

Chemorecepce

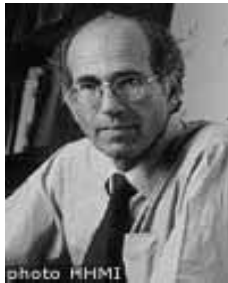


Čich

**The Nobel Prize in Physiology or
Medicine 2004**



**"for their discoveries of odorant receptors and the organization
of the olfactory system"**



Richard Axel

1/2 of the prize

USA

**Columbia University
New York, NY, USA; Howard
Hughes Medical Institute**

b. 1946



Linda B. Buck

1/2 of the prize

USA

**Fred Hutchinson Cancer
Research Center
Seattle, WA, USA; Howard
Hughes Medical Institute**

b. 1947

Distanční chemorecepce

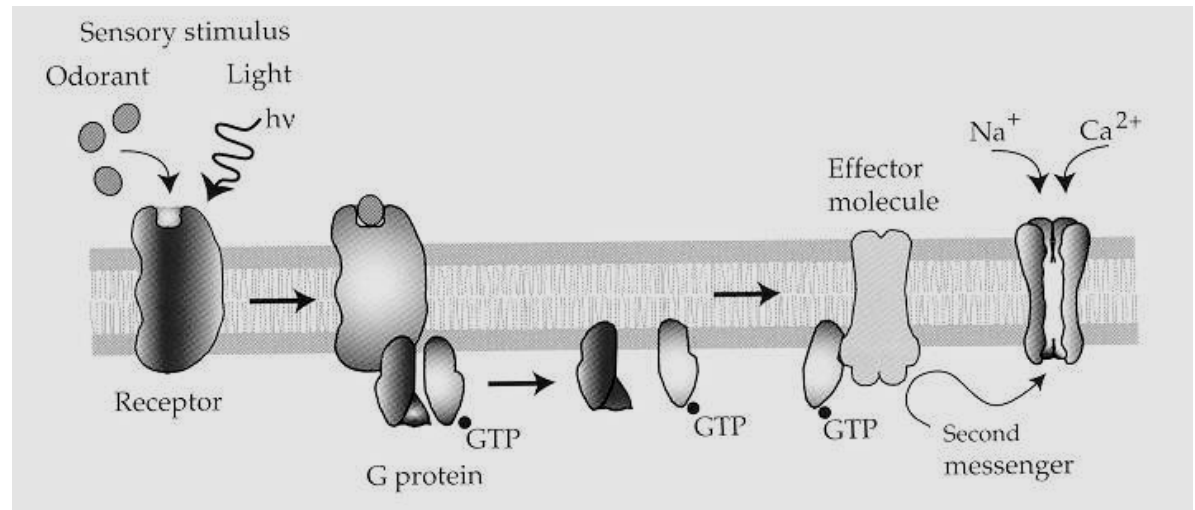
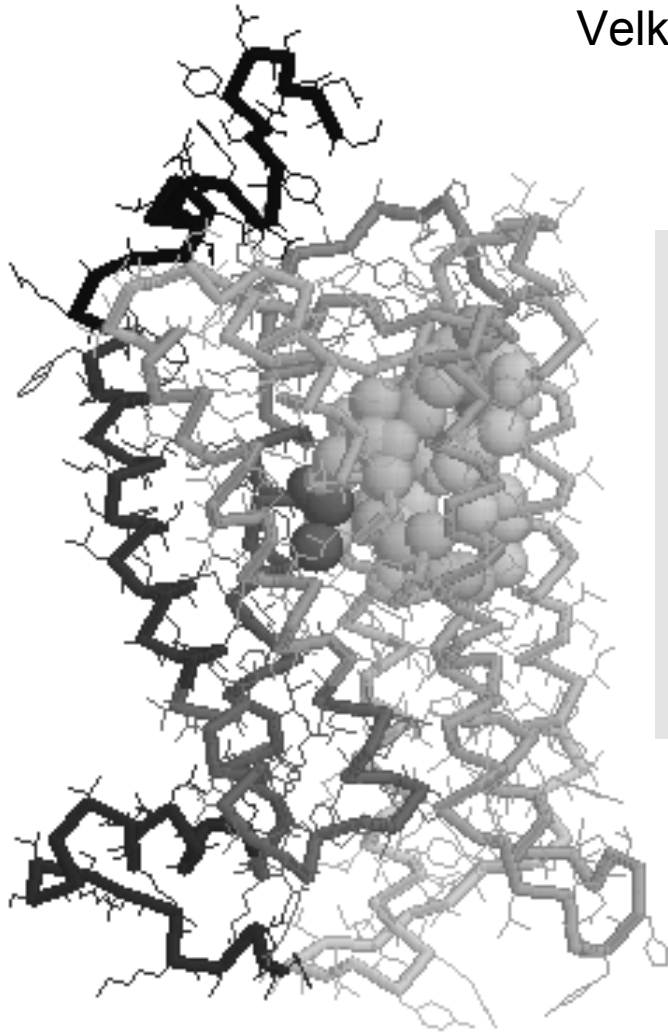
Modelový objekt pro mnoho dalších signálových drah

7TM receptory

Metabotropní signalizace prostřednictvím G proteinů

Otevřený systém podobný imunitnímu

Velká část (4%) genomu věnovaná čichovým receptorům

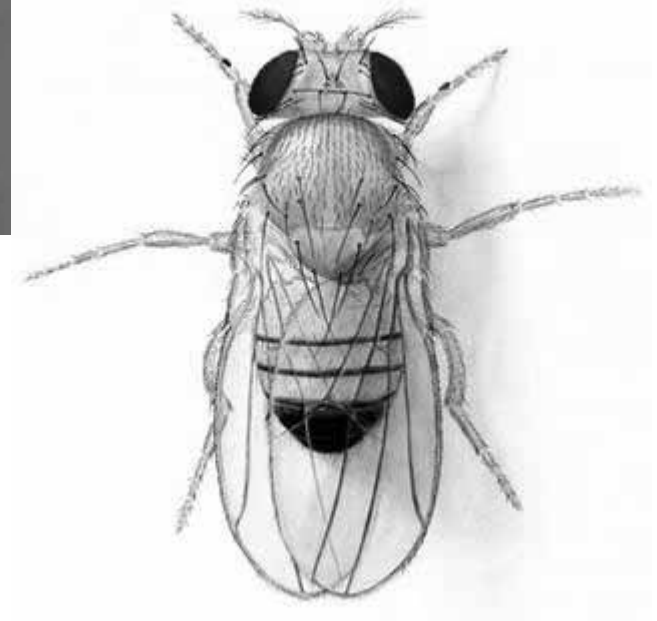


Savci: 1000 genů pro čichové receptory – největší genová rodina

Člověk: 350 funkčních genů

Háďátko: 1500

Drosophila: 62



E.coli

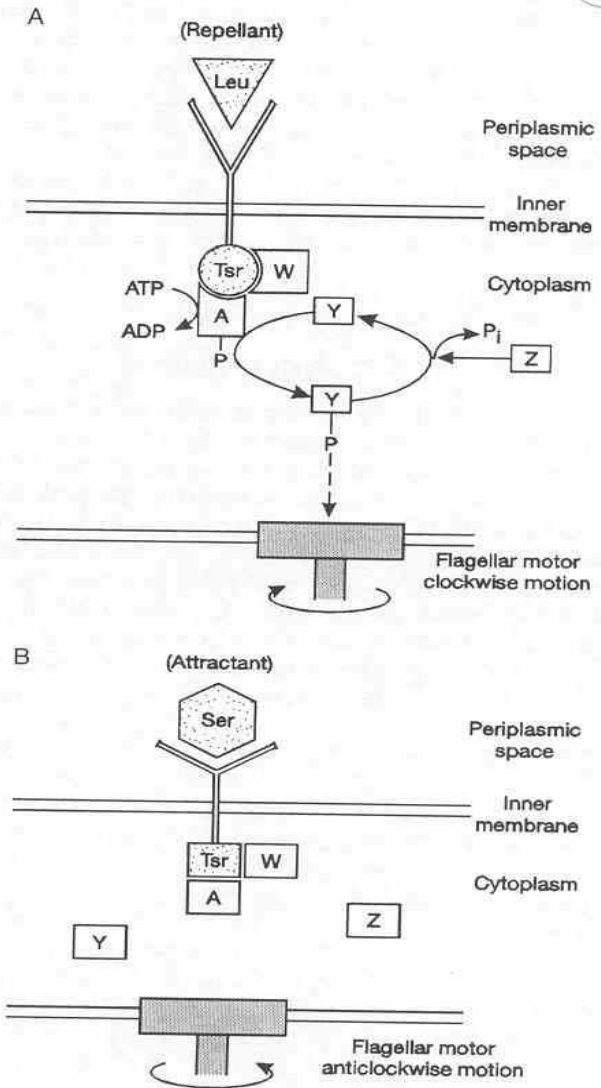
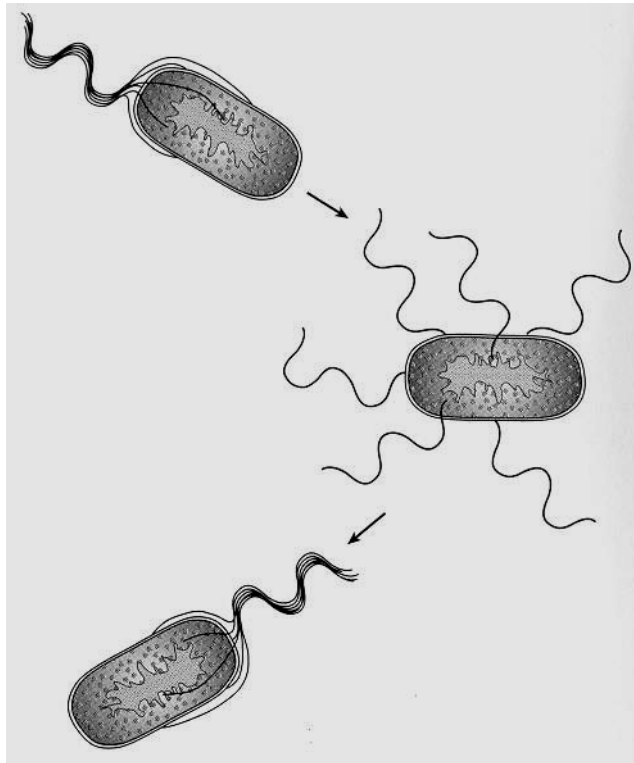
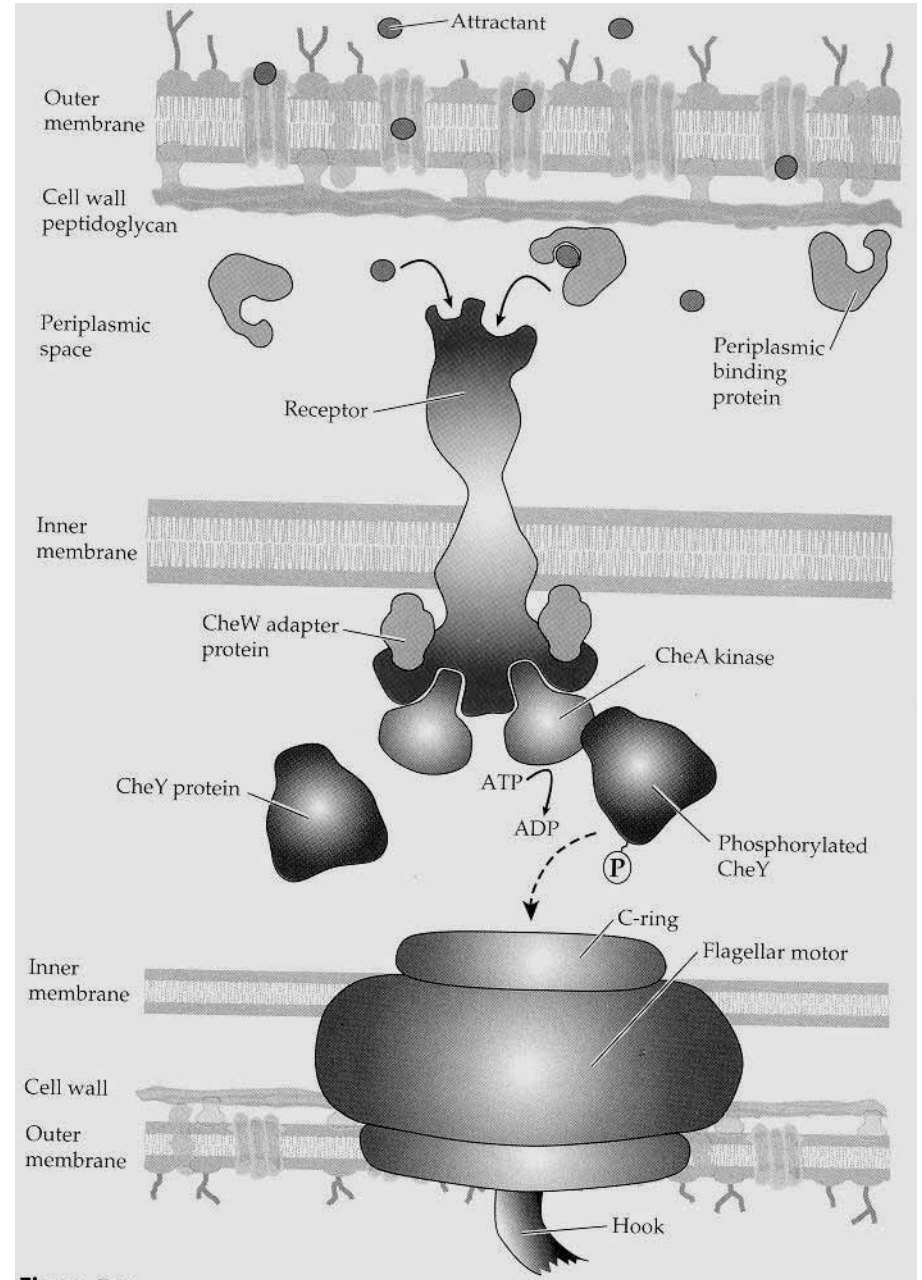
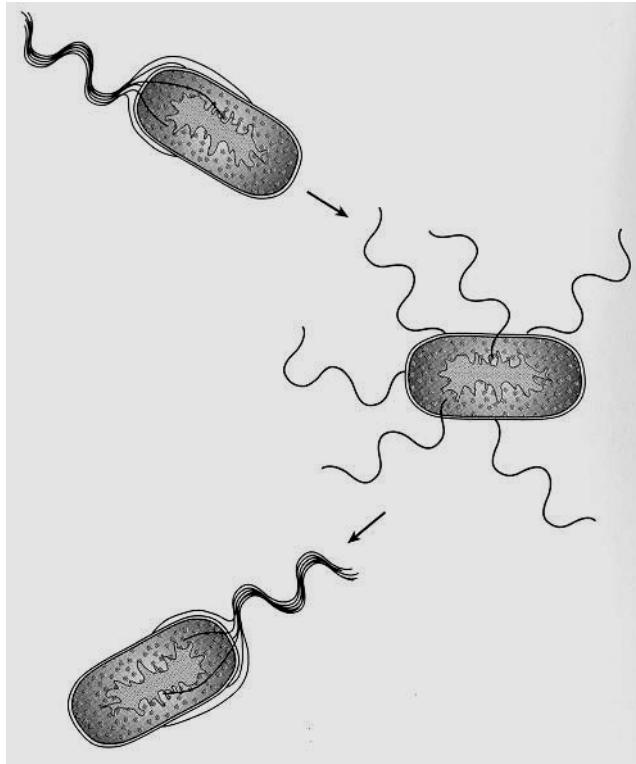
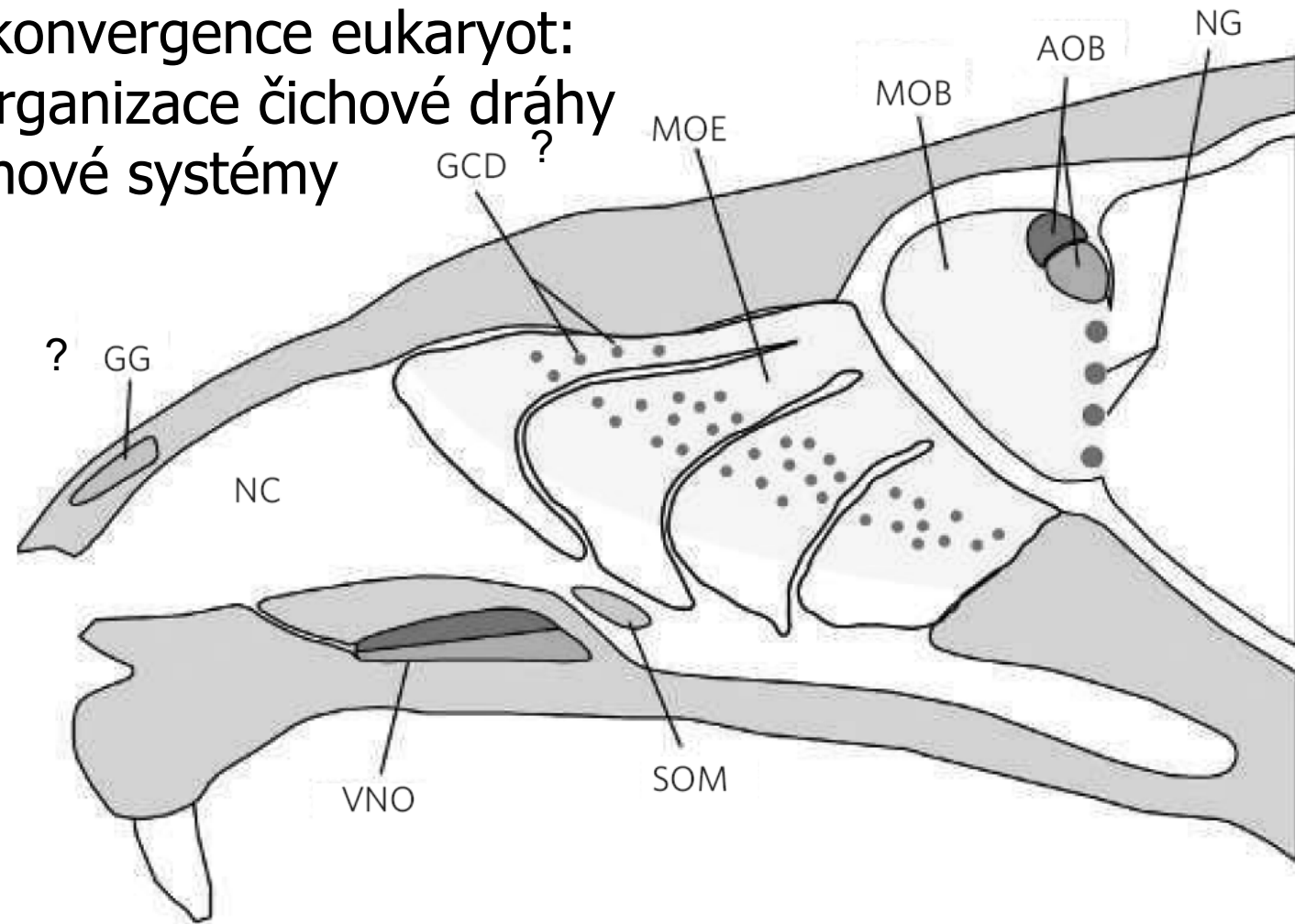


Figure 10.6 Molecular signalling in the *E. coli* chemosensory system. (a) The Tsr receptor-transducer protein accepts a repellent molecule (Leu). CheW and CheA are activated. CheA accepts phosphate from ATP and passes it on CheY. CheY diffuses to the flagellar motor and induces a clockwise rotation and hence tumbling. CheY is eventually dephosphorylated by CheZ. (b) The Tsr receptor-transducer accepts an attractant molecule (Ser). The consequent conformational change inactivates CheA and CheW so that CheY remains unphosphorylated and consequently inactive. The flagellum resumes its anticlockwise motion and the bacterium swims smoothly forward. A = CheA; W = CheW; Y = CheY; Z = CheZ. Data from Bourrett, Borkovich and Simon, 1991

E.coli



Pozoruhodná konvergence eukaryot:
Transdukce, organizace čichové dráhy
2 paralelní čichové systémy



accessory olfactory bulb (AOB).

vomeronasal organ (VNO)

main olfactory epithelium (MOE) consists predominantly of ciliated olfactory sensory neurons (OSNs), which project to the main olfactory bulb (MOB)

Dva chemosensitivní systémy savců

Hlavní čichový epitel (MOE):

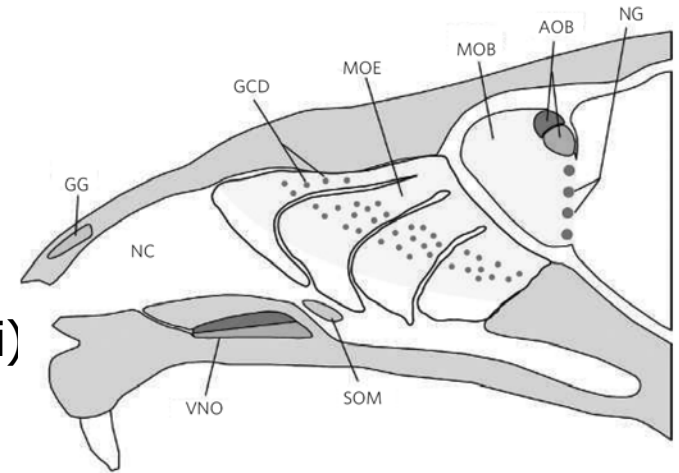
ciliární čichové buňky

Projekce do čichového laloku

Každá buňka exprimuje jediný typ receptoru (1300 u myši)

Proud vzduchu při nadechování (a vydechování)

Identifikace potravy, predátora, značení teritoria ...



Vomeronasální orgán (VNO):

Slepá dutinka

Mikrovilární morfologie

Projekce do přídatného čichového laloku (AOB)

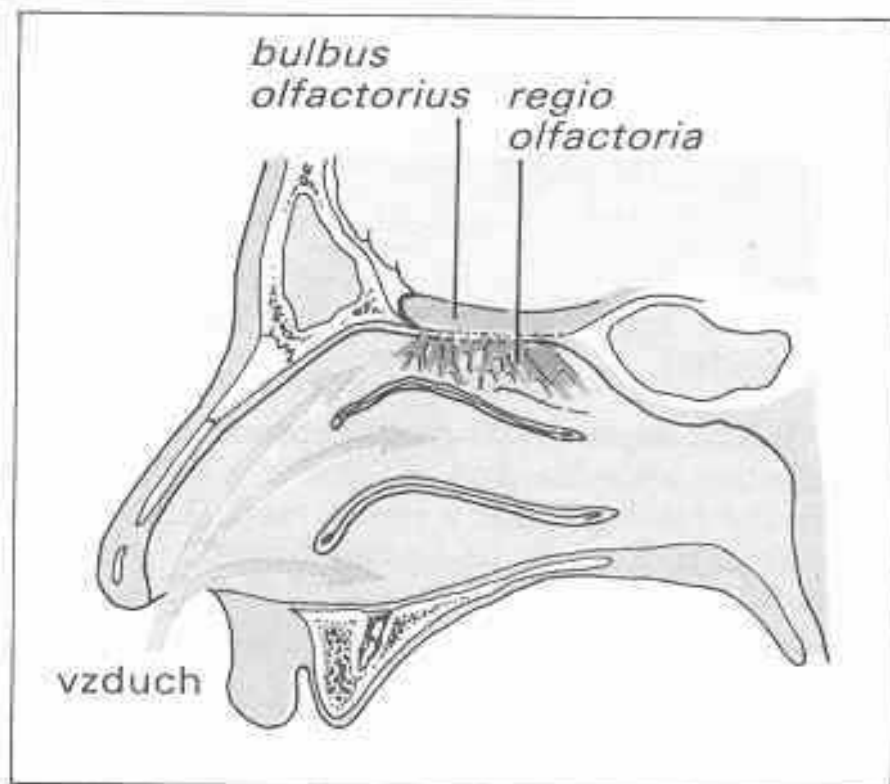
2 třídy receptorů (G protein, ale málo příbuzné čichovým, asi 200 celkem)

Vzduch přichází „pumpováním“ při vzrušení (spíše přímým kontaktem)

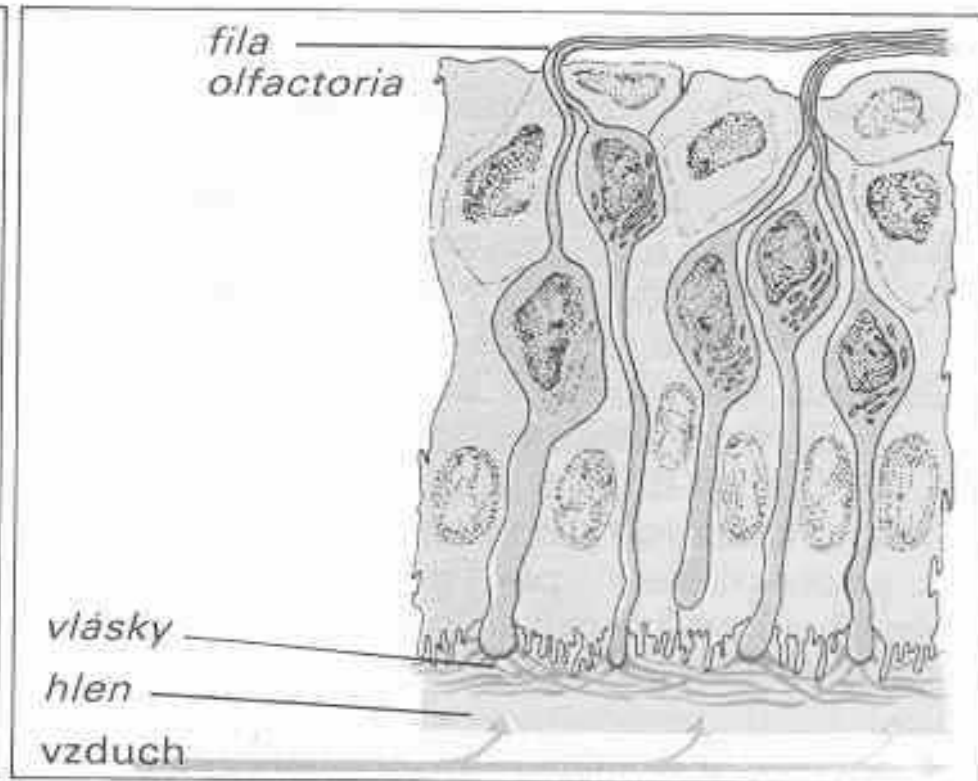
Detekce feromonů, vnitrodruhová signalizace mezi pohlavími, rozmnožování, péči o ml.

V poslední době se ale ukazuje podobnost funkce



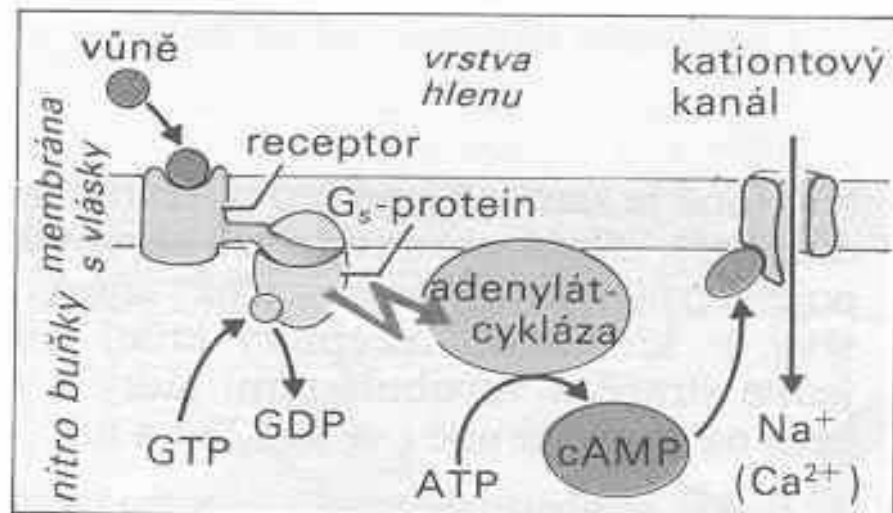


A. Nosní dutina a čichový orgán

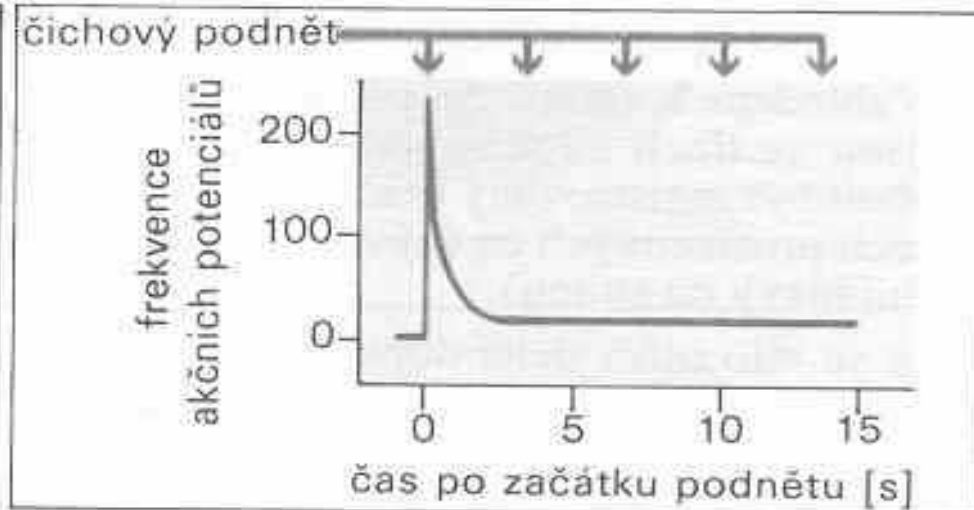


B. Čichový epitel

(podle Andrese)

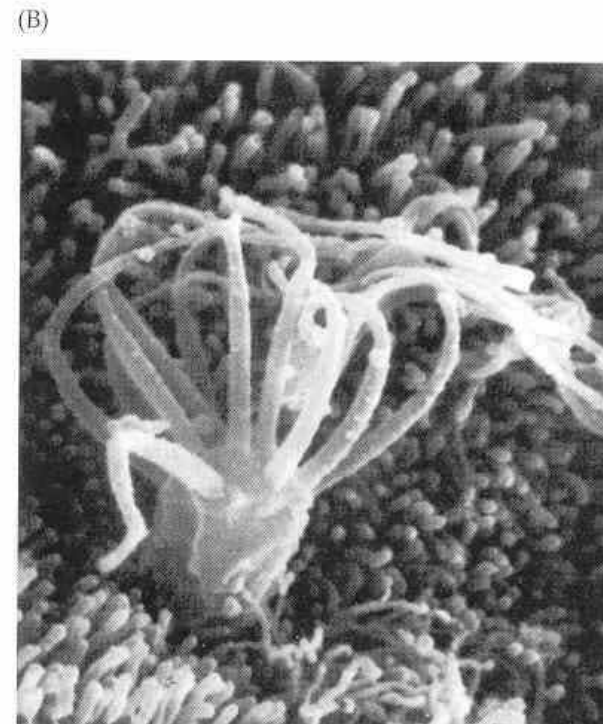
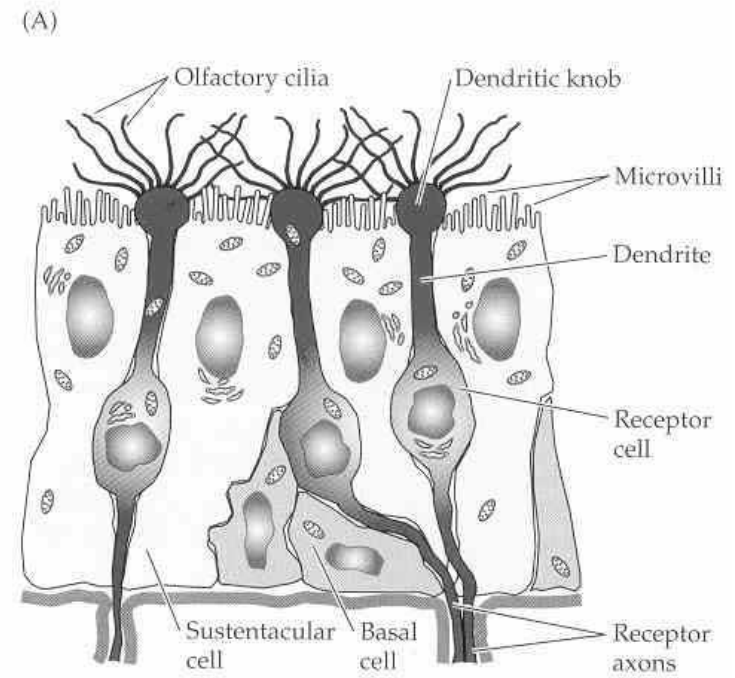


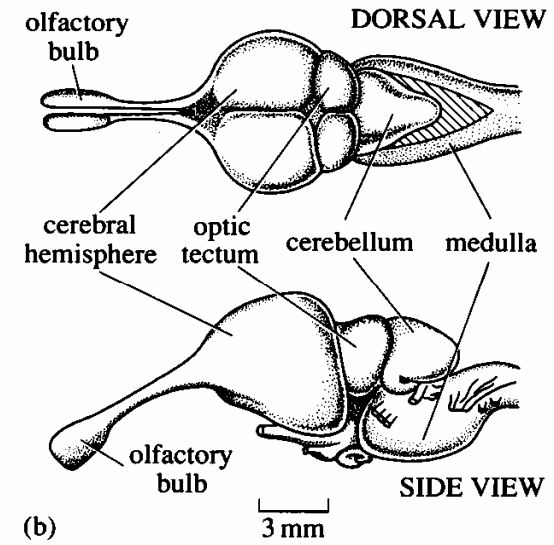
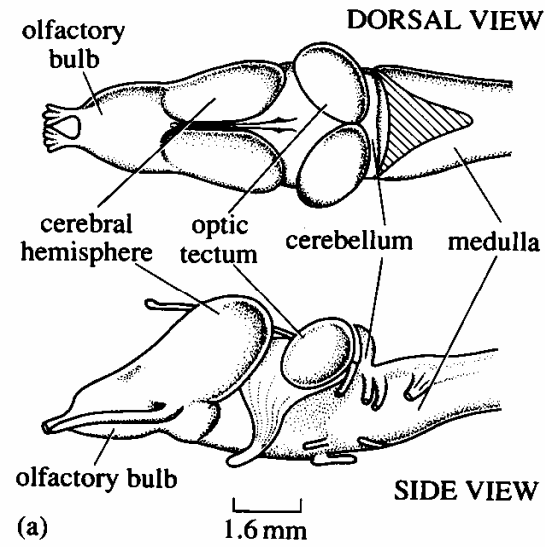
C. Transdukce čichového podnětu



D. Adaptace čichu

Figure 7.7
Olfactory epithelium (A) Schematic cross section of olfactory epithelium. (B) Scanning micrograph of a dendritic knob and dendrites of a human olfactory receptor neuron. Magnification: 18,500 \times . (From Morrison and Costanzo, 1990.)





