What We Now Know About Flavor Perception

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What people remember about how flavor perception works depends, at least in part, on what was known when they learned about it.

Most people recall that flavor perception has two aspects:

Taste

Smell

We now know that there are actually three aspects:

- Taste
- Smell
- Chemesthesis

Taste

Tongue maps

At one time sensory textbooks contained diagrams showing regions of the tongue that were sensitive for particular tastes.

We now know that the tongue map idea is incorrect.

There are taste buds located all over the tongue, as well as on other oral surfaces (including cheeks, soft palate, and epiglottis). These contain all of the taste receptor types.

Most people remember four tastes:

- Sweet
- Sour
- Salty
- Bitter

And many people have heard of a fifth taste:

- Sweet
- Sour
- Salty
- Bitter
- Umami (savory)

People sometimes think of umami as being relatively recently discovered.

In fact it was first proposed by Kikunae Ikeda in 1908 and only later generally accepted.

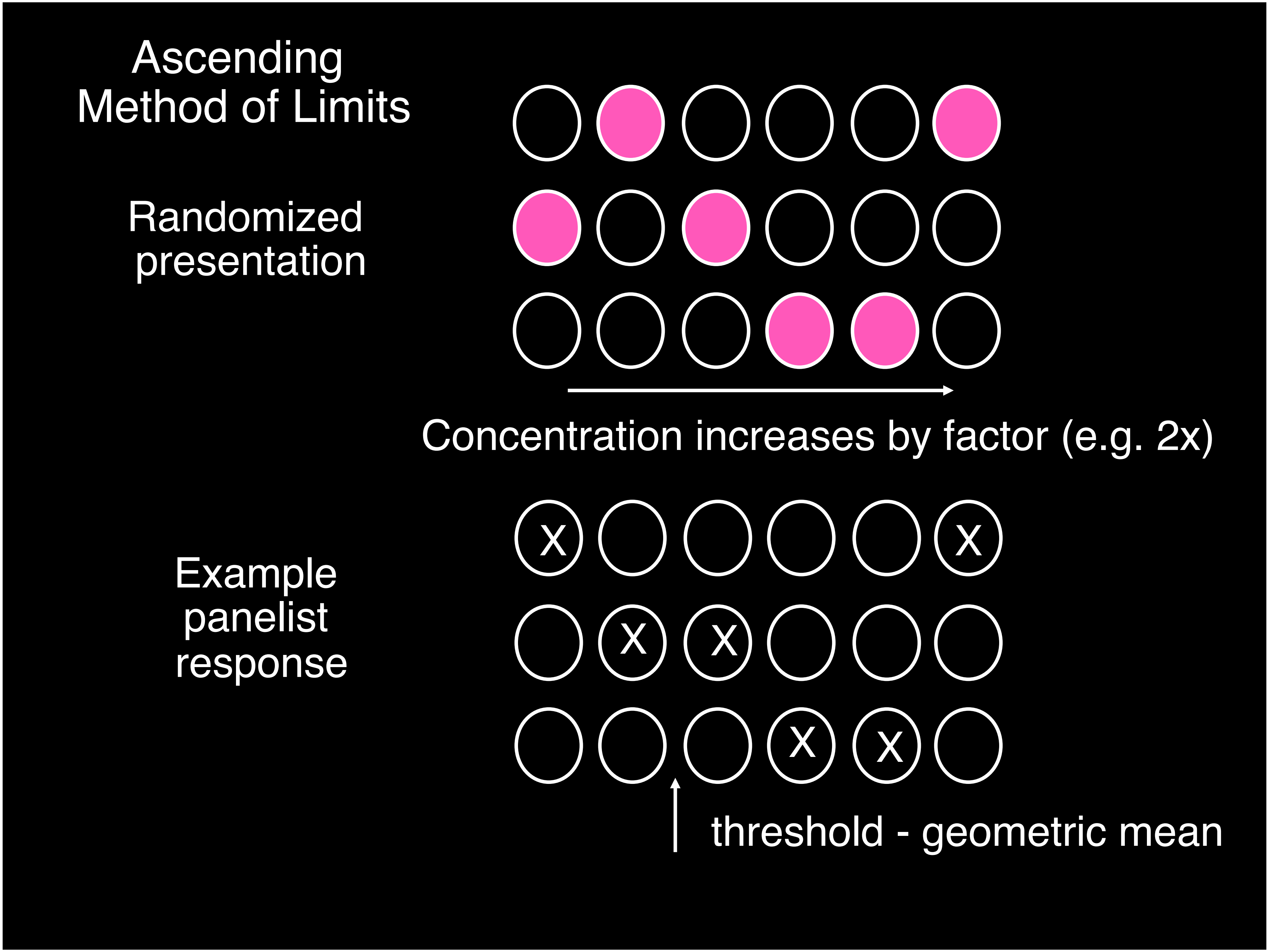
A sixth taste, oleogustus, or ‘fatty’, was recently described (Running, Craig & Mattes, *Chem. Senses 40*: 507-516, 2015) and is likely to be generally accepted fairly soon.

