

A few questions on the content of the
previous lecture

slido



The vestibular pathway begins with

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slido



The primary motor cortex (BA 4) is organized

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The basal ganglia

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Any questions/remarks before we begin
today's lecture?

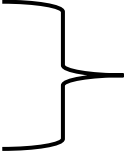


Smell, Taste, and Touch

Dr. Lavinia Carmen Uscătescu

December 18th 2023

Outline

1. Smell: the olfactory circuit
 2. Taste: the gustatory processing network
 3. Touch: the somatosensory system
- 
- the chemical senses

Smell: the olfactory circuit

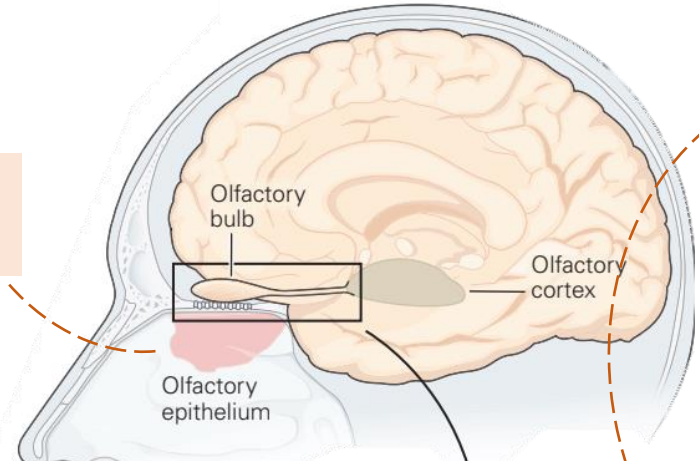
Overview

~5 cm²; contains **sensory neurons** and **glia-like supporting cells**

odorants = volatile chemicals that are perceived as odors

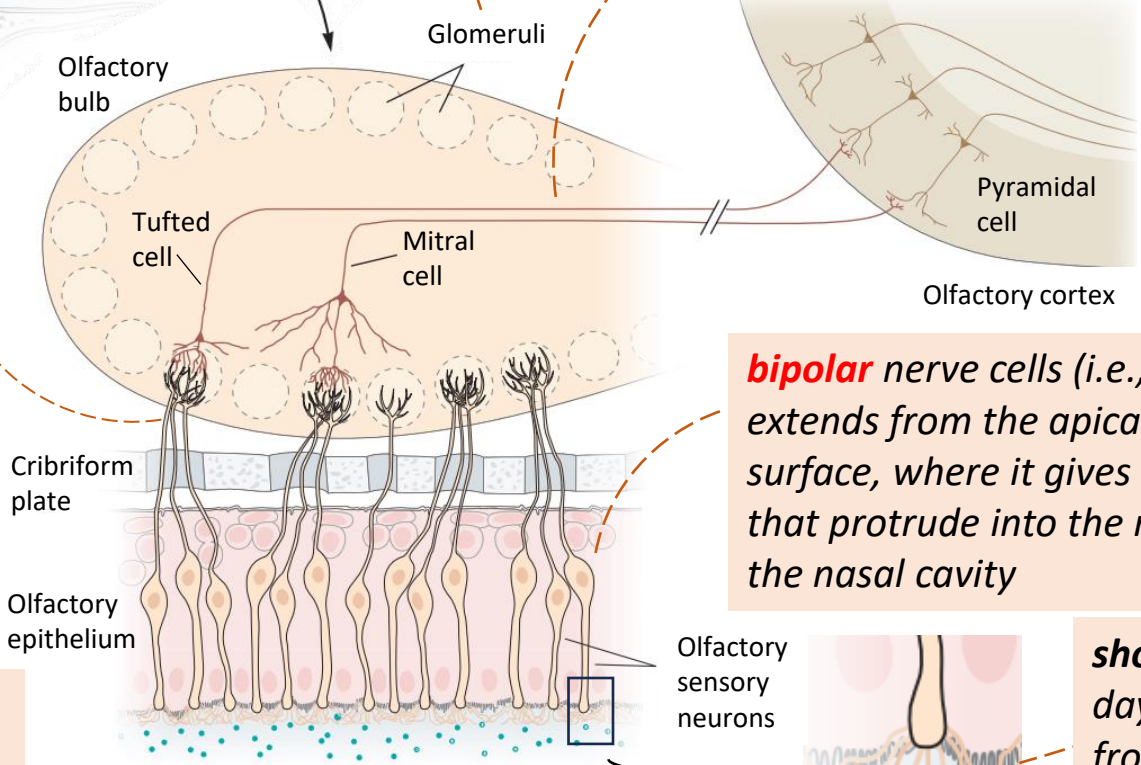
the **axons of olfactory sensory neurons** pass through the **cribriform plate** and project to the **olfactory bulb**, where they terminate on the **dendrites of mitral and tufted cell relay neurons** within **glomeruli**

cribriform plate = perforated region in the **ethmoid bone** above the nasal cavity



cluster of synapses that collects information from **olfactory neurons** expressing **a single type of receptor**

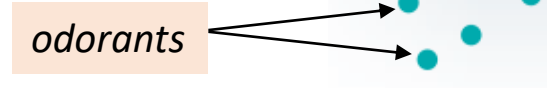
axons of the **relay neurons** project to the **olfactory cortex**, where they terminate on the **dendrites of pyramidal neurons** whose **axons** project to other brain areas



bipolar nerve cells (i.e., **a single dendrite** extends from the apical end to the epithelial surface, where it gives rise to numerous thin **cilia** that protrude into the mucus that coats the nasal cavity

short life span (30 to 60 days); continuously replaced from a layer of **basal stem cells** in the epithelium

adapted from Kandel et al. (2021), p. 683



Odorant receptors

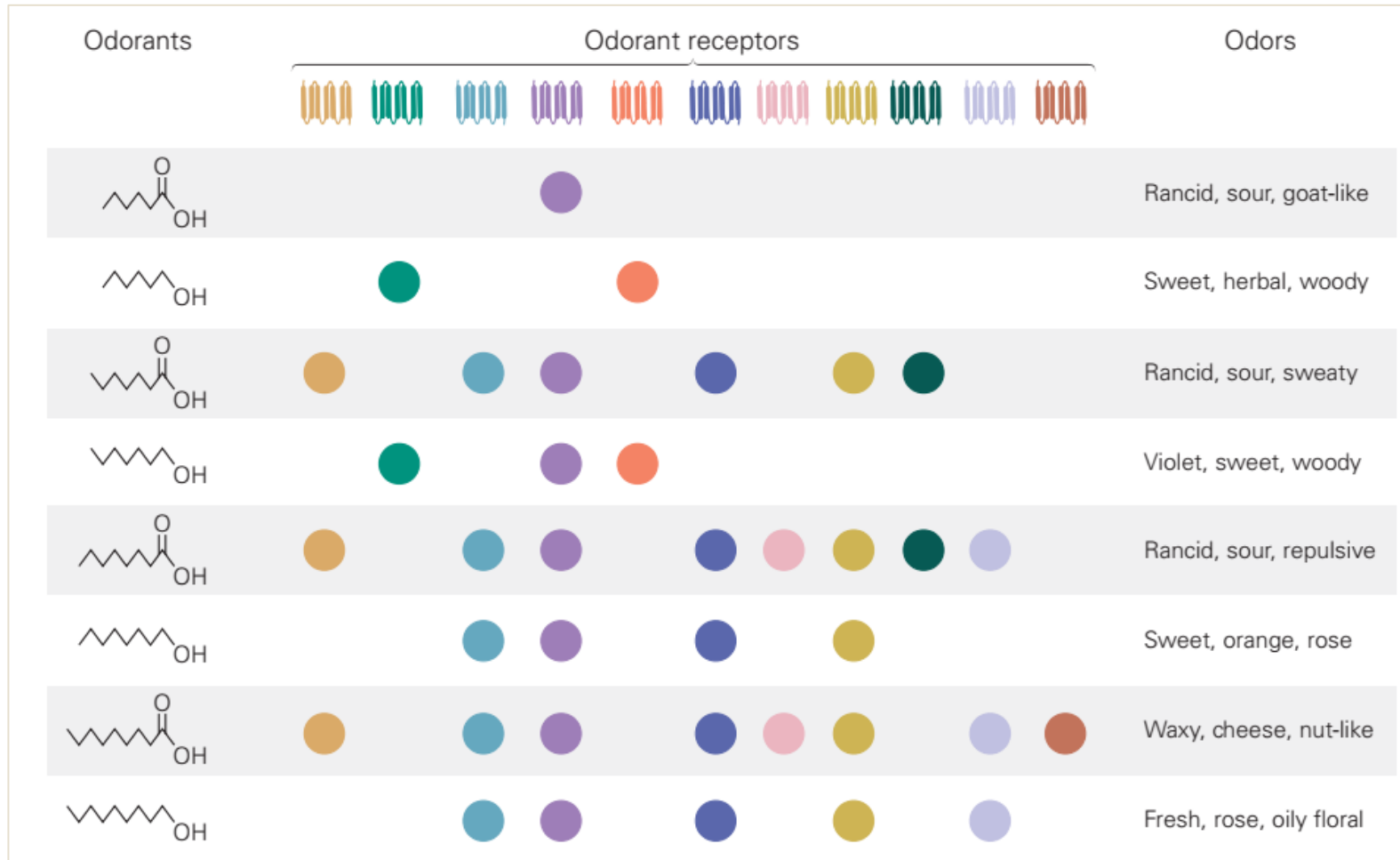


Figure 29–4 Each odorant is recognized by a unique combination of receptors. A single odorant receptor can recognize multiple odorants, but different odorants are detected, and thus encoded, by different combinations of receptors. This combinatorial coding explains how mammals can distinguish odorants with similar chemical structures as having different scents.

Kandel et al. (2021), p. 686

Odorant receptors belong to the **G protein-coupled receptor** superfamily.

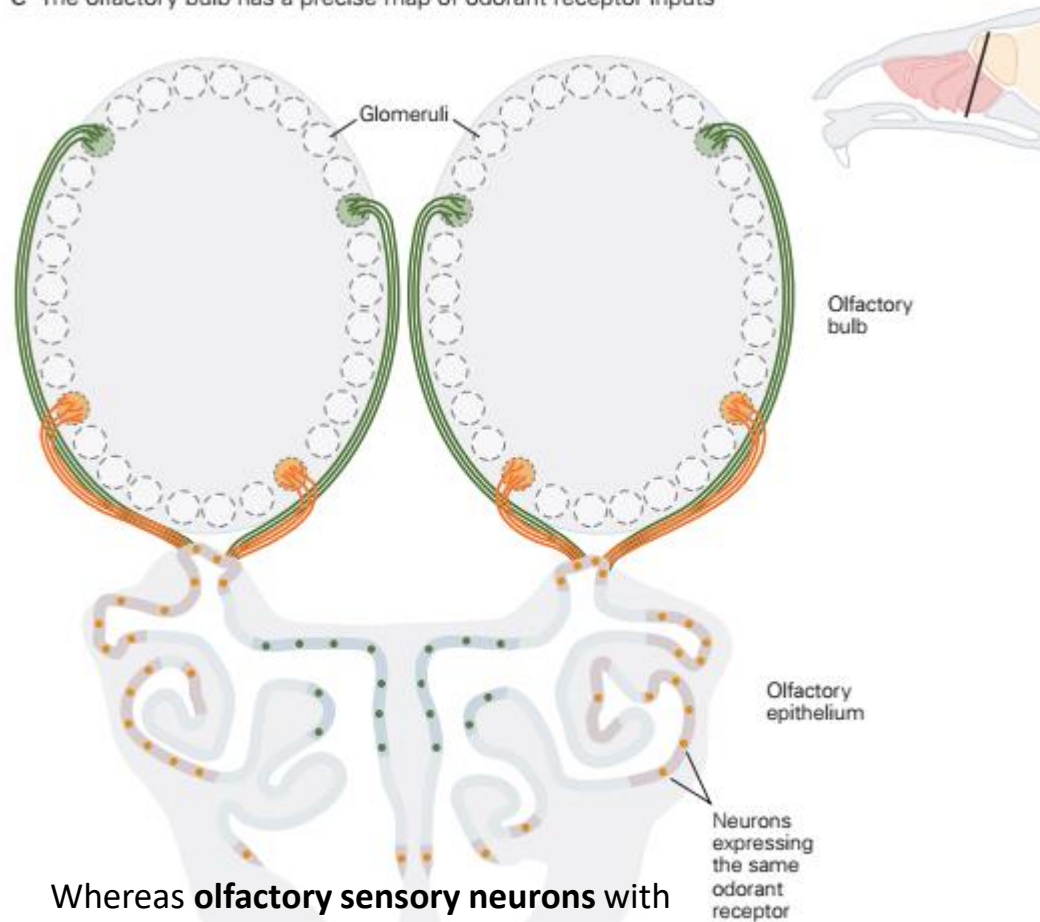
Binding of an odorant to its receptor => **depolarization of the olfactory sensory neuron** => **action potentials** are generated and conducted to the **olfactory bulb**.

Dynamic **adaptation** to odors & recovery of **sensitivity** => mechanism not understood.

A **slight change** in the **chemical structure** of an **odorant** => dramatic **perceptual changes** (e.g., from *rose* to *sour*). The same happens for **different concentrations** of the **same odorant**.

The olfactory glomerulus

C The olfactory bulb has a precise map of odorant receptor inputs



Whereas **olfactory sensory neurons** with the **same odorant receptor** are randomly scattered in one epithelial zone, their **axons** typically **converge** in **two glomeruli** at specific locations, one on either side of the olfactory bulb.

