Gustation: How Your Brain Decodes Every Flavor

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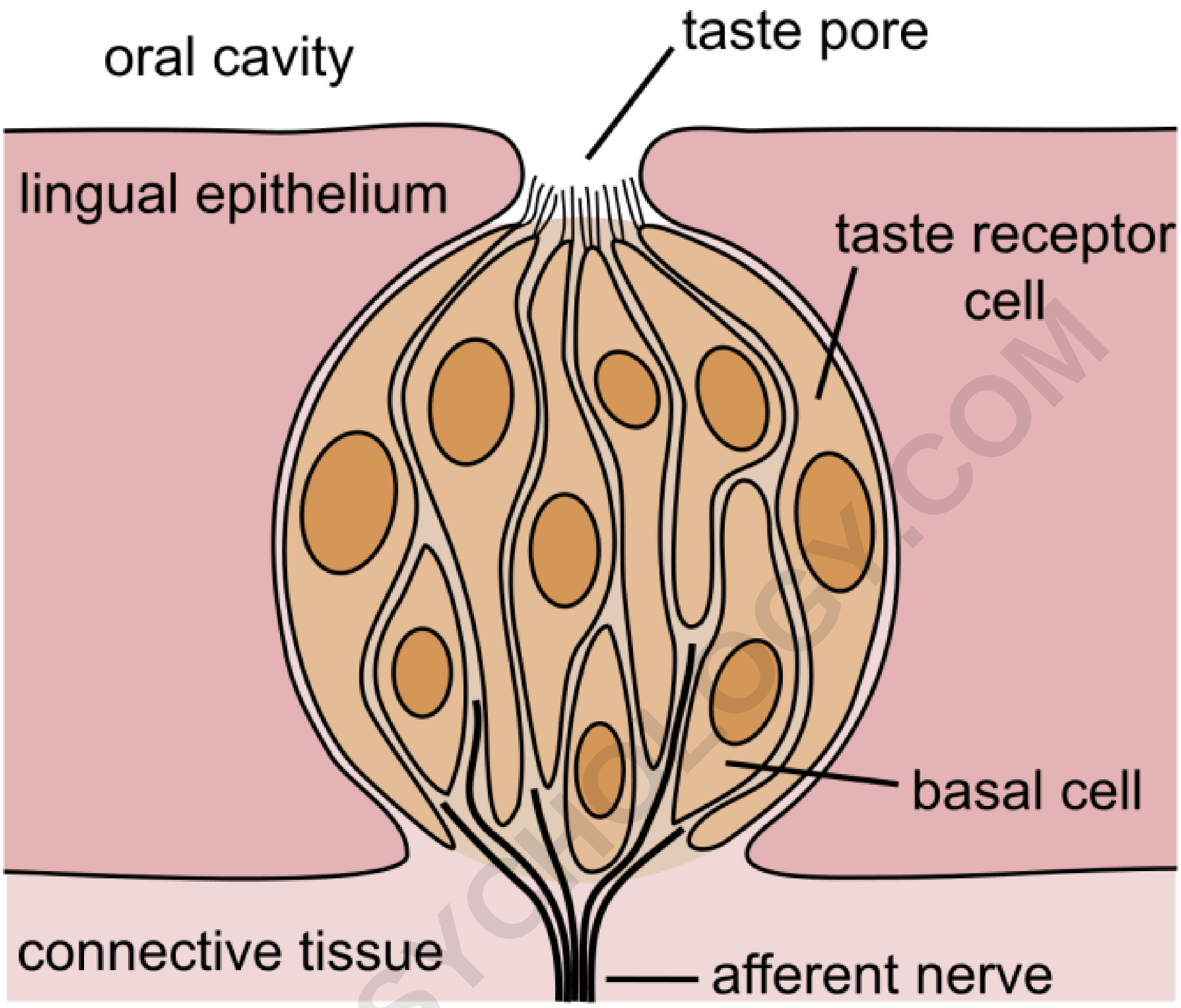

Taste bud

Taste, gustatory perception, or gustation is one of the five traditional senses that belongs to the gustatory system.