All of the tastes are caused by compounds that are soluble in saliva. That means compounds that tend to be polar.

Flavor strengths are indicated by flavor thresholds. Substances with relatively low flavor thresholds are more potent (a lower concentration can be detected).

Tthe thresholds given here are addition thresholds in beer, typically determined by the Ascending Method of Limits.

Panelists were generally free to use any nose or mouth sensation to perceive a test compound. Appearance was usually masked by serving in dark colored glasses.


Ascending
Method of Limits
Randomized
presentation
Concentration increases by factor (e.g. 2x)
Example
panelist
response
X
X
X
X
X
X
threshold - geometric mean

Sweet Taste

Sugars

Artificial sweeteners

In beer, mainly simple sugars (mono- and disaccharides) have thresholds in a similar range:

Sucrose	2600 mg/l (= 0.26%)
Glucose	3400 mg/L (= 0.34% est.)
Fructose	1780 mg/L (= 0.18% est.)

Sour Taste

In general, substances contributing H^+ to solution (i.e. organic and inorganic acids) produce a sour taste.

Acetic acid threshold in beer: 175, 200 mg/L

We know that acid flavor is more complicated than just [H^+]. For organic acids, thresholds are lower with low numbers of double bonds, greater hydrophobicity and low numbers of polar groups (Siebert, *Food Qual. & Pref. 10:* 129-137, 1999)

Salty Taste

Saltiness is a taste produced primarily by the presence of sodium ions. Other ions of the alkali metals group (first column of the periodic table) also taste salty, but the further from sodium, the less salty the sensation is.

Na^+ threshold: >2400 mg/L (>0.24%)

Bitter Taste

Bitter taste is evoked by some organic compounds:

- quinine
- caffeine
- isoalpha acids

Different isoalpha acid isomers have slightly different and quite low thresholds:

- 4-7 mg/L

Umami Taste

- Savory flavor
- Compounds
  - monosodium glutamate
    - glutamic acid threshold >300 mg/L
  - Some nucleotide monomers especially
    - inositol monophosphate
    - guanosine monophosphate
      - threshold 6 mg/L

Oleogustus Taste

- Fatty taste
- Free fatty acids with 10 or more carbon atoms

Some beers, particularly those not fermented to dryness or those ‘primed’ with sugar (usually sucrose) just before packaging, have some sweetness.

Significant sourness is found mainly in lambic and gueuze style beers, but in lesser amounts in a few other types. Essentially this is caused by acids, but not entirely explained by $[H^+]$ alone.