Kandel et al., (2021), p. 689

There are ~350 different **types of olfactory receptors** => ~350 different **types of glomeruli** spread throughout the olfactory bulb.

The **axon of an olfactory sensory neuron** as well as the **primary dendrite of each mitral and tufted relay neuron** terminate in a single glomerulus. In each glomerulus, the axons of **several thousand sensory neurons** converge on the dendrites of **~40 to 50 relay neurons**.

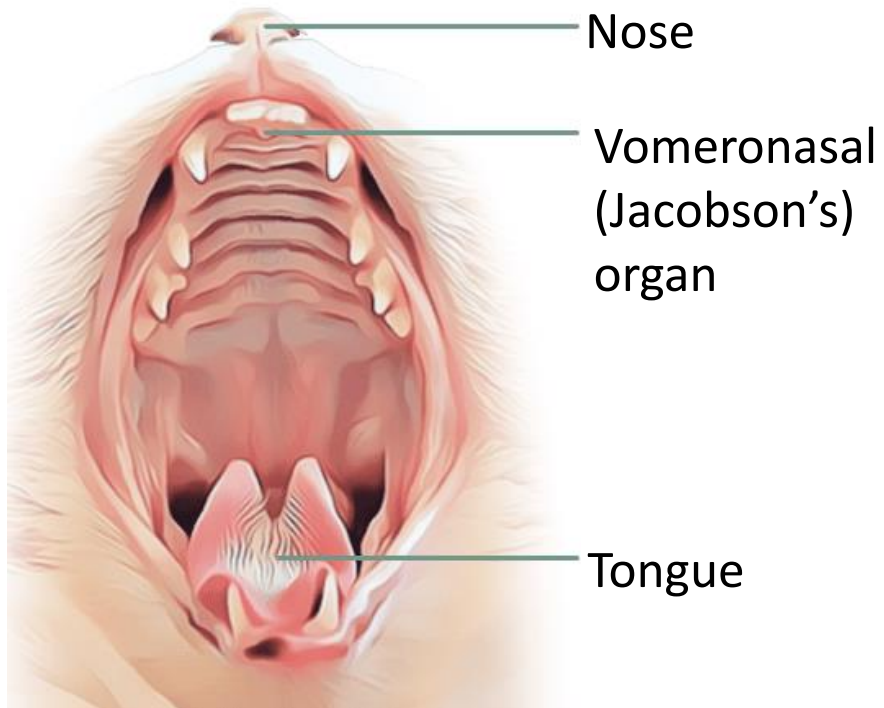
Each glomerulus, and each mitral and tufted relay neuron connected to it, receives input from **just one type of odorant receptor**. The result is a precise arrangement of sensory inputs from different odorant receptors, one that is similar between individuals (i.e., **chemotopic map**).

Because **each odorant** is recognized by a **unique combination** of receptor types, each also activates a **particular combination of glomeruli** in the olfactory bulb.

The vomeronasal organ

pheromones

chemicals capable of acting like **hormones** outside the body of the secreting individual, to affect the behavior of the receiving individuals



<http://tinyurl.com/ycy8n439>

The Flehmen response: <http://tinyurl.com/zwmc5mmz>

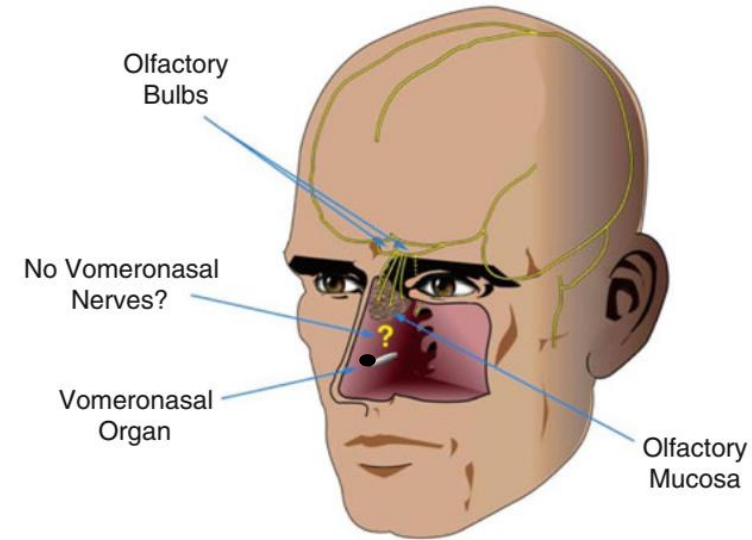


Fig. 4 The diagram shows the location of the **vomeronasal organ in adult humans**. There is no obvious bulge in the nasal septum indicating its position. The duct opening (VNO pit), which can be observed with an endoscope in most adult humans, is at the anterior end (black dot next to arrowhead). There is **no evidence for true vomeronasal sensory nerves connecting the organ to the brain**. There are nerves running behind the VNO and extending back to the brain (? on the diagram), but they may be only nervus terminalis, trigeminal, and autonomic nerve branches. **The organ shows some differences in structure compared with other mammalian organs. It has no obvious thick sensory epithelium but does have a few cells that have been described as similar to bipolar sensory neurons but lacking an axon.** The location and structure suggest that **the human organ, if functional, might be stimulated by airborne chemicals rather than by stimuli dissolved in mucus.** Studies of the human genome indicate that a gene thought to be essential for vomeronasal sensory neuron function in other species is nonfunctional in humans, apes, and other old-world primates. The accessory olfactory bulbs, to which VN nerves normally project in mammals, also have not been identified in humans, raising additional questions about human VNO function. **The central target of VNO input in mammals, the cortico-medial amygdala, is present in humans and does receive chemosensory input (from the main olfactory system).** It surely shares some functions with the amygdala in other mammals, but it is not yet clear whether these include the receipt of purely vomeronasal input or the analysis of pheromone-related information (whether or not from the vomeronasal system). (From <http://www.neuro.fsu.edu/~mmered/vomer/human.htm>. Text and Images © Dr. Michael Meredith and Program in Neuroscience, Florida State University)

Pfaff et al., (2022), p. 1239

The olfactory tract

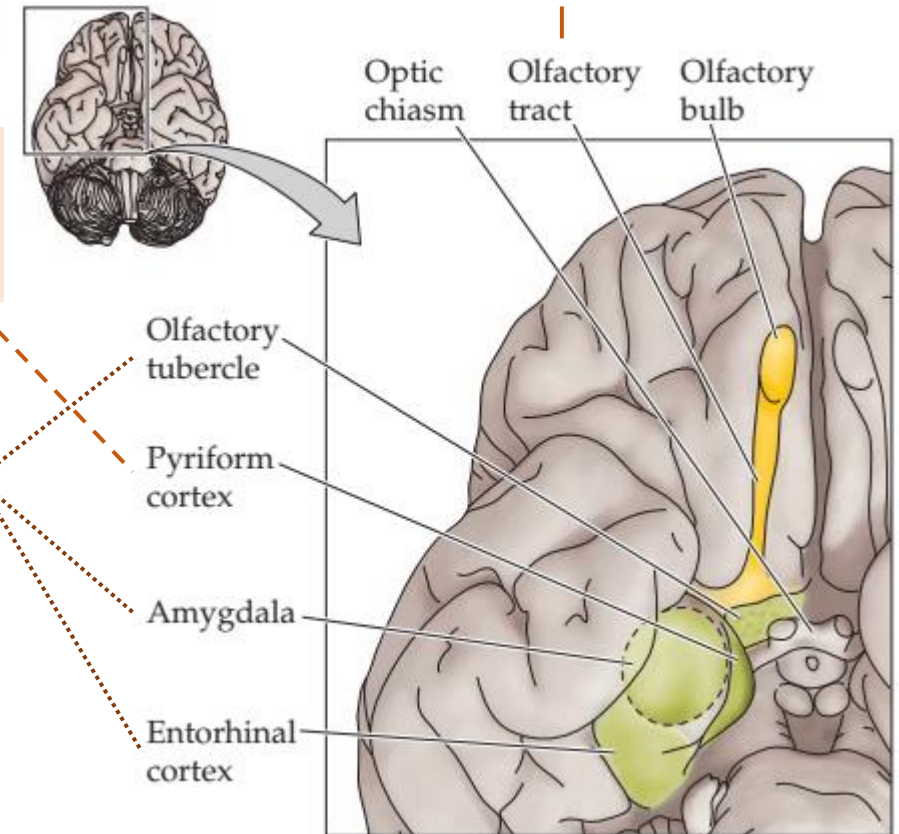
From a functional point of view, the brain regions involved in olfaction can be divided into those that are part of the **neocortex** (**orbitofrontal cortex**) and are related to the awareness of smell, and those that are part of the **limbic system**.

The **limbic system** includes **amygdala** (processing of **smell-related fear** and threat stimuli), **entorhinal cortex** (interface between hippocampus and cerebral cortex important for creating **olfactory memories**), and **hippocampus** (incorporation of **long-term olfactory memories**).

*analogous to the **primary sensory cortices** in vision, audition, and somatic sensation*

*analogous to the **higher-order processing regions** in these other systems*

composed of the **axons of mitral and tufted cells**

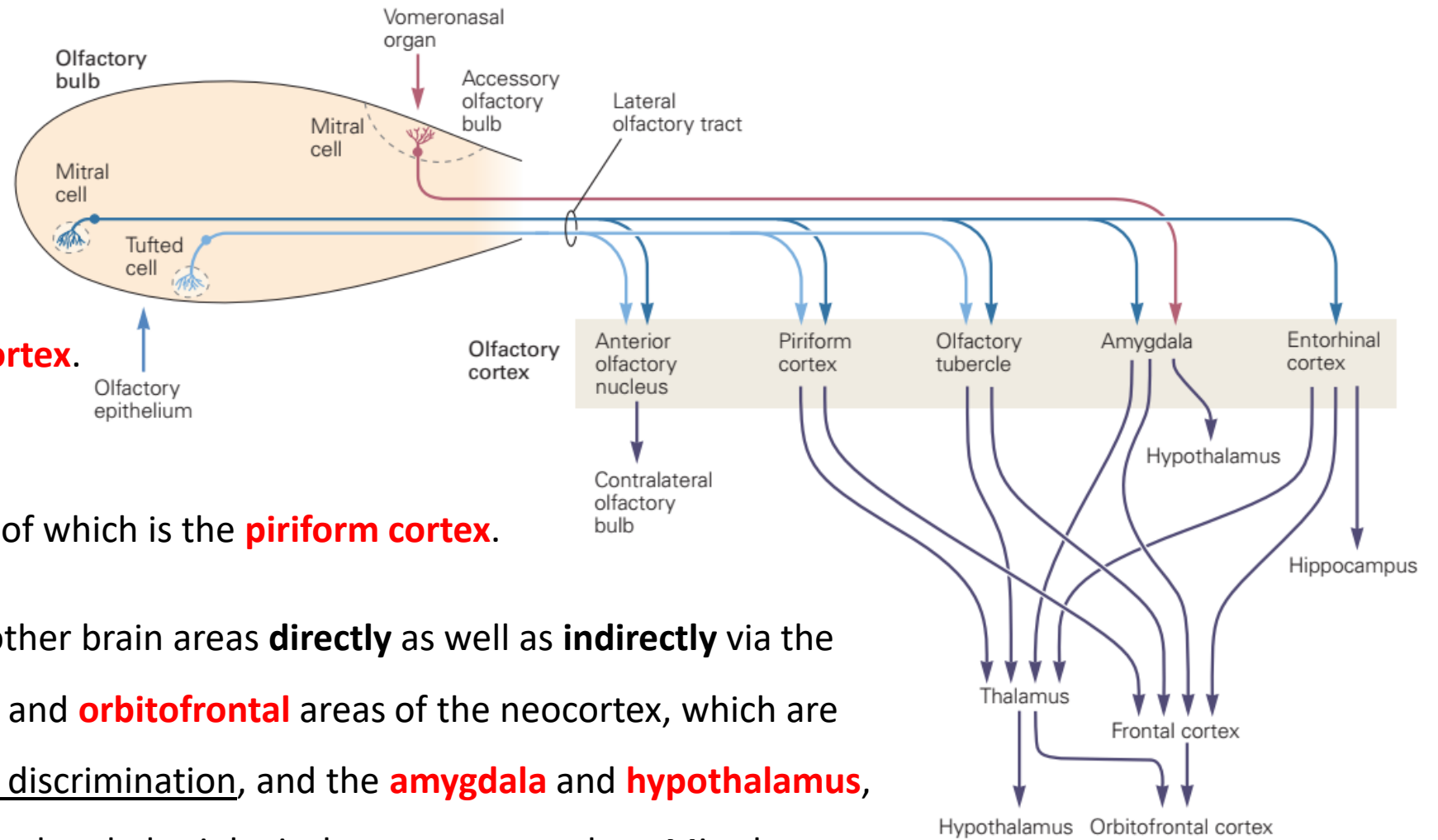


Purves et al., (2018), p. 324

The axons of mitral and tufted relay neurons of the **olfactory bulb** project through the **lateral olfactory tract** to the **olfactory cortex**.

The **olfactory cortex** consists of several distinct areas, the largest of which is the **piriform cortex**.