Taste is the sensation produced when a substance in the mouth reacts chemically with taste receptor cells located on taste buds in the oral cavity, mostly on the tongue. Taste, along with smell (olfaction) and trigeminal nerve stimulation (registering texture, pain, and temperature), determines flavors of food or other substances. Humans have taste receptors on taste buds (gustatory calyculi) and other areas including the upper surface of the tongue and the epiglottis. The gustatory cortex is responsible for the perception of taste.

The tongue is covered with thousands of small bumps called papillae, which are visible to the naked eye. Within each papilla are hundreds of taste buds. The exception to this is the filiform papillae that do not contain taste buds. There are between 2000 and 5000 taste buds that are located on the back and front of the tongue. Others are located on the roof, sides and back of the mouth, and in the throat. Each taste bud contains 50 to 100 taste receptor cells.

The sensation of taste includes five established basic tastes: sweetness, sourness, saltiness, bitterness, and umami. Scientific experiments have proven that these five tastes exist and are distinct from one another. Taste buds are able to differentiate among different tastes through detecting interaction with different molecules or ions. Sweet, umami, and bitter tastes are triggered by the binding of molecules to G protein-coupled receptors on the cell membranes of taste buds. Saltiness and sourness are perceived when alkali metal or hydrogen ions enter taste buds, respectively.

The basic tastes contribute only partially to the sensation and flavor of food in the mouth--other factors include smell, detected by the olfactory epithelium of the nose; texture, detected through a variety of mechanoreceptors, muscle nerves, etc.; temperature, detected by thermoreceptors; and "coolness" (such as of menthol) and "hotness" (pungency), through chemesthesis.

As taste senses both harmful and beneficial things, all basic tastes are classified as either aversive or appetitive, depending upon the effect the things they sense have on our bodies. Sweetness helps to identify energy-rich foods, while bitterness serves as a warning sign of poisons.

Among humans, taste perception begins to fade around 50 years of age because of loss of tongue papillae and a general decrease in saliva production. Humans can also have distortion of tastes through dysgeusia. Not all mammals share the same taste senses: some rodents can taste starch (which humans cannot), cats cannot taste sweetness, and several other carnivores including hyenas, dolphins, and sea lions, have lost the ability to sense up to four of their ancestral five taste senses.

Basic tastes

Taste in the gustatory system allows humans to distinguish between safe and harmful food, and to gauge foods' nutritional value. Digestive enzymes in saliva begin to dissolve food into base chemicals that are washed over the papillae and detected as tastes by the taste buds. The tongue is covered with thousands of small bumps called papillae, which are visible to the naked eye. Within each papilla are hundreds of taste buds. The exception to this are the filiform papillae that do not contain taste buds. There are between 2000 and 5000 taste buds that are located on the back and front of the tongue. Others are located on the roof, sides and back of the mouth, and in the throat. Each taste bud contains 50 to 100 taste receptor cells.

Bitter foods are generally found unpleasant, while sour, salty, sweet, and meaty tasting foods generally provide a pleasurable sensation. The five specific tastes received by taste receptors are saltiness, sweetness, bitterness, sourness, and umami, which means 'delicious' in Japanese and is

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sometimes translated as "savory" in English. As of the early twentieth century, Western physiologists and psychologists believed there were four basic tastes: sweetness, sourness, saltiness, and bitterness. At that time umami was not identified but now a large number of authorities recognize it as the fifth taste.

One study found that both salt and sour taste mechanisms detect, in different ways, the presence of sodium chloride (salt) in the mouth, however, acids are also detected and perceived as sour. The detection of salt is important to many organisms, but specifically mammals, as it serves a critical role in ion and water homeostasis in the body. It is specifically needed in the mammalian kidney as an osmotically active compound which facilitates passive re-uptake of water into the blood. Because of this, salt elicits a pleasant taste in most humans.

Sour and salt tastes can be pleasant in small quantities, but in larger quantities become more and more unpleasant to taste. For sour taste this is presumably because the sour taste can signal under-ripe fruit, rotten meat, and other spoiled foods, which can be dangerous to the body because of bacteria which grow in such media. Additionally, sour taste signals acids, which can cause serious tissue damage.

