Olfatto e gusto

due sensi chimici

L'olfatto e il gusto sono definiti 'sensi chimici' perché ci consentono di analizzare le molecole dell'ambiente esterno con le quali veniamo in contatto respirando e nutrendoci.

forme di sensibilità filogeneticamente più antiche

L’esperienza sensoriale del gusto dipende non solo dalla stimolazione dei recettori gustativi, ma anche di quelli olfattivi .

Taste (gusto) is often thought to be synonymous with flavor (aroma).

However,

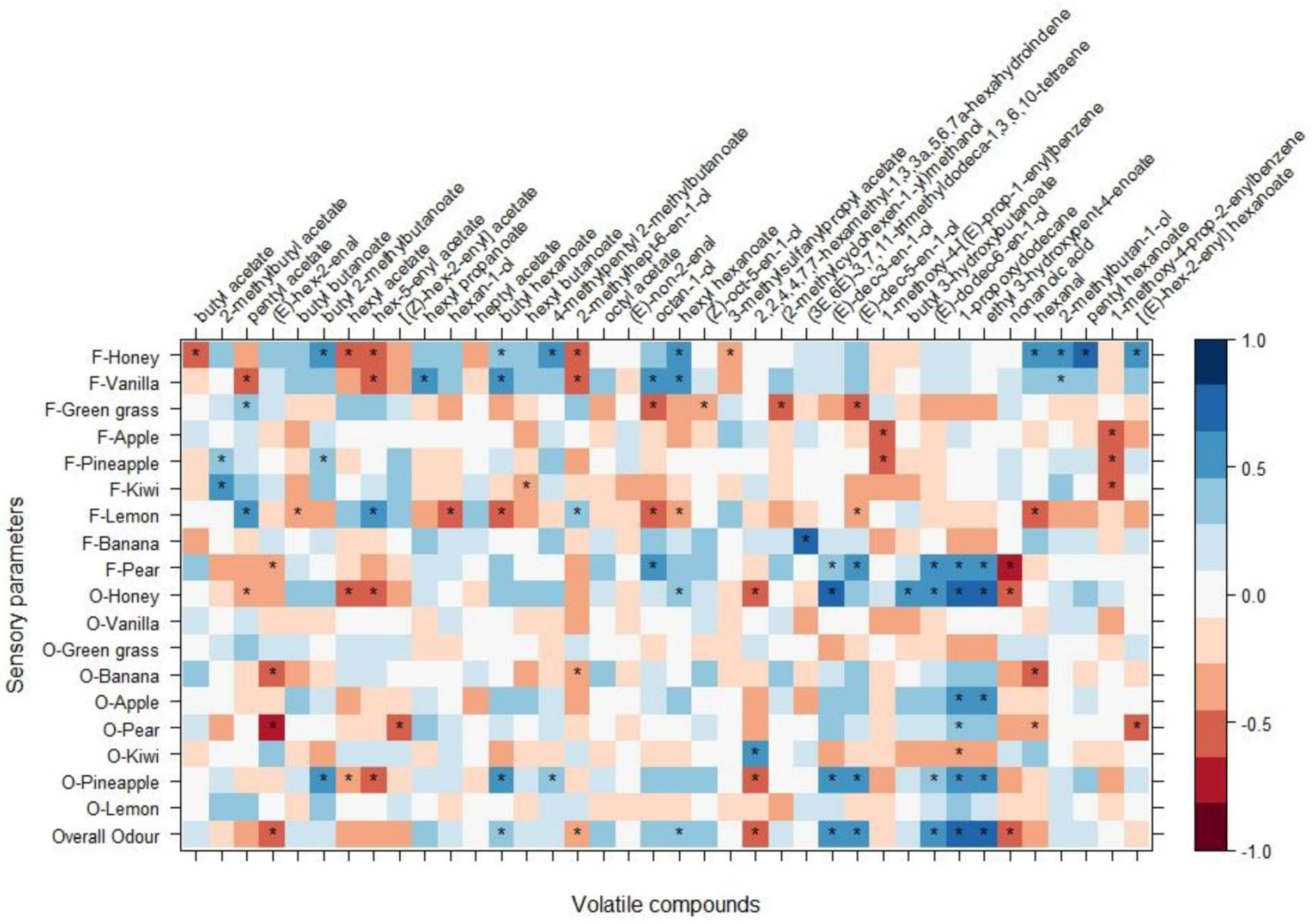
taste (gusto) refers strictly to the qualities encoded in the gustatory system,

whereas

flavor, with its rich and varied qualities, actually stems from a combination of inputs from the gustatory, olfactory, and somatosensory systems

Il senso dell'olfatto (dal latino *olfàcere,* annusare) permette di riconoscere un gran numero di molecole odorose volatili.

Quelli che comunemente vengono definiti "odori" sono in realtà miscele, a volte molto complesse, di molecole volatili strutturalmente diverse tra loro che trasportano informazioni riguardanti l'ambiente esterno.

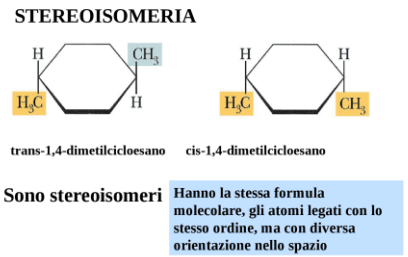


La discriminazione di odori dipende

- da **recettori specifici** localizzati sui cellule olfattive e gustative
- che **interagiscono stericamente** (cioè grazie alla loro forma specifica) con le varie sostanze.

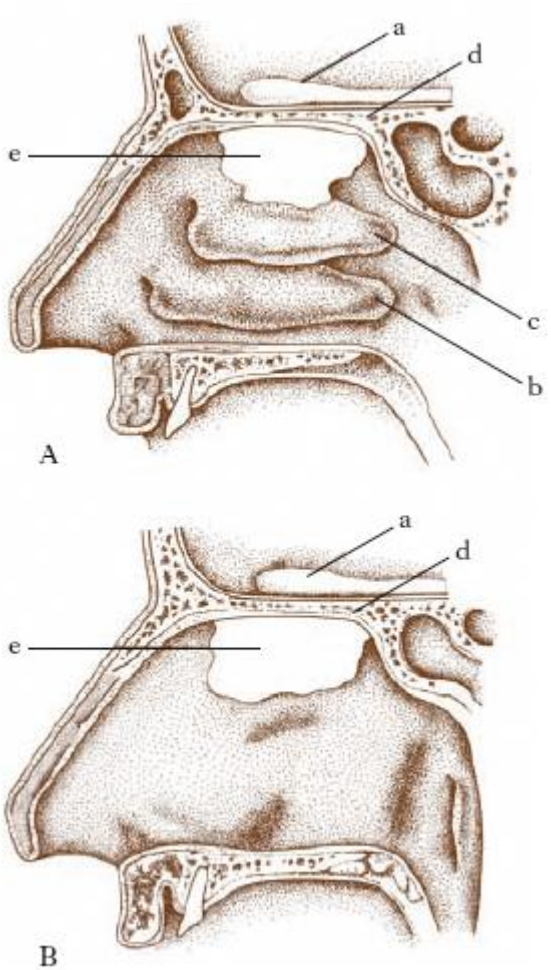
L'assenza del recettore specifico rende insensibili alla sostanza corrispondente. Ad esempio coloro che esprimono il recettore per la feniltiourea la sentono amara, mentre quelli che non lo esprimono non la percepiscono proprio.

Stereoisomeri di una stessa sostanza, chimicamente uguali, ma diversi per la loro forma tridimensionale non producono la stessa sensazione.



Chemocettori

localizzati in un’area ristretta della mucosa nasale, la mucosa olfattoria con pigmentazione giallastra.



Mammiferi microsmatici

Strettamente legata alla funzione “gustativa”

Mammiferi macrosmatici

molecole liberate

- sudore
- escrementi
- altri secreti

Vengono percepite dal s. olfattivo e servono

- per marcare il territorio
- per attirare un partner sessuale
- per la funzione riproduttiva (ovulazione)e parentali
- per riconoscere i conspecifici
- Per comportamenti di attacco e fuga
- per lanciare un allarme

Esempi

Nelle femmine in estro dei Roditori il contatto con l'urina di un maschio della stessa specie determina l'ovulazione per l'azione di segnali olfattivi sui neuroni endocrini dell'ipotalamo che controllano l'asse ipofisi-ovaio.

Animali sotto stress lasciano nell'ambiente tracce chimiche che possono indurre un corrispondente stato neuroendocrino di stress in altri animali che successivamente occupino quell'ambiente.

ma

Nella specie umana le femmine in età riproduttiva

ritengono più gradevole

l'odore di magliette indossate da maschi con MHC dissimile dal loro

Rispetto

a quello di magliette indossate da maschi con MHC simile

ma non è ancora noto se questa preferenza influenzi effettivamente le scelte sessuali e riproduttive

Il complesso maggiore di istocompatibilità (MHC)
gruppo di geni altamente variabile da individuo a individuo, ma non fra gemelli monozigotici, che determina l'assetto immunitario individuale

frontiers in Psychology

ORIGINAL RESEARCH
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Do Single Men Smell and Look Different to Partnered Men?

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Previous research indicates human body odor (BO) can signal kinship, sickness and genetic compatibility. Based on research indicating single males have higher testosterone levels than partnered males and that higher testosterone levels are associated with stronger smelling BO, the current study aimed to determine if, by extension of previous findings, single males' BO smells stronger than partnered males' BO. Eighty-two heterosexual women aged 18–35 years rated the BO and faces of six different males also aged 18–35 years. Consistent with the hypothesis, single men's BO smelled stronger than partnered men's BO and single men's faces were rated as more masculine than partnered men's faces. The possible advantages of females being able to identify single males are addressed in the Discussion.

OPEN ACCESS

Keywords: mate preferences, mate attraction, masculinity, body odor, face attractiveness

Un componente del sudore derivato da ormoni gonadici, l'androstenone, sta acquistando popolarità nel commercio dei profumi perché in alcune specie (per es., nei cinghiali e forse anche nell'uomo) aumenta l'attrazione olfattiva delle femmine verso i maschi.

Sincronizzazione dei cicli mestruali

i ***ferormoni*** influenzano l'attività endocrina dell'ipotalamo umano

Ad esempio:

sincronizzano il ciclo mestruale in donne che vivono in comunità.

Sostanze presenti nel sudore ascellare, per lo più inodori, che vengono secrete in determinate fasi del ciclo mestruale:

•Sostanze secrete verso la fine della fase pre-ovulatoriatoria accelerano l'ovulazione e accorciano il ciclo nelle donne che le inalano.

•Sostanze secrete in fase post-ovulatoria ritardano l'ovulazione e allungano il ciclo.

La sincronizzazione del ciclo mestruale in donne conviventi è il risultato della combinazione dei due effetti.

Soglia assoluta

L'olfatto dell'uomo ha una sensibilità è tale da far sì che

la presenza di un odore sia rilevata a una concentrazione di 10^7 molecole per 1 ml d'aria

e la sua identità sia riconosciuta a una concentrazione solo dieci volte superiore.

Soglia differenziale

Per *soglia differenziale* si intende la differenza minima di intensità che uno stimolo deve avere da un altro affinché vengano percepiti come diversi.

In addition to detecting minute quantities of odor humans detect subtle variation in concentration.

The smallest discernable difference in concentration, or magnitude, constitutes the standard psychophysical entity of “just noticeable difference” (JND). As a rule, JNDs are in constant proportion to the initial stimulus .

This proportion, called the Weber fraction, can be as low as ~7% in olfaction), which is similar if not smaller than Weber fractions in human vision and audition (Mueller, 1951).

Capacità discriminativa

In addition to small differences in concentration, humans can discriminate the smallest alterations in molecular structure.

For example, humans can discriminate

•aliphatic odorants equal in number of carbons, but differing in functional group (Laska et al., 2000).

•odorants that differ in chain length by one carbon, and the greater the difference in carbon chain length between any two odorants, the easier they are to discriminate (Laska and Freyer, 1997).

•between certain enantiomer pairs like (+) and (−) carvone

La capacità discriminativa dell'olfatto umano è meno sviluppata rispetto a quella di molti animali

Tuttavia

odor chemists estimate that the human olfactory system may be capable of detecting more than 10,000 different volatile chemicals.

Perfumers who are highly trained to discriminate odorants can distinguish as many as 5,000 different types of odorants

wine tasters can discern more than 100 different components of taste based on combinations of taste (gusto) and aroma.

La capacità di discriminare le diverse sostanze volatili consente di attribuire **un label semantico** (che cosa è) agli oggetti che emettono un insieme di sostanze volatili nel 50% dei casi

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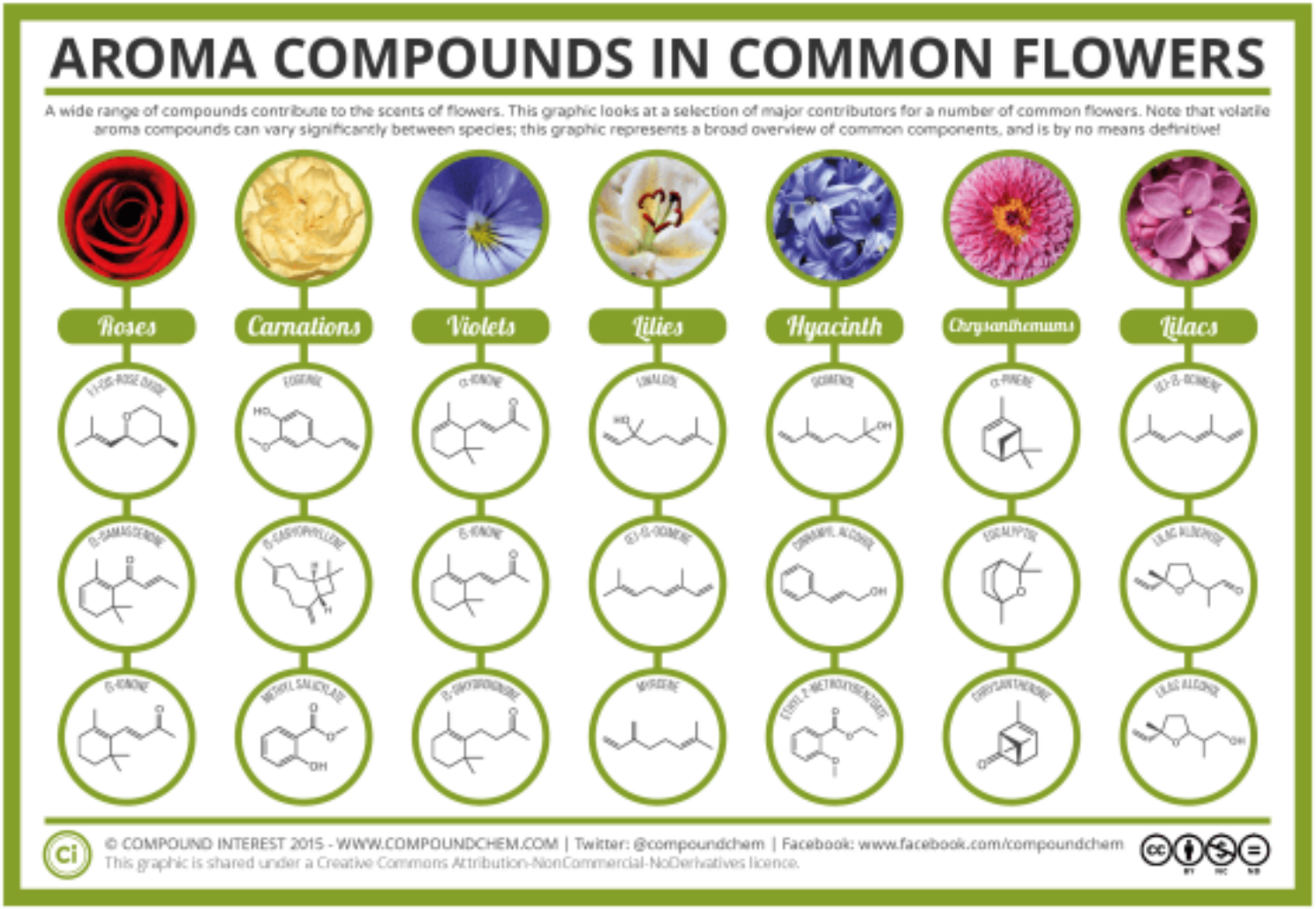
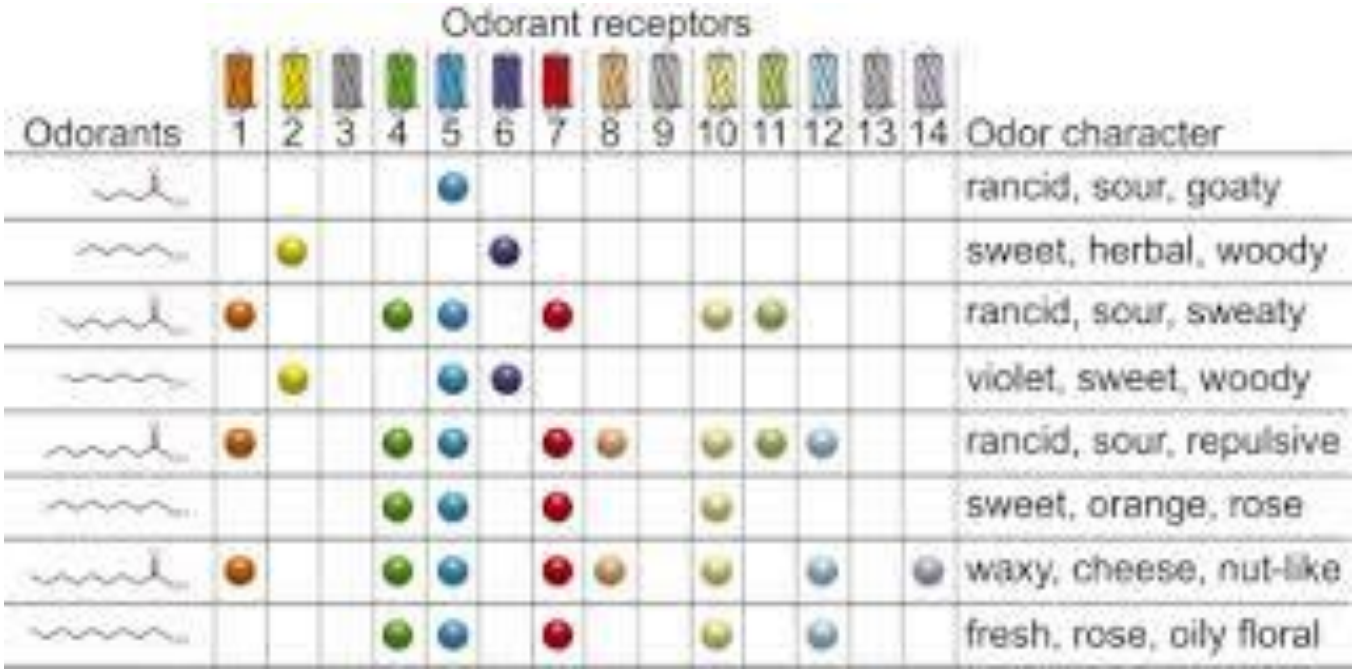


Nel rimanente 50% dei casi pur non associando l'odore ad un oggetto

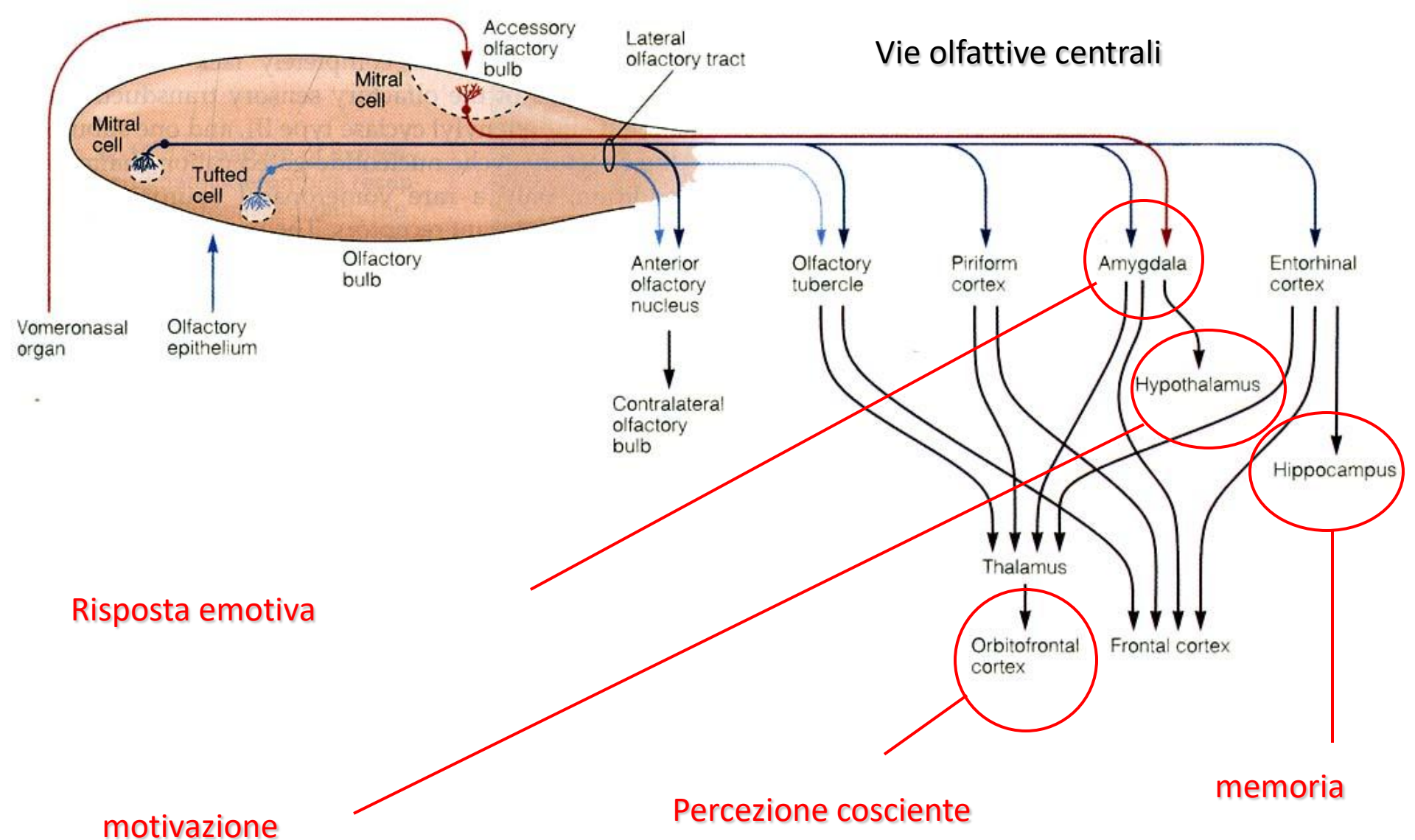
i soggetti sono capaci di **usare descrittori generici** che si riferiscono ad una qualità di generica un odore

prevalgono derscrittori legati all'aspetto affettivo: es piacevole/disgustoso , famigliare/sconosciuto



Anatomia e fisiologia dell’olfatto

Vie olfattive centrali



Risposta emotiva

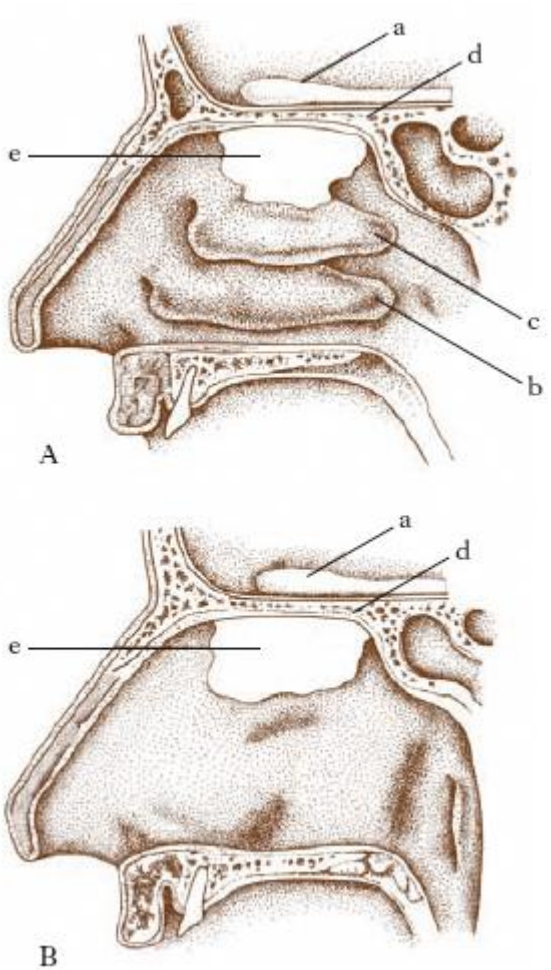
motivazione

Percezione cosciente

memoria

Chemocettori

localizzati in un’area ristretta della mucosa nasale, la mucosa olfattoria con pigmentazione giallastra.



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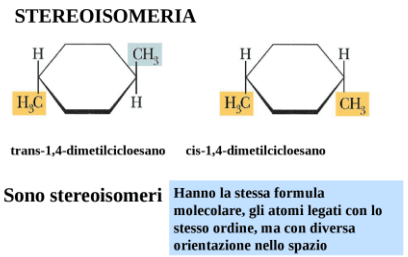
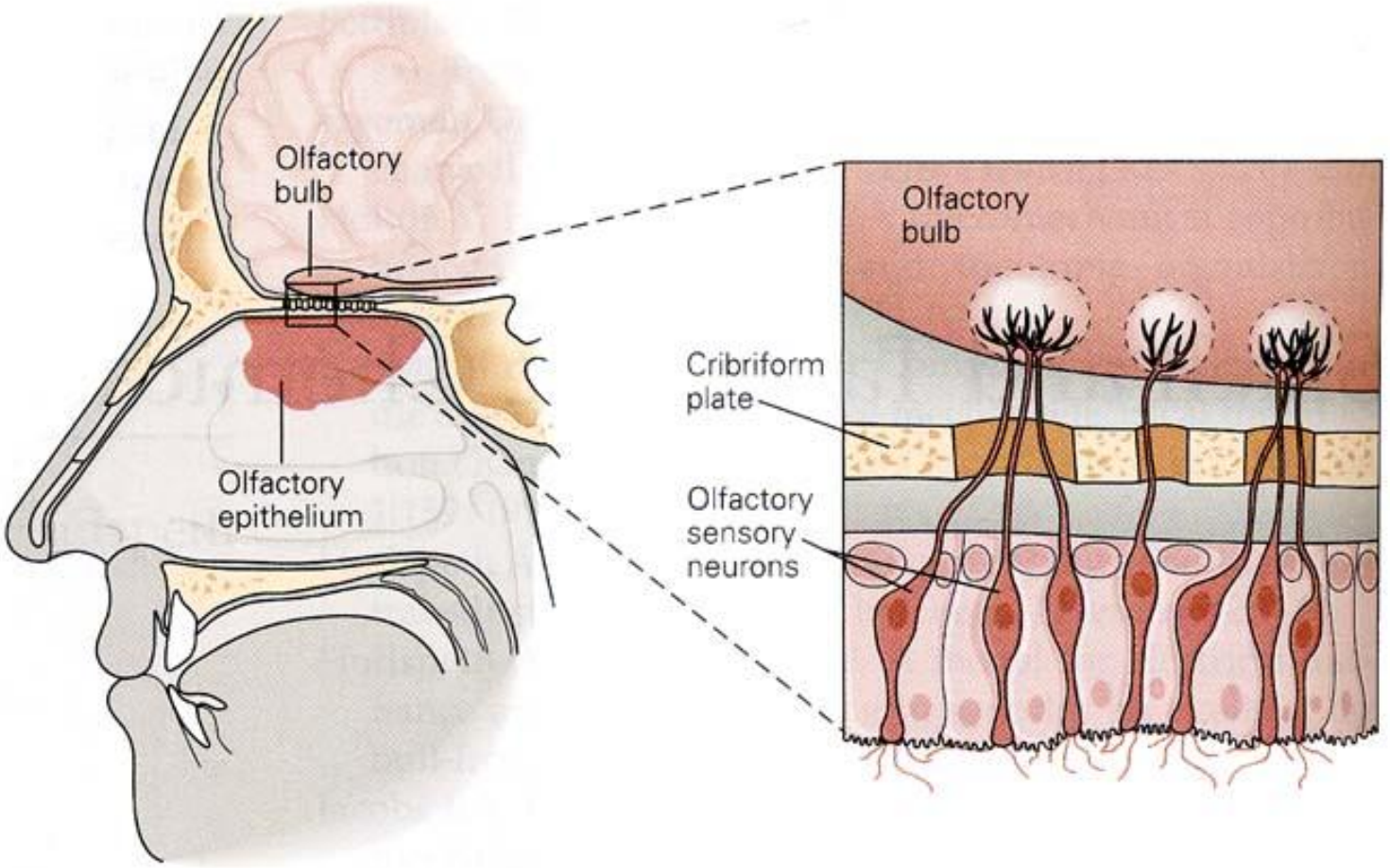
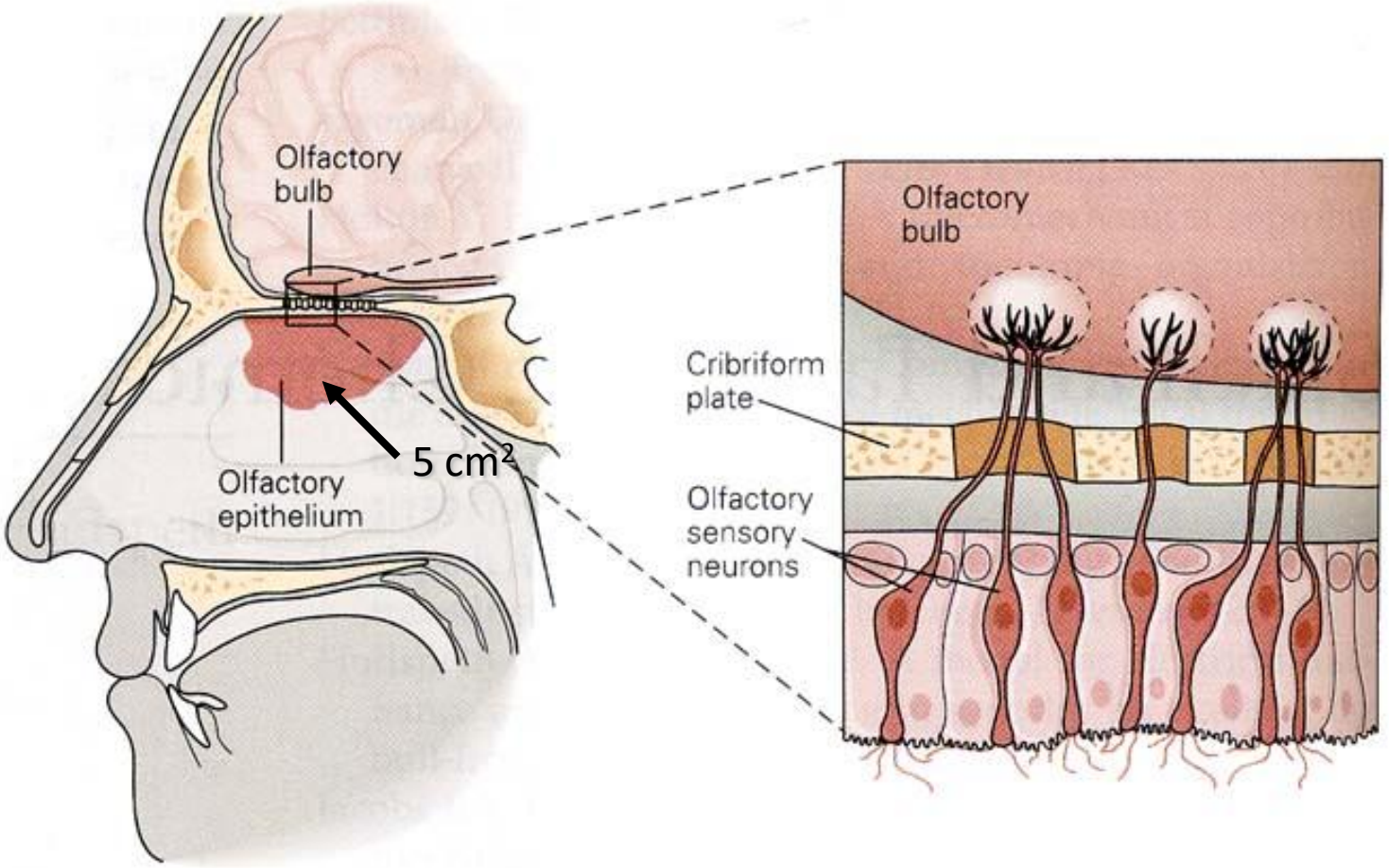


I recettori olfattivi sono cellule localizzate nella parte posteriore della cavità nasale





Le molecole odorose raggiungono l'epitelio olfattivo non solo attraverso le narici *(via ortonasale)*, ma anche attraverso la rinofaringe *(via retronasale)*. Questo processo svolge un ruolo molto importante nel determinare l'aroma dei cibi, poiché le molecole volatili provenienti dal cibo ingerito raggiungono i recettori olfattivi.

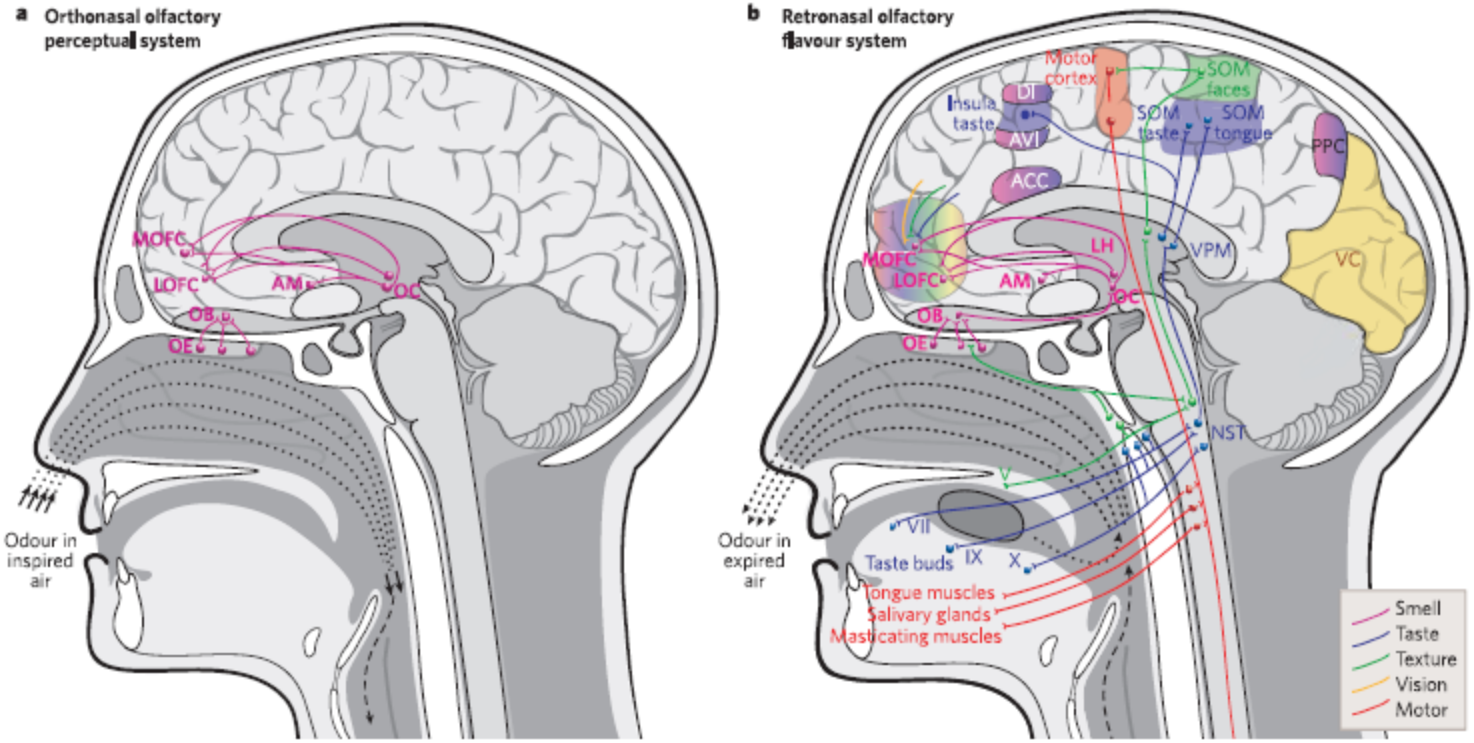


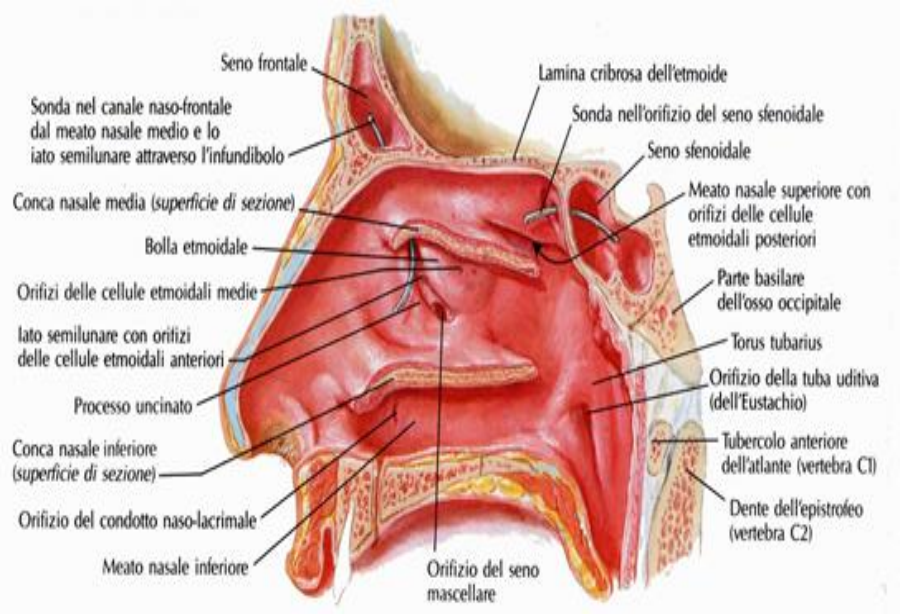
Figure 2 | The dual olfactory system. **a,** Brain systems involved in smell perception during orthonasal olfaction (sniffing in). **b,** Brain systems involved in smell perception during retronasal olfaction (breathing out), with food in the oral cavity. Air flows indicated by dashed and dotted lines; 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.

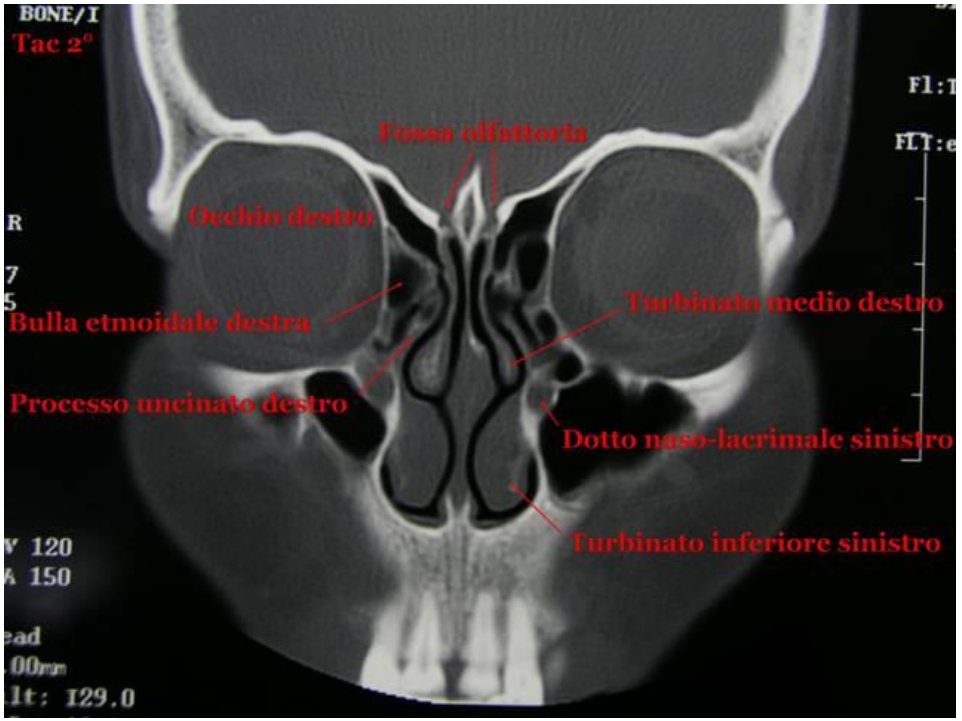
Table 1 | The dual olfactory system

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.

Il naso ha una struttura tridimensionale complessa che ha un ruolo importante nel regolare il flusso delle molecole odorose verso le strutture recettoriali.

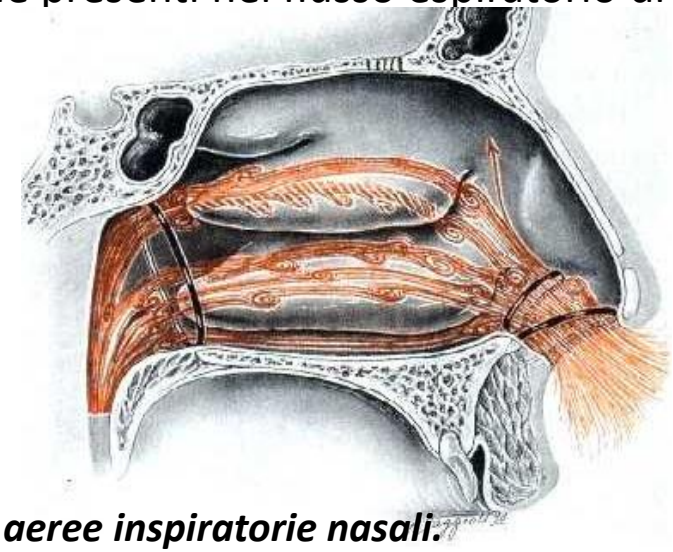




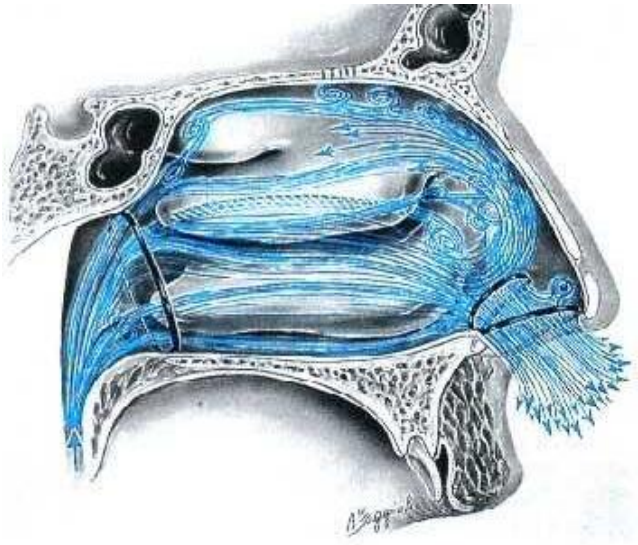
Misurazioni del flusso d'aria attraverso le vie respiratorie superiori rivelano che i flussi inspiratori ed espiratori hanno proprietà differenti.

l'inalazione genera un flusso d'aria multidirezionale e laminare. Durante l'inspirazione le molecole volatili raggiungono l'*epitelio olfattivo,* un tessuto epiteliale specializzato, situato sulla volta della cavità nasale sotto la placca cribriforme e il turbinato superiore

l'esalazione determina un flusso stretto e turbolento, che impedisce alla maggior parte delle molecole presenti nel flusso espiratorio di essere nuovamente inalate.



