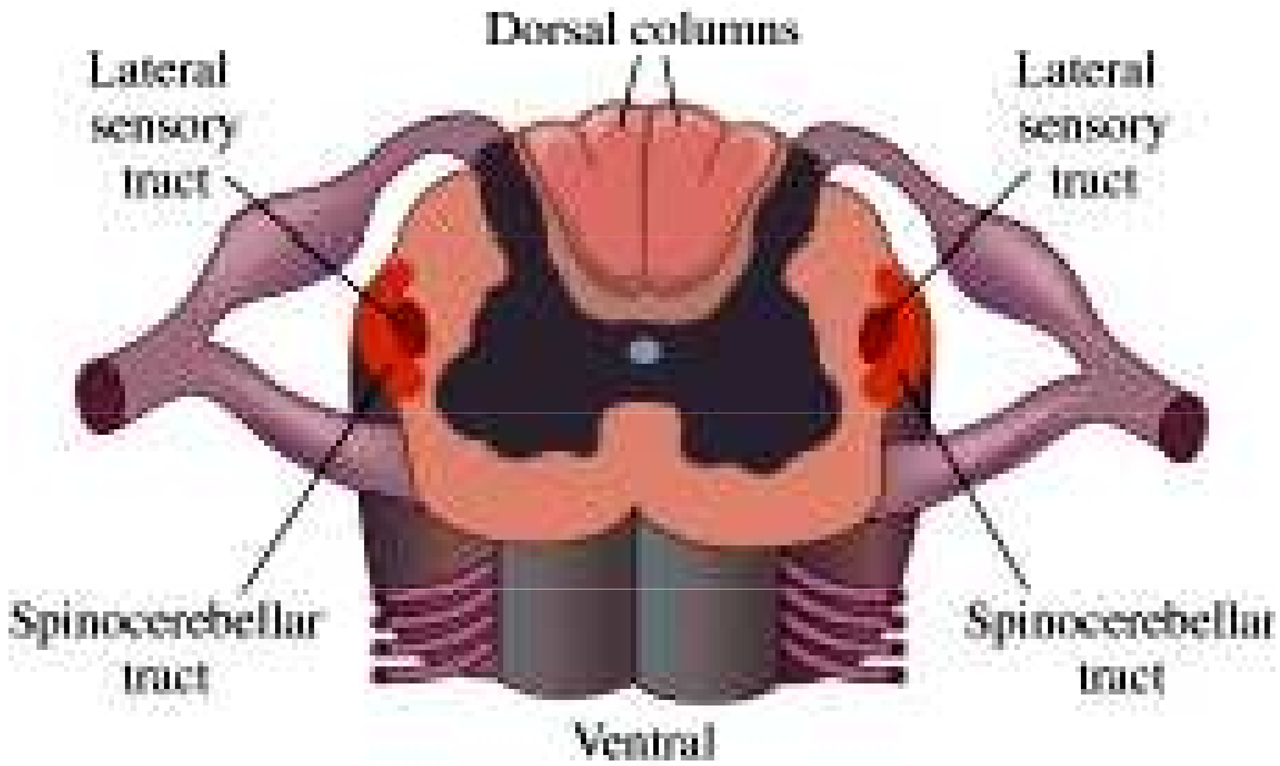


Fig. 12.5 Experimental analysis of transduction in the Pacinian corpuscle. **A.** Diagram showing probe for stimulating the intact corpuscle, and recording from the nerve. *(Below)* recordings of the receptor potential and impulse discharge. **B.