The bitter taste is almost universally unpleasant to humans. This is because many nitrogenous organic molecules which have a pharmacological effect on humans taste bitter. These include caffeine, nicotine, and strychnine, which respectively compose the stimulant in coffee, addictive agent in cigarettes, and active compound in many pesticides. It appears that some psychological process allows humans to overcome their innate aversion to bitter taste, as caffeinated drinks are widely consumed and enjoyed around the world. It is also interesting to note that many common medicines have a bitter taste if chewed; the gustatory system apparently interprets these compounds as poisons. In this manner, the unpleasant reaction to the bitter taste is a last-line warning system before the compound is ingested and can do damage.

Sweet taste signals the presence of carbohydrates in solution. Since carbohydrates have a very high calorie count (saccharides have many bonds, therefore much energy), they are desirable to the human body, which evolved to seek out the highest calorie intake foods. They are used as direct energy (sugars) and storage of energy (glycogen). However, there are many non-carbohydrate molecules that trigger a sweet response, leading to the development of many artificial sweeteners, including saccharin, sucralose, and aspartame. It is still unclear how these substances activate the sweet receptors and what adaptational significance this has had.

The umami taste, identified by Japanese chemist Kikunae Ikeda of Tokyo Imperial University, which signals the presence of the amino acid L-glutamate, triggers a pleasurable response and thus encourages the intake of peptides and proteins. The amino acids in proteins are used in the body to build muscles and organs, transport molecules (hemoglobin), antibodies, and the organic catalysts known as enzymes. These are all critical molecules, and as such it is important to have a

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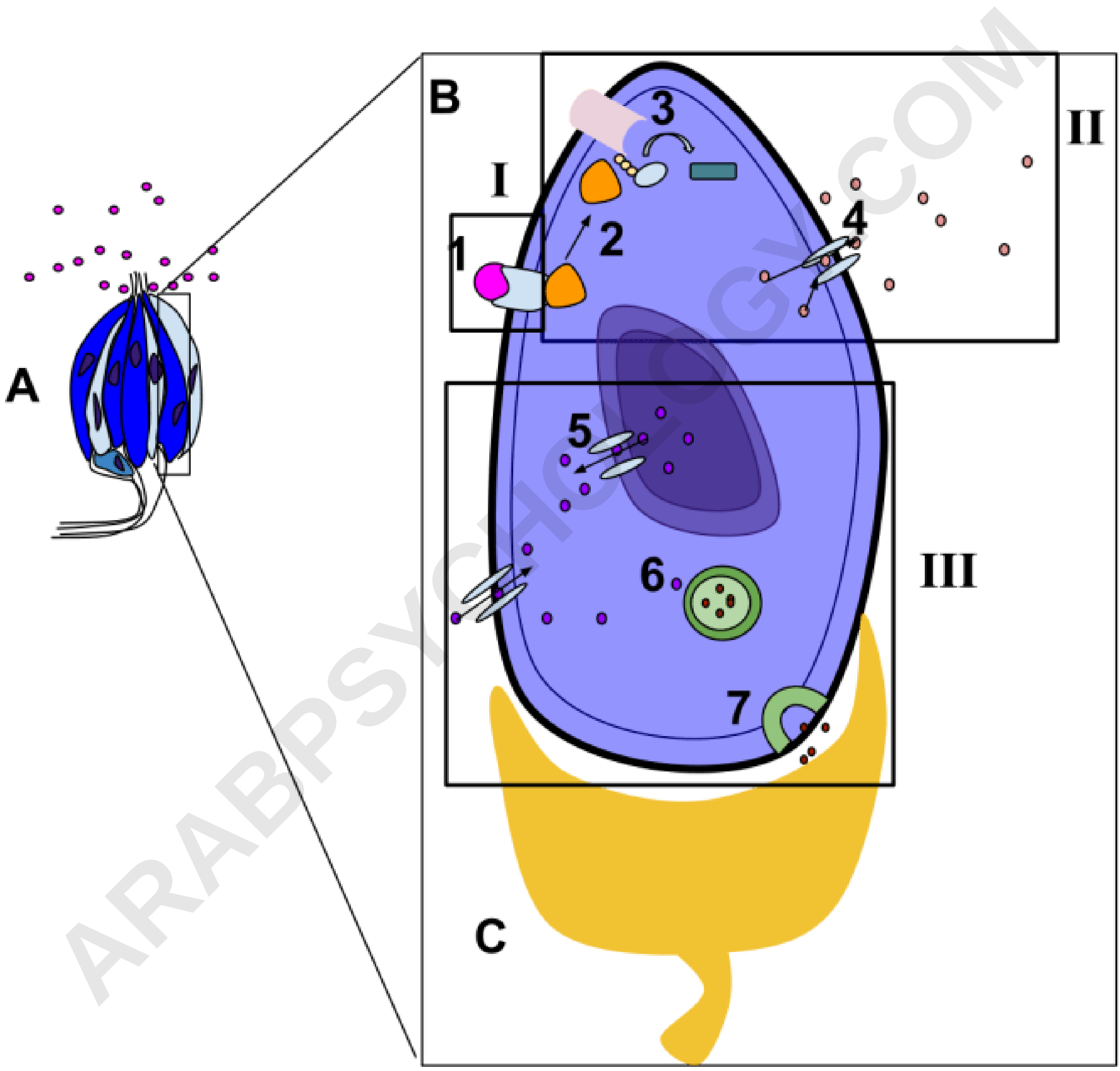
steady supply of amino acids, hence the pleasurable response to their presence in the mouth.