The **olfactory cortex** projects to other brain areas **directly** as well as **indirectly** via the **thalamus**. Targets include **frontal** and **orbitofrontal** areas of the neocortex, which are thought to be important for odor discrimination, and the **amygdala** and **hypothalamus**, which may be involved in emotional and physiological responses to odors. Mitral cells in the **accessory olfactory bulb** project to specific areas of the **amygdala** that transmit signals to the **hypothalamus**.



Kandel et al., (2021), p. 690

The Nobel Prize in Physiology or Medicine 2004



Photo from the Nobel Foundation archive.

Richard Axel

Prize share: 1/2



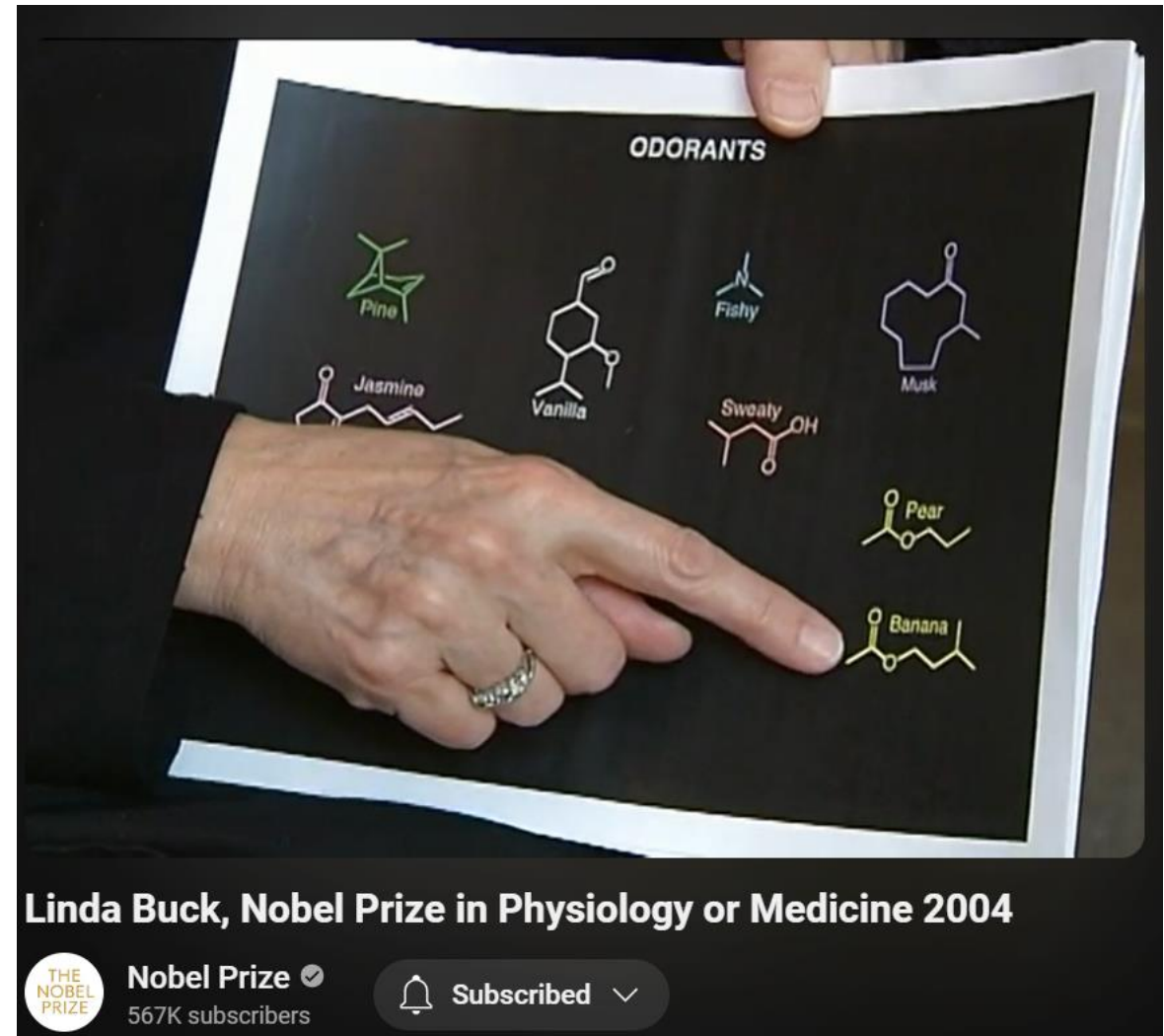
Photo from the Nobel Foundation archive.

Linda B. Buck

Prize share: 1/2

The Nobel Prize in Physiology or Medicine 2004 was awarded jointly to Richard Axel and Linda B. Buck "for their discoveries of odorant receptors and the organization of the olfactory system"

<https://www.nobelprize.org/prizes/medicine/2004/summary/>



Linda Buck, Nobel Prize in Physiology or Medicine 2004

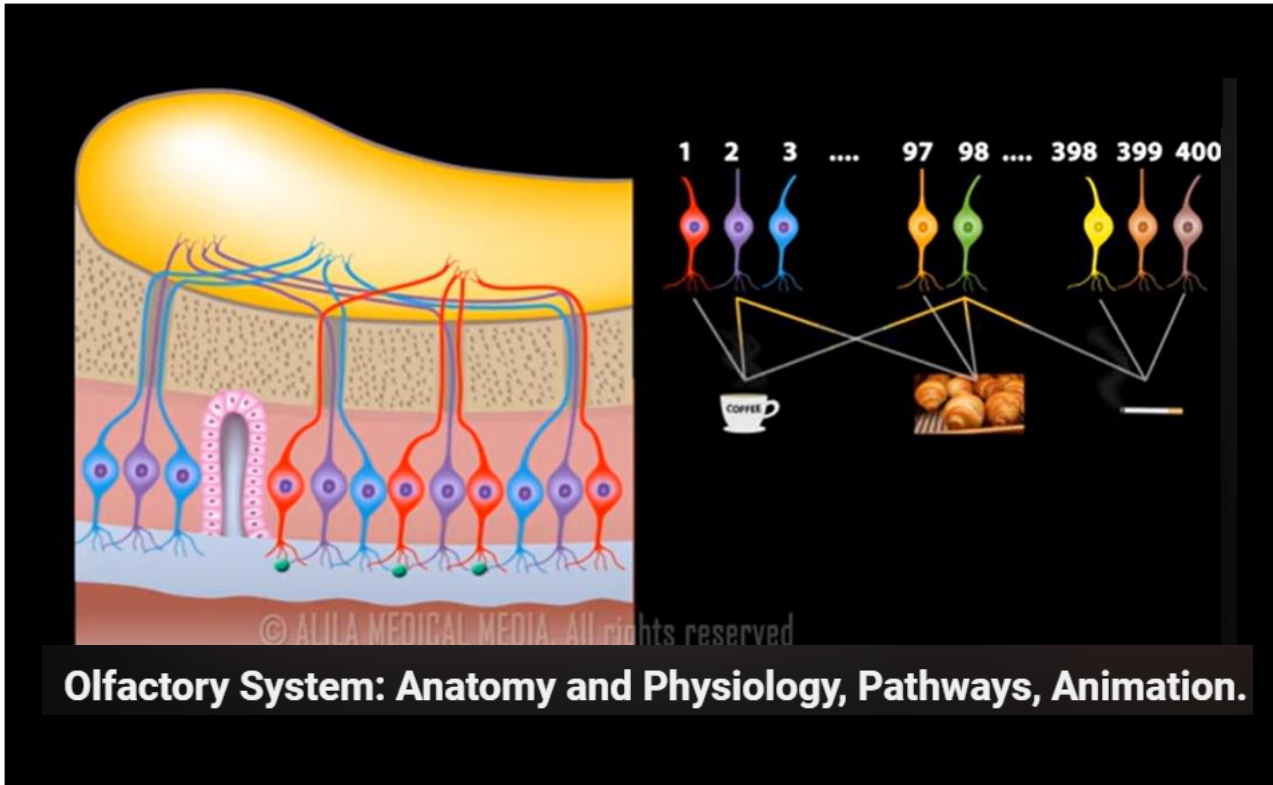


Nobel Prize ✓
567K subscribers

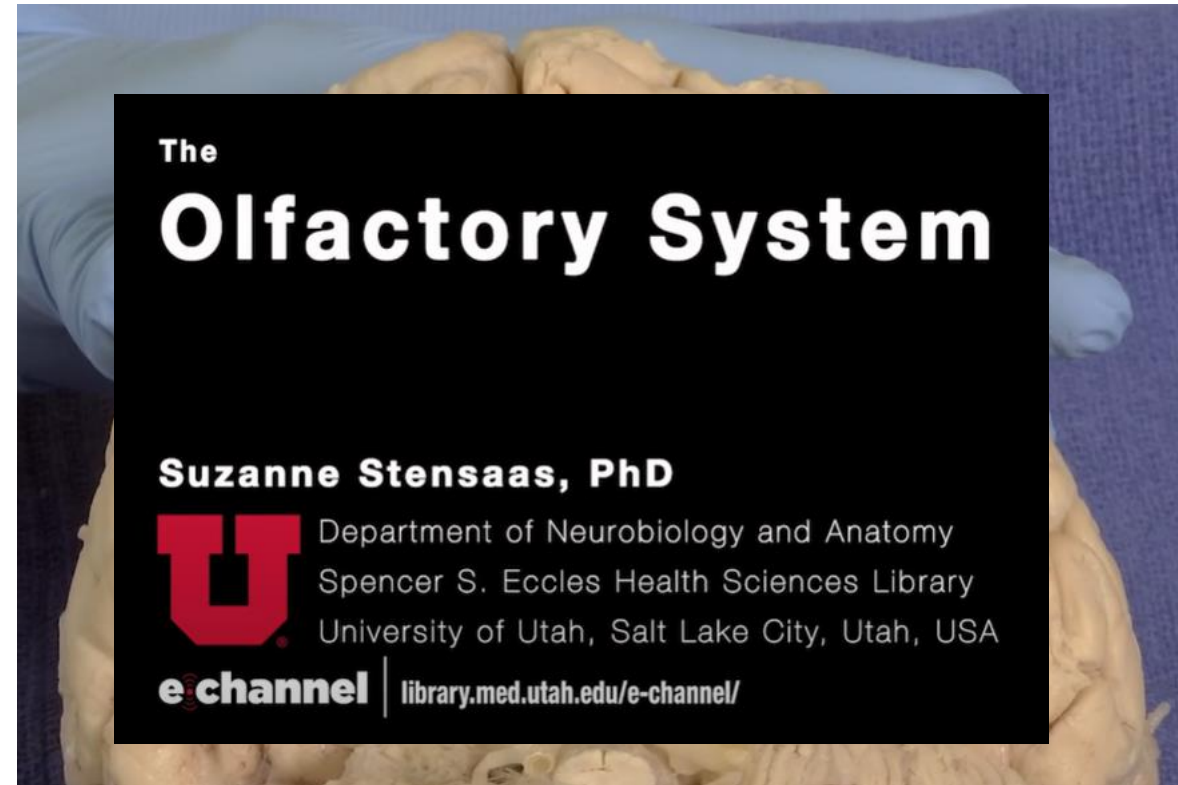
Subscribed ✓

<https://www.youtube.com/watch?v=BvV3vYsOzMk>

In summary



<https://www.youtube.com/watch?v=wQJbsOWc344>



<https://www.youtube.com/watch?v=8NrZdv3c0cA>

Taste: the gustatory processing network

Five basic taste qualities: **sweet**, **bitter**, **salty**, **sour**, and **umami** (i.e., a Japanese word meaning *delicious* and associated with the “savory” taste of **amino acids**).

This limited palate detects all essential dietary requirements: **sweet** taste invites consumption of **energy rich foods**; **bitter** taste warns against the ingestion of **toxic, noxious chemicals**; **salty** taste promotes a diet that maintains proper **electrolyte balance**; **sour** taste signals **acidic, unripened, or fermented foods**; and **umami** indicates **protein-rich foods**. Both **sweet** and **umami** tastants are innately **pleasurable**, while **bitter** and **sour** tastants elicit innately **aversive** responses.

Taste is often thought to be synonymous with **flavor**. However, taste refers strictly to the five qualities encoded in the gustatory system, whereas flavor stems from the **multisensory integration** of inputs from the **gustatory**, **olfactory**, and **somatosensory** systems (e.g., **texture** and **temperature**).