Čichový lalok – součást
koncového mozku

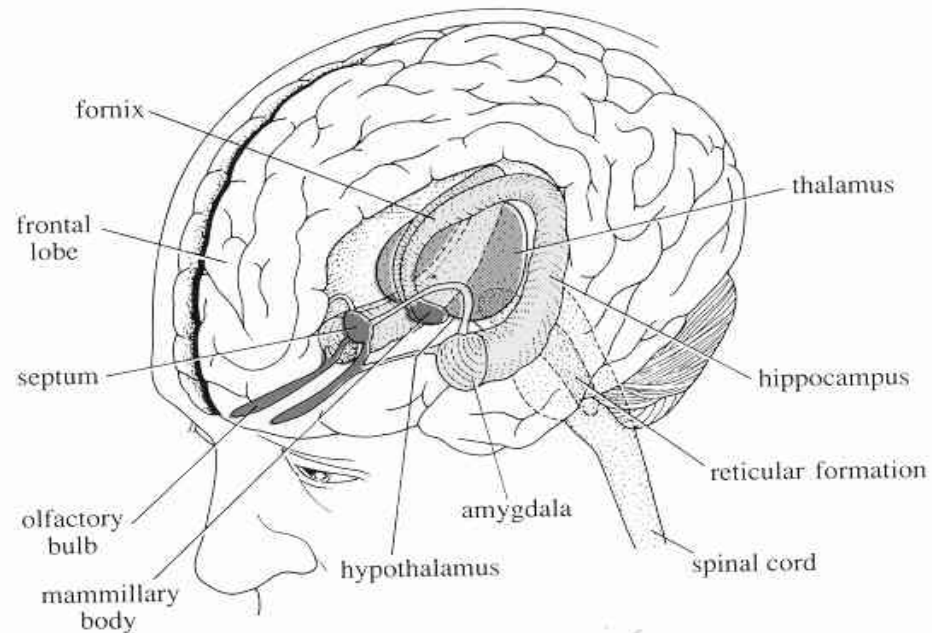
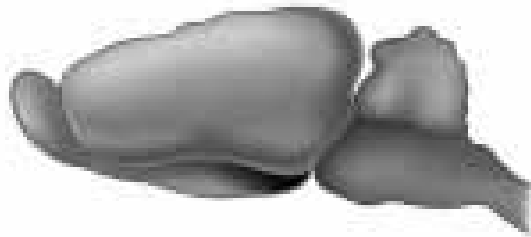


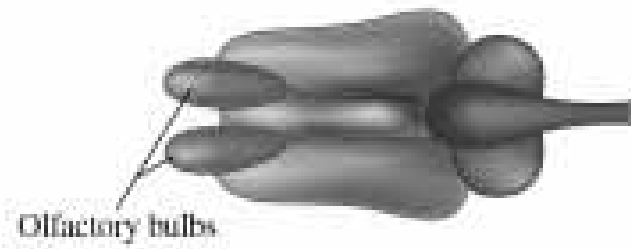
Figure 10.1 The limbic system (the main limbic system structures are shown in

Rat

Side view



Bottom view

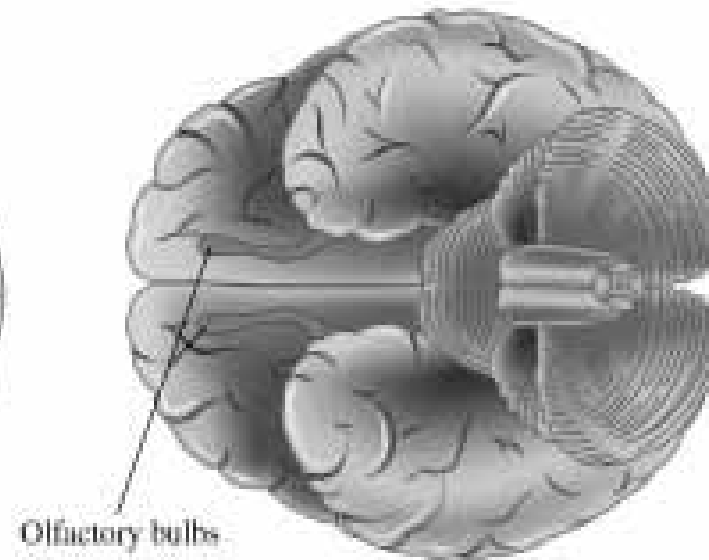


Human

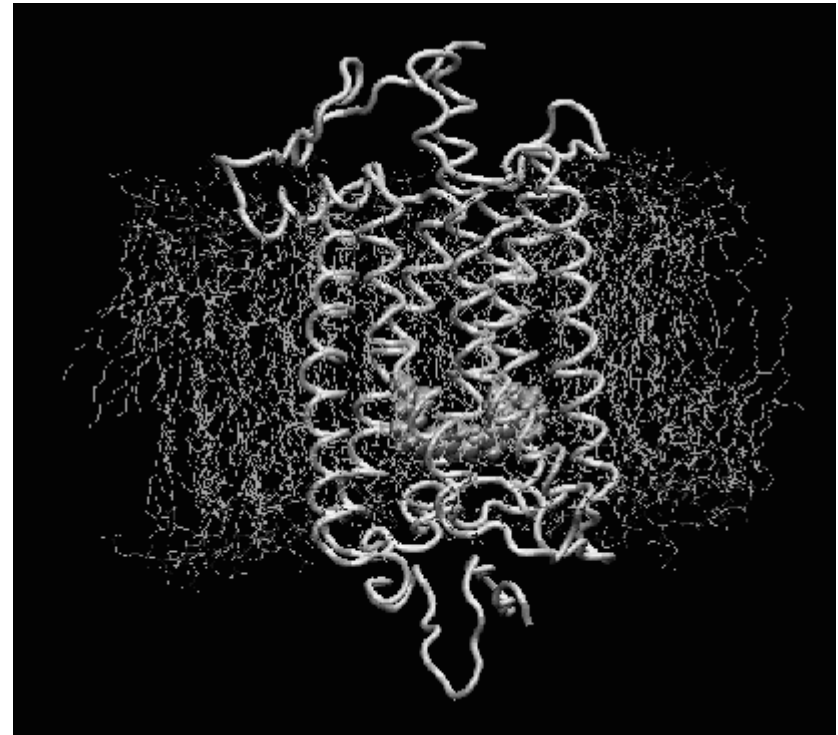
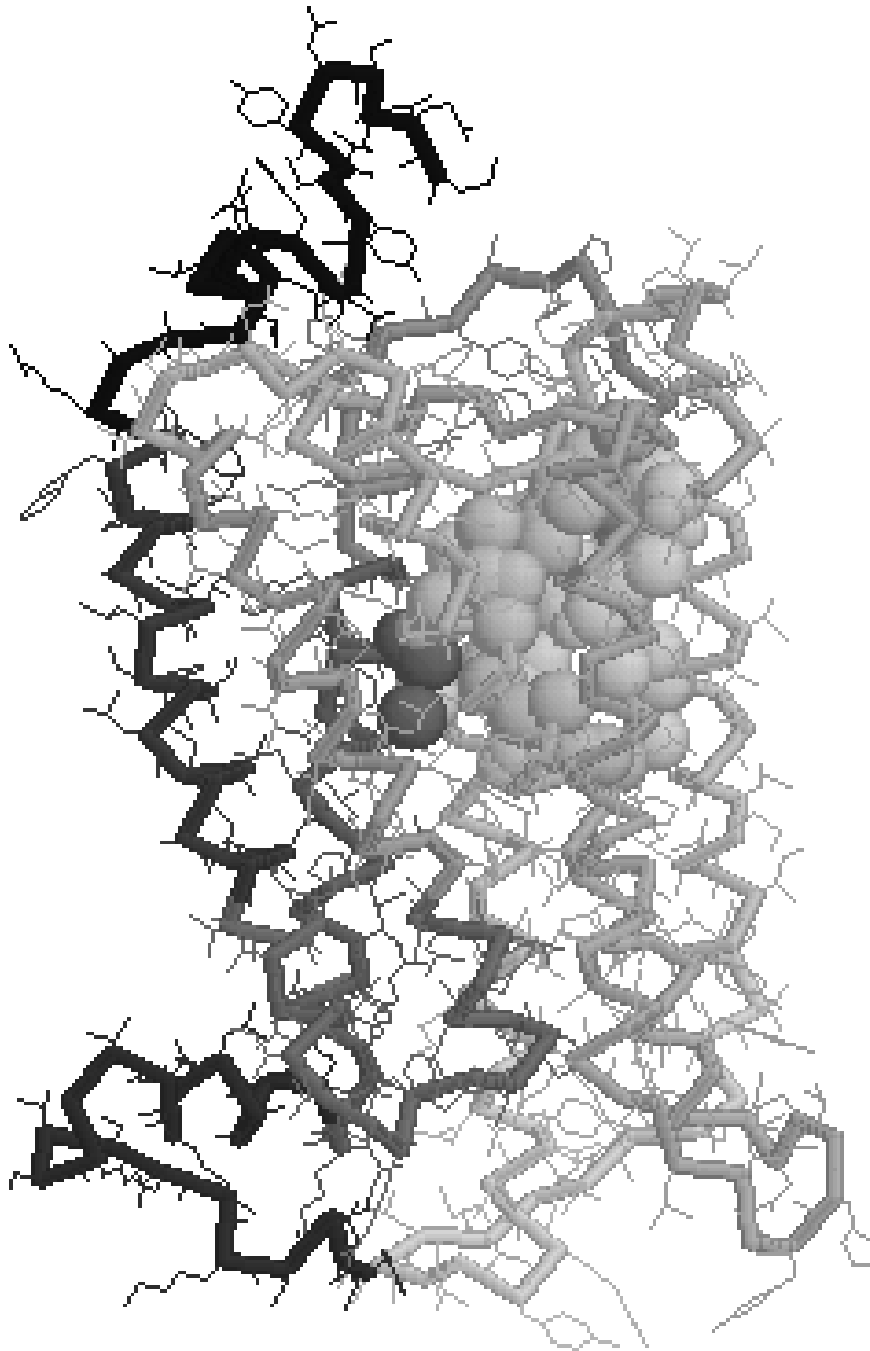
Side view

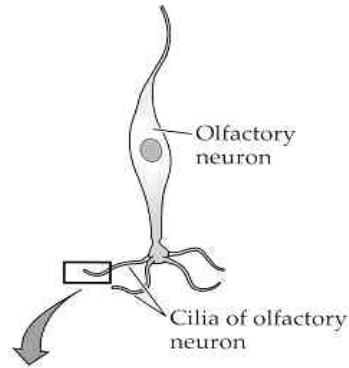


Bottom view

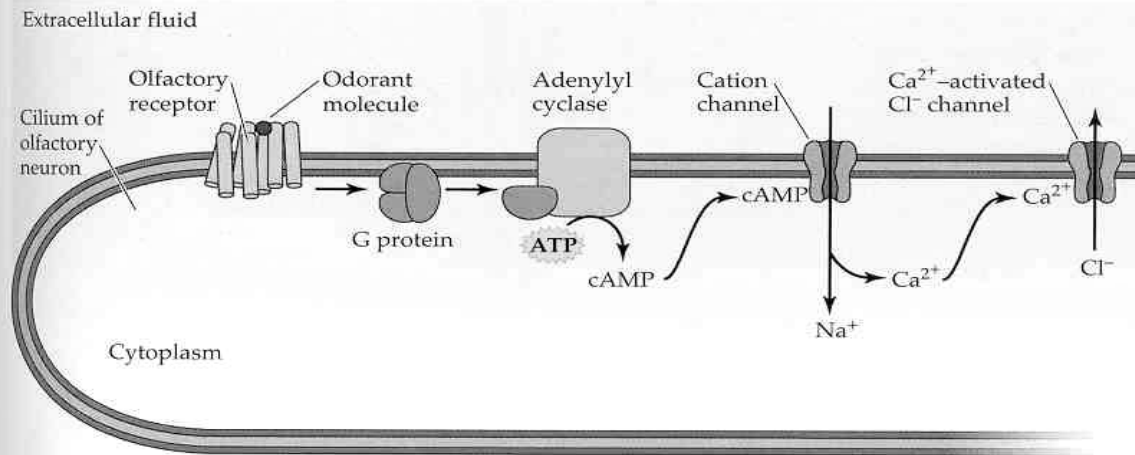


Univerzální receptor G prot signální dráhy
7TM a-helix receptor





(a) Increase in cAMP



(b) Increase in IP₃

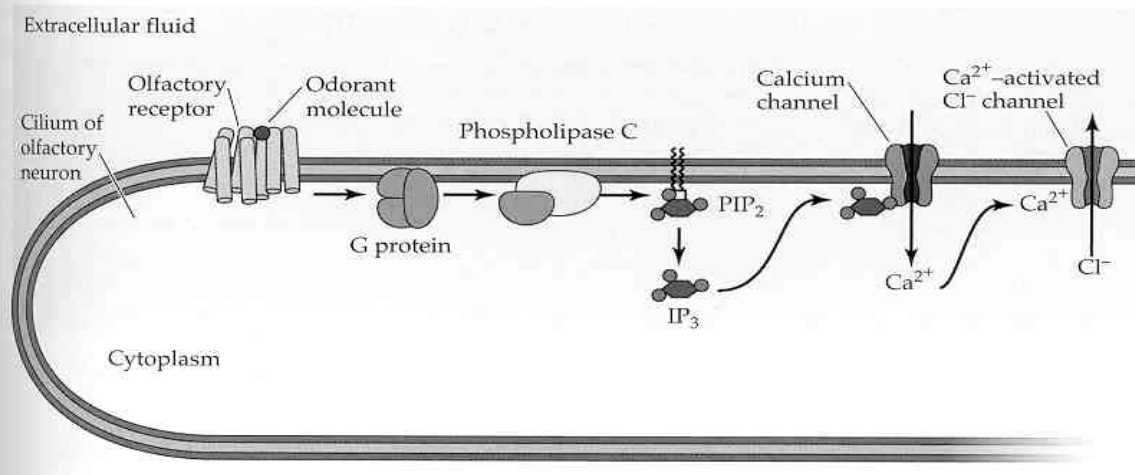
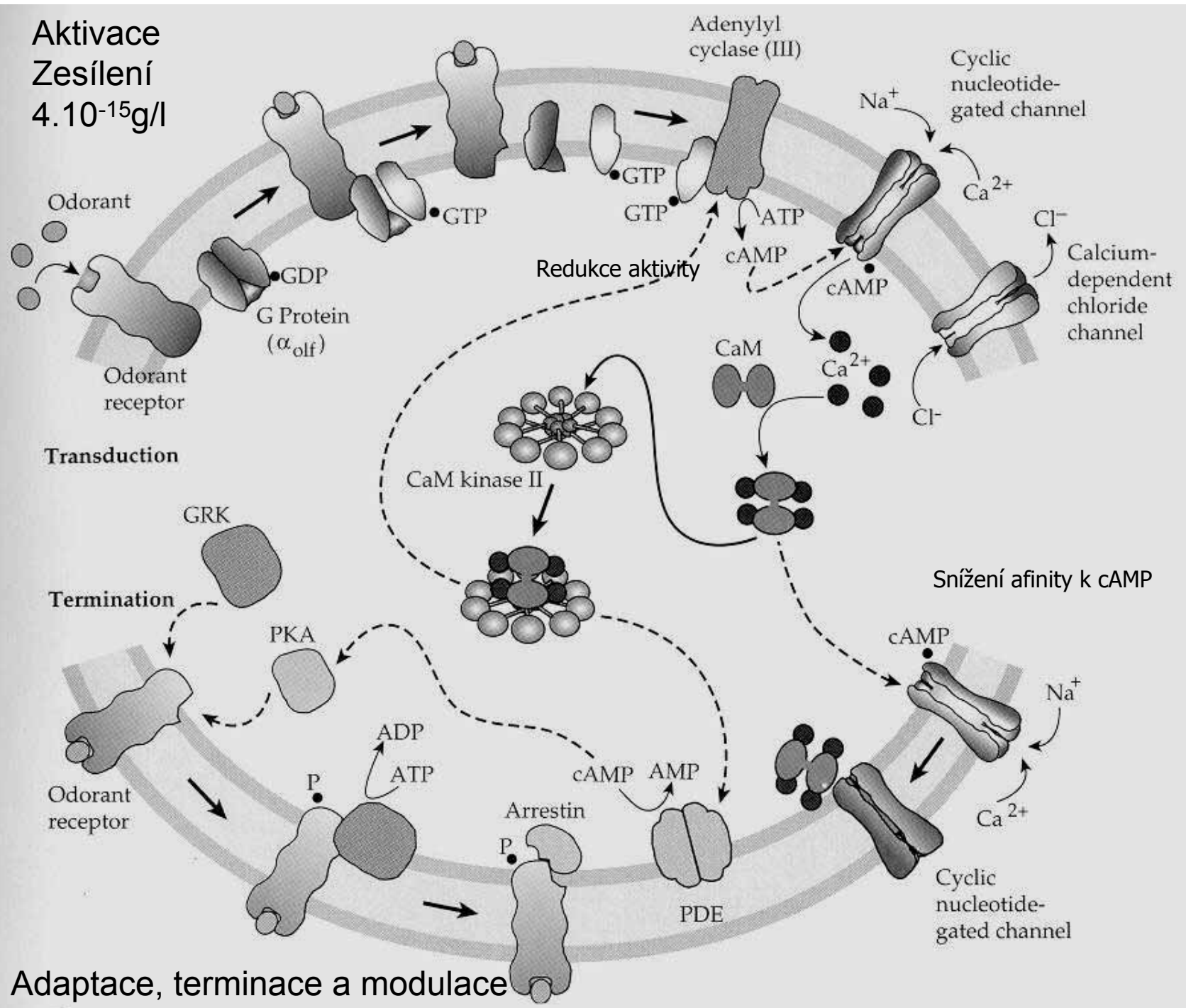


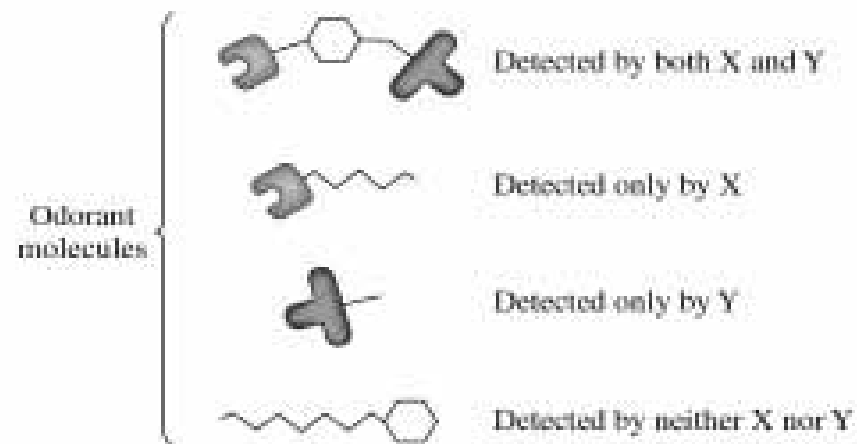
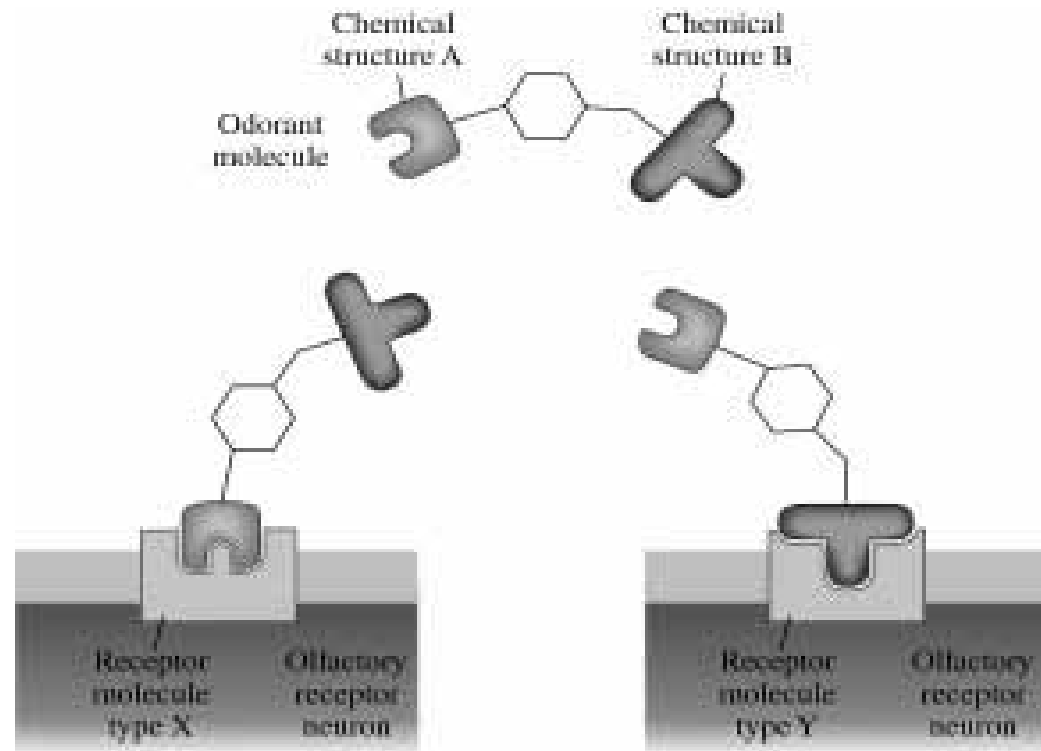
Figure 13.36 Olfactory transduction mechanisms in cilia membranes of olfactory neurons (a) Many odorants act to increase cyclic AMP. The odorant binds to an odorant receptor on the ciliary membrane; the receptor activates a G protein to activate adenylyl cyclase, producing cAMP. Cyclic AMP binds to and opens a cation channel, allowing entry of Na⁺ and Ca²⁺ ions to depolarize the cell. Ca²⁺ binds to Ca²⁺-activated Cl⁻ channels, augmenting the depolarization. (b) Some olfactory responses increase IP₃. This mechanism also starts with odorant binding to a G protein-coupled receptor, but in this case the G protein activates phospholipase C, forming IP₃ from PIP₂ (see Figure 12.21). IP₃ binds to and opens a calcium channel, letting Ca²⁺ enter to depolarize the cell. As in (a), Ca²⁺-activated Cl⁻ channels augment the depolarization.

Aktivace
Zesílení
 $4 \cdot 10^{-15} \text{g/l}$



Adaptace, terminace a modulace

Specializace receptorů
Kombinace cca 350 receptorů
3.000-100.000 (?)



Periferie
čichové dráhy

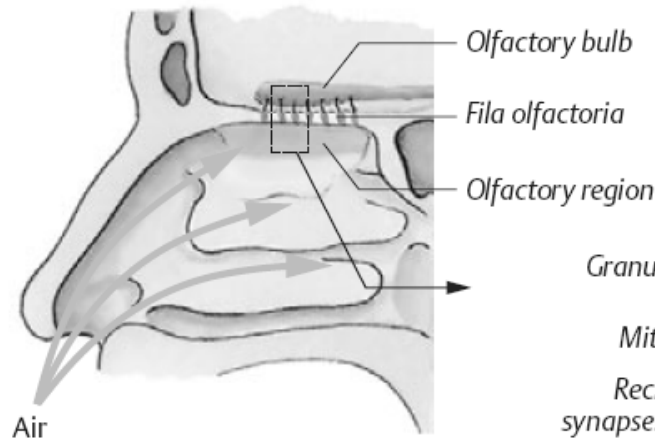
Rozlišování chem.
Struktury

Laterální inhibice
Kontrastování

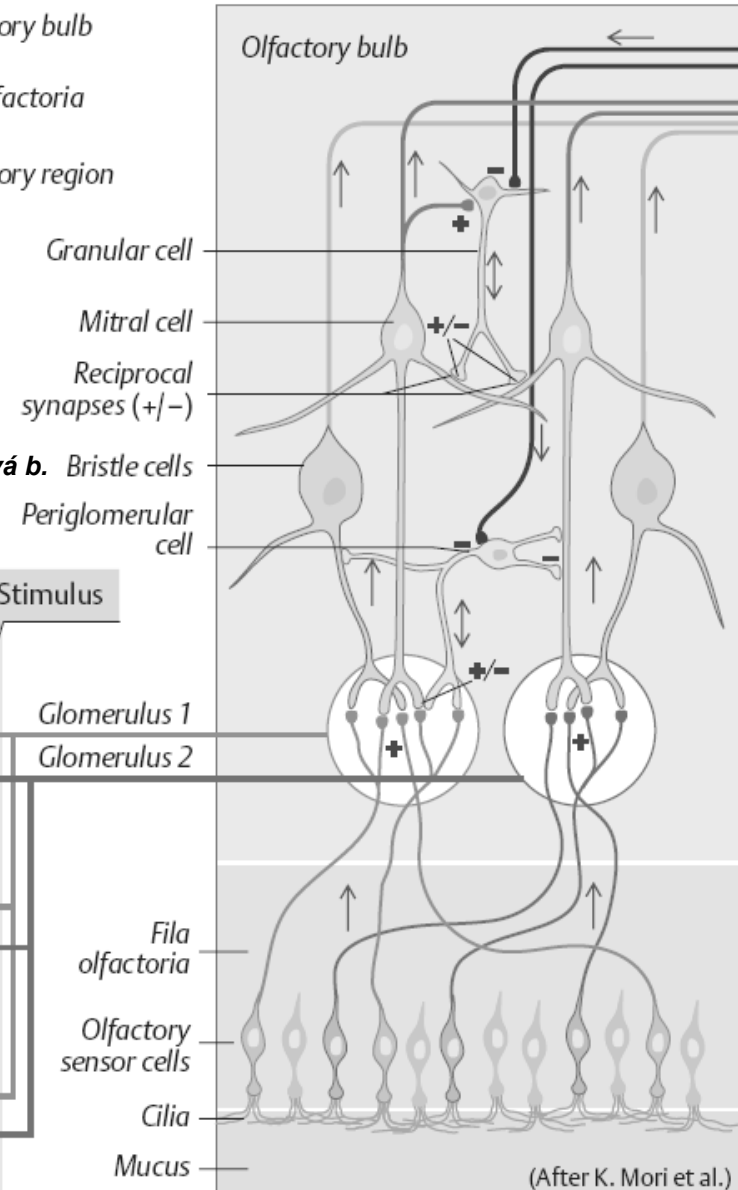
Eferentní inhibice

A. Olfactory pathway and olfactory sensor specificity

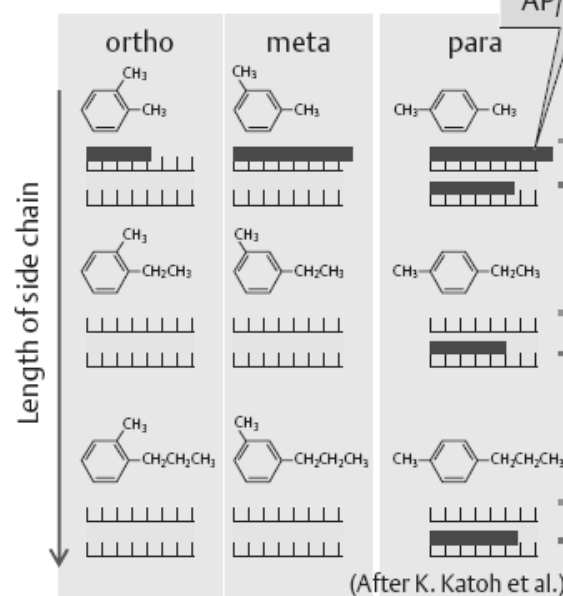
1 Nasal cavity



2 Olfactory pathway

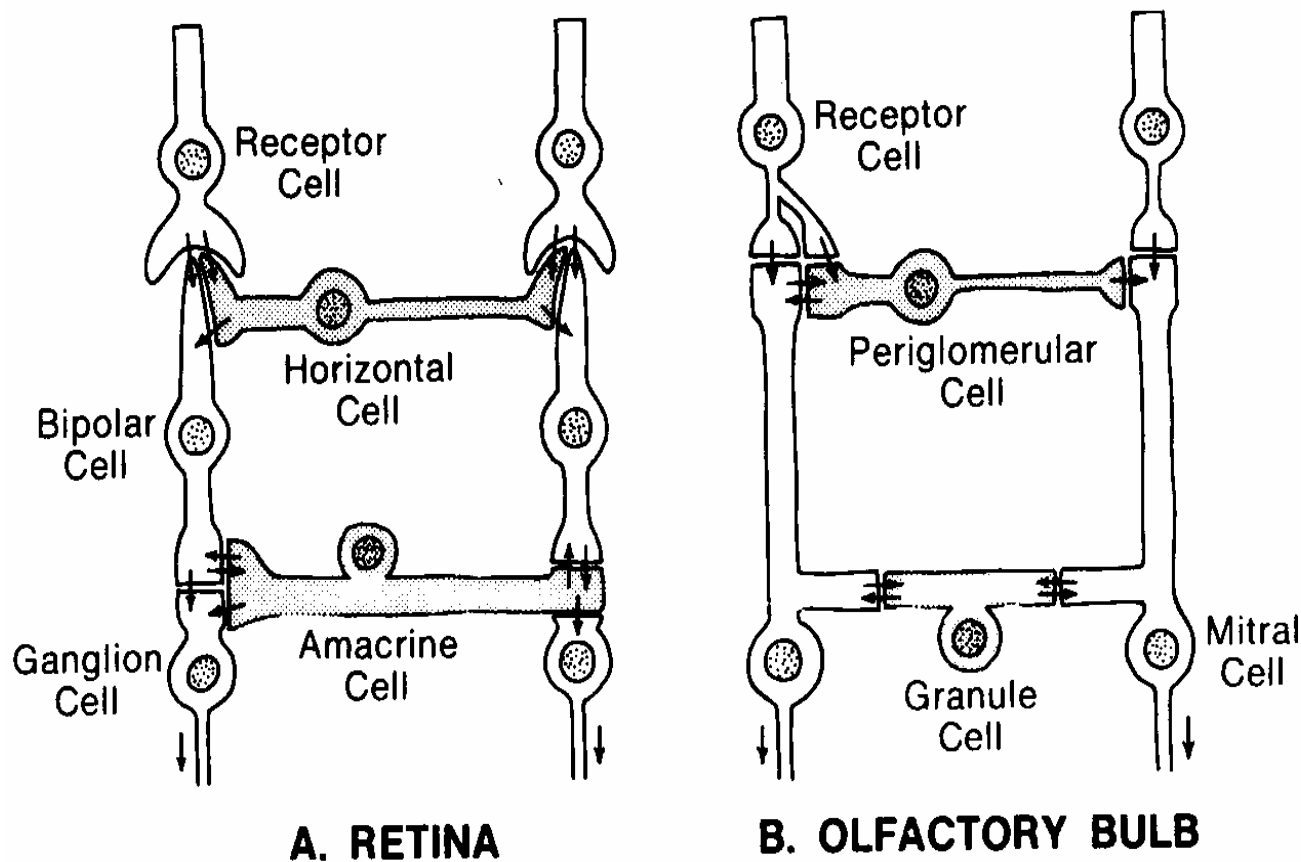


3 Sensor specificity (example)

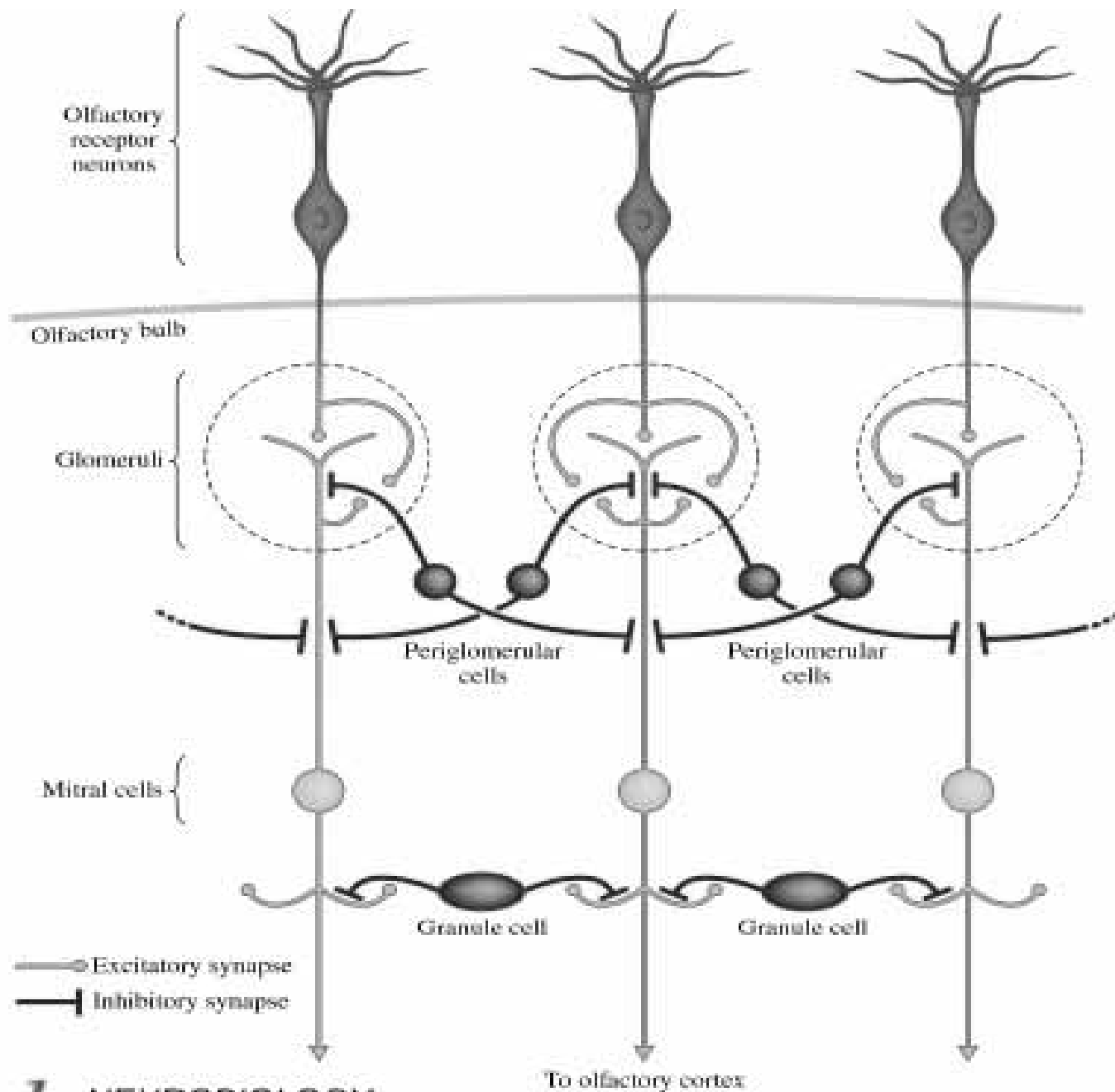


(After K. Mori et al.)