In Asian countries within the sphere of mainly Chinese and Indian cultural influence, pungency (piquancy or hotness) had traditionally been considered a sixth basic taste. In 2015, researchers at Purdue University suggested a new basic taste (of fats) called oleogustus.

Sweetness



The diagram above depicts the signal transduction pathway of the sweet taste. Object A is a taste bud, object B is one taste cell of the taste bud, and object C is the neuron attached to the taste cell. I. Part I shows the reception of a molecule. 1. Sugar, the first messenger, binds to a protein receptor on the cell membrane. II. Part II shows the transduction of the relay molecules. 2. G Protein-coupled receptors, second messengers, are activated. 3. G Proteins activate adenylate cyclase, an enzyme, which increases the cAMP concentration. Depolarization occurs. 4. The energy, from step 3, is given to activate the K+, potassium, protein channels.III. Part III shows the response of the taste cell. 5. Ca+, calcium, protein channels is activated.6. The increased Ca+ concentration activates neurotransmitter vesicles. 7. The neuron connected to the taste bud is stimulated by the neurotransmitters.

Sweetness, usually regarded as a pleasurable sensation, is produced by the presence of sugars and a few other substances. Sweetness is often connected to aldehydes and ketones, which contain a carbonyl group. Sweetness is detected by a variety of G protein coupled receptors coupled to the G protein gustducin found on the taste buds. At least two different variants of the "sweetness receptors" must be activated for the brain to register sweetness. Compounds the brain senses as sweet are thus compounds that can bind with varying bond strength to two different sweetness receptors. These receptors are T1R2+3 (heterodimer) and T1R3 (homodimer), which account for all sweet sensing in humans and animals. Taste detection thresholds for sweet substances are rated relative to sucrose, which has an index of 1. The average human detection threshold for sucrose is 10 millimoles per liter. For lactose it is 30 millimoles per liter, with a sweetness index of 0.3, and 5-Nitro-2-propoxyaniline 0.002 millimoles per liter. "Natural" sweeteners such as saccharides activate the GPCR, which releases gustducin. The gustducin then activates the molecule adenylate cyclase, which catalyzes the production of the molecule cAMP, or adenosine 3′, 5′-cyclic monophosphate. This molecule closes potassium ion channels, leading to depolarization and neurotransmitter release. Synthetic sweeteners such as saccharin activate different GPCRs and induce taste receptor cell depolarization by an alternate pathway.