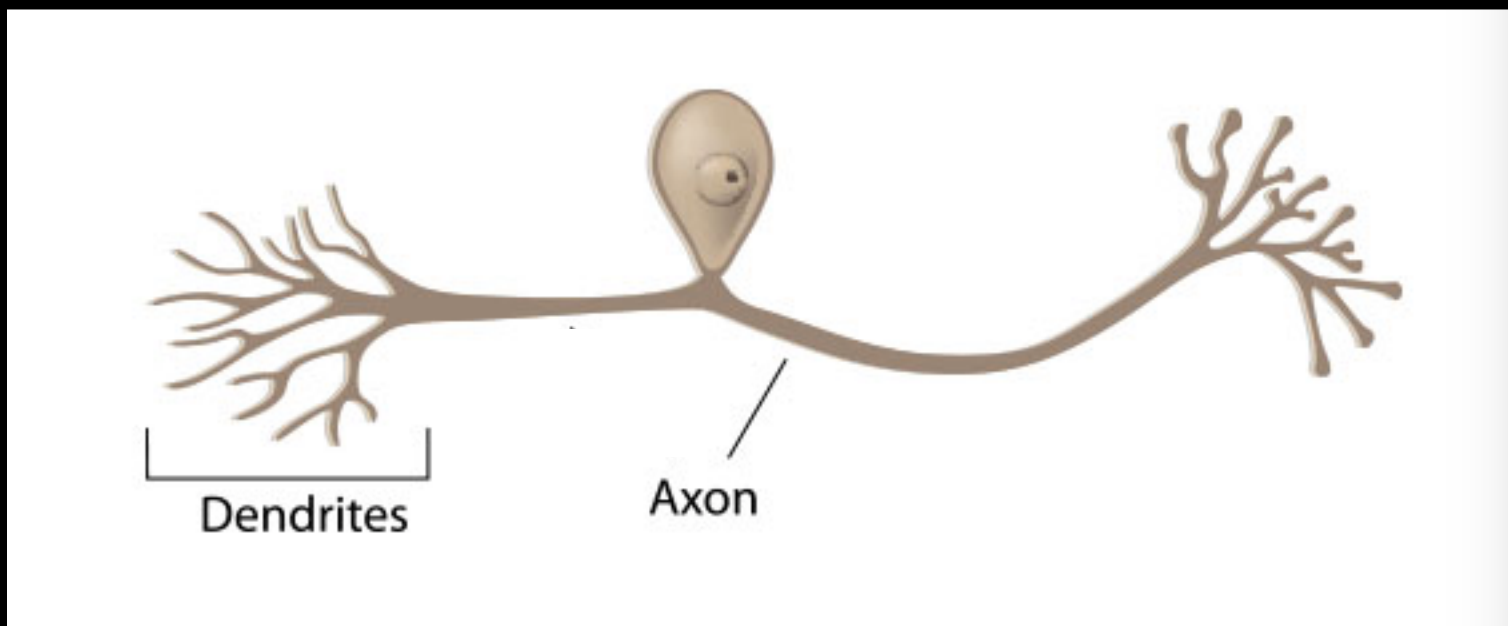
Minor saltiness may be noted in some beers.

Umami and oleogustus tastes are rarely associated with beer.