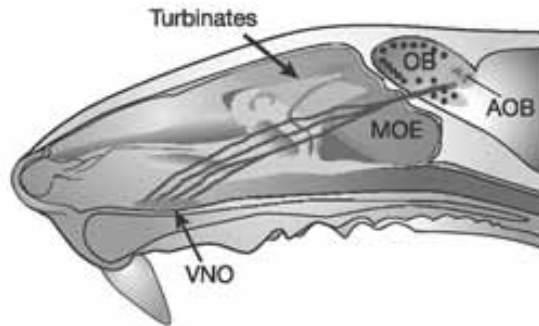
Podobnost architektury sensorických obvodů a drah



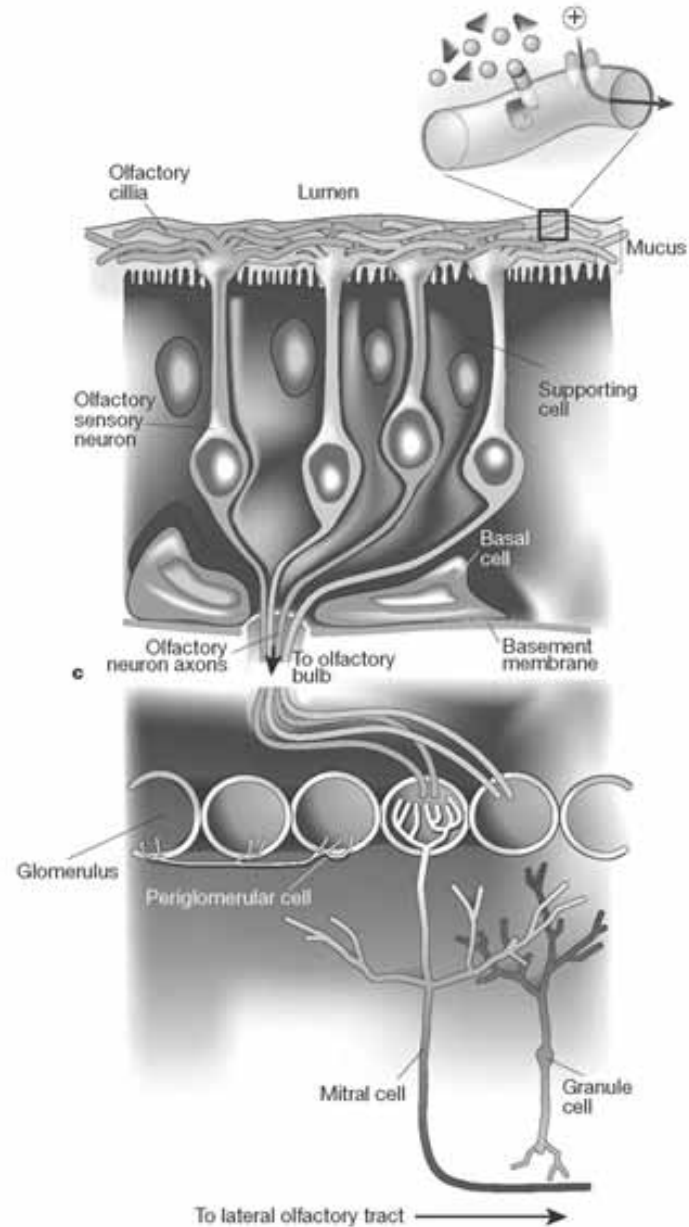
Comparison between simplified basic circuit diagrams of the vertebrate retina and olfactory bulb. (After Shepherd, 1978)



Konvergence na příslušný glomerulus (100 - 1000/1)



MOE = main olfactory epithelium.
OB = olfactory bulb.
AOB = accessory olfactory bulb.
VNO = vomeronasal organ.



Mapa vůní – vzorec aktivovaných glomerulů
 Konvergence neprostorového parametru
 na prostorový

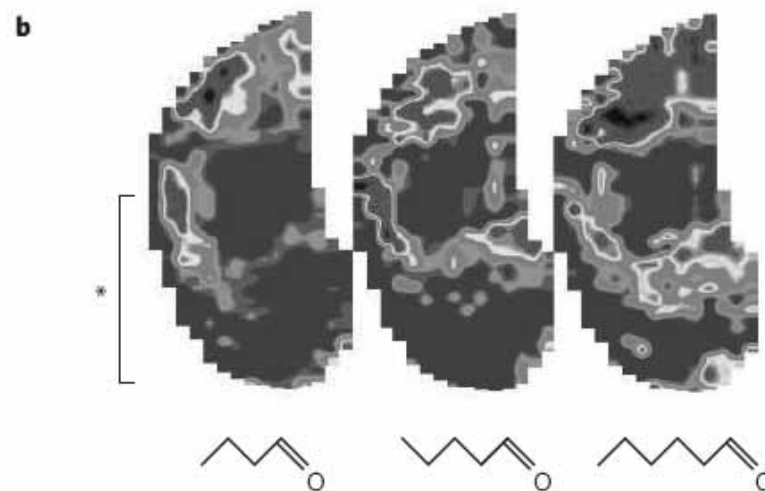
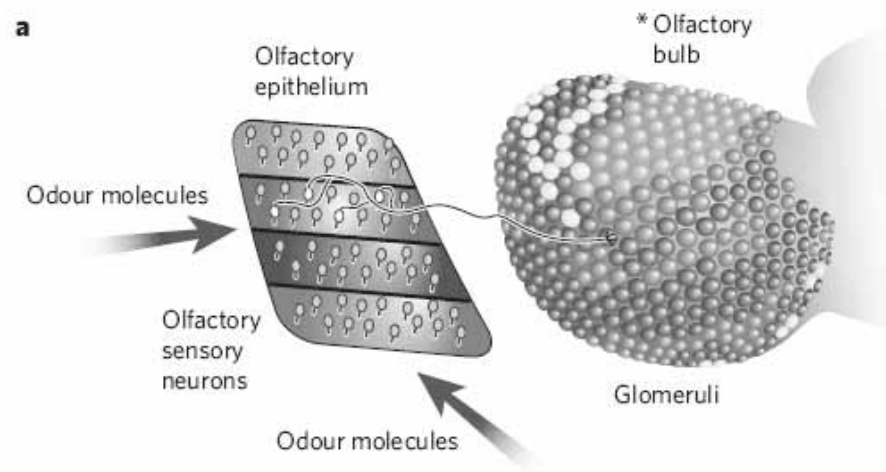
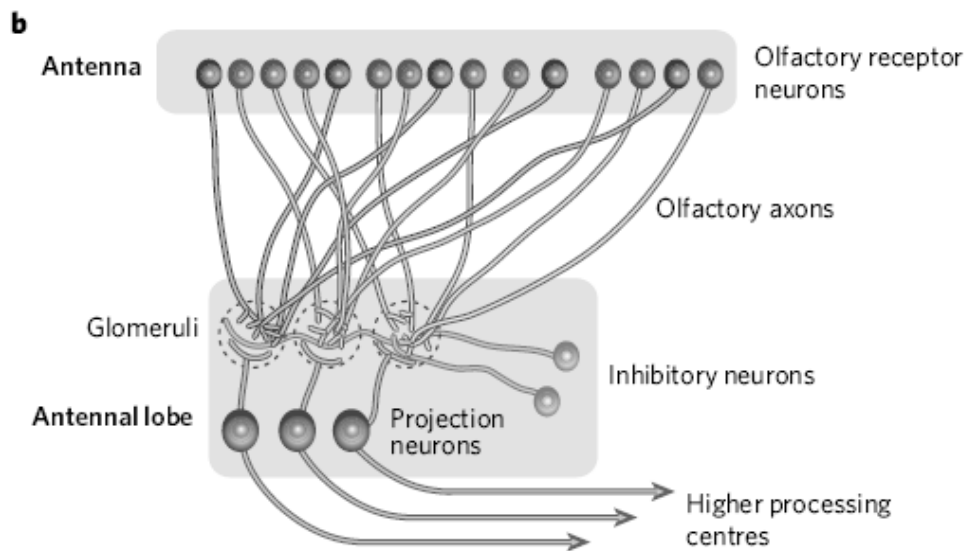


Figure 1 | Odour images in the olfactory glomerular layer. **a**, Diagram showing the relationship between the olfactory receptor cell sheet in the nose and the glomeruli of the olfactory bulb⁵³. **b**, fMRI images of the different but overlapping activity patterns seen in the glomerular layer of the olfactory bulb of a mouse exposed to members of the straight-chain aldehyde series, varying from four to six carbon atoms. The lower part of the image in the left panel corresponds to the image on the medial side of the olfactory glomerular layer as shown in **a** (see asterisk). (Image in **a** adapted, with permission, from ref. 53; image in **b** adapted, with permission, from ref. 10.)

Podobnost architektury sensorických obvodů a drah

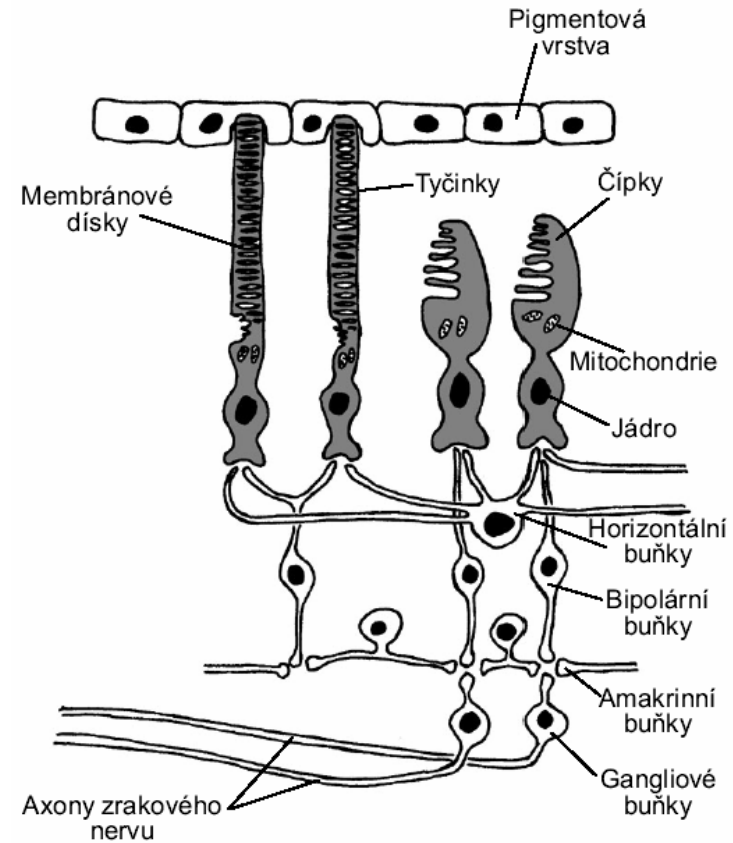
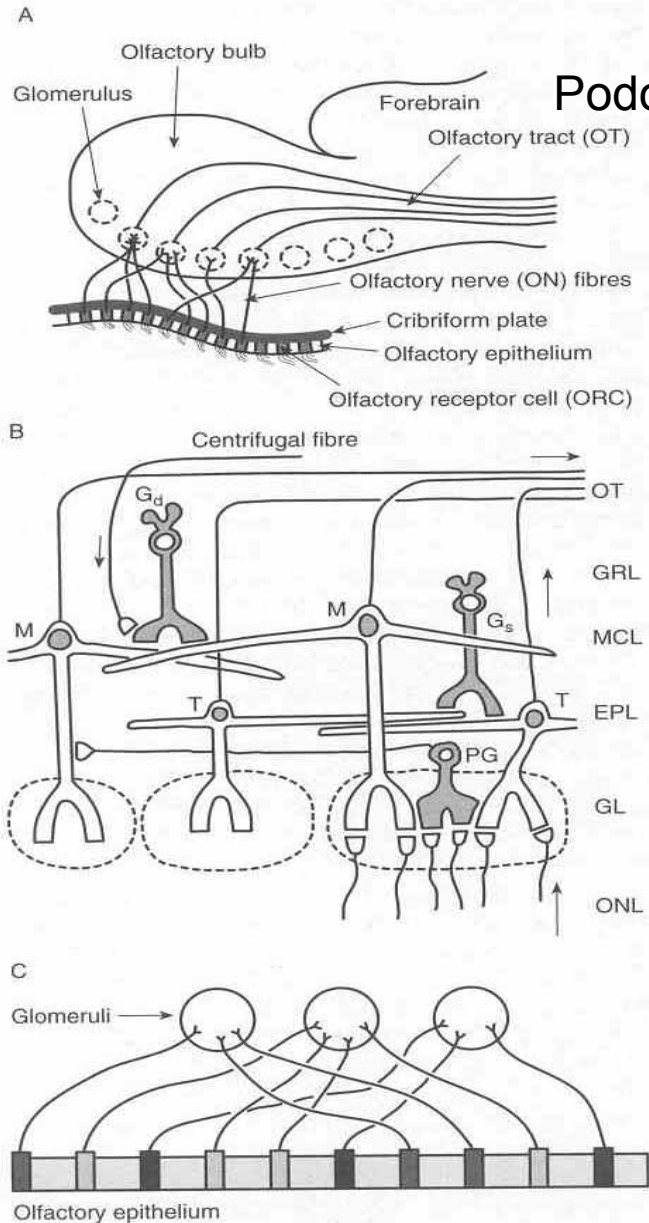


Figure 13.7 Olfactory bulb. (a) The figure shows olfactory axons passing through the cribriform plate to end in glomeruli in the olfactory bulb. (b) Basic circuit of the mammalian olfactory bulb. Layers: EPL = external plexiform layer; GL = glomerular layer; GRL = granule cell layer; OT = olfactory tract; MCL = mitral cell layer. Cells: G_d = deep granule cell; G_s = superficial granule cell; M = mitral cell; PG = periglomerular cell; T = tufted cell. Inhibitory cells stippled. Simplified from

Podobnost architektury sensorických obvodů a drah

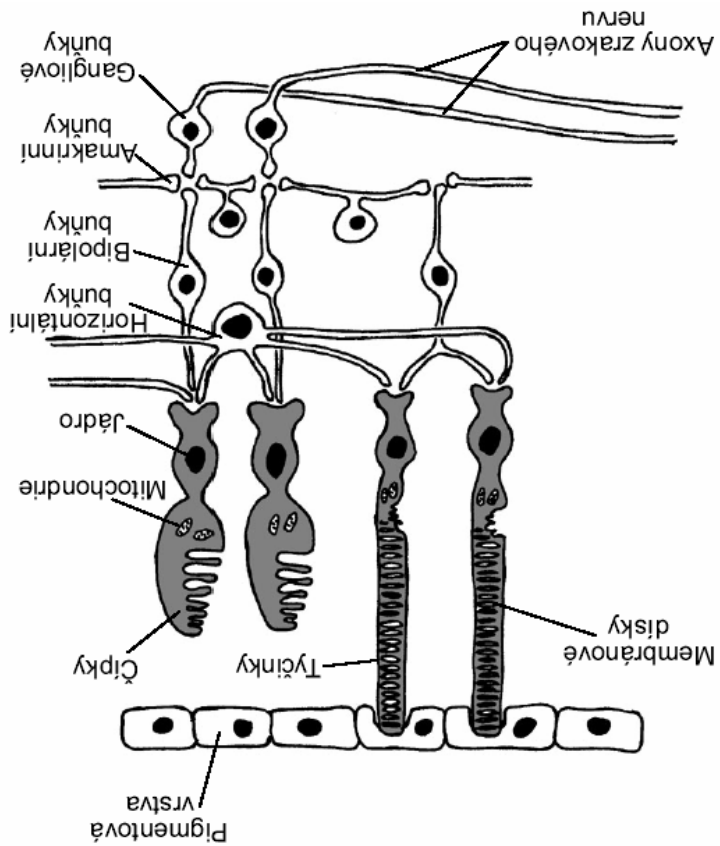
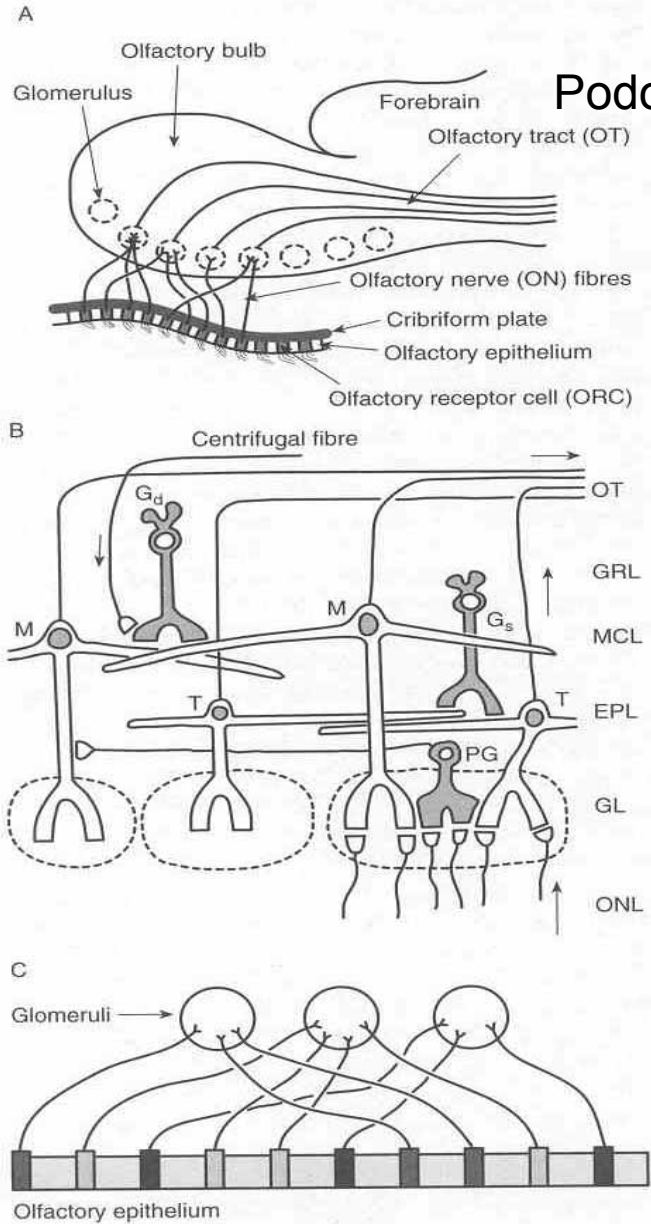
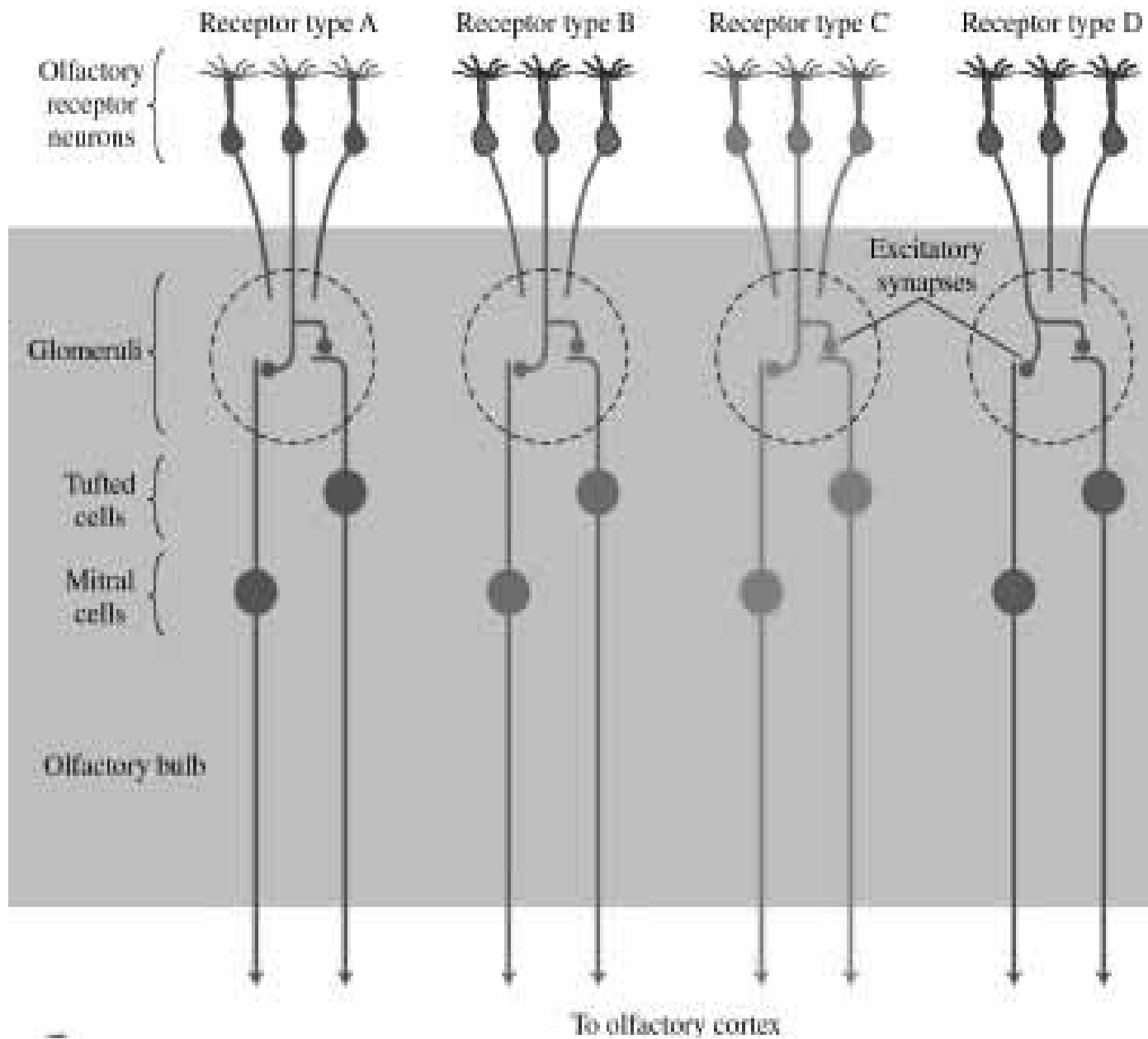
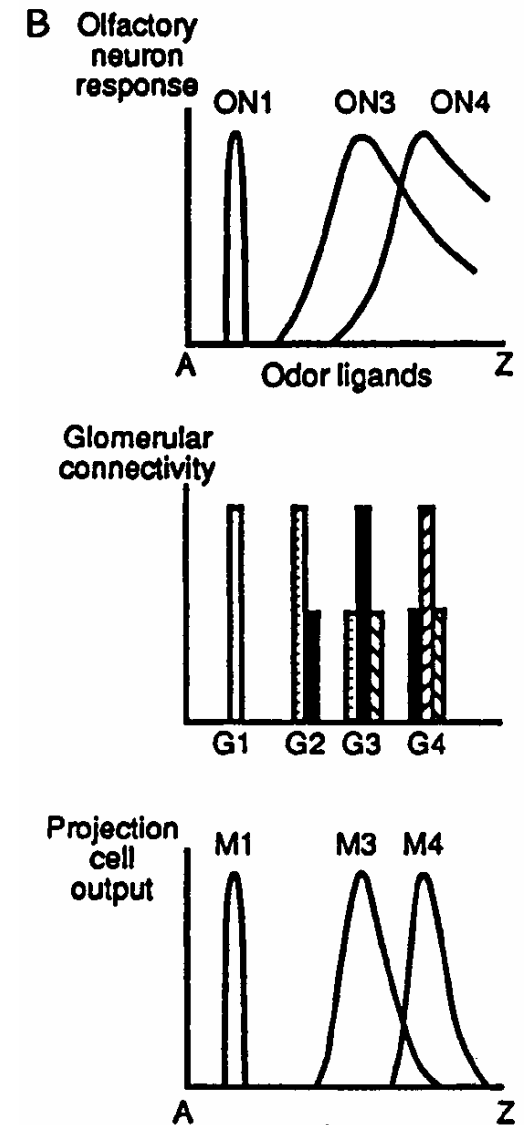


Figure 13.7 Olfactory bulb. (a) The figure shows olfactory axons passing through the cribriform plate to end in glomeruli in the olfactory bulb. (b) Basic circuit of the mammalian olfactory bulb. Layers: EPL = external plexiform layer; GL = glomerular layer; GRL = granule cell layer; OT = olfactory tract; MCL = mitral cell layer. Cells: G_d = deep granule cell; G_s = superficial granule cell; M = mitral cell; PG = periglomerular cell; T = tufted cell. Inhibitory cells stippled. Simplified from



Překryv



„Zostření“ naladění ve vyšších patrech dráhy

Také adaptace může být na úrovni vyšších pater smyslové dráhy

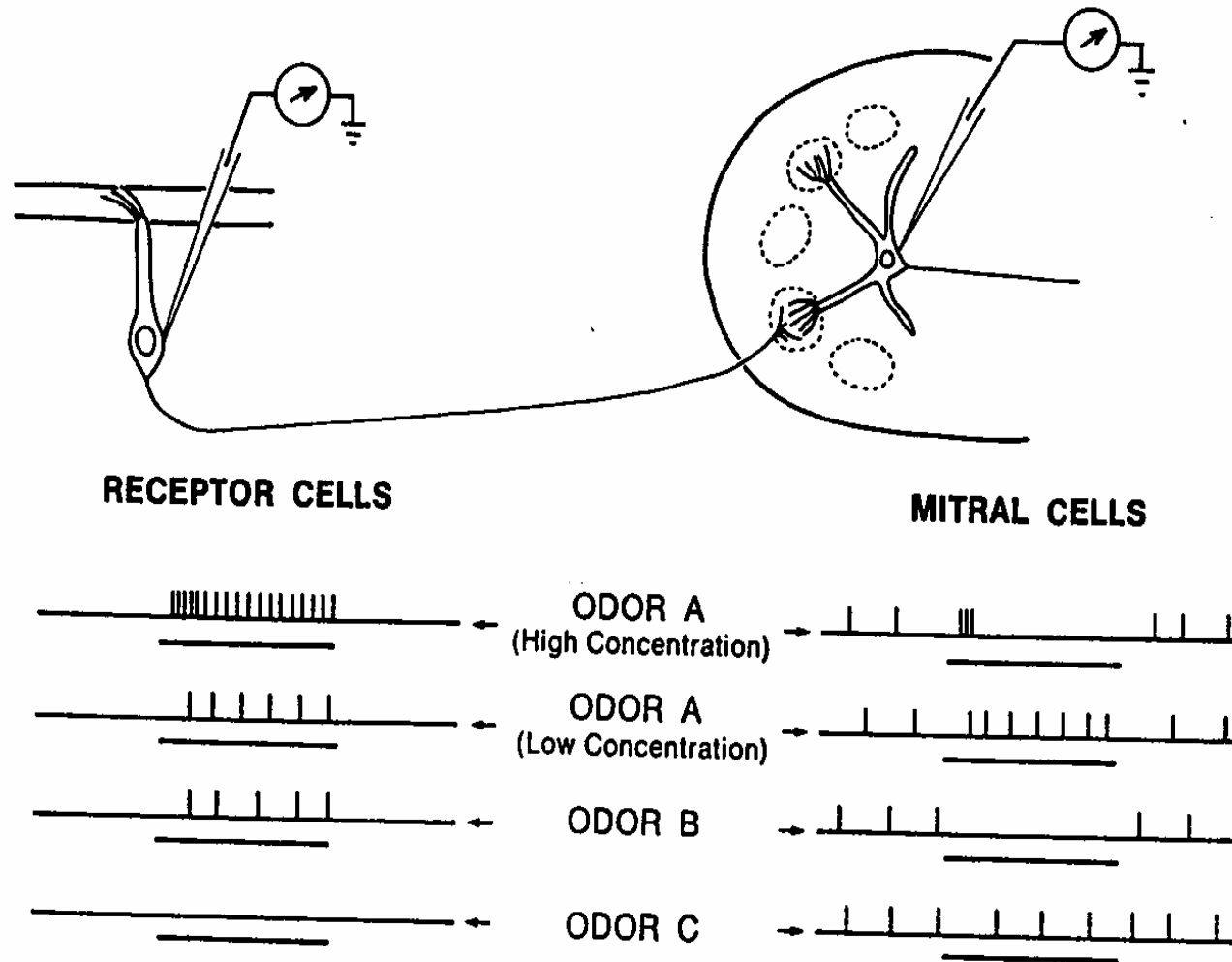
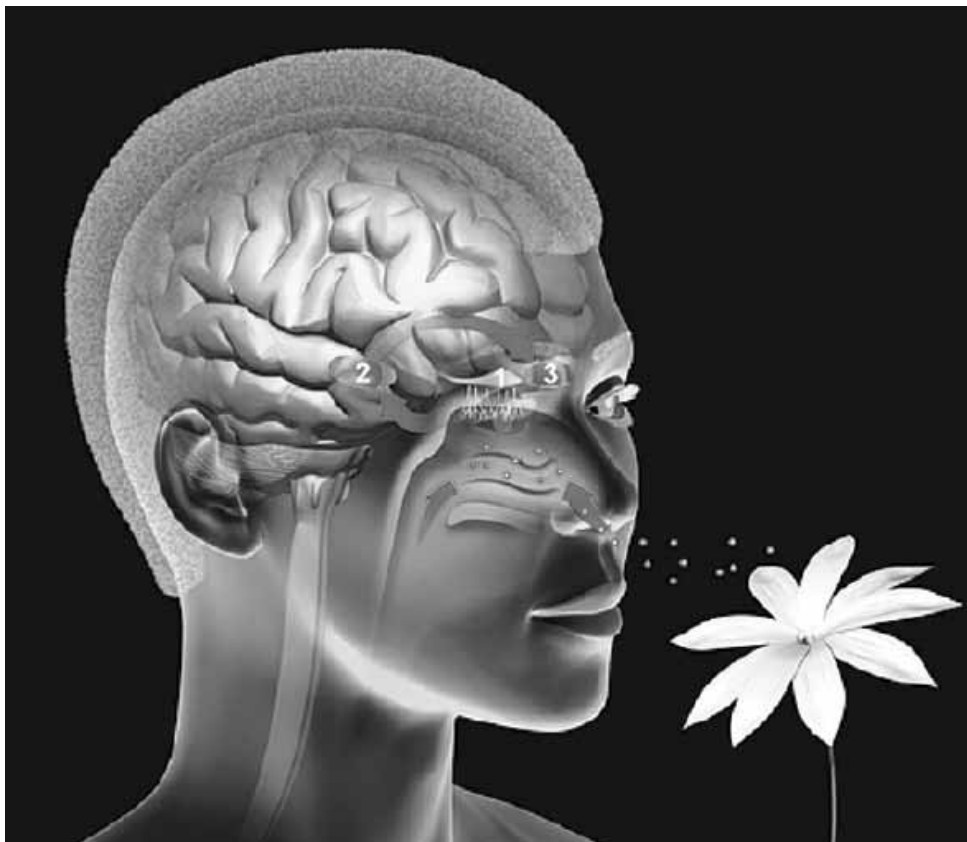