Correnti aeree inspiratorie nasali.
Una corrente a colonna entra nella narice, incontra le prime resistenze nel cul-de-sac superiore, si concentra per attraversare l'area valvolare, si dilata nelle cavità nasali per concentrarsi di nuovo in corrispondenza del registrimento coanale, con un'angolatura a 90° si dirige nella faringe per procedere poi nella laringe.



Correnti aeree espiratorie.
Dalla faringe la corrente calda e satura di umidità penetra nella cavità nasale. Il gioco dei flussi vorticosi permette all'aria di cedere calore e umidità prima di uscire all'esterno.

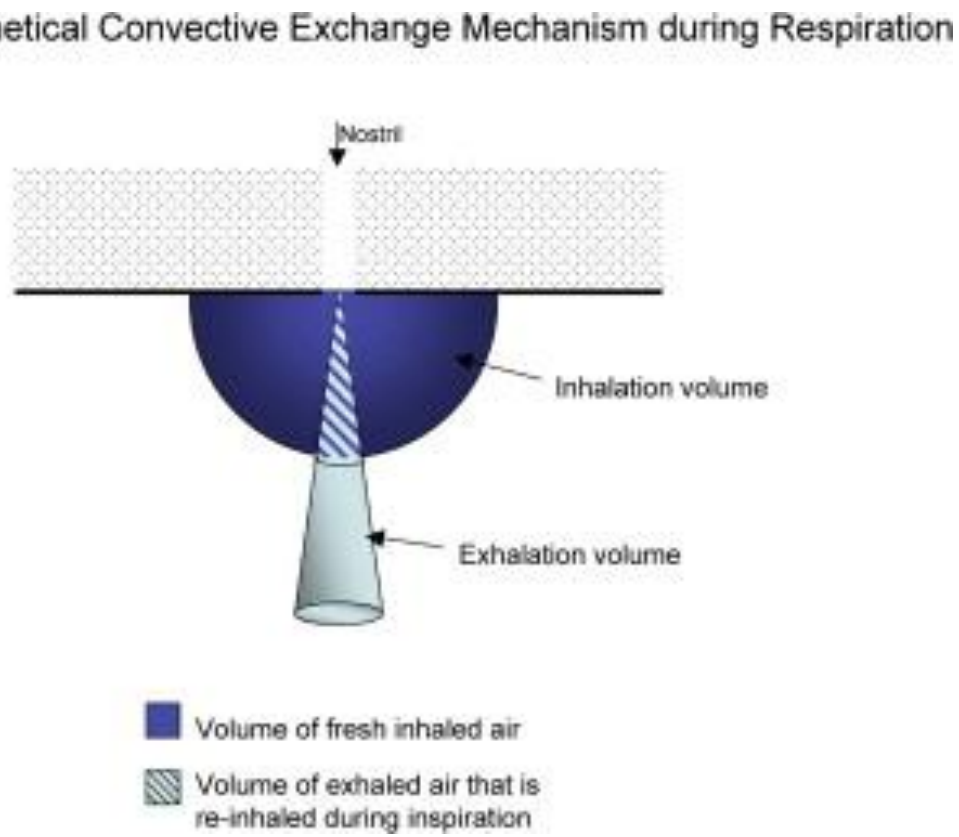


Figure 2. Schematic Diagram Showing the Operation of the Hypothetical Convective Exchange Mechanism that Takes Place during Respiration through the NoseShown is the position of the expired gas immediately after expiration and the position of the inhaled gas im...

Christina Zelano, Noam Sobel

Humans as an Animal Model for Systems-Level Organization of Olfaction

null, Volume 48, Issue 3, 2005, 431–454

http://dx.doi.org/10.1016/j.neuron.2005.10.009

Different Perception through Different Nostrils

Humans as an Animal Model for Systems-Level Organization of Olfaction

Christina Zelano, Noam Sobel

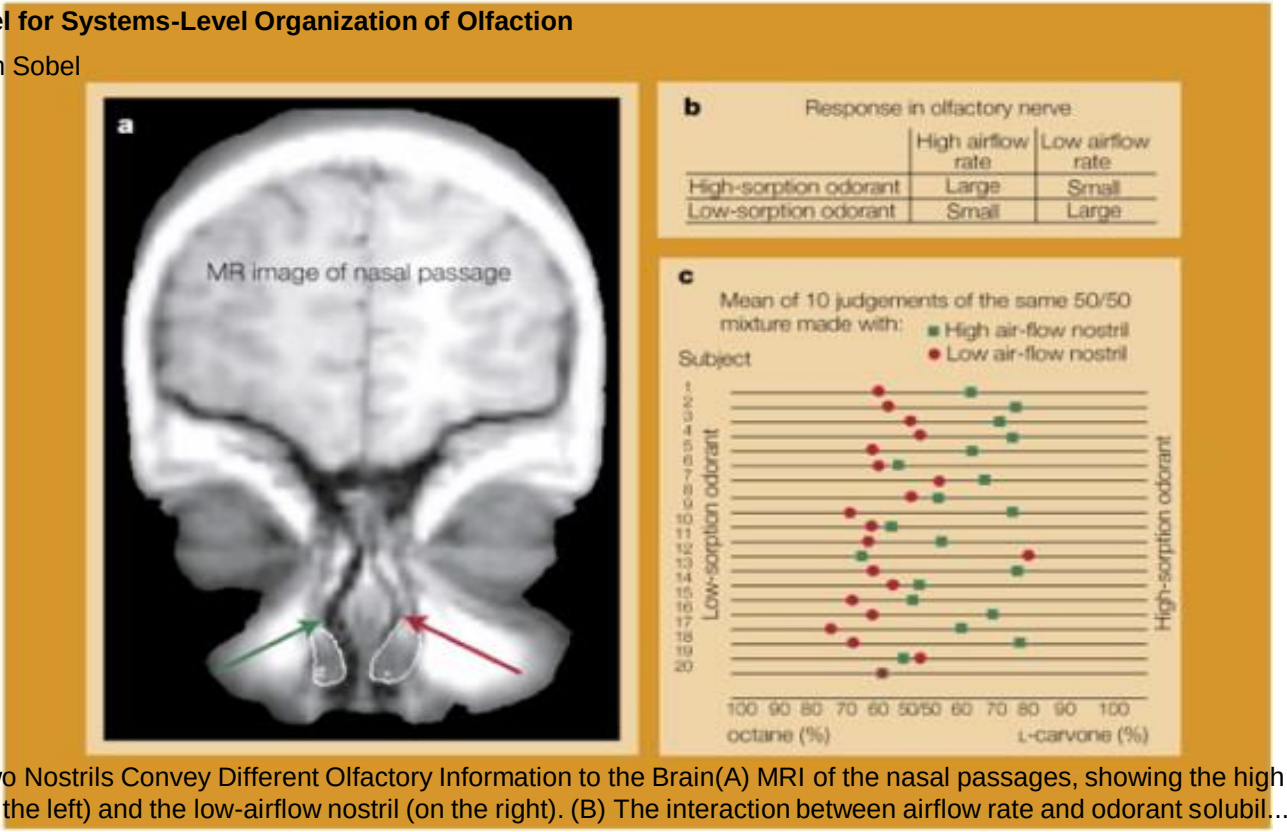


Figure 4. The Two Nostrils Convey Different Olfactory Information to the Brain(A) MRI of the nasal passages, showing the high-airflow nostril (on the left) and the low-airflow nostril (on the right). (B) The interaction between airflow rate and odorant solubil...

On each of ten trials, subjects smelled an identical binary mixture of octane and (−) carvone, using either the left or right nostril. They then judged the composition of the mixture. Using the high-flow rate nostril (green), the average judgment was that the mixture consisted of 55% (−) carvone and 45% octane. Using the low-flow rate nostril (red), the judgment was that it consisted of 61% octane and 39% (−) carvone

differences in timing or intensity could provide information about where an odor-emanating object is located in space
(http://dx.doi.org/10.1016/j.neuron.2005.10.009

In condizioni di riposo (respirazione tranquilla) solo il 5-10% del flusso d'aria che attraversa le narici durante la respirazione raggiunge l'epitelio olfattivo.

Il *processo dell'annusare*

per rivelare la presenza di molecole odorose.

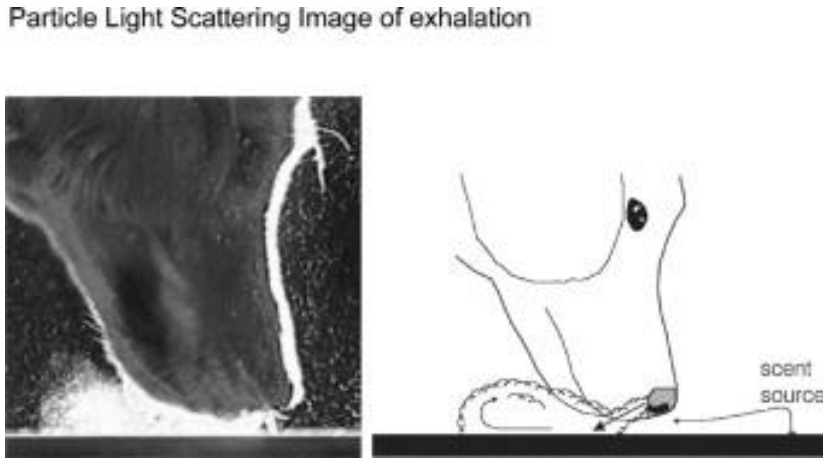
Malgrado durante la respirazione tranquilla un gran numero di molecole possono sfuggire alla rilevazione olfattiva è possibile esplorare la presenza di molecole odorose nell'ambiente annusando

Il processo consiste nell'aspirare con forza dal naso, tramite ripetute e veloci inalazioni che permettono all'aria di raggiungere l'epitelio olfattivo senza arrivare ai polmoni.

Infatti, quando si annusa, i muscoli respiratori regolano il volume dell'aria inalata e la durata di ogni inalazione in rapporto alle caratteristiche di concentrazione e di gradevolezza dello stimolo odoroso.

La tipica durata del processo d'inalazione, quando si annusa, è di circa 1,6 s che, con una velocità di inalazione di 27 I min^{-1}, permette l'ingresso di circa 500 cm^3 di aria.

Inoltre



Organisms utilize a sniffing nose to shape and enhance the vapor pulse that is finally presented to the sensory machinery, rather than simply reflect the spatial and temporal properties of the original stimulus outside the nose.

Figure 3. Imaging the Canine SniffOn the left, an image of a dog performing olfactory exploration, obtained using particle light scattering to show the effect of entrainment by expired air jets. On the right is a diagram highlighting the effects of the directi...

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La percezione sensoriale implica processi di esplorazione attiva

Per l’olfatto

L’atto di annusare

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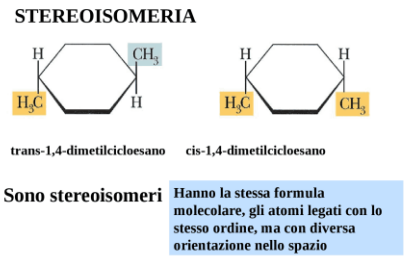
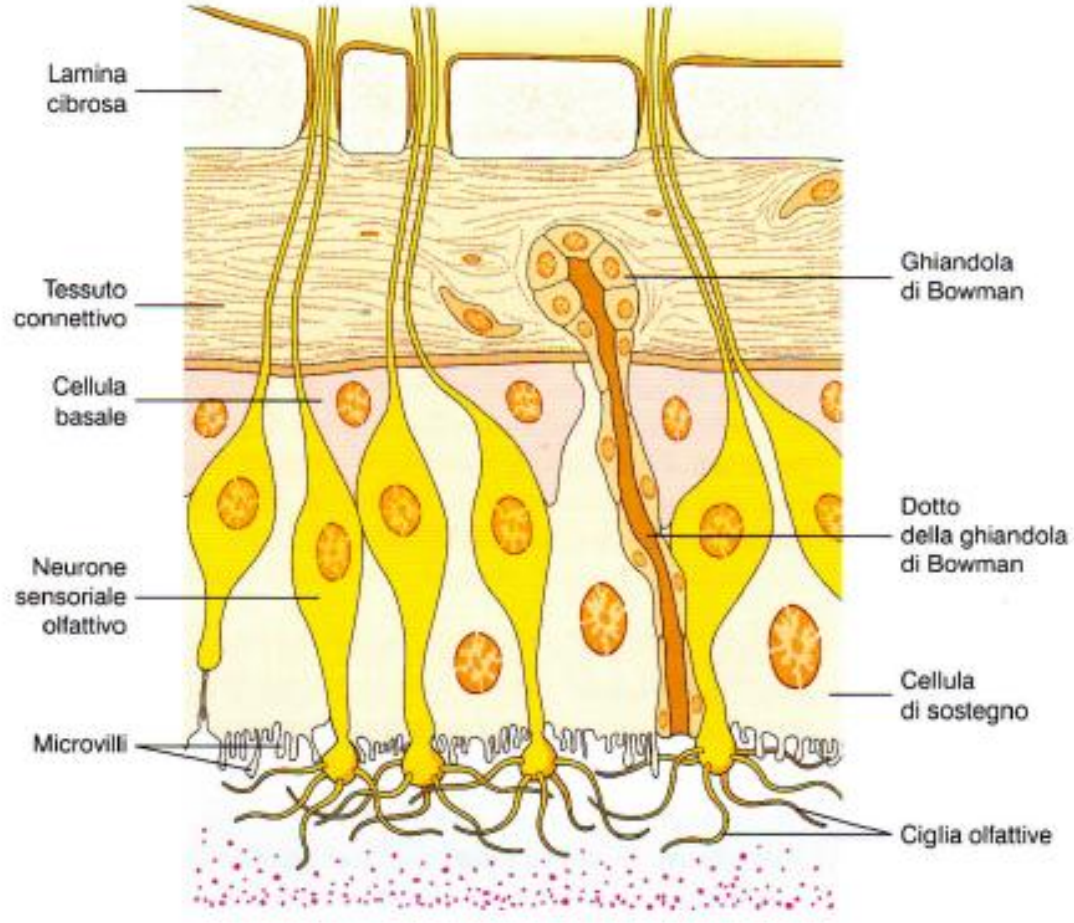
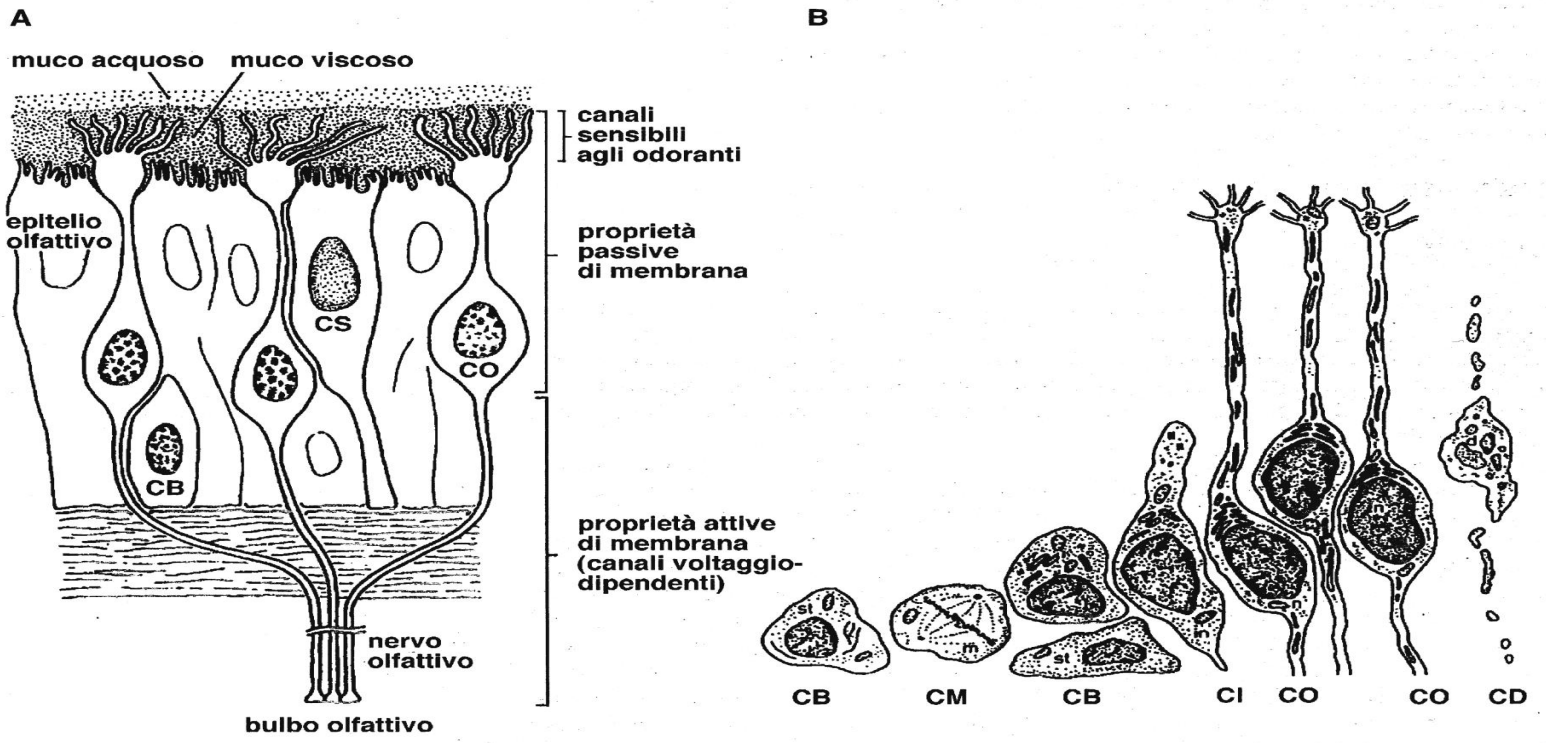


Quello olfattivo è un epitelio pseudostratificato specializzato che, nell'uomo, copre un'area di circa 5 cm^2.

È costituito da tre tipi principali di cellule:

- neuroni sensoriali olfattivi
- cellule basali
- cellule di sostegno



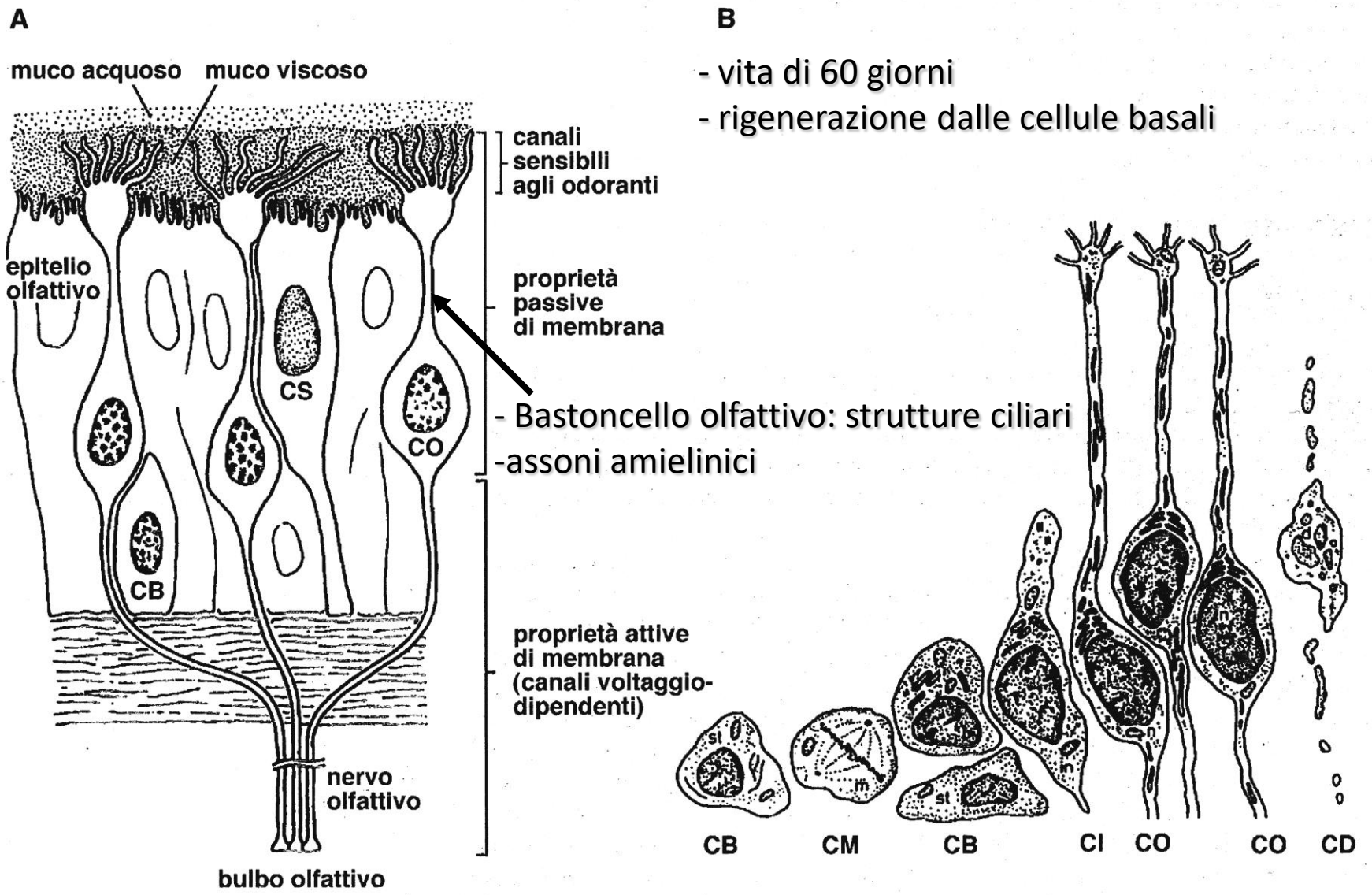


I *neuroni sensoriali olfattivi sono i neuroni sensoriali* primari, la cui funzione consiste nel trasformare l'energia proveniente dal legame con molecole odorose in potenziali d'azione, che vengono trasmessi ai neuroni secondari. L'epitelio olfattivo di ogni cavità nasale contiene circa sei milioni di neuroni sensoriali, che sono tipici *neuroni bipolari. Il* soma, il cui diametro è 5-7 micron è localizzato nella parte submediale dell'epitelio. Nella **parte apicale** del neurone si trova un *dendrite che termina con* una piccola protuberanza, dalla quale si dipartono cinque-venti *ciglia*. Le **ciglia** sono le strutture specializzate per la trasduzione olfattiva e si estendono in uno spesso strato di muco che ricopre la superficie dell'epitelio che è in diretto contatto con l'aria . Dalla **parte basale** del neurone olfattivo si diparte un *assone amielinico, che raggiunge i neuroni secondari nel* bulbo olfattivo, attraverso i fori della lamina cribrosa dell'osso etmoide.

Le *cellule basali hanno forma globosa, non raggiungono* la superficie epiteliale e costituiscono le **cellule staminali** responsabili della rigenerazione dei neuroni sensoriali olfattivi. Infatti, i neuroni sensoriali olfattivi, a differenza della maggior parte degli altri tipi di neuroni, sono in grado di rigenerarsi. Nell'epitelio olfattivo normale adulto i neuroni olfattivi hanno una vita media di trenta-sessanta giorni e vengono continuamente rigenerati a partire dalle cellule basali.

Le *cellule di sostegno sono cellule epiteliali con* forma colonnare che attraversano l'intero spessore dell'epitelio e presentano microvilli all'estremità

I neuroni dell'epitelio olfattivo sono gli unici che non vivono in un ambiente protetto e termoregolato. La natura labile e la necessità del continuo rinnovamento sia dei recettori gustativi sia di quelli olfattivi è, almeno in parte, spiegata dal fatto che tanto la mucosa nasale quanto quella orale sono esposte direttamente all'ambiente esterno e quindi a condizioni potenzialmente lesive, come forti cambiamenti della temperatura locale (inspirazione di aria molto fredda, ingestione di alimenti molto caldi o gelati), stimoli nocivi fisici o chimici (polveri e gas irritanti nell'aria inspirata, cibi solidi abradenti, bevande acide), infezioni ricorrenti (raffreddore comune, stomatiti).



- vita di 60 giorni
- rigenerazione dalle cellule basali

- Bastoncello olfattivo: strutture ciliari
-assoni amielinici

- Sostanze odorose: si sciolgono nel muco
- Legame con proteine: presentazione o rimozione
- Interazione con il recettore e variazione di conduttanza
- Potenziale di recettore e scarica di PDA

Non esistono odori primari

Per molto tempo si è ritenuto:

- che le sostanze odorose fossero raggruppabili in poche classi di odori primari (floreale, etereo, muschiato, canforaceo, dolce, putrescente, pungente)

- che nei neuroni olfattivi esistessero recettori specifici per tali classi di odori.

In realtà esiste un gran numero di recettori a cui si legano i composti volatili diversi

La varietà dei recettori permette di intercettare un gran numero di molecole

E’ dalla combinazione dei recettori attivati che emerge la specifica sensazione odorosa

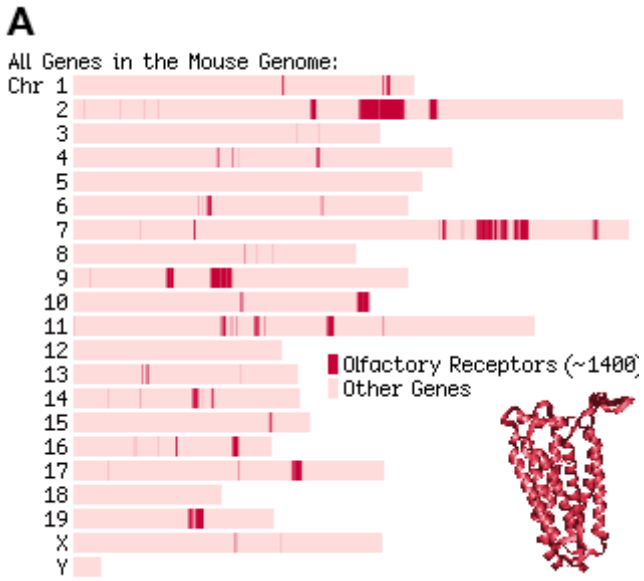
Nel topo sono stati identificati circa mille recettori olfattivi.

Nell'uomo si stima che ne esistano più di trecento.

La varietà dei recettori permette la discriminazione tra un gran numero di molecole odorose

Figura 21.3 Immagine al microscopio elettronico di un neurone sensoriale olfattivo umano. Sono ben visibili la parte apicale del dendrite e le ciglia che emergono da essa (E.E. Morrison, R.M. Costanzo, Morphology of the human olfactory epithelium, J Comp Neurol 297: 1-13, 1990, riproduzione autorizzata da Wiley-Liss, Inc.).

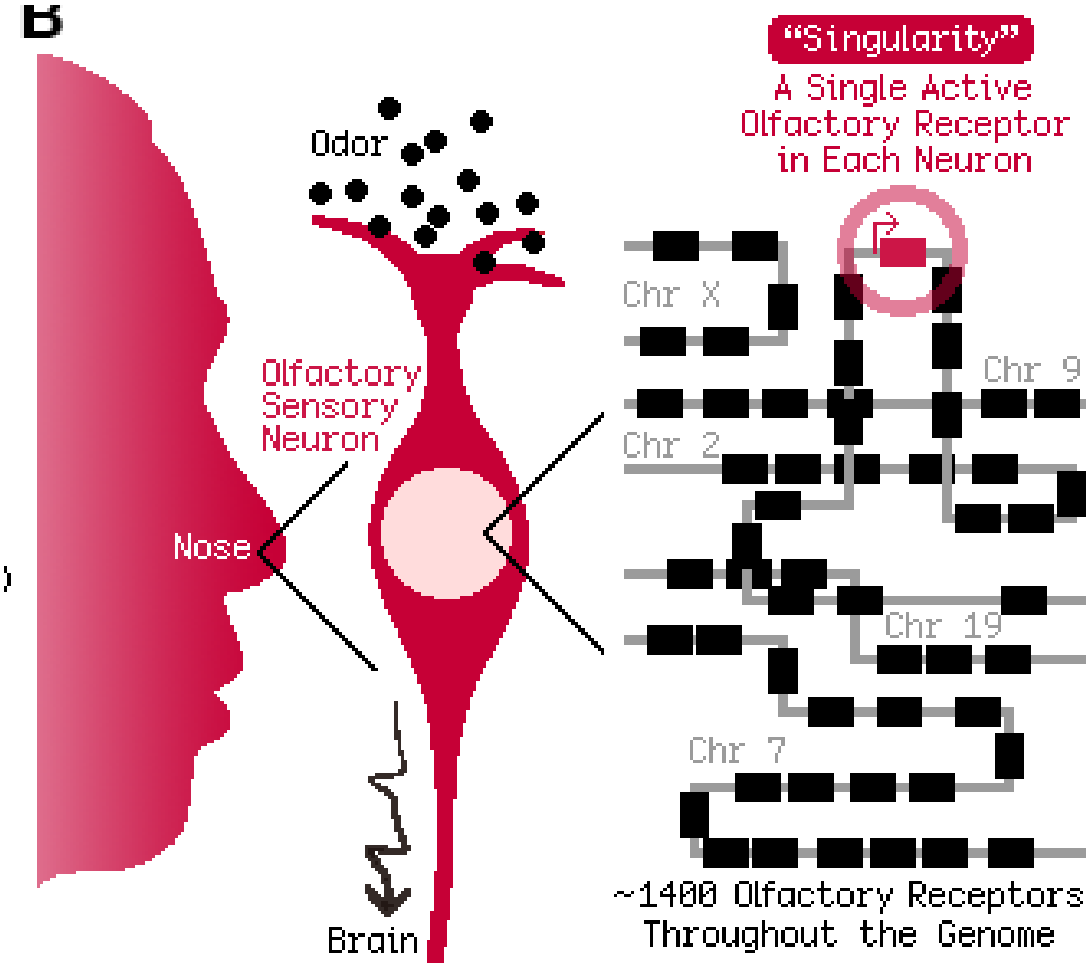
I geni dei recettori olfattivi costituiscono la più grande famiglia genica nel genoma dei vertebrati e permettono la discriminazione tra un gran numero di molecole odorose



In mammals, the sense of smell relies on their massive array of genes encoding olfactory receptors (ORs).

Ors constitute the largest gene family in mammalian genomes. For example, mice carry ~1,400 different OR genes, and together accounting for 6% of all genes in the mouse genome (Figure 1A).

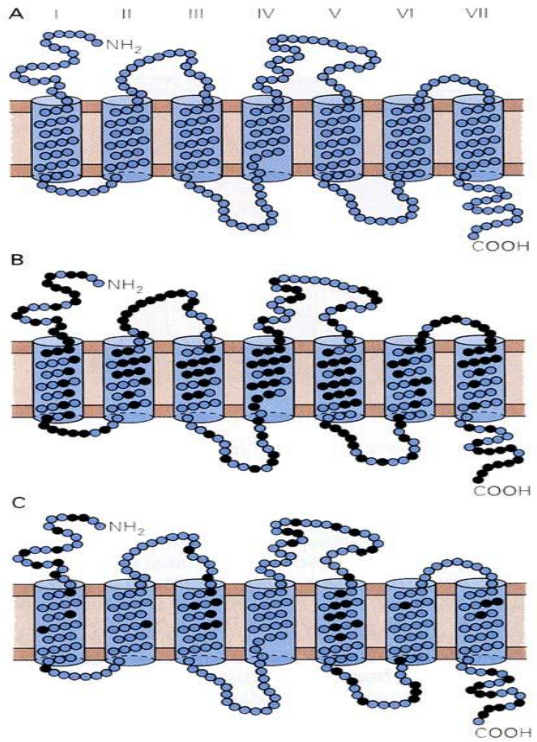
Ciascun neurone sensoriale esprime un solo gene recettoriale quindi le ciglia contengono un solo tipo di recettore



I recettori olfattivi appartengono alla famiglia dei recettori accoppiati alle proteine G e hanno una struttura caratteristica con sette regioni idrofobiche transmembrana.

Le varie centinaia di recettori olfattivi differiscono tra loro nella sequenza aminoacidica, specialmente a livello della terza, quarta e quinta regione transmembrana, dove si trova

il sito di legame delle molecole odorose.



Recettori olfattivi. In B e C i pallini neri indicano aminoacidi diversi rispetto ad A. La variabilità delle regioni transmembranarie fa supporre che anche queste partecipino al legame con la molecola odorosa.

Ogni neurone sensoriale olfattivo esprime un solo tipo di recettore.

Ogni recettore riconosce multipli odoranti (molecole odorose)

Ogni odorante viene rilevato da diversi tipi di recettori..

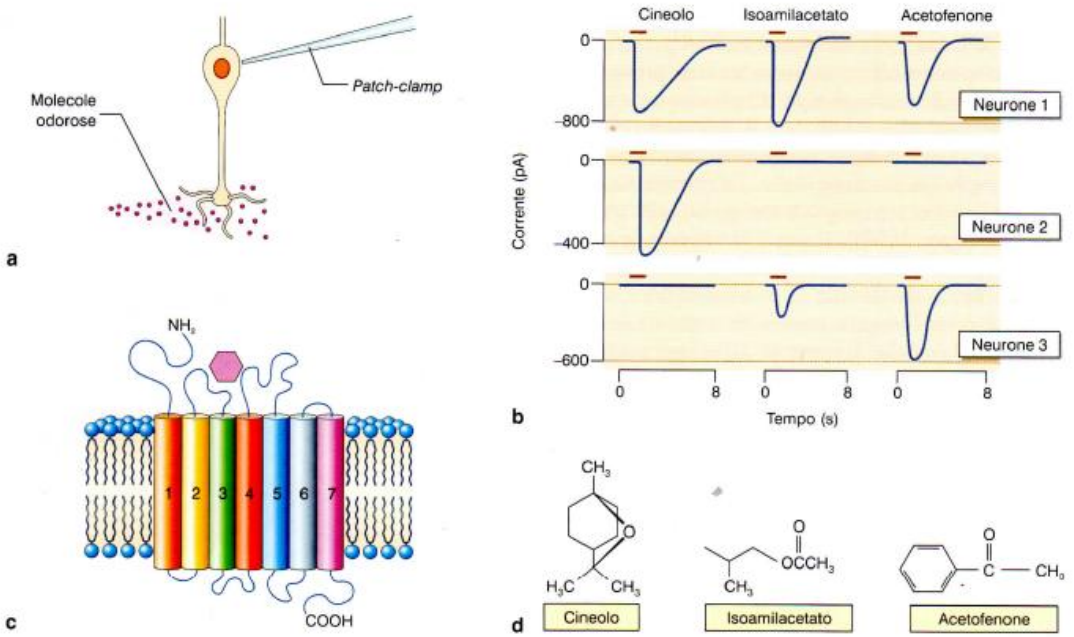


Figura 21.4 Risposte di tre diversi neuroni sensoriali olfattivi a stimoli odorosi. **a**, Metodo sperimentale. Un neurone sensoriale olfattivo isolato viene stimolato con molecole odorose, mentre la risposta elettrica viene misurata con la tecnica del *patch-clamp* nella configurazione di *whole-cell*. **b**, Risposte di tre neuroni olfattivi a varie molecole odorose. Il potenziale della membrana è mantenuto costante a −55 mV. Il neurone 1 risponde a tutti e tre gli odori, il neurone 2 risponde solo a un odore e il neurone 3 risponde a due odori. **c**, Struttura generica di un recettore olfattivo con le sette regioni transmembrana. **d**, Struttura delle molecole odorose utilizzate nell'esperimento in **b**.

Come può il sistema allora distingure i diversi odoranti?

Codifica Combinatoria

Per essere distinte percettivamente le diverse molecole odorose devono causare segnali diversi da trasmettere al SNC

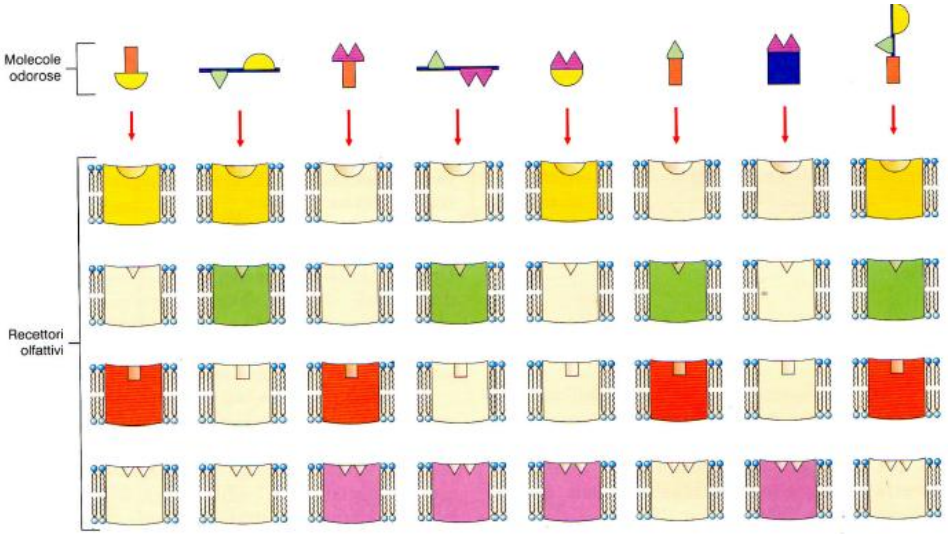


Figura 21.5 Schema di codice combinatorio dei recettori olfattivi per il riconoscimento delle molecole odorose. Nelle quattro fila sono schematizzati quattro recettori distinti con un diverso sito di legame rappresentato da una particolare incisione alla sommità. In alto sono rappresentate otto possibili molecole odorose con caratteristiche strutturali che possono essere riconosciute dai diversi siti di legame dei recettori. In ogni riga i recettori colorati corrispondono a quelli che riconoscono una caratteristica della molecola rappresentata sopra. Ogni recettore olfattivo viene utilizzato nel codice combinatorio come un componente per riconoscere varie molecole. Ogni molecola attiva un'unica combinazione di recettori (modificata da B. Malnic et al., Combinatorial receptor codes for odors, Cell 96: 713-23, 1999).

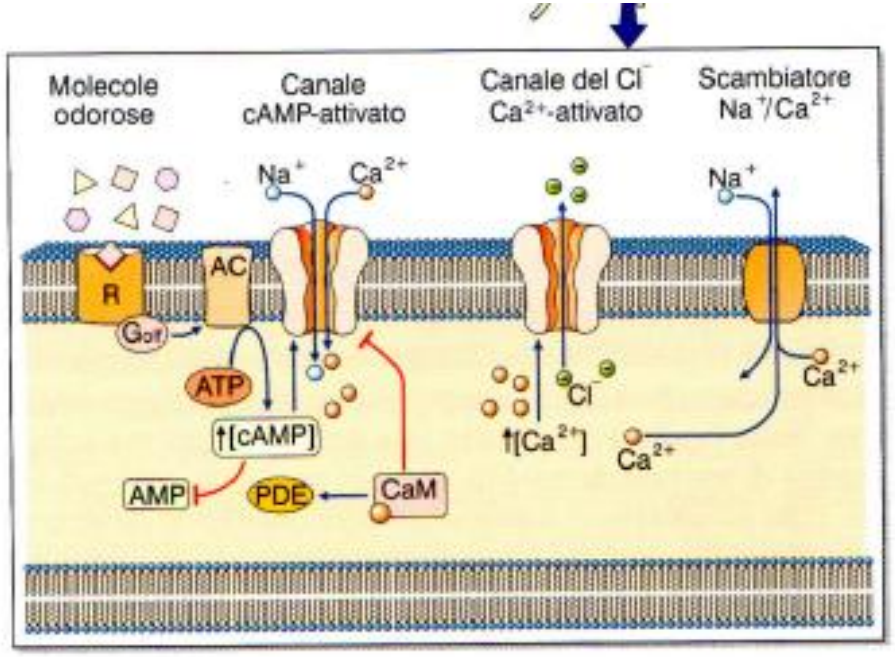
La presenza di ogni molecola odorosa viene rilevata da una costellazione unica di recettori

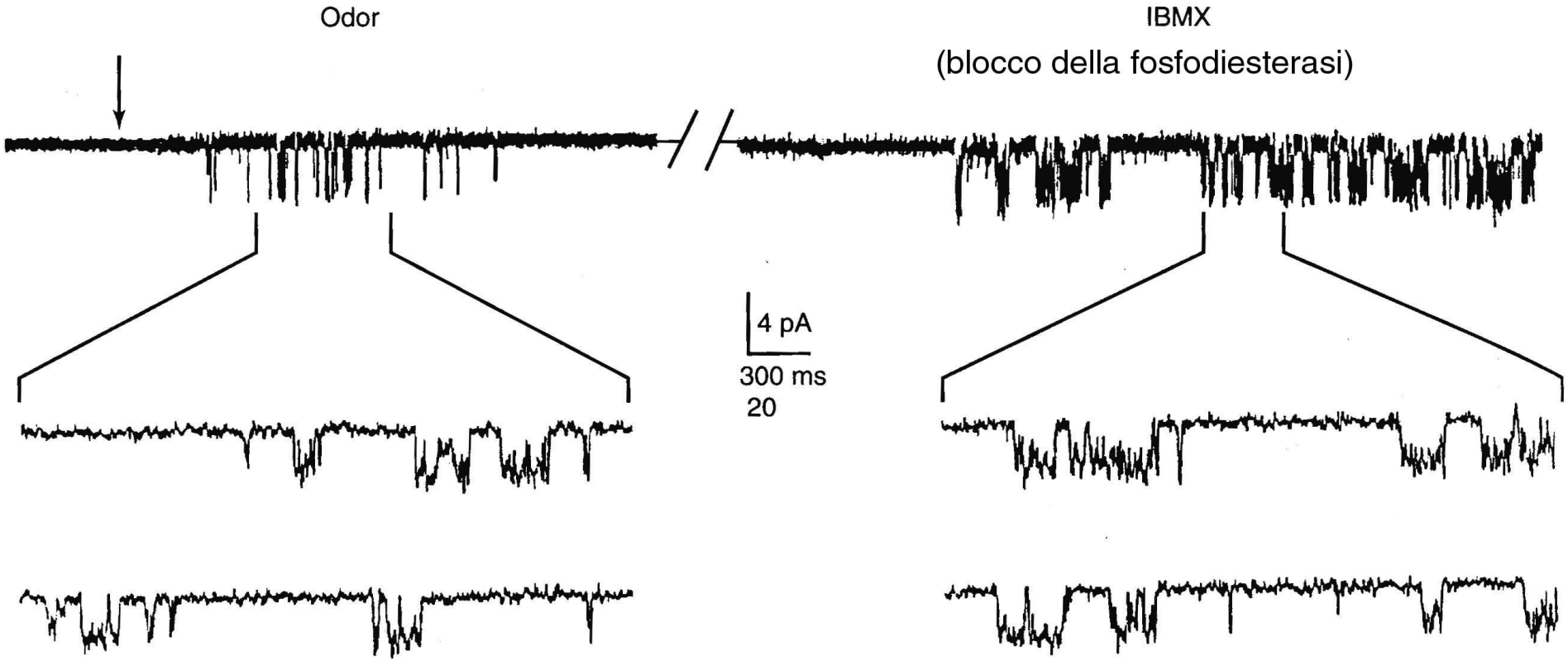
Provoca così un pattern caratteristico di segnali da trasmettere al cervello

La codifica combinatoria di odoranti consente di ampliare notevolmente il potere discriminatorio del sistema olfattivo .