Sourness

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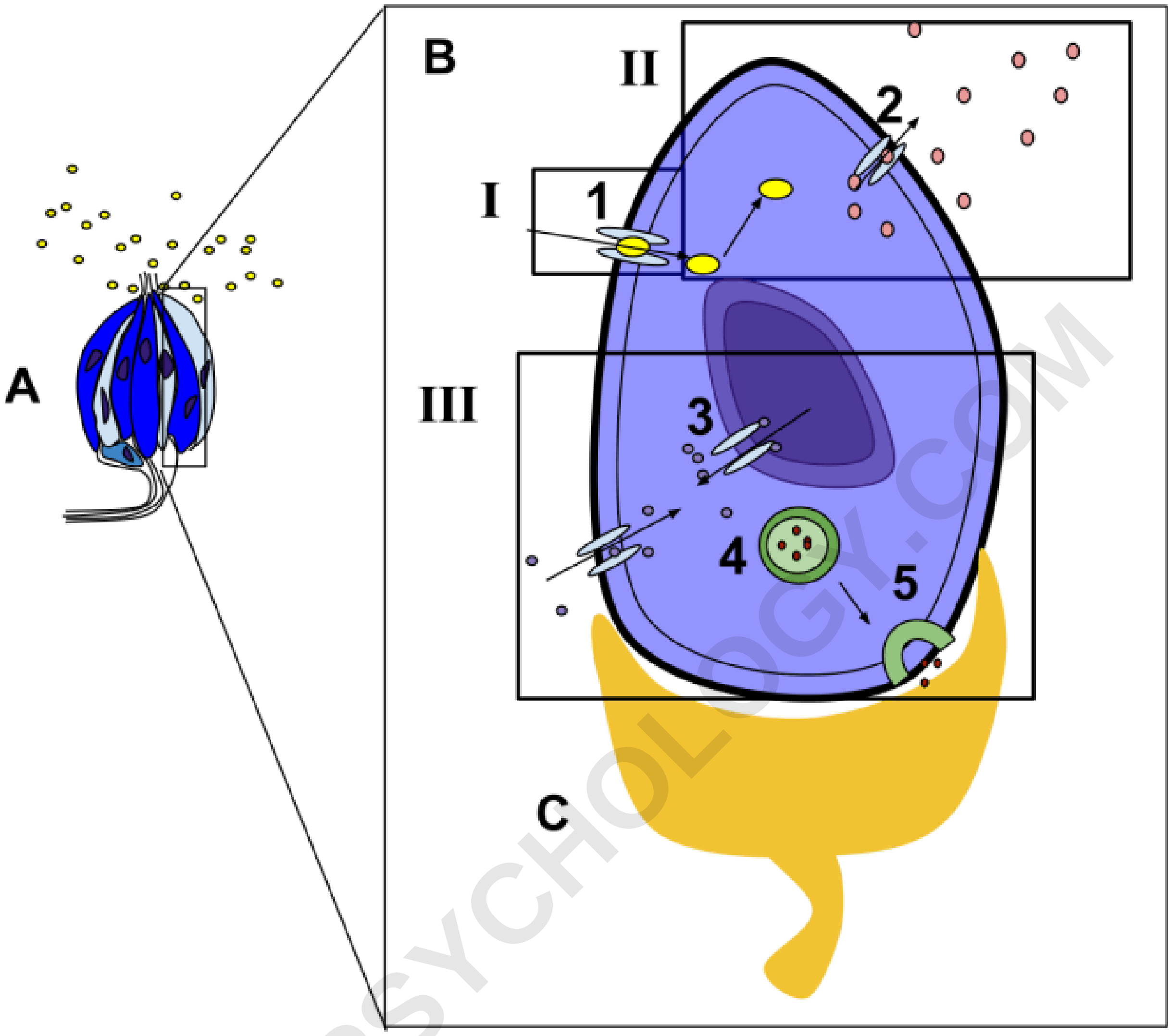

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The diagram depicts the signal transduction pathway of the sour or salty taste. Object A is a taste bud, object B is a taste receptor cell within object A, and object C is the neuron attached to object B. I. Part I is the reception of hydrogen ions or sodium ions. 1. If the taste is sour, H+ ions, from an acidic substances, pass through their specific ion channel. Some can go through the Na+ channels. If the taste is salty Na+, sodium, molecules pass through the Na+ channels. Depolarization takes place II. Part II is the transduction pathway of the relay molecules.2. Cation, such as K+, channels are opened. III. Part III is the response of the cell. 3. An influx of Ca+ ions is activated.4. The Ca+ activates neurotransmitters. 5. A signal is sent to the neuron attached to the taste bud.