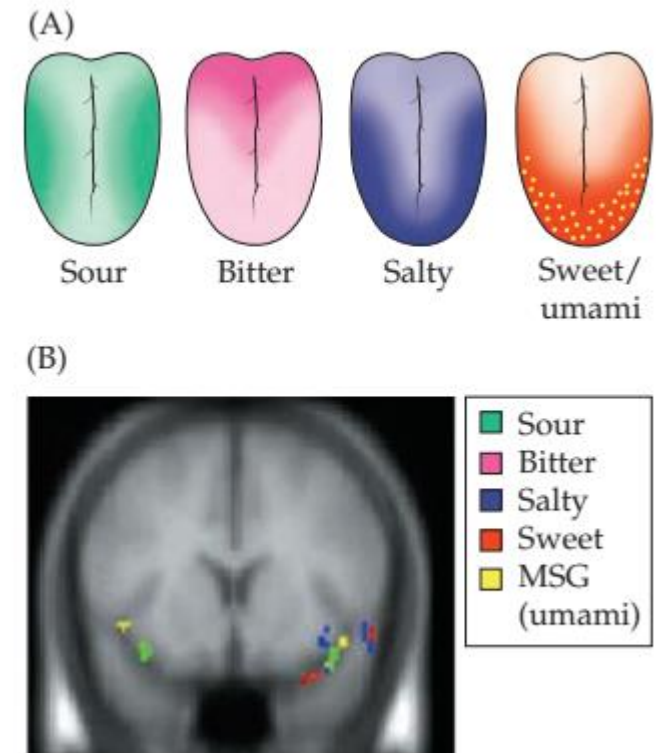
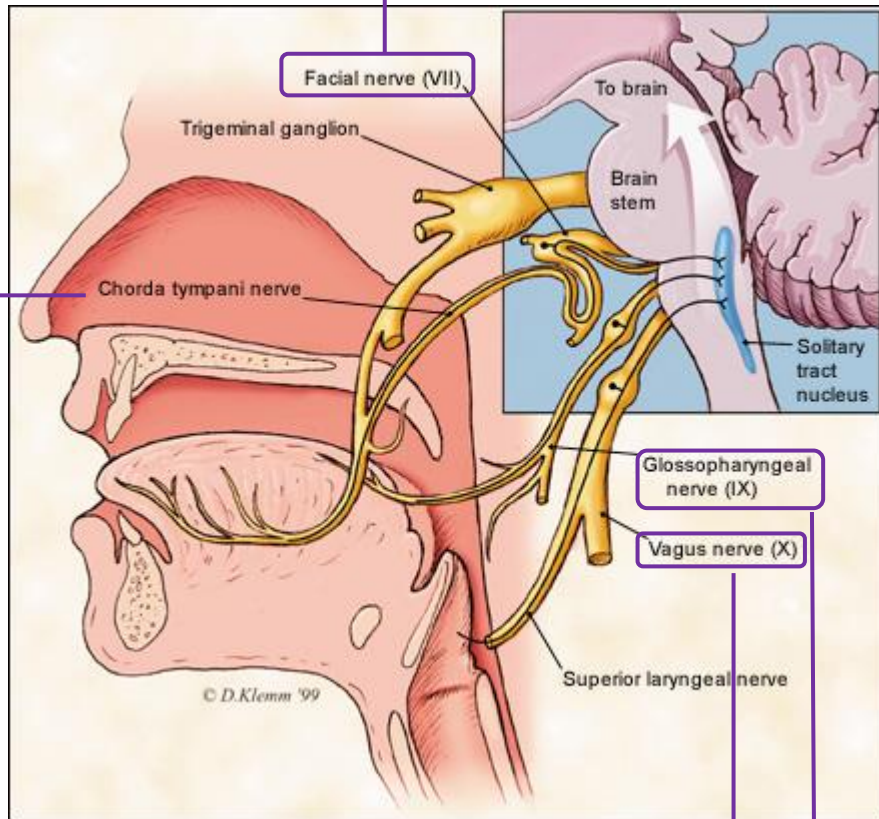


FIGURE 15.22 Peripheral innervation of the tongue. (A) Responses to sweet/umami, salty, sour, and bitter tastants recorded in the **three cranial nerves** that innervate the **tongue and epiglottis**. (B) **Composite fMRI** showing the different locations of focal activation in the **insular cortex** in response to each of the tastes encoded by taste receptors. (B from Schoenfeld et al., 2004.)

Purves et al., (2018), p. 349

innervates the **anterior two-thirds of the tongue**



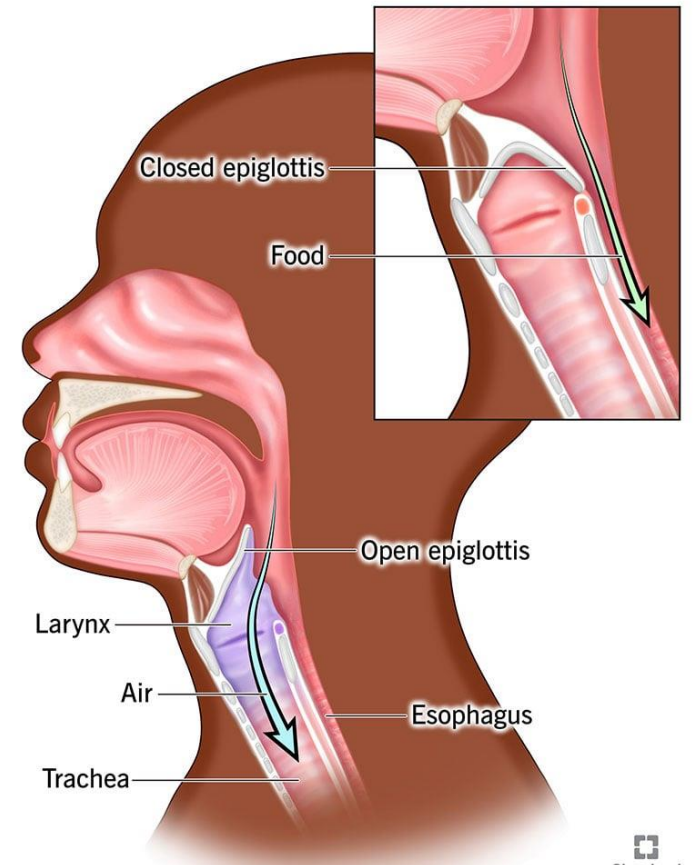
<http://tinyurl.com/yjxf56x8>

innervates the **epiglottis**

innervates the **posterior third of the tongue**

branch of the **facial nerve**
that innervates the **anterior two-thirds of the tongue**

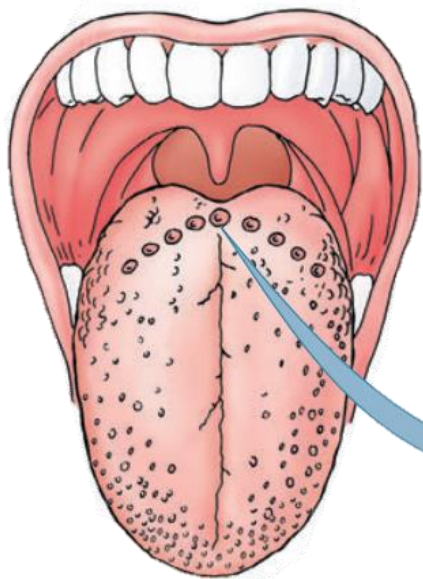
Epiglottis



<http://tinyurl.com/2tpv4xzh>

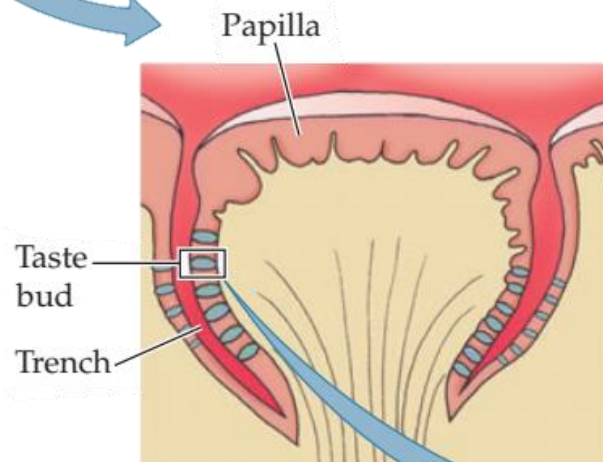
epiglottis

elastic **cartilage** that protects the larynx
and enables swallowing



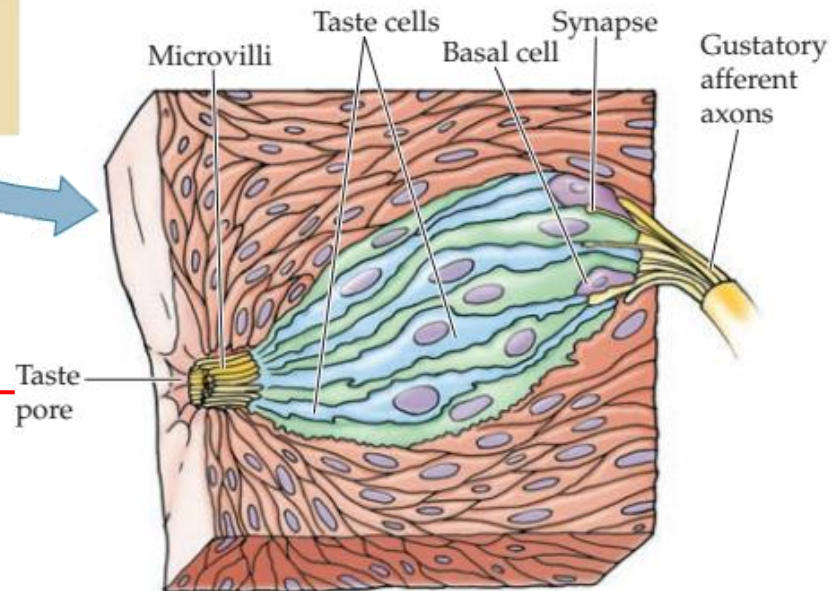
The **papillae** are multicellular protuberances surrounded by local invaginations in the tongue epithelium (i.e., **trenches**) to concentrate solubilized tastants.

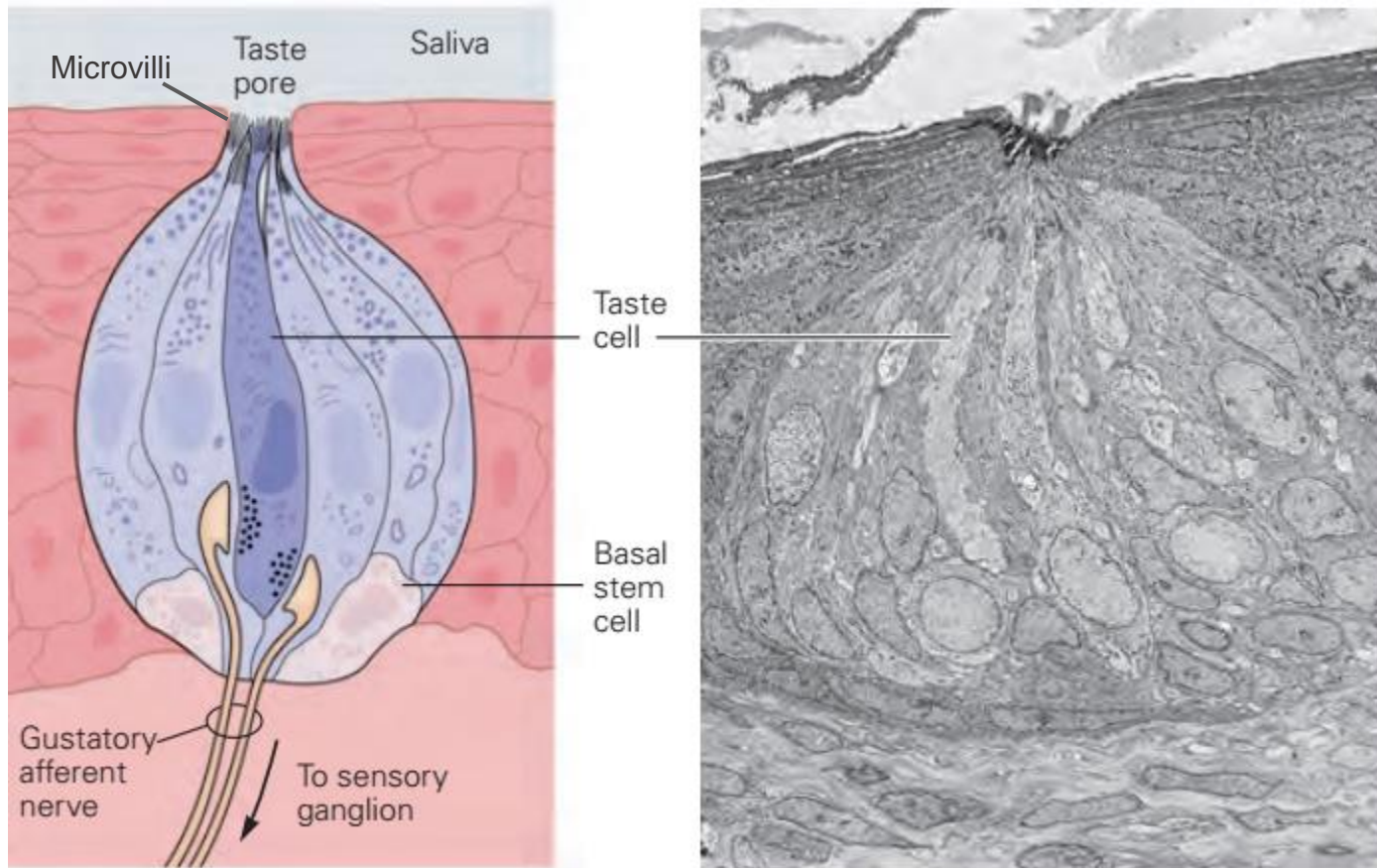
Taste buds (~ 4000 in humans) are distributed along the lateral surfaces of the **papillar protuberance** as well as in the **trench walls**. They consist of specialized neuroepithelial **receptor cells** called **taste cells** (~ 2 weeks lifespan), some supporting cells, and occasional **basal cells** (i.e., the local **stem cells** which help replace the dead taste cells).