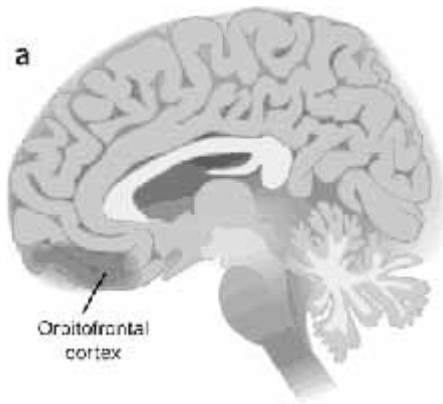
Fig. 11.11 Extracellular single-unit recordings of responses to odors of receptor cells (*left*) and mitral cells (*right*) in the salamander, showing different types of responses and different temporal patterns of activity. (After Kauer, 1974, and Getchell and Shepherd, 1978)



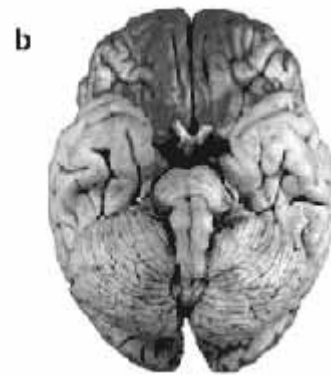
Centrální části čichové dráhy

1. Čichový lalok
2. Piriformní kůra
3. Orbitofrontální kůra

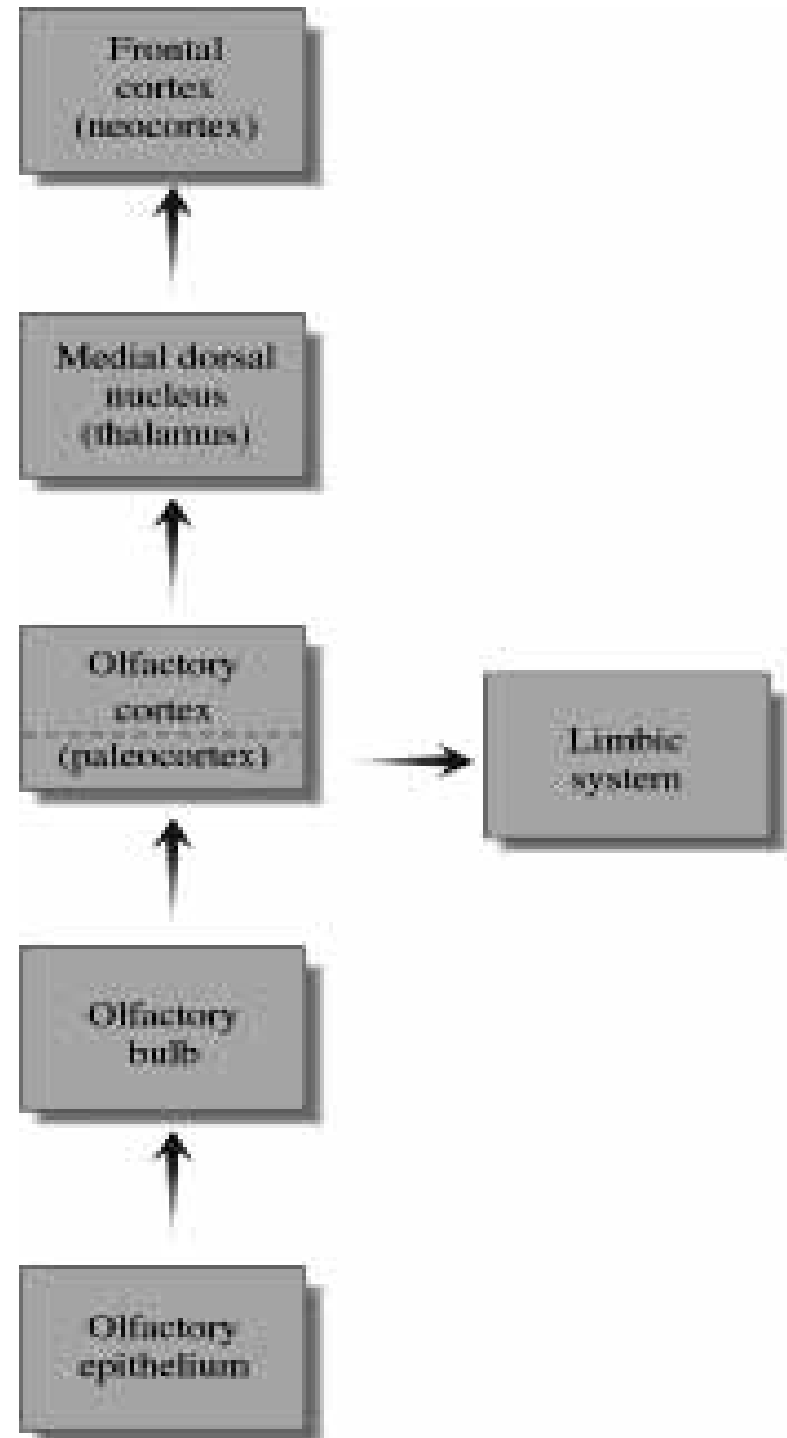
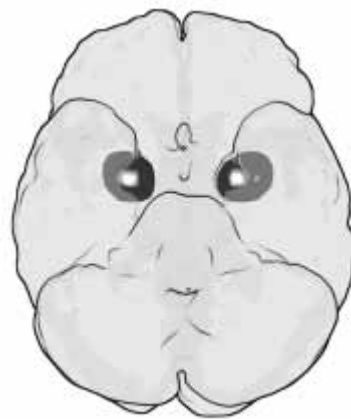
Figure 1. Schematic overview of the basic steps of the central processing of odorous stimuli. Odorants are first detected by receptors at the top of the nasal cavity, and from there, the signal travels to the olfactory bulb (1). This signal is then routed to the piriform cortex (2) and subsequently to the orbitofrontal cortex (3), among other structures. Note the dual route that odorants can take to reach the receptors at the top of the nasal cavity. The route via the nostrils is known as orthonasal olfaction, whereas the route via the back of the throat is known as retronasal olfaction. See the text for



Orbitofrontální kůra

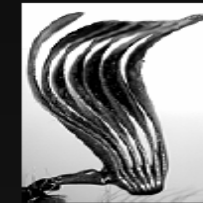
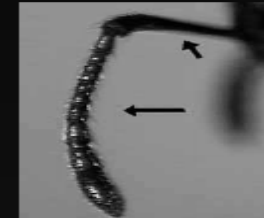


Piriformní kůra

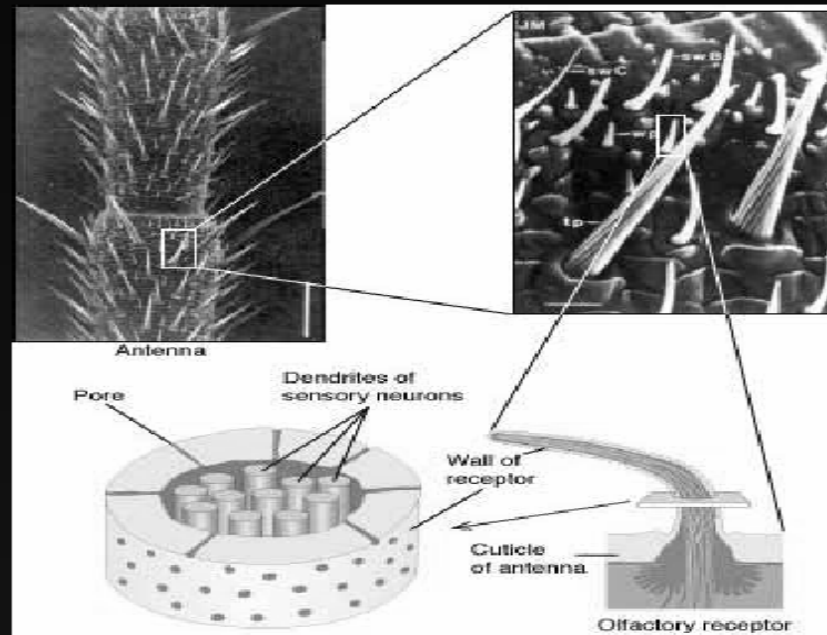


A co hmyz ?

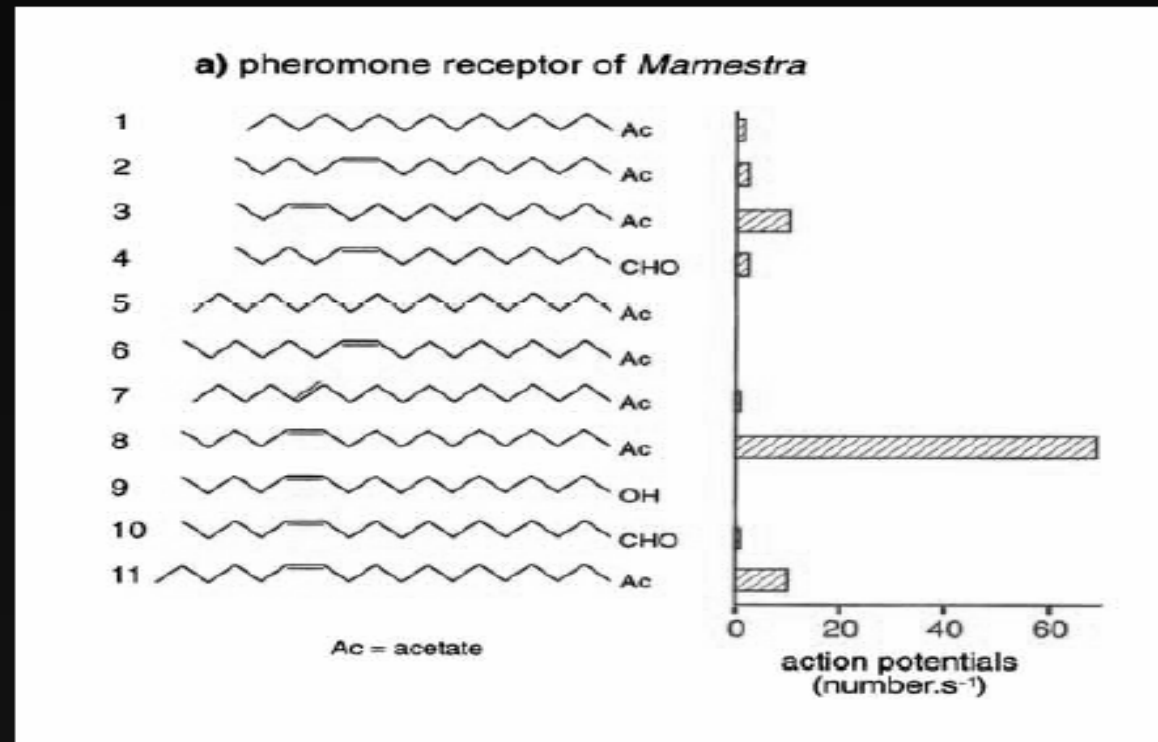
Antennal morphology diversity



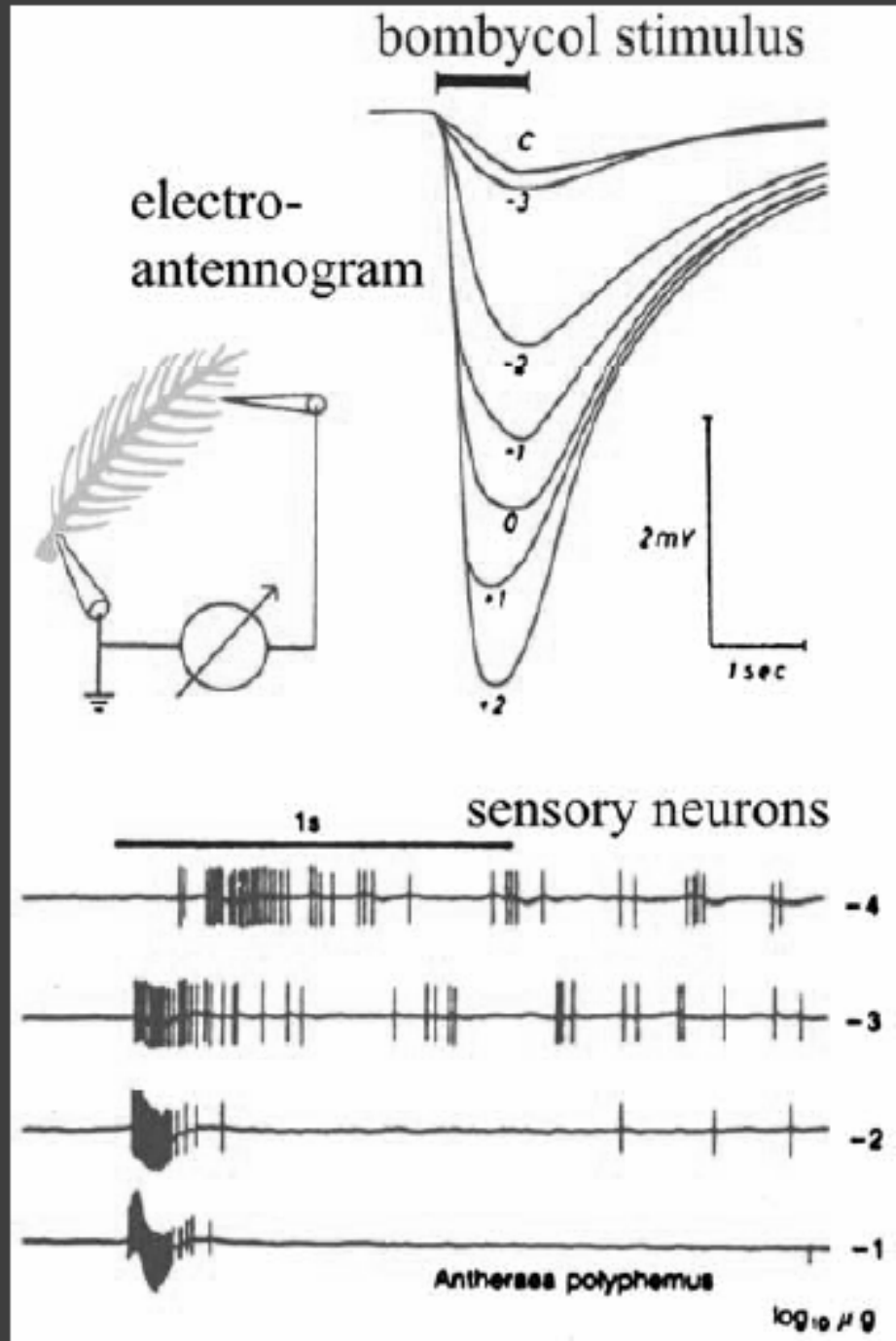
Anatomy of an antennal sensilla



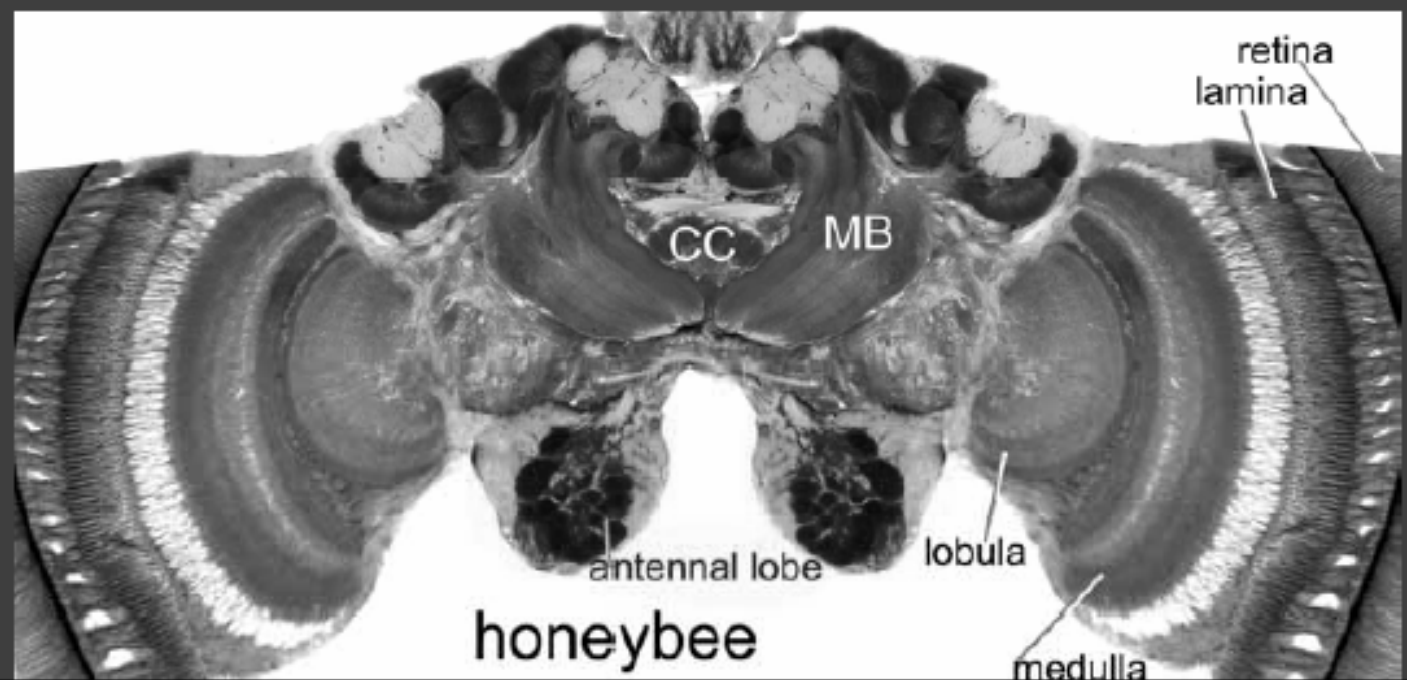
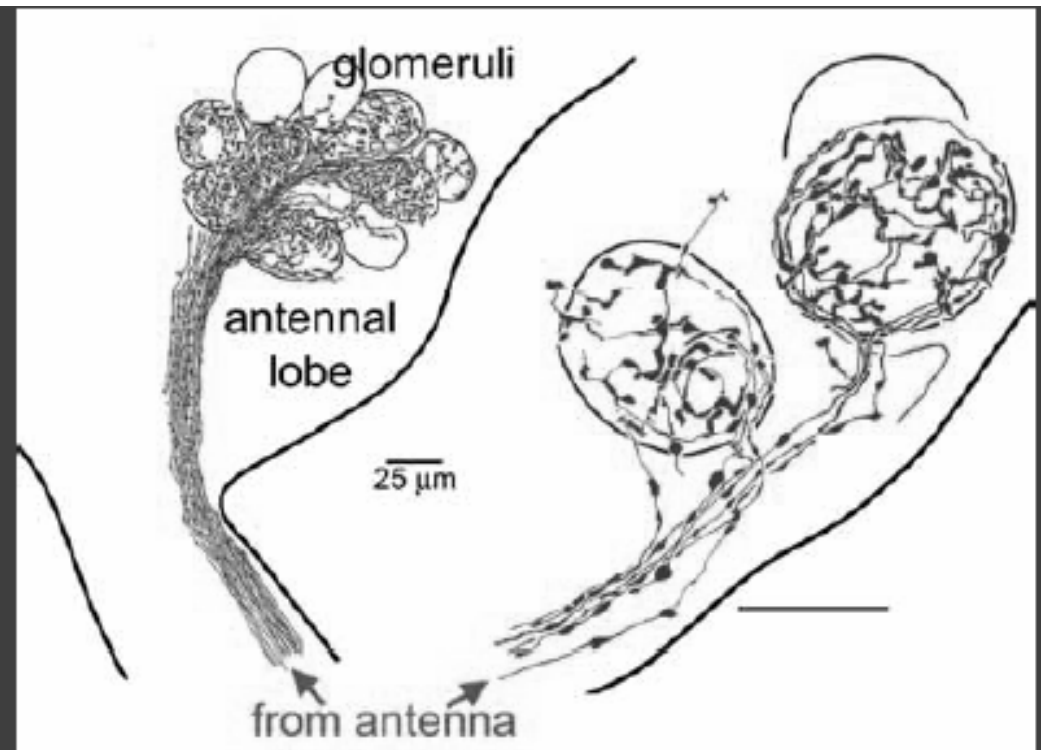
Response specificity to size and composition of odorant molecule



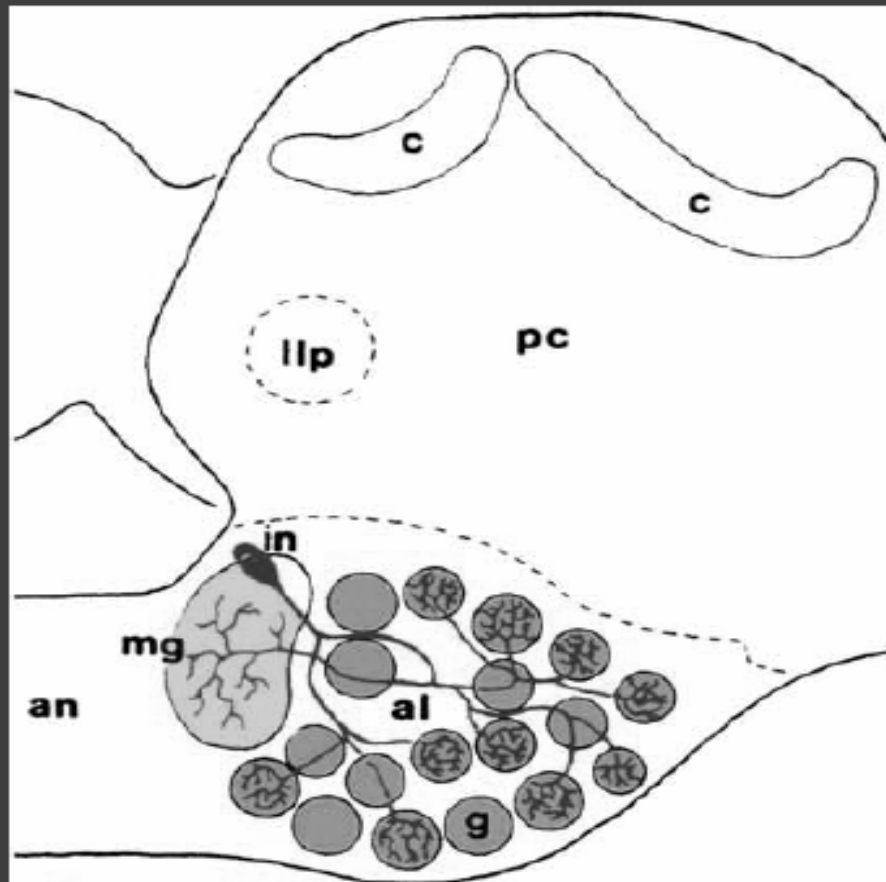
Olfactory receptor neurons respond to odorants



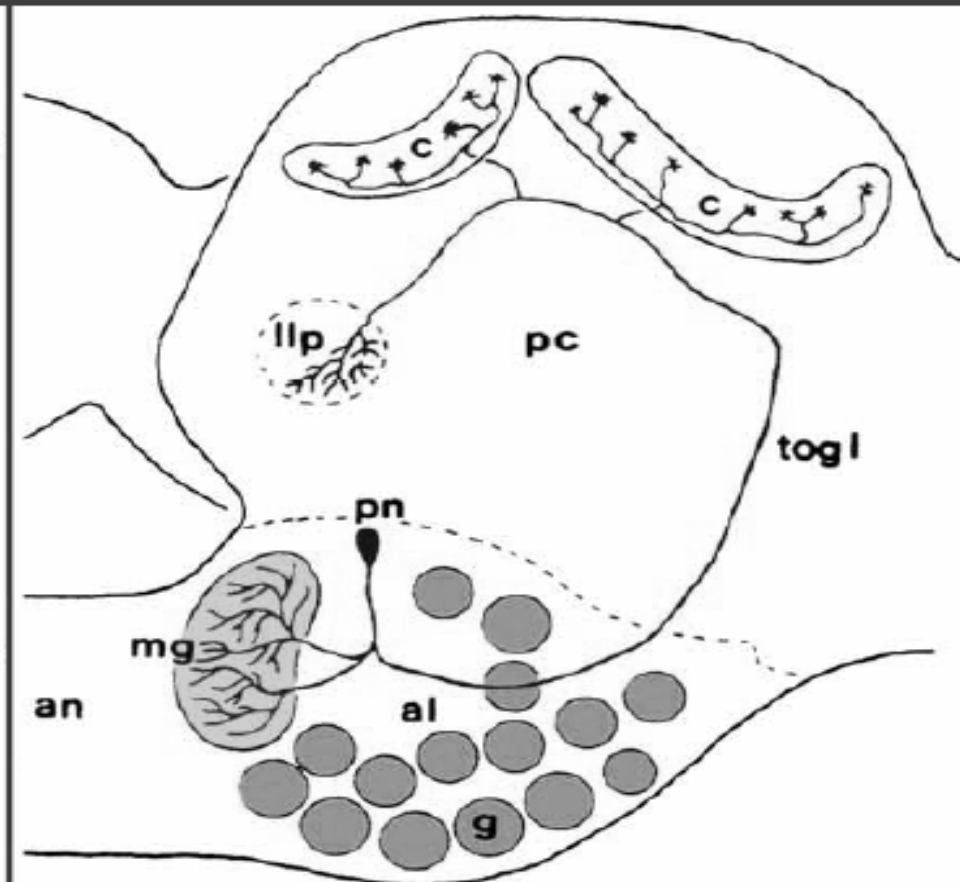
Antennal
olfactory receptor
neurons terminate
in antennal lobe
glomeruli



Antennal lobe: two major classes of neurons

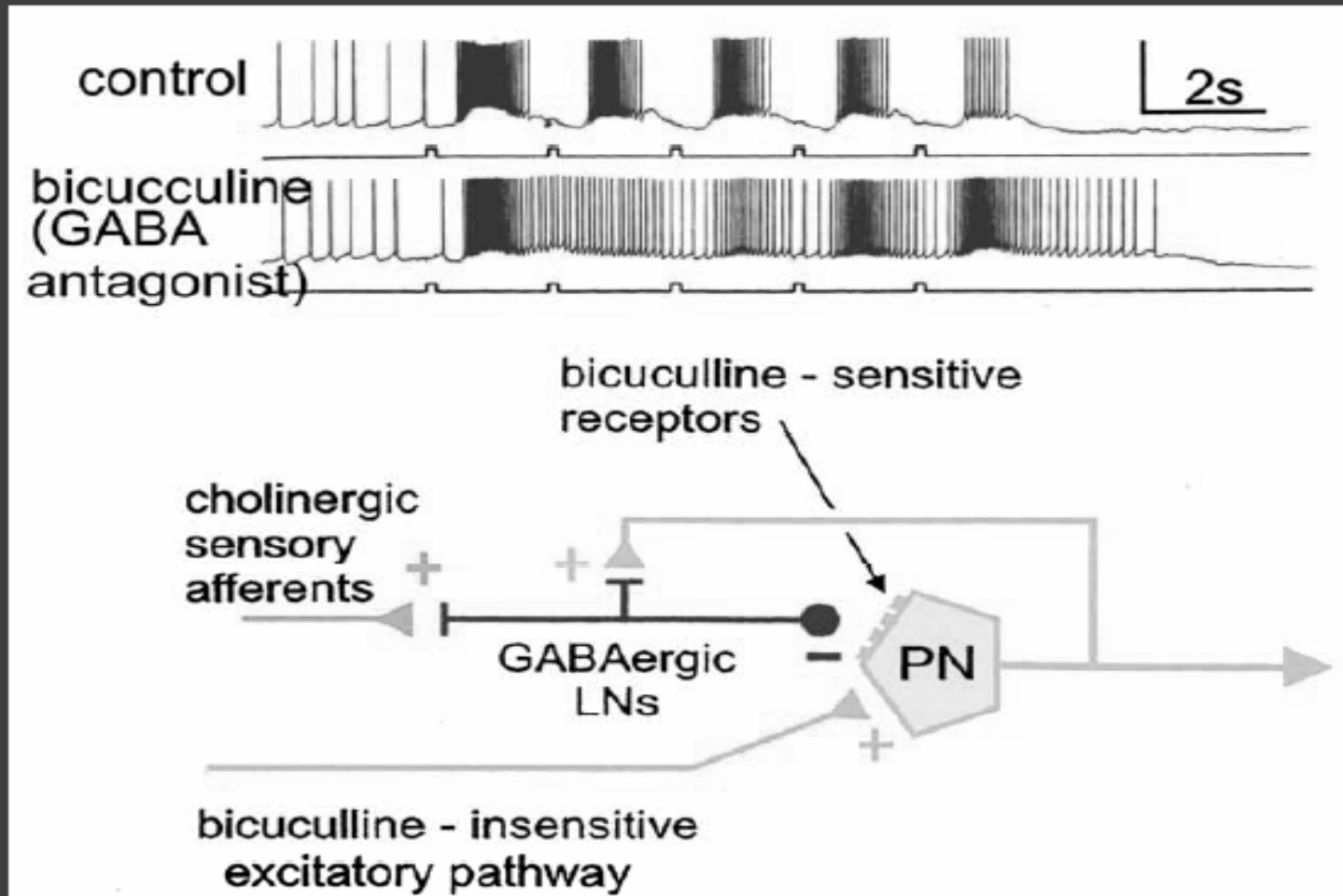


local interneuron

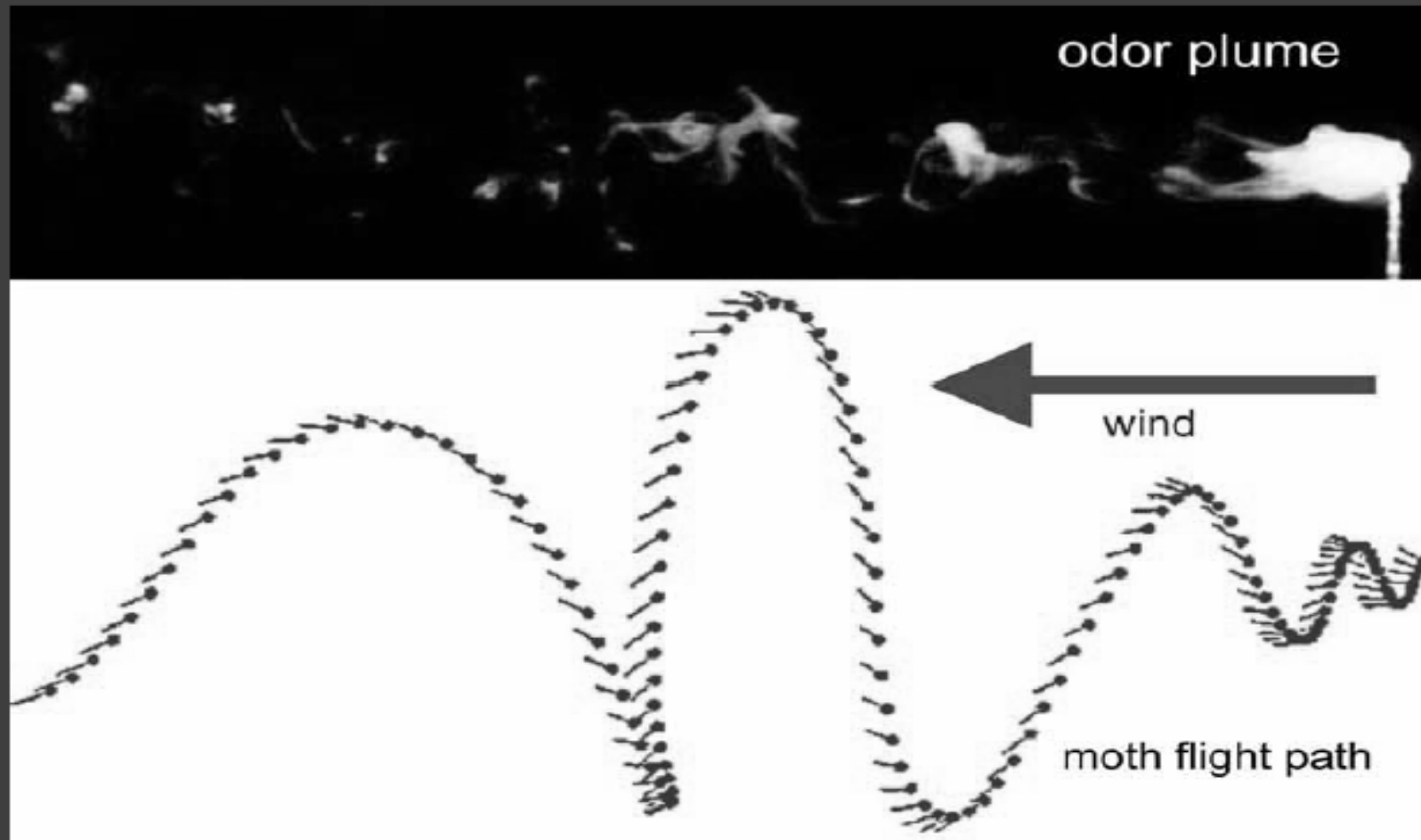


projection neuron

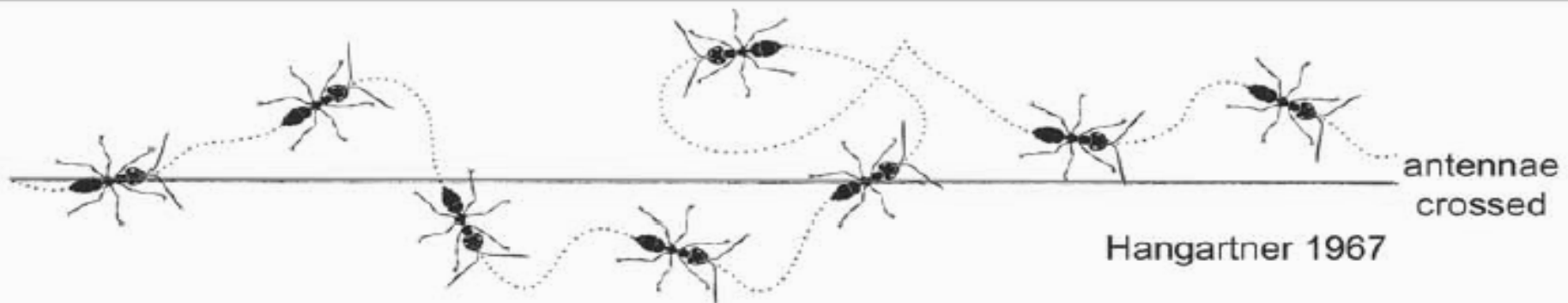
Inhibition 'sharpens' the PN response (temporal and odor discrimination)