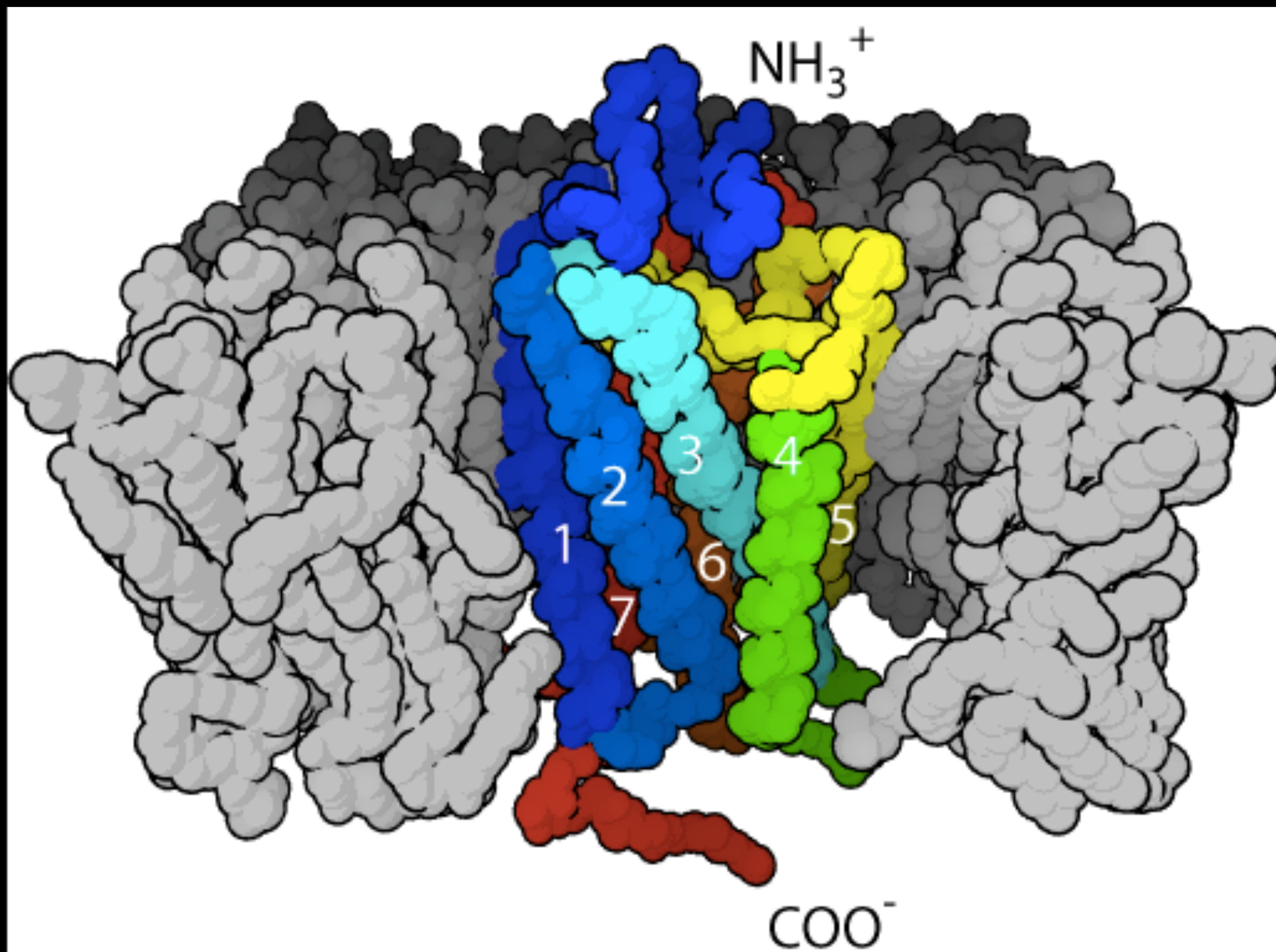
Taste Mechanisms

Sweet, umami and bitter are triggered by the binding of molecules to G-protein coupled receptors (GPCRs) on