Trasduzione olfattiva

Figura 21.6 Trasduzione olfattiva. La trasduzione olfattiva avviene nelle ciglia dei neuroni sensoriali olfattivi. Molecole odorose si legano ai recettori olfattivi (R) che si trovano nella membrana delle ciglia, attivando la proteina G (Golf) che a sua volta attiva l'adenilatociclasi (AC), causando l'aumento nella produzione di adenosin-monofosfato ciclico (cAMP) da adenosin-trifosfato (ATP). Il cAMP apre canali ionici nella membrana delle ciglia, causando l'ingresso di ioni sodio e calcio. Il calcio amplifica ulteriormente il segnale attivando una corrente al cloro. Questi flussi ionici causano una depolarizzazione. Azioni inibitorie (in rosso) sono dovute al complesso calcio-calmodulina (CaM), che causa una riduzione nella probabilità di apertura dei canali attivati dal cAMP. La CaM produce anche un aumento dell'attività della fosfodiesterasi (PDE) che idrolizza il cAMP. Il calcio viene, quindi, estruso dallo scambiatore sodio-calcio.

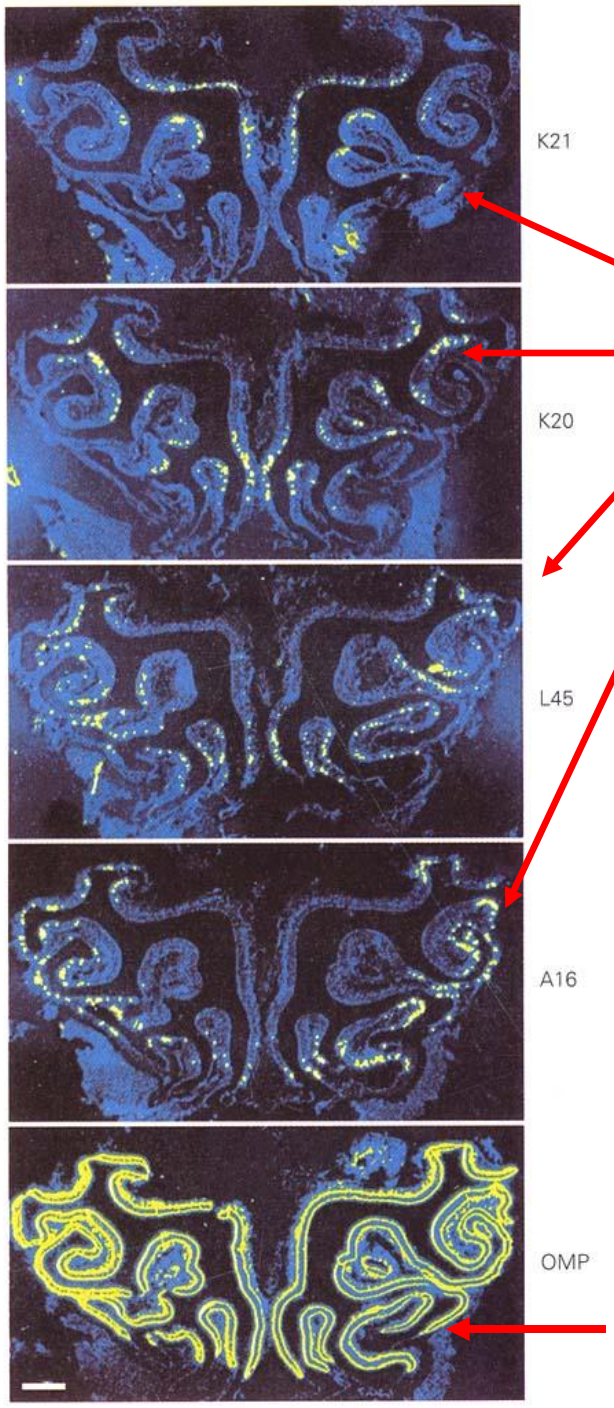




Trasduzione
- proteina G, adenilato ciclasi
- aumento del cAMP
- Apertura canale per il Na+ regolato dal cAMP

L'enzima **fosfodiesterasi** catalizza la degradazione di **cAMP** ad AMP

Segregazione spaziale dei geni che codificano per recettori diversi nell'epitelio olfattivo



Espressione di geni codificanti famiglie diverse di proteine recettoriali

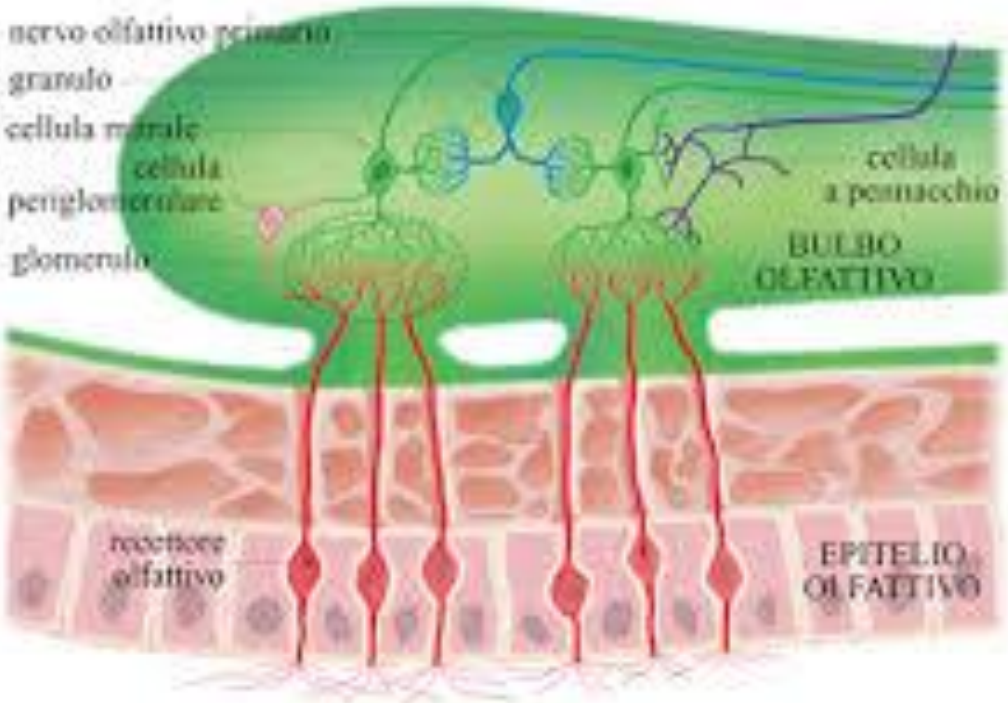
Diversi tipi di recettori olfattivi sono espressi in diverse zone dell'epitelio olfattivo.

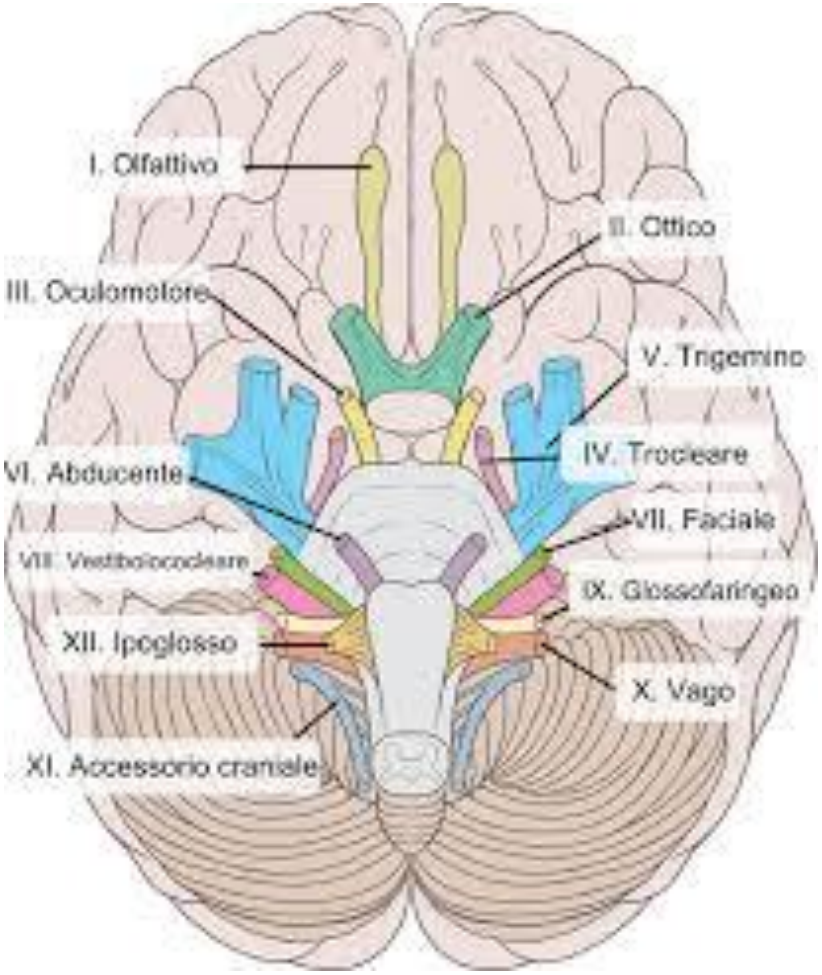
Ogni tipo di recettore è espresso in circa 5.000 neuroni

I neuroni con lo stesso recettore sono sparsi in modo casuale all'interno della zona in modo che i neuroni con recettori diversi sono intervallati.

Tutte le zone contengono una varietà di recettori, in modo che una specifica molecola odorosa può essere riconosciuta da recettori in varie zone differenti .

Marker generico delle cellule olfattive





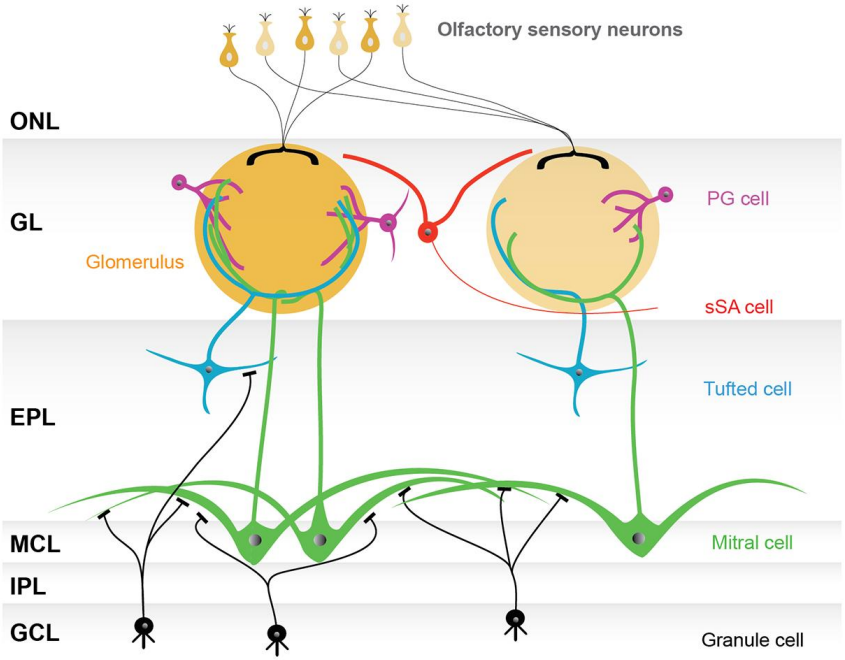
Hopfield fig. 3

Il bulbo olfattivo forma una rete neuronale in cui troviamo diversi tipi di neuroni variamente interconessi tra di loro

Cellule Mitrali

Cellule a Pennacchio

Interneuroni Gabaergici
Cellule dei granuli
Cellule periglomerulari



Presenta

uno stadio di ingresso delle informazioni (assoni dei recettori)

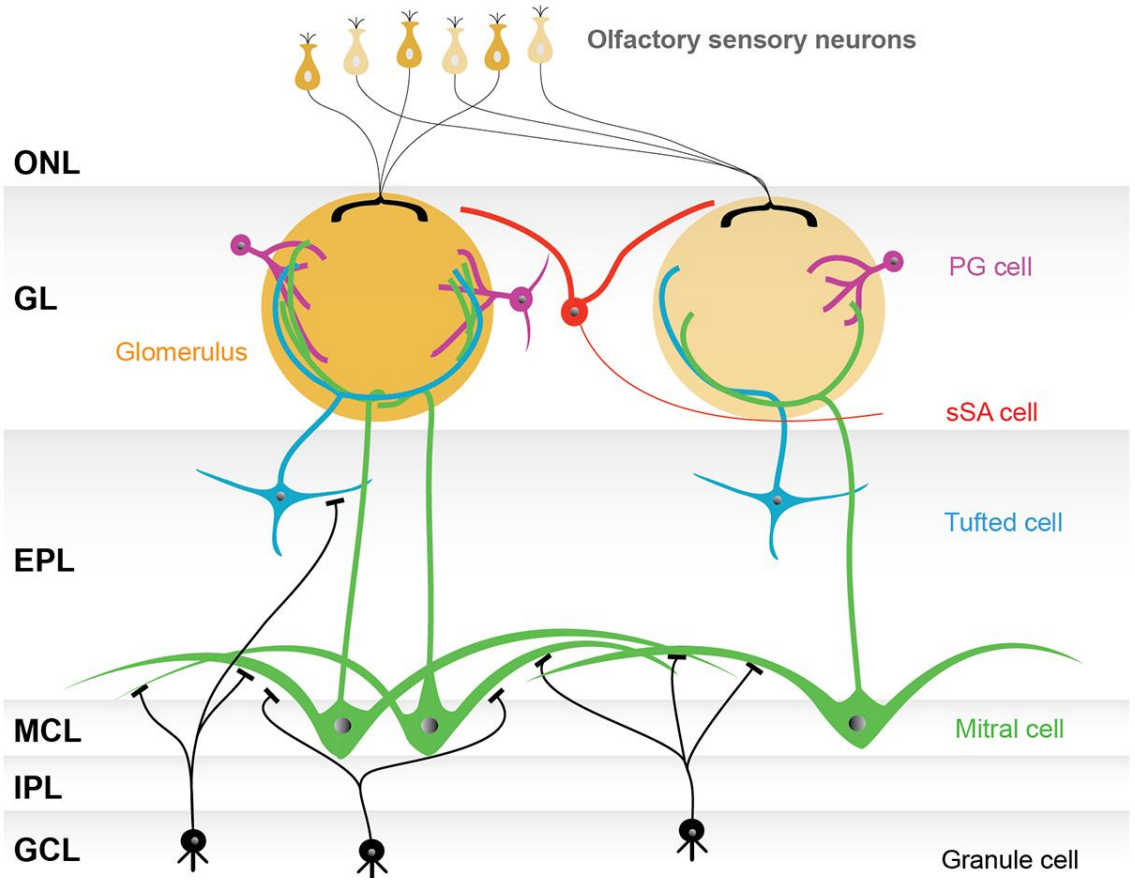
Uno stadio di uscita attraverso gli assoni delle cellule Mitrali e a Pennacchio

(neuroni glutammatergici)

Il bulbo olfattivo ha una struttura a strati

e

una caratteristica struttura : il glomerulo



Glomerural layer

External plexiform layer

Mitral cell layer

Internal plexiform layer

Granule cell layer

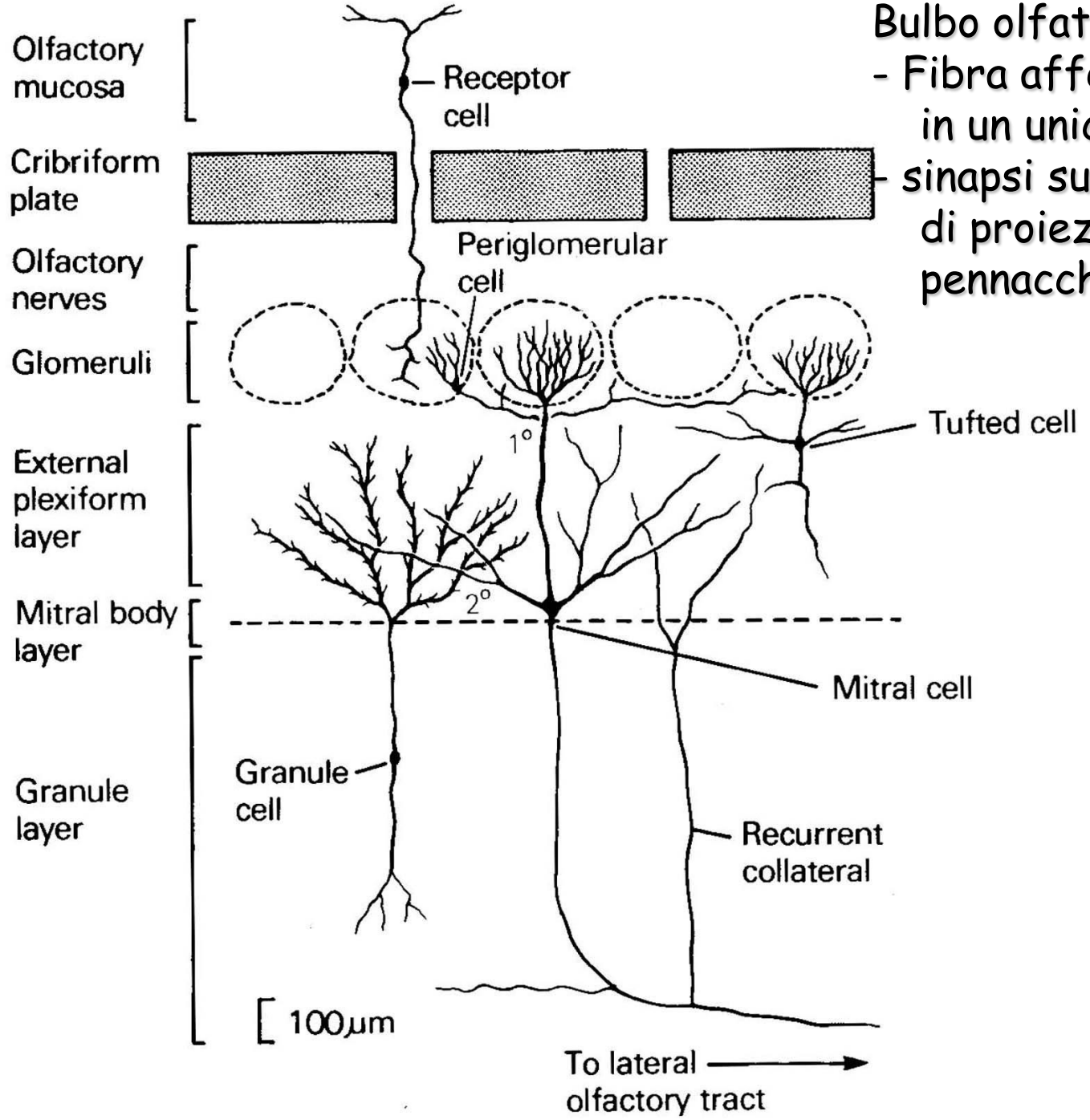
FIGURE 1 | Basic model of the olfactory bulb network. The illustrated olfactory bulb network is based on the conventional categorization of participating neurons. The axons of olfactory sensory neurons make synapses in the glomerular layer (GL), consisting of spherical structures called glomeruli. Although there are several thousand glomeruli at the surface of the rodent olfactory bulb, olfactory sensory neurons expressing the same type of odorant receptor converge their axons into only a few glomeruli, and thus each glomerulus represents a single odorant receptor. Neurons surrounding glomeruli in the GL are called juxtaglomerular cells (JG cells), consisting of three morphologically distinct cell types: periglomerular (PG) cells, external tufted (ET) cells (not shown), and superficial short-axon (sSA) cells. There are two types of projection neurons, the mitral cells and the tufted cells, which send their axons to the olfactory cortex. The somata of mitral cells are located in the mitral cell layer (MCL), while the tufted cells are scattered throughout the EPL. Both mitral and tufted cells project a single primary dendrite into a single glomerulus, where they receive synaptic inputs from the axons of olfactory sensory neurons and make reciprocal synapses with the dendrites of PG cells. Secondary dendrites of mitral and tufted cells are elongated in the external plexiform layer (EPL), where reciprocal synapses are formed with granule cell dendrites. The internal plexiform layer (IPL), in which axons from mitral cells and axon collaterals of ET cells run, and the granule cell layer (GCL), which is largely composed of granule cells, both lie beneath the MCL. Granule cells are axon-less interneurons extending dendrites apically into the EPL. Abbreviation: ONL, olfactory nerve layer.

Ogni recettore olfattivo manda il suo assone ad un glomerulo

Migliaia di assoni di neuroni olfattivi esprimenti la stessa molecola recettrice convergono su uno o due glomeruli

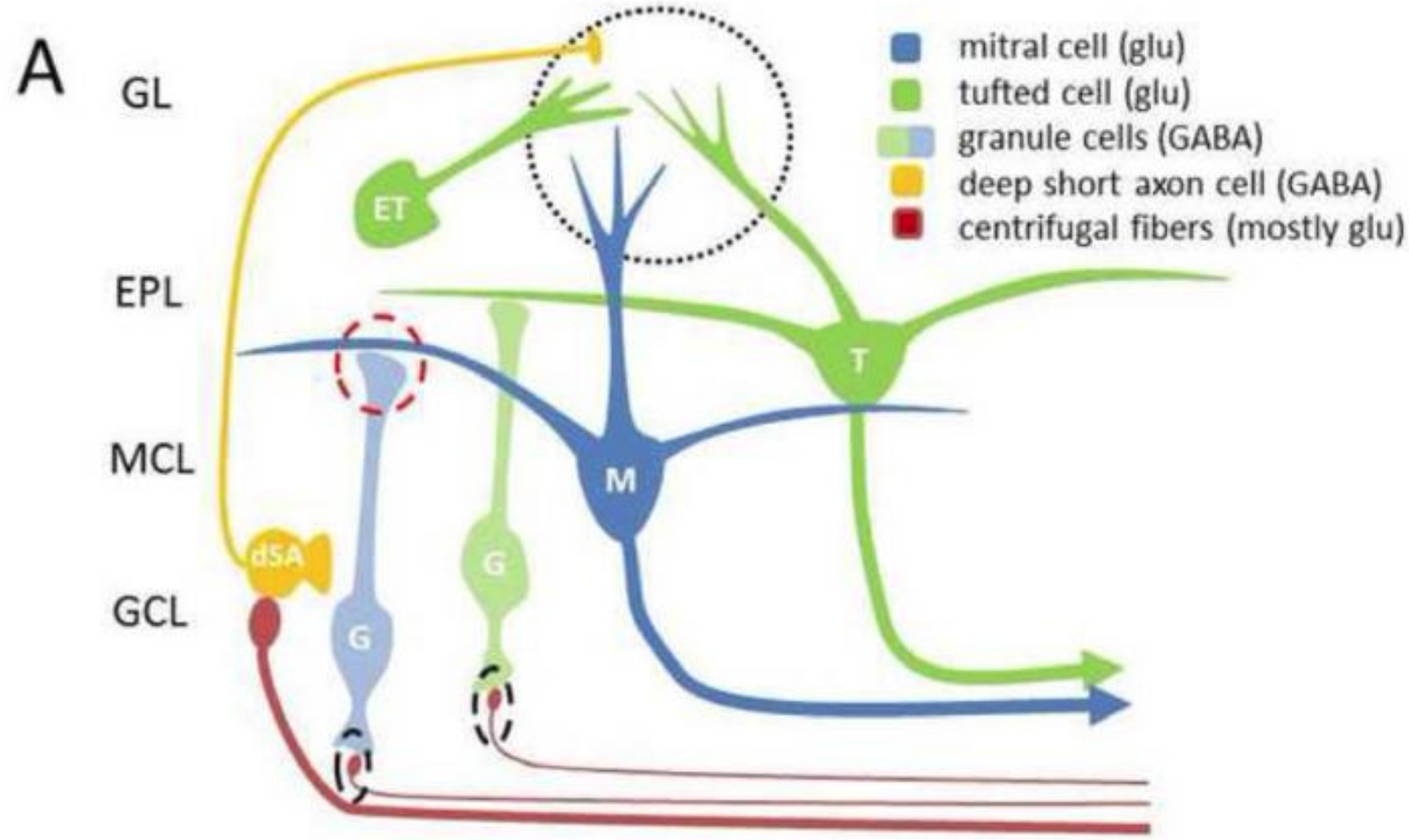
per prendere contatto sinaptico con le cellule mitrali e con quelle a **pennacchio**, cellule di proiezione che utilizzano il glutammato come trasmettitore

Le interazioni fra i glomeruli e tra le cellule di proiezione del bulbo olfattivo sono assicurate da cellule intrinseche del bulbo, le periglomerulari e i granuli, che utilizzano come trasmettitore sinaptico l'acido *γ*-amminobutirrico (GABA).



Bulbo olfattivo

- Fibra afferente: terminazione in un unico glomerulo
- sinapsi sui dendriti delle cellule di proiezione (mitrali e a pennacchio)


A
GL
EPL
MCL
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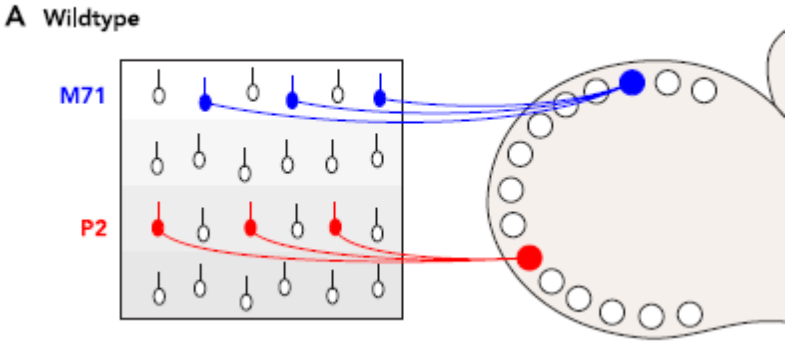
ET
T
M
dSA
G
G
mitral cell (glu)
tufted cell (glu)
granule cells (GABA)
deep short axon cell (GABA)
centrifugal fibers (mostly glu)

Convergenza

Each olfactory sensory neuron innervates a single glomerulus, and each glomerulus is innervated by sensory neurons expressing the same type of receptor only
Thus, this processing stage enables a powerful convergence of input.



In addition to input from olfactory sensory neurons, mitral and tufted (a pennacchio) cells receive extensive centrifugal input from central brain mechanisms, and numerous local interneurons form connections between cells within the bulb.

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

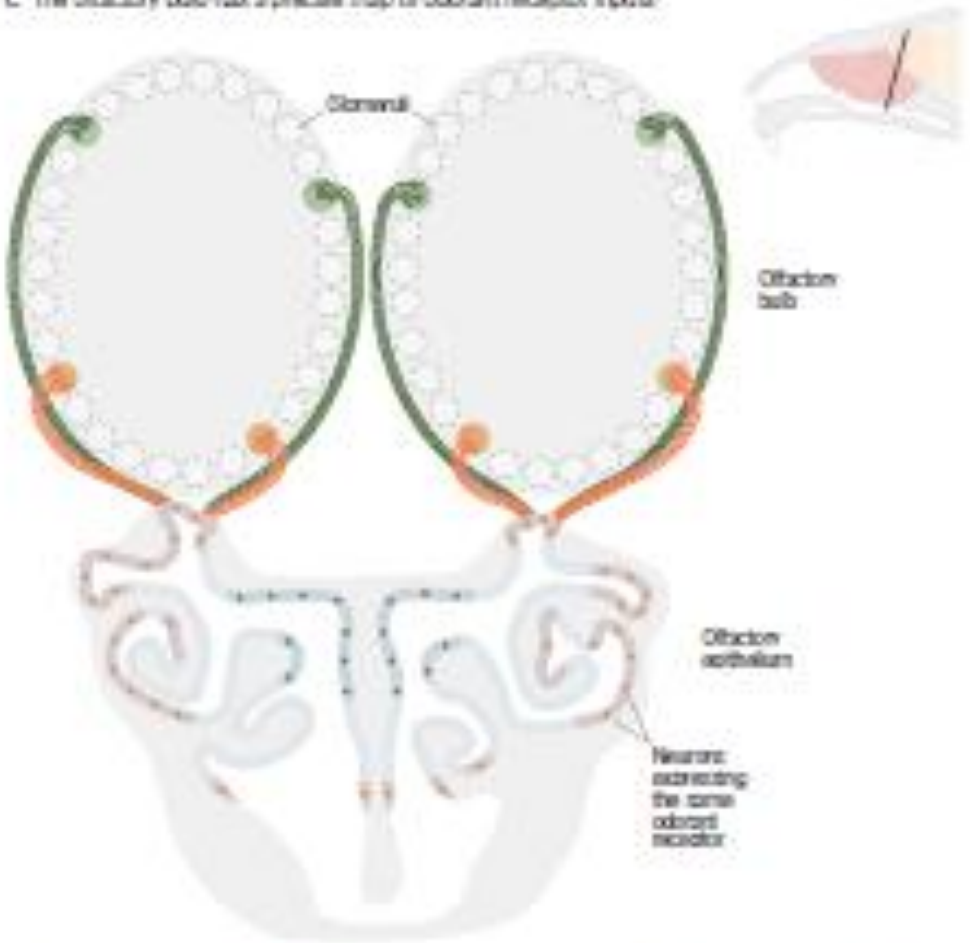


Figure 22–7 Odor responses in the olfactory bulb.

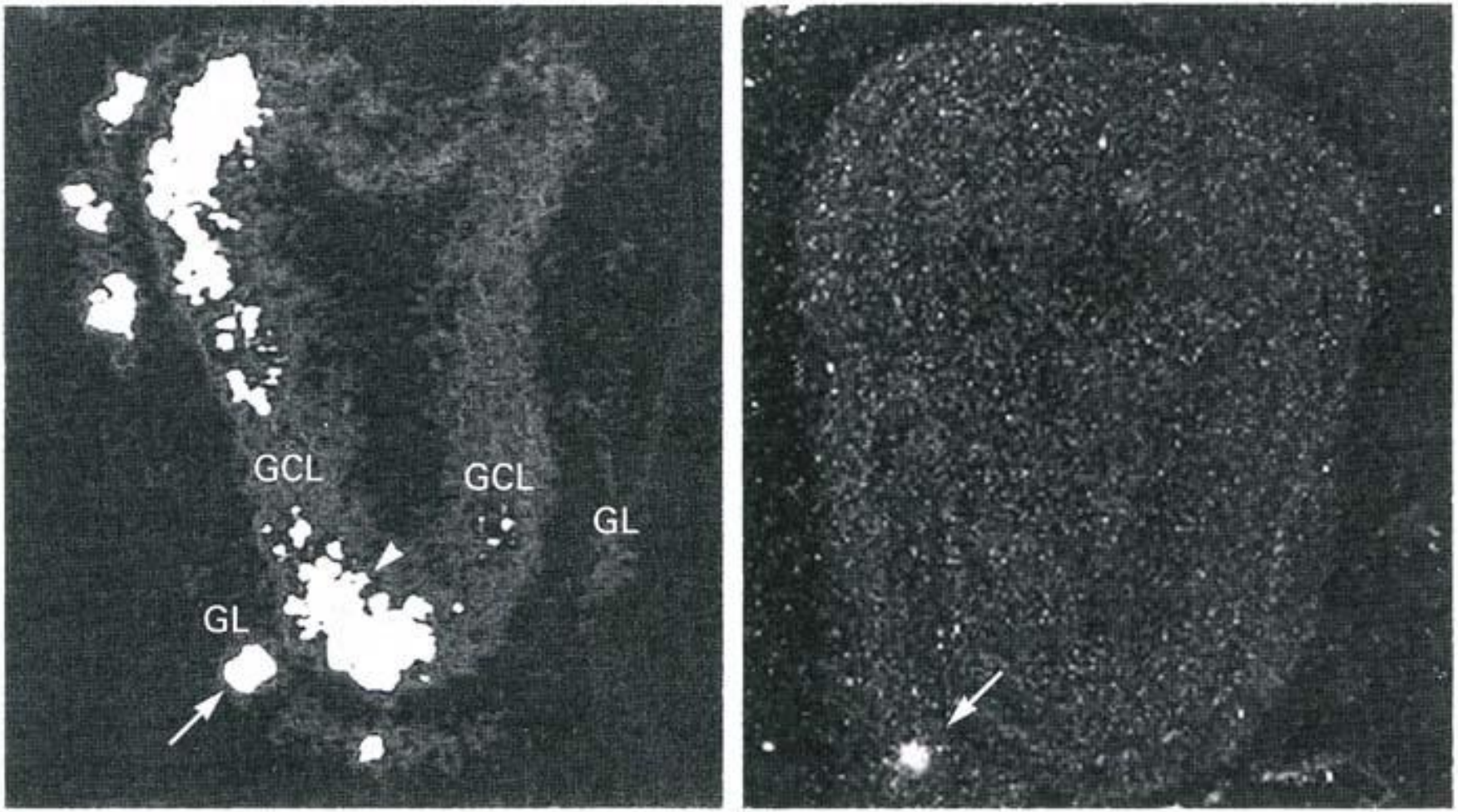
A. The axons from neurons in one epithelial zone with the same odorant receptor type usually converge to two glomeruli, one on each side of the olfactory bulb. Here a probe specific for one odorant receptor gene labeled a glomerulus on the medial side (left) and lateral side (right) of a mouse olfactory bulb. The probe hybridized to receptor messenger RNAs present in sensory axons in these coronal sections. (Adapted from Ressler, Sullivan, and Buck 1994.)

B. This section of a rat olfactory bulb shows the uptake of radiolabeled 2-deoxyglucose at multiple foci (red) following exposure of the animal to the odorant methyl benzoate. The labeled foci correspond to numerous glomeruli at different locations in the olfactory bulb. (Reproduced, with permission, from Johnson, Farahbod, and Leon 2006.)

C. The olfactory bulb has a precise map of odorant receptor inputs because each glomerulus is dedicated to only one type of receptor. The maps in the two olfactory bulbs are bilaterally symmetrical and are nearly identical across individuals. The maps on the medial and lateral sides of each bulb are similar, but slightly displaced along the dorsal-ventral and anterior-posterior axes.

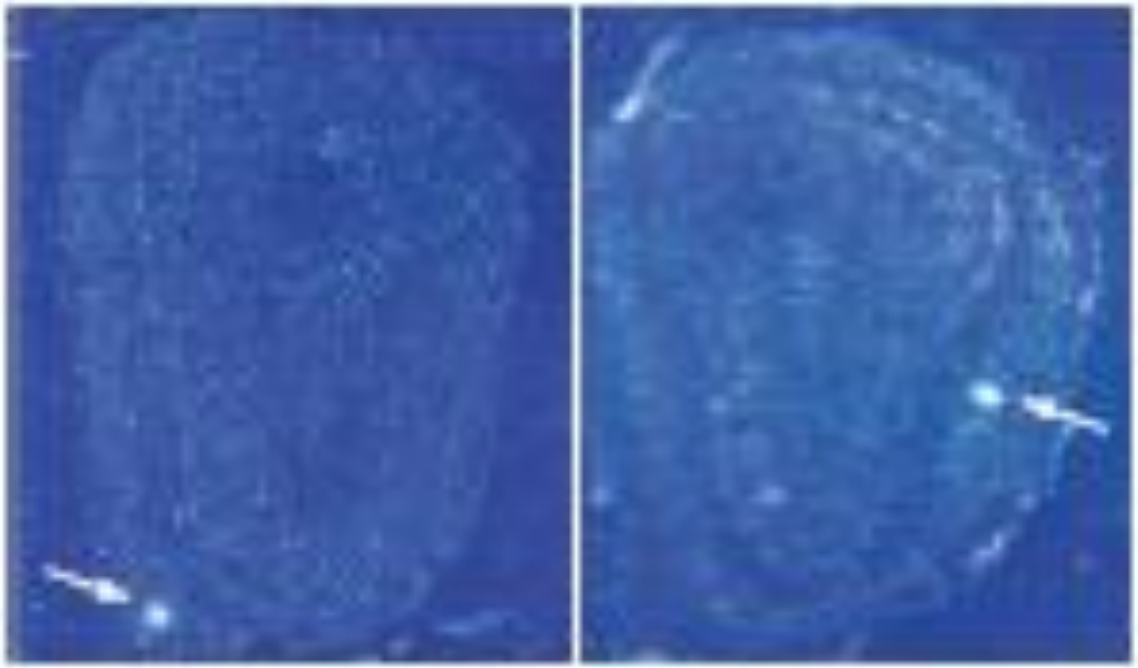
A Attivazione del bulbo olfattivo

B Marker per un recettore specifico

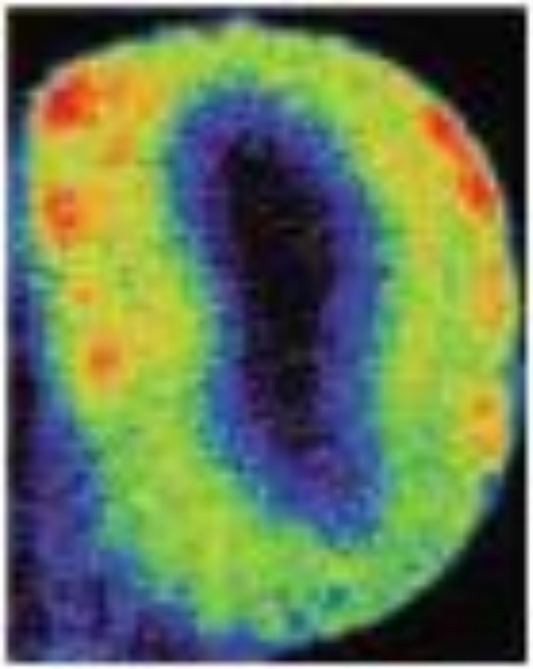


Ogni glomerulo riceve informazioni da un solo tipo di recettore

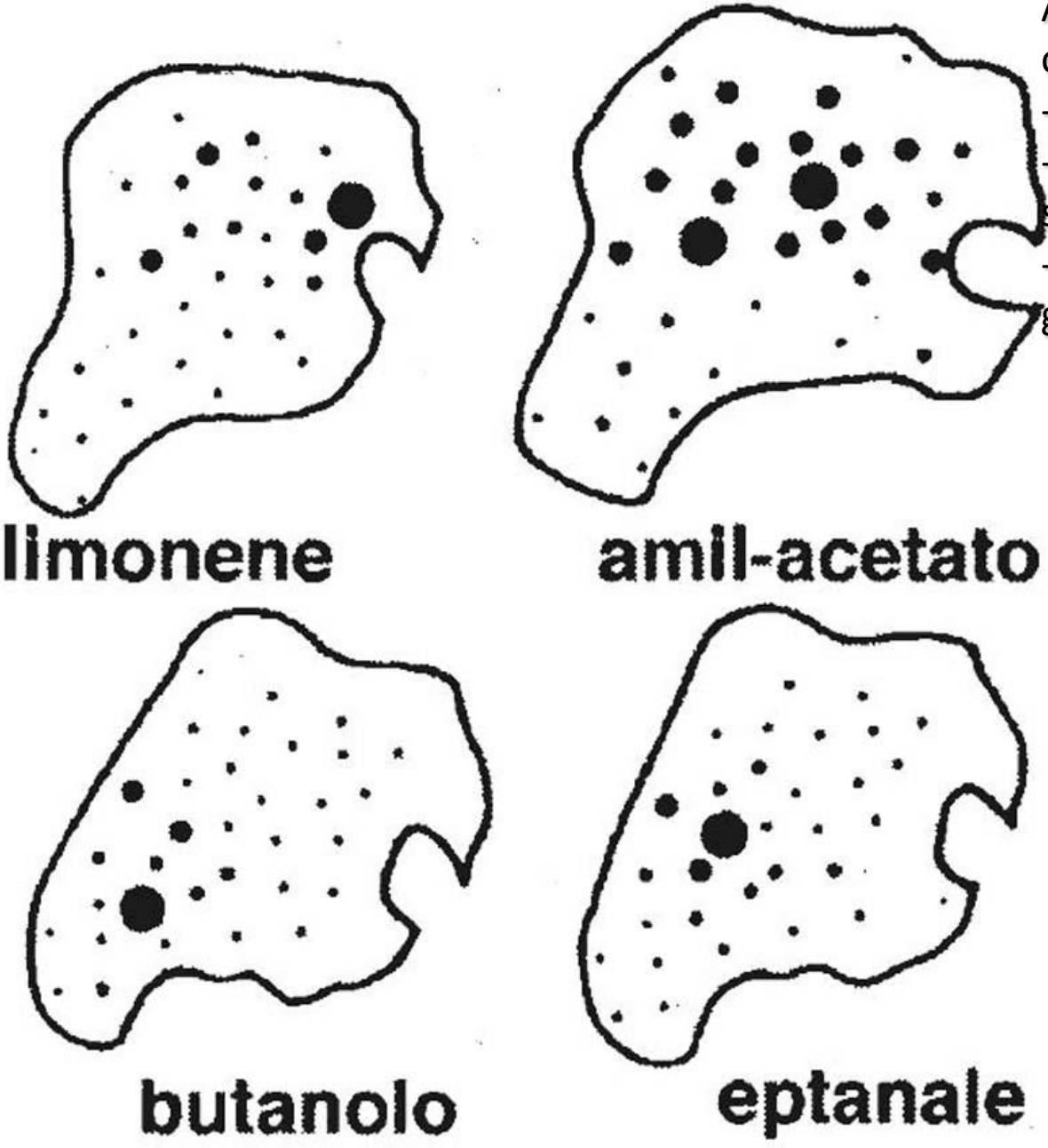
A Axons of neurons with the same odorant receptor converge on a few glomeruli

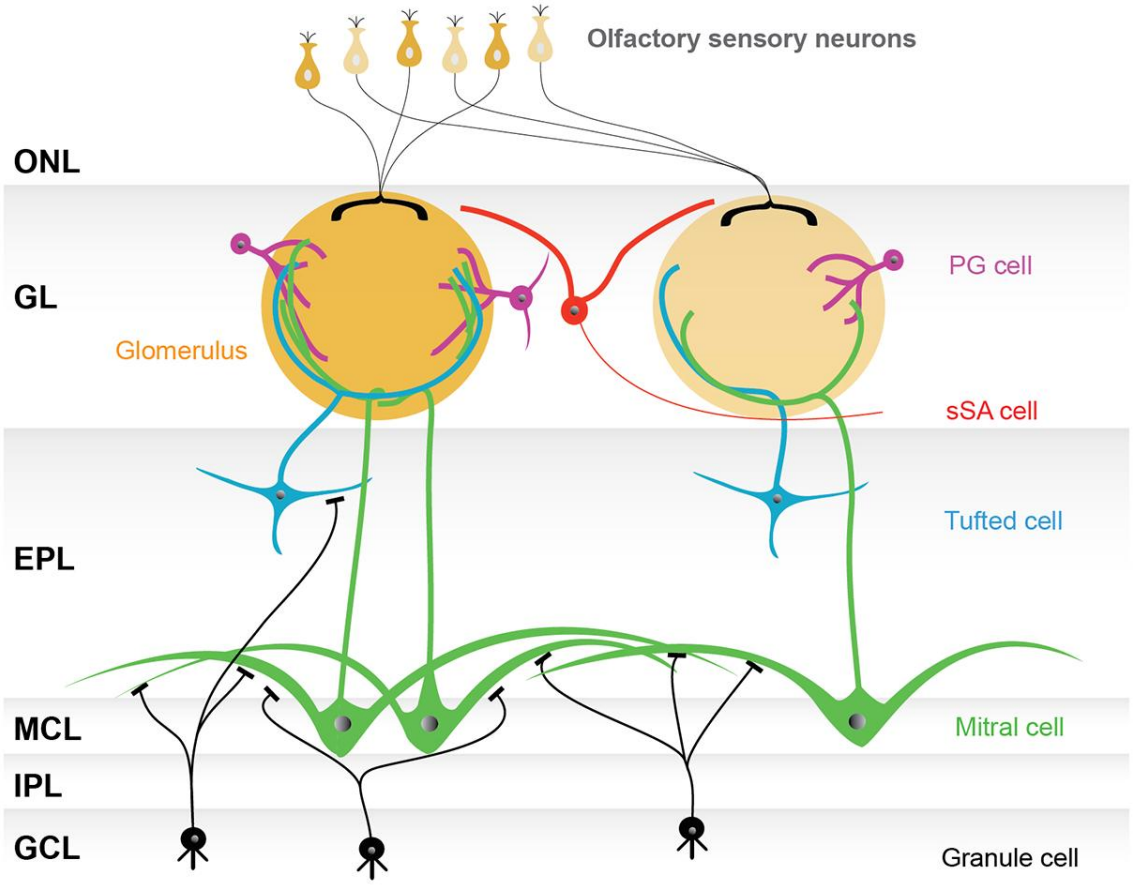


B One odorant can activate many glomeruli



Attivazione del bulbo da parte di odori diversi
-2 deossiglucosio
-un odore, un quadro di attivazione specifico
-un odore attiva più glomeruli e un glomerulo è attivato da più odori