** Repeat of experiment after removal of lamellae. C. Sensitivity of Pacinian corpuscle to vibratory stimulation at different frequencies. Sensitivity of Meissner's corpuscle is shown by dotted line. (A, B based on Loewenstein, 1971; C modified from Schmidt, 1978)

různé dráhy do somatosensorické kůry



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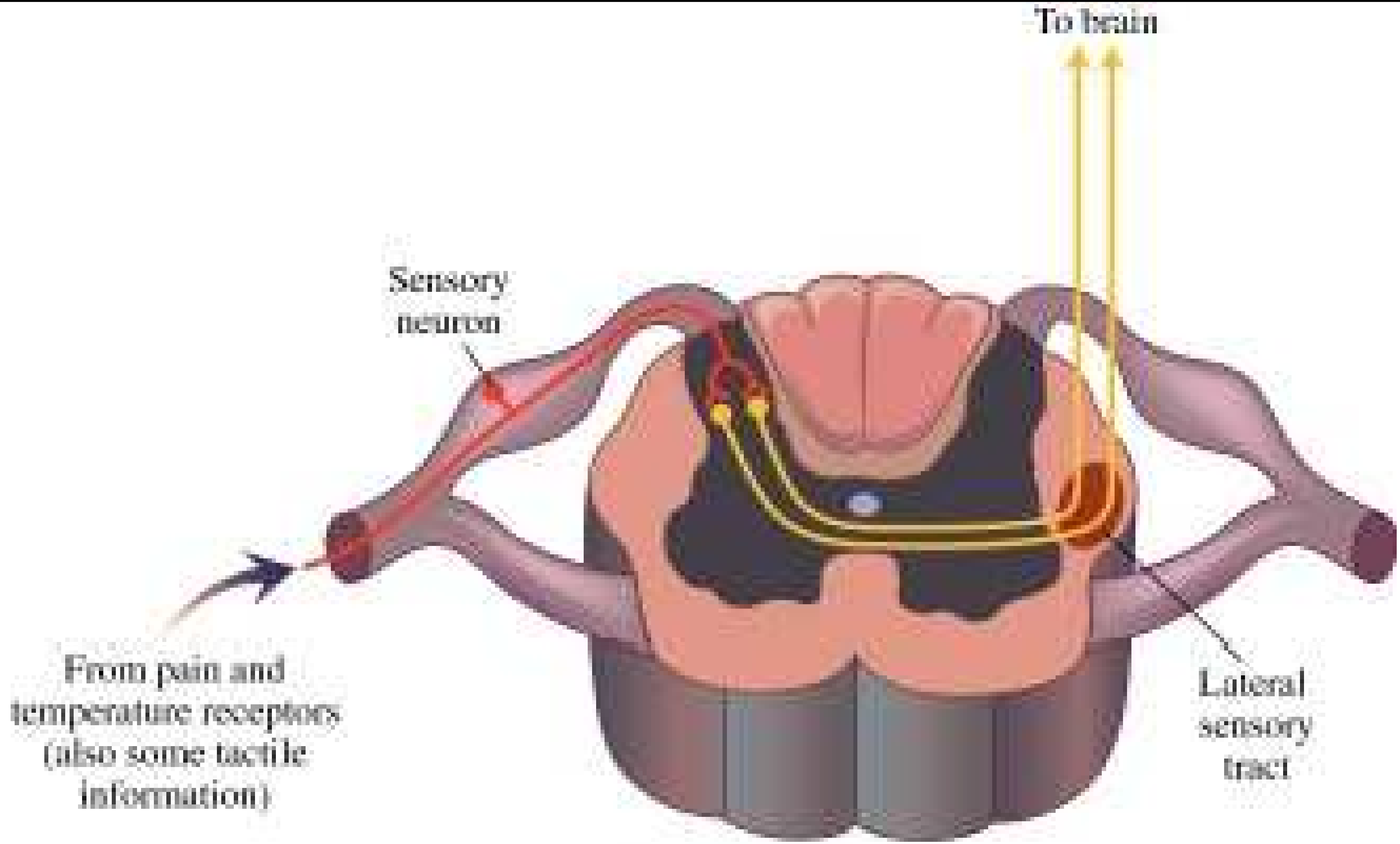

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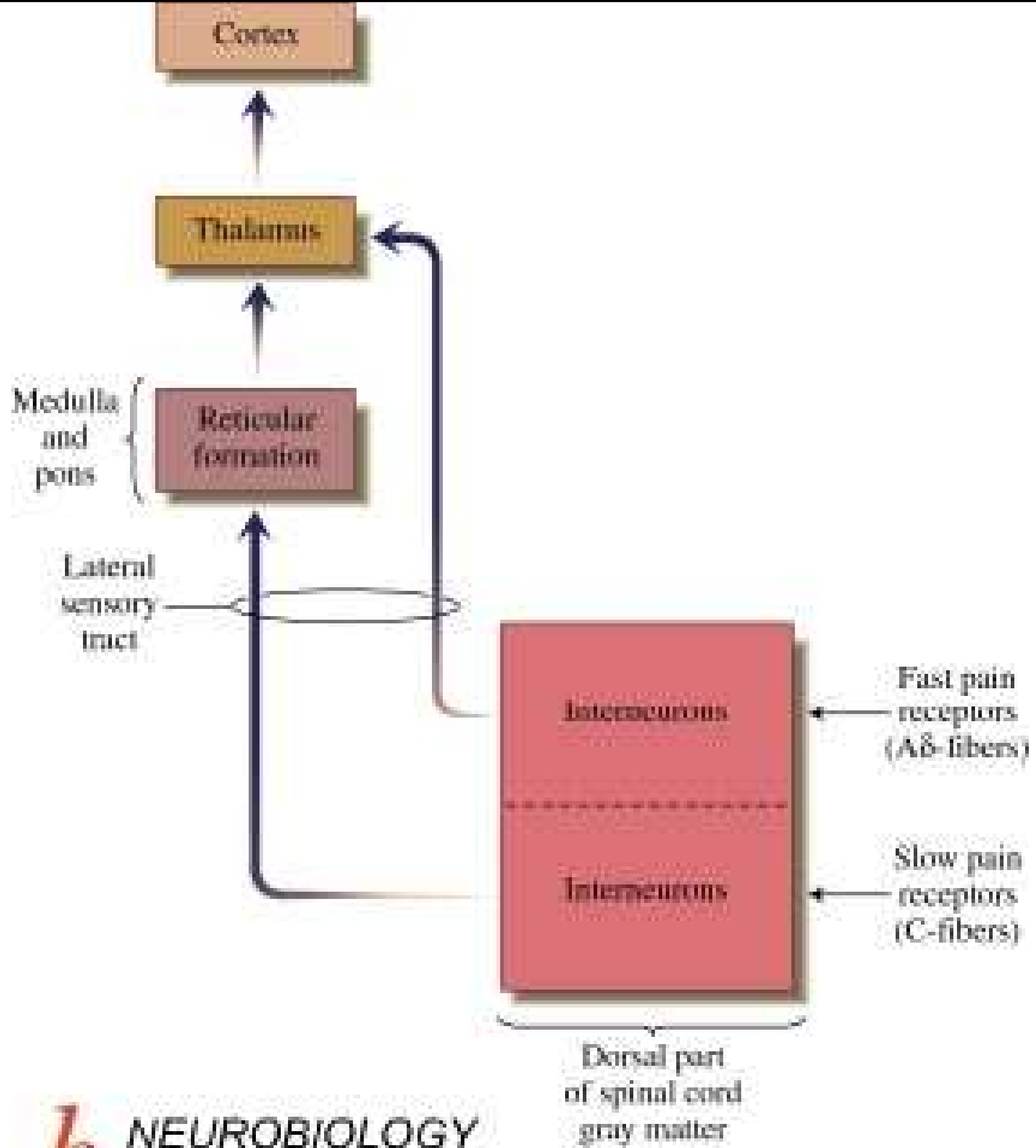

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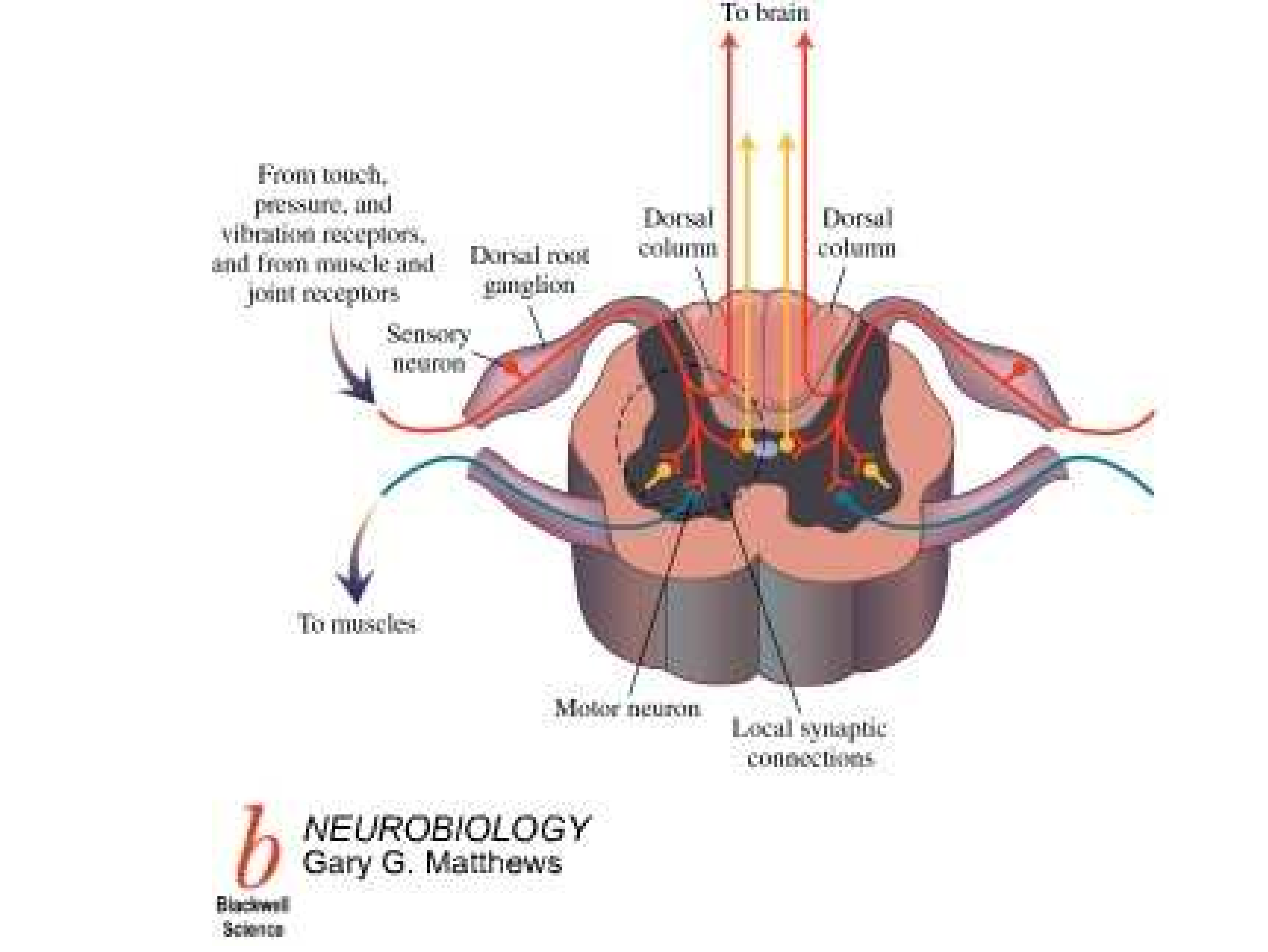
To brain