adapted from Purves et al., (2012), p. 123
and Purves et al., (2018), p 348

opening at the epithelial surface;
the point of contact with tastants





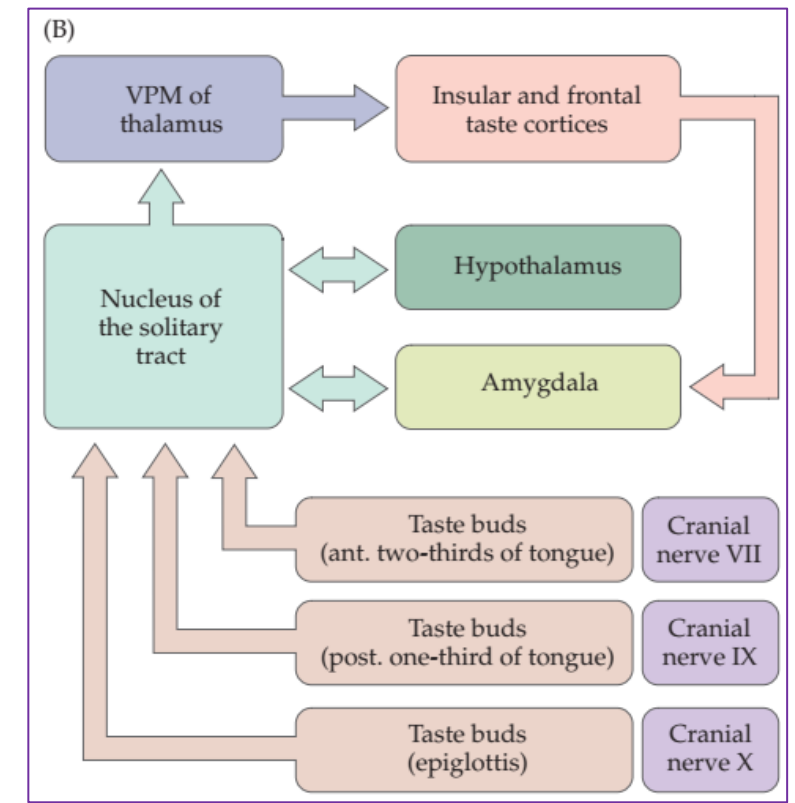
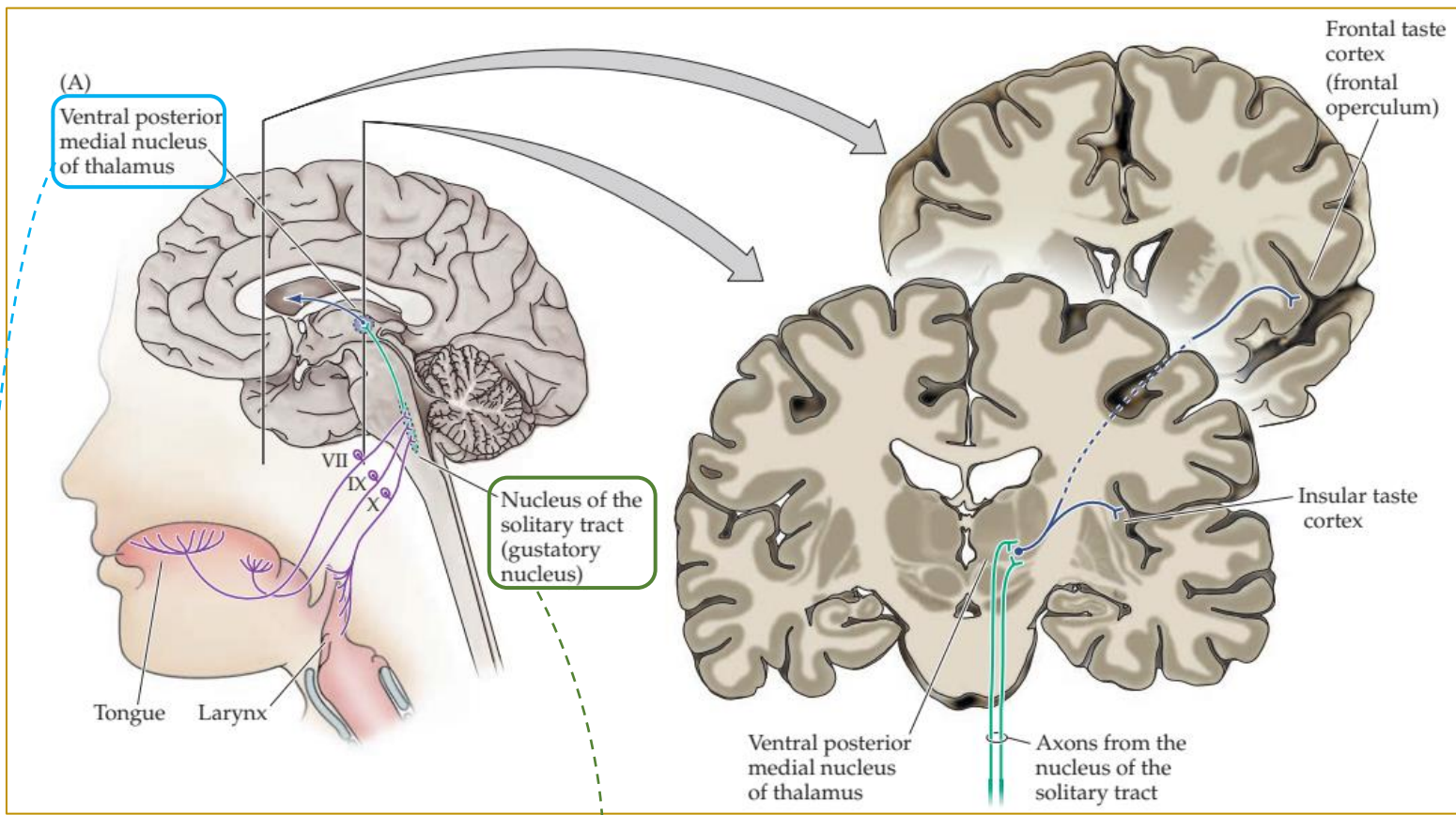
Kandel et al., (2021), p. 697

Each **taste bud** contains approximately 100 **taste receptor cells** (taste cells), elongated cells that stretch from the taste pore to the basal area of the bud.

Each **taste cell** extends **microvilli** into the **taste pore**, allowing the cell to contact chemicals dissolved in saliva at the epithelial surface.

At its basal end, the taste cell contacts the **afferent fibers of gustatory sensory neurons**.

Taste cells are **nonneural**, but their contacts with the gustatory sensory neurons have the morphological characteristics of **chemical synapses**, including **clustered presynaptic vesicles**. Taste cells also resemble neurons in that they are **electrically excitable**; they have **voltage-gated Na⁺, K⁺, and Ca²⁺ channels** and can generate **action potentials**.



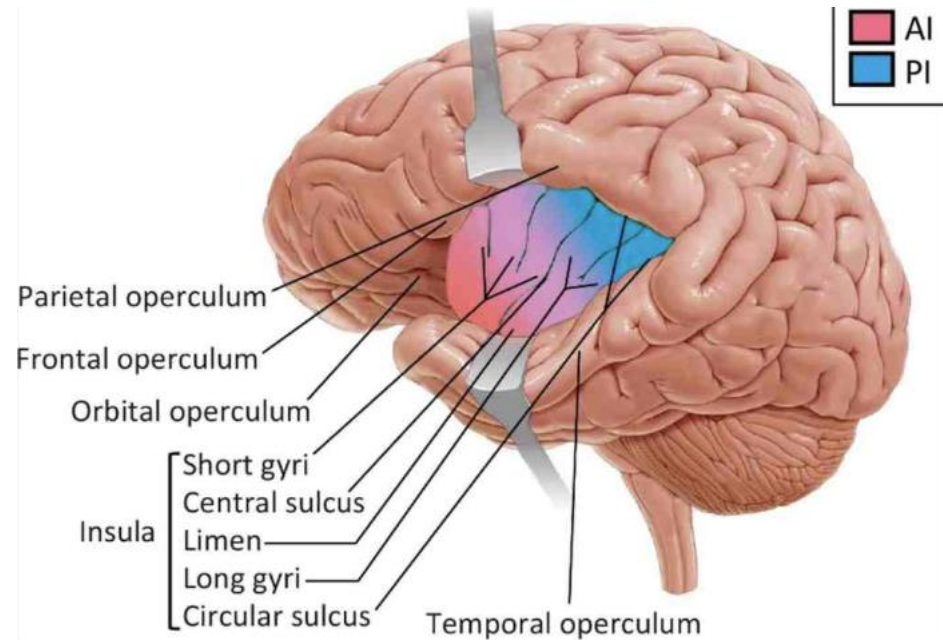
cell bodies of the taste receptor cells reside in specific sensory ganglia (i.e., nucleus of the solitary tract and ventral posterior medial nucleus of the thalamus)

FIGURE 15.20 The human taste system. (A) The drawing shows the relationship between receptors in the mouth and upper alimentary canal, and the nucleus of the solitary tract in the medulla. The coronal section shows the ventral posterior medial (VPM) nucleus of the thalamus and its connection with gustatory regions of the cerebral cortex. (B) Basic pathways for processing taste information. (C) Functional MRI of a typical person consuming food. Note bilateral focal activation (red) in the insular cortex (arrows), with a bias for greater activation in the dominant hemisphere (left in most humans). (C from Schoenfeld et al., 2004.)




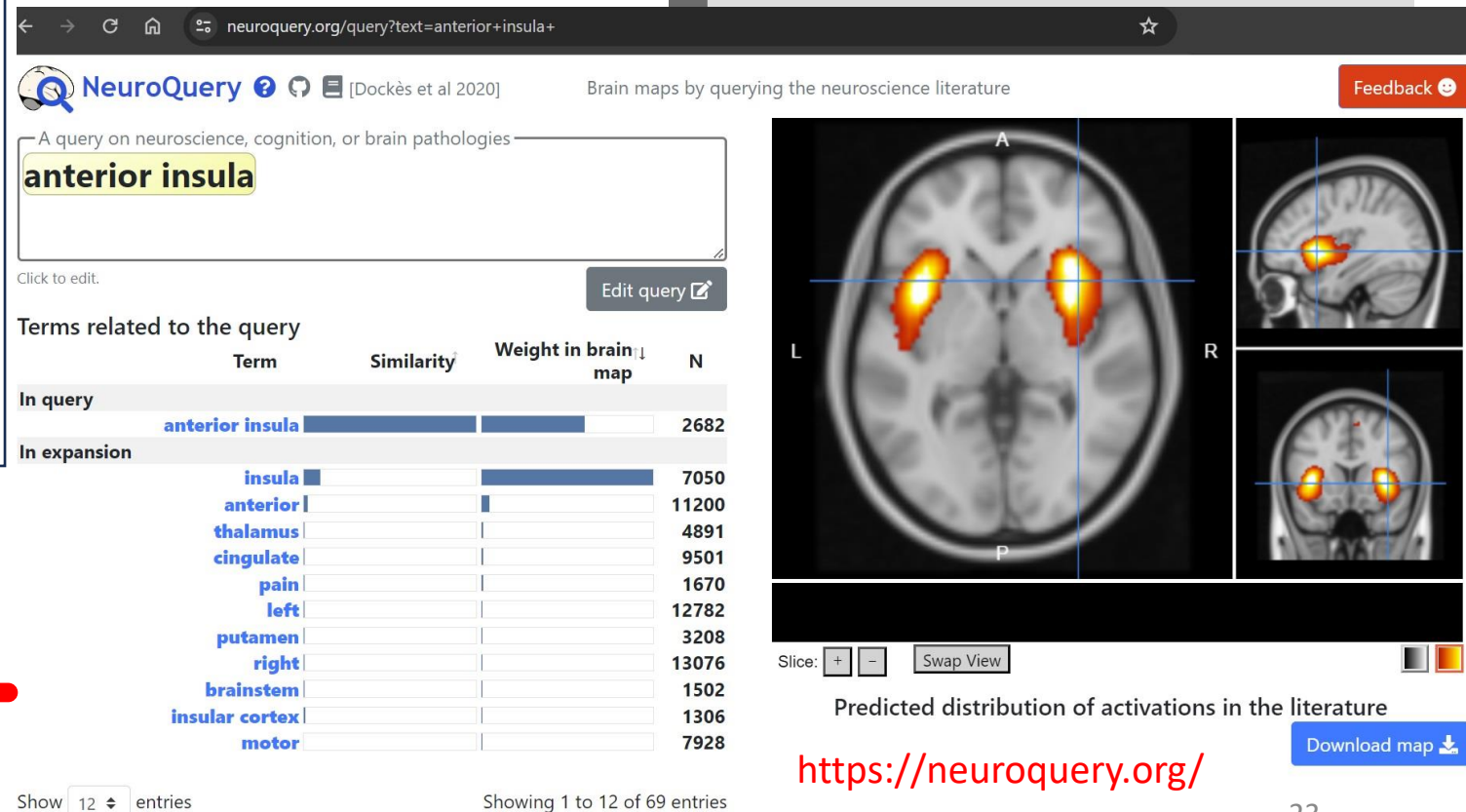
Whenever in doubt: visualize!