Sourness is the taste that detects acidity. The sourness of substances is rated relative to dilute hydrochloric acid, which has a sourness index of 1. By comparison, tartaric acid has a sourness index of 0.7, citric acid an index of 0.46, and carbonic acid an index of 0.06.

Sour taste is detected by a small subset of cells that are distributed across all taste buds in the tongue. Sour taste cells can be identified by expression of the protein PKD2L1, although this gene is not required for sour responses. There is evidence that the protons that are abundant in sour substances can directly enter the sour taste cells through apically located ion channels. This transfer of positive charge into the cell can itself trigger an electrical response. It has also been proposed that weak acids such as acetic acid, which are not fully dissociated at physiological pH values, can penetrate taste cells and thereby elicit an electrical response. According to this mechanism, intracellular hydrogen ions inhibit potassium channels, which normally function to hyperpolarize the cell. By a combination of direct intake of hydrogen ions (which itself depolarizes the cell) and the inhibition of the hyperpolarizing channel, sourness causes the taste cell to fire action potentials and release neurotransmitter.

The most common food group that contains naturally sour foods is fruit, such as lemon, grape, orange, tamarind, and sometimes melon. Wine also usually has a sour tinge to its flavor, and if not kept correctly, milk can spoil and develop a sour taste. Children in the US and UK show a greater enjoyment of sour flavors than adults, and sour candy is popular in North America including Cry Babies, Warheads, Lemon drops, Shock Tarts and sour versions of Skittles and Starburst. Many of these candies contain citric acid.