Glomerural layer

External plexiform layer

Mitral cell layer

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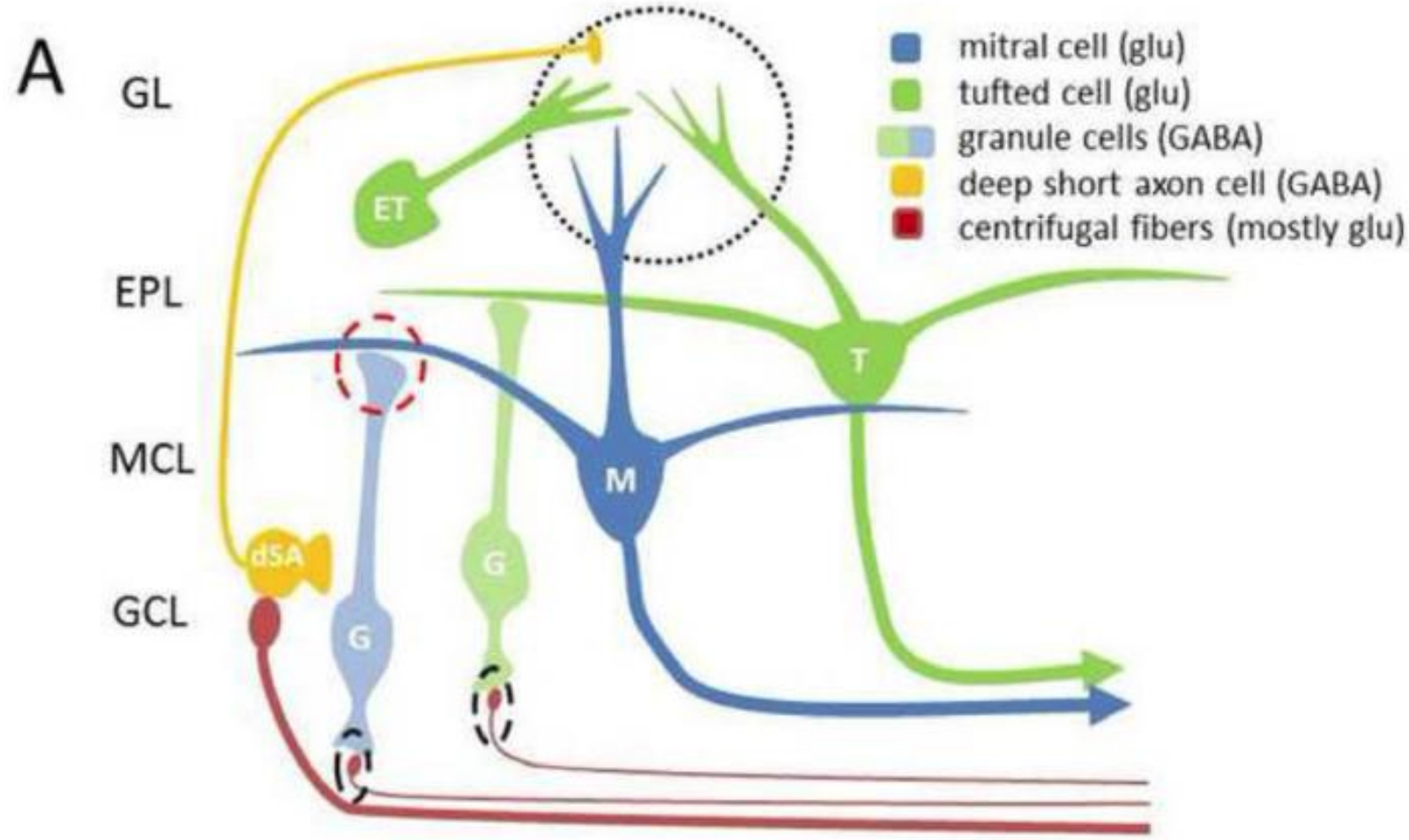
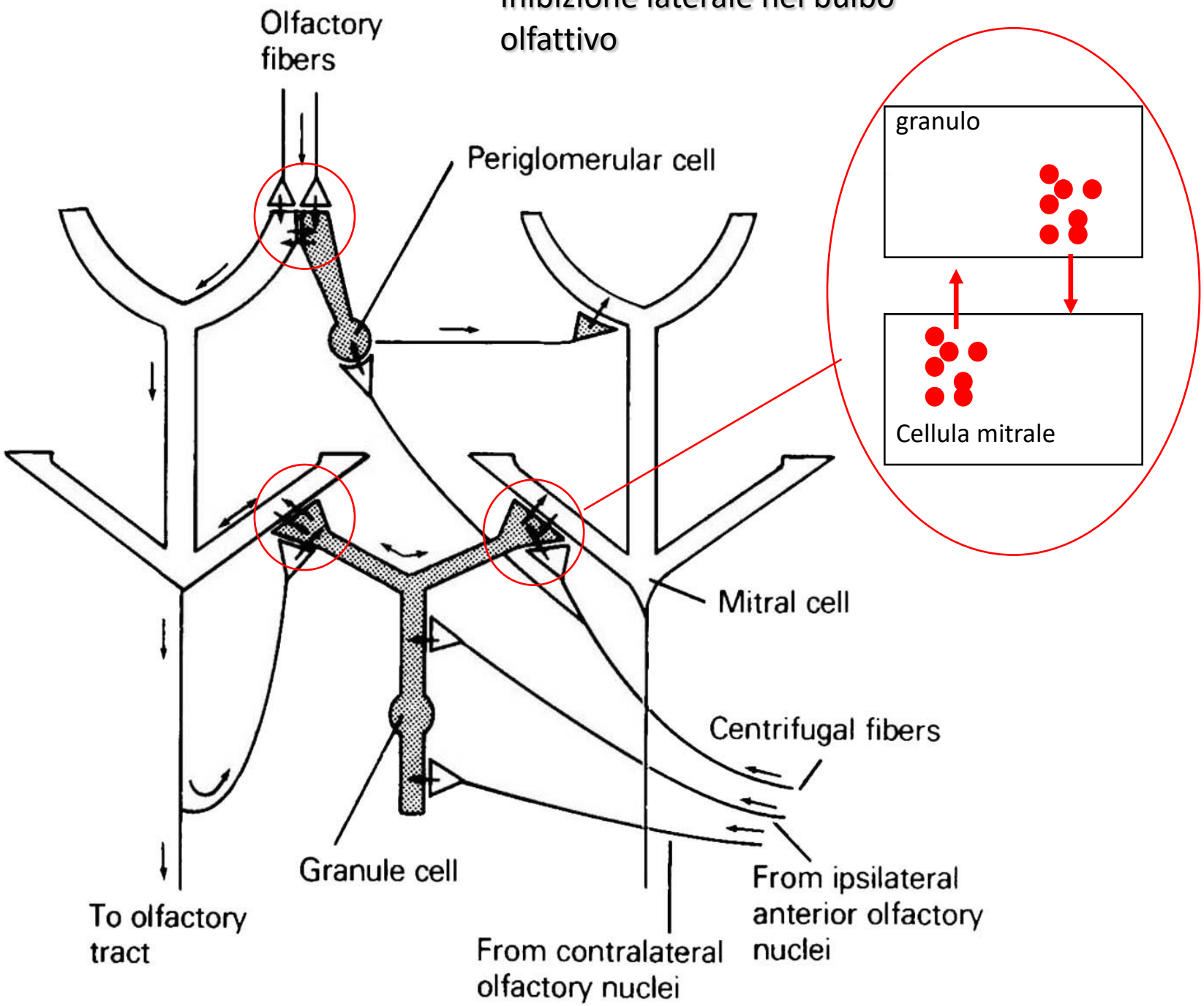
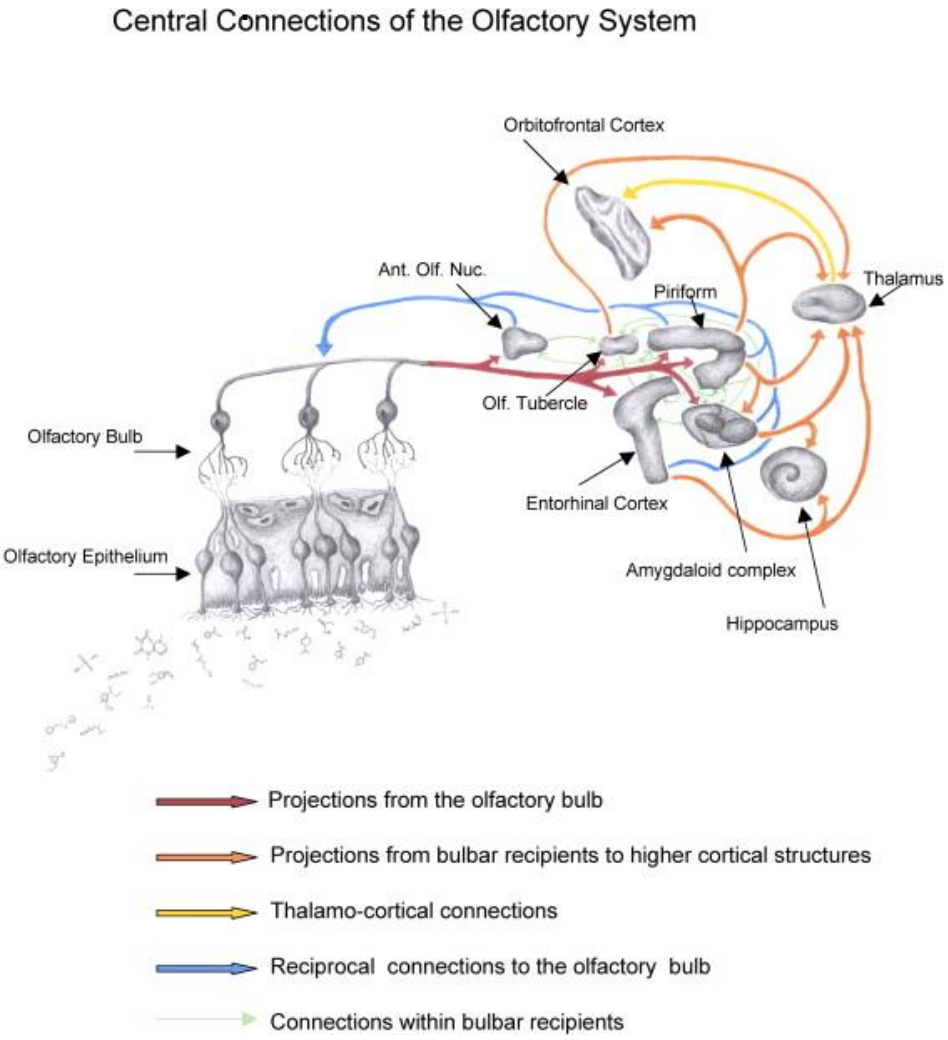
Controllo Top-down


A
GL
EPL
MCL
GCL
ET
T
M
dSA
G
G
mitral cell (glu)
tufted cell (glu)
granule cells (GABA)
deep short axon cell (GABA)
centrifugal fibers (mostly glu)

Inibizione laterale nel bulbo olfattivo



The final processing occurs in higher-order brain structures



These higher centers include the

anterior olfactory nucleus, which connects the two olfactory bulbs through a portion of the anterior commissure,

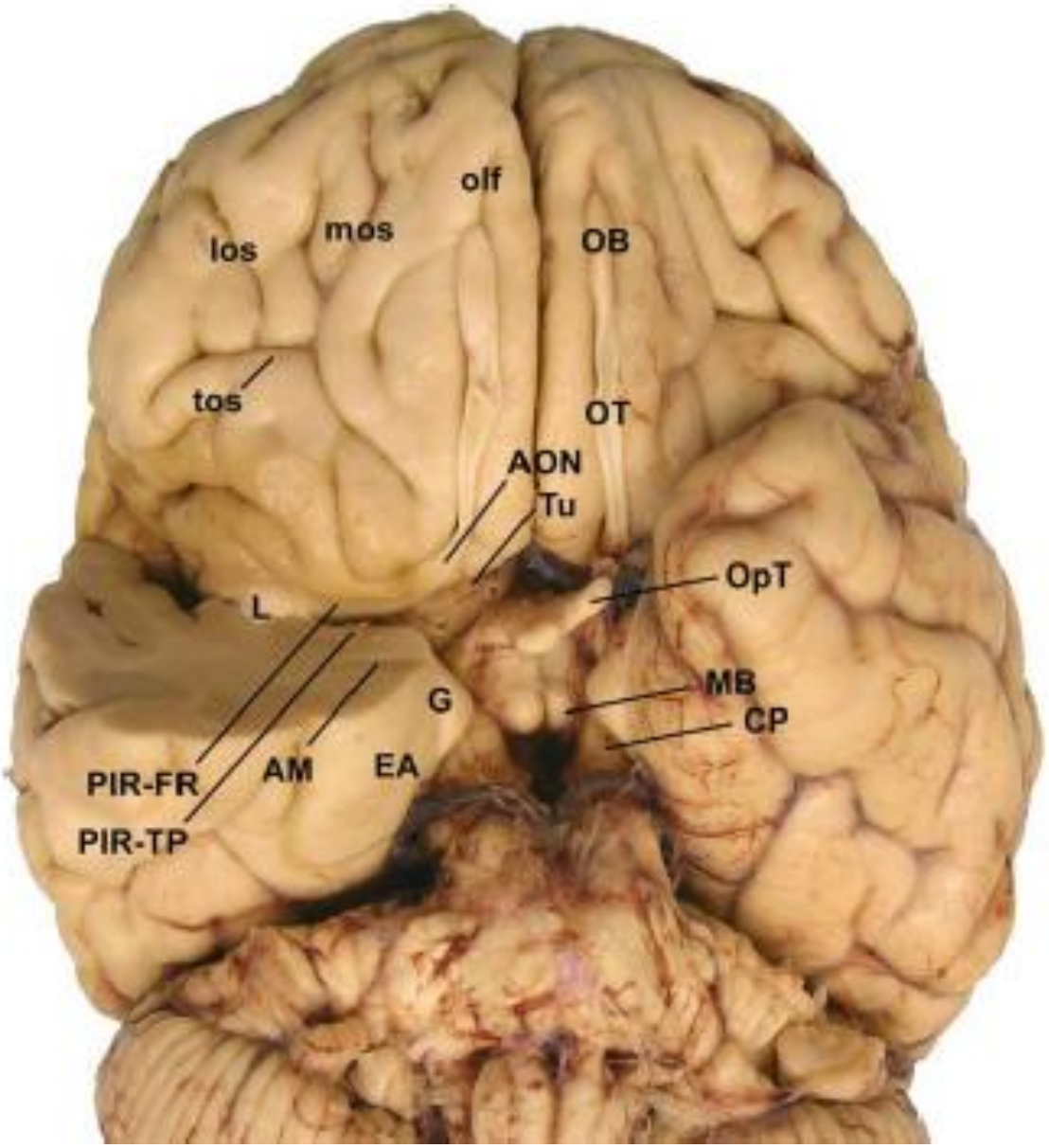
olfactory tubercle

anterior and posterior piriform cortex (considered to be the primary olfactory cortex)

cortical nucleus of the amygdala

entorhinal area

The axons of bulbar output neurons project in the olfactory tract to higher-order brain structures without contacting the thalamus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L
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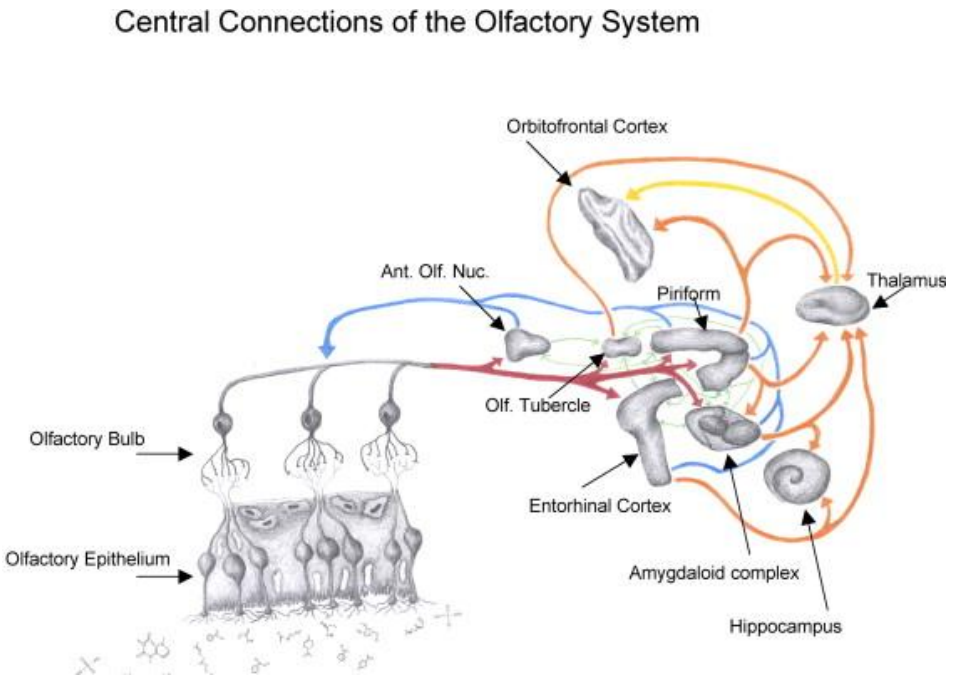
G
CP
PIR-FR
AM
EA
PIR-TP

VIA TALAMICA

Nevertheless, olfactory information is ultimately relayed through the thalamus to the neocortex, similar to other sensory systems.

The olfactory tubercle projects to the medial dorsal nucleus of the thalamus, which in turn projects to the orbitofrontal cortex, the region of cortex thought to beinvolved in the conscious perception of smell (377).



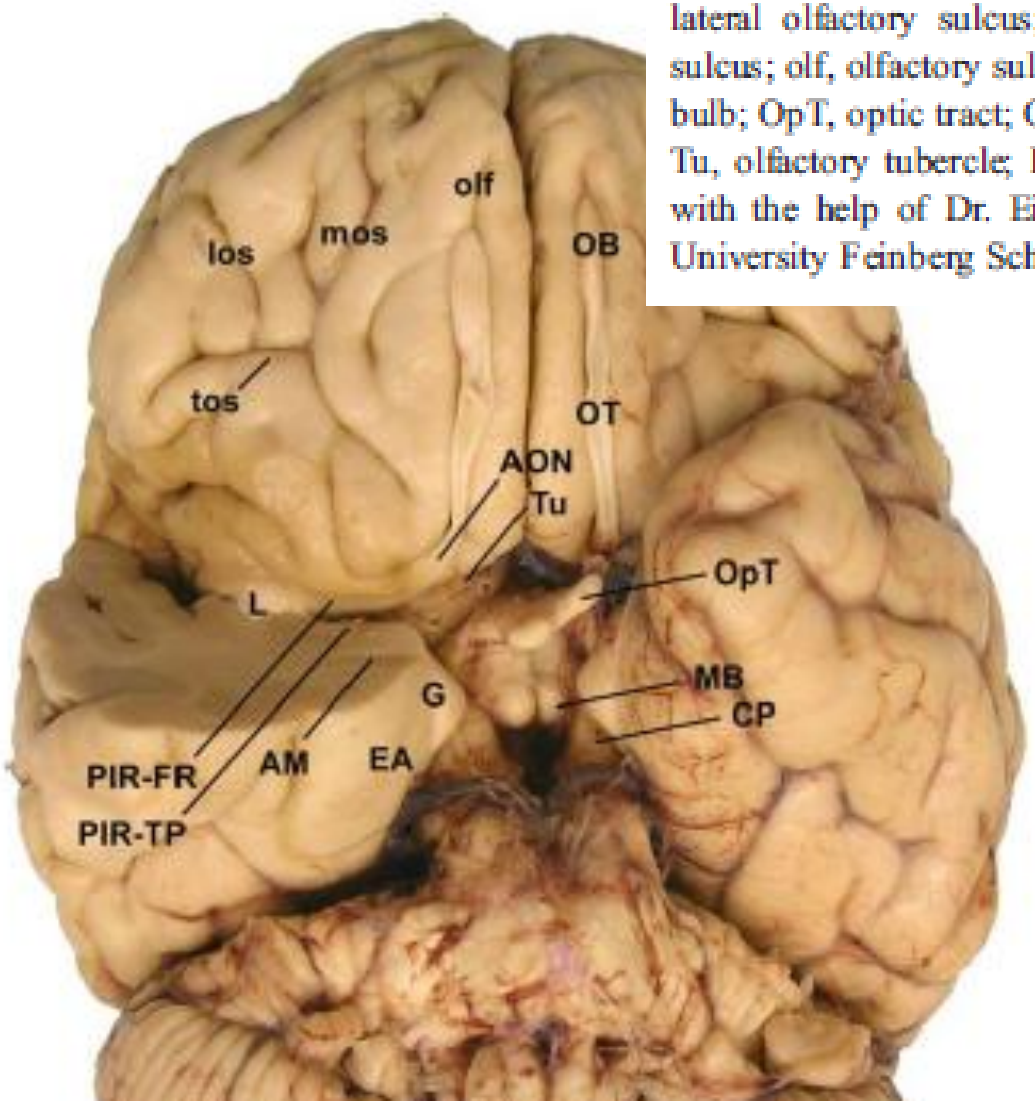
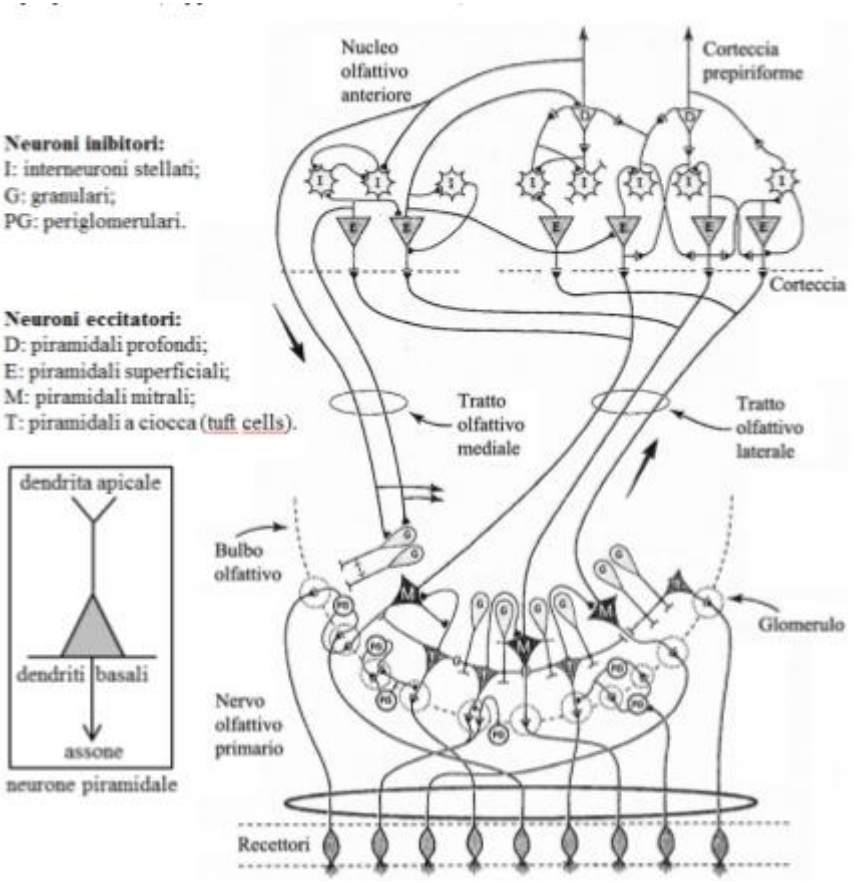
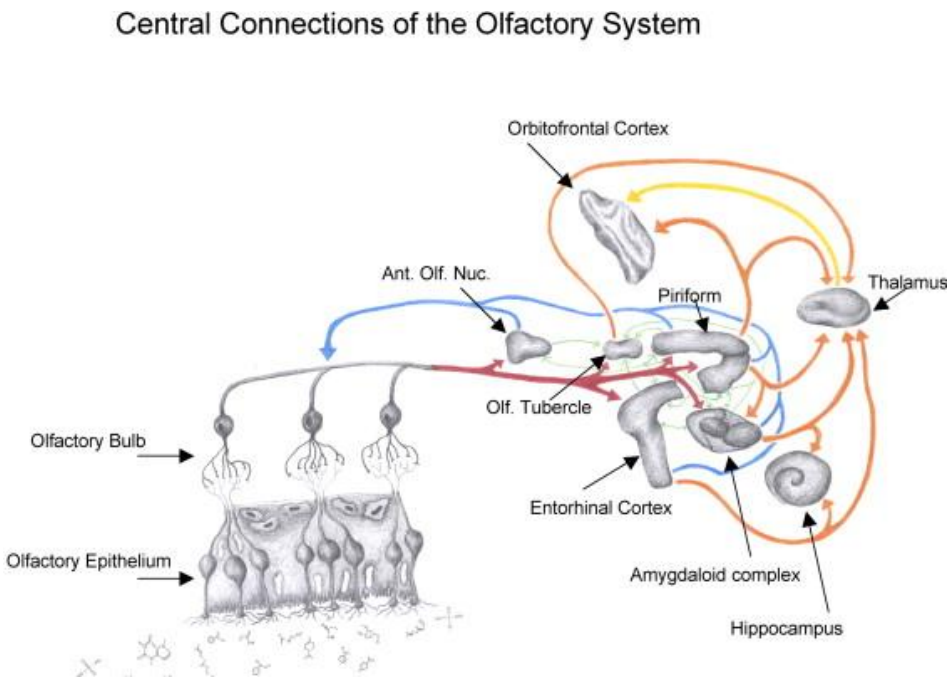


Fig. 1. Macroscopic view of the human ventral forebrain and medial temporal lobes, depicting the olfactory tract, its primary projections, and surrounding non-olfactory structures. The right medial temporal lobe has been resected horizontally through the mid-portion of the amygdala (AM) to expose olfactory cortex. AON, anterior olfactory nucleus; CP, cerebral peduncle; EA, entorhinal area; G, gyrus ambiens; L, limen insula; los, lateral olfactory sulcus; MB, mammillary body; mos, medial olfactory sulcus; olf, olfactory sulcus; PIR-FR, frontal piriform cortex; OB, olfactory bulb; OpT, optic tract; OT, olfactory tract; tos, transverse olfactory sulcus; Tu, olfactory tubercle; PIR-TP, temporal piriform cortex. Figure prepared with the help of Dr. Eileen H. Bigio, Dept. of Pathology, Northwestern University Feinberg School of Medicine, Chicago, IL.

Vie top-down oltre che bottom-up





La corteccia olfattiva fa parte della Allocortex

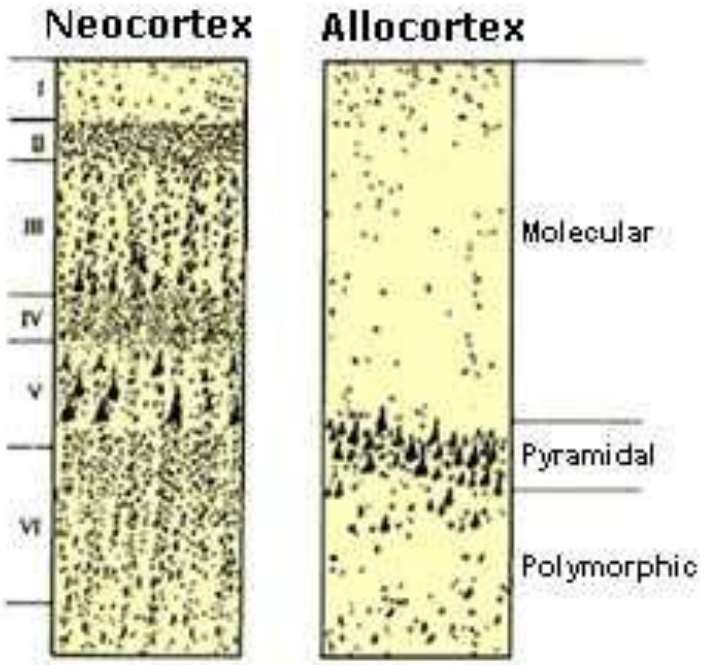
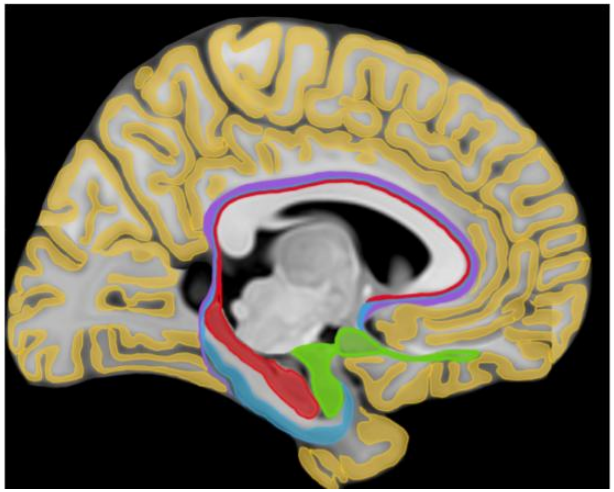
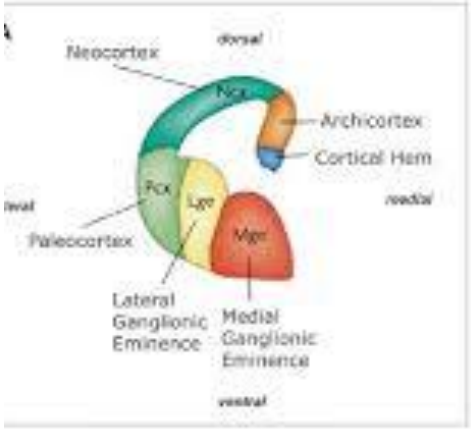
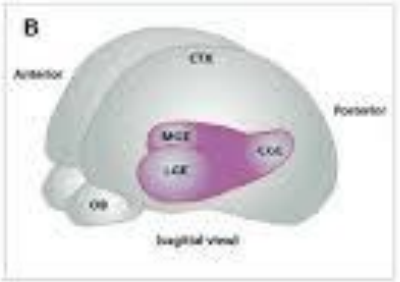


Figure 1: Schematic representation of the subdivisions of the human cerebral cortex into paleocortex (in green), archicortex (in red), periarchicortex (in blue), proisocortex (in purple) and neocortex (in yellow). Modified from Zilles and Amunts, 2012.

Note: we created a modified sagittal representation of the MRI template by fusing various parasagittal slices that allowed the delineation of the five ROIs in the same figure.

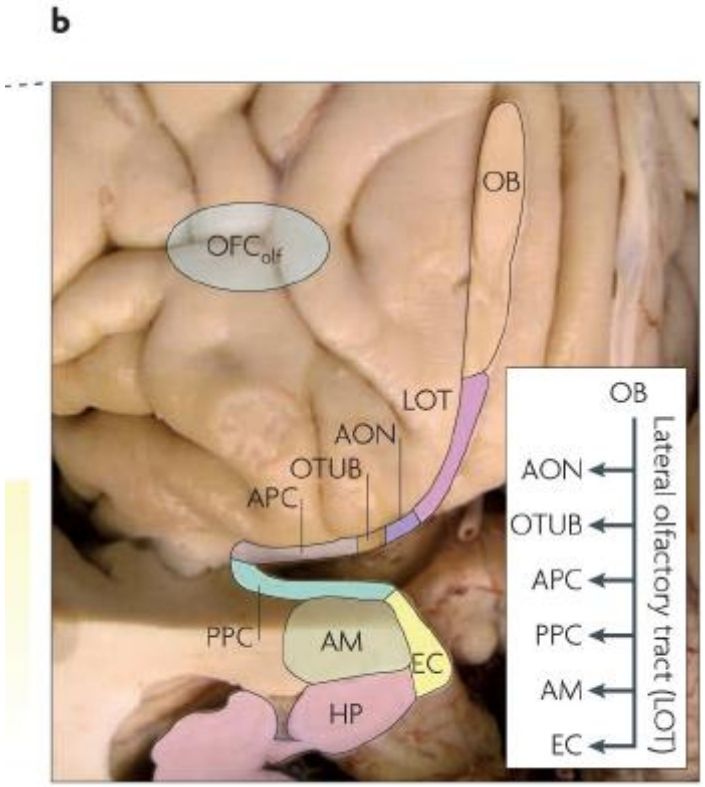


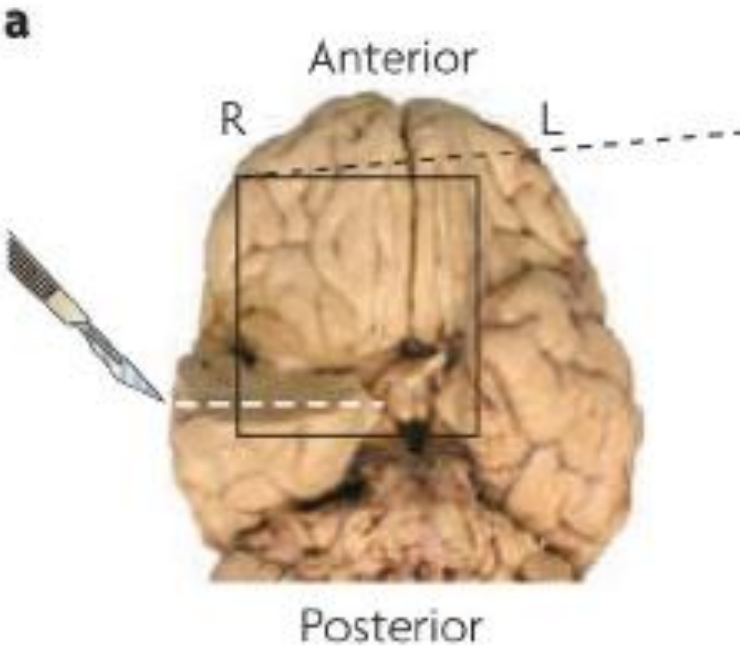




Piriform cortex

Anterior
And
Posterior





L’elaborazione seriale dell’informazione lungo la “via olfattiva”

Differenze fra bulbo olfattorio e corteccia piriforme anteriore

An object that is newly presented to the senses can be perceived only if irrelevant (background) stimulus information can be effectively filtered or tuned out. This property is known as **figure–ground segmentation**, and its principles apply as much to odour object perception as to object perception in other sensory modes.
In the olfactory system, sensory habituation is one method of segmenting a novel odour from older (background) odours.

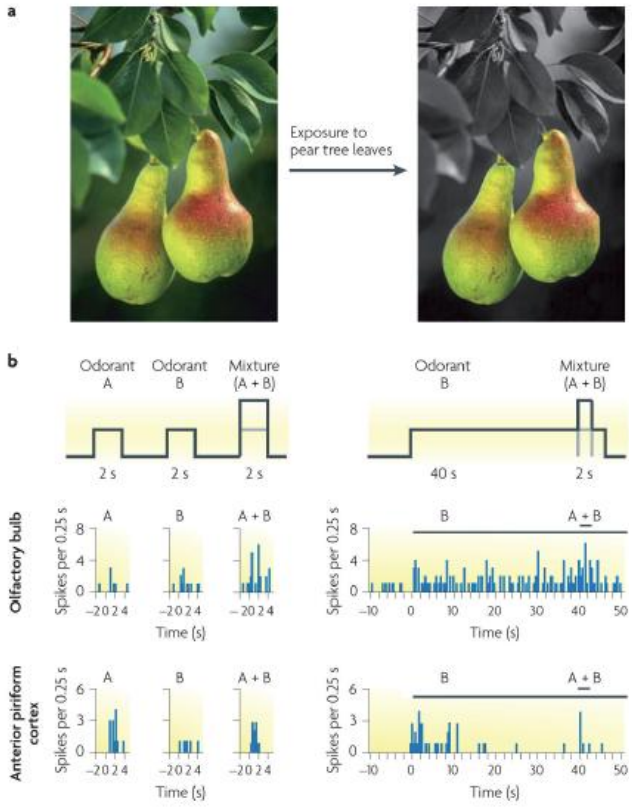
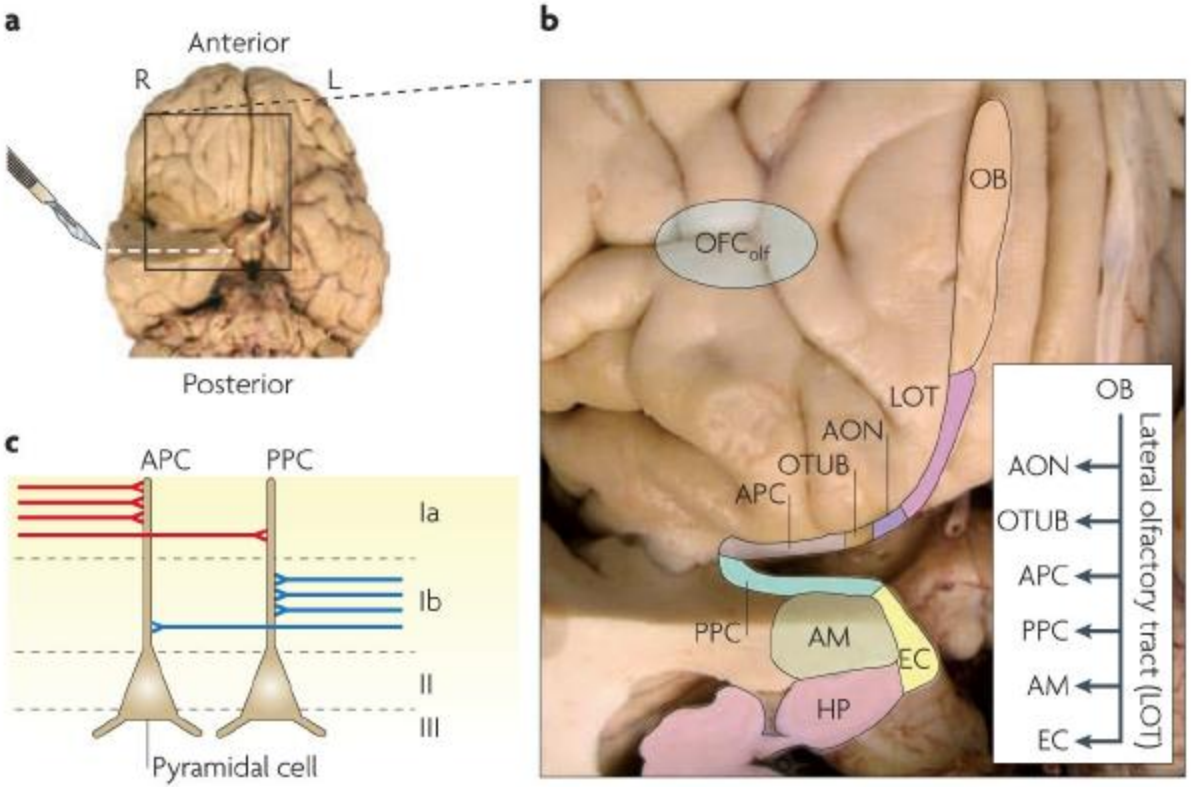


Figure 3. Odour-background segmentation
a | When considering pears hanging from a tree as an odour object, the olfactory features that arise from the leaves of the pear tree constitute the background stimulus. Prolonged exposure to this background stimulus induces sensory-specific habituation in the piriform cortex, thereby bringing the smell of pears to the foreground of perception. **b** | In a study performed in rodents, odorants 'A' and 'B' were presented individually or as a mixture ('A + B') on separate trials that lasted for 2 s (top part, left side). In a subsequent habituation phase, B was continuously presented for 40 s, followed by a presentation of the mixture for 2 s (top part, right side). In this presentation of the mixture, B constituted the background against which A was presented. During habituation to B, single-unit activity persisted in the olfactory bulb, showing a constant profile resembling that elicited by the 2-s presentation (middle part, right side), but in the anterior piriform cortex, the activity declined progressively during habituation to B (bottom part, right side). When A was presented together with B immediately after habituation, firing rates in the olfactory bulb were similar to those evoked by individual presentations of A + B (middle part, left side). By contrast, anterior piriform cortex firing rates in response to presentation of the mixture (bottom part, right side) were more similar to those evoked by A alone (bottom part, left side), reflecting the effective segregation of odorant A from the background (odorant B). Part **b** is modified, with permission, from REF. 122 © (2006) The American Physiological Society.

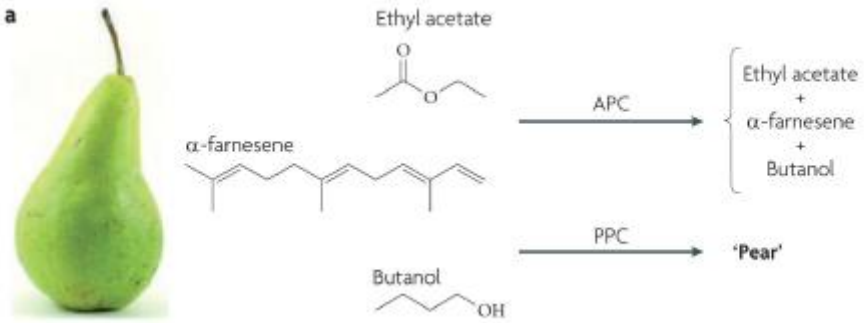
Piriform cortex

Anterior And Posterior



regions are then reciprocally interconnected (not shown). **c** | Schematic representation of the cellular organization of the piriform cortex. Pyramidal neurons are located in cell body layers II and III, and their apical dendrites project to molecular layer I. Layer I is subdivided into a superficial layer (Ia) that contains the sensory afferents from the olfactory bulb (shown in red) and a deeper layer (Ib) that contains the associative inputs from other areas of the primary olfactory cortex and higher-order areas (shown in blue)[33]. The majority of layer Ia afferents terminate in the APC, whereas the majority of layer Ib associative inputs terminate in posterior piriform cortex (PPC). Photographs in parts **a** and **b** prepared with the help of E. H. Bigio, Northwestern University Feinberg School of Medicine, USA.

Differenze fra corteccia piriforme anteriore e posteriore



The hierarchical transformation of information coding from APC (ant piriform) PPC (post piriform) closely agrees with their anatomical connectivity: most afferent fibres from the olfactory bulb innervate the **APC,** which is therefore ideally suited to represent elemental features of an odour, whereas the **PPC** mainly receives associative projections, allowing elemental representations to be unified into perceptual wholes.