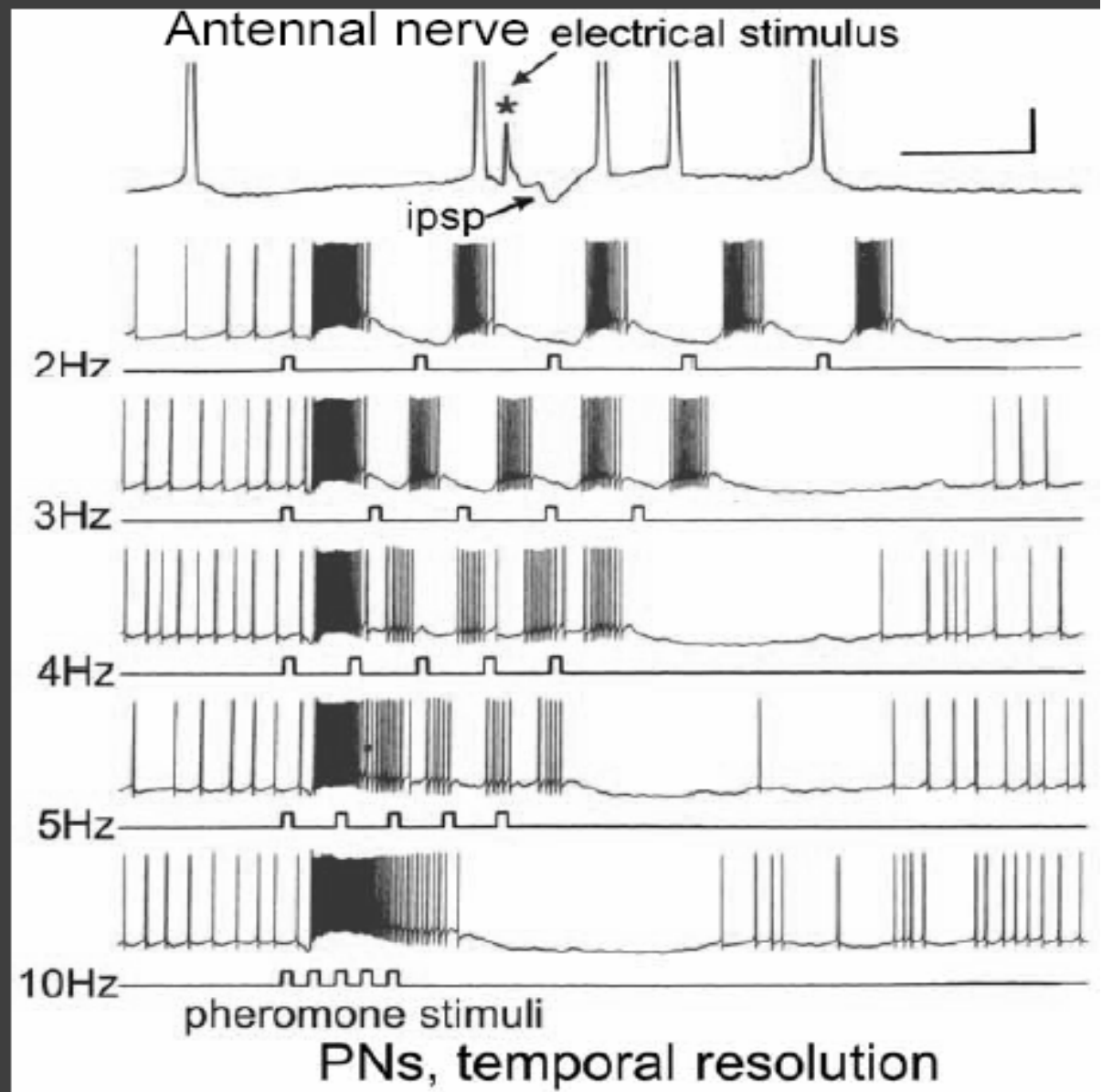
Odor is discontinuously distributed in air



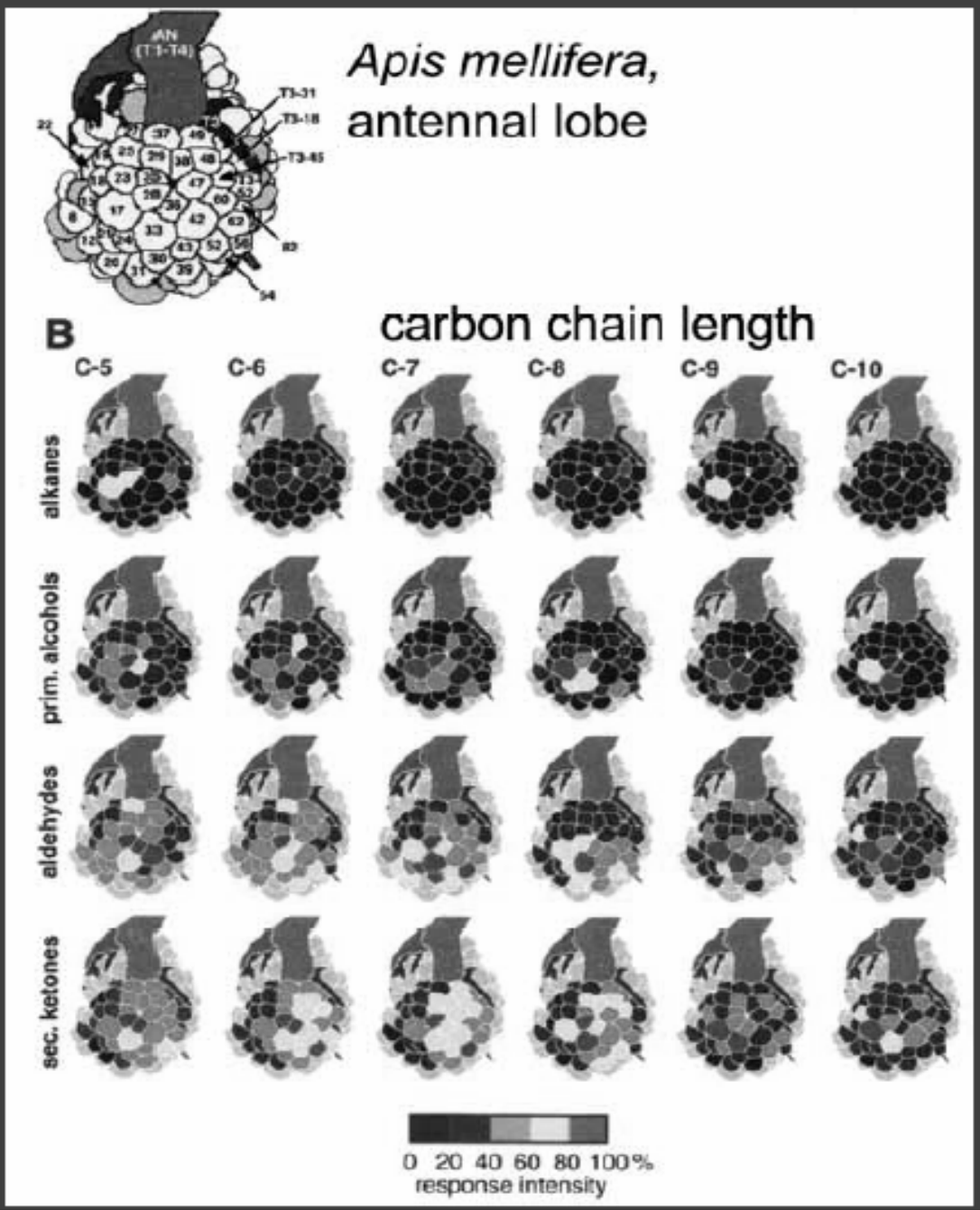
Even when following an odor trace, perception is discontinuous



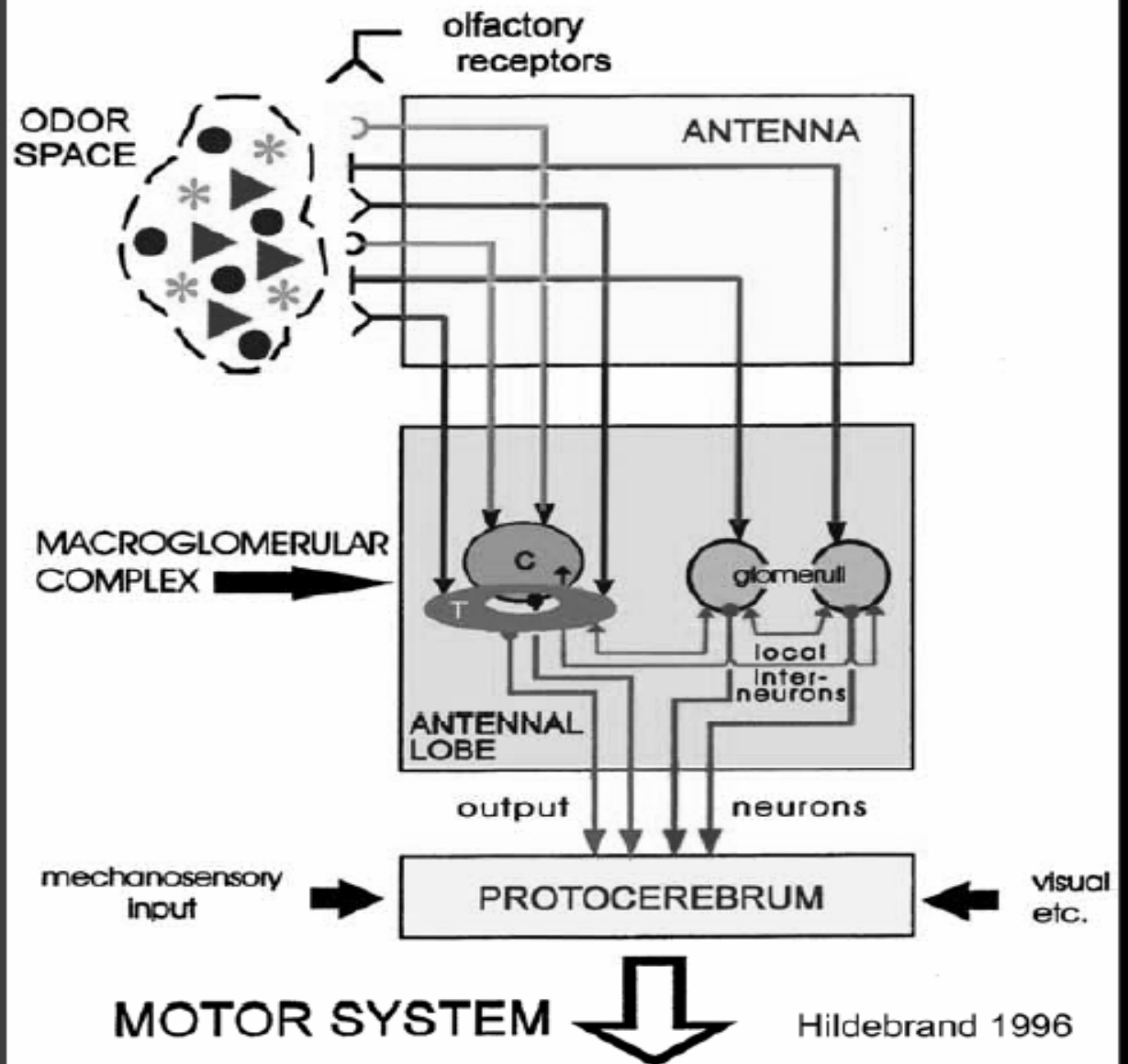
Temporal resolution is limited



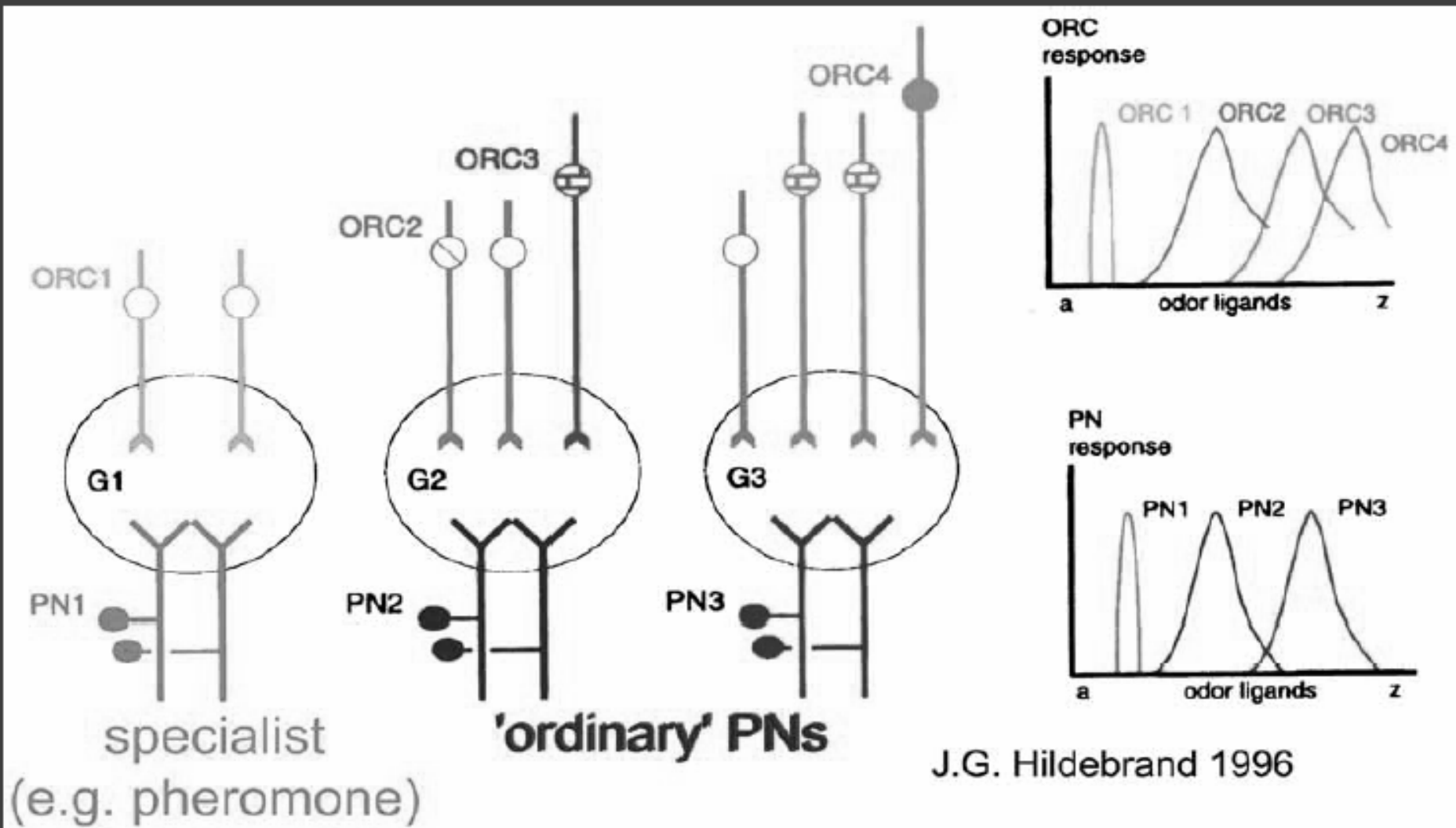
Glomeruli responses reflect odorants' structural properties (chain length, residues, polarity etc.):
odor map



(sex)
pheromones
and
'ordinary'
odors are
processed by
two different
pathways



PNs may have narrower response spectra than receptor neurons



Podobnost mezi hmyzem a obratlovci jen omezená

Class	Receptors	Ligands	Oligomeric state	Localization
<i>Vertebrates</i>				
GPCRs	OR	Odours	Monomer	Main olfactory epithelium, Grüneberg ganglion, vomeronasal organ and exogenic expression
	TAAR	Amines	Monomer	Main olfactory epithelium and Grüneberg ganglion
	FPR	Pathogen- and inflammation-related compounds	Unknown	Apical layer of vomeronasal organ
	V1R	Small, volatile molecules and sulphated steroids	Monomer	Apical layer of vomeronasal organ and main olfactory epithelium
	V2R	Peptides (ESP1 and MHC peptides), MUPs and sulphated steroids	Monomer and heteromer with H2-Mv proteins and B2M	Basal layer of vomeronasal organ and Grüneberg ganglion
Monotopic receptors (RTK type)	GCD	Extracellular: uroguanylin and guanylin Intracellular: bicarbonate, Ca ²⁺ and neurocalcin- δ	Dimer	Main olfactory epithelium
	GCG	Unknown	Unknown	Grüneberg ganglion
<i>Insects</i>				
Ionotropic '7-TM' receptors	OR	Food odours and pheromones	Heterodimer (OrX–Or83b)	Antenna (basiconic, trichoid and coeloconic sensilla) and maxillary palp
	GR	CO ₂	Heterodimer (Gr21a–Gr63a)	Antenna (basiconic sensilla)
Ionotropic 'glutamate' receptors	IR	Ammonia, amines, water vapour and alcohols	Multimeric	Antenna (coeloconic sensilla)

B2M, β 2 microglobulin; ESP1, exocrine gland-secreting peptide 1; FPR, formyl peptide receptors; GCD and GCG, guanylate cyclase type D and G; GPCR, G protein-coupled receptor; GR, gustatory receptor; Gr21a and Gr63a, *Drosophila melanogaster* gustatory receptors 21a and 63a; H2-Mv, non-classical class I major histocompatibility genes; IR, ionotropic receptor; MHC, major histocompatibility complex; MUP, major urinary protein; OR, odorant receptor; RTK, receptor tyrosine kinase; OrX–Or83b, heteromeric *D. melanogaster* odorant receptor composed of Or83b and another OR (OrX); TAAR, trace amine-associated receptor; 7-TM, seven-transmembrane; V1R and V2R, vomeronasal receptors type 1 and 2.

Podle: Čich hmyz a obratlovci, 2010

Podobnost mezi hmyzem a obratlovci jen omezená

Table 2 | **Commonalities and differences of olfactory receptors in vertebrates and insects**

Characteristic	Vertebrates	Insects
Class	GPCR	Non-GPCR
Repertoire	Large, variable	Smaller, constant
Topology	Heptahelical	Inverse heptahelical
Activation	Metabotropic	Ionotropic
Pseudogene fraction	High	None to low
Stoichiometry	Monomers	Heteromers
One receptor–one neuron rule	Yes	Yes*
Gene selection	Stochastic	Deterministic
Expression pattern	Zonal and random	Zonal and random
Instructive role	Yes	Unknown
Ectopic expression	Yes	Unknown
Inhibitory action of odorants	Rare	Common
Convergence of axons to glomeruli	Yes	Yes
Glomeruli per receptor type	Variable, ≤ 2 up to 20	~ 1

GPCR, G protein-coupled receptor. *There are notable exceptions to this rule, which have been excluded from this table for clarity.

Feromony u obratlovců

Interindividuální komunikace

- Spouštěče: vyvolávají okamžitý behaviorální projev
- Primery: pomalejší změny vývoje nebo metabolismu
- Modulátory (?): ovlivňující emoce, náladu lidí

Chemické složení: velikost, polarita, těkavost:

Atraktanty nebo poplachové feromony – malé a těkavé (alkoholy)

Individuální feromony – netěkavé (proteiny)

Dva chemosensitivní systémy savců

Hlavní čichový epitel (MOE):

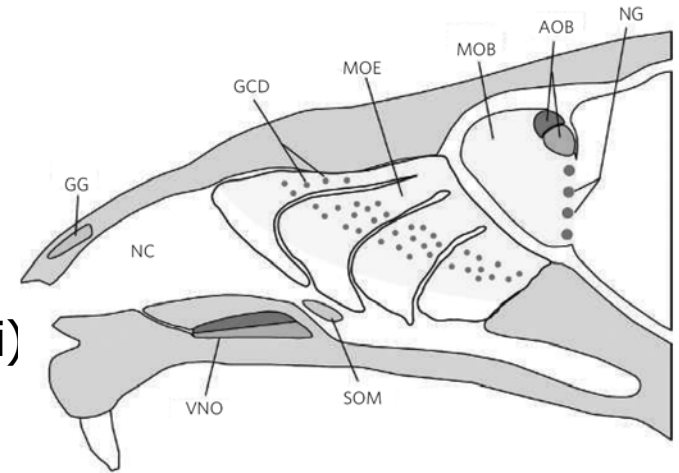
ciliární čichové buňky

Projekce do čichového laloku

Každá buňka exprimuje jediný typ receptoru (1300 u myši)

Proud vzduchu při nadechování (a vydechování)

Identifikace potravy, predátora, značení teritoria ...



Vomeronasální orgán (VNO):

Slepá dutinka

Mikrovilární morfologie

Projekce do přídatného čichového laloku (AOB)

2 třídy receptorů (G protein, ale málo příbuzné čichovým, asi 200 celkem)

Vzduch přichází „pumpováním“ při vzrušení (spíše přímým kontaktem)

Detekce feromonů, vnitrodruhová signalizace mezi pohlavími, rozmnožování, péči o ml.

V poslední době se ale ukazuje podobnost funkce



U člověka také?

AOB u dospělců nenalezen, ani inervace ne.

Izolace dvou feromonů:

Mužského z potu, ženského z moči

MRI a PET ukázaly „rozsvícení“ čichové kůry

Žen u ženského f. a hypotalamu u mužského f.

Muži reagovali opačně.

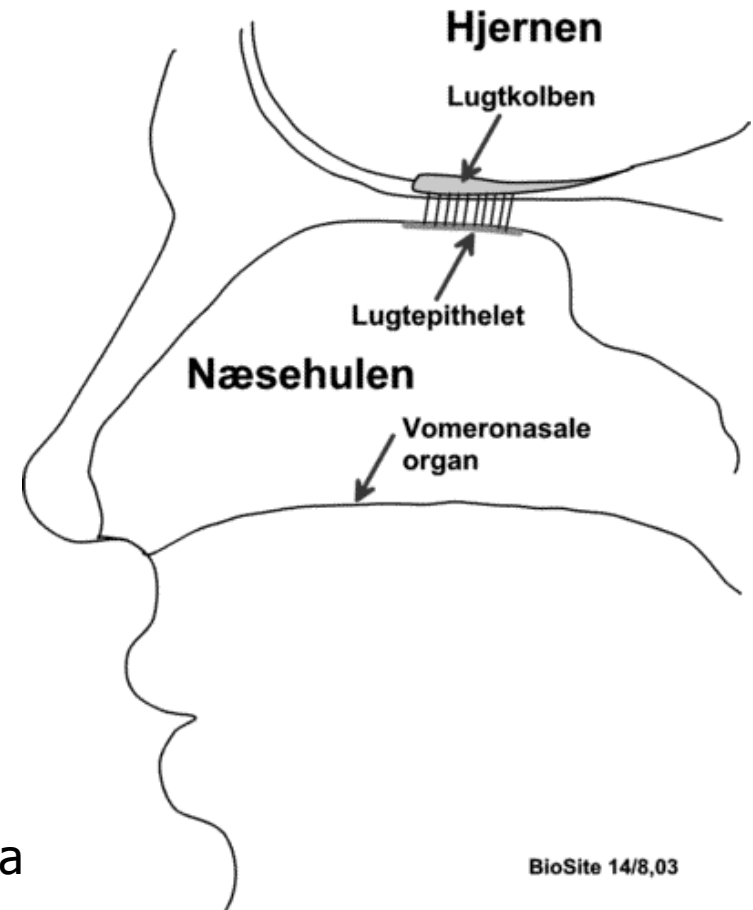
Gayové jako ženy.

MHC nepříbuznost detekovaná čichem?

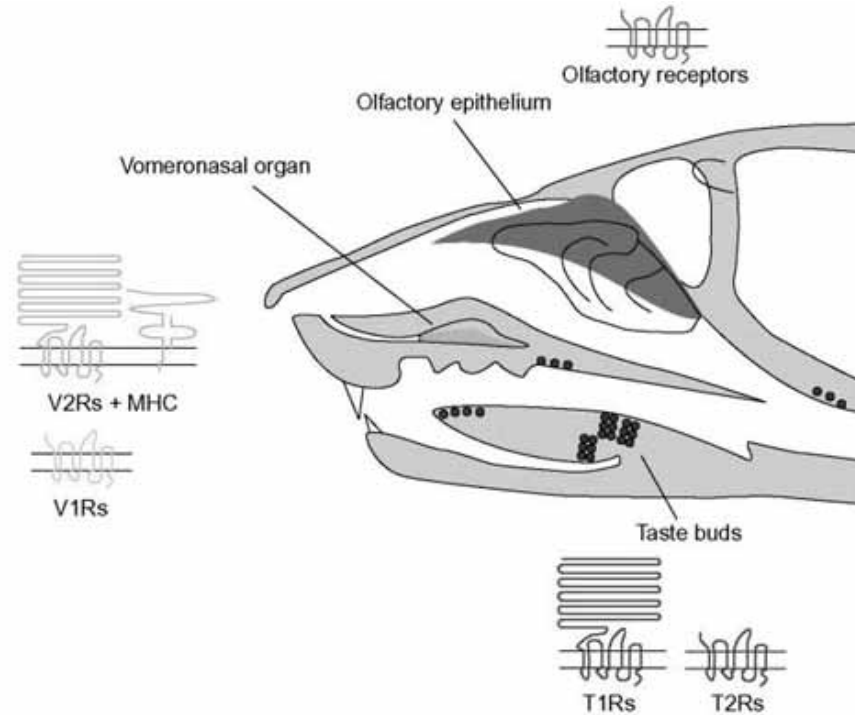
MHC molekuly ovlivňují složení těkavých látek moči a

Potu = Individualita na dálku

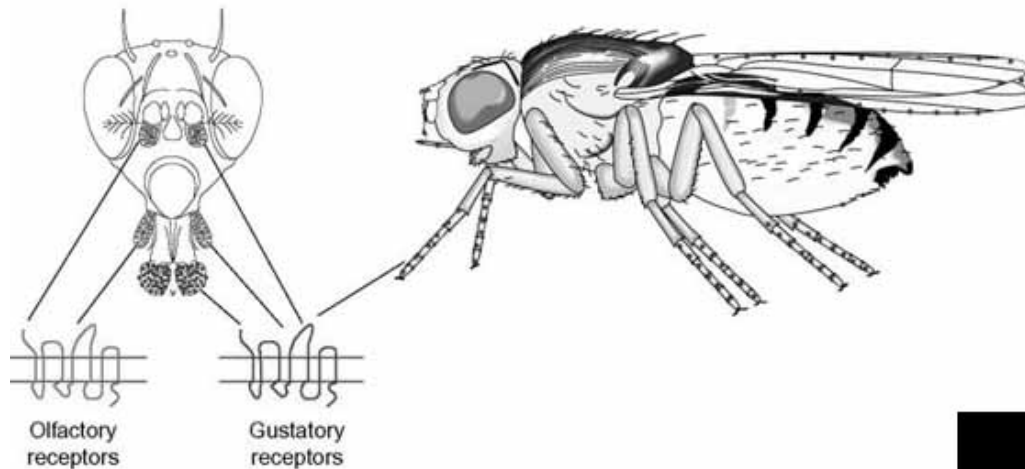
Volba partnera, afrodiziaka, parfémy...



(a)



(b)



The location of chemosensory organs in the mouse and *Drosophila*. **(a)** A sensory neuron in the olfactory epithelium of mice expresses one of about 1,000 olfactory receptors. Neurons in the apical and basal layers of the vomeronasal organ express distinct, unrelated classes of G-protein-coupled pheromone receptors (V1Rs in the apical and V2Rs in the basal layer). In addition, a small family of MHC class I-like molecules is coexpressed with V2Rs in neurons of the basal layer. The taste cells in the tongue, palate and pharynx express other classes of GPCRs, one encoding sweet-taste receptors (T1Rs) and one encoding receptors for bitter compounds (T2Rs). Note that V1Rs and T2Rs are related to each other, as are V2Rs and T1Rs, respectively. **(b)** The olfactory neurons of *Drosophila* are located in two pairs of appendages in the head, the third antennal segment and the maxillary palps, and each neuron expresses very few, possibly just one, of the 61 olfactory receptor genes identified so far. The gustatory or taste sensory neurons are located in numerous organs, including the two labial palps on the head, internal sensory clusters in the pharynx (not shown), all the legs and the anterior wing margin. Each neuron expresses a few, possibly just one, gustatory receptor gene. A few gustatory receptor genes are also expressed in olfactory neurons of the antenna and maxillary palps.

Čich a chuť



Aroma, příchuť – kromě orthonasálního ještě i retronasální olfaktorický vjem

FIGURE 14.1 Molecules released into the air inside our mouths as we chew and swallow food travel up through the retronasal passage into the nose, where they then move upward and contact the olfactory epithelium.