From touch, pressure, and vibration receptors, and from muscle and joint receptors
Dorsal root ganglion
Dorsal column
Dorsal column
Sensory neuron
To muscles
Motor neuron
Local synaptic connections
NEUROBIOLOGY
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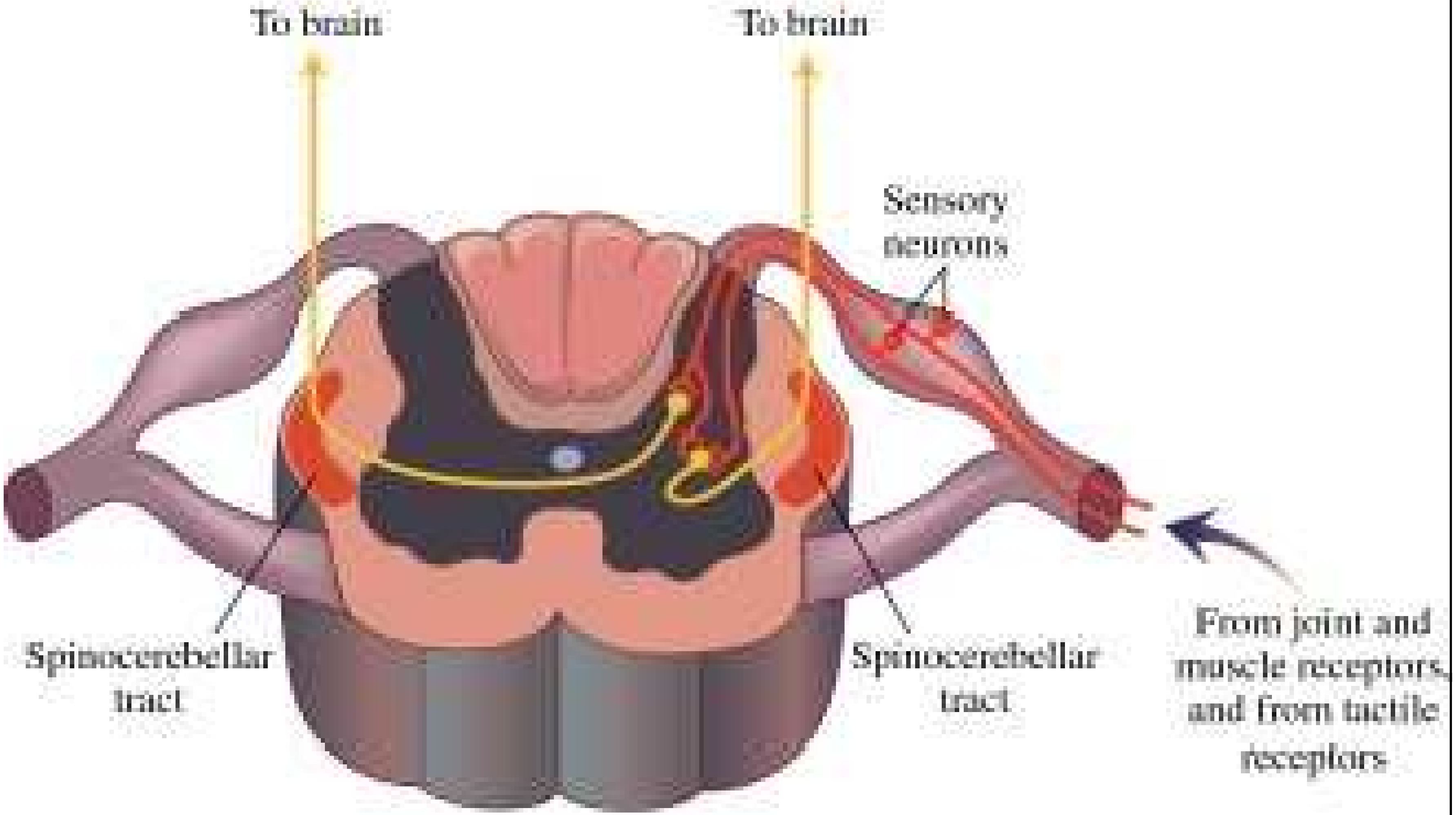