The gustatory cortex: anterior insula & frontal operculum



<https://tinyurl.com/2p9kk2h3>

Use this open-source software to load neuroimaging files for visualization 



neuroquery.org/query?text=anterior+insula+

NeuroQuery [Dockès et al 2020] Brain maps by querying the neuroscience literature Feedback

A query on neuroscience, cognition, or brain pathologies

anterior insula


Click to edit. Edit query

Term	Similarity	Weight in brain map	N
In query			
anterior insula			2682
In expansion			
insula			7050
anterior			11200
thalamus			4891
cingulate			9501
pain			1670
left			12782
putamen			3208
right			13076
brainstem			1502
insular cortex			1306
motor			7928

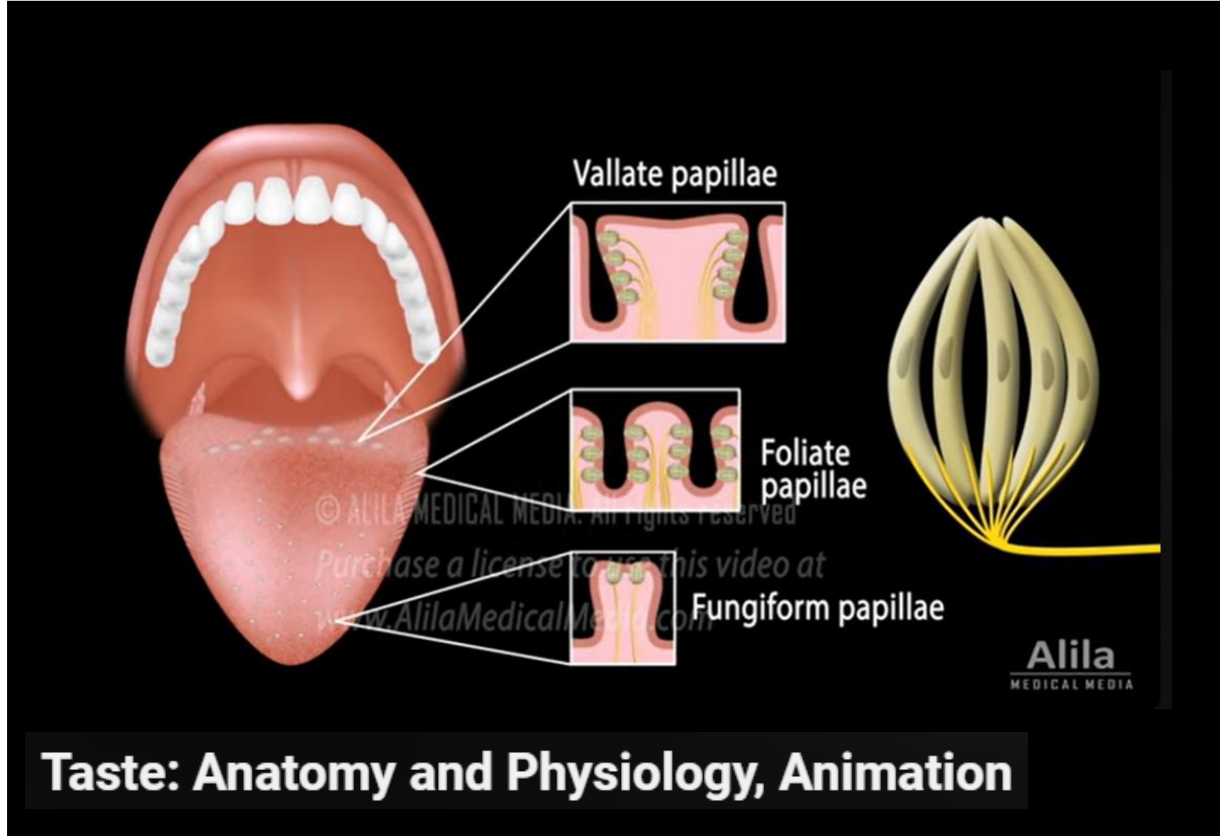
Showing 12 entries Showing 1 to 12 of 69 entries

Brain maps showing predicted distribution of activations in the literature. Includes controls for slice (+, -) and Swap View. Download map button.

<https://neuroquery.org/>

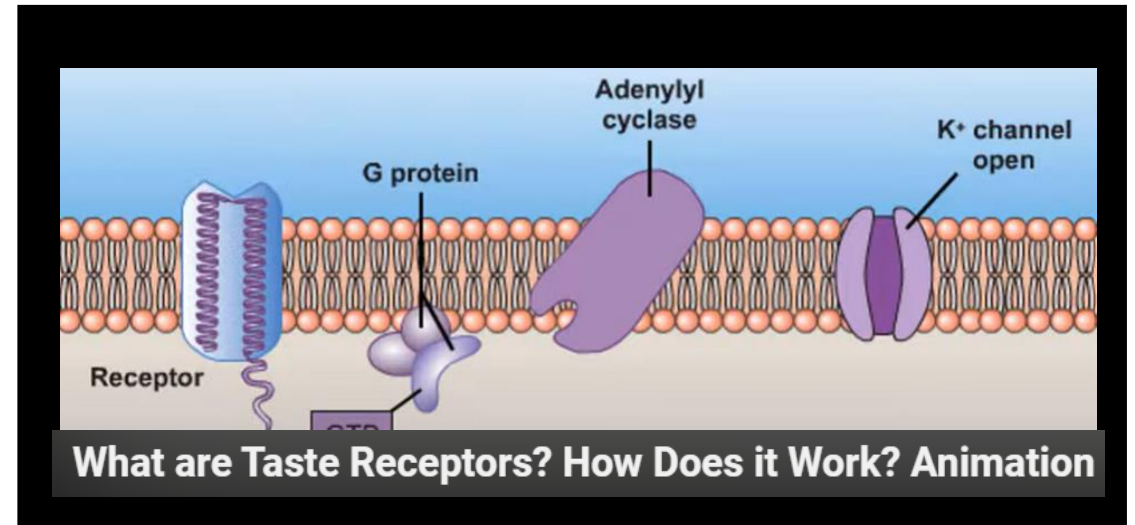
Use this website to see and download activation maps (in .nii.gz format; nii = Neuroimaging Informatics Technology; gz = compressed using Gnu Zip (gzip) software) 

In summary



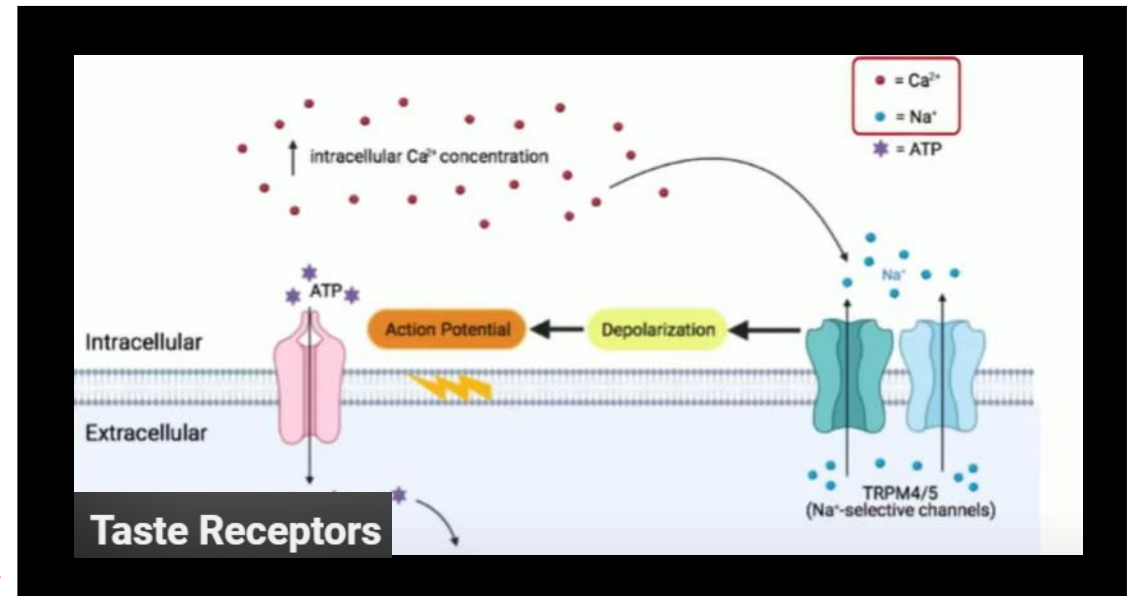
Taste: Anatomy and Physiology, Animation

<https://www.youtube.com/watch?v=K9JSBzEEA0o>



What are Taste Receptors? How Does it Work? Animation

<https://www.youtube.com/watch?v=9H5fcl7legE>



Taste Receptors

<https://www.youtube.com/watch?v=3q2SWm9dheo>

kokumi = “rich taste” (e.g., the richness and complexity of aged wines) ←

Touch: the somatosensory system

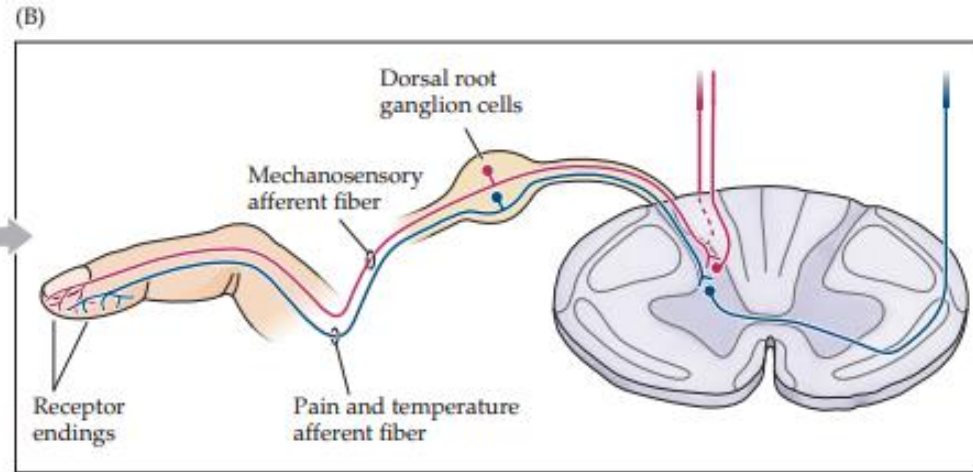
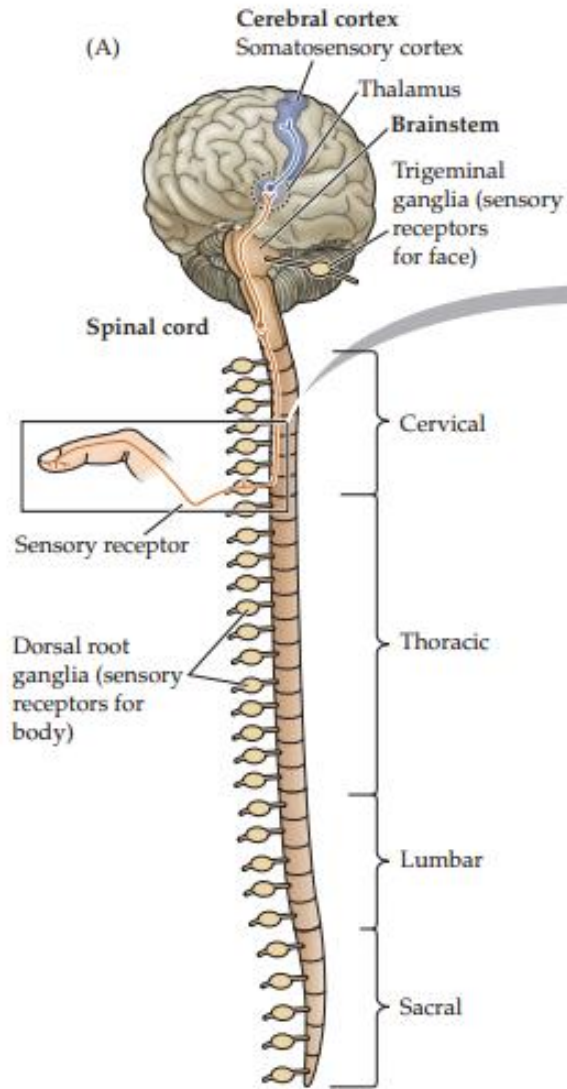


FIGURE 9.1 Somatosensory afferents convey information from the skin surface to central circuits. (A) The cell bodies of somatosensory afferent fibers conveying information about the body reside in a series of dorsal root ganglia that lie along the spinal cord; those conveying information about the head are found primarily in the trigeminal ganglia. (B) Pseudounipolar neurons in the dorsal root ganglia give rise to peripheral processes that ramify within the skin (or muscles or joints) and central processes that synapse with neurons located in the spinal cord and at higher levels of the nervous system. The peripheral processes of mechanoreceptor afferents are encapsulated by specialized receptor cells; afferents carrying pain and temperature information terminate in the periphery as free endings.