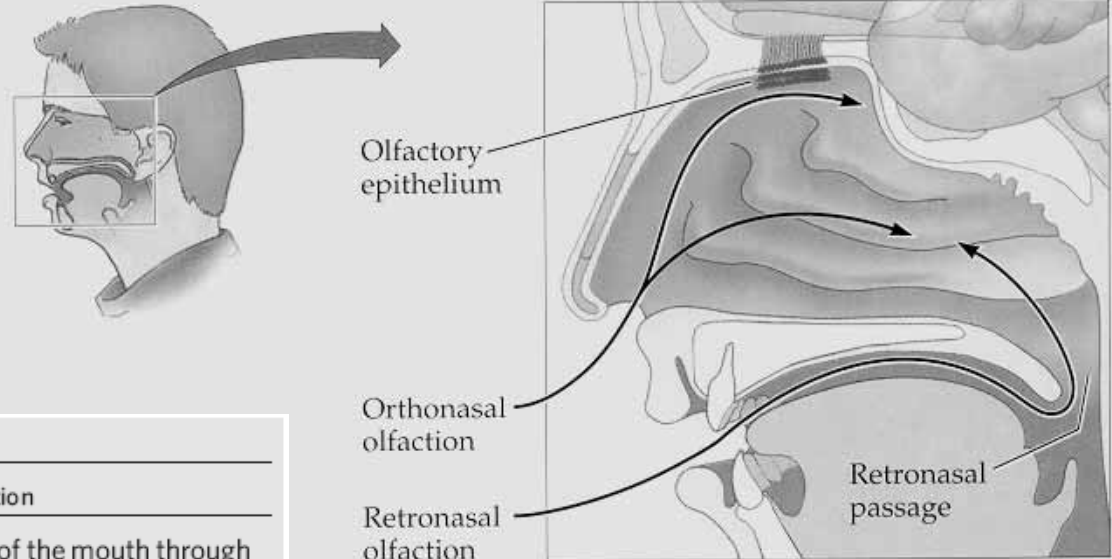


Table 1 | The dual olfactory system

Operations	Orthonasal olfaction	Retronasal olfaction
Stimulation route	Through the external nares	From the back of the mouth through the nasopharynx
Stimuli	Floral scents Perfumes Smoke Food aromas Prey/predator smells Social odors Pheromones MHC molecules	Food volatiles
Processed by	Olfactory pathway influenced by the visual pathway	Olfactory pathway combined with pathways for taste, touch, sound and active sensing by proprioception form a 'flavour system'

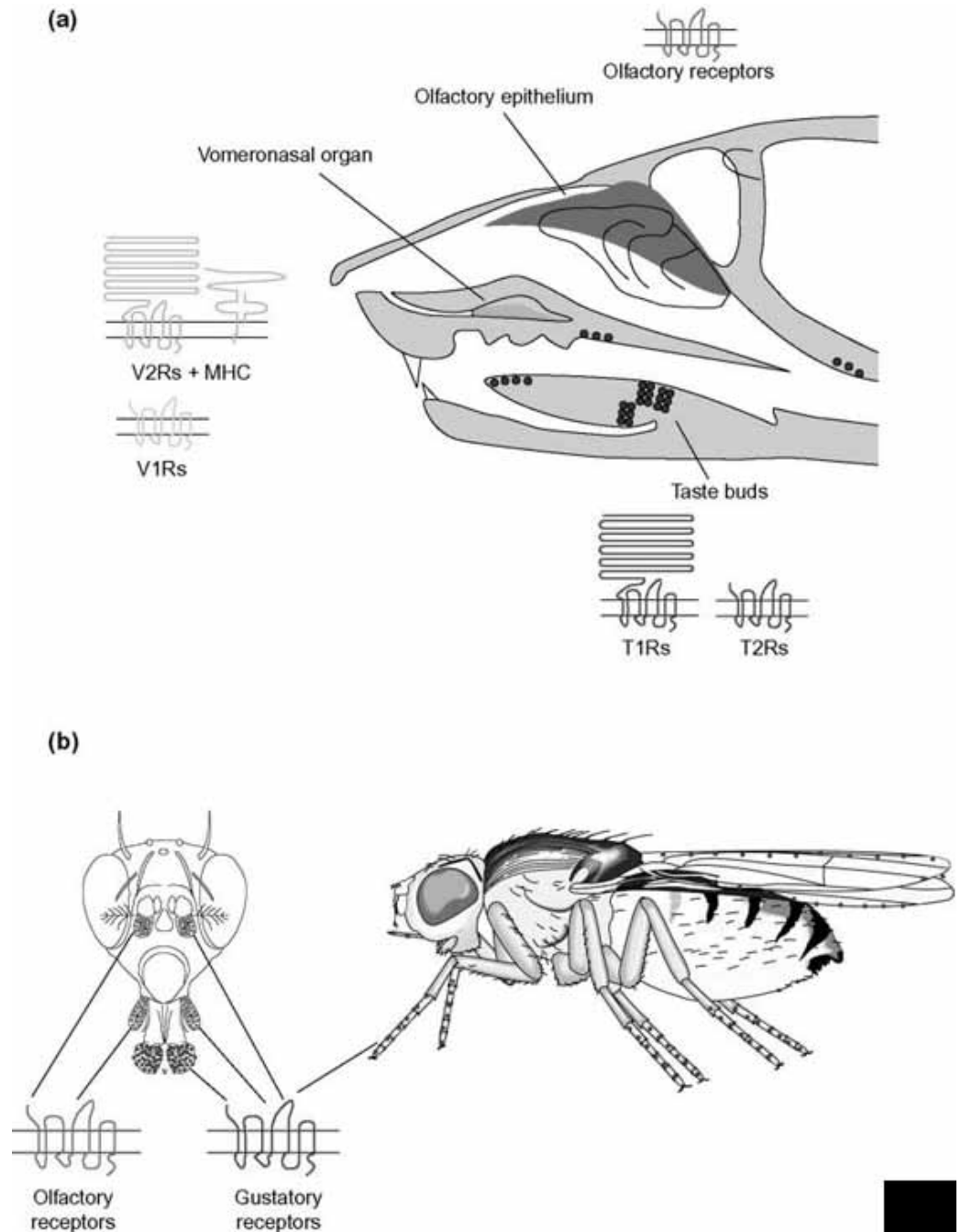
Note the interesting contrast, that orthonasal olfactory perception involves a wide range of types of odors processed through only the olfactory pathway, in comparison with retronasal olfactory perception which involves only food volatiles but processed in combination with many brain pathways.

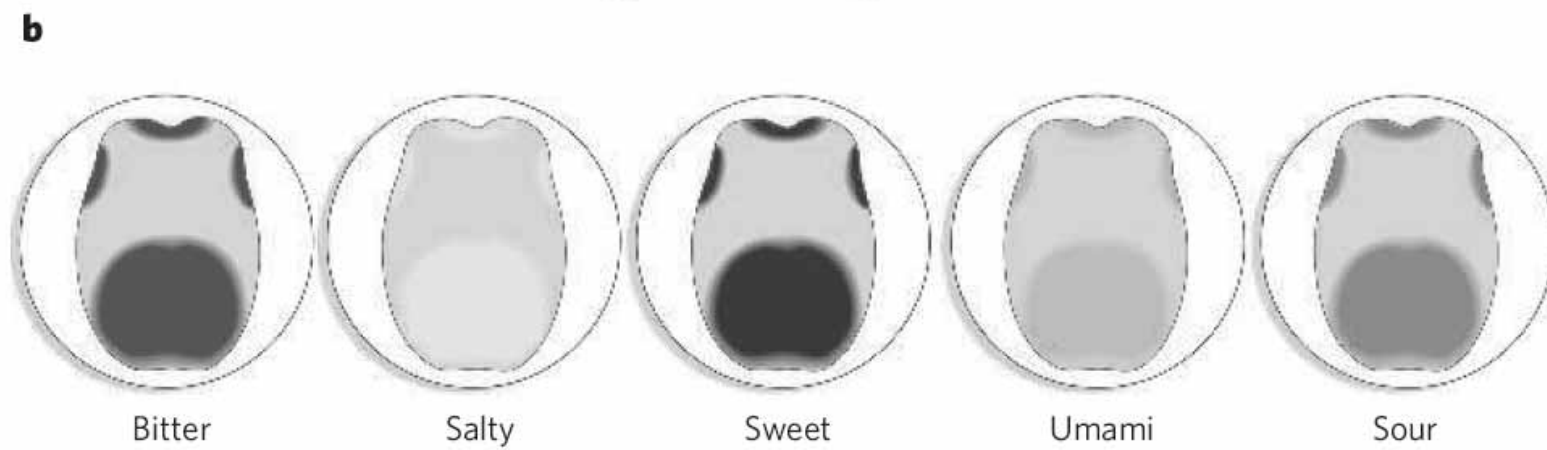
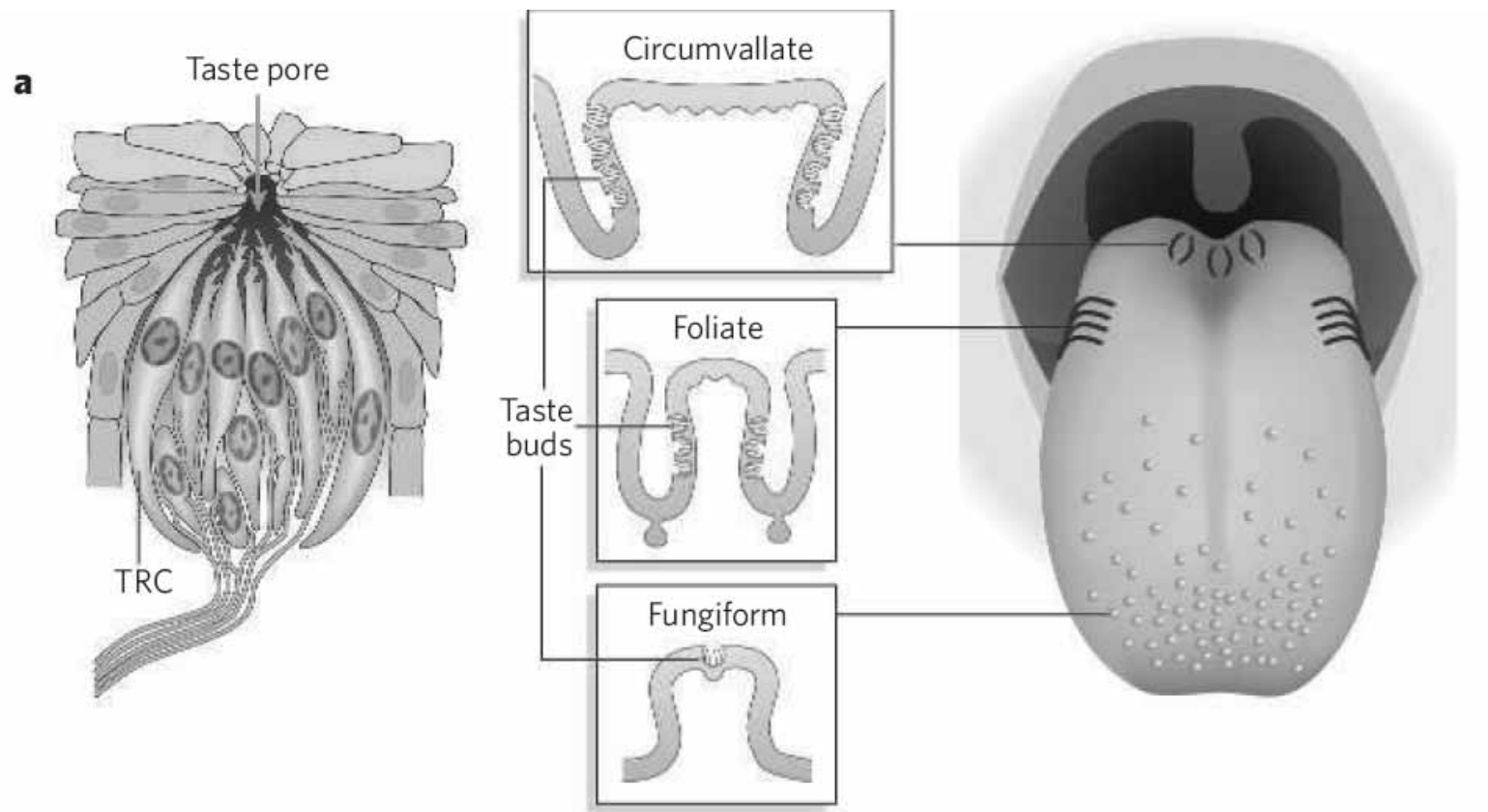
Chut'

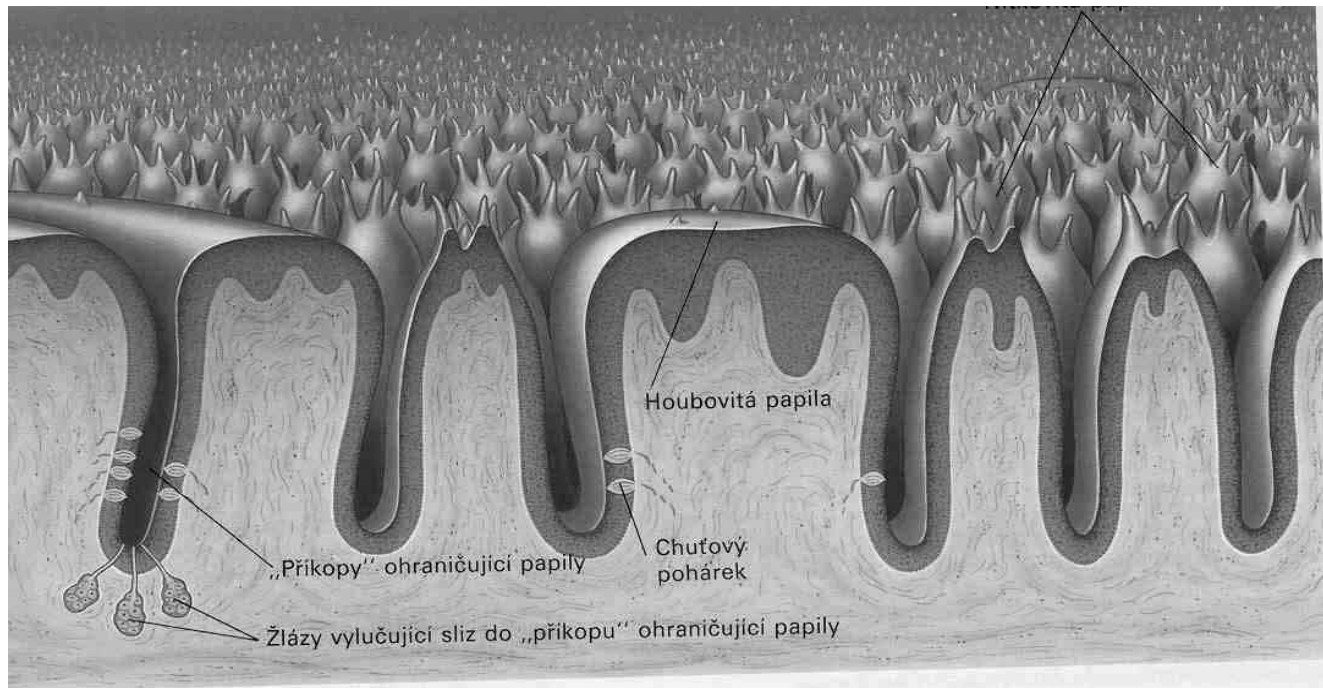


Chuť

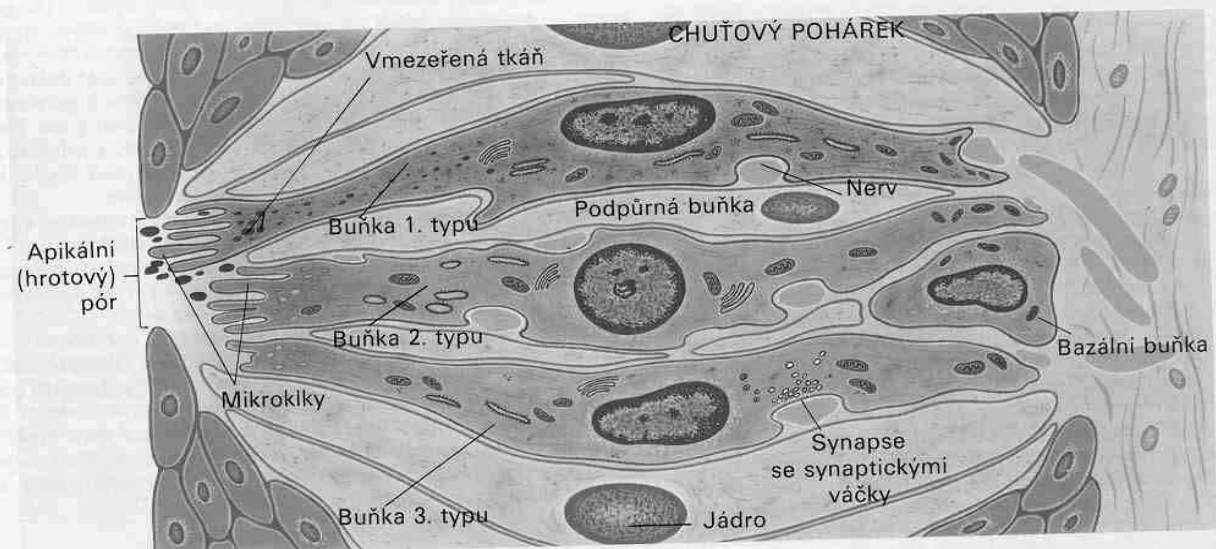
Na rozdíl od čichu je to smysl, kontaktní, méně citlivý, má mnohem méně receptorů, ale překvapivě různá transdukční schémata.



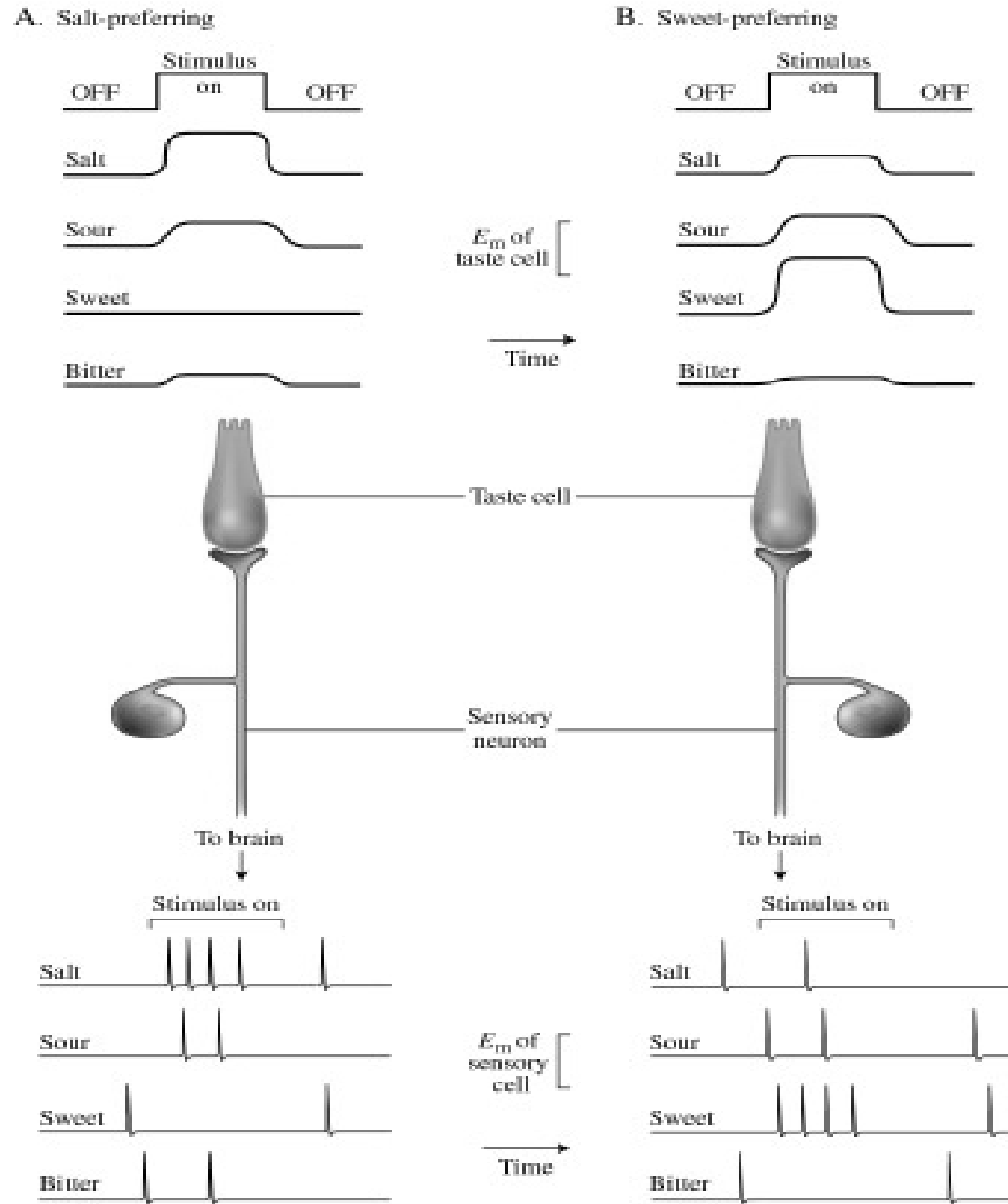




v „přikopech“ obklopujících jejich centrální val, reagují na chutě hořké. Mezery mezi papilami zvlhčuje sliz, vylučovaný žlázami umístěnými na bázi těchto mezer. Chuťové molekuly se musí v tomto vlhkém prostředí nejprve rozptýlit, a teprve poté je mohou chuťové pohárky detekovat.



Selektivita omezená.



Transdukční schémata

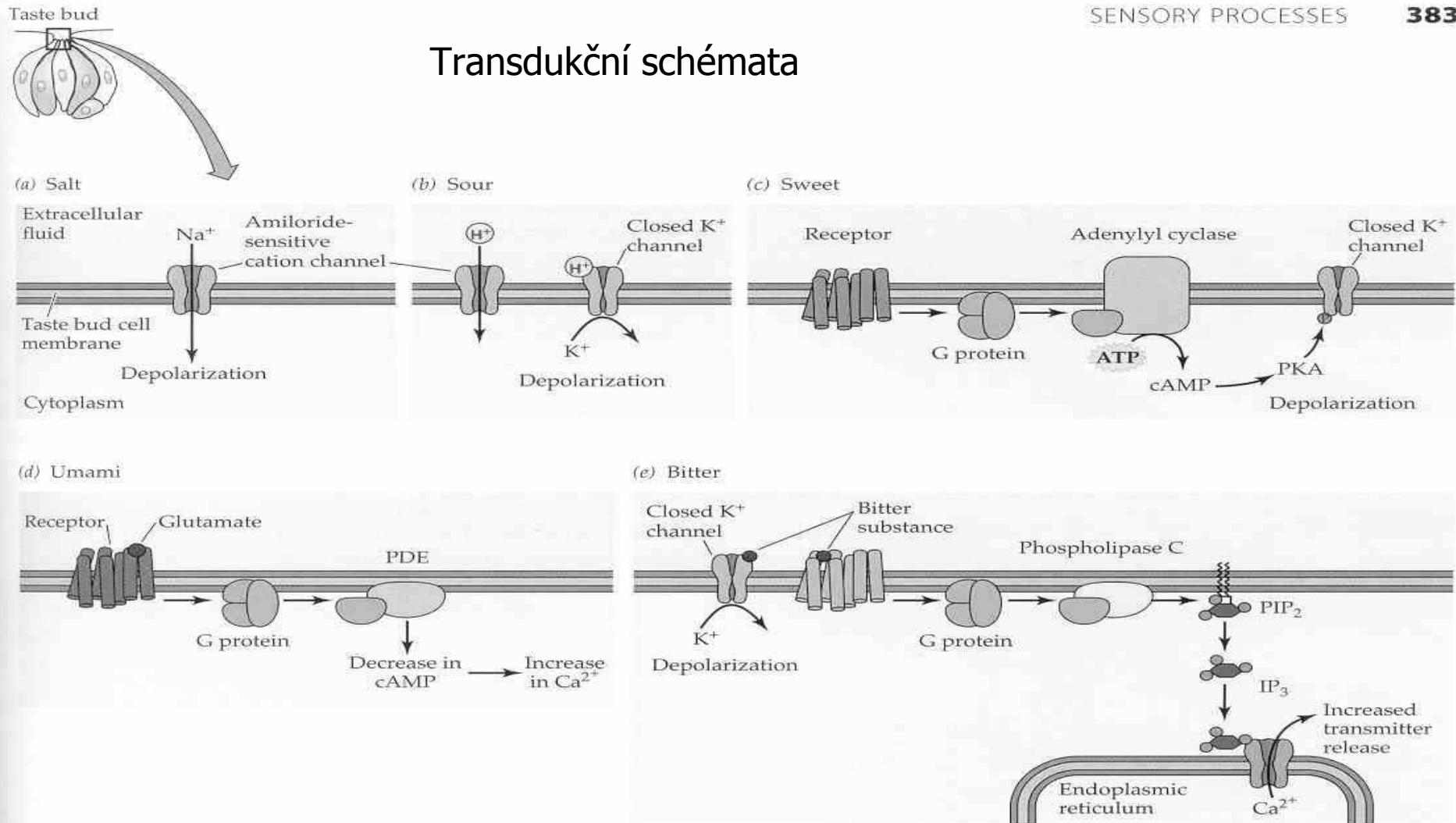
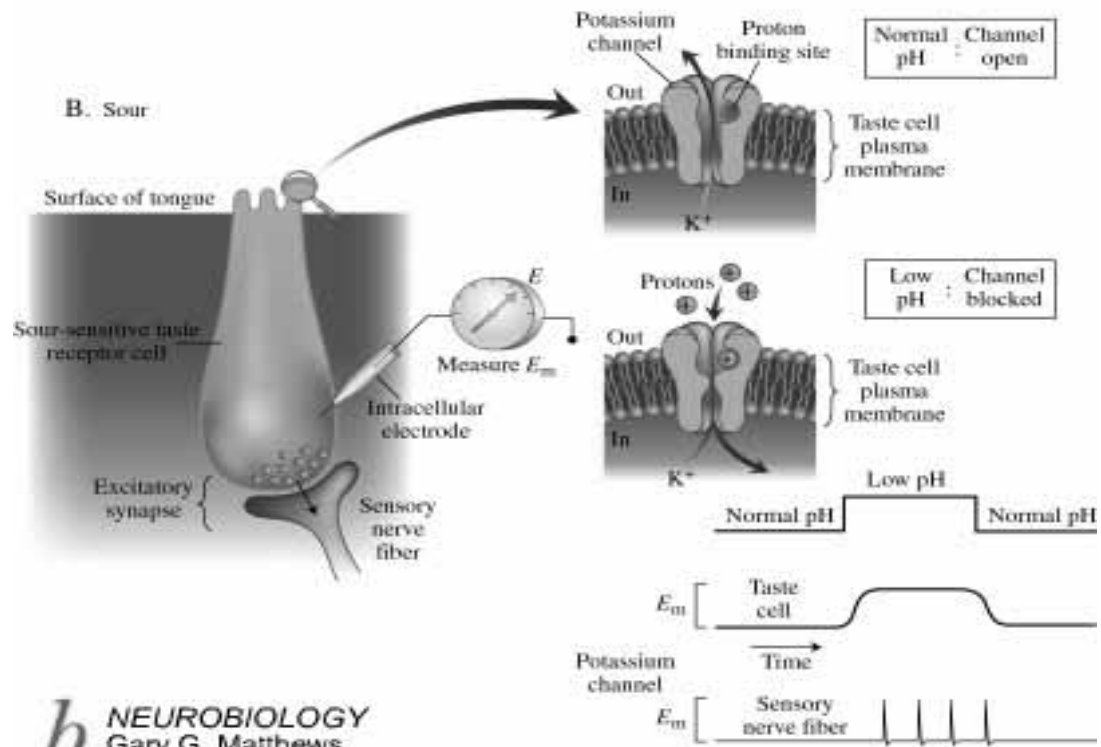
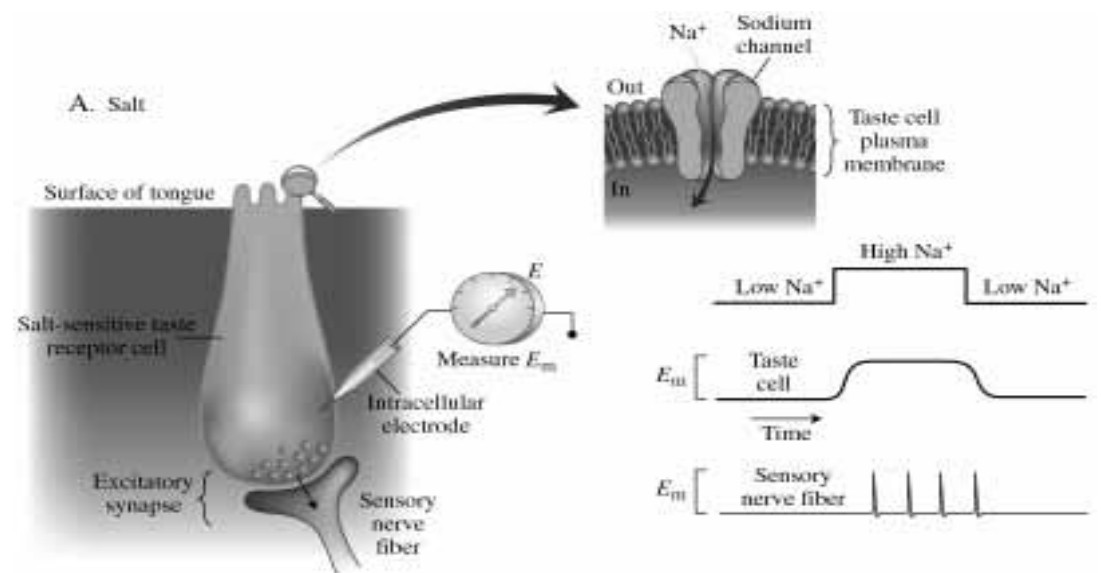


Figure 13.34 Taste-transduction mechanisms differ for different taste qualities All transduction mechanisms except the IP_3 action in (e) lead to *depolarization*, which spreads to the basal end of the cell and opens voltage-gated Ca^{2+} channels to allow Ca^{2+} entry and transmitter release. (a) For salt taste, sodium ions enter a taste bud cell through amiloride-sensitive cation channels, directly depolarizing the cell. (b) In sour taste, either H^+ ions enter the cell through amiloride-sensitive cation channels, or they close K^+ channels to produce depolarization. (c) Sweet taste is most commonly mediated by the binding of sugars to a G protein-coupled receptor, which acts via a G protein to activate adenylyl cyclase and produce cyclic AMP. Cyclic AMP then activates protein kinase A (PKA) to close a K^+ channel (by phosphorylating

it), producing depolarization. (d) The amino acid glutamate (monosodium glutamate, MSG) stimulates the taste quality umami (a savory or meaty quality). Glutamate binds to a G protein-coupled receptor (related to synaptic metabotropic glutamate receptors) to activate a phosphodiesterase (PDE) and decrease the concentration of cAMP. The decrease in cAMP leads to an increase in intracellular Ca^{2+} concentration. (e) Bitter taste mechanisms can involve a G protein-coupled receptor for bitter substances that acts via a G protein and phospholipase C to produce IP_3 . IP_3 liberates Ca^{2+} ions from intracellular stores, eliciting transmitter release without requiring depolarization. Other bitter substances bind to K^+ channels and close them to depolarize the cell.