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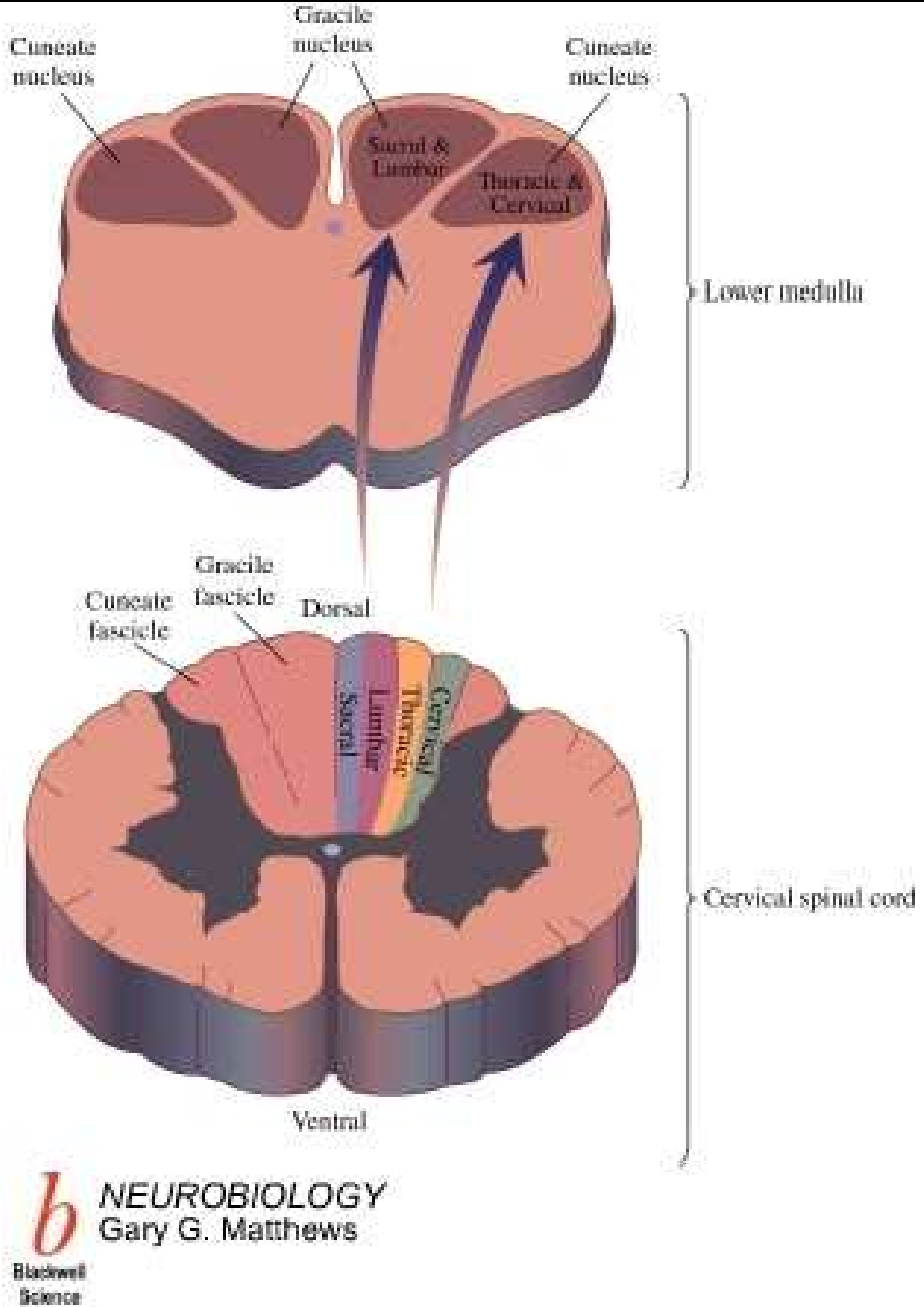
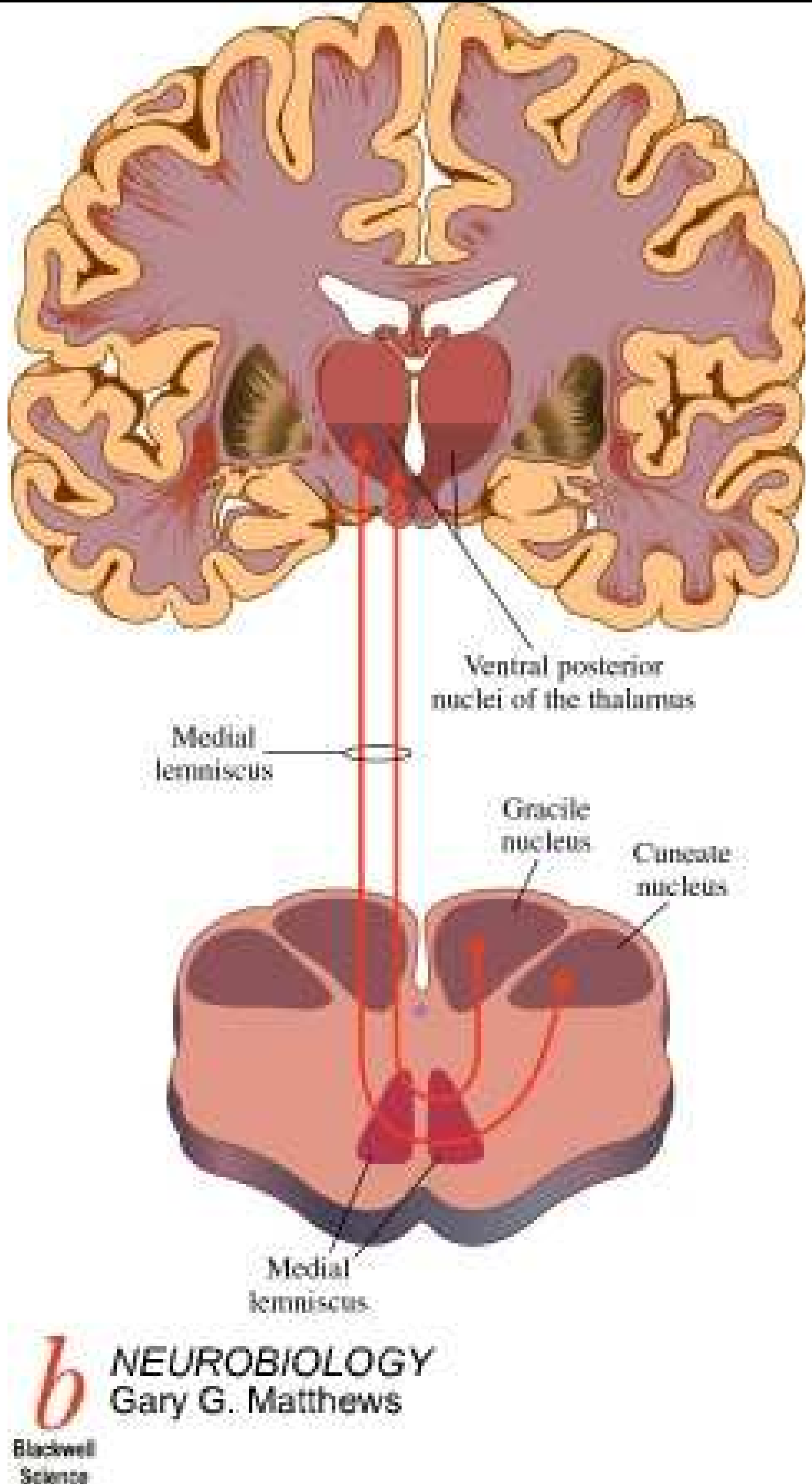
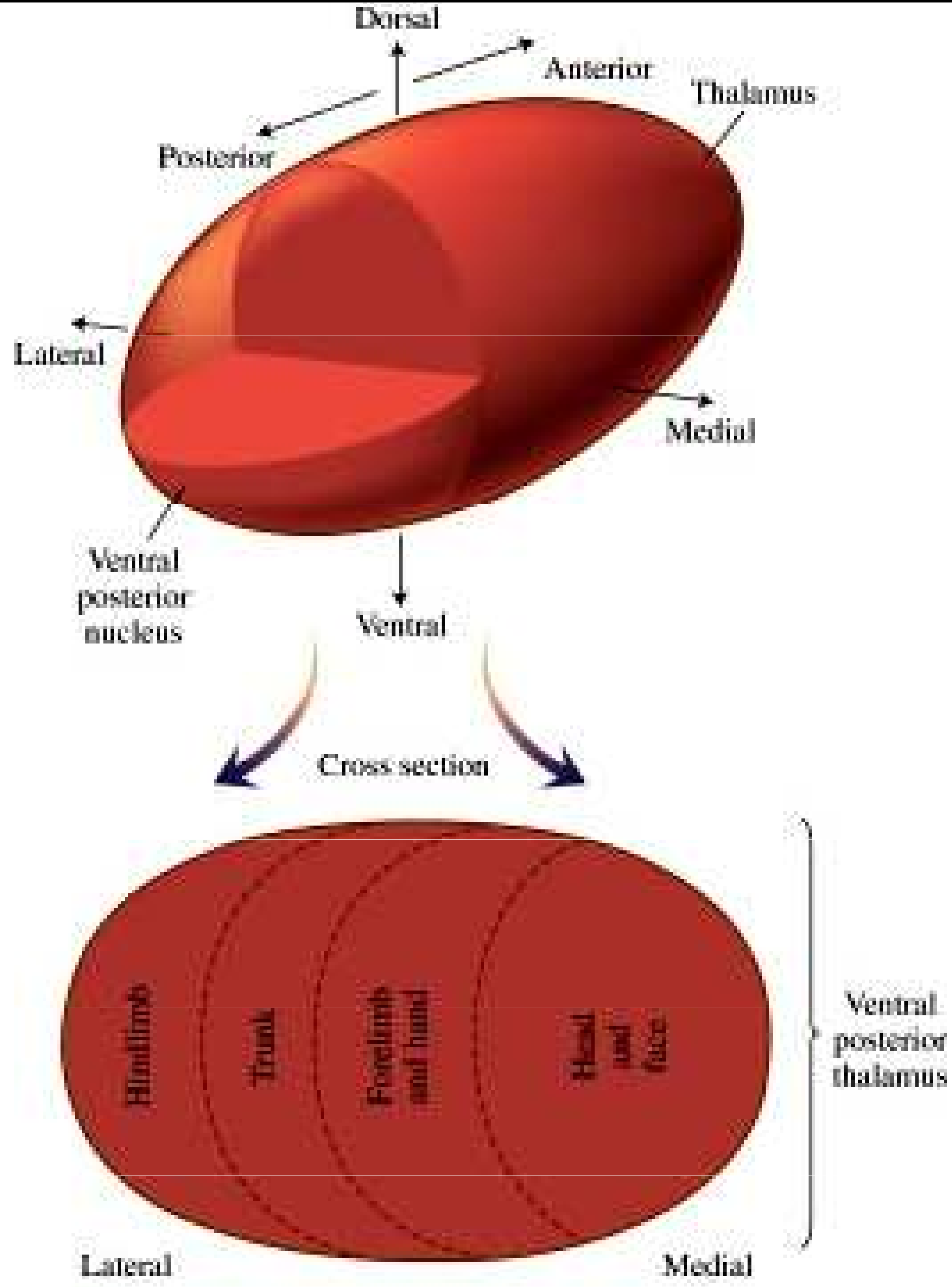
Somatotopie



Somatotopie



Somatotopie



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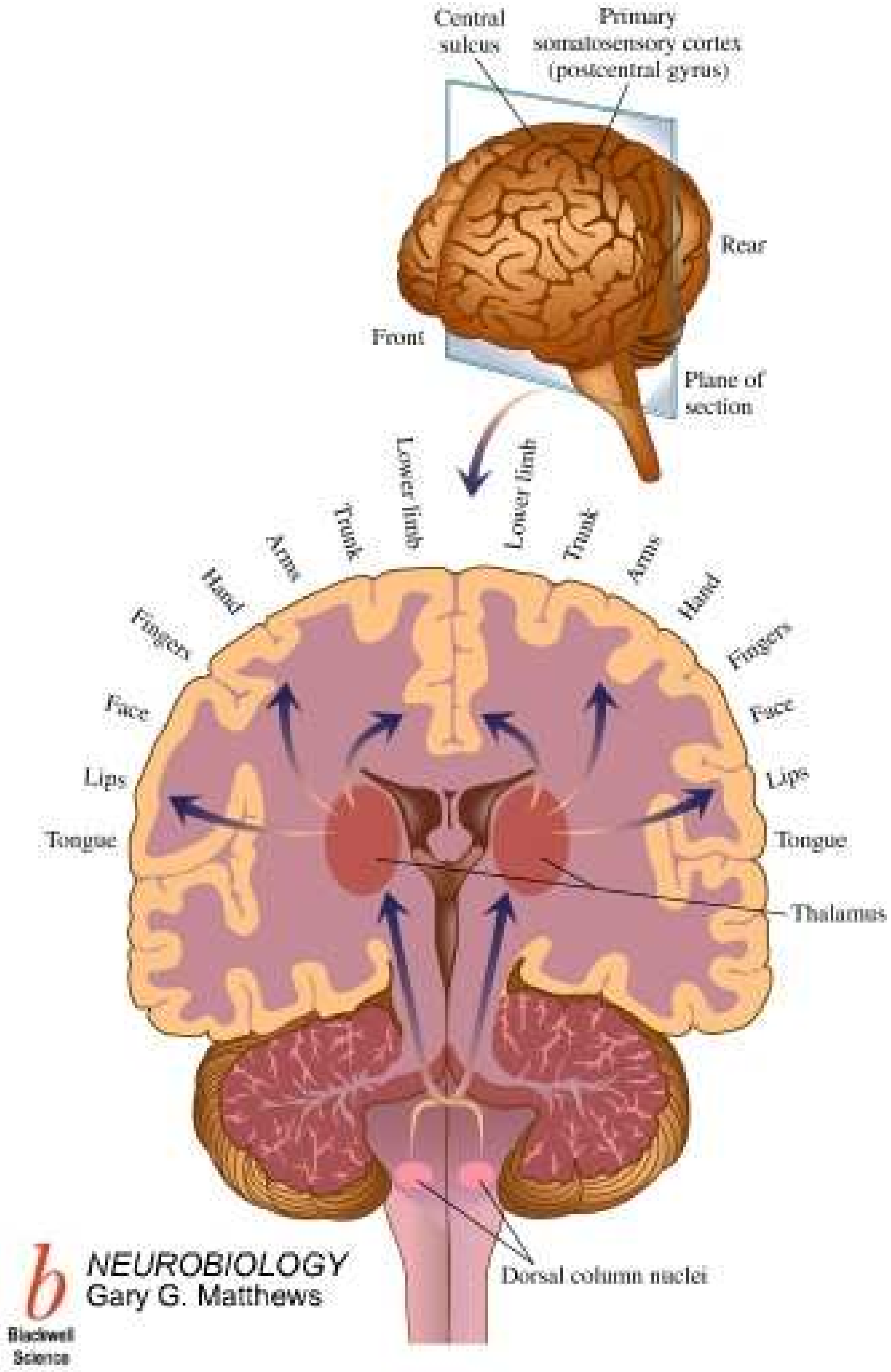