the cell membranes of taste buds.

Sensory Neuron



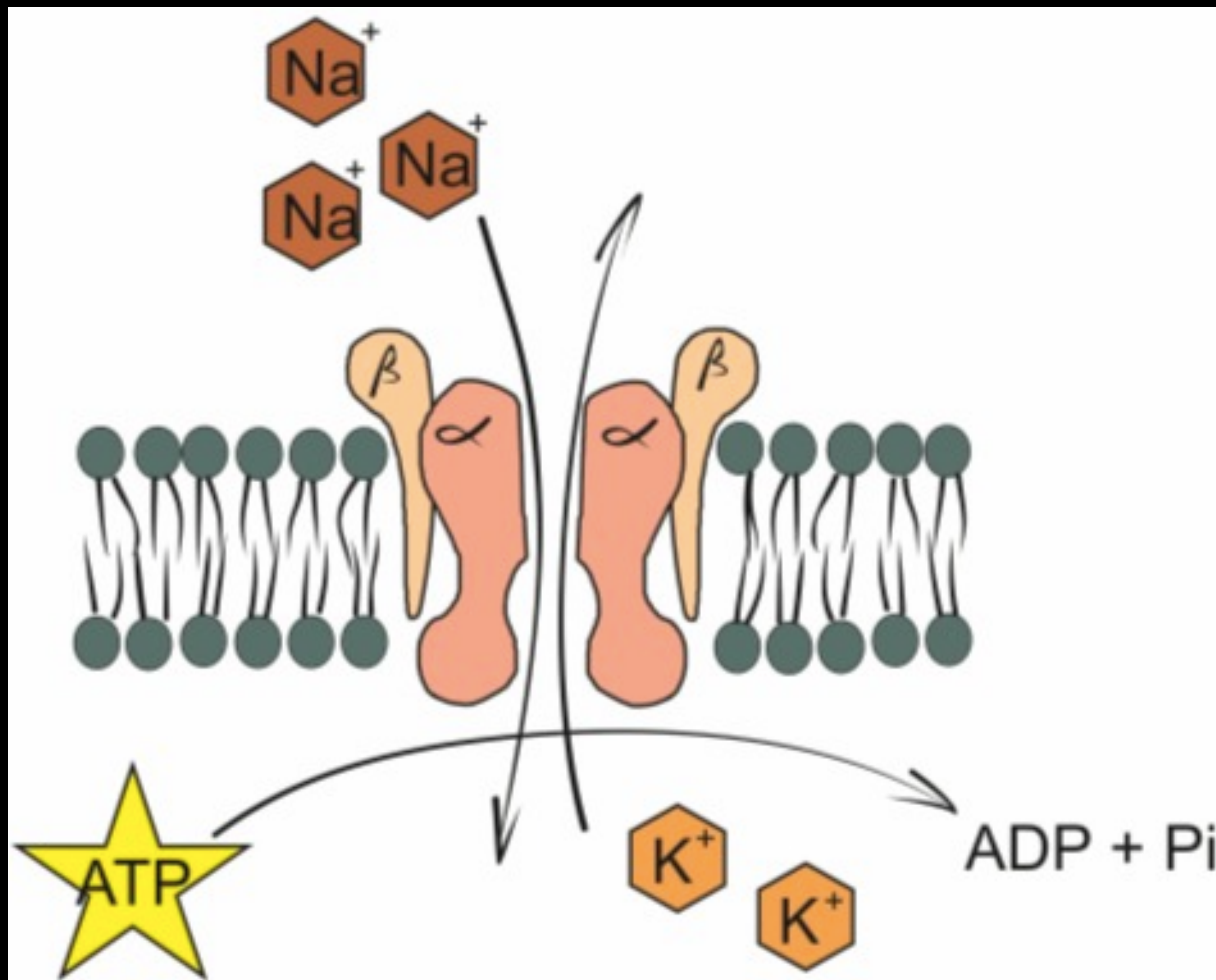
The seven-transmembrane α-helix structure of a G protein-coupled receptor