Purves et al., (2018), p. 194

REMEMBER: the **trigeminal nerve** (i.e., cranial nerve V) innervates the **face**

stimulation on skin

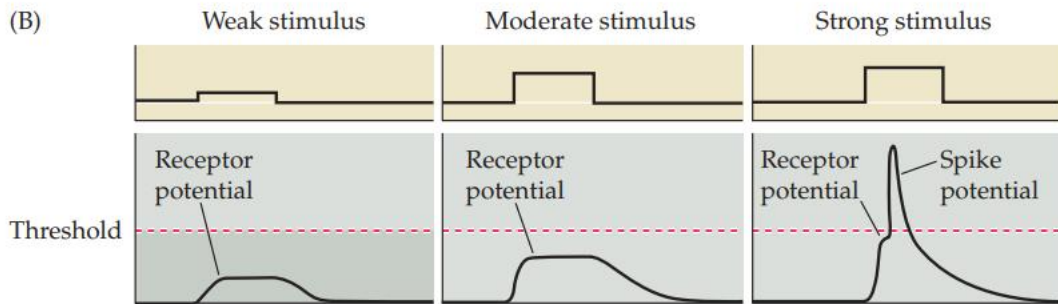
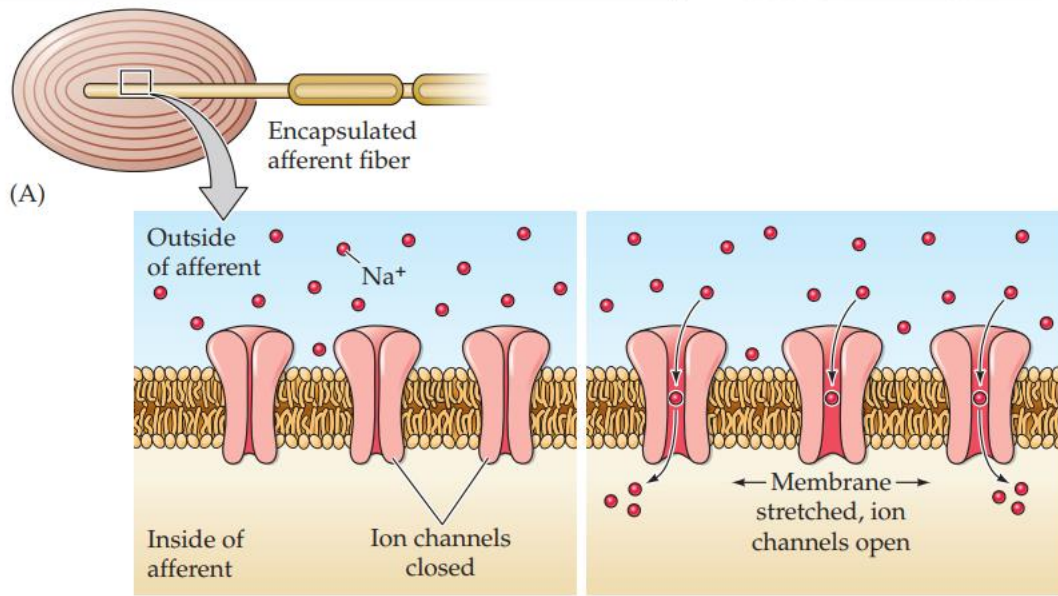


sensory transduction

(i.e., the process of **converting** the energy of a **stimulus** into an **electrical signal**) => **receptor potential** proportional to **stimulation intensity**



action potentials are generated in **afferent fibers** whose cell bodies are in the **dorsal root ganglia**



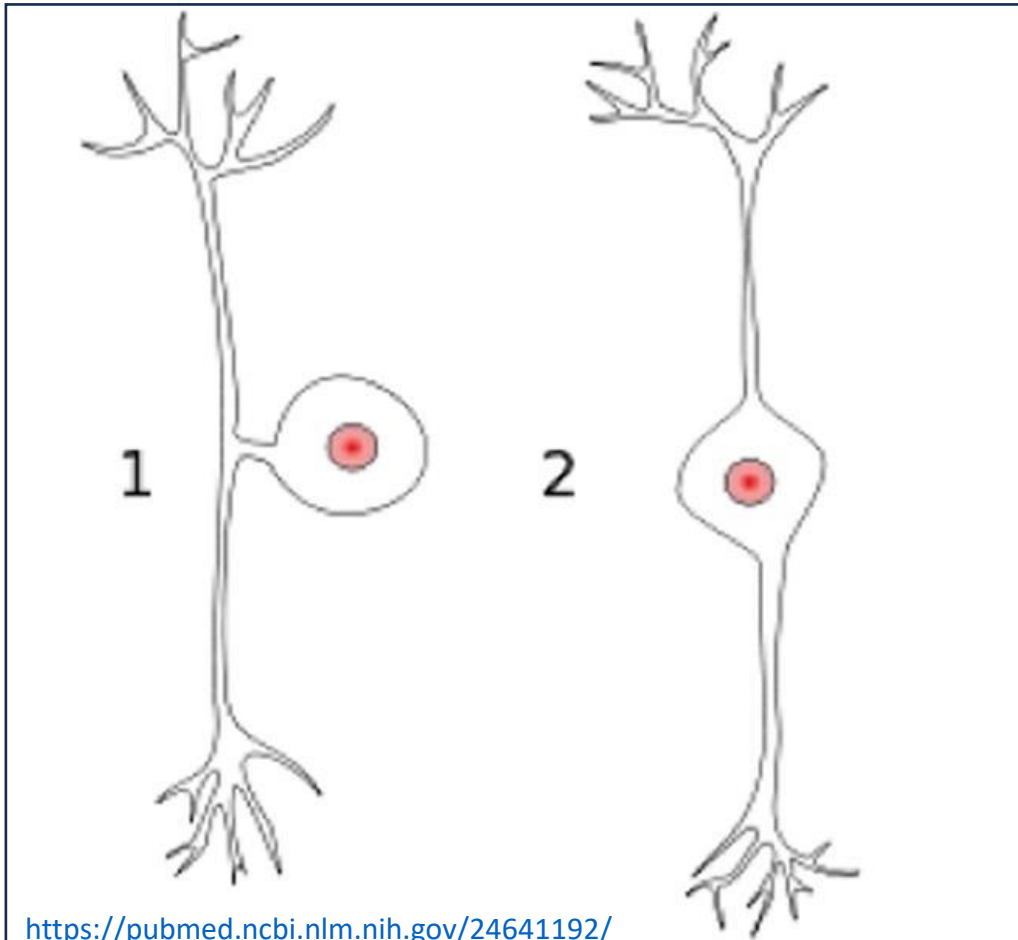
**FIGURE 9.2 Transduction in a mech-
anosensory afferent.** The process is
illustrated here for a Pacinian corpuscle.
(A) Deformation of the capsule leads to
a stretching of the membrane of the af-
ferent fiber, increasing the probability of
opening mechanotransduction channels
in the membrane. (B) Opening of these
cation channels leads to depolarization
of the afferent fiber (receptor potential). If
the afferent is sufficiently depolarized,
an action potential is generated and propa-
gates to central targets.

Purves et al., (2018), p. 195

Most afferent fiber terminals that **detect** and **transmit touch** sensory stimuli are **encapsulated** by **specialized receptor cells** that help tune the afferent fiber to somatic stimulation. The encapsulated fibers terminals generally have **lower thresholds** for action potential generation => **more sensitive** to sensory stimulation compared to free nerve endings.

Unencapsulated afferent fibers are called **free nerve endings** and are especially important in the sensation of pain (i.e., **nociception**).

Sensory neurons



<https://pubmed.ncbi.nlm.nih.gov/24641192/>

(1) A **pseudounipolar sensory neuron**. A pseudounipolar neuron has **one axon** that is divided into two separate branches, one from the periphery to the body and one from the body to the spinal cord. There are **no dendrites**. Unipolar cells are not to be confused with bipolar cells (2) where the body lies within the path of the axon. Unipolar cells have a T-stem axon that is away from the main axon.

Because sensory neurons are **pseudounipolar**, conduction of electrical activity through the membrane of the **cell body** is not an obligatory step in conveying sensory information to **central targets**. Nevertheless, cell bodies of sensory afferents play a **critical role** in maintaining the cellular mechanisms that mediate **transduction, conduction, and transmission** by sensory afferent fibers.

transduction

occurs in the **peripheral terminals** of primary afferent neurons where different forms of **energy** (e.g., mechanical), are converted to electrical activity (**action potentials**)

conduction

the **movement of an action potential** across the peripheral process to the central process where it depolarizes the presynaptic terminal

transmission

the process by which **electrical activity** induced by a stimulus is conducted **through the nervous system**

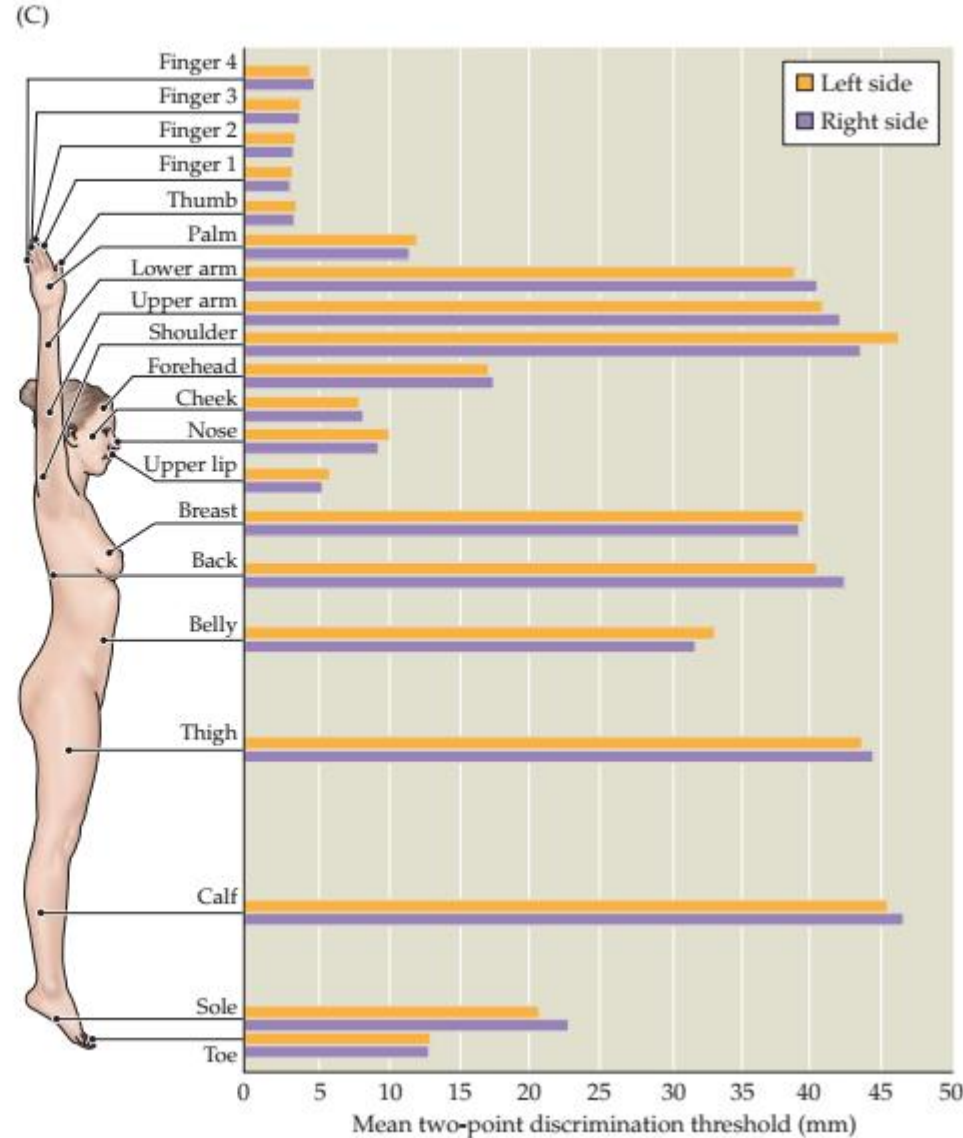
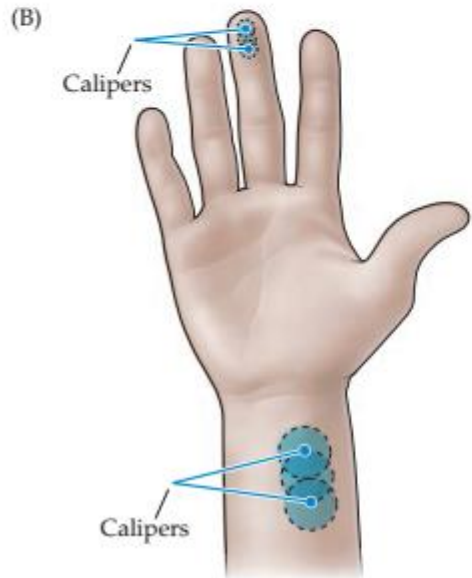
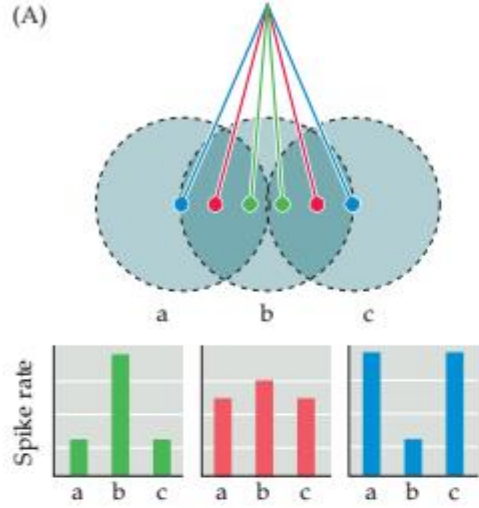


FIGURE 9.3 Receptive fields and the two-point discrimination threshold. (A) Patterns of activity in three mechanosensory afferent fibers with overlapping receptive fields a, b, and c on the skin surface. When two-point discrimination stimuli are closely spaced (green dots and histogram), there is a single focus of neural activity, with afferent b firing most actively. As the stimuli are moved farther apart (red dots and histogram), the activity in afferents a and c increases and the activity in b decreases. At some separation distance (blue dots and histogram), the activity in a and c exceeds that in b to such an extent that two discrete foci of stimulation can be identified. This differential pattern of activity forms the basis for the two-point discrimination threshold. Stimulation applied to the center of the receptive field tends to evoke stronger responses than stimuli applied at more eccentric locations within the receptive field (see Figure 1.14). (B) The two-point discrimination threshold in the fingers is much finer than that in the wrist because of differences in the sizes of afferent receptive fields—that is, the separation distance necessary to produce two distinct foci of neural activity in the population of afferents innervating the lower arm is much greater than that for the afferents innervating the fingertips. (C) Differences in the two-point discrimination threshold across the surface of the body. Somatic acuity is much higher in the fingers, toes, and face than in the arms, legs, or torso. (C after Weinstein, 1968.)