Somatotopie



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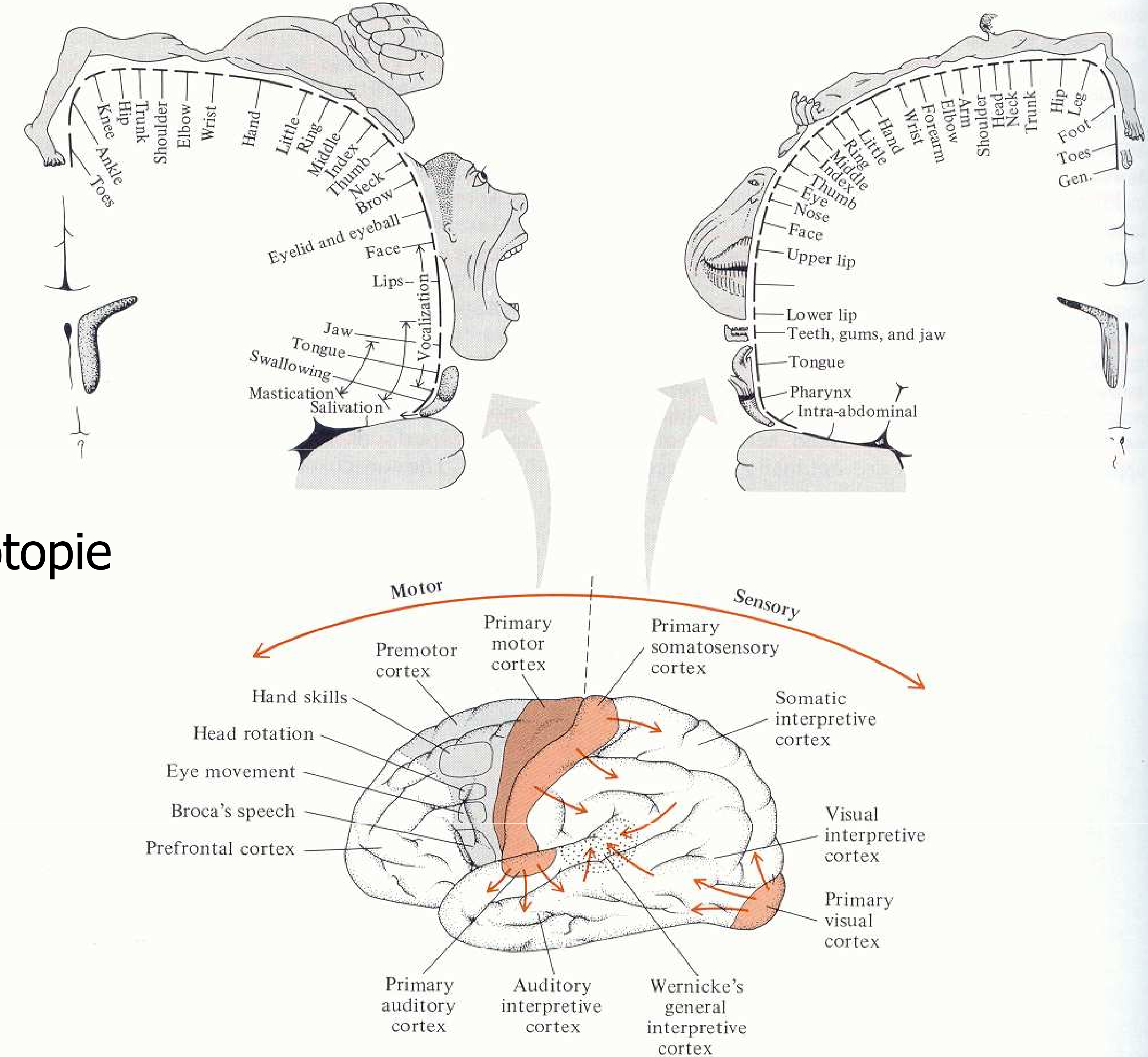
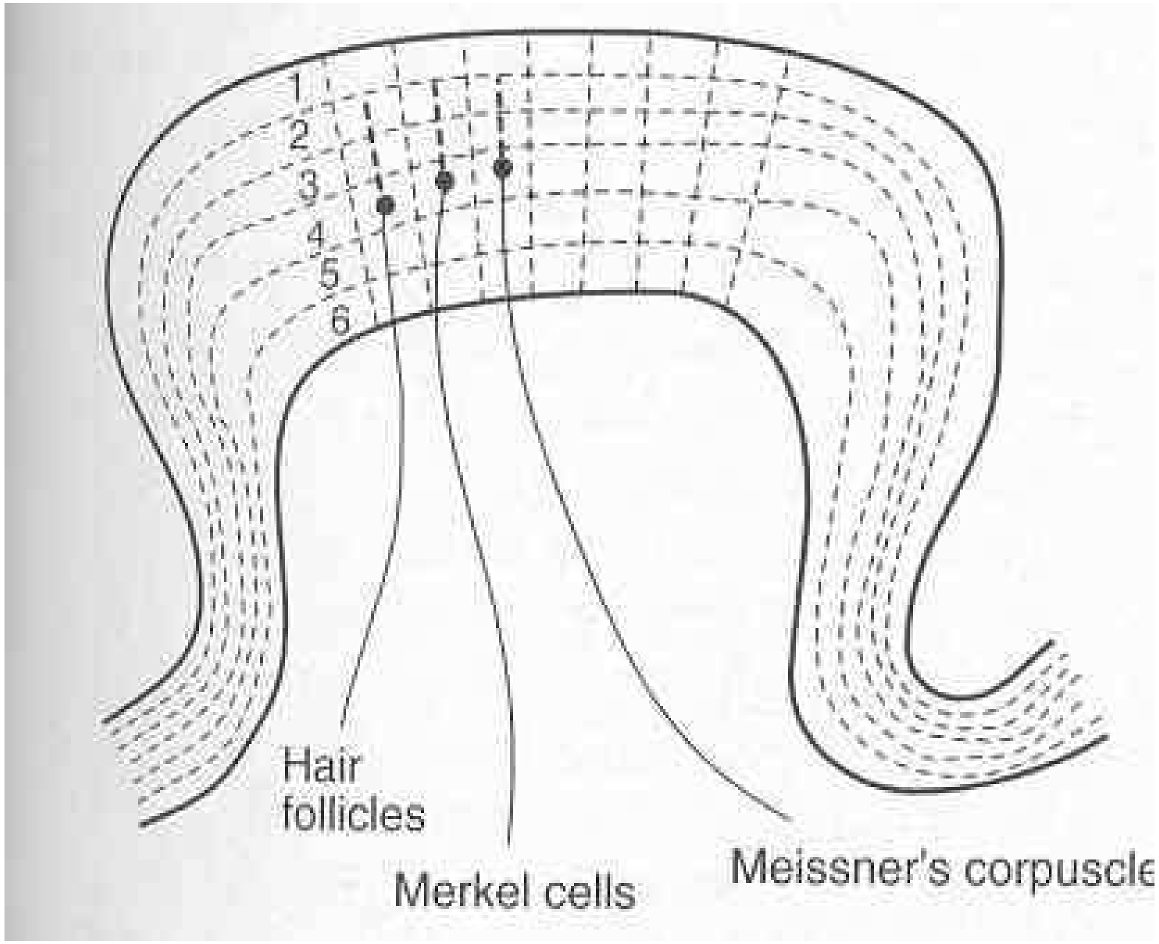


Somatotopie



Plasticita somatosenzorické kůry

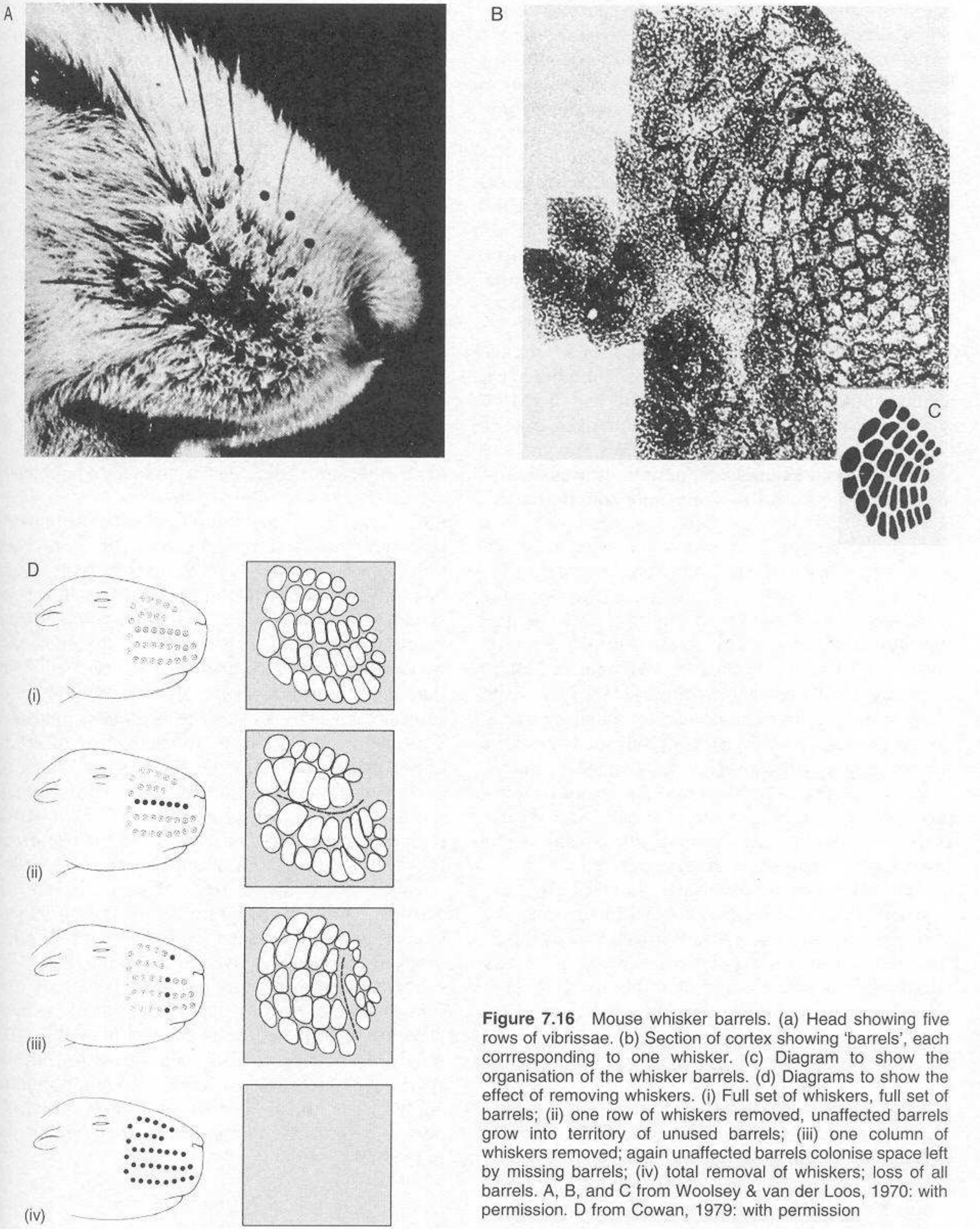


Figure 7.16 Mouse whisker barrels. (a) Head showing five rows of vibrissae. (b) Section of cortex showing 'barrels', each corrresponding to one whisker. (c) Diagram to show the organisation of the whisker barrels. (d) Diagrams to show the effect of removing whiskers. (i) Full set of whiskers, full set of barrels; (ii) one row of whiskers removed, unaffected barrels grow into territory of unused barrels; (iii) one column of whiskers removed; again unaffected barrels colonise space left by missing barrels; (iv) total removal of whiskers; loss of all barrels. A, B, and C from Woolsey & van der Loos, 1970: with permission. D from Cowan, 1979: with permission