When a ligand (in this case a sensed molecule) attaches to a GPCR on the outside of a dendrite, it catalyzes a series of chemical reactions inside the neuron that lead to transmission of signal through the axon.

Salty and sour are perceived when alkali metal or hydrogen ions enter taste buds through ion channels.

Ion Channel in Cell Membrane



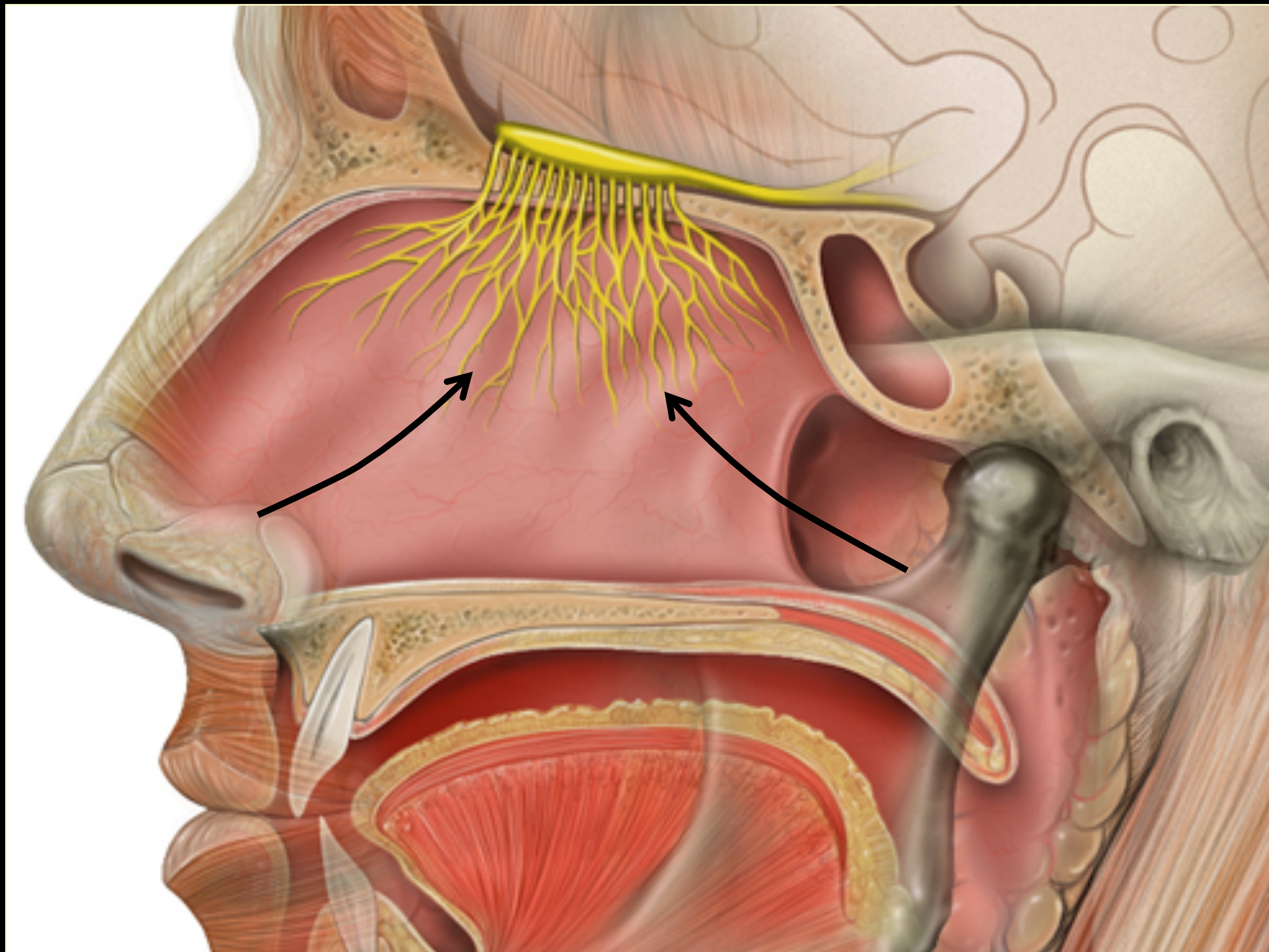
Smell

Smell (olfaction)

Smells are perceived when volatile compounds reach the olfactory epithelium.

This can happen when inhaling (orthonasal olfaction) or when exhaling (retronasal olfaction). In the latter case, substances in the throat and gut that have been ingested are warmed (and in some cases volatilized) and carried to the olfactory epithelium when exhaling.

Nerves from the olfactory epithelium directly enter the brain.



The dendrites of each olfactory sensory neuron contain receptors that span the cell membrane (G-protein coupled receptors) and the axon enters the olfactory bulb of the brain. When an odorant binds to a receptor, this causes a series of events that transmit a signal to the brain.

Source: “Olfaction: The Nasal Cavity and Smell.” *Boundless Psychology*. Boundless, 2016.

Olfactory receptor genes form the largest known multigene family in the human genome (Niimura and Nei, *Proc. Natl. Acad. Sci. USA.* Oct 14; 100(21): 12235-40 2003).

Presumably smell was important in evolutionary terms.

The ~900 human olfactory receptor genes are expressed as 300-500 receptor types.

A single odorant compound is sensed to varying degrees by multiple receptor types.

That results in thousands of different patterns that can be perceived.

Smell (olfaction)

Compounds that are smelled must be volatile at ambient temperature and are mainly low molecular weight (<300 Da) organic compounds.

A few ‘inorganic’ compounds can be smelled – e.g. SO_2, H_2S

Flavor thresholds for compounds perceived by smell are generally lower than those perceived by taste, and may be vastly lower (e.g. methyl mercaptan threshold = 0.00015 mg/L [0.15 ppb]).