Corteccia Piriforme Posteriore e l'apprendimento discrimimat

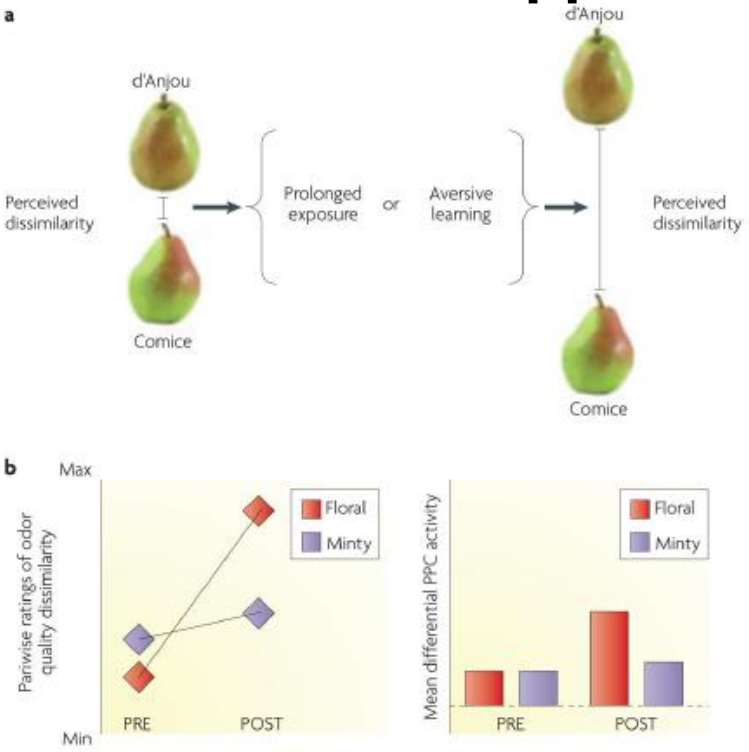


Figure 5. Odour object discrimination
a | Perceptual learning. Two varieties of pears, the d'Anjou and the Comice, have similar smells (left part). The ability to discriminate between the two can increase after prolonged exposure to their odours or after aversive learning (middle and right parts). This is an example of learning-induced perceptual plasticity in humans. **b** | In a functional MRI study of olfactory perceptual learning in humans[129], prolonged exposure to one odorant enhanced perceptual differentiation among qualitatively related odorants. After continuous delivery of a floral odorant for 3.5 min, the ratings of odour quality dissimilarity given by subjects increased between floral odorants (left part, shown in red) but not between minty odorants (left part, shown in purple), demonstrating the category-specificity of these learning effects. In the same subjects, experience-dependent changes were observed in the right posterior piriform cortex (PPC) (right part), with greater differences in mean fMRI activity in response to floral odours pre-exposure (PRE) compared with post-exposure (POST), showing how perceptual experience can modulate neural representations of odour quality. **c** |

The ability to group different objects into the same category must be tempered with the flexibility to discriminate among the individual objects. A stereotyped response to all members of a category is non-adaptive. Discriminating among different exemplars of an object category is facilitated by perceptual learning and experience. In the case of odour objects, one simple mechanism for object discrimination is olfactory habituation, which is a form of non-associative perceptual learning that arises from passive, prolonged exposure to a smell.
In humans, continuous exposure (habituation) to 1 odorant for 3 min enhanced the ability to differentiate between categorically similar odorants.
Hence, after prolonged experience with a floral-like odorant, subjects were better able to distinguish among different floral odorants, effectively becoming floral 'experts'. These perceptual changes were paralleled by an odour-evoked enhancement of mean fMRI activity in the PPC and OFC (but not in the APC), implying that these regions are involved in refining odour quality information. Interestingly, across the group of subjects, the magnitude of the learning-induced fMRI signal change in the OFC correlated with the ability to discriminate the odours, suggesting that the OFC may play an active role in mediating this phenomenon.

Olfactory Orbitofrontal cortex

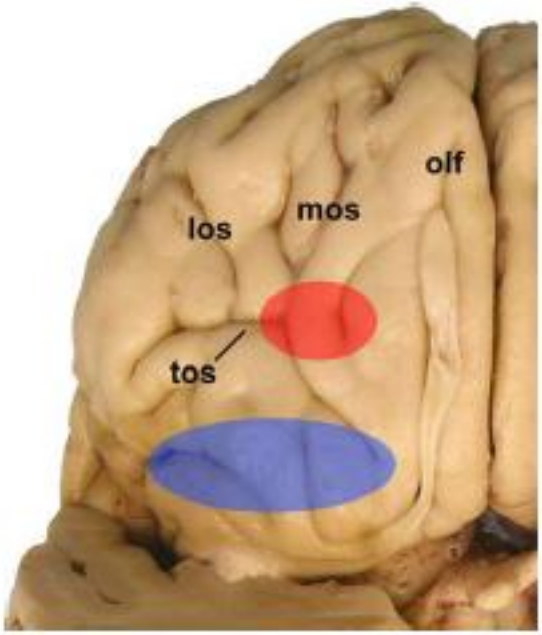


Fig. 6. Cross-species mismatch between predicted and observed olfactory OFC. The blue area signifies the olfactory projection area in monkey OFC, as based on electrophysiological [87,92] and anatomic tracer [14] studies, whereas the red area denotes the putative human olfactory projection area, as based on the neuroimaging meta-analysis presented here and recent cross-species anatomical comparisons of OFC [17,55]. See Fig. 1 for key to abbreviations. The diagram clearly indicates that the human olfactory region is located considerably more anterior than the monkey counterpart. Possible explanations for this anatomical discrepancy are discussed in the text.

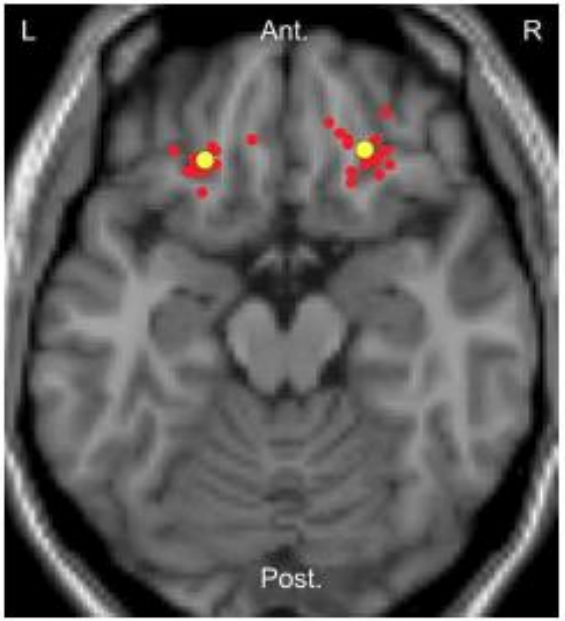


Fig. 5. Localization of olfactory OFC in humans. The peak activation coordinates (23 voxels: red dots) from 13 neuroimaging studies of basic olfactory processing are plotted on a canonical T1-weighted anatomical MRI scan in Talairach space. The yellow circles indicate the mean voxel coordinates for right and left sides. For presentation, coordinates are collapsed across the *z* axis (superior–inferior) in order to depict all voxels on a single image.

Orbitofrontal cortex

In termini evolutivi, l'OFC (corteccia orbitofrontale) arriva tardi sulla scena.

Il fatto che i vertebrati non mammiferi processino gli stimoli olfattivi senza OFC suggerisce che questa struttura non è essenziale per i comportamenti guidati dall'olfatto.

La corteccia orbitofrontale , ancor più della corteccia piriforme posteriore, è coinvolta

- nell'integrazione multisensoriale
- nell'apprendimento discriminativo degli odori
- nell'assegnare al cibo una salienza incentivante
- nella capacità di inibire le risposte prepotenti evocate dallo stimolo olfattivo , conferendo una flessibilità comportamentale cosa che è difficile da raggiungere per gli animali "inferiori"
- nella memoria degli odori assieme al circuito ippocampale
- nella percezione cosciente **????**

Interestingly, human patients with focal orbitofrontal lesions have notable difficulties with odour discrimination, identification and memory, whereas odour detection is relatively spared..

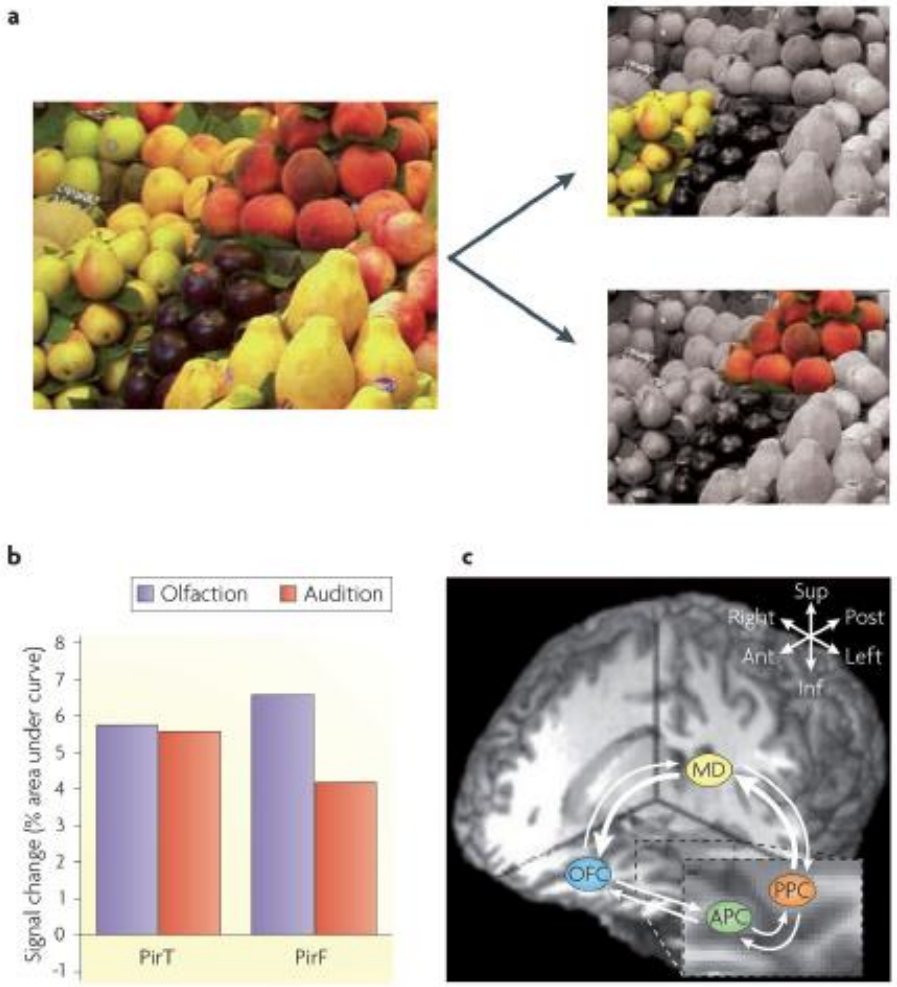
A recent clinical report suggests that olfactory conscious awareness relies on an intact right OFC:

> a 33-year-old man developed **anosmia** following **right** orbitofrontal injury but demonstrated **preserved odour-evoked autonomic responses to unpleasant smells, with concomitant activation of the piriform cortex** (bilaterally) **and the left OFC.**
>
> > These findings imply a central role of the right OFC in transforming olfactory inputs into conscious percepts, and suggest that the left olfactory pathway is not sufficient to sustain conscious olfaction.

Un circuito corteccia piriforme posteriore frontale-talamo-corteccia orbito frontale si attiva

Permettendoci di dirigere selettivamente il focus attentivo cosciente verso un particolare stimolo odoroso

Il circuito attenzionale corteccia piriforme posteriore frontale-talamo-corteccia orbito frontale



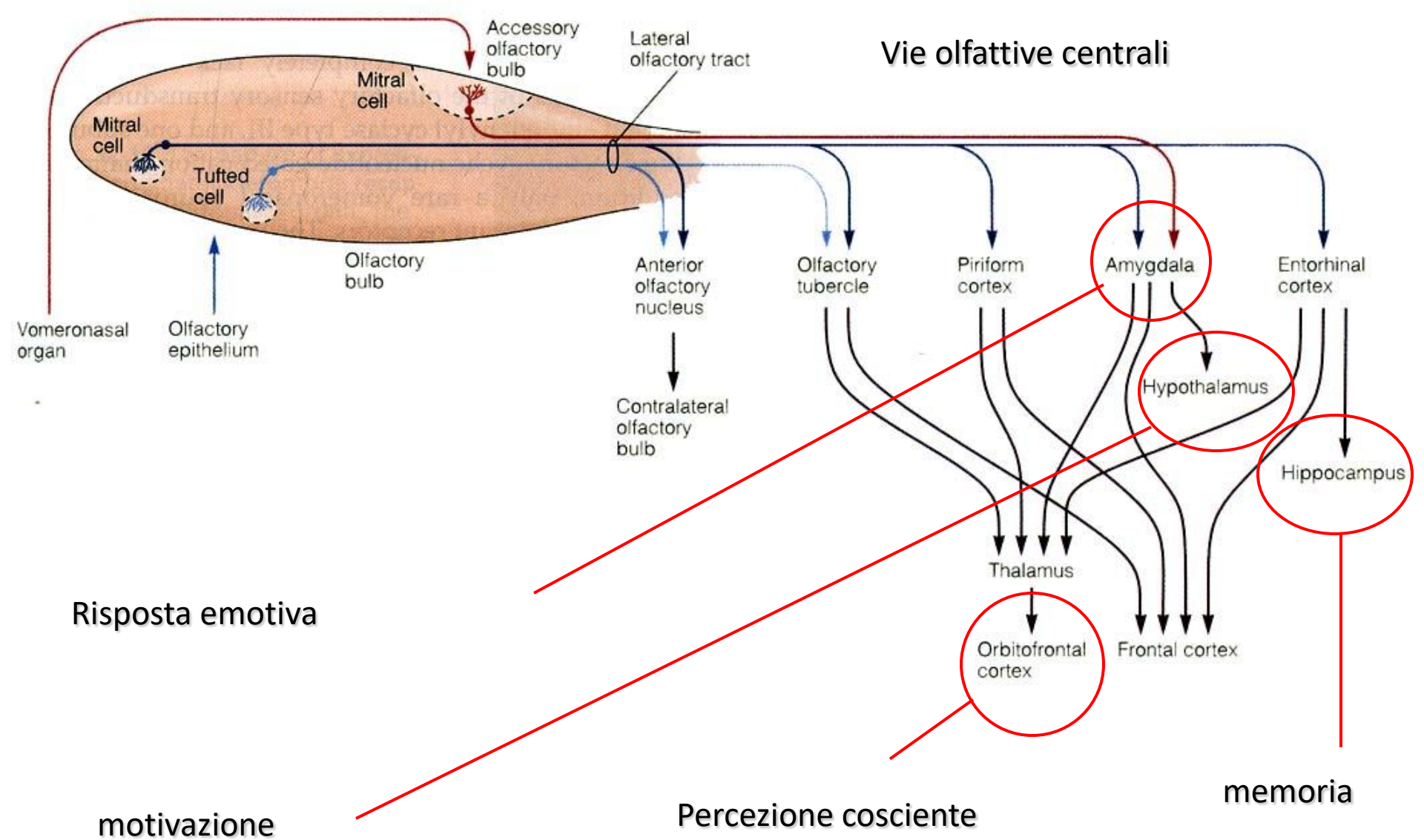
The studies described here make a strong case for the piriform cortex as an important substrate of odour object perception. The data suggest that the APC and the PPC have different roles in this process.

Odorant identity, the composite sum of an odorant's molecular and chemical constituents, is encoded in the **APC**, where signal fidelity of the original stimulus can be preserved.

Odour quality is encoded in the **PPC**, a sensory associative area where object representations are defined and updated through learning and experience. Thus, the APC retains a more static snapshot of the olfactory environment, which in the PPC is transformed into a dynamic percept that varies according to an individual's past history, present circumstances and future expectations.

Finally, the proposed role of the **OFC** in guiding experience-dependent perceptual plasticity is in agreement with the idea that this region provides a top-down signal that helps to resolve odour object representations in the piriform cortex, particularly under conditions of high stimulus uncertainty

Vie olfattive centrali



Risposta emotiva

motivazione

Percezione cosciente

memoria

IL GUSTO

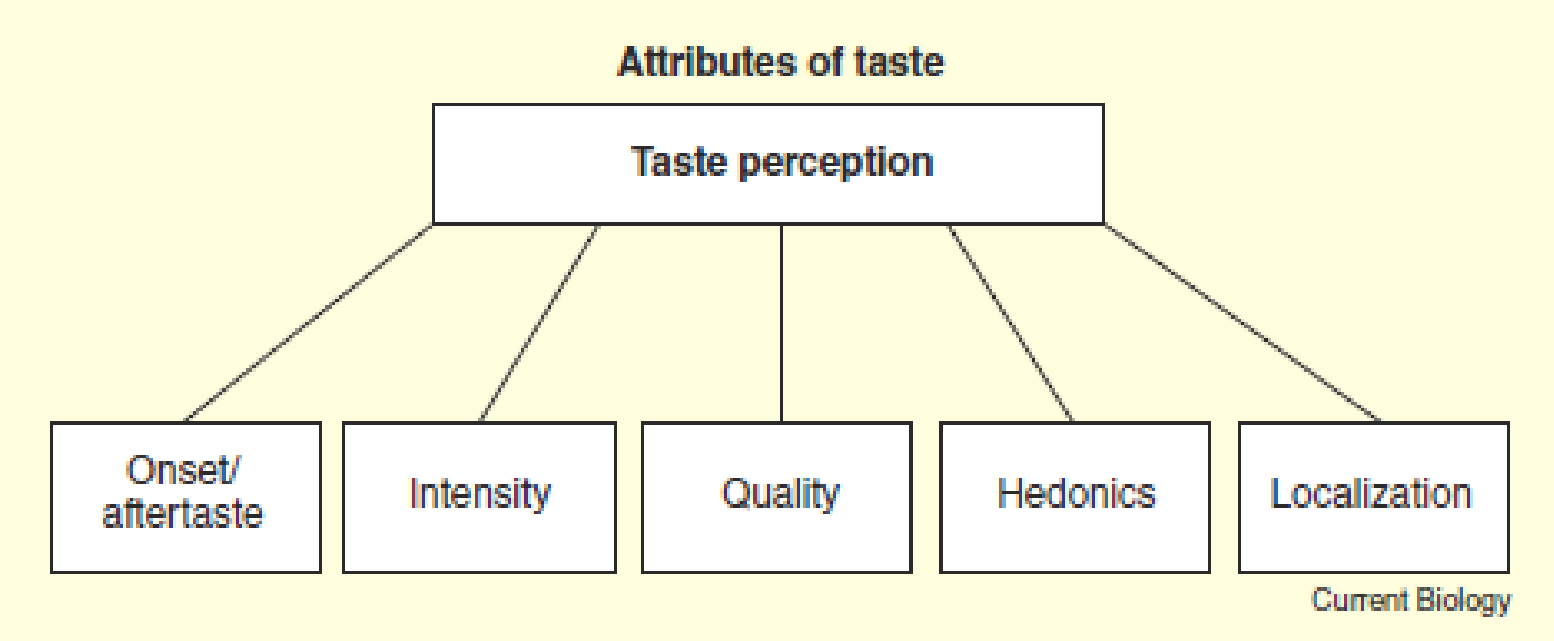


Figure 2. The psychological attributes of a taste percept.

The percept of taste from any given stimulus or solution is principally thought to consist of qualitative experiences labeled salty, sweet, bitter, sour and umami. Most taste percepts will also be composed of distinct additional attributes: intensity, hedonic, oral localization, and temporal features (rise and decay and aftertaste).

Qualità

Esistono 5 gusti primari

dolce, amaro, salato, acido e umami associato agli amino acidi.

Chemicals (tastants) perceived

as sweet are associated with food high in caloric content

those sensed as umami are indicative of protein.

Noncanonical Taste Qualities in Mammals

Grassi

they qualify as bona fide tastes is still an open question. Fats are detected by several routes, including olfaction and somatosensation, and they elicit postingestive effects that promote consumption. But are they tasted? Several lines of evidence argue that the answer is yes. The observation that mice prefer water spiked with free fatty acids, which are breakdown product of triacylglycerides that are found in vegetable and animal-derived products, supports a role for the taste system in detecting this rich source of calories (Gaillard et al., 2008). Taste cells express putative receptors for fat taste including K^+ channels that are sensitive to polyunsaturated fatty acids, a fatty acid transporter (CD36), and two fat-sensitive GPCRs, GPR40 and GPR120 (Liu et al., 2011). The most promising of these candidate receptors is GPR120, which is required for preference to fatty acids in mice (Cartoni et al., 2010) and is expressed in human TRCs

Calcio

Another noncanonical sensory attribute encoded by taste cells is referred to as "calcium taste." Ca^{2+}, an ion required for a vast array of cellular functions, is attractive to Ca^{2+}–deprived animals, but is rejected by Ca^{2+}-sated animals. Paradoxically, the aver-

Acqua

Last among these noncanonical tastes is the taste of water. Animals can detect wetness across their body by virtue of the somatosensory system, and this system is also likely to contribute to the sensing of aqueous solutions in the oral cavity.

Intensità

Soglia assoluta

- per evocare sensazioni **gustative** sono necessarie concentrazioni da 10^{14} a 10^{20} molecole per 1 ml di soluzione

Tab. 10-2. Soglia gustativa di alcune sostanze.

Sostanza	Gusto	Concentrazione soglia (μmol/l)
Acido cloridrico	Acido	100
Sodio cloruro	Salato	2000
Stricnina cloridrato	Amaro	1,6
Glucosio	Dolce	80000
Saccarosio	Dolce	10000
Saccarina	Dolce	23

il senso del gusto

è meno discriminativo e sensibile dell'olfatto

riconosce infatti solo cinque sapori fondamentali:

i quattro classici
(acido, amaro, dolce, salato)

e l'*umami*

(parola giapponese che indica il sapore gradevole della carne e degli alimenti contenenti glutammato)..

La minore sensibilità del gusto rispetto all'olfatto è attestata dal fatto che

- per evocare sensazioni **gustative** sono necessarie concentrazioni da 10^{14} a 10^{20} molecole per 1 ml di soluzione

- per evocare sensazioni **olfattive** la soglia assoluta è 10^{7} molecole per 1 ml d'aria

L'esperienza sensoriale del gusto si associa ad una esperienza affettiva di piacevolezza o di disgusto

Consistent with the nutritional importance of carbohydrates and proteins, both sweet and umami tastants elicit pleasurable sensations in humans and are attractants for animals.

In contrast, bitter tastants, which are often found in poisonous plants, elicit an aversive response that is innate in animals as well as human infants and likely prevents the ingestion of toxic substances.

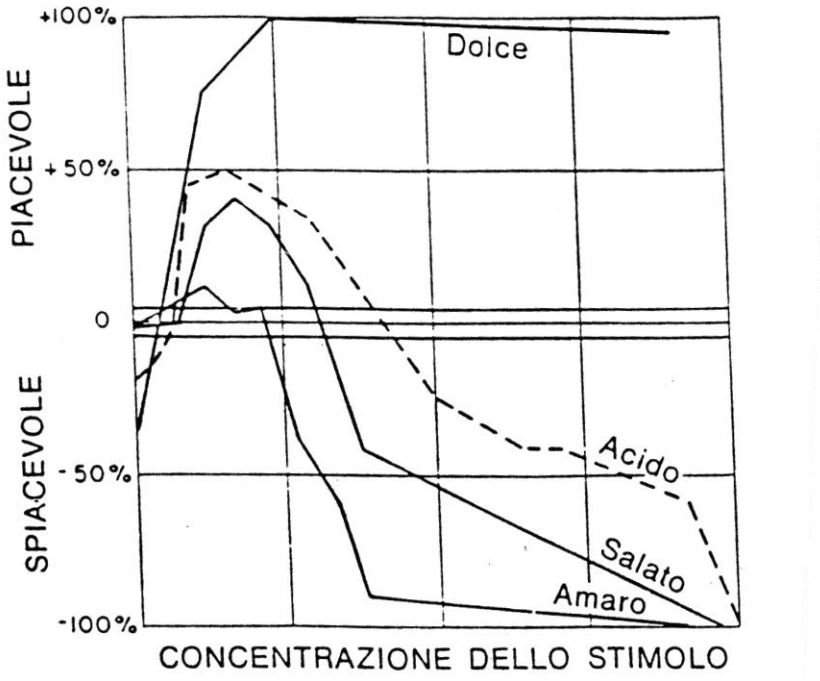
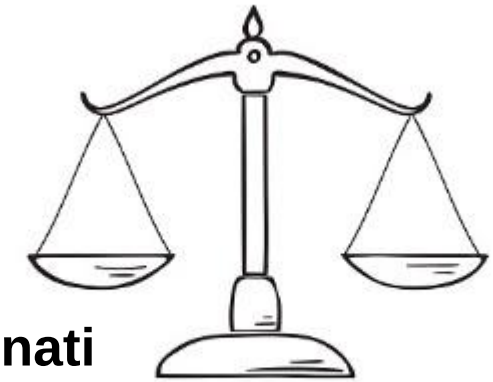


Figura 62-3. Tonalità affettiva dei differenti sapori fondamentali alle differenti intensità di stimolazione. (Da Engel in Woodworth and Schlosberg: Experimental Psychology. Holt Rinekart & Winston, Inc. 1954).

La valenza affettiva associata alle emozioni evocate dal gusto

dipende



Meccanismi innati **Meccanismi appresi**

La valenza affettiva associata ai sapori primari dipende da un meccanismo innato

Le esperienze emotive

di piacevolezza associate al dolce ed umami

di disgusto associate all'amaro

sembrano innate e non apprese

A. Positive Affective Reactions

B. Aversive Reactions

12

5

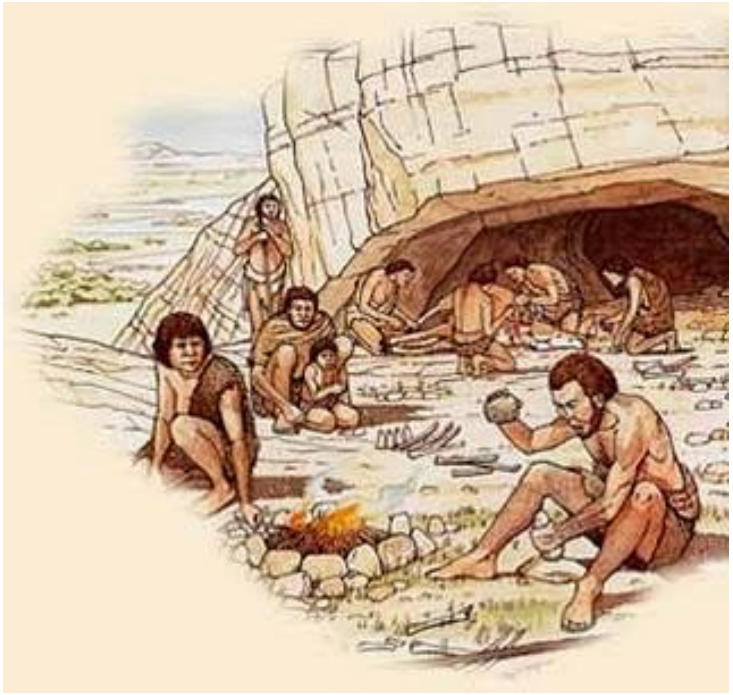
from there extends to the primary taste cortex (Fig. 2b). A key fact about taste stimuli is that they elicit the most basic human emotions of pleasure (sweet) and disgust (bitter), which are not learned; they are hard-wired in the brainstem from birth[28,29]. In contrast to taste, the affective responses to odour images seem to be mostly learned, which presumably accounts for the enormous diversity of flavours in the world's cuisines.

Le risposte emotive ai gusti primari hanno condizionato le nostre scelte alimentari e ci hanno fatto sopravvivere nella caverna.

Cibi dolci, salati e ad alta densità energetica

⇩

Piacere



Avversione

⇩

amaro e acido (veleni,tossine)

…fenoli, alcaloidi, glicosidi,terpeni,steroidi, peptidi, aminoacidi, amidi,amine,acidi grassi,composti eterociclici, tiouree, carbamidi, esteri, lattoni, composti carbonilici……

Il 10% delle specie vegetali sintetizza metaboliti secondari tossici

La mimica facciale legata alla espressione della sensazione gustativa ha una componente riflessa di origine troncoencefalica

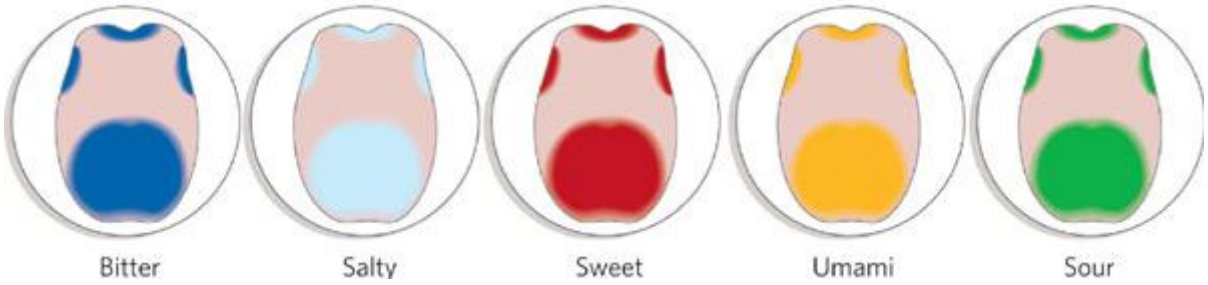
La si ritrova infatti anche in animali decerebrati

from there extends to the primary taste cortex (Fig. 2b). A key fact about taste stimuli is that they elicit the most basic human emotions of pleasure (sweet) and disgust (bitter), which are not learned; they are hard-wired in the brainstem from birth[28,29]. In contrast to taste, the affective responses to odour images seem to be mostly learned, which presumably accounts for the enormous diversity of flavours in the world's cuisines.

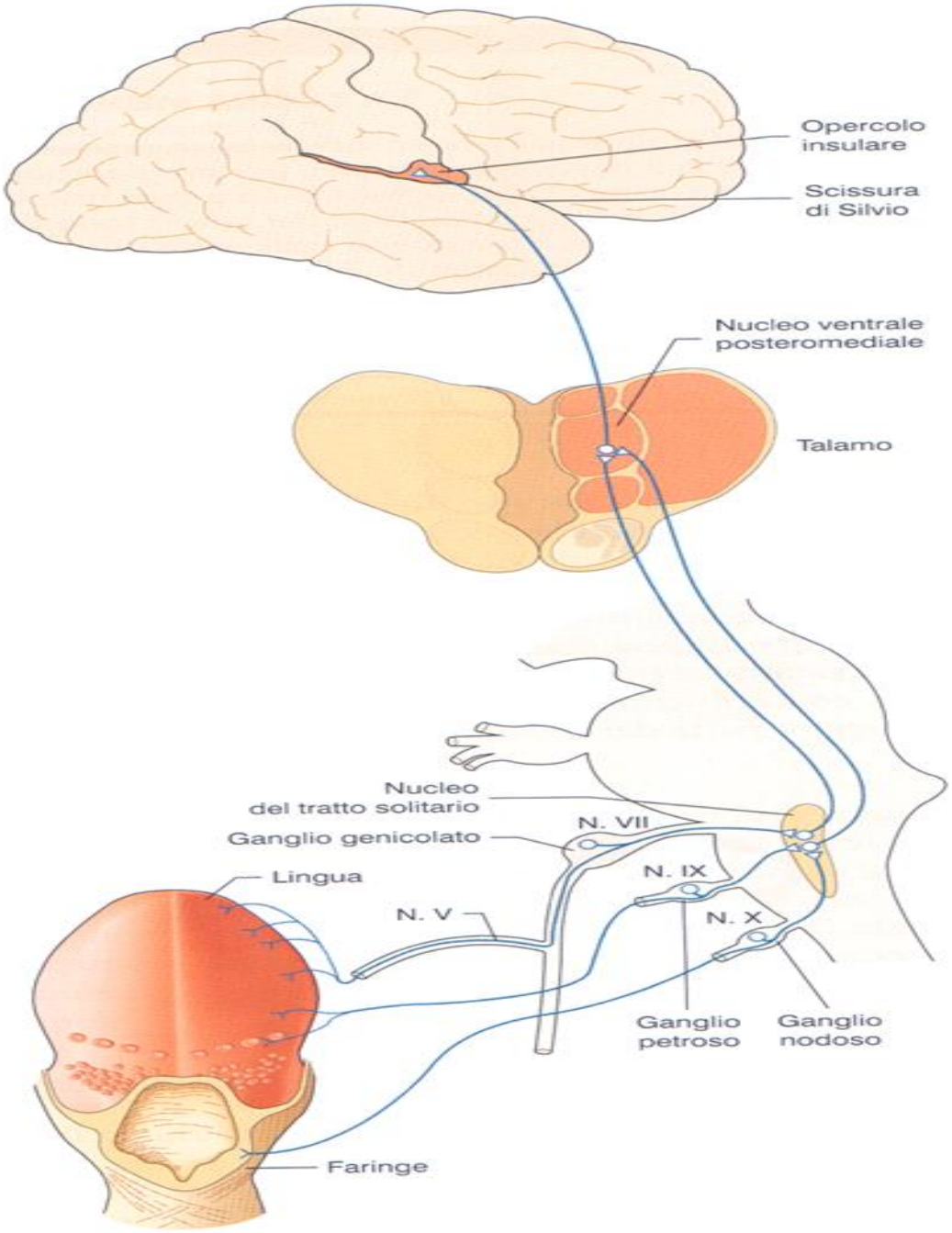
I recettori e le vie del gusto

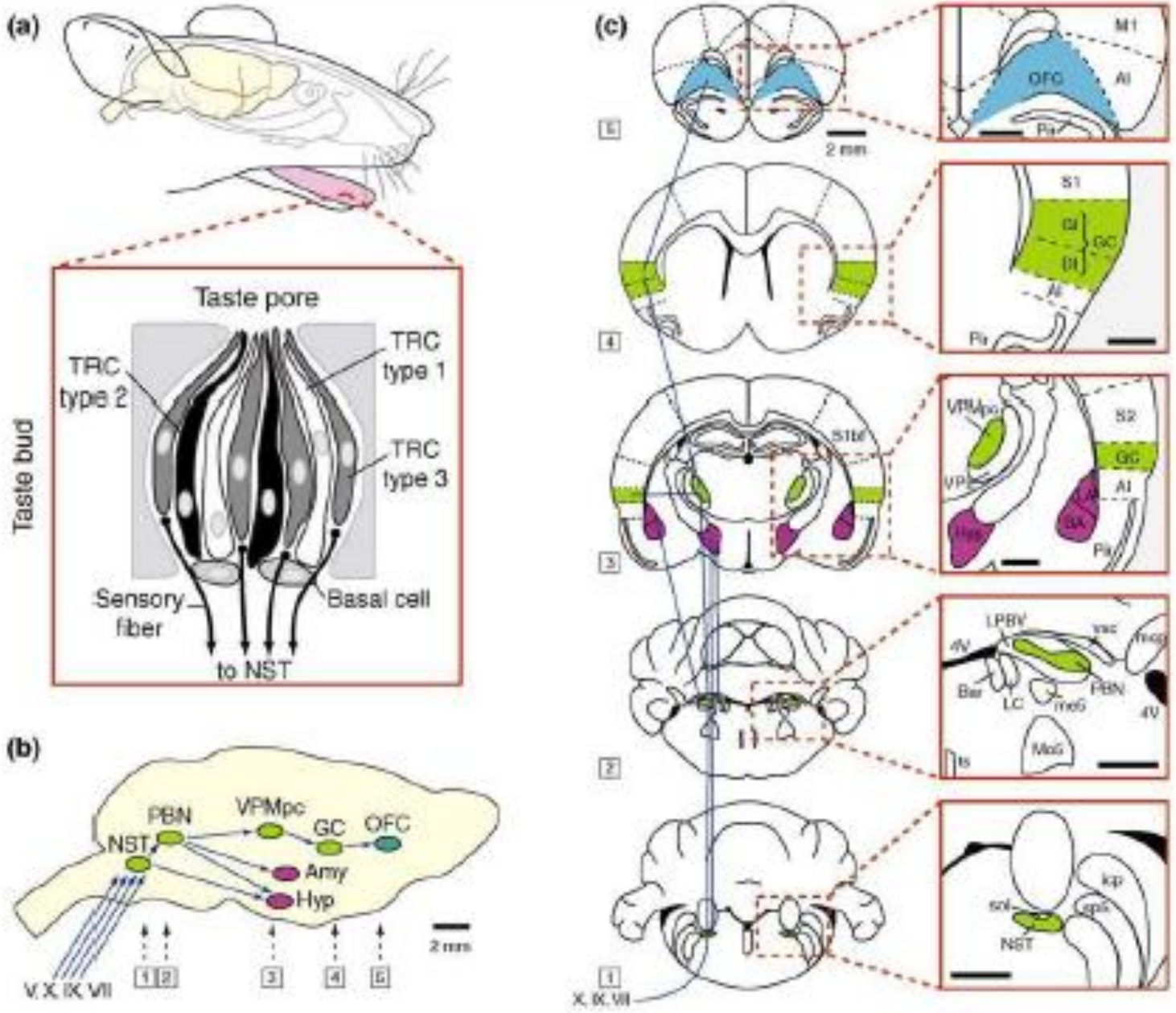
Quadro d’insieme

La sensazione gustativa dipende da recettori localizzati nel cavo oro-faringeo



Le vie del gusto


Opercolo insulare
Scissura di Silvio
Nucleo ventrale posteromediale
Talamo
Nucleo del tratto solitario
Ganglio genicolato
N. VII
N. IX
N. X
Lingua
N. V
Ganglio petroso
Ganglio nodoso
Faringe



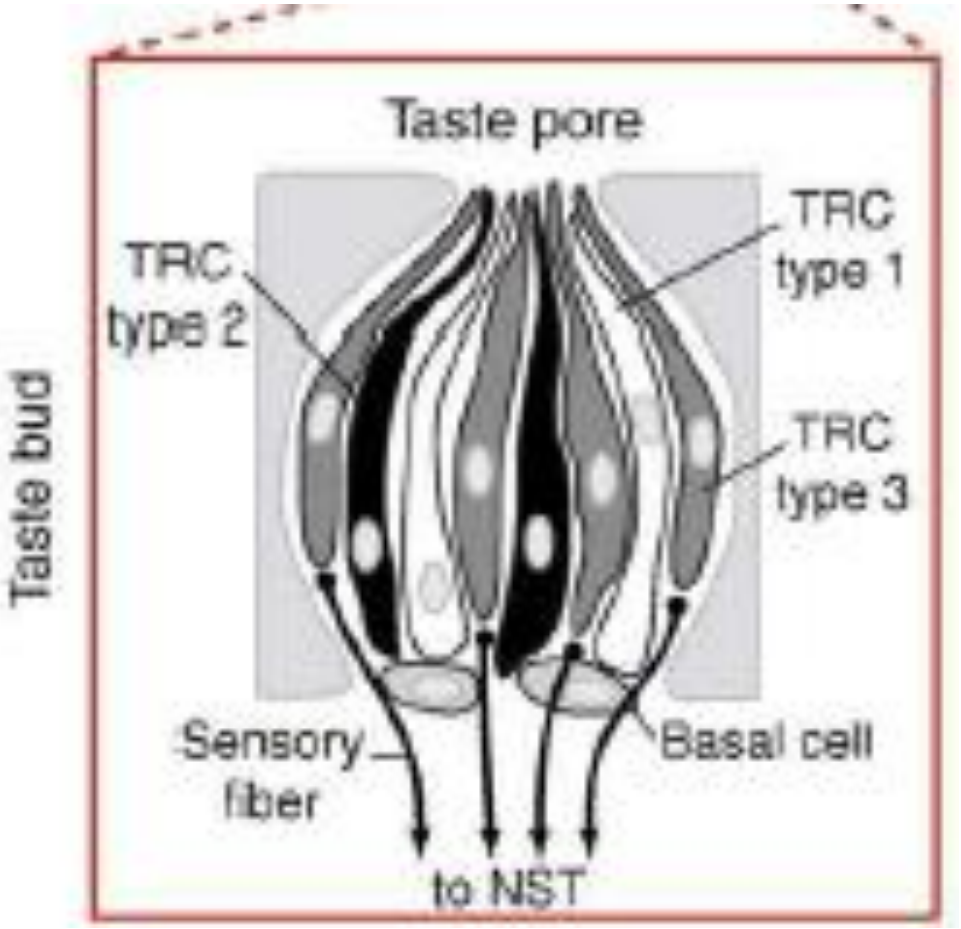
TRENDS in Neurosciences

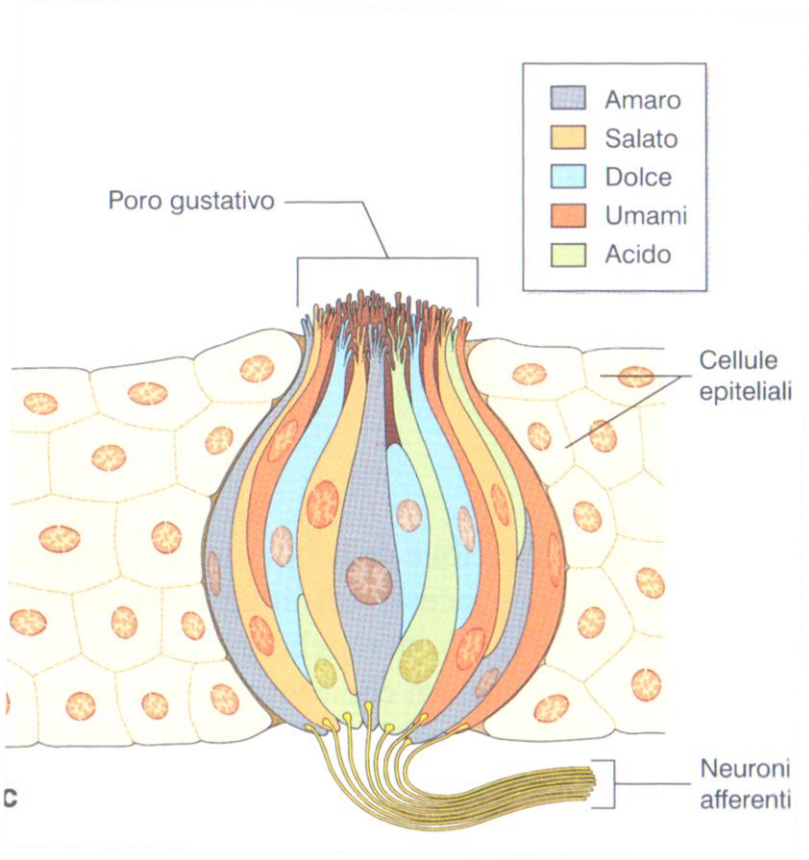
I recettori gustativi di trovano in strutture chiamate