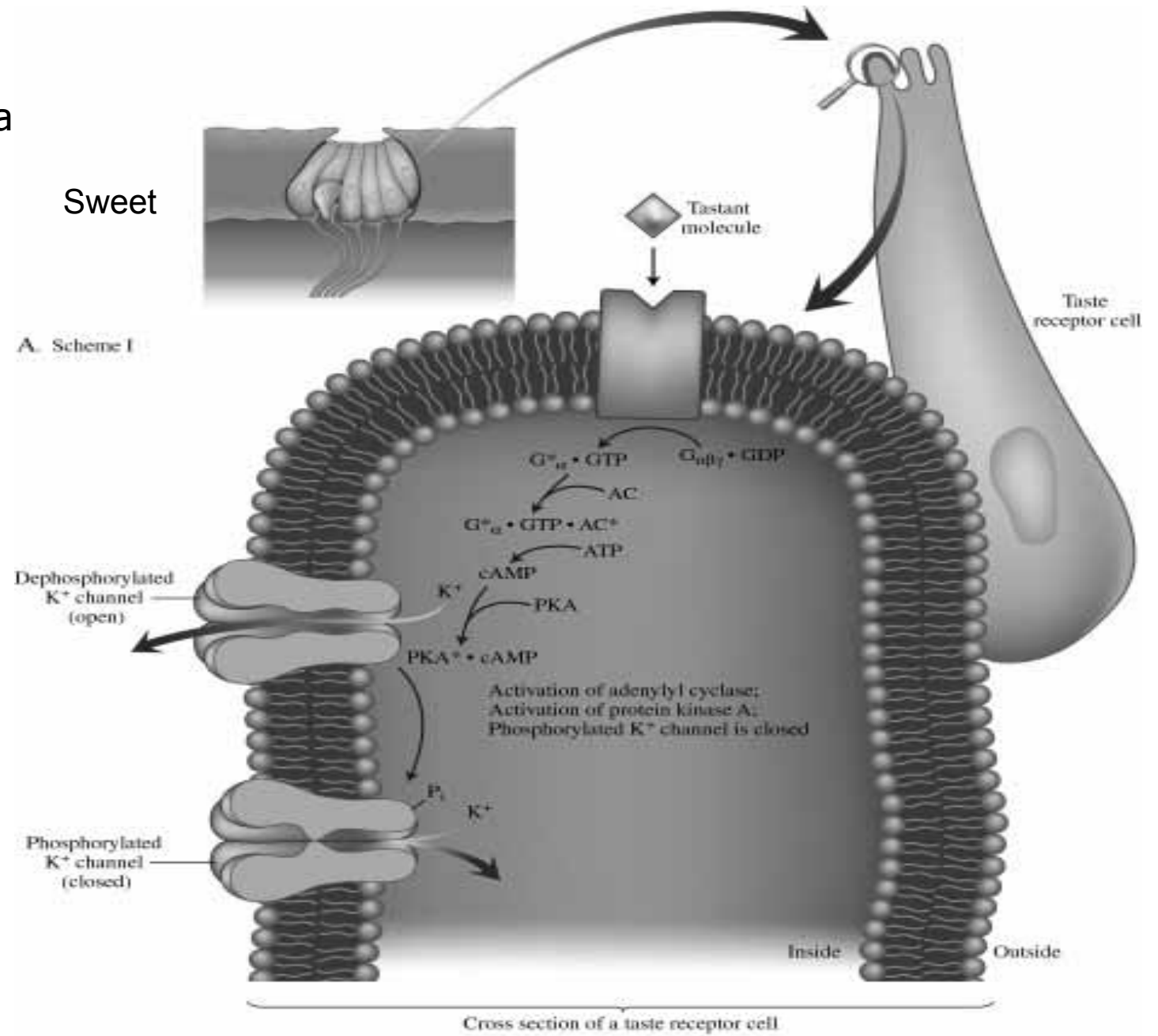
Transdukční schémata



Transdukční schémata

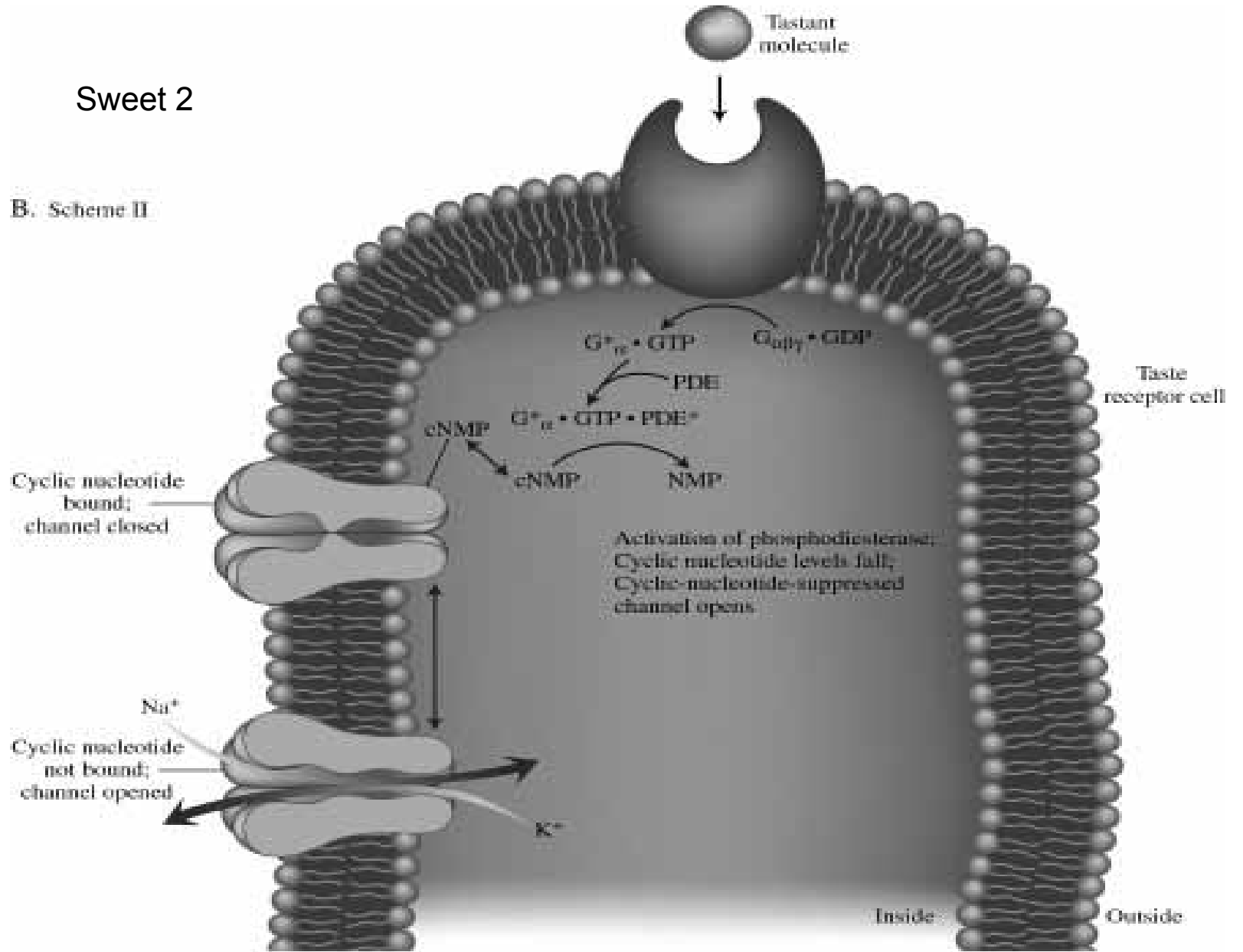
Sweet

A. Scheme 1



Sweet 2

B. Scheme II



Bitter

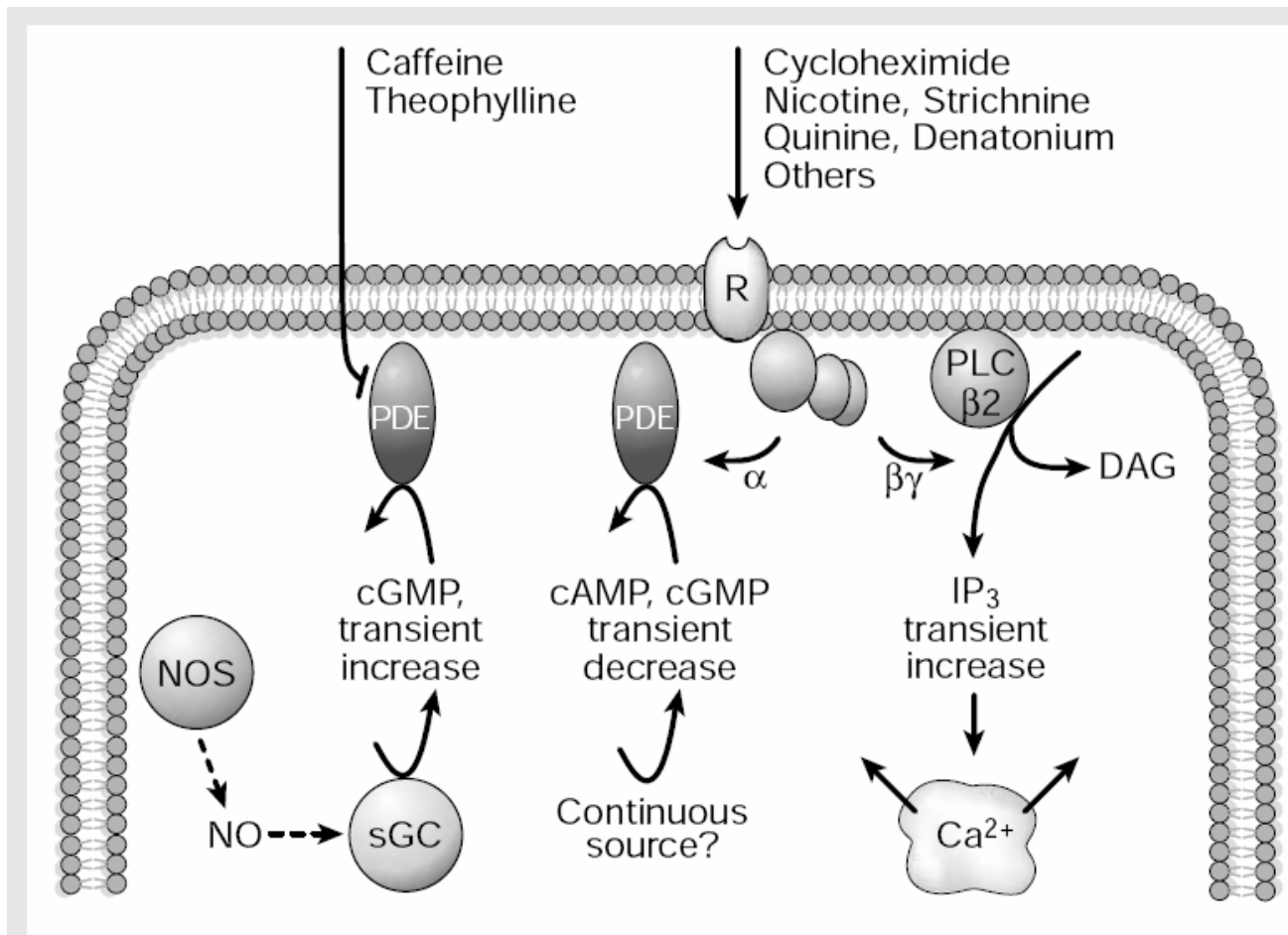


Figure 3 Transduction of bitter taste as elicited by a variety of ligands. Rs, multiple GPCRs of the T2R family, coupled to the G protein gustducin⁴⁷⁻⁴⁹; α , α -subunit of gustducin^{6,57}; $\beta\gamma$, G-protein subunits β 3 and γ 13 (refs 60-62); PLC β 2, phospholipase C subtype⁶¹; Ins(1,4,5)P $_3$, inositol-1,4,5-trisphosphate⁵⁹; PDE, taste-specific phosphodiesterase⁵⁸; cAMP, cyclic adenosine monophosphate⁵⁹; cGMP, cyclic guanosine monophosphate⁵⁹; sGC, soluble guanylate cyclase⁵⁵; NO, nitric oxide⁵⁵; NOS, NO synthase⁵⁶. For second-messenger kinetics, see refs 55,59,63,64.

Kódování chuťové kvality: labeled lines (analogie sluchu) nebo specifické vzorce aktivity (analogie b.vidění nebo čichu – jeden receptor o kvalitě nic neříká a směs dvou dává třetí kvalitu)

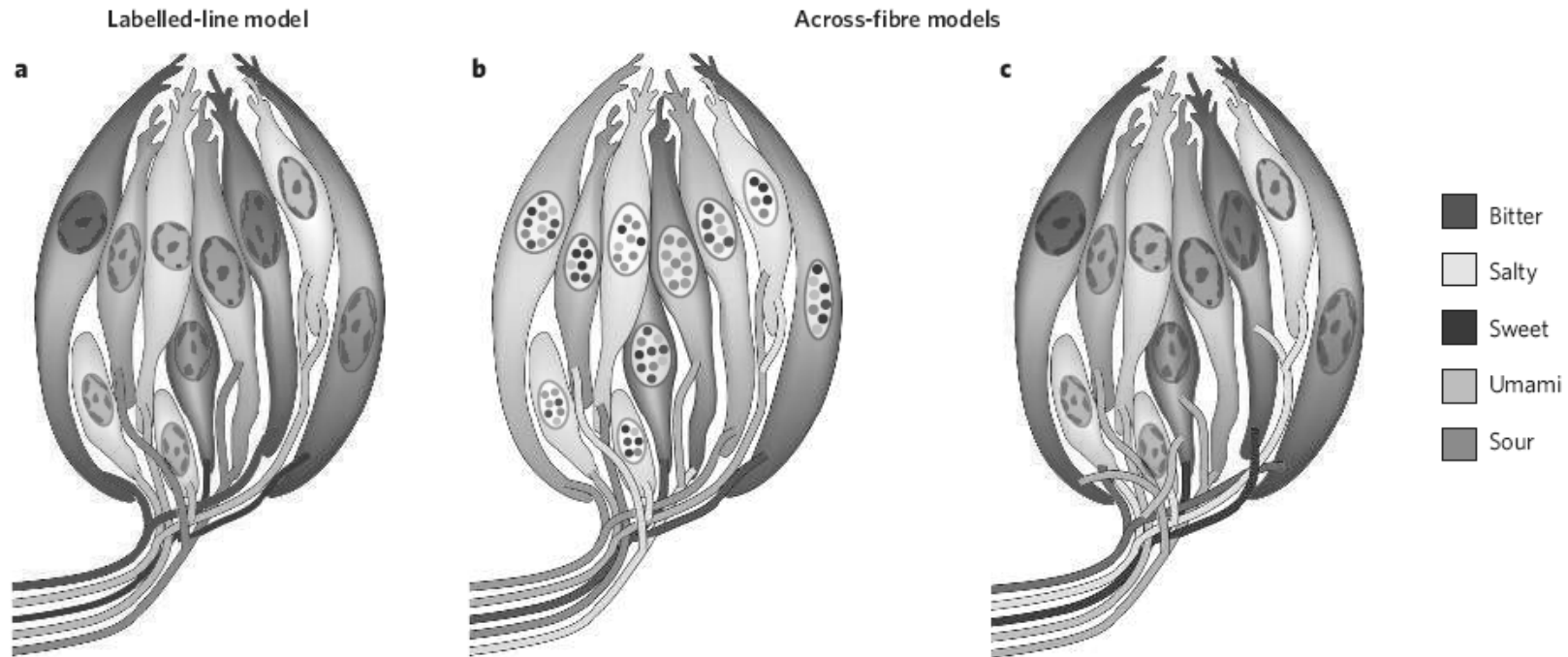
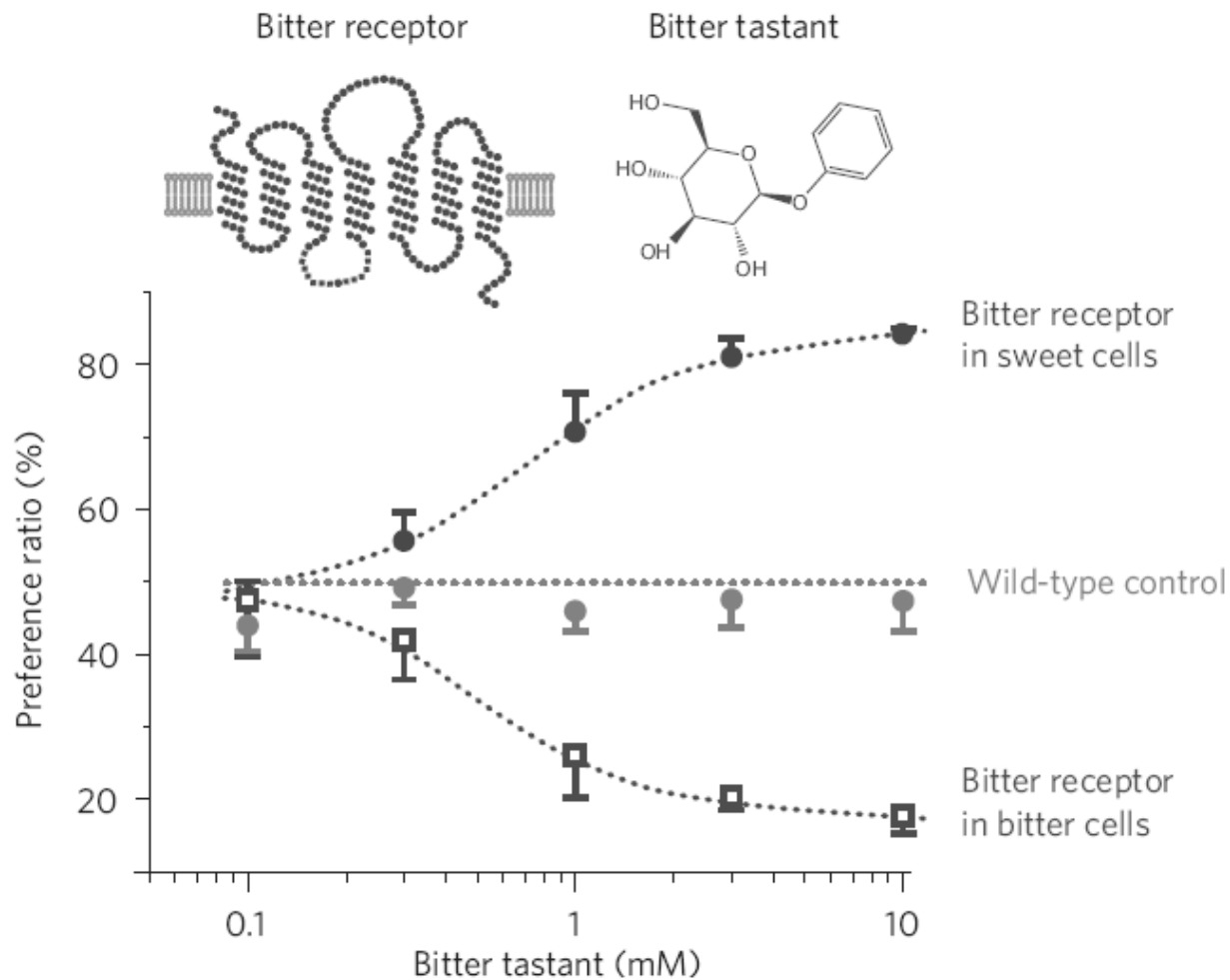


Figure 2 | Encoding of taste qualities at the periphery. There are two opposing views of how taste qualities are encoded in the periphery. **a**, In the labelled-line model, receptor cells are tuned to respond to single taste modalities — sweet, bitter, sour, salty or umami — and are innervated by individually tuned nerve fibres. In this case, each taste quality is specified by the activity of non-overlapping cells and fibres. **b, c**, Two contrasting models of what is known as the ‘across-fibre pattern’. This states that either individual TRCs are tuned to multiple taste qualities (indicated by various tones of grey and multicoloured stippled nuclei), and consequently the same afferent fibre carries information for more than one taste modality (**b**), or that TRCs are still tuned to single taste qualities but the same afferent fibre carries information for more than one taste modality (**c**). In these two models, the specification of any one taste quality is embedded in a complex pattern of activity across various lines. Recent molecular and functional studies in mice have demonstrated that different TRCs define the different taste modalities, and that activation of a single type of TRC is sufficient to encode taste quality, strongly supporting the labelled-line model.

Transgenní myši



Vnímání sladkého nebo hořkého odráží aktivaci jen určitých buněk bez ohledu na vlastnosti receptoru nebo chuťových molekul

Každou jednotlivou chuť rozeznáme i ve směsi chutí – ochrana.

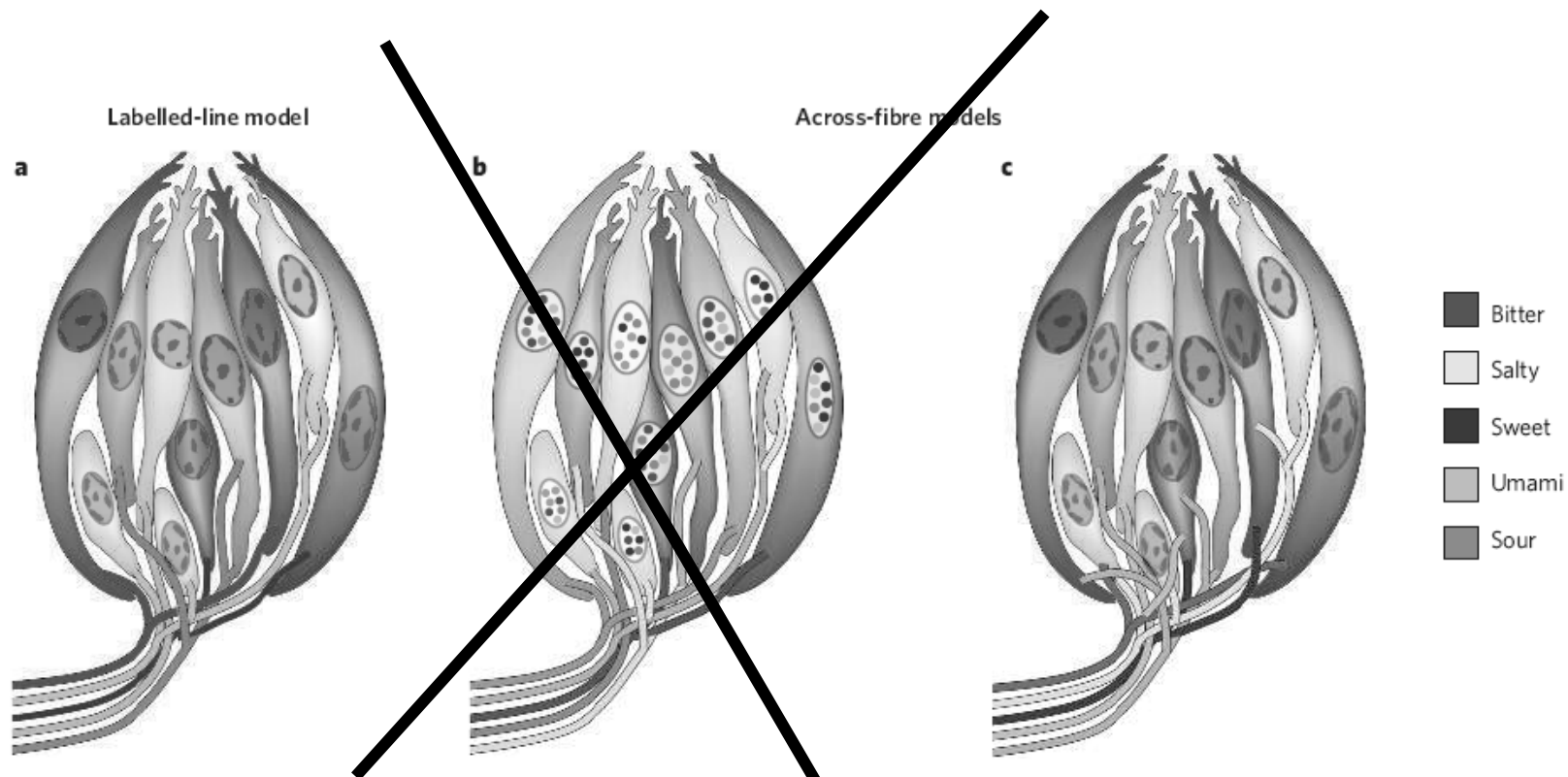
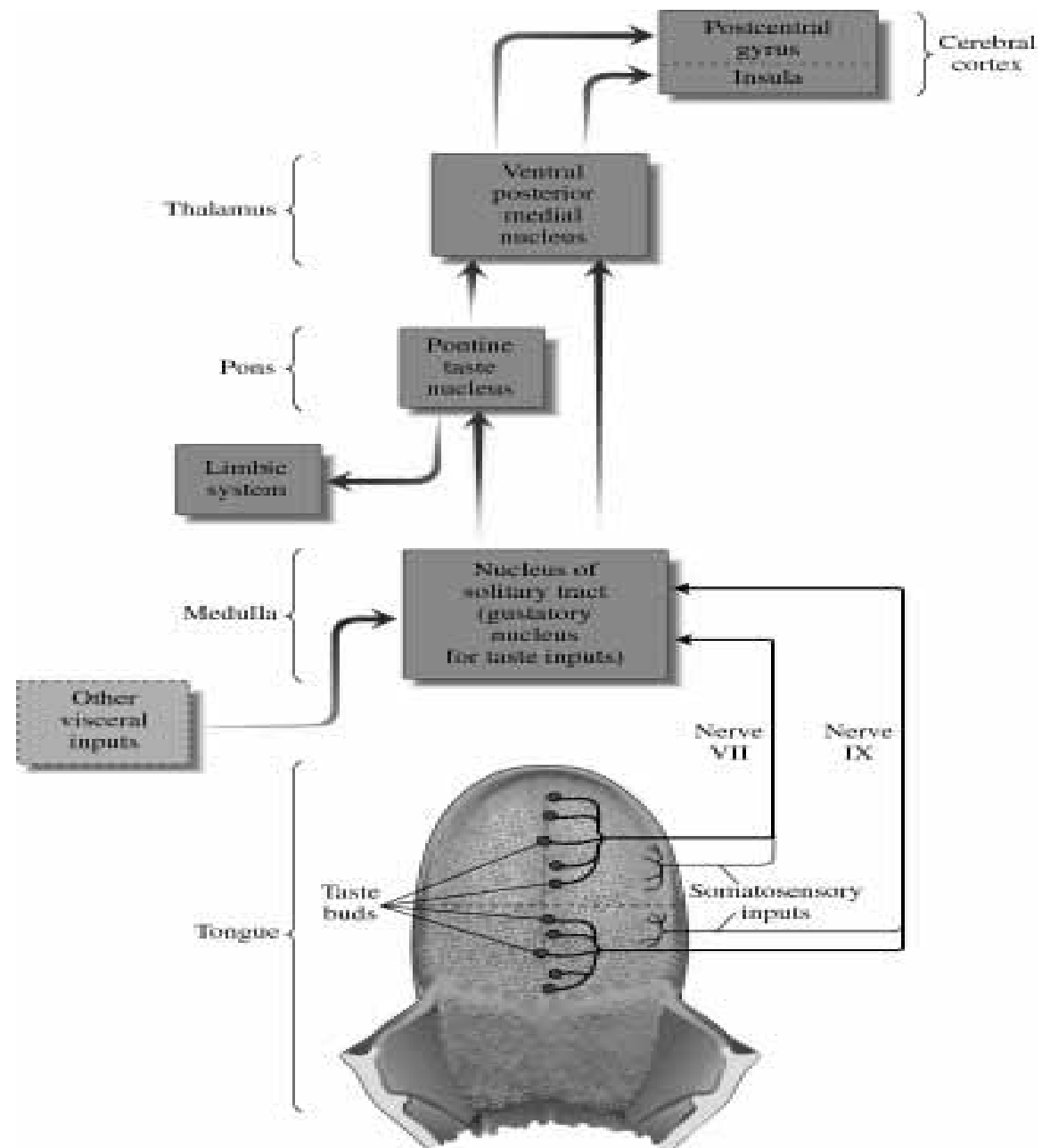
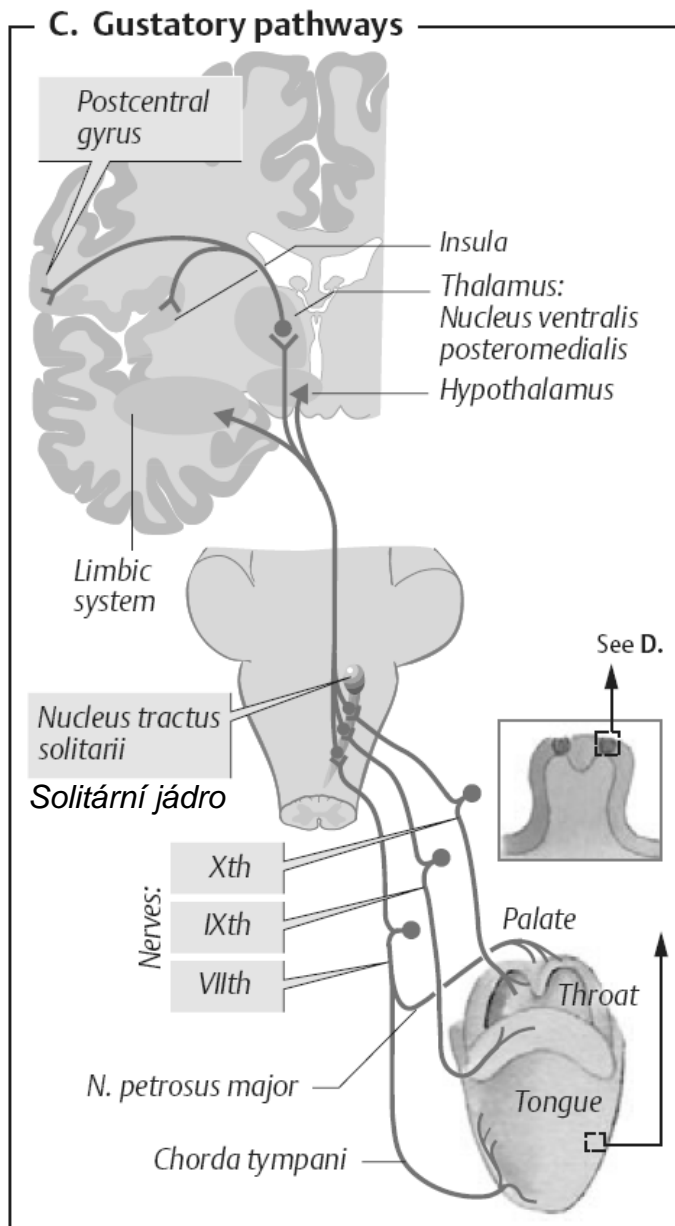
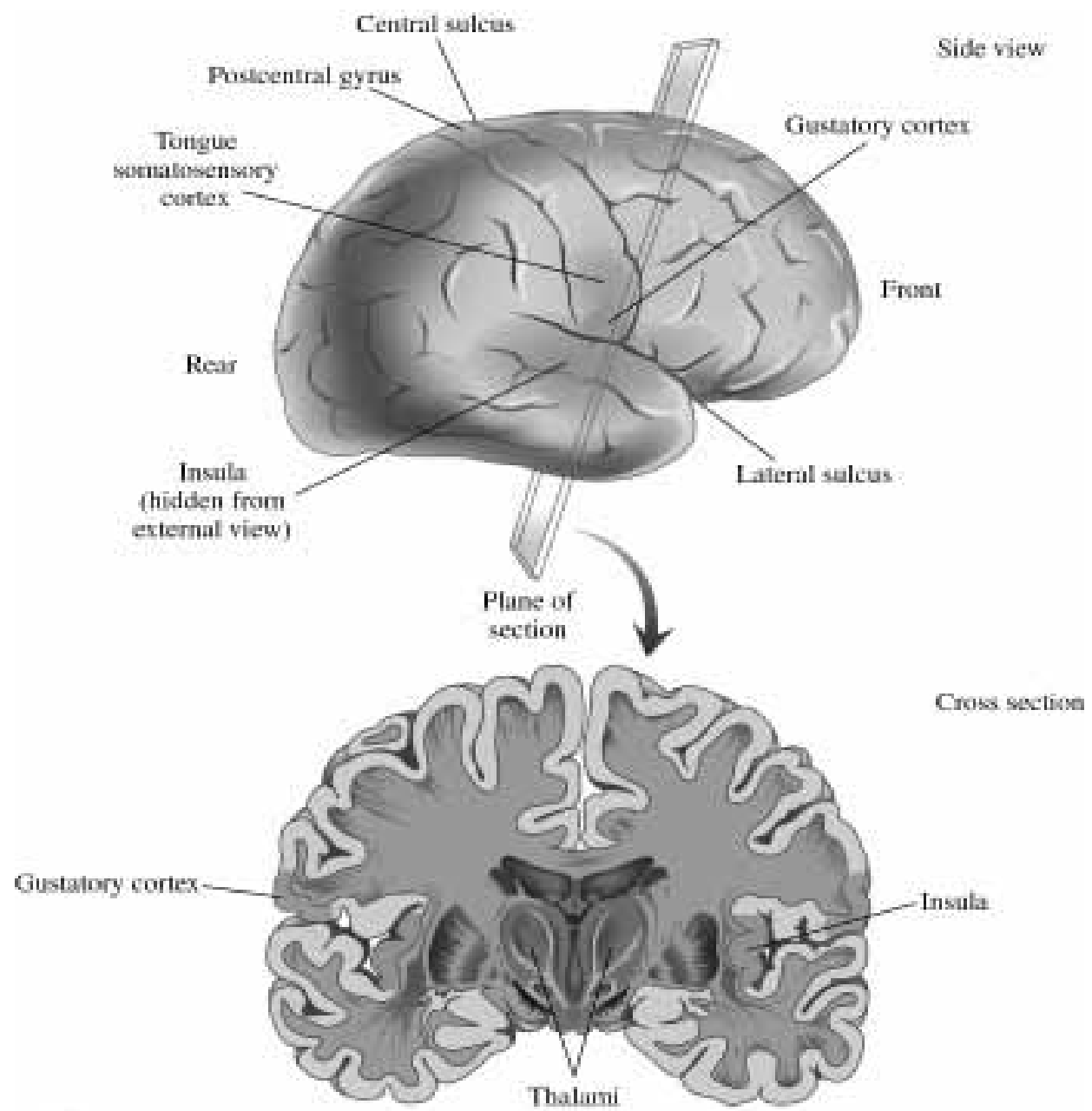


Figure 2 | Encoding of taste qualities at the periphery. There are two opposing views of how taste qualities are encoded in the periphery. **a**, In the labelled-line model, receptor cells are tuned to respond to single taste modalities — sweet, bitter, sour, salty or umami — and are innervated by individually tuned nerve fibres. In this case, each taste quality is specified by the activity of non-overlapping cells and fibres. **b, c**, Two contrasting models of what is known as the ‘across-fibre pattern’. This states that either individual TRCs are tuned to multiple taste qualities (indicated by various tones of grey and multicoloured stippled nuclei), and consequently the same afferent fibre carries information for more than one taste modality (**b**), or that TRCs are still tuned to single taste qualities but the same afferent fibre carries information for more than one taste modality (**c**). In these two models, the specification of any one taste quality is embedded in a complex pattern of activity across various lines. Recent molecular and functional studies in mice have demonstrated that different TRCs define the different taste modalities, and that activation of a single type of TRC is sufficient to encode taste quality, strongly supporting the labelled-line model.





Potěšení z chutí - vrozené prospěšné reflexy. Zvýšená chuť na chybějící složku.