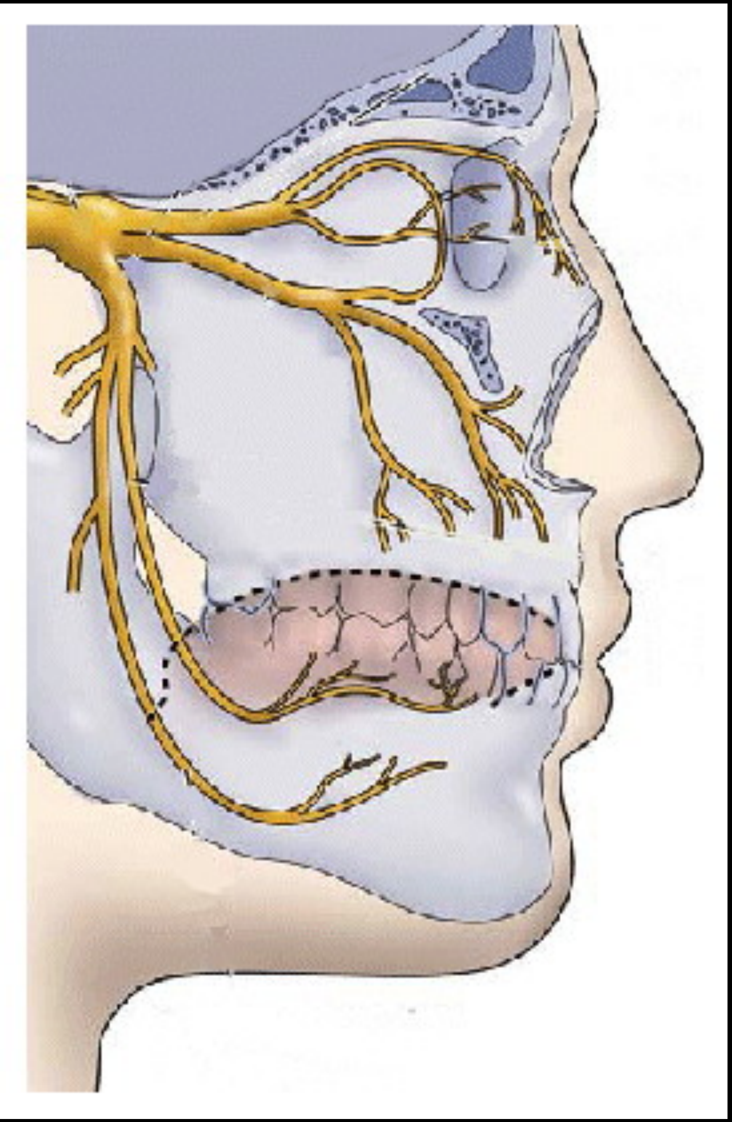
Chemesthesis

Chemesthesis

Chemesthesis is the result of perceptions made by the trigeminal nerve, which wraps around the nose and throat.

The trigeminal nerve provides touch-position and pain-temperature sensations.

The Trigeminal Nerve



Chemesthesis

Chemesthesis perceptions include mainly physical factors, such as:

- Hot
- Cold
- Smoothness
- Astringency
- Tingling of CO_2

Hotness

Four different sensors respond at different temperatures:

- 25-34°C (77-93°F)
- 33°C (91°F)
- >42°C (>108°F)
- >52°C (>126°F)

The hot sensation is also triggered by some chemicals including:

- capsaicin (hot peppers)
- gingerol (ginger)
- piperine (black pepper)
- ethanol
- eugenol

Coldness

Two sensors respond at different temperatures:

<25ºC (<77ºF)

<17ºC (<63ºF)

The cold sensation is also triggered by some chemicals including:

menthol

icilin

eugenol

geraniol

1-carvone eucalyptol

Much more information about trigeminal hot and cold sensations can be seen at:

Bandell, Macpherson, and Patapoutian, *Curr. Opin. Neurobiol. 17*(4): 490–497, 2007.

- Astringency and smoothness appear to be largely opposite sides of the same coin. A lack of astringency leads to smoothness (Siebert & Xu, unpublished).

- Several different classes of compounds produce astringency:
  - polyphenols & tannins
  - acids
  - ethanol and some other solvents
  - multivalent metal ions e.g. Al^{3+} as in alum [mixed aluminum sulfate salts]

Polyphenol Astringency

Polyphenol astringency is generally recognized as the result of interactions between proline-rich proteins (PRPs) in saliva and ingested polyphenols.