GEMME GUSTATIVE

Gemme gustative

Strutture composte da 50-100 cellule gustative,





Le gemme gustative si concentrano nelle papille gustative

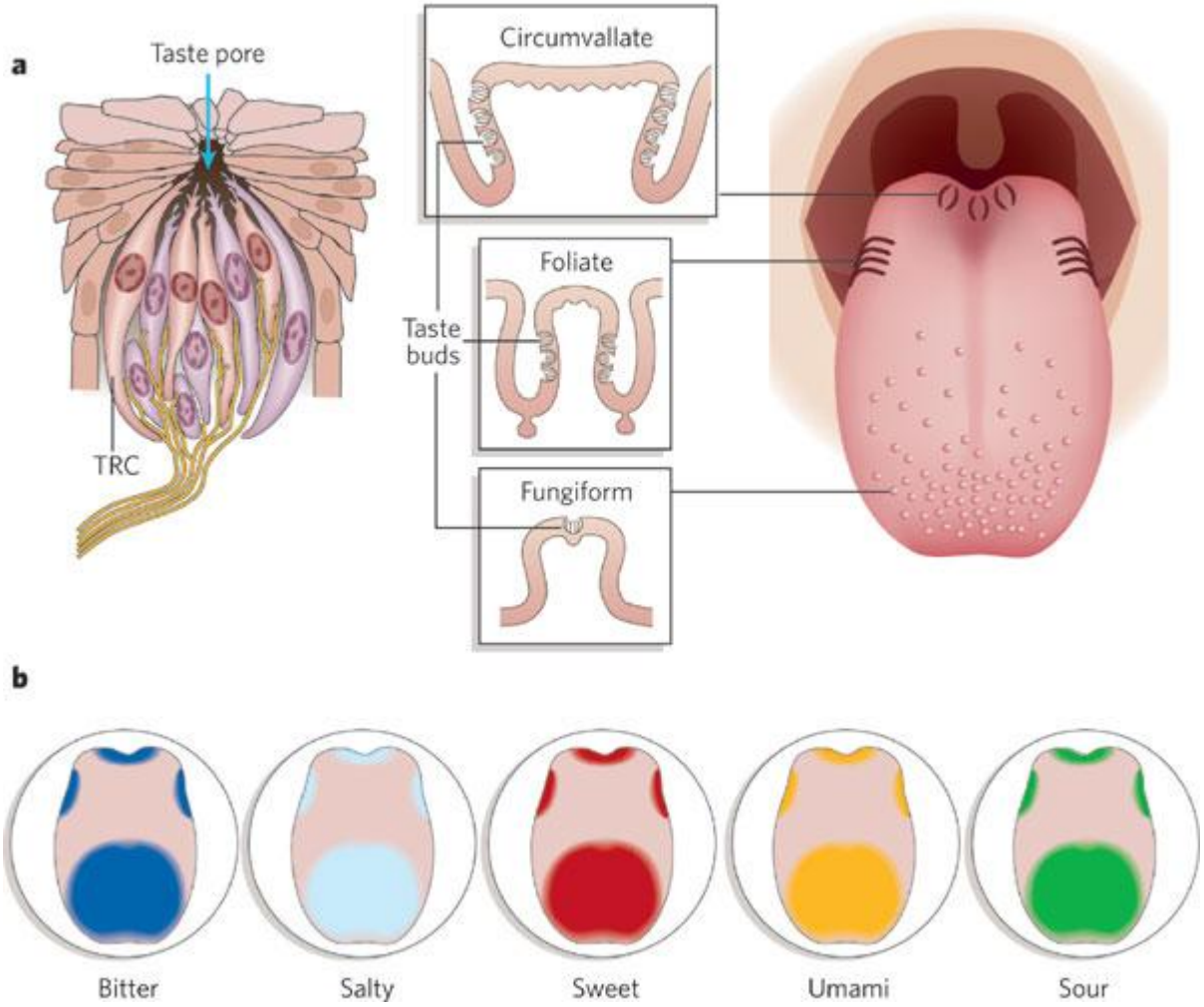
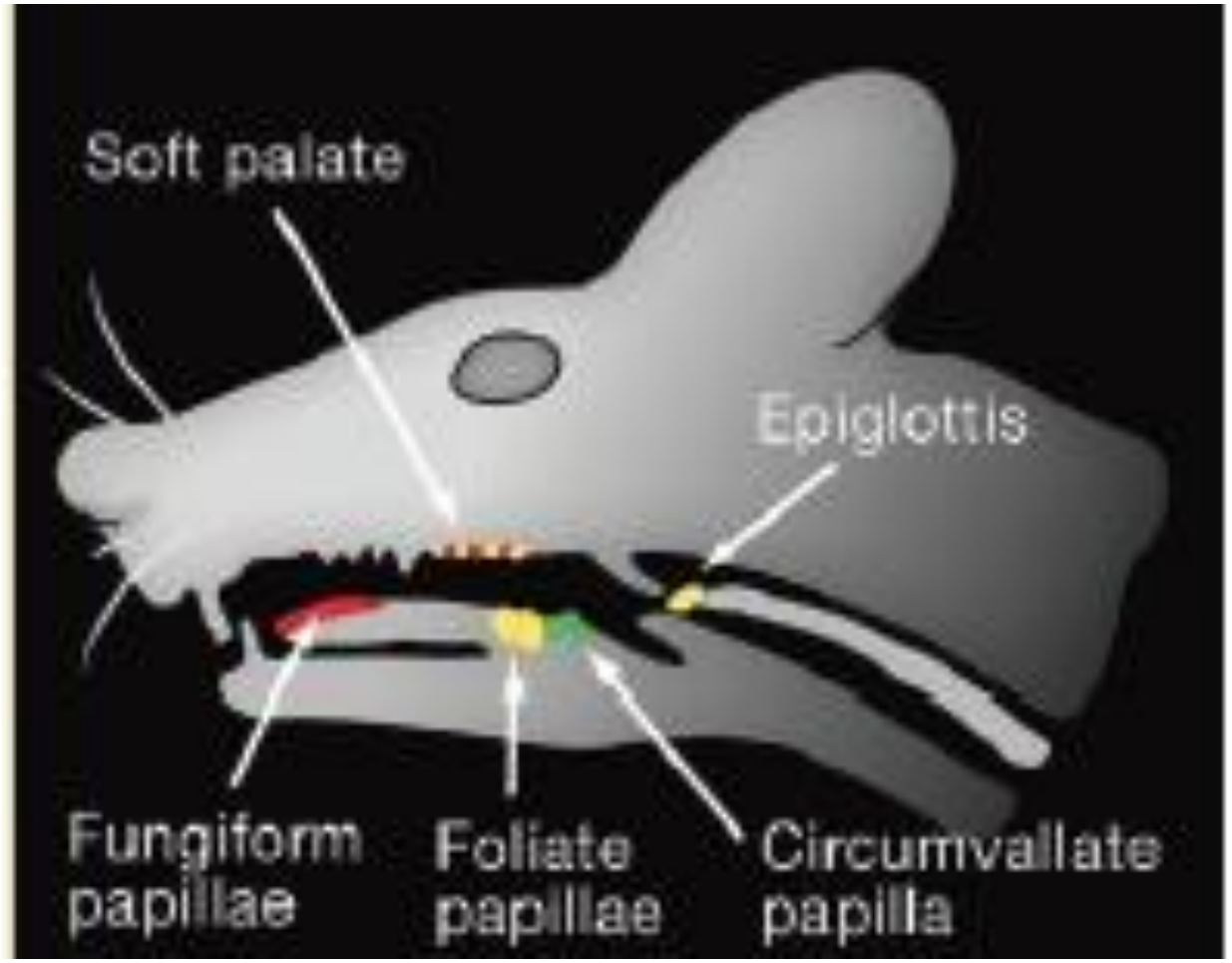
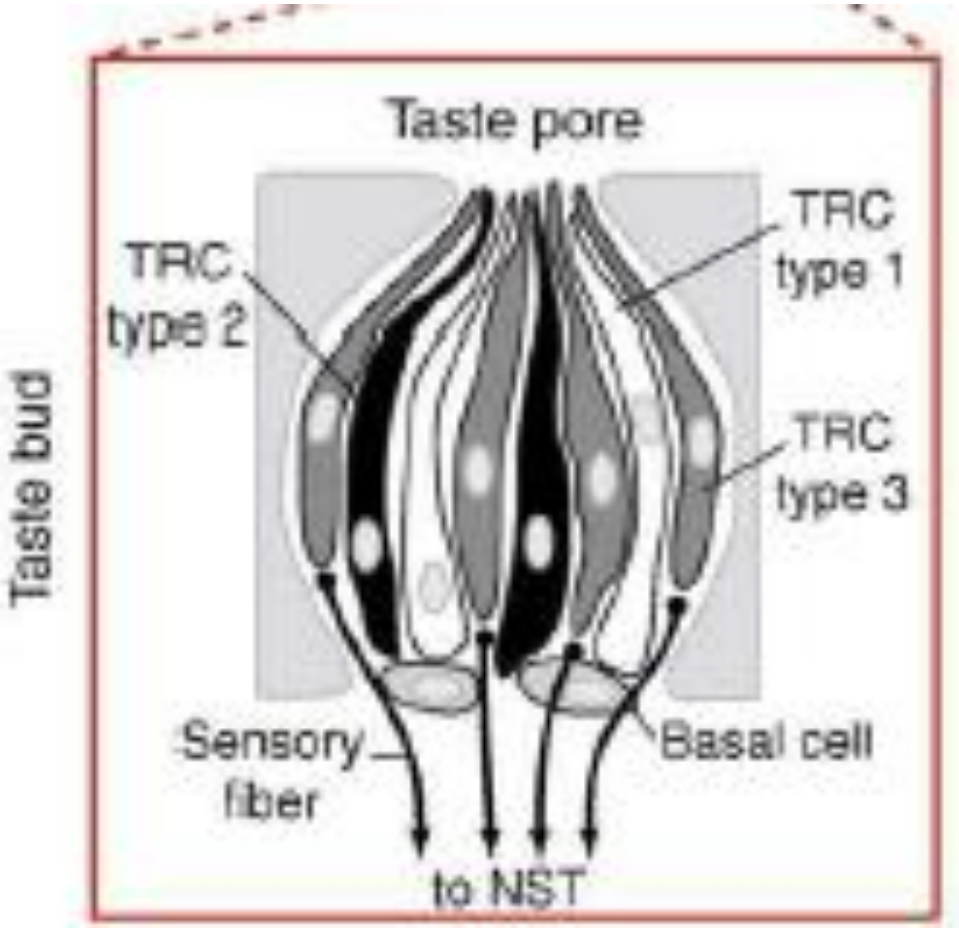
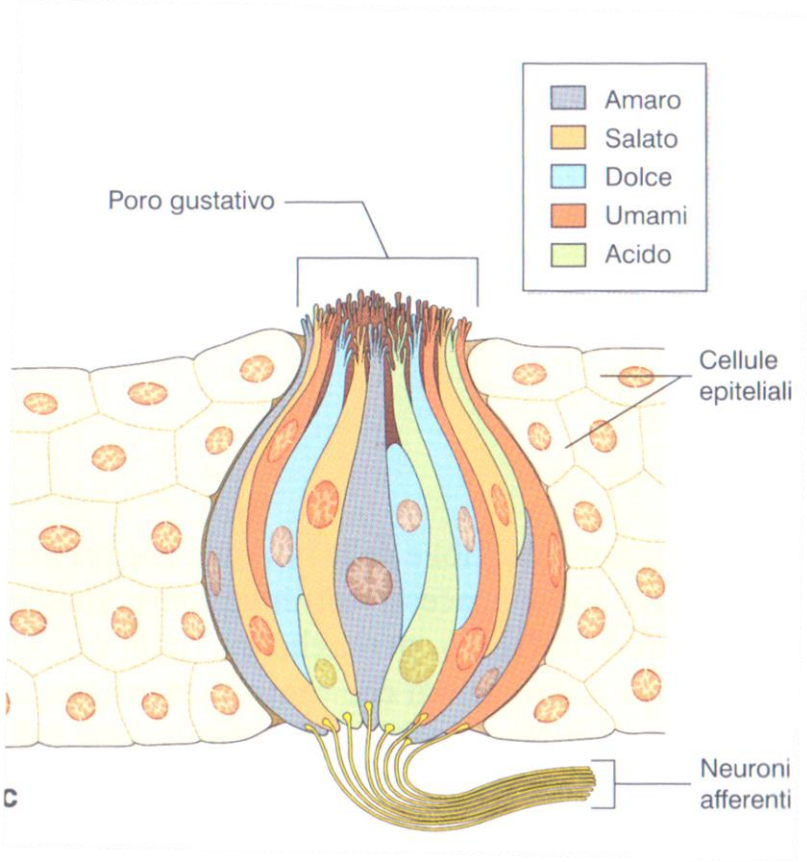


Figure 1 | Taste-receptor cells, buds and papillae. **a**, Taste buds (left) are composed of 50–150 TRCs (depending on the species), distributed across different papillae. Circumvallate papillae are found at the very back of the tongue and contain hundreds (mice) to thousands (human) of taste buds. Foliate papillae are present at the posterior lateral edge of the tongue and contain a dozen to hundreds of taste buds. Fungiform papillae contain one or a few taste buds and are found in the anterior two-thirds of the tongue. TRCs project microvillae to the apical surface of the taste bud, where they form the 'taste pore'; this is the site of interaction with tastants. **b**, Recent molecular and functional data have revealed that, contrary to popular belief, there is no tongue 'map': responsiveness to the five basic modalities — bitter, sour, sweet, salty and umami — is present in all areas of the tongue[6,8,9,32,78].


Soft palate
Epiglottis
Fungiform papillae
Foliate papillae
Circumvallate papilla


Taste bud
Taste pore
TRC type 2
TRC type 1
TRC type 3
Sensory fiber
Basal cell
to NST


Amaro
Salato
Dolce
Umami
Acido
Poro gustativo
Cellule epiteliali
Neuroni afferenti
c

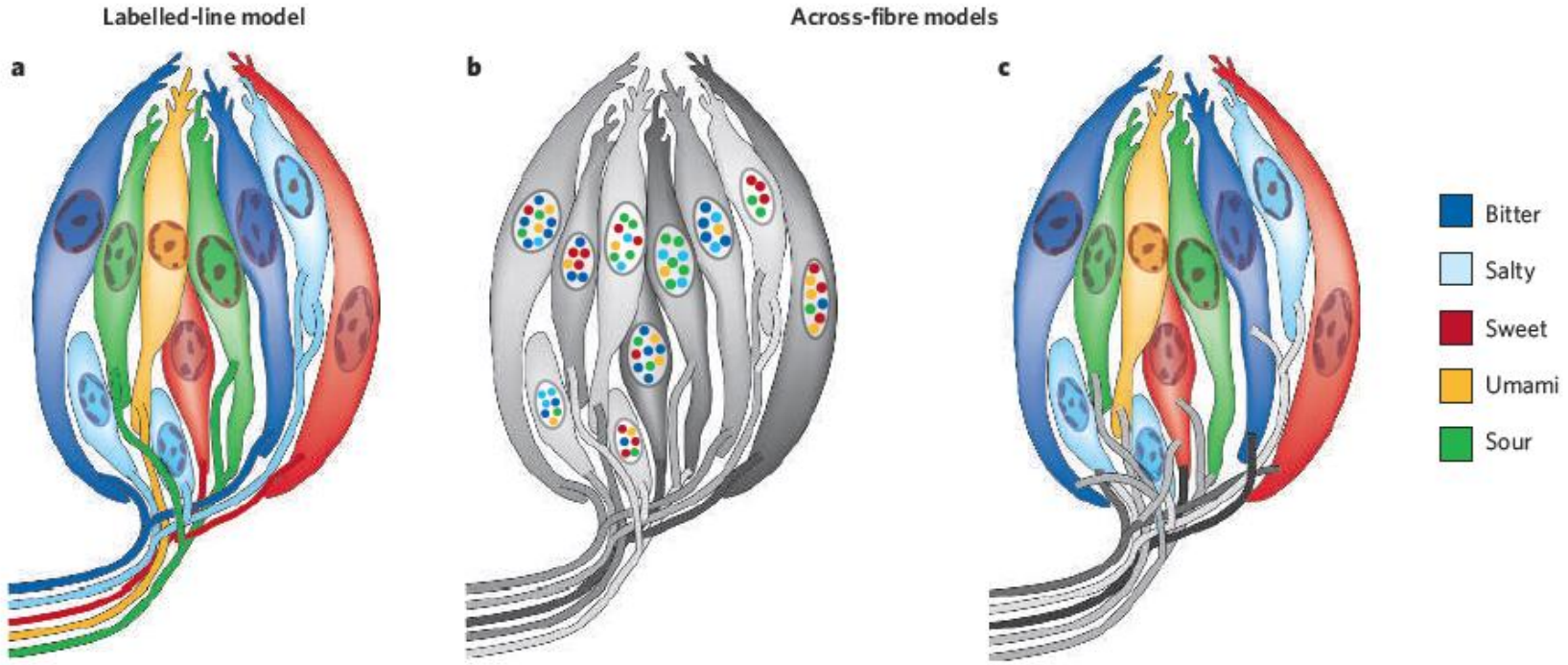


Figure 2 | Encoding of taste qualities at the periphery. There are two opposing views of how taste qualities are encoded in the periphery. **a**, In the labelled-line model, receptor cells are tuned to respond to single taste modalities — sweet, bitter, sour, salty or umami — and are innervated by individually 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.

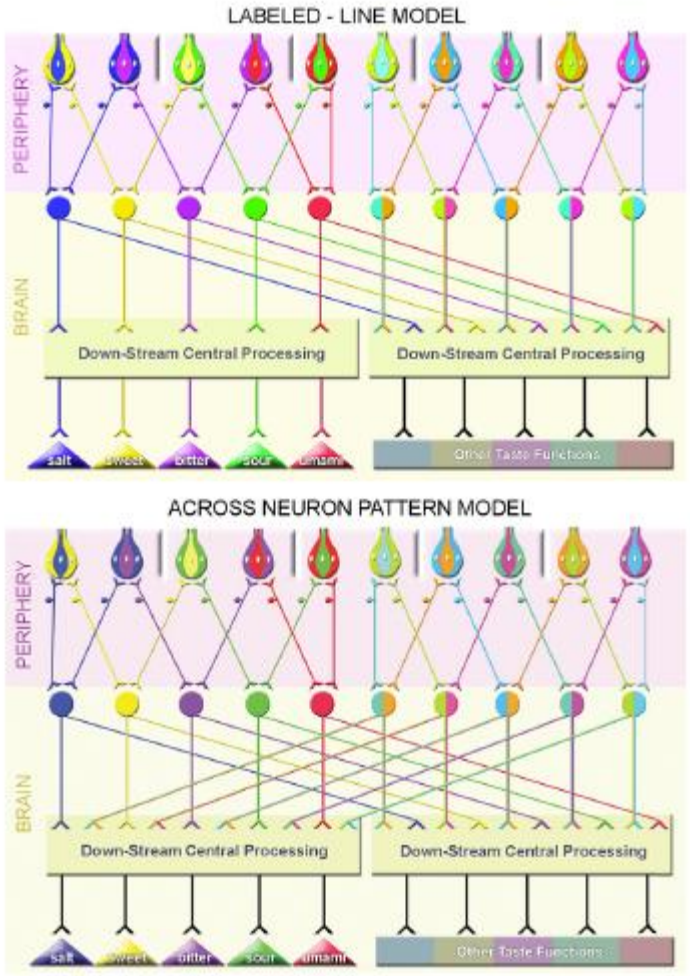


Figure 3. Idealized models of labeled-line versus across-neuron pattern coding of taste quality. The top panel depicts labeled-line coding of quality and the bottom panel depicts across-neuron pattern coding. In the idealized version of labeled-line coding, activity in a dedicated subset of relatively narrowly tuned neurons gives rise to a specific taste quality perception (left side of panel). Activity in these neurons is necessary and sufficient for the specific quality perception to occur. Thus, the elimination of such a neuronal subset should affect the perception of its associated taste quality without affecting the others. Importantly, this model of quality coding does not preclude the existence of broadly tuned taste neurons (right side of panel). In the idealized version of across-neuron pattern of quality coding patterns of activity in large ensembles of both narrowly and broadly tuned neurons lead to the perception of specific taste qualities (left and right side of panel). Different patterns lead to different qualitative perceptions. Various incarnations and subcomponents of these models have appeared in the literature. Whether the specific features of these models hold true for all or any mammalian species is hotly debated.

La valenza affettiva dello stimolo è legata al tipo di linea attivata

Se si attiva la linea che codifica per il dolce si associa l'effetto piacevolezza

Se si attiva la linea che codifica per l'amaro si associa l'effetto disgusto

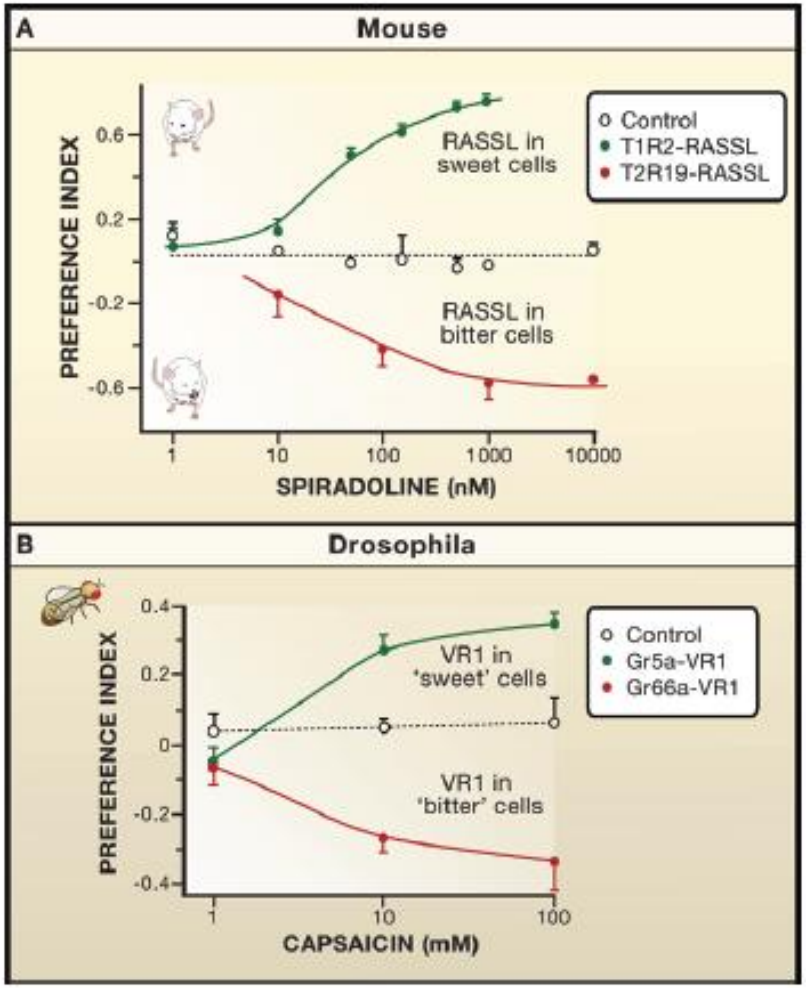


Figure 4. Behavioral Attraction and Aversion Are Hardwired
Mice and flies have converged on a similar organization of taste coding at the periphery. In both cases, dedicated cells tuned to selective taste qualities are hardwired to trigger specific behavioral responses. The synthetic opiate spiradoline is normally tasteless to mice (A, open circles). However, after targeted expression of the spiradoline receptor (RASSL) to sweet cells, mice exhibit dose-dependent attraction to spiradoline (Zhao et al., 2003). In marked contrast, directing expression of the very same RASSL receptor to bitter cells results in strong aversion to the ligand (Mueller et al., 2005). Similarly, activation of selective populations of gustatory receptor neurons in flies (B) mediates robust innate behavioral responses (Marella et al., 2006). Expression of the mammalian ion channel TrpV1 in sugar-sensing GRNs (Gr5a-TrpV1) results in strong behavioral preference for capsaicin. In contrast, expression of TrpV1 in the "bitter-responsive" Gr66a cells makes capsaicin an aversive tastant. Normal flies do not respond to capsaicin (open circles); preference index = (tastant – control)/total.

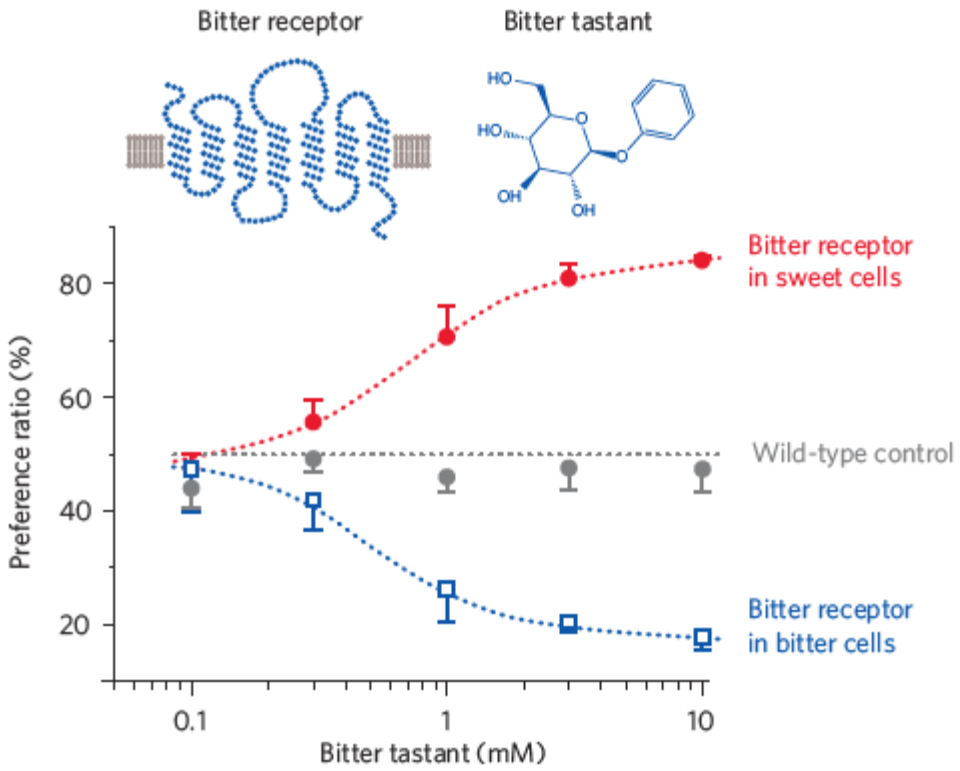
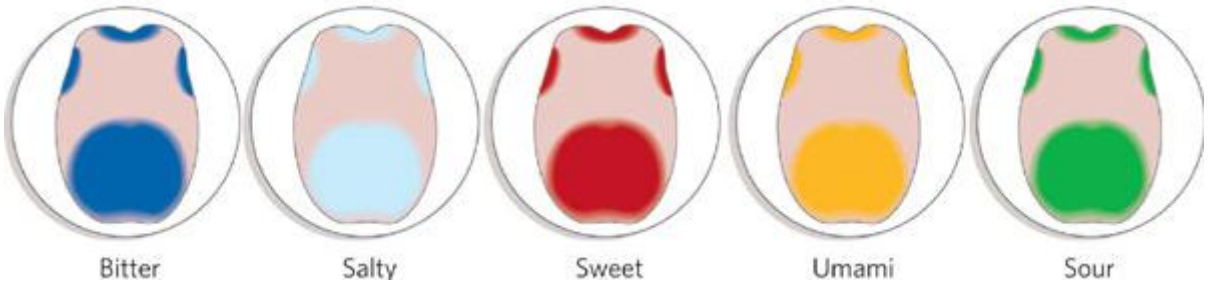


Figure 5 | Behavioural attraction and aversion are mediated by dedicated taste-receptor cells. Targeted expression of a novel bitter receptor to bitter (T2R-expressing) cells results in dose-dependent aversion to the specific bitter tastant (open blue squares). In marked contrast, directing expression of the same receptor to sweet cells produces animals that are strongly attracted to this bitter tastant (filled red circles). Control animals lacking the receptor (filled grey circles) are indifferent to the tastant.

Assenza di segregazione anatomica delle 5 modalità gustative nella cavità orofaringea



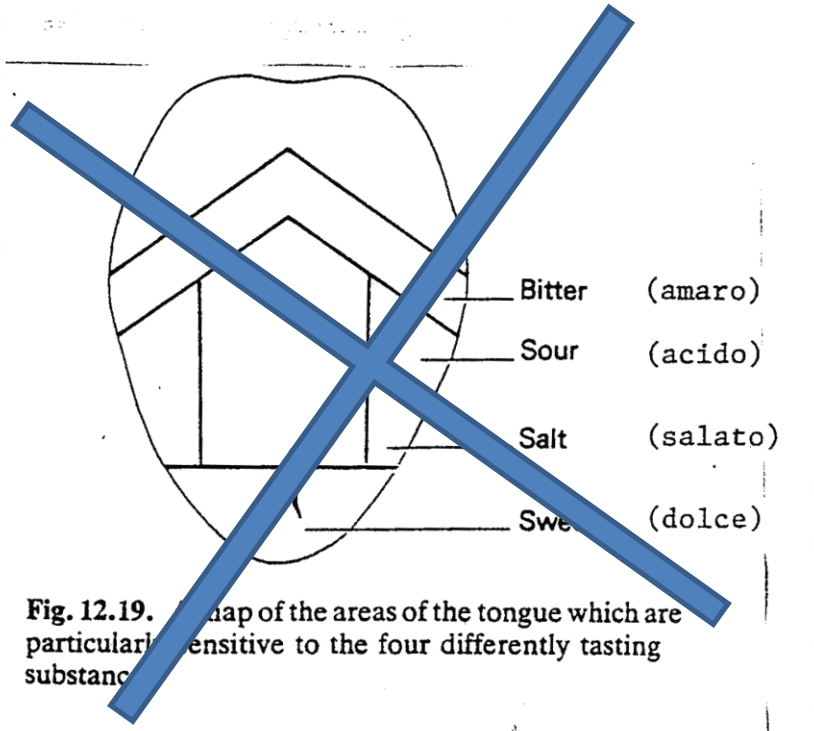
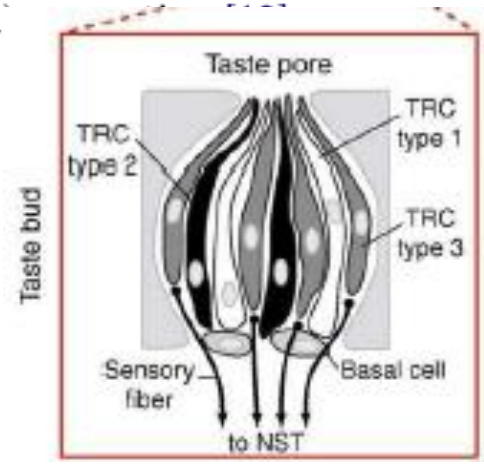


Fig. 12.19. ap of the areas of the tongue which are particularl ensitive to the four differently tasting substanc

TYPE I

of TBs [9,10]. Type I cells were initially believed to be supporting (or 'glial-like') cells because they express enzymes involved in transmitter uptake and degradation. However, recent studies showed that they express an amiloride-sensitive epithelial sodium channel (ENaC) [11,12] that has been demonstrated to be the major sensor for salt (NaCl

Salato



TYPE II

Dolce (T1R2, T1R3) Amaro (T2Rs) Umami (T1R1

There is, however, general agreement regarding the roles of type II TRCs. These cells contain G-protein-coupled receptors (GPCRs) that selectively respond (at concentrations that can be considered close to physiological) to sweet tastants (T1R2, T1R3), bitter tastants (T2Rs) and amino acids/umami (T1R1–T1R3), because deletion of the receptors (or of the type II cells that contain them) selectively prevents both whole-nerve cell responses and behavioral responses – ingestion for sweet tastants and rejection for bitter tastants (Figure 2a) [14]. Crucial signaling molecules that have been identified as being downstream from these GPCRs include a phospholipase (PLC-β2) and a transient receptor potential (TRP) channel (TRPM5) that is activated by IP3-induced increases in intracellular calcium [14,15].

TYPE III

Acido

For responses to acid it was found that type III TRCs contain a TRP channel termed PKD2L1. Deletion of these PKD2L1-expressing cells selectively eliminates whole-nerve responses to acid (Figure 2a) [16]. In addition, taste cells containing PKD2L1 also express CAR4 [17], an extracellular glycosylphosphatidylinositol (GPI)-anchored carbonic anhydrase, along with intracellular forms of carbonic anhydrase [17,18]. Both forms play essential roles in modulating the conversion of CO_2 to bicarbonate (HCO_3^-) and hydrogen that, in principle, could produce a perception of sour taste (note: CO_2 is also a trigeminal nerve stimulant, giving rise to painful and tingling sensations [19]). As

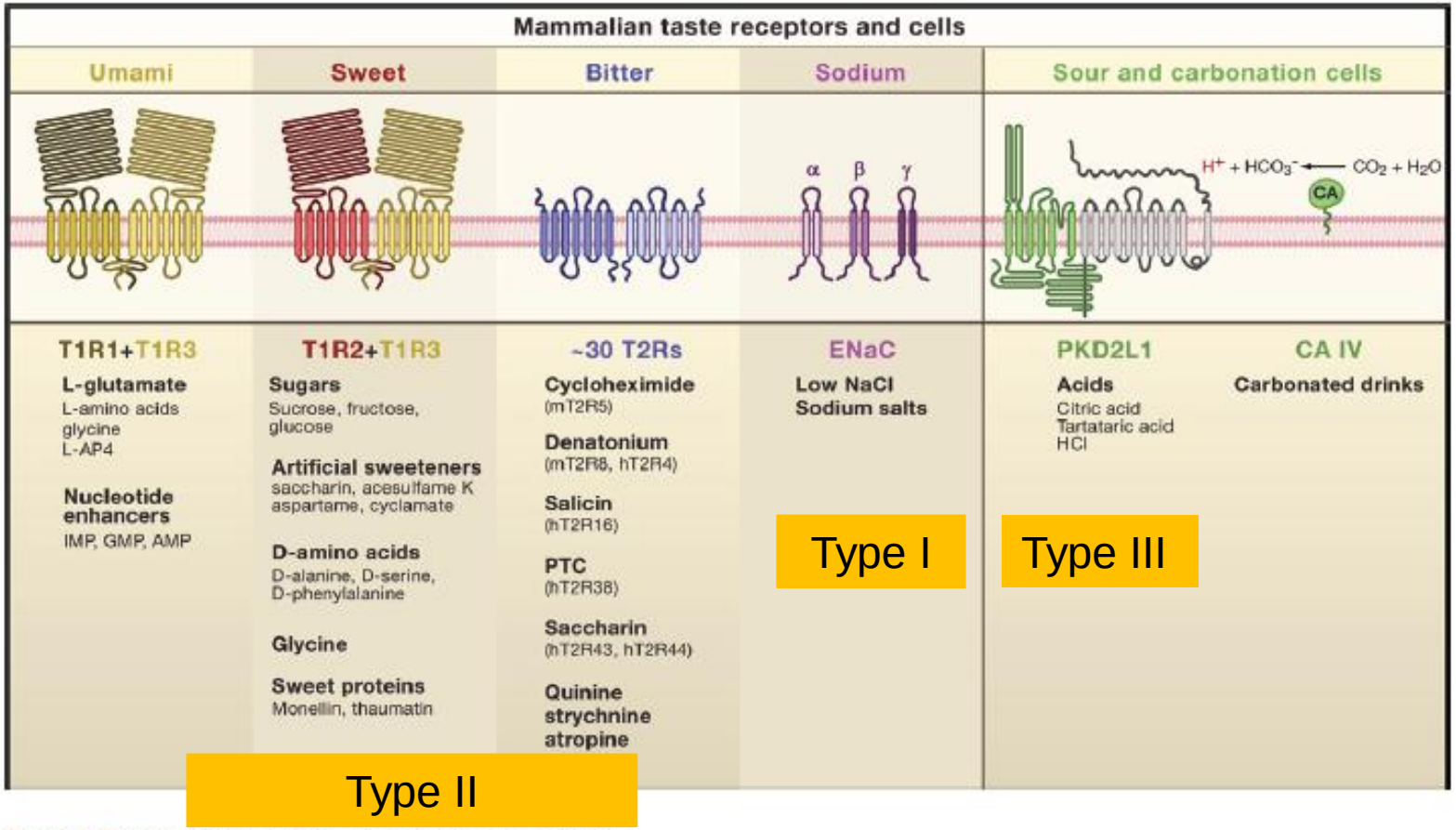


Figure 2. Mammalian Taste Receptors, Cells, and Ligands

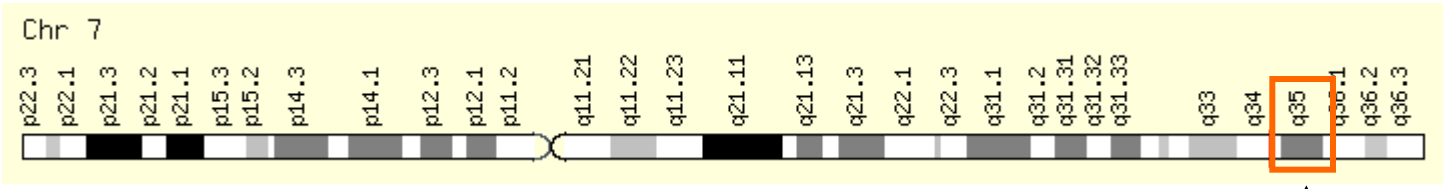
Detection of the gustatory world is mediated by several distinct classes of taste receptors and taste receptor cells. Sweet and umami compounds are sensed by T1R heterodimers (Nelson et al., 2001, 2002; Li et al., 2002), while bitter compounds activate T2R receptors (Chandrashekar et al., 2000; Mueller et al., 2005; Meyerhof et al., 2005). Salt is detected via several mechanisms, one of which is thought to rely on the sodium channel ENaC (Heck et al., 1984). Sour-sensing cells are defined by the expression of PKD2L1 (Huang et al., 2006), whereas gustatory responses to carbonation are mediated by the membrane-tethered carbonic anhydrase CA IV (Chandrashekar et al., 2009).

Table 1 | Tastant selectivity of candidate mammalian taste receptors

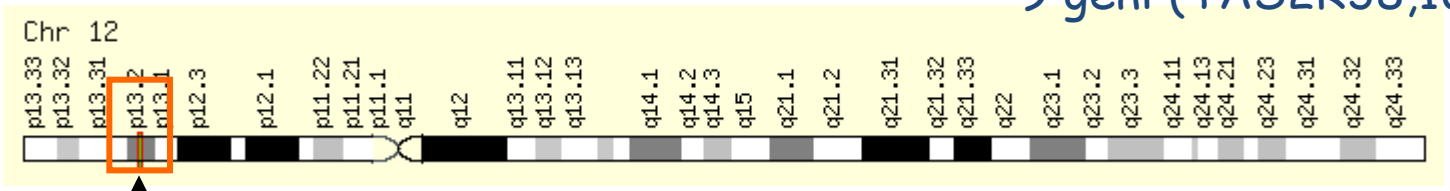
Tastant quality	Receptor(s)	Class of tastant	Examples of tastants
Umami	T1R1+T1R3	Amino acids	L-Glutamate, L-AP4, glycine*, L-amino acids*
		Nucleotide enhancers	IMP, GMP, AMP
Sweet	T1R2+T1R3	Sugars†	Sucrose, fructose, glucose, maltose
		Artificial sweeteners	Saccharin, acesulfame-K, cyclamate‡, aspartame‡
		D-amino acids	D-Phenylalanine, D-alanine, D-serine (also some selective L-amino acids)
		Sweet proteins‡	Monellin, thaumatin, curculin
Bitter§	T2R5¶		Cycloheximide
	T2R8¶, T2R4, T2R44		Denatonium
	T2R16		Salicin‡
	T2R38		PTC‡
	T2R43, T2R44		Saccharin
	Not known	Other toxic/noxious compounds	Quinine, strychnine, atropine
Sour	PKD2L1	Acids	Citric acid, tartaric acid, acetic acid, hydrochloric acid

*Preferentially activates mouse but not human receptors.
†High concentrations of sugars, but not other sweet tastants, can also be detected by T1R3 alone[15].
‡Activates human but not mouse receptors and does not elicit behavioural responses in wild-type mice.
§About 30 T2Rs are involved in bitter-tastant recognition.
¶Mouse T2Rs; all others shown are human. There are 25 human and 35 mouse T2R bitter-taste receptors. For illustrative purposes we have included receptor–ligand matches for a number of de-orphaned T2Rs (for example, mouse T2R5 is the receptor for the protein synthesis inhibitor toxin cycloheximide).

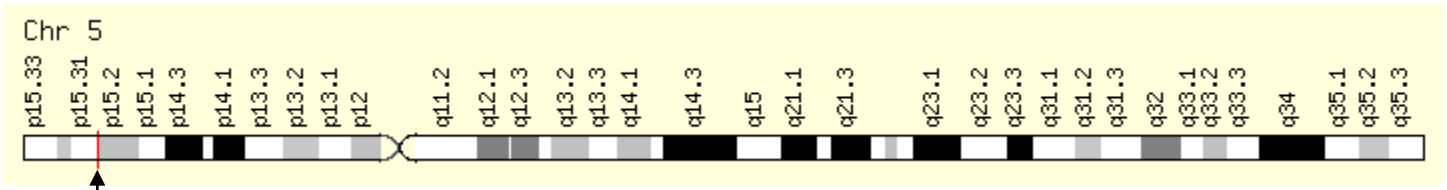
T2RS: 25 geni umani che mappano in cluster su 3 cromosomi



9 geni (TAS2R38,16,3,4,5)



18 geni (TAS2R19,43,44)



TAS2R1

12 TAS2R espressi a livelli elevati nel 10% delle cellule recettoriali
6 espressi a livelli moderati nel <5%
7 espressi solo nell' 1%

GENE	POLIMORFISMO	PROTEINA	LIGANDO	VARIANZA
TAS2R19	rs10772420 A>G	Cys299Arg	Chinino	5,9%
TAS2R38	rs713598 G>C rs1726866 A>G Rs10246939 C>T	Ala49Pro Val262Ala Ile296Val	Feniltiocarbamide e Propiltiuracile	65-80%
TAS2 R43 **TAS2 R44**	no dbSNP no dbSNP	W35S W35R	Saccarina	34%
TAS2 R3	rs765007 C>T	5'UTR	Caffeina	16%
TAS2R4	rs2234001 C>G	Val96Leu	Caffeina	
TAS2 R5	rs2234012 G>A	5'UTR	Caffeina	
TAS2 R5	rs2227264 T>G	Ser26Ile	Caffeina	
TAS2 R16	rs846664 G>T	Lys172Asp	Salicina	10%

Meccanismi di trasduzione recettoriale

Trasduzione amaro, dolce, umani

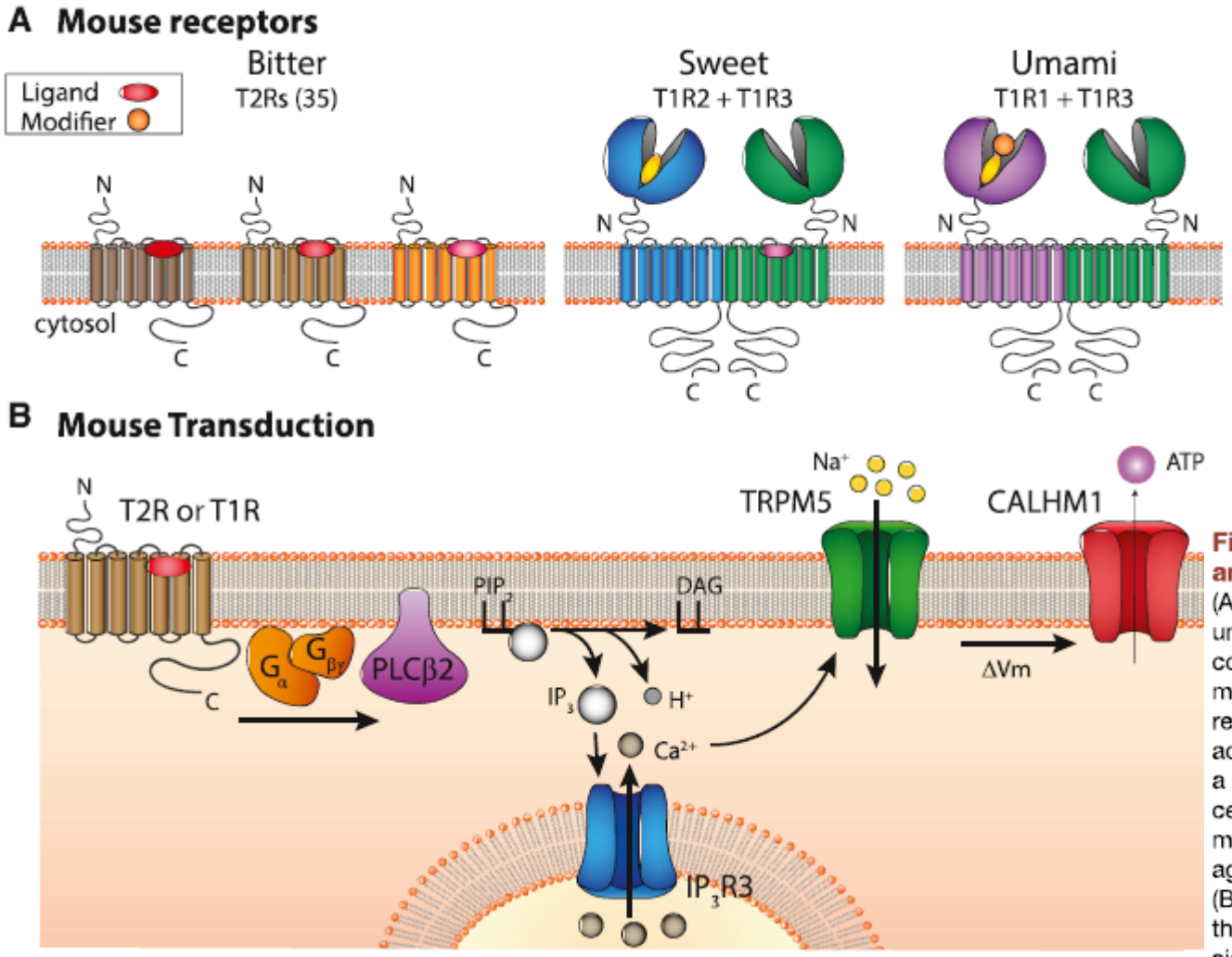


Figure 2. Mouse and Fly Taste Receptors and Transduction in the Mouse

(A) Transmembrane topology of bitter, sweet, and umami receptors in the mouse. All are G protein–coupled receptors. Bitter receptors (35 total in mice) are Class A GPCRs, while sweet and umami receptors (two each) are Class C receptors, characterized by a large N-terminal domain that forms a Venus flytrap structure. Sweet and umami receptors bind both ligands (ovals) and allosteric modifiers (circles) that can increase potency of the agonist.