Purves et al., (2018), p. 196

Two-Point Discrimination Test (psychophysics)

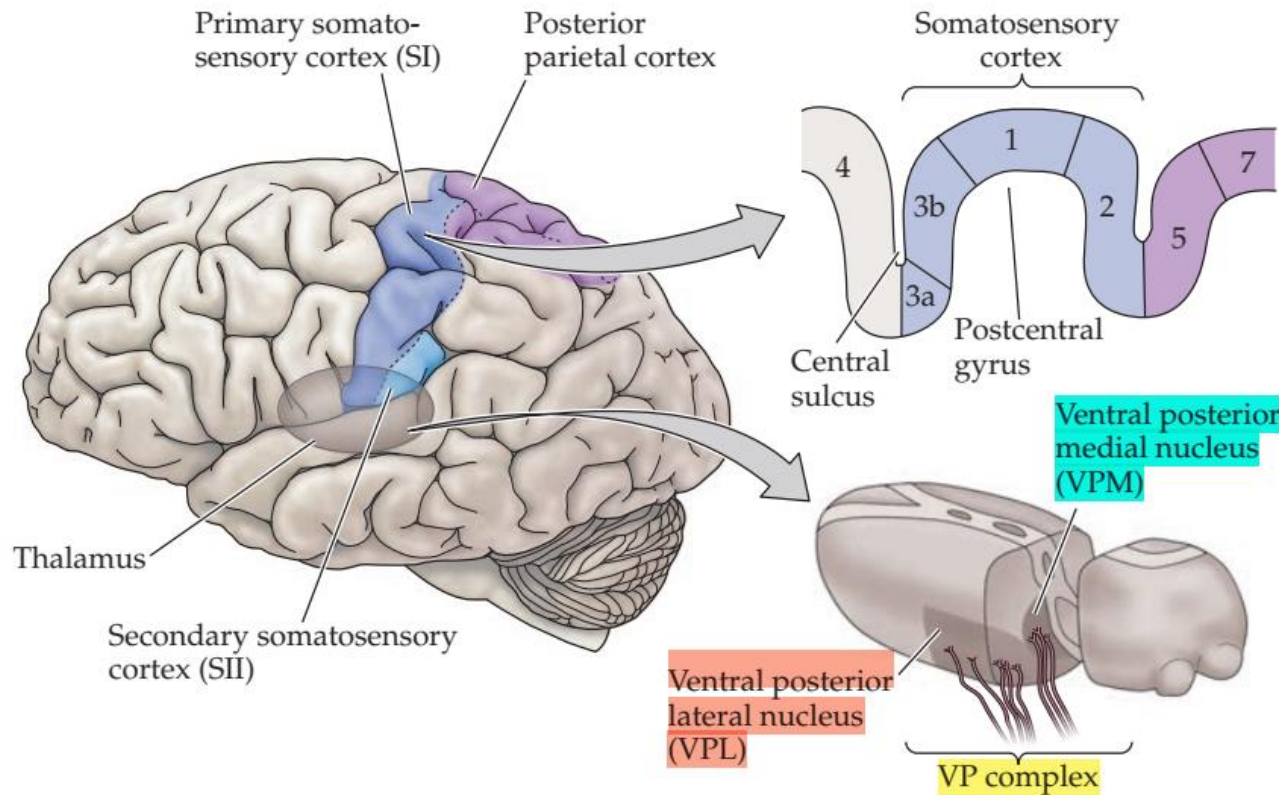


<https://www.youtube.com/watch?v=f488-BNid8>

examples of calipers



Primary somatosensory cortex



Each of the several **ascending somatosensory pathways** originating in the **spinal cord and brainstem** converges on the **ventral posterior complex** of the **thalamus** and terminates in an organized fashion (**somatotopy**).

Purves et al., (2018), p. 206

FIGURE 9.10 Somatosensory portions of the thalamus and their cortical targets in the postcentral gyrus. The **ventral posterior nuclear complex** comprises the **VPM**, which **relays somatosensory information carried by the trigeminal system from the face**, and the **VPL**, which **relays somatosensory information from the rest of the body**. The diagram at the upper right shows the organization of the primary somatosensory cortex in the postcentral gyrus, shown here in a section cutting across the gyrus from anterior to posterior. (After Brodal, 1992 and Jones et al., 1982.)

Somatotopic organization of the primary somatosensory cortex

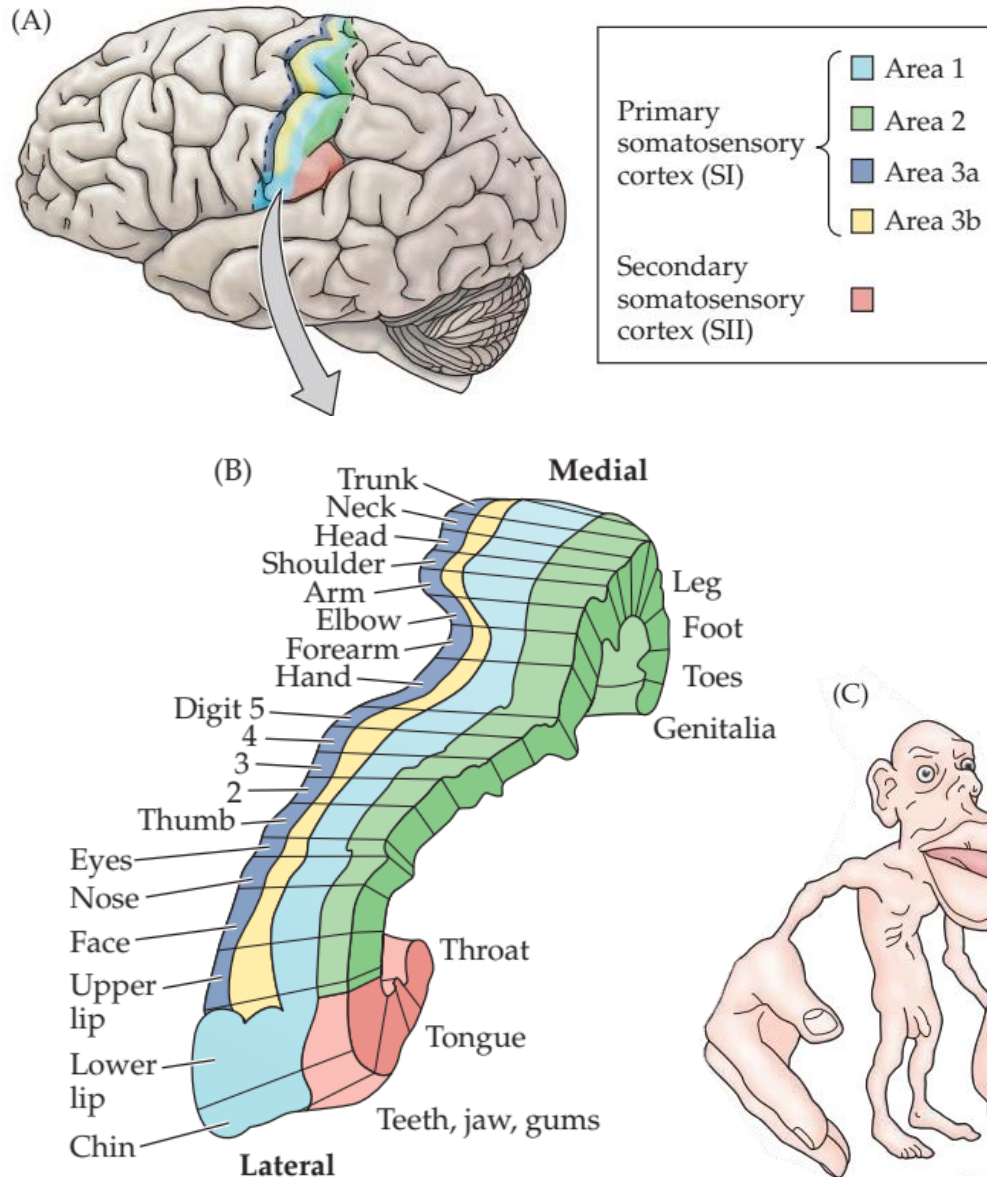
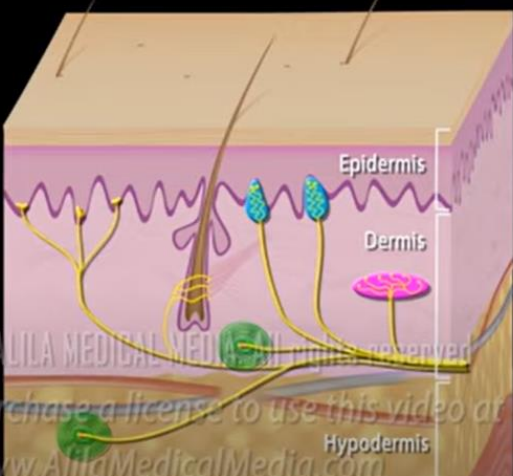


FIGURE 9.11 Somatotopic order in the human primary somatosensory cortex. (A) Diagram showing the region of the human cortex from which electrical activity is recorded following mechanosensory stimulation of different parts of the body. (The patients in the study were undergoing neurosurgical procedures for which such mapping was required.) Although modern imaging methods are now refining these classical data, the human somatotopic map defined in the 1930s has remained generally valid. (B) Diagram showing the somatotopic representation of body parts from medial to lateral. (C) Cartoon of the homunculus constructed on the basis of such mapping. Note that the amount of somatosensory cortex devoted to the hands and face is much larger than the relative amount of body surface in these regions. A similar disproportion is apparent in the primary motor cortex, for much the same reasons (see Chapter 17). (After Penfield and Rasmussen, 1950, and Corsi, 1991.)

remember the homunculus of Wilder Penfield

In summary

Major types of tactile receptors



The diagram shows a cross-section of skin with three layers: Epidermis, Dermis, and Hypodermis. Various receptors are shown: yellow branching structures (Merkel's discs) in the epidermis, blue oval structures (Meissner's corpuscles) at the dermal papillae, and green oval structures (Pacian corpuscles) in the dermis. A pink structure (Ruffini's corpuscles) is also shown in the dermis.

Merkel's discs:

- unencapsulated
- slowly-adapting
- light touch
- small receptive field

Pacian corpuscles:

- encapsulated
- rapidly-adapting
- heavy pressure

Meissner's corpuscles:

- encapsulated
- rapidly-adapting
- light touch
- small receptive field

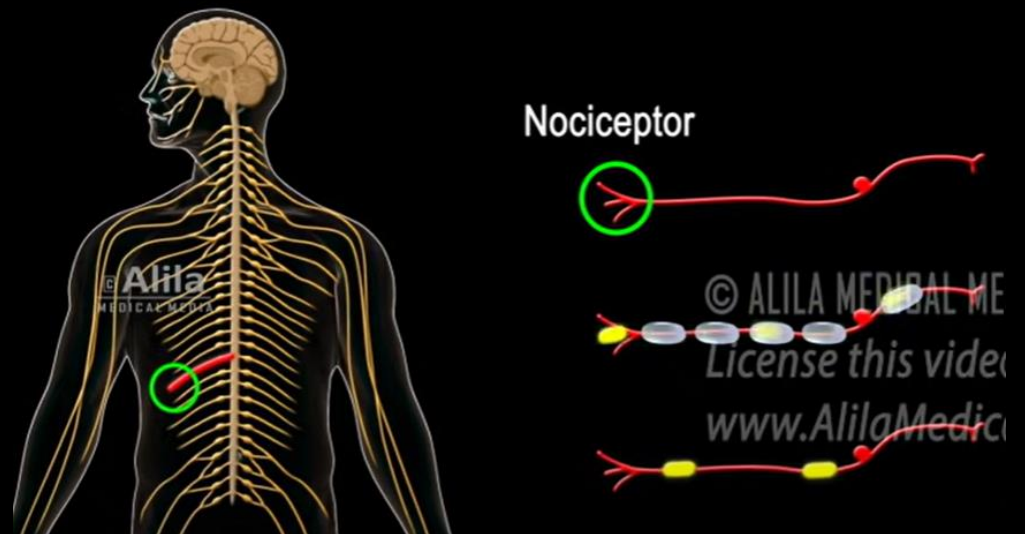
Ruffini's corpuscles:

- encapsulated
- slowly-adapting
- heavy pressure

Physiology of Touch: Receptors and Pathways, Animation

<https://www.youtube.com/watch?v=udzhuFz3HKw>

Nociceptor



The diagram shows a human torso with the nervous system highlighted. A green circle highlights a nociceptor in the skin. To the right, a detailed view of a nociceptor is shown, consisting of a red fiber with a green circle at the end, and a yellow fiber with a red circle at the end. The text 'Nociceptor' is written above the diagram.

Physiology of Pain, Animation.

<https://www.youtube.com/watch?v=uOaiaYDoUnA>

Real world applications



For Amputees, Reactivating the Sense of Touch

<https://www.youtube.com/watch?v=lrn5HbQjkm8>

Further resources



Linda Buck interview on the Science of Smell (2005)

<https://www.youtube.com/watch?v=X9Cy0Y6YYOA>