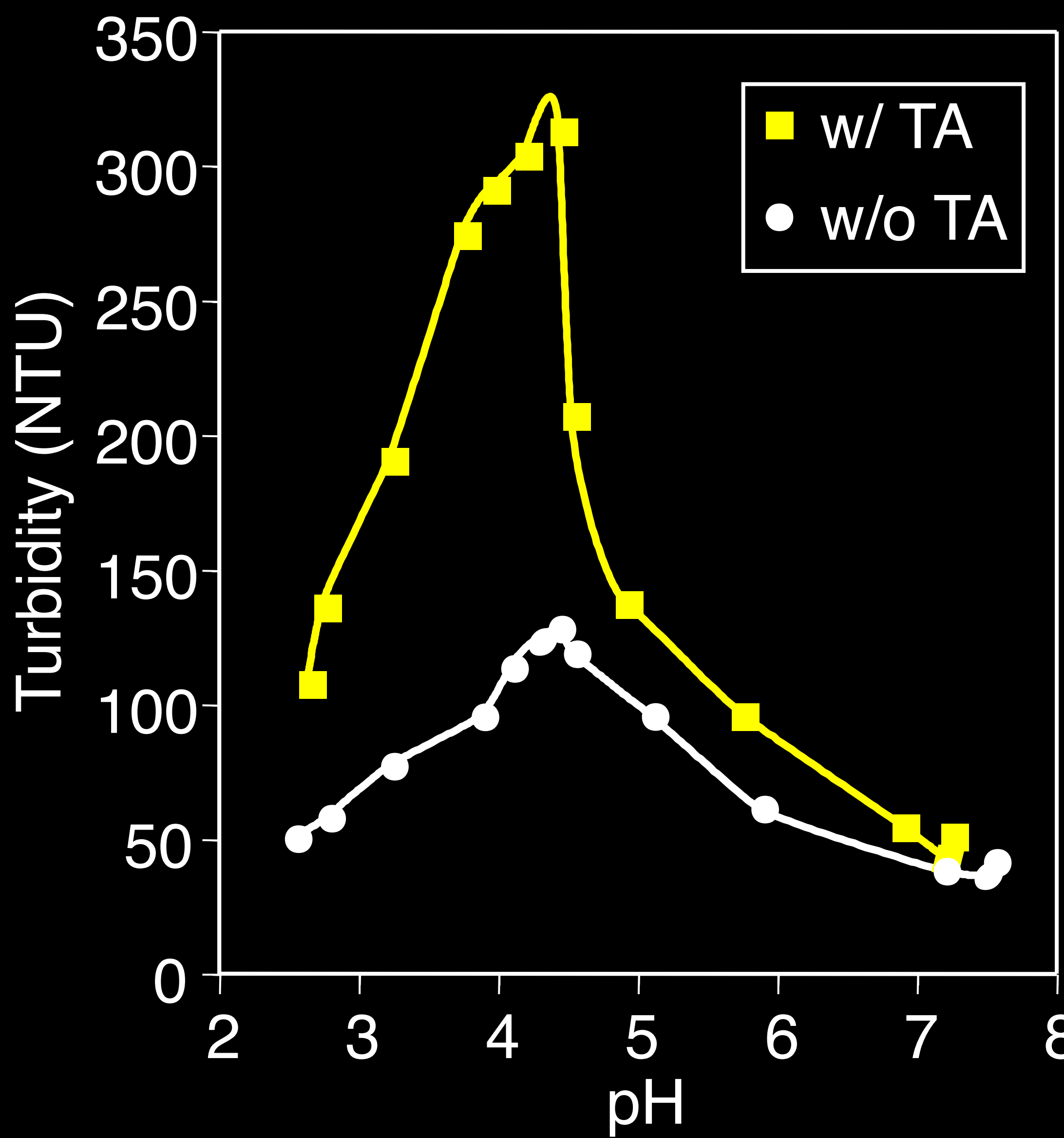
The PRPs and polyphenols combine to form colloidal particles and this removes the lubricity provided by the PRPs in solution.

Bate-Smith, 1973; Gawel, 1997

This is very similar to the mechanism of haze formation in beer, where proline-rich proteins (derived from barley hordein) are bridged together by polyphenols to form insoluble particles that scatter light.

And adding tannic acid to saliva also results in light scattering.

Effect of pH Adjustment of Saliva (●) and Saliva + Tannic Acid (■) on Light Scattering



Siebert & Chassy, *Food Qual. & Pref. 15*: 13-18, 2004.

Polyphenols are normally present in saliva and the level is affected by dietary habits. At saliva pH (6.5-7.0), they do not interact much with salivary PRPs. When acid is ingested, the saliva pH drops to the point that stronger PRP–polyphenol interaction occurs. This removes the lubrication of the PRPs, resulting in astringency.

Siebert, Maekawa & Lynn, *Food Qual. & Pref. 22*: 157-164, 2011

Chemesthesis Mechanism

Mechanoreceptors sense pressure and texture

Thermoreceptors sense hot and cold

Nociceptors sense pain

Chemesthetic sensations can also be produced when chemicals activate ion channels on sensory nerve fibers, often through transient receptor potential (TRP) channels.

In typical flavor perception, the brain combines the taste, olfaction, and chemesthetic sensations to produce a few prominent perceptions.