(B) Transduction of bitter, sweet, and umami in the vertebrate is mediated by a canonical PLC-signaling cascade, which culminates in the opening of the TRPM5 ion channel. This produces a depolarization that may allow CALMH1 channels to open and release ATP, which serves as a neurotransmitter.

Trasduzione acido

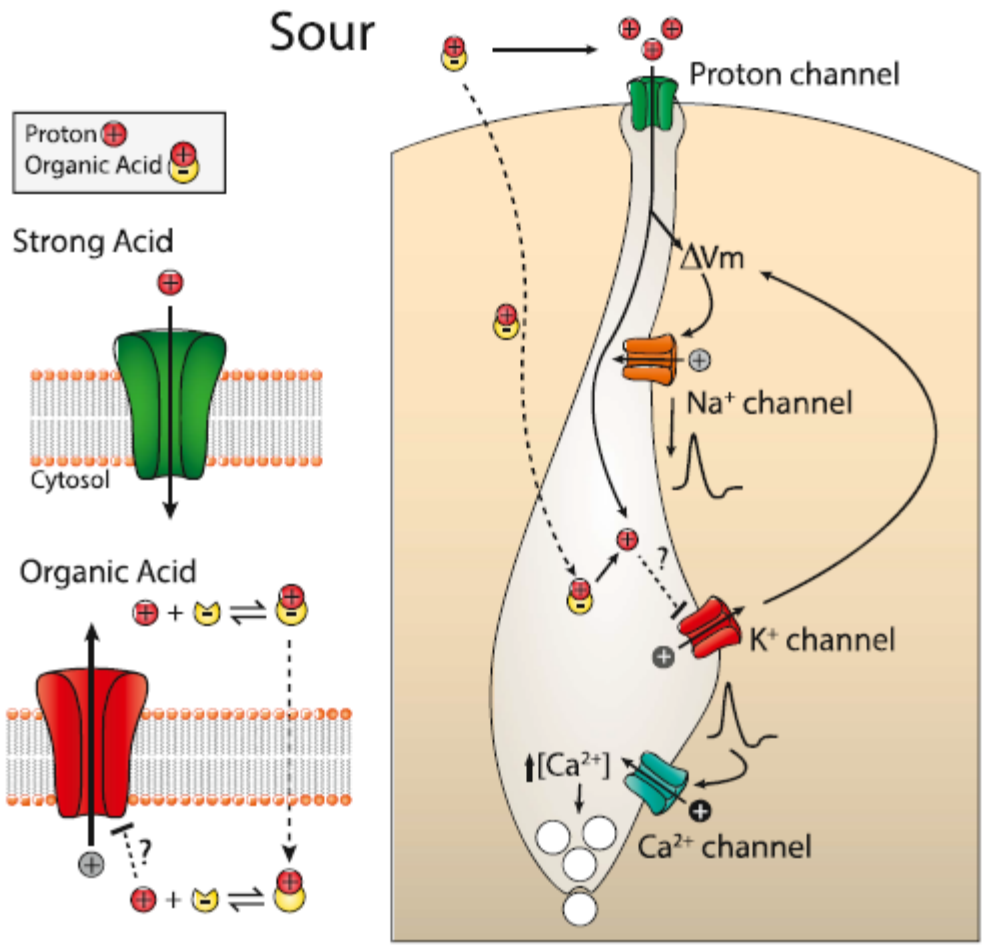
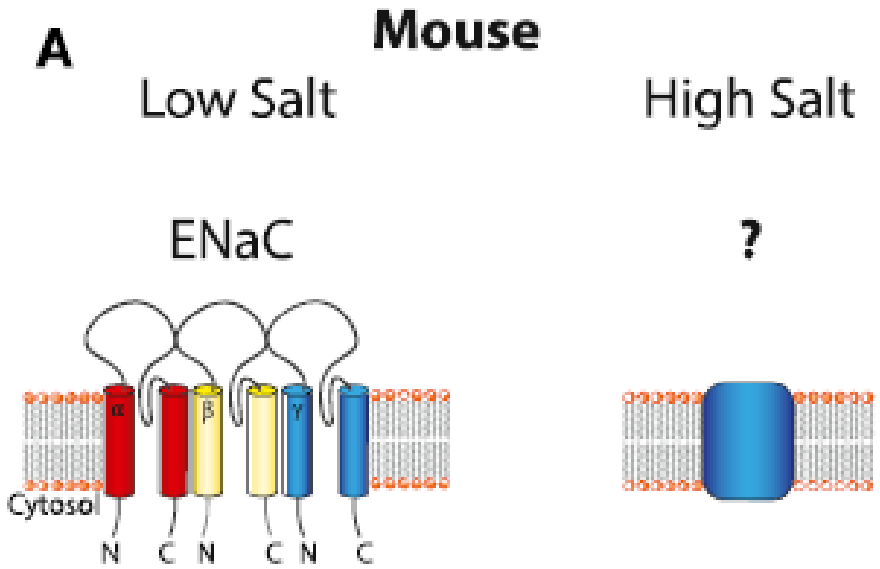


Figure 3. Sour Taste
Sour taste in vertebrates is initiated when protons enter through an apically located proton-selective ion channel. Weak acids may also activate sour cells by penetrating the cell membrane and acidifying the cytosol, leading to closure of resting K^+ channels and membrane depolarization.

Trasduzione salato

Salt Taste Receptors

The taste of salt is complex from two perspectives. First, while we frequently think of salt taste as the sensation of Na^+, other cations such as Li^+ or K^+ may also be perceived as salty, although less potently than Na^+. Second, salt can be attractive or aversive depending on concentration, with lower concentrations (<100 mM) being attractive. This dichotomy reflects the fact that moderate levels of salt are necessary to maintain muscle contraction, action potentials, and many other functions, while excessive salt intake is deleterious and in humans can lead to hypertension.



Noncanonical Taste Qualities in Mammals

Grassi

they qualify as bona fide tastes is still an open question. Fats are detected by several routes, including olfaction and somatosensation, and they elicit postingestive effects that promote consumption. But are they tasted? Several lines of evidence argue that the answer is yes. The observation that mice prefer water spiked with free fatty acids, which are breakdown product of triacylglycerides that are found in vegetable and animal-derived products, supports a role for the taste system in detecting this rich source of calories (Gaillard et al., 2008). Taste cells express putative receptors for fat taste including K^+ channels that are sensitive to polyunsaturated fatty acids, a fatty acid transporter (CD36), and two fat-sensitive GPCRs, GPR40 and GPR120 (Liu et al., 2011). The most promising of these candidate receptors is GPR120, which is required for preference to fatty acids in mice (Cartoni et al., 2010) and is expressed in human TRCs

Calcio

Another noncanonical sensory attribute encoded by taste cells is referred to as "calcium taste." Ca^{2+}, an ion required for a vast array of cellular functions, is attractive to Ca^{2+}–deprived animals, but is rejected by Ca^{2+}-sated animals. Paradoxically, the aver-

Acqua

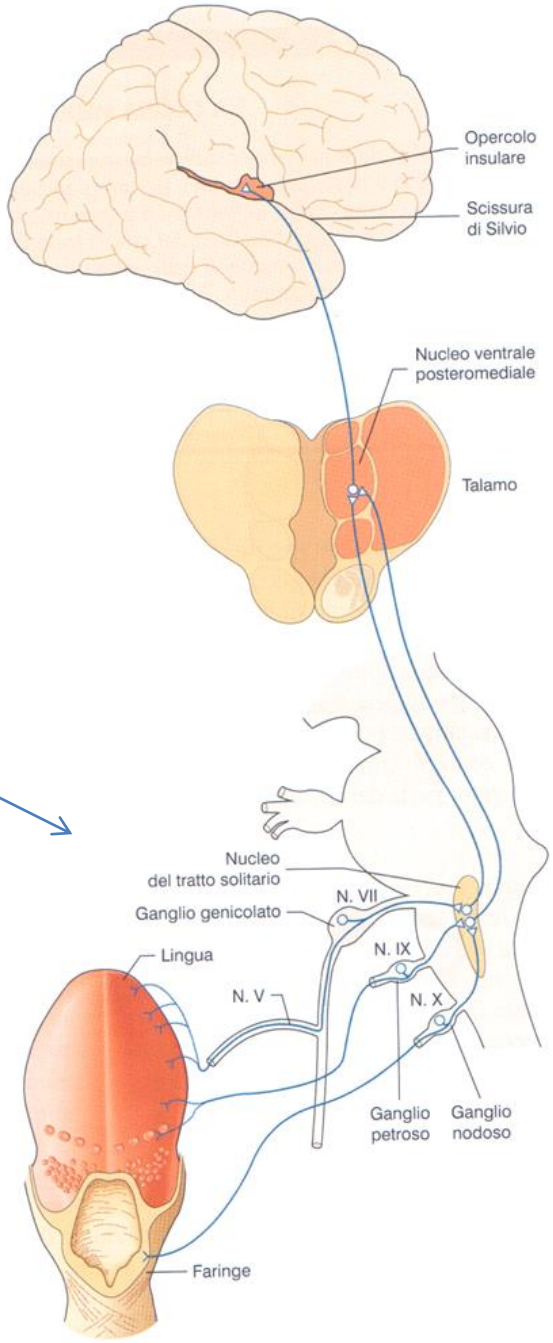
Last among these noncanonical tastes is the taste of water. Animals can detect wetness across their body by virtue of the somatosensory system, and this system is also likely to contribute to the sensing of aqueous solutions in the oral cavity.

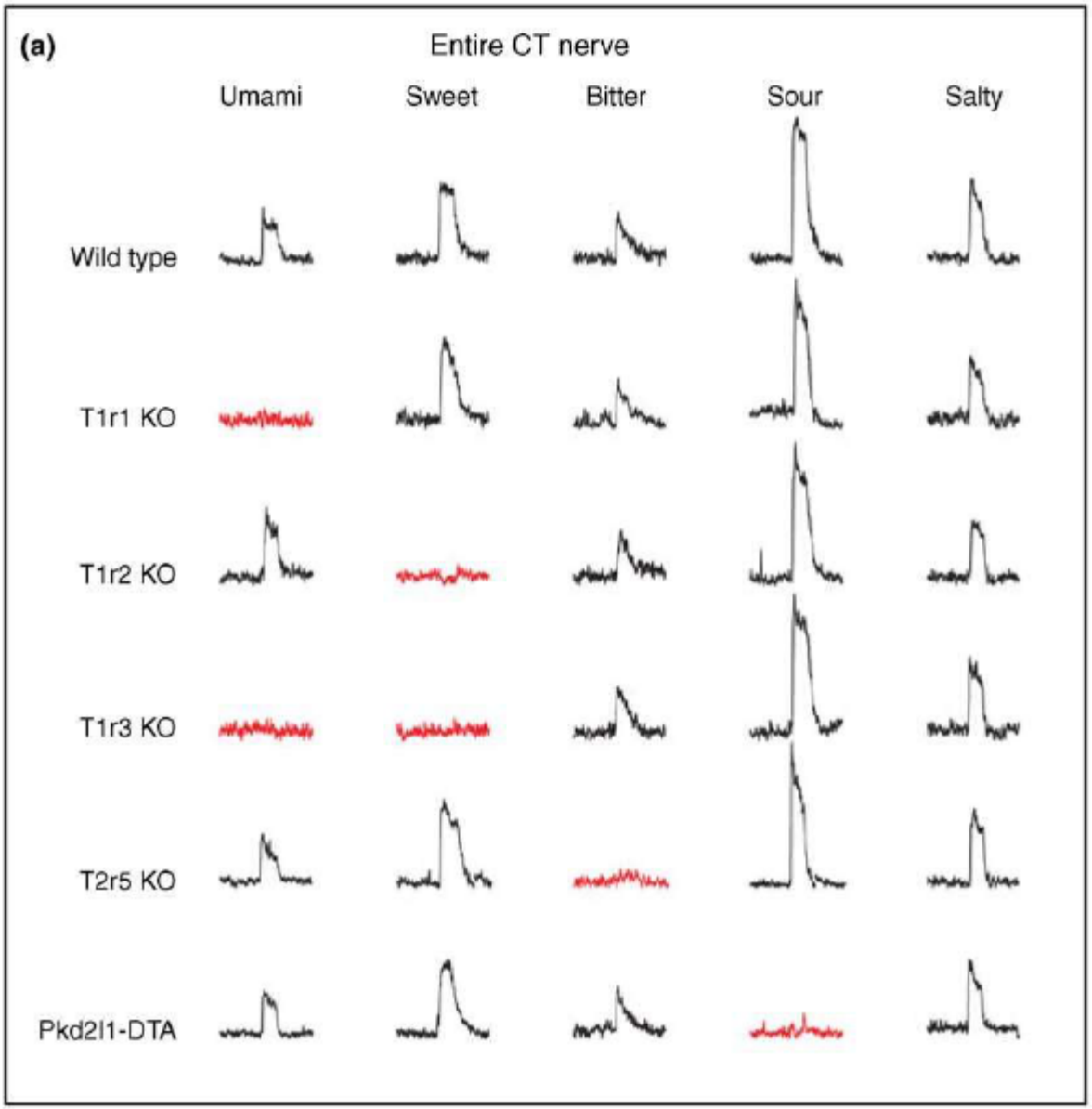
Vie afferenti Periferiche

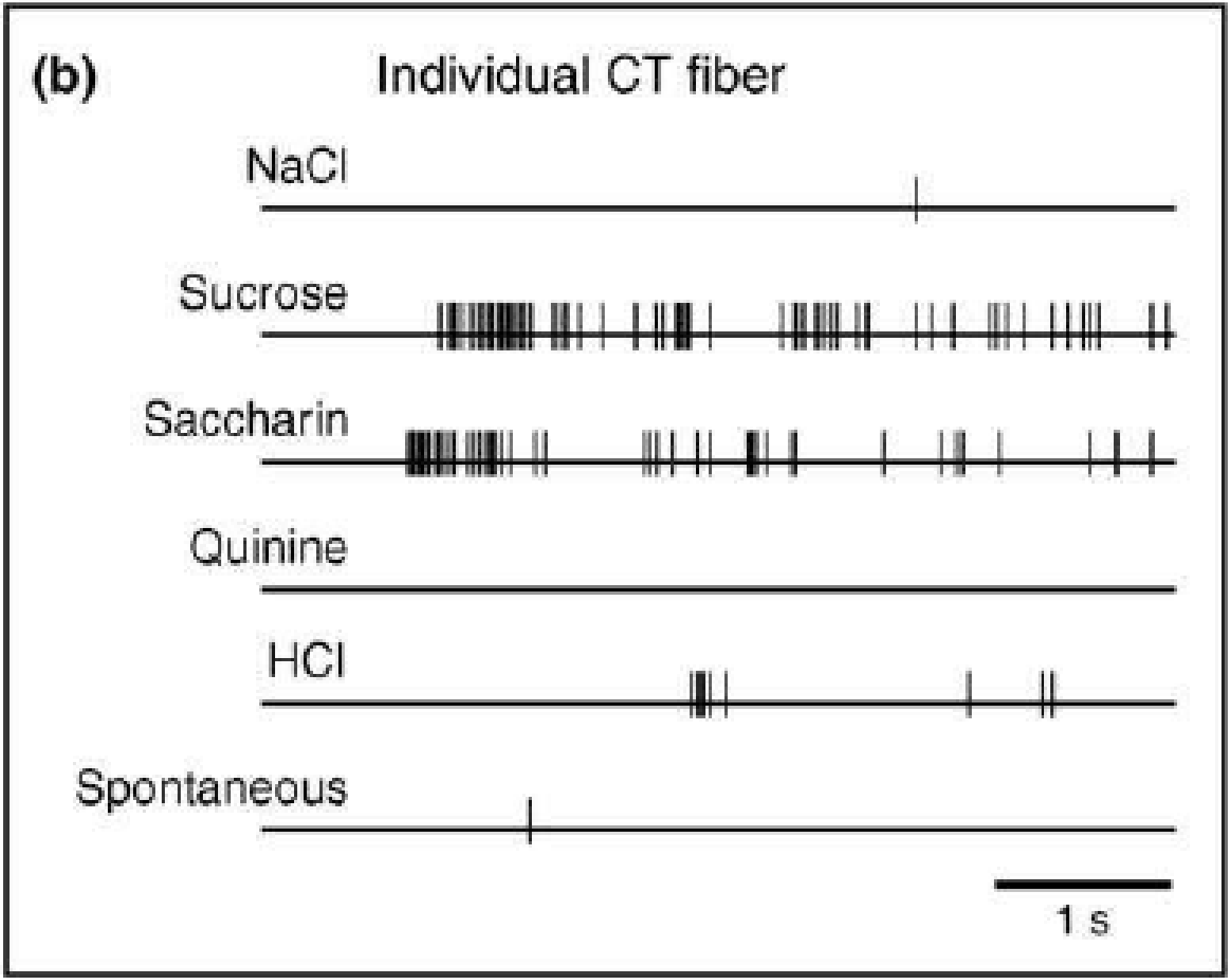
V n.c. n.trigemino

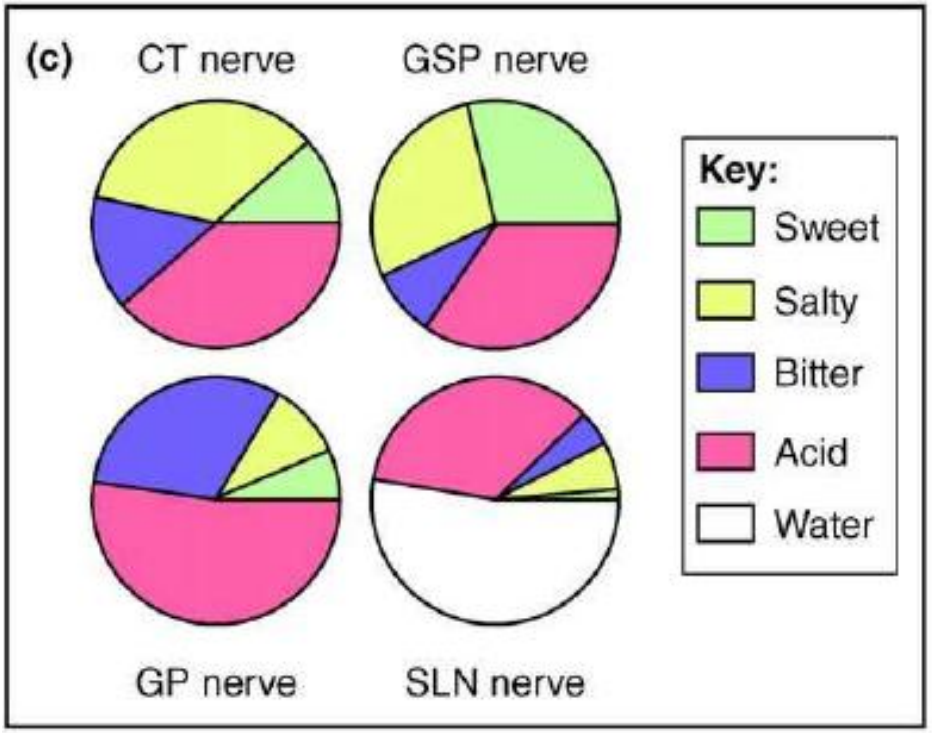
IX n.c. n.glosso faringeo

X n.c. n. vago




(a)
Entire CT nerve
Umami
Sweet
Bitter
Sour
Salty
Wild type
T1r1 KO
T1r2 KO
T1r3 KO
T2r5 KO
Pkd2l1-DTA


(b)
Individual CT fiber
NaCl
Sucrose
Saccharin
Quinine
HCl
Spontaneous
1 s



CT : **corda tympani origina dal VII, c.c. nel ganglio genicolato e si congiunge al n. linguale (ramo del mandibolare del V paio)**

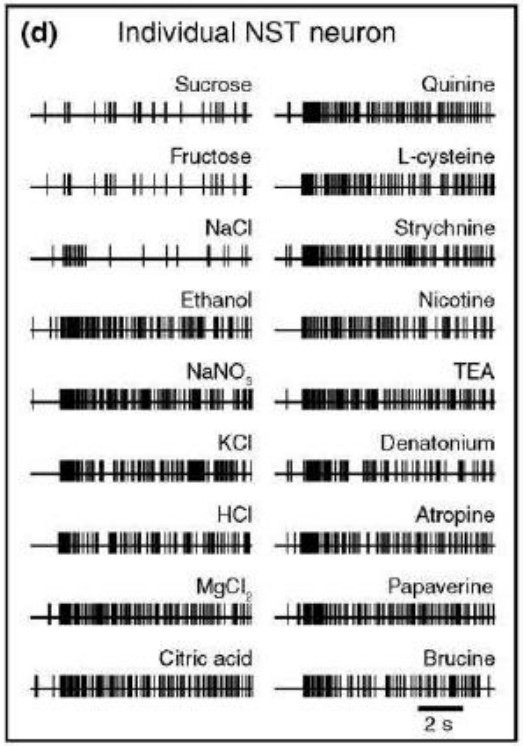
GSP: **greater (superficial) petrosal nerve (VII paio, c.c. nel G genicolato)**

GP: **nervo grande palatino (ramo del mascellare, V paio)**

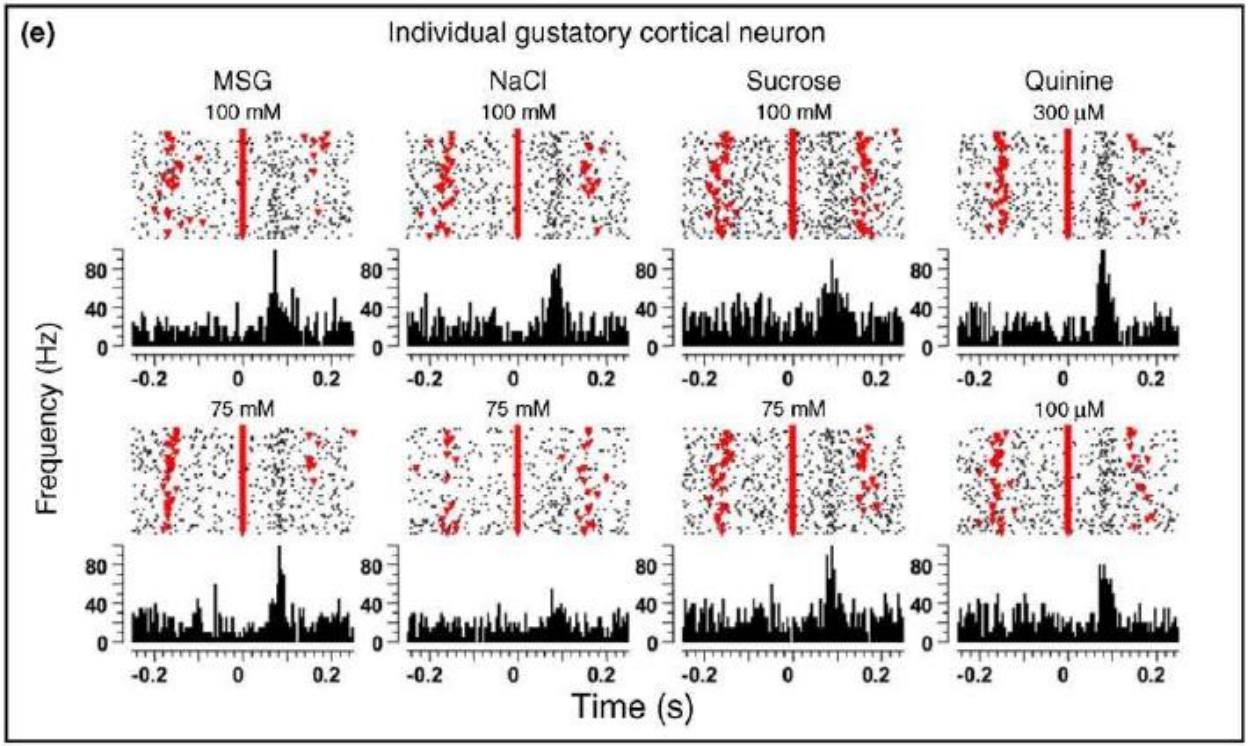
SLN: **nervo laringeo superiore (ramo del vago , c.c nel ganglio inf del vago)**

Le stazioni centrali

Nucleo Tratto Solitario



Neuroni corticali



TRENDS in Neurosciences

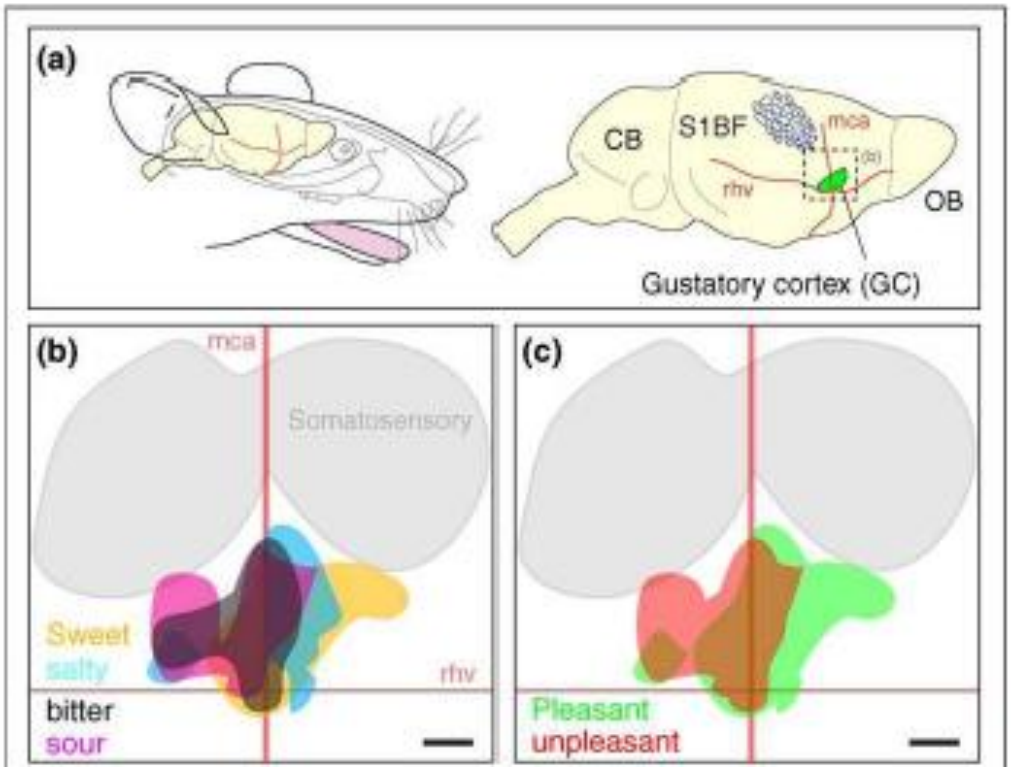


Figure 3. Topographical representations in the rat gustatory cortex. **(a)** Approximate size and location of the GC with respect to anatomical landmarks (blood vessels: middle cerebral artery, mca; rhv, rhinal veins) and other sensory areas of the brain (olfactory bulb, OB; primary somatosensory cortex barrel field, S1BF). **(b)** Schematic representation of the cortical territories activated following stimulation with four stimuli representing four different taste modalities (sweet, salty, bitter, sour). The orientation is the same as in (a). **(c)** Pleasant (sweet, salty) and unpleasant (bitter, sour) regions appear to be spatially distinguishable. Responses to pleasant stimuli seem to be represented more rostrally than responses to unpleasant stimuli. **(d)** Relationship between behavioral state and cortical state in the gustatory cortex. In a naïve (i.e. control) rat, cortical representations of the hedonically positive (saccharin; orange) and negative (quinine; grey) tastants are quite different, although commonly-activated cortical territories exist. After conditioned taste aversion (CTA) training, in which the malaise-inducing agent lithium chloride (LiCl) is paired with the ingestion of saccharin, the normally positive stimulus of the latter becomes aversive and the pattern changes accordingly to become more similar (highly correlative) to the quinine response. After saccharin aversion extinction (Glossary) the hedonic value of saccharin reverts to a positive response, and its cortical map is again less similar (low correlation) to the quinine pattern. Note that the new representation of saccharin after extinction might not be a simple return to the same one that existed prior to conditioning.

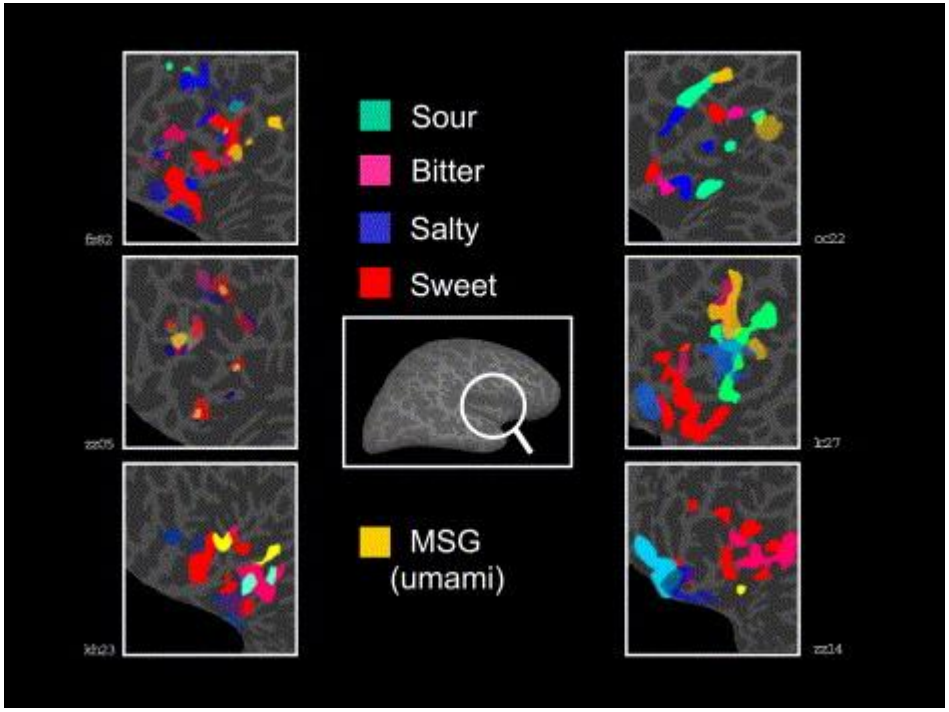
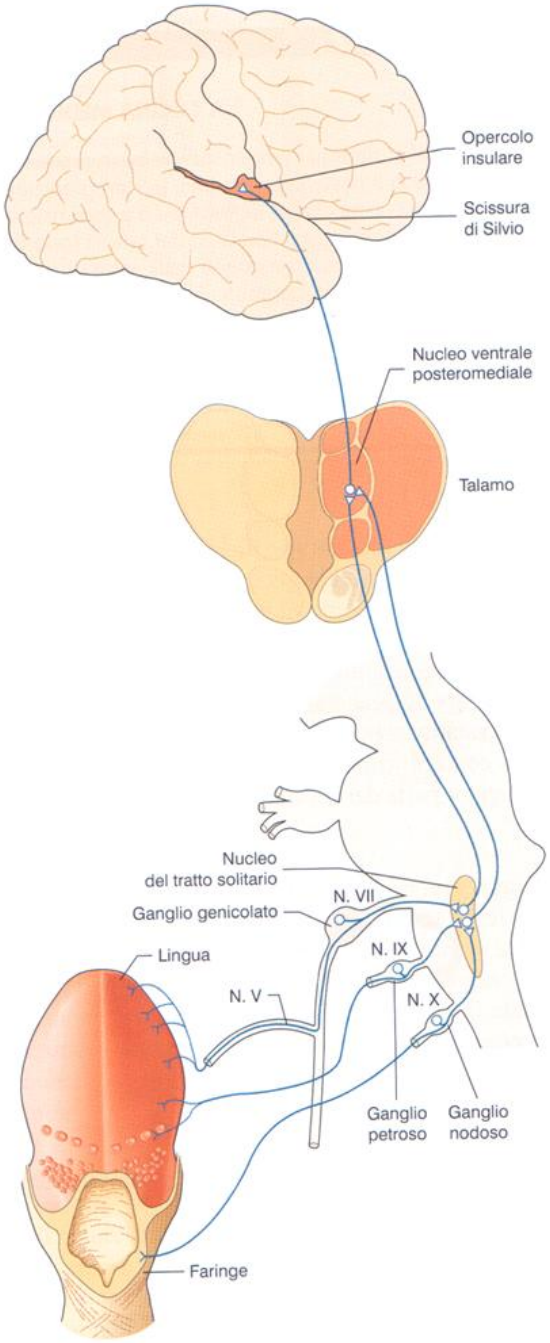


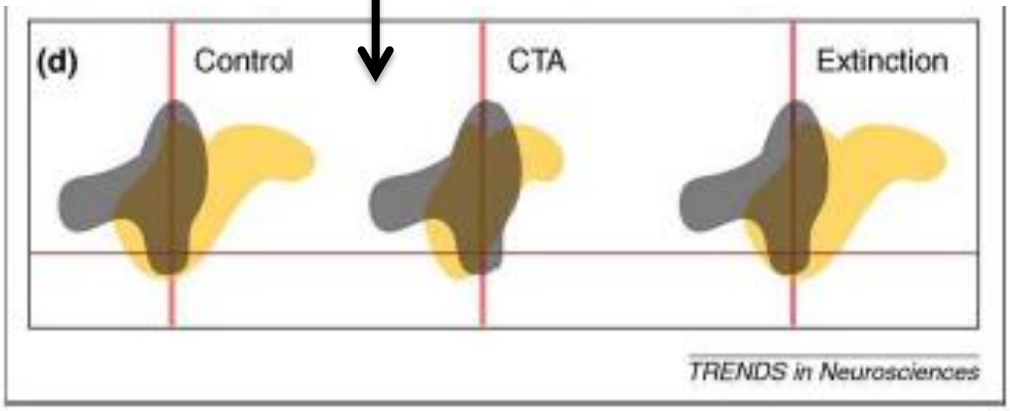
Fig. 1. The figure shows the individual activity maps for all investigated taste stimuli on the flattened cortical surfaces of the insular/opercular cortex of the right hemisphere of **six subjects**. In the center of the figure the picture shows the location of the patches on an unfolded brain. Note the high inter-individual variability of the activations.



Plasticità delle mappe corticali dopo apprendimento
Rilevanza dell'aspetto affettivo

Mappa corticale di attivazione da stimoli gustativi

Dopo condizionamento avversivo
[Saccarina (CS) + avvelenamento con litio LiCl (US)]



Arancio: saccarina

Grigio: chinino

Sviluppo del gusto

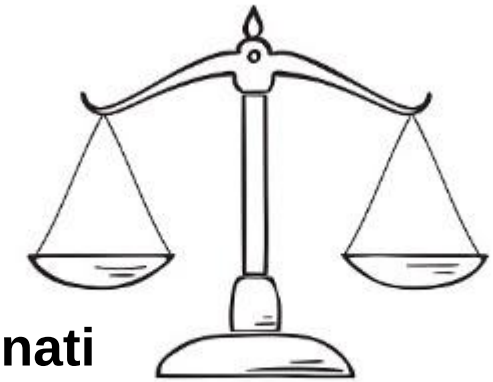
Quanto è ereditario del gusto ?

Ereditarietà : Il gusto tra gemelli

- Cibo proteico = 78%
- Frutta = 51%
- Vegetali = 37%
- Dolciumi = 37%

La valenza affettiva associata alle emozioni evocate da stimolazioni gustative

dipende



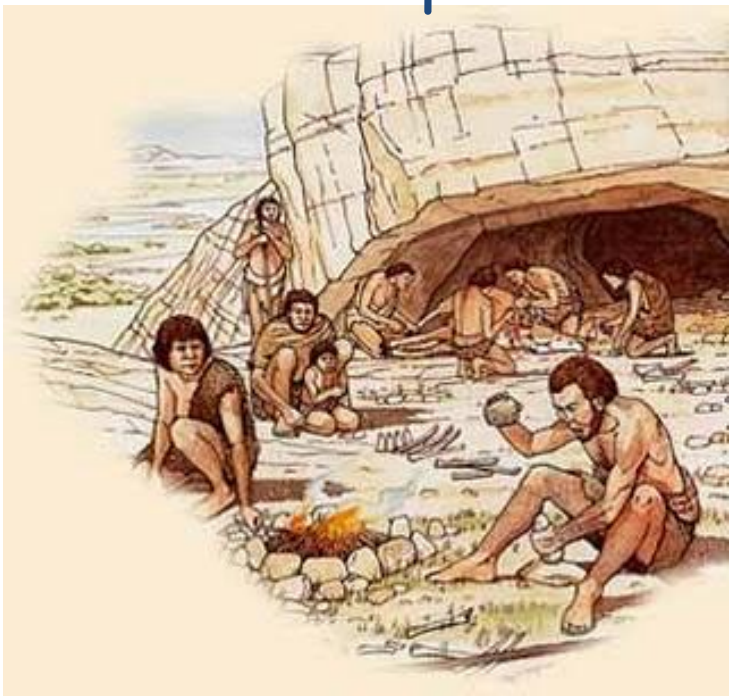
Meccanismi innati **Meccanismi appresi**

Alcune emozioni piacevoli/spiacevoli sono in maniera innata associate a particolari sapori ed hanno contribuito alla sopravvivenza della specie

Cibi dolci, salati e ad alta densità energetica

⇩

Piacere



Avversione

⇩

amaro e acido (veleni,tossine)

…fenoli, alcaloidi, glicosidi,terpeni,steroidi, peptidi, aminoacidi, amidi,amine,acidi grassi,composti eterociclici, tiouree, carbamidi, esteri, lattoni, composti carbonilici……

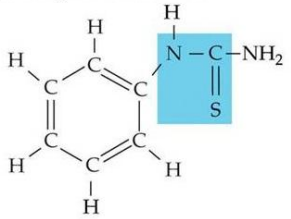
Il 10% delle specie vegetali sintetizza metaboliti secondari tossici

Esistono fattori genetici individuali condizionano la sensibilità ai sapori ed alle emozioni da essi evocate

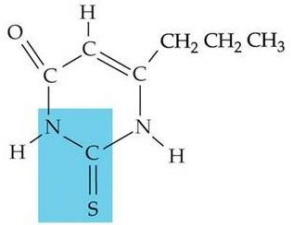
La variabilità tra individui (polimorfismo) è stata messa in relazione con una serie di **polimorfismi genetici** (SNPs) , tra i quali la **sensibilità all'amaro** per certe sostanze quali la feniltiocarbamide (PTC) e il 6-n-propiltiouracile (PROP) ed è dovuta alla presenza e funzionalità di un particolare **recettore dell'amaro**, il TAS2R38 (Duffy et Al., Physiology & Behavior, 2004, 82, 435–445).