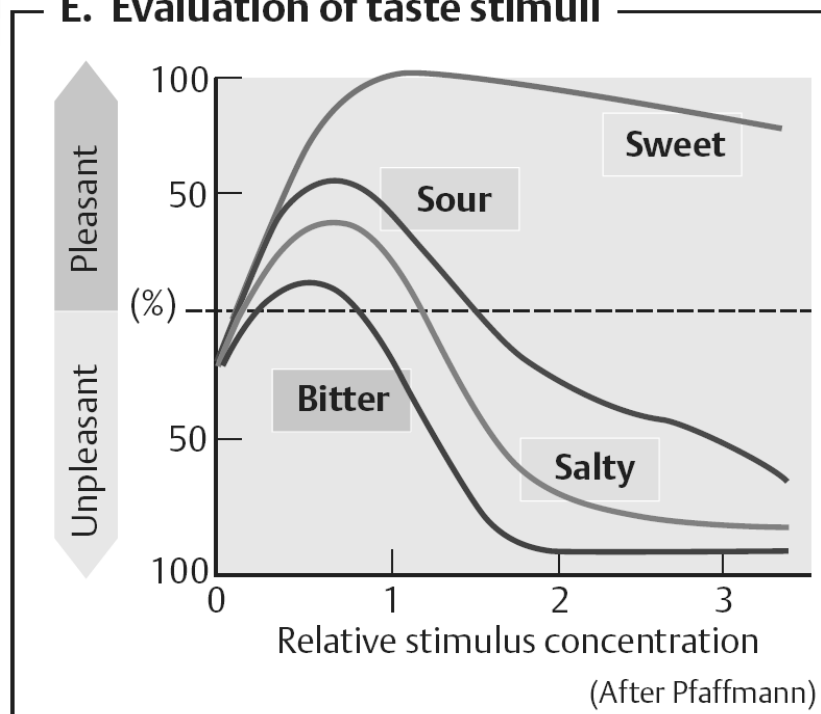
(a)



(b)



E. Evaluation of taste stimuli



Hygroreceptor

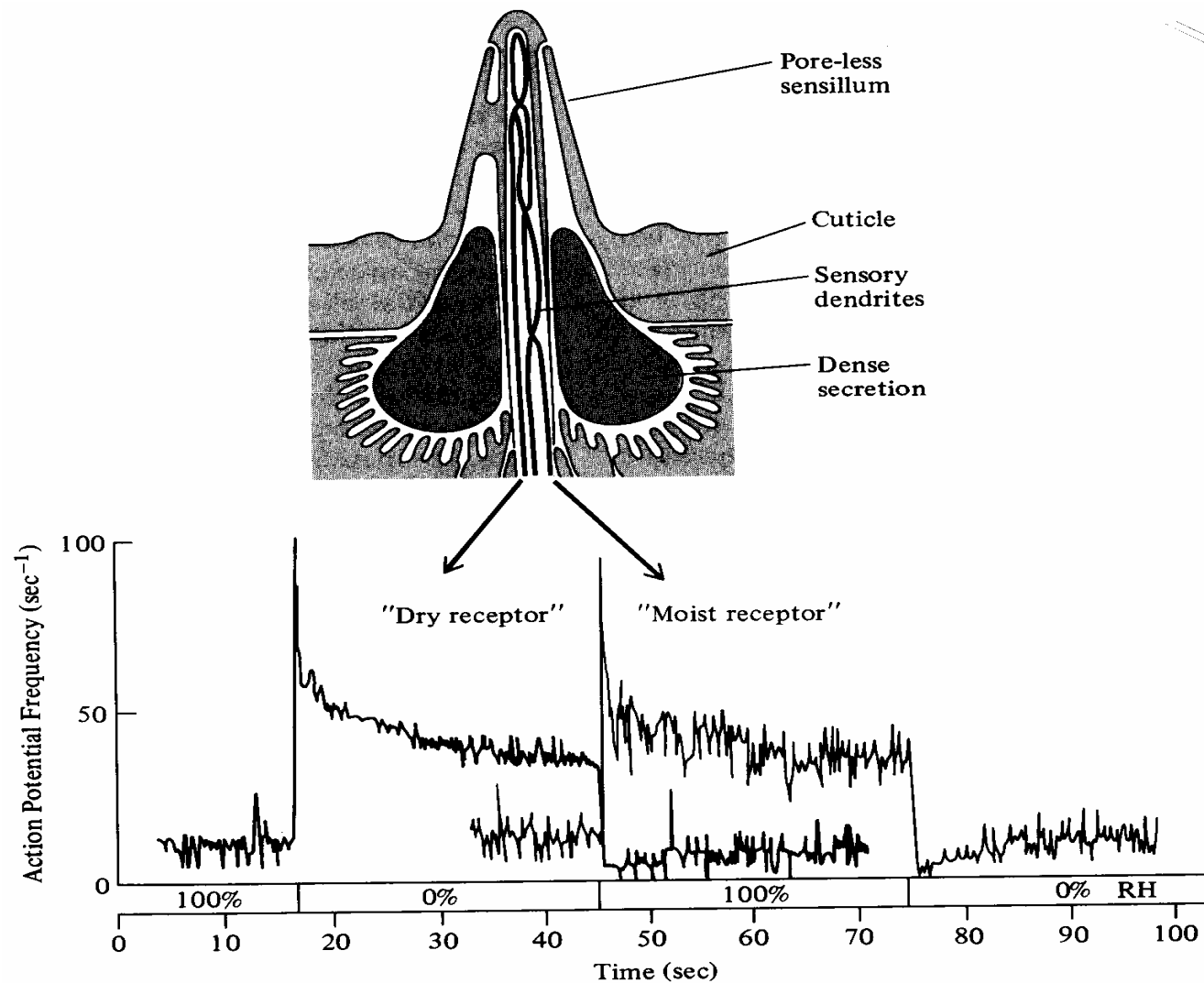


FIGURE 7-18 The “cold-moist-dry” triad sensory sensillum of the cockroach contains three bipolar sensory neurons; one neuron of the hygroreceptor responds to high humidity (“moist” receptor) and one to low humidity (“dry” receptor). The receptor cavity of the poreless sensillum is filled with a dense secretion. (Modified from Yokohari and Tateda 1976; Schaller 1978.)

Termorecepce

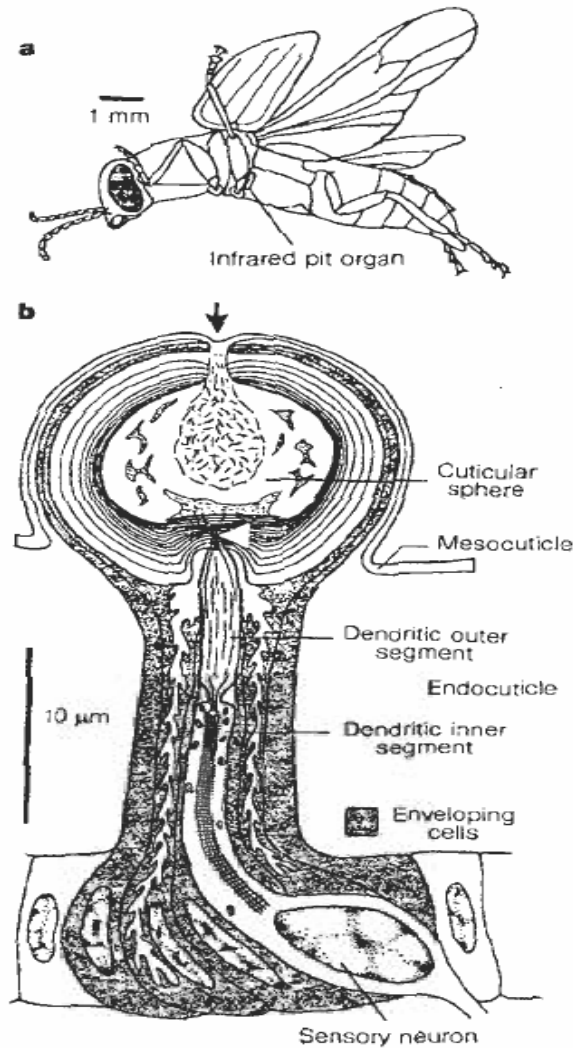


Figure 1 a, Diagram of *Melanophila* (body length 10 mm). The infrared pit organs, situated next to the coxae of the middle legs, are completely exposed during flight. b, An infrared sensillum, redrawn from ref. 3.

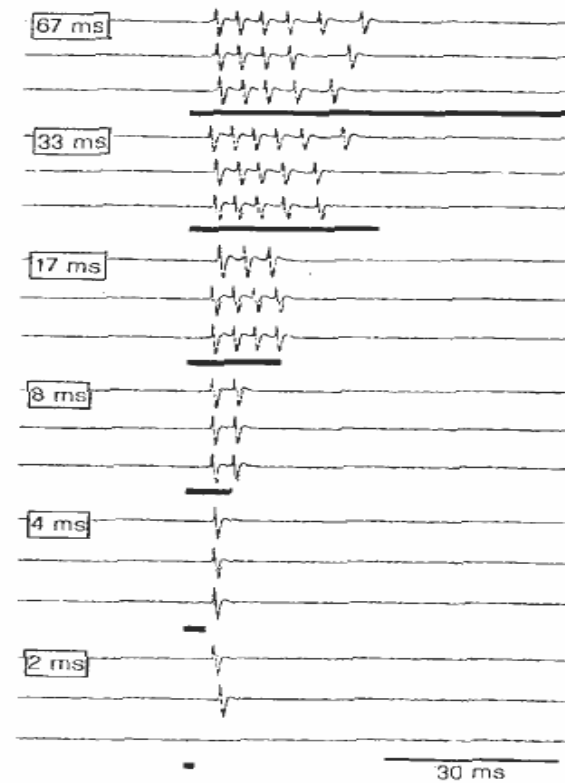


Figure 2 The responses of a neuron, recorded from the pit organ, to various infrared stimuli. Each trace shows the original response to one stimulus. Horizontal bars indicate exposure times. Each trial was repeated three times. The number of action potentials decreases with decreasing stimulus duration; 2 ms was sufficient to generate a response. If the mirror was covered, no response was recorded at any of the infrared intensities and shutter speeds tested.

pass infrared filter (50% cut-on at 1.8 μm) and neutral-density filters. At a radiation intensity of 24 mW cm⁻² single neurons

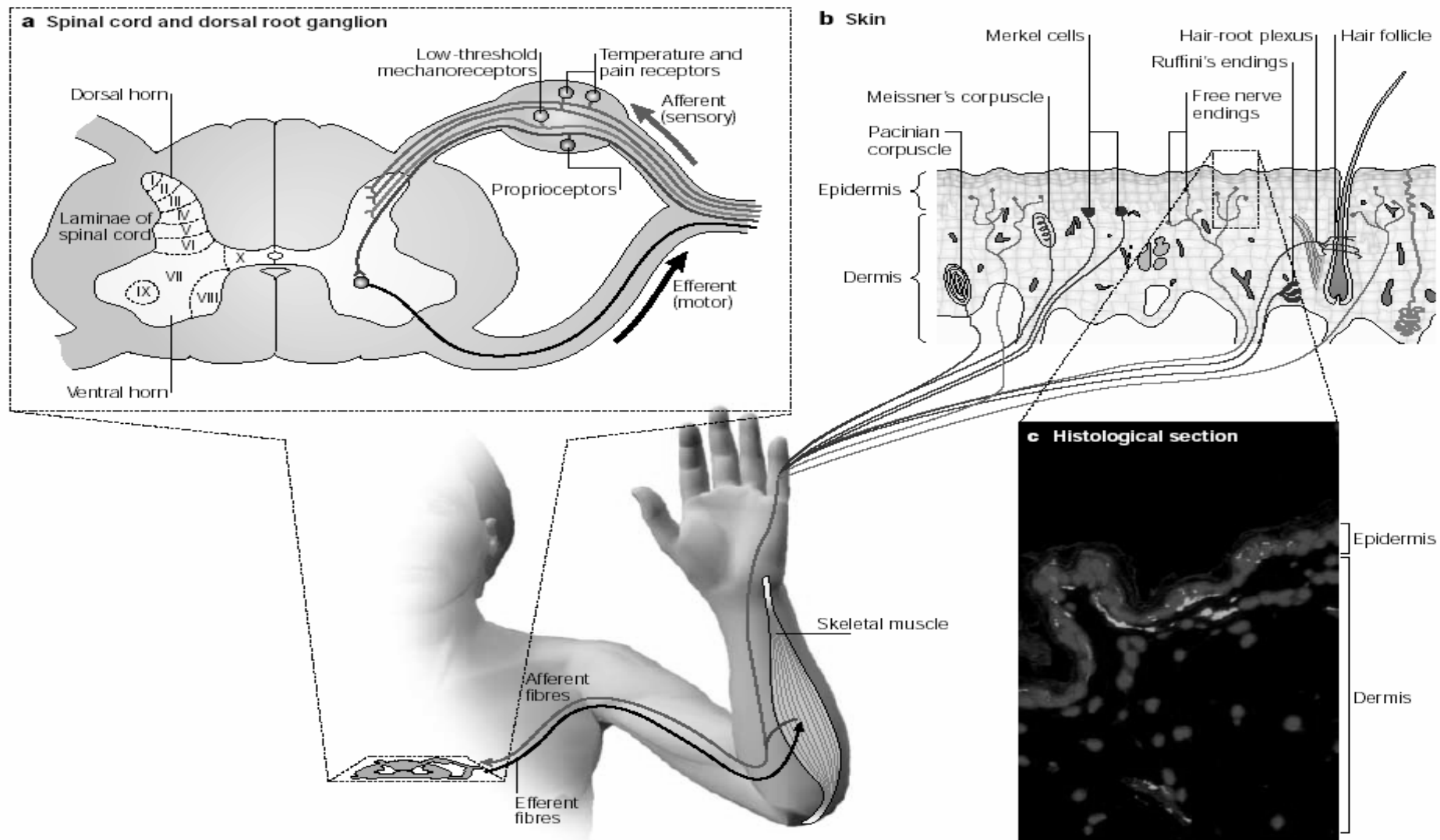


Figure 1 | **Anatomic and functional organization of touch.** **a** | Spinal nerves formed by the joining of afferent (sensory) and efferent (motor) roots provide peripheral innervation to skin, skeletal muscle, viscera and glands. Arrows denote the direction of incoming sensory and outgoing motor impulses. The cell bodies of motor neurons are located within the ventral horn (laminae VII-IX) of the spinal cord. Cell bodies of sensory neurons are located in the dorsal root ganglia (DRG). Within the DRG there are subclasses of sensory neurons known as proprioceptive (blue), low-threshold mechanosensitive (red) and temperature- and pain-sensing neurons (green). These neurons project centrally to dorsal horn interneurons (laminae I-VI of the spinal cord) and peripherally to target tissues. Proprioceptive neurons (blue fibre) project to specialized structures within target tissues such as muscle, and sense muscle stretch. **b** | Low-threshold mechanosensitive neurons (red fibres) project to end organs that transmit mechanical stimuli. Five types of mechanosensitive assemblies have been described and are illustrated in the figure. Temperature and pain sensing neurons (green) do not project to specialized end organs; instead they terminate as free nerve endings in all layers of the skin, and near blood vessels and hair follicles. **c** | Section of skin showing free nerve endings (green fibres) stained with the pan-neuronal marker PGP9.5. The nuclei of skin cells are stained (blue) with 4,6-diamidino-2-phenylindole (DAPI). Free nerve endings are found in both the epidermal and dermal layers.

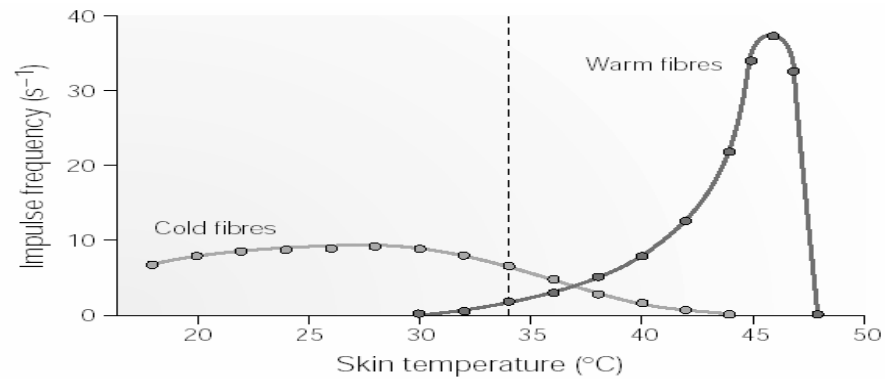


Figure 2 | **Average discharge frequency of individual cold- and warm-sensitive fibres in response to changes in skin temperature.** The dotted line indicates the normal skin temperature (33°C). Cold-sensitive fibres respond only to cooling, whereas warm-sensitive fibres respond to warming. Neither type of fibre responds to mechanical stimulation. Adapted, with permission, from REF. 13 © (1969) The Physiological Society.

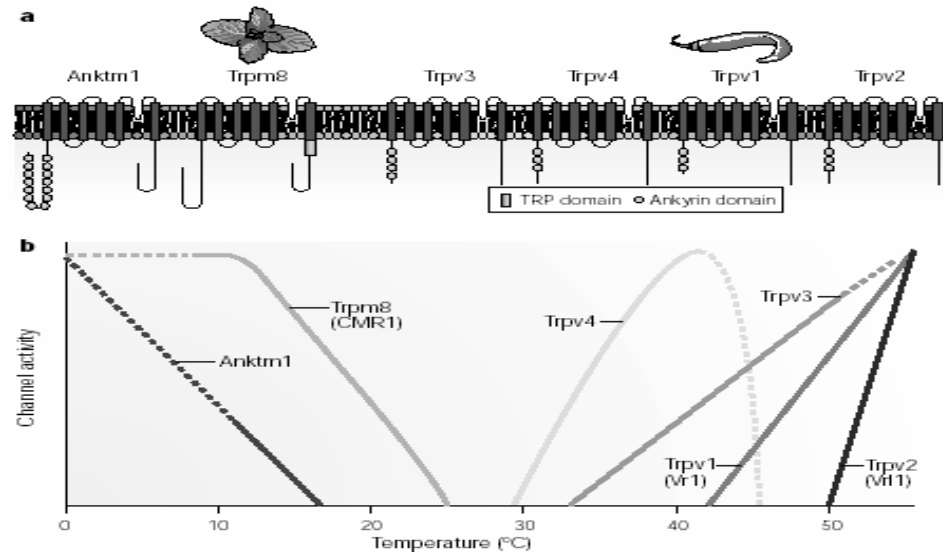


Figure 3 | **Domain organization and temperature thresholds of temperature-activated transient receptor potential ion channels (thermoTRPs).** a | TRP channels are composed of six putative membrane-spanning units and cytoplasmic amino and carboxyl termini. Some TRPs also have variable numbers of ankyrin repeats at the amino terminus, or a conserved TRP domain of 25 amino acids after the transmembrane regions. b | Temperatures ranging from noxious heat to noxious cold activate several members of the TRP family. The cooling compound menthol and capsaicin (the hot ingredient of chilli pepper) act as non-thermal activators of Trpm8 and Trpv1, respectively. The thresholds of activation and maximal activation are based on activity of these channels in heterologous systems; some of these thresholds are averaged values from different studies. Dashed lines indicate an uncertainty in the exact slope of the lines.

Shepherd, Smell...

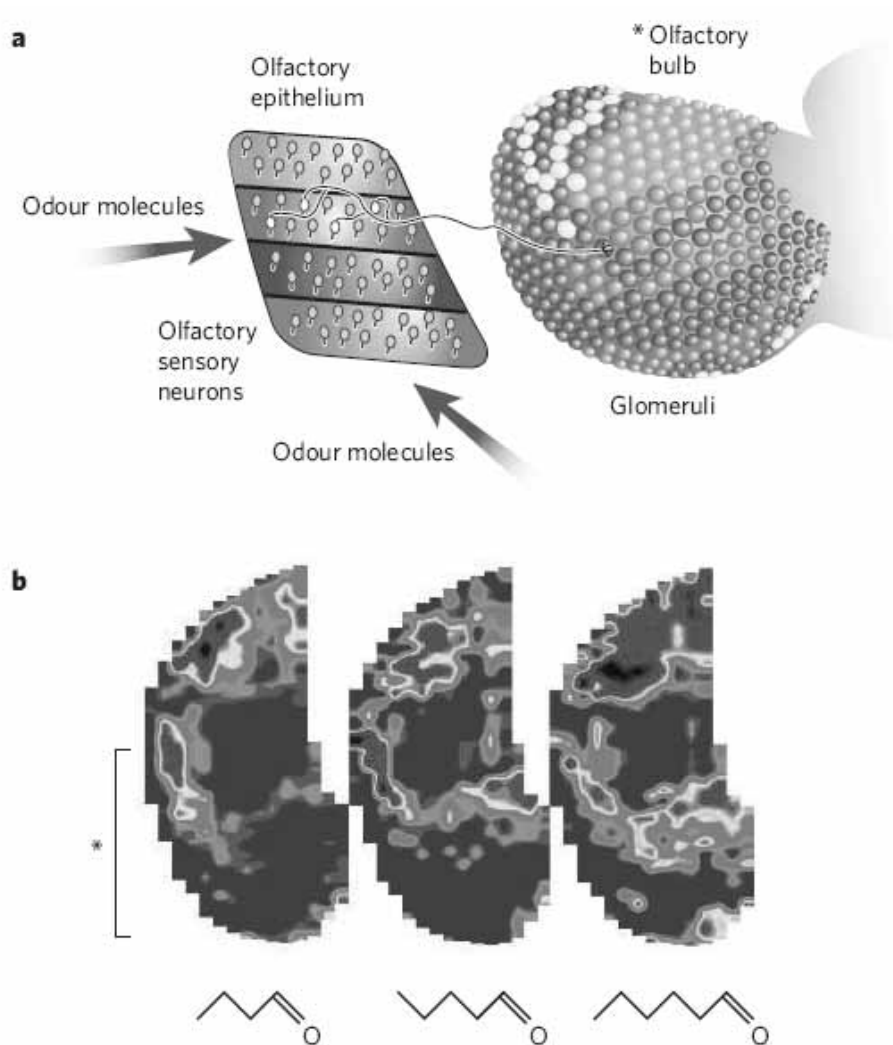


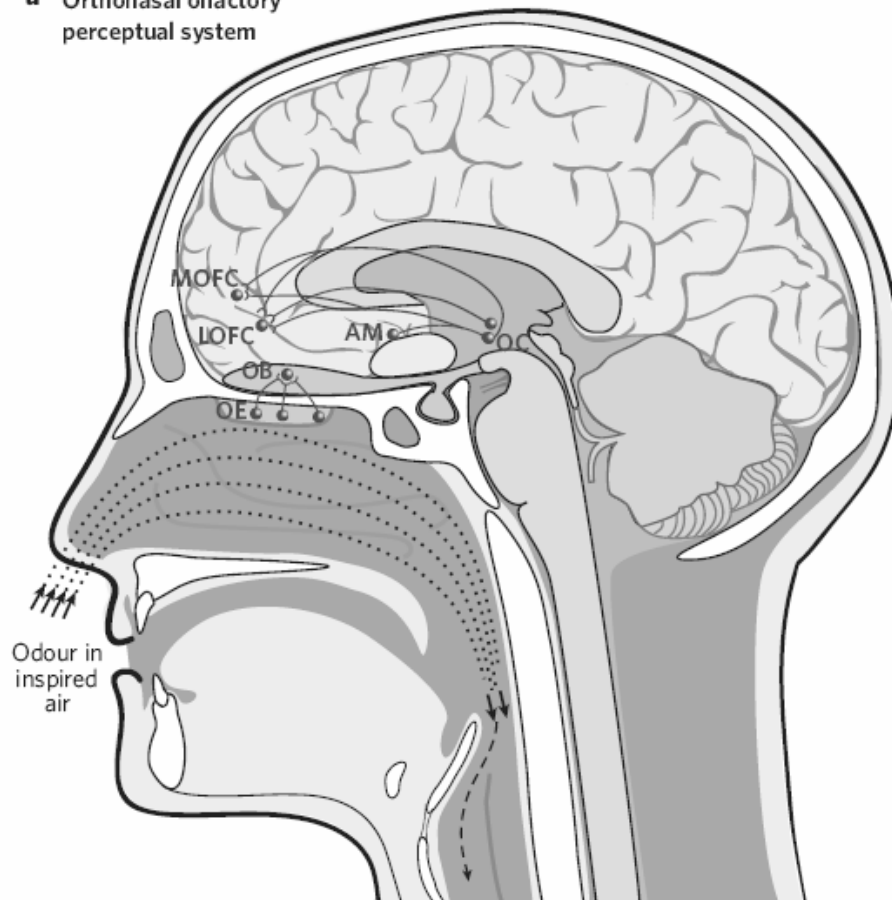
Figure 1 | Odour images in the olfactory glomerular layer. **a**, Diagram showing the relationship between the olfactory receptor cell sheet in the nose and the glomeruli of the olfactory bulb⁵³. **b**, fMRI images of the different but overlapping activity patterns seen in the glomerular layer of the olfactory bulb of a mouse exposed to members of the straight-chain aldehyde series, varying from four to six carbon atoms. The lower part of the image in the left panel corresponds to the image on the medial side of the olfactory glomerular layer as shown in **a** (see asterisk). (Image in **a** adapted, with permission, from ref. 53; image in **b** adapted, with permission, from ref. 10.)

Table 1 | The dual olfactory system

Operations	Orthonasal olfaction	Retronasal olfaction
Stimulation route	Through the external nares	From the back of the mouth through the nasopharynx
Stimuli	Floral scents Perfumes Smoke Food aromas Prey/predator smells Social odors Pheromones MHC molecules	Food volatiles
Processed by	Olfactory pathway influenced by the visual pathway	Olfactory pathway combined with pathways for taste, touch, sound and active sensing by proprioception form a 'flavour system'

Note the interesting contrast, that orthonasal olfactory perception involves a wide range of types of odors processed through only the olfactory pathway, in comparison with retronasal olfactory perception which involves only food volatiles but processed in combination with many brain pathways.

a Orthonasal olfactory perceptual system



b Retronasal olfactory flavour system

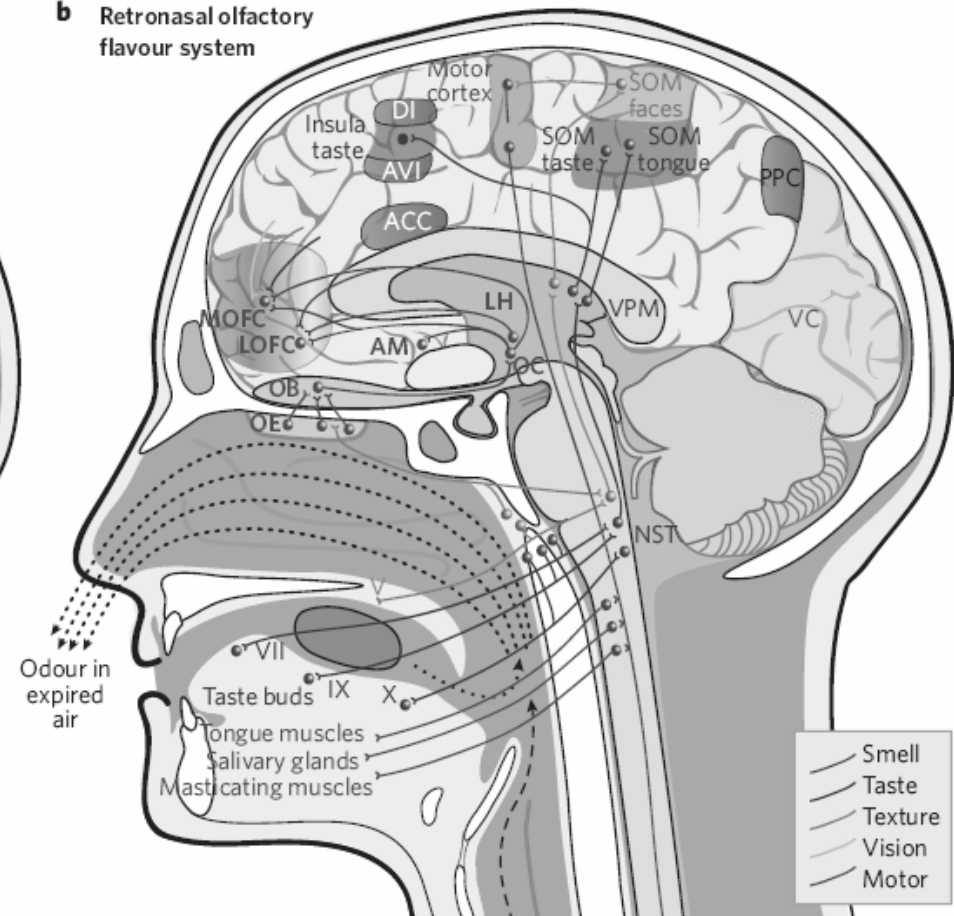


Figure 2 | The dual olfactory system. **a**, Brain systems involved in smell perception during orthonasal olfaction (sniffing in). **b**, Brain systems involved in smell perception during retronasal olfaction (breathing out), with food in the oral cavity. Air flows indicated by dashed and dotted lines; dotted lines indicate air carrying odour molecules. ACC, accumbens; AM, amygdala; AVI, anterior ventral insular cortex; DI, dorsal insular cortex; LH, lateral hypothalamus; LOFC, lateral orbitofrontal cortex; MOFC, medial orbitofrontal cortex; NST, nucleus of the solitary tract; OB, olfactory bulb; OC, olfactory cortex; OE, olfactory epithelium; PPC, posterior parietal cortex; SOM, somatosensory cortex; V, VII, IX, X, cranial nerves; VC, primary visual cortex; VPM, ventral posteromedial thalamic nucleus.

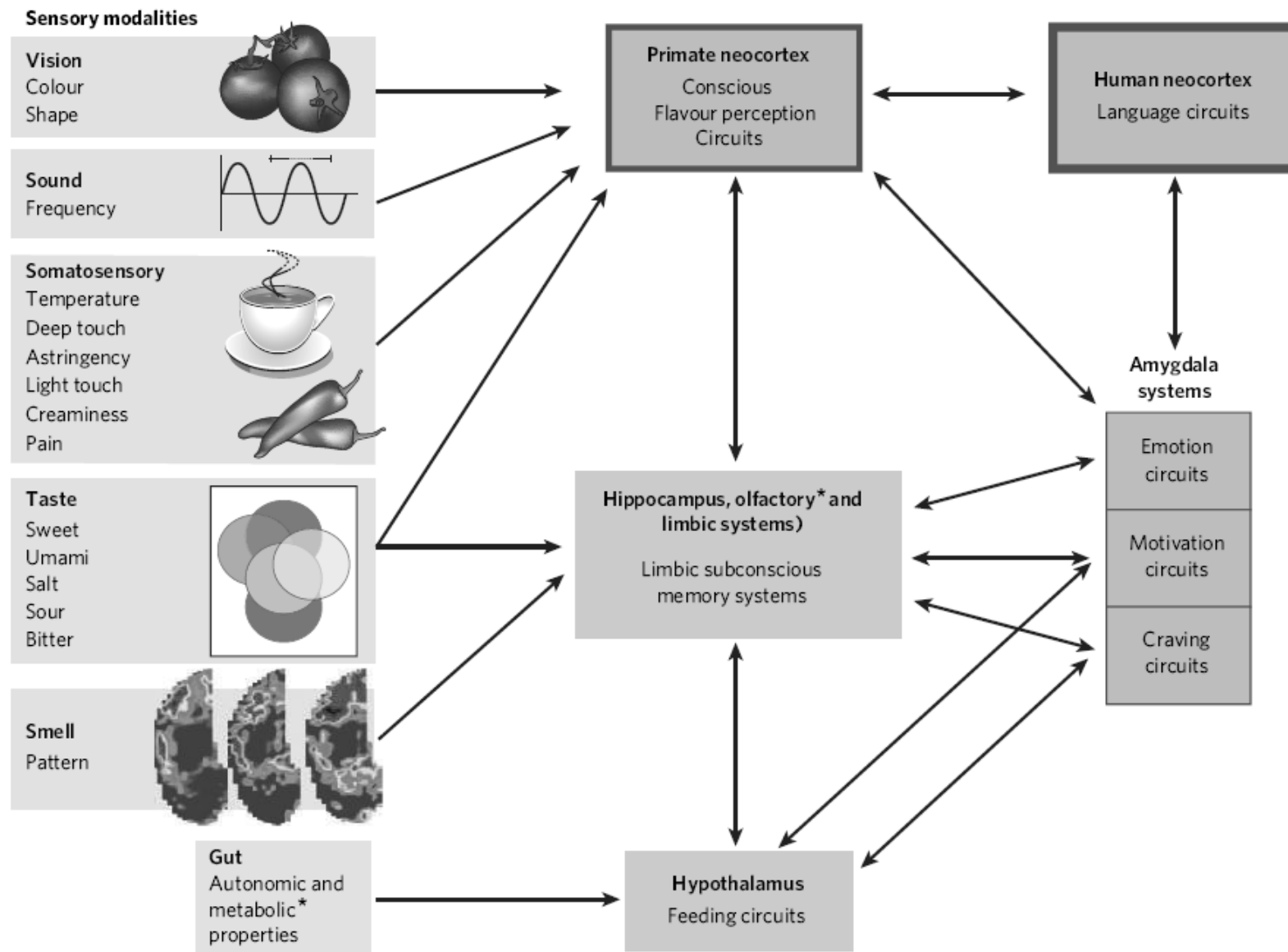


Figure 3 | The human brain flavour systems that evaluate and regulate food intake. The diagram shows the areas involved in the perceptual, emotional, memory-related, motivational and linguistic aspects of food evaluation mediated by flavour inputs^{32,41,54,55}. Left, different sensory modalities and submodalities that contribute to flavour perception. Middle and right, brain flavour system that evaluates and regulates food intake. Red regions mediate conscious sensory perception; thicker outlines indicate their greater importance in humans and other primates. Green regions mediate subconscious feeding regulation. Deficiencies in essential amino acids are sensed by the anterior olfactory cortex (asterisk).