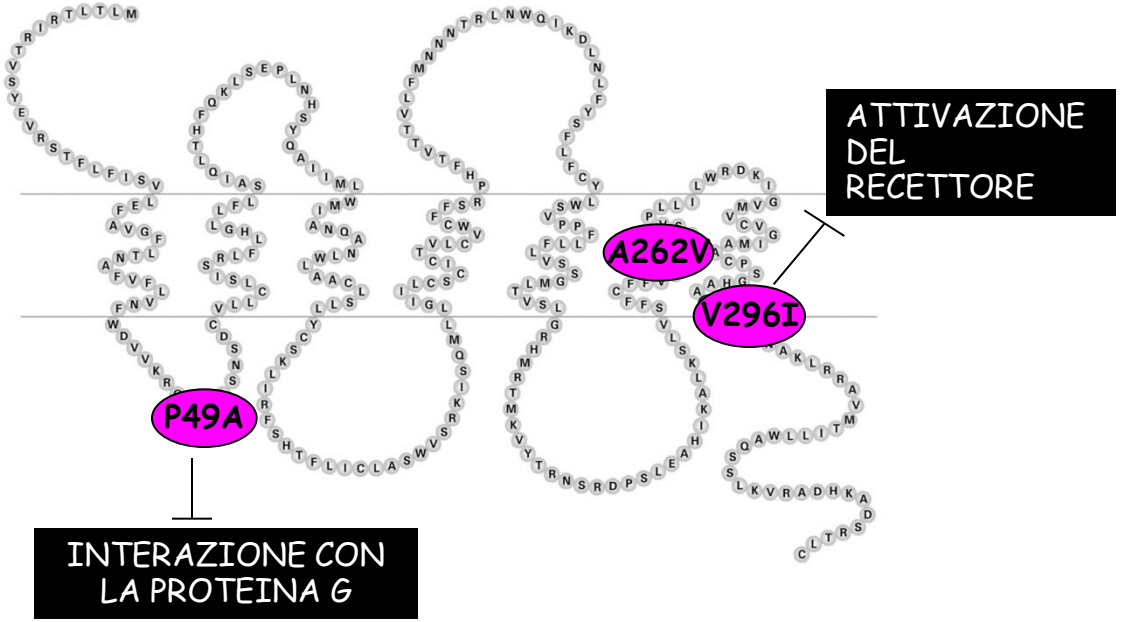
Il recettore dell'amaro TAS2R38 esibisce polimorfismi genetici che distinguono **Percettori**, da non **Percettori** e da **Super-percettori**

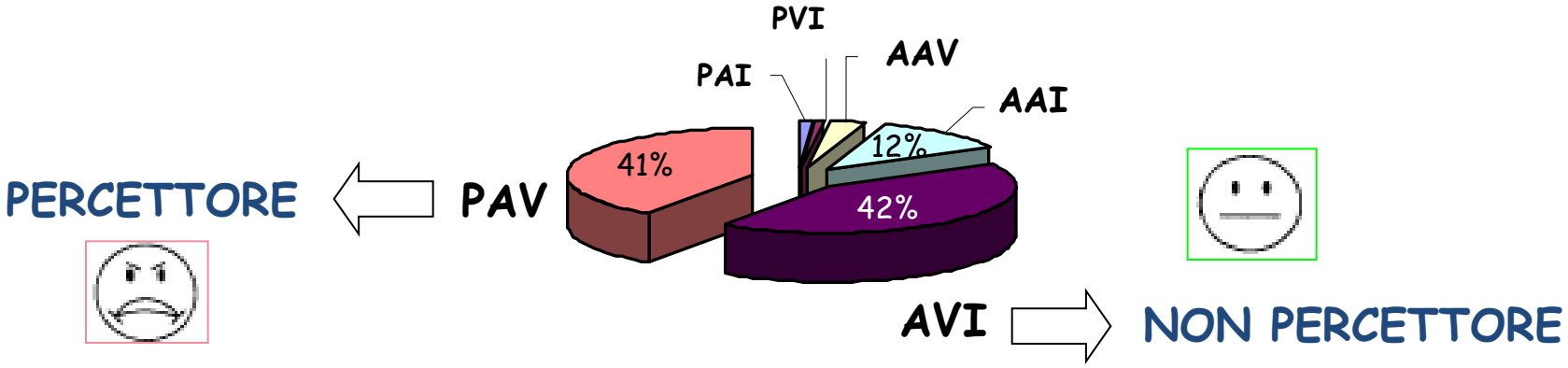
(*a*) Phenylthiolcarbamide



(*b*) Propylthiouracil







Il gusto Amaro del Propiltiouracile

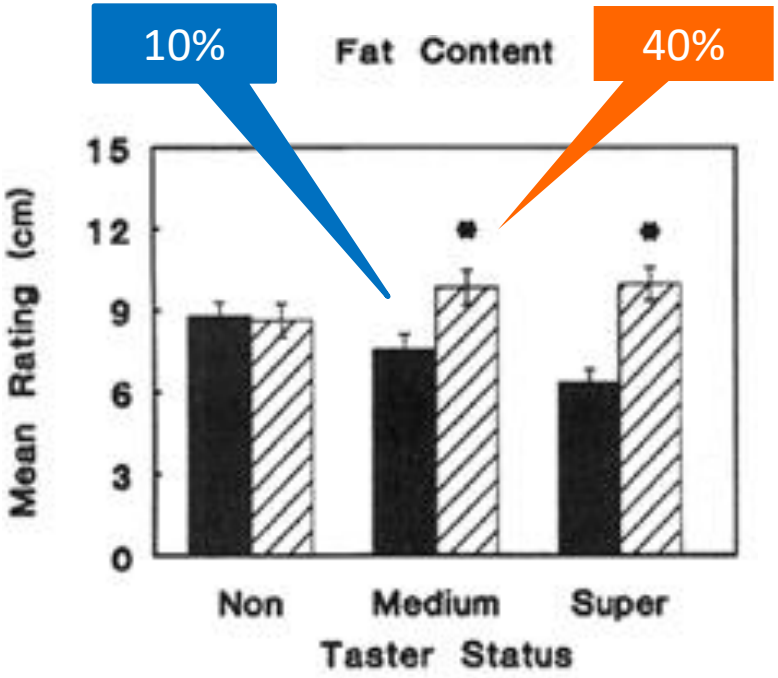
- Poco sensibili all'amaro = 30%
- Sensibili all'amaro = 60%
- Iper sensibili all'amaro = 10%

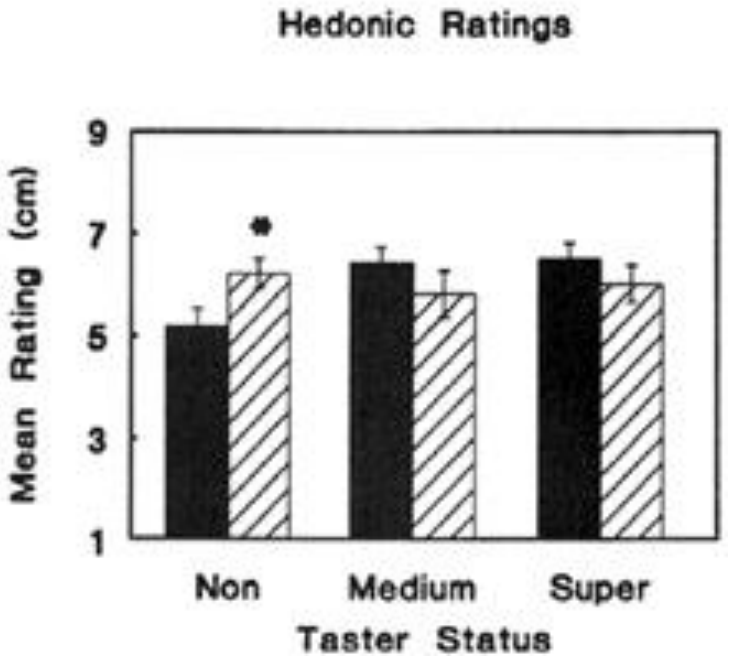
Il differente gradimento di alcuni alimenti è associato alla sensibilità al PROP

Non Percettore

Super Percettore

I percettori hanno maggiore sensibilità per i grassi



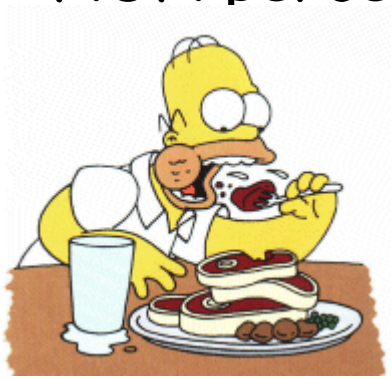


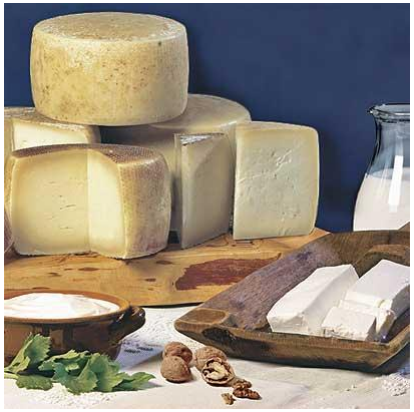
e li gradiscono di meno!

Tepper BJ et al. Ann N Y Acad Sci. (1998)

I superpercettori sono più sensibili al grasso, al piccante e al dolce e le scelte alimentari ne sono influenzate

NON percettori

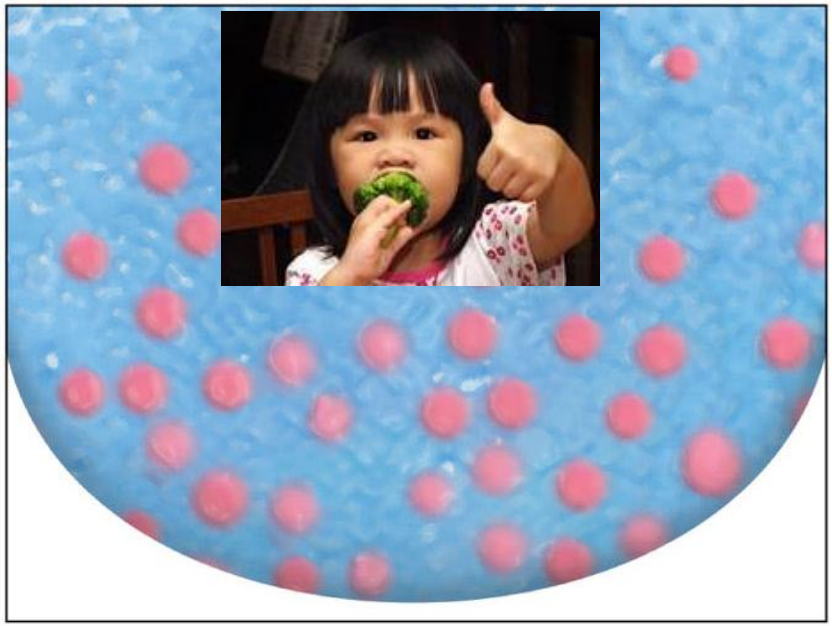




SUPERpercettori

I SuperPercettori hanno una maggiore densità di papille e più gemme gustative rispetto ai Non Percettori

NON percettore

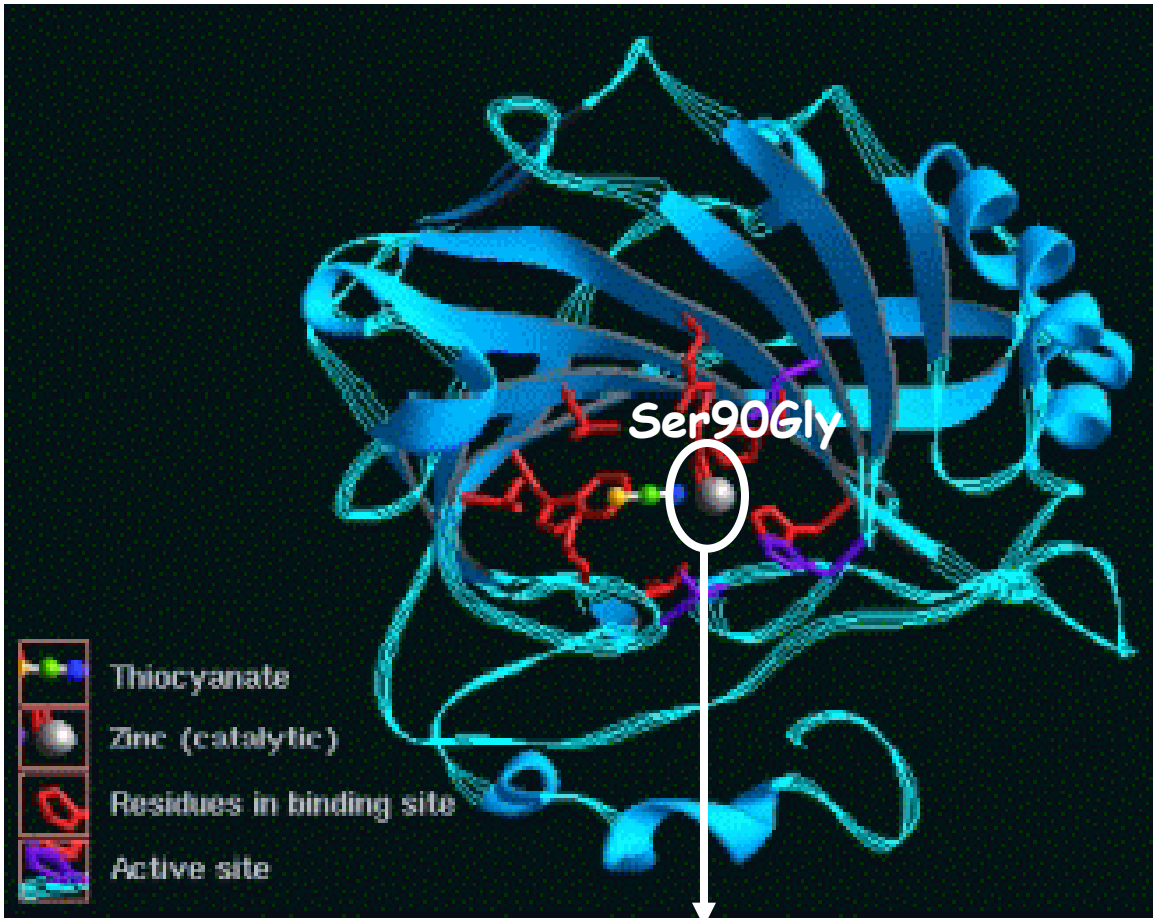


SUPER percettore

…le gemme gustative sono riccamente innervate dal trigemino che conduce sensazioni chemoestetiche responsabili della percezione della consistenza e della densità calorica dei cibi

SENSATION AND PERCEPTION, Figure 14.3 © 2006 Sinauer Associates, Inc.

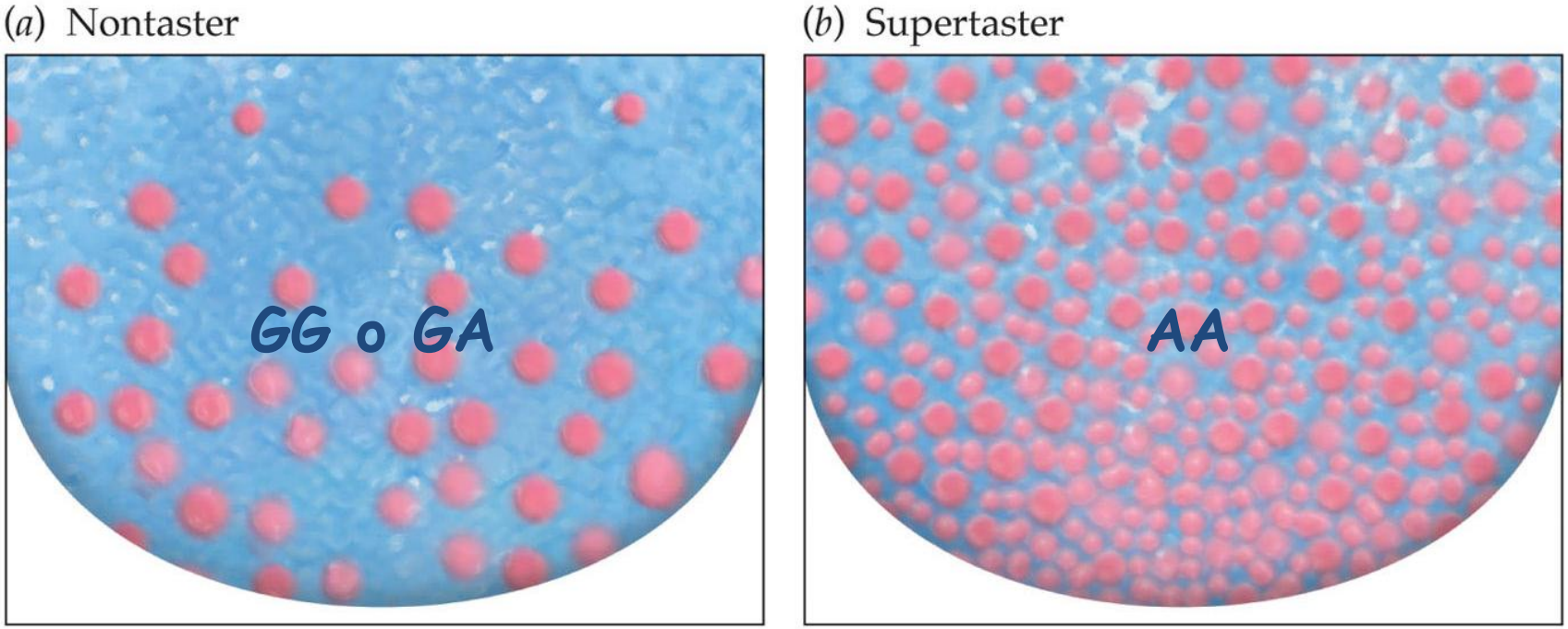
Geni modificatori: la GUSTINA



Allele A (Ser): proteina funzionale
Allele G (Gly): proteina non funzionale

La GUSTINA è un fattore trofico per le papille gustative

LA RIDOTTA FUNZIONALITÀ DELLA GUSTINA SI ASSOCIA AD UNA DENSITÀ INFERIORE DI PAPILLE GUSTATIVE ED UNA MINORE ABILITÀ CHEMOSENSORIALE



I SUPERpercettori sono più frequentemente omozigoti per l'allele funzionale della GUSTINA, mentre i NON percettori sono generalmente omozigoti o eterozigoti per l'allele non funzionale

SENSATION AND PERCEPTION, **Figure 14.3**

loci genetici che contribuiscono al fenotipo

Percezione chemosensoriale

Scelte alimentari ?

Lo sviluppo del gusto nel neonato

Alla nascita **Preferisce il Dolce** :

- Carboidrati e calorie

Non piace l'Amaro e l'Acido

- si protegge da tossine , veleni e batteri

Dal 4° mese sviluppa il gusto per il **Salato**

(anche se allattato al seno)

sviluppa il **gusto UMAMI**

Il latte che riceve da lattante condizionerà lo sviluppo del gusto a 5 anni !

- **Al seno** riceve i sapori scelti dalla madre
- Se beve **idrolisati** continua a preferire il sapore del latte e ***l'acido'***
- ***s***e beve la **soia** preferisce ***l'amaro*** ed i broccoli
- Mennella J, Early Hum Develop, 2002 , 68 : 71-82

Piace la Densità Calorica dei Cibi

- Avverte l'esperienza di '***sazietà'*** dei cibi ad alta densità calorica dopo l'ingestione
- Apprende così a preferire , per lo stesso gusto, il cibo a maggiore densità

  (per es : zuppa con amido aggiunto, yogurth più grasso)
- Sviluppa un '**flavour-consequence learning'** vitale nelle scelte della foresta del passato, mortale nell'ambiente obesogenico attuale

NEOFOBIA : Il bambino rifiuta il nuovo !

Per ottenere che un bimbo si adatti ad un alimento è necessario un lungo e paziente training : sono necessarie almeno 7-8 esposizioni prima che il bambino lo accetti in modo stabile (Maier 2007).

Neofobia : rifiutare cibi nuovi

- **20-30% dei bambini sono neofobici (78% familiarità)**
- La neofobia a 3 anni correla con neofobia ad 8
- Neofobia = meno frutta, vegetali e proteine
- Non c'è neofobia per amidi, farine, zuccheri e grassi
- La Neofobia è sinergica con il disgusto per cibi meno 'facili'
- I neofobici hanno una dieta più ristretta

L’esperienza sensoriale del gusto dipende non solo dalla stimolazione dei recettori gustativi, ma anche di quelli olfattivi .

Taste (gusto) is often thought to be synonymous with flavor (aroma).

However,

taste (gusto) refers strictly to the qualities encoded in the gustatory system,

whereas

flavor, with its rich and varied qualities, actually stems from a combination of inputs from the gustatory, olfactory, and somatosensory systems

from there extends to the primary taste cortex (Fig. 2b). A key fact about taste stimuli is that they elicit the most basic human emotions of pleasure (sweet) and disgust (bitter), which are not learned; they are hard-wired in the brainstem from birth[28,29]. In contrast to taste, the affective responses to odour images seem to be mostly learned, which presumably accounts for the enormous diversity of flavours in the world's cuisines.

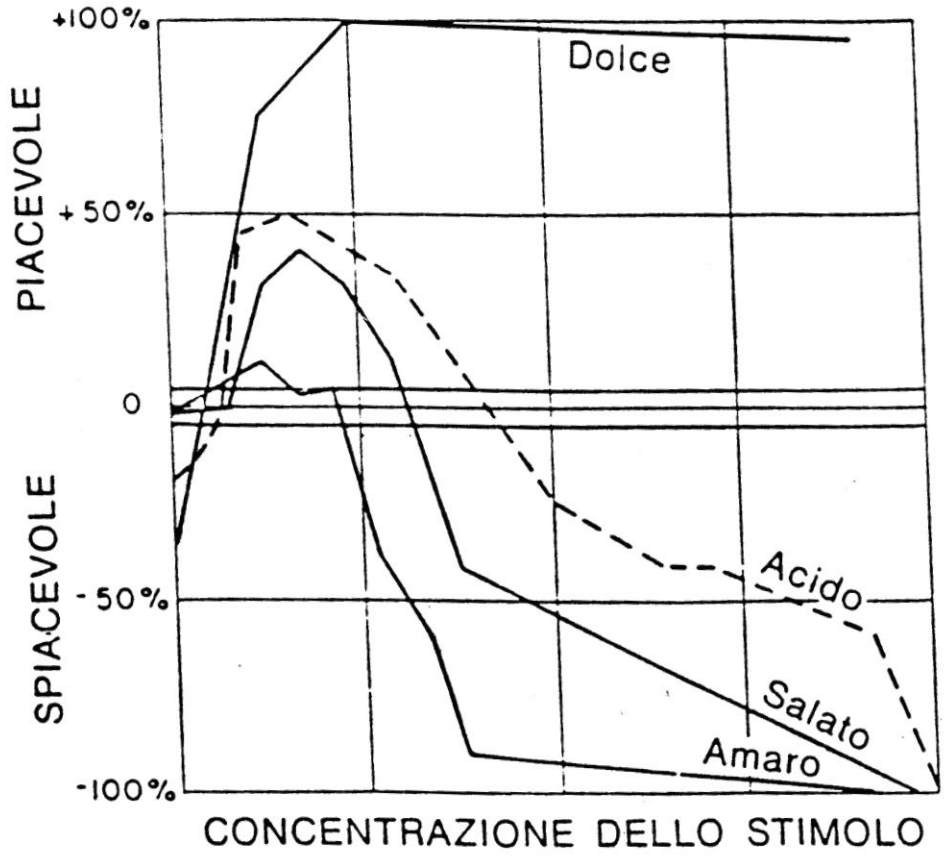


Figura 62-3. Tonalità affettiva dei differenti sapori fondamentali alle differenti intensità di stimolazione. (Da Engel in Woodworth and Schlosberg: Experimental Psychology. Holt Rinekart & Winston, Inc. 1954).

Flavor involves the combination of gustatory and olfactory stimuli, giving rise to descriptors such as “fruity,” “meaty,” “floral,” “herbal,” etc.

Here, it is important to distinguish between

orthonasal smell when we sniff (that tells us about the aroma of food, the bouquet of the wine)

retronasal smell when air is pulsed out from the back of the nose as we swallow (e.g., Rozin, 1982).

Different neural substrates may actually be involved in processing these two kinds of olfactory information (see Small et al., 2005).

It is the retronasal aromas that are combined with gustatory cues to give rise to flavors. On top of these two senses, trigeminal inputs also contribute to flavor perception.

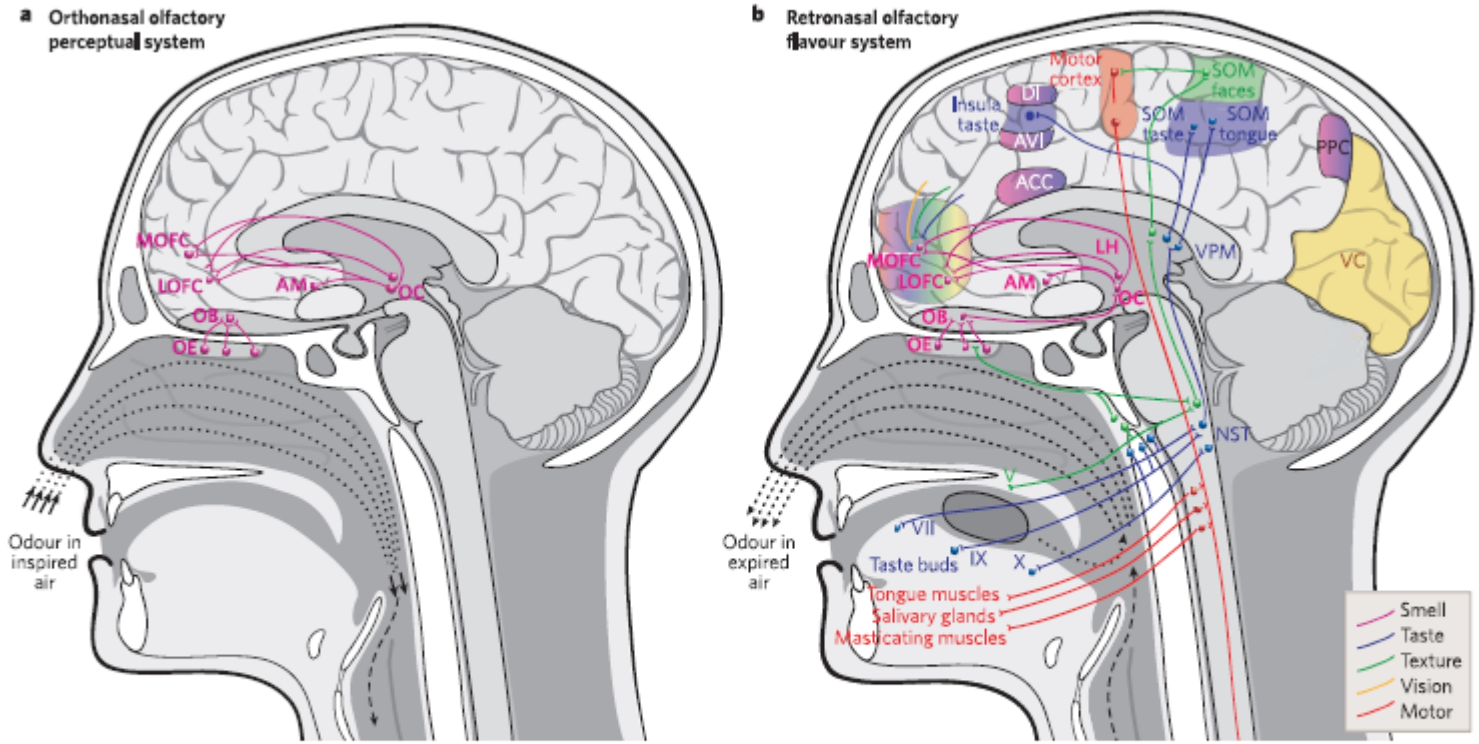


Figure 2 | The dual olfactory system. **a,** Brain systems involved in smell perception during orthonasal olfaction (sniffing in). **b,** Brain systems involved in smell perception during retronasal olfaction (breathing out), with food in the oral cavity. Air flows indicated by dashed and dotted lines; 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.

Integrazione tra olfatto e gusto

Participants in their studies were given two pairs of bottles to sniff, each containing a clear odorless liquid. An almond-cherry-like scent (i.e., benzaldehyde) had been added to one of the bottles. On each trial, the participants had to try and determine which bottle contained the benzaldehyde. The concentration of the olfactant was varied on a trial-by-trial basis in order to home in on each participant's detection threshold. Surprisingly, when the participants performed this task while holding a sub-threshold solution of saccharin in their mouths (i.e., a solution that had no discernible taste or smell), the cherry-almond smell was perceived as being significantly more intense relative to a baseline condition in which a tasteless water solution was held in the mouth instead (see Figure 1).

Integrazione multisensoriale

Profumo di ciliegia

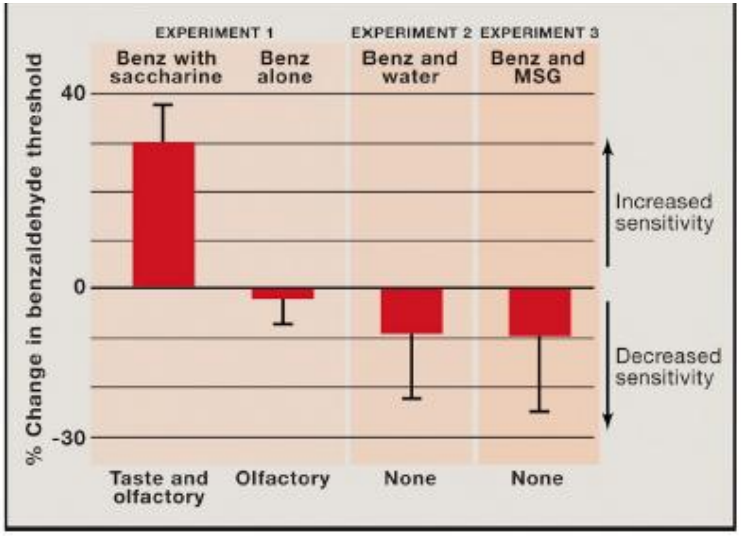


Figure 1. Multisensory Interactions between Olfaction and Gustation in Multisensory Flavor Perception

Results of a series of experiments by Dalton et al. (2000), showing the integration of orthonasal olfactory and gustatory cues. Figure reprinted with permission from Figure 6.2 of Spence and Piqueras-Fiszman (2014).

Integrazione gusto e sistema uditivo

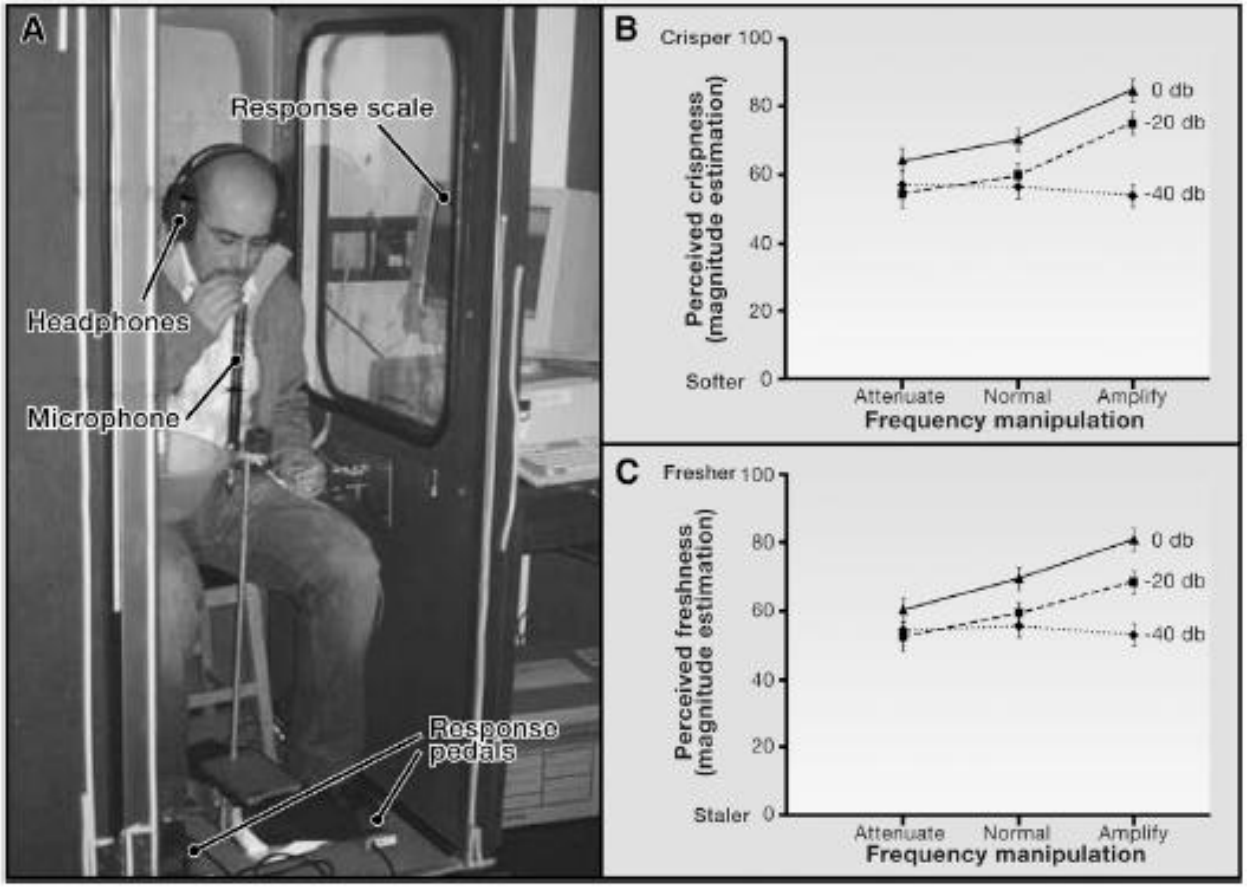


Figure 5. The "Sonic Chip" Experiment
(A) Schematic view of the apparatus and participant in Zampini and Spence (2004) study demonstrating the influence of biting sounds on crispness and freshness perception. The door of the experimental booth was closed during the experiment, and the response scale was viewed through the window in the left-side wall of the booth. Mean responses for the soft-crisp (B), and fresh-stale (C) response scales for the three overall attenuation levels (0 dB, −20 dB, or −40 dB) against the three frequency manipulations (high frequencies attenuated, veridical auditory feedback, or high frequencies amplified) are reported. Error bars represent the between-participants standard errors of the means. Figure reprinted with permission from Figure 1 of Zampini and Spence (2004).

Integrazione gusto e sistema visivo

Tre esempi

Esempio 1°

Integrazione gusto e sistema visivo

One of the most common observations has been that changing the hue of a drink changes the perceived flavor. Many people will, for example, say that a cherry-flavored drink tastes of lime if colored green while perceiving it to taste of orange if colored orange (see Zampini et al., 2007, 2008). One intriguing but as yet unconfirmed observation in this area comes from Zampini et al. (2008). These researchers found that supertasters were significantly less influenced by inappropriate coloring of a beverage than were medium tasters who, themselves, were less influenced than were the non-tasters (see Figure 2).

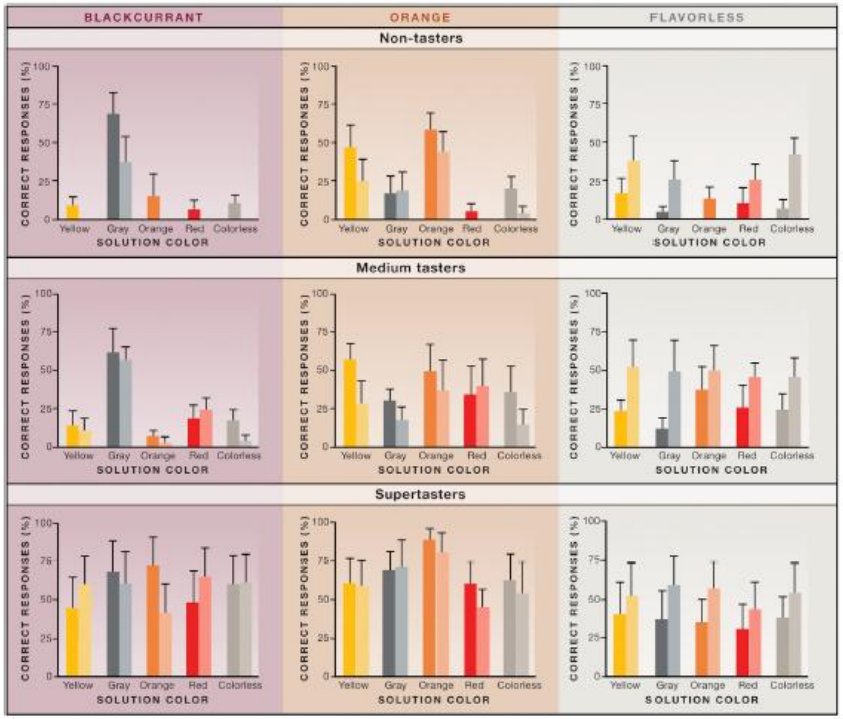


Figure 2. The Influence of Color on Flavor Identification as a Function of Taster Status
Mean percentages of correct flavor identification responses for the three groups of participants (non-tasters, medium tasters, and supertasters) for the blackcurrant, orange, and flavorless solutions presented in Zampini et al.'s study (2008) of the effects of color cues on multisensory flavor perception in humans. The darker columns represent solutions where fruit acids had been added, and the lighter columns represent solutions without fruit acids. The error bars represent the between-participants standard errors of the means. Figure reprinted with permission from Figure 1 of Zampini et al. (2007).

Figure 2. The Influence of Color on Flavor Identification as a Function of Taster Status

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Esempio 2°

Quale dei due dessert alla fragola è più dolce?

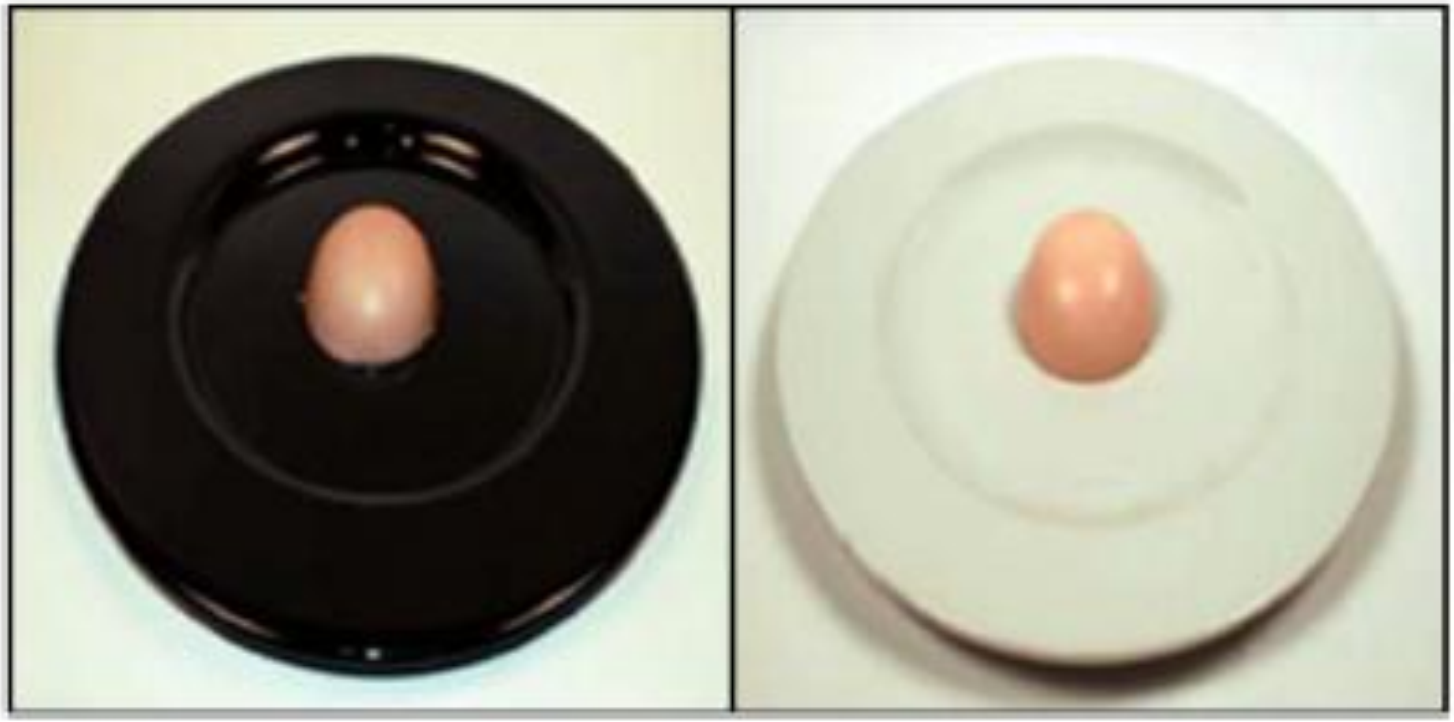

Figure 3. Can You Taste the Plate?
Black and white plates with red frozen strawberry dessert. Participants rated the dessert tasted from the white plate as tasting significantly sweeter and more flavorful than exactly the same food when served from the black plate instead. Figure reprinted with permission from Figure 2 of Piqueras-Fiszman et al. (2012).

Esempio 3°

Quale delle tre insalate vi sembra più appetitosa?

Quanto sareste disposti a pagare per ciascuno dei tre piatti?

Esempio 2°

Figure 4. Salad Three Ways

(A) Three different presentations of exactly the same ingredients served to participants in Michel et al.'s Kandinsky on a plate study (2014a). Plating inspired by Kandinsky's "Painting number 201," hanging (the other way up) in the MoMA in New York (see http://www.moma.org/collection/browse_results.php?object_id=79452).

(B) Same ingredients now served as a regular tossed salad.

(C) The ingredients laid out side by side—an effortful presentation, but not an especially aesthetically pleasing one. No surprises for guessing that those participants served the artistic version of the salad liked it more and were willing to pay significantly more for the food. Figure adapted and reprinted with permission from Figure 1 of Michel et al. (2014a).

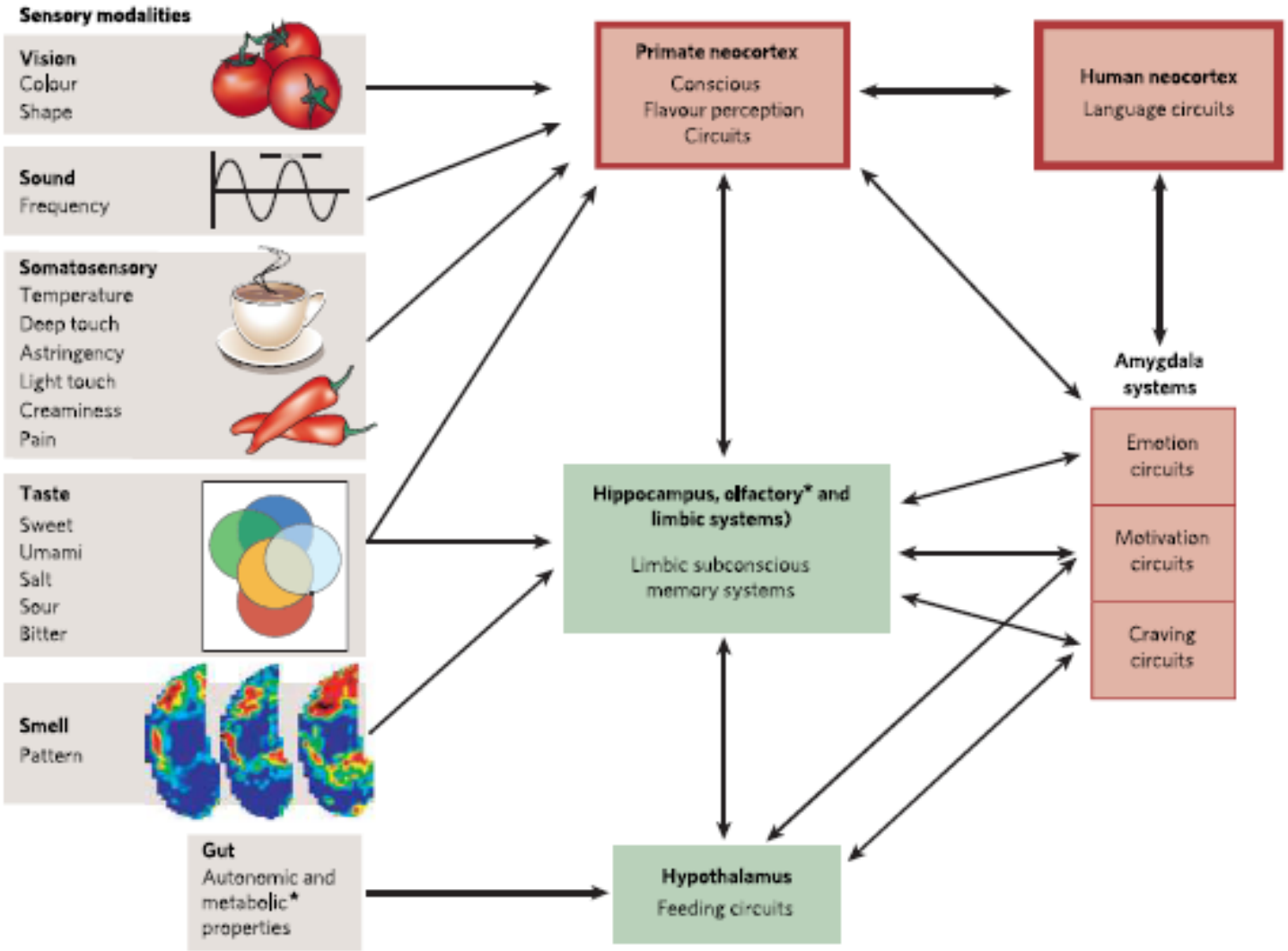

Figure 3 | The human brain flavour systems that evaluate and regulate food intake. The diagram shows the areas involved in the perceptual, emotional, memory-related, motivational and linguistic aspects of food evaluation mediated by flavour inputs[32,41,54,55]. Left, different sensory modalities and 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).