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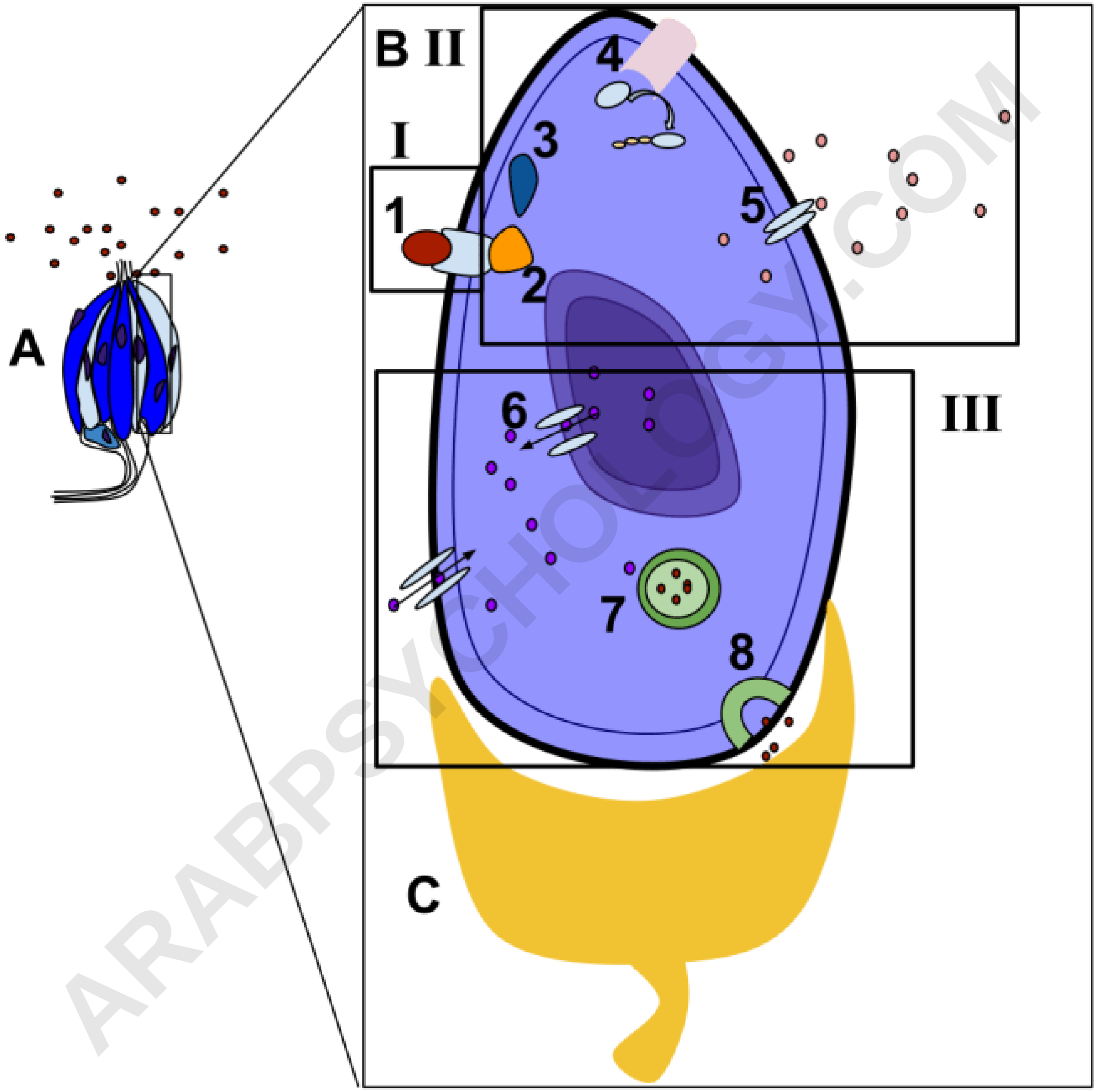
Saltiness

The simplest receptor found in the mouth is the sodium chloride (salt) receptor. Saltiness is a taste produced primarily by the presence of sodium ions. Other ions of the alkali metals group also taste salty, but the further from sodium, the less salty the sensation is. A sodium channel in the taste cell wall allows sodium cations to enter the cell. This on its own depolarizes the cell, and opens voltage-dependent calcium channels, flooding the cell with positive calcium ions and leading to neurotransmitter release. This sodium channel is known as an epithelial sodium channel (ENaC) and is composed of three subunits. An ENaC can be blocked by the drug amiloride in many mammals, especially rats. The sensitivity of the salt taste to amiloride in humans, however, is much less pronounced, leading to conjecture that there may be additional receptor proteins besides ENaC to be discovered.

The size of lithium and potassium ions most closely resemble those of sodium, and thus the saltiness is most similar. In contrast, rubidium and cesium ions are far larger, so their salty taste differs accordingly. The saltiness of substances is rated relative to sodium chloride (NaCl), which has an index of 1. Potassium, as potassium chloride (KCl), is the principal ingredient in salt substitutes and has a saltiness index of 0.6.

Other monovalent cations, e.g. ammonium, $NH4+$, and divalent cations of the alkali earth metal group of the periodic table, e.g. calcium, $Ca2+$, ions generally elicit a bitter rather than a salty taste even though they, too, can pass directly through ion channels in the tongue, generating an action potential.

Bitterness



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The diagram depicted above shows the signal transduction pathway of the bitter taste. Bitter taste has many different receptors and signal transduction pathways. Bitter indicates poison to animals. It is most similar to sweet. Object A is a taste bud, object B is one taste cell, and object C is a neuron attached to object B. I. Part I is the reception of a molecule.1. A bitter substance such as quinine, is consumed and binds to G Protein-coupled receptors.II. Part II is the transduction pathway 2. Gustducin, a G protein second messenger, is activated. 3. Phosphodiesterase, an enzyme, is then activated. 4. Cyclic nucleotide, cNMP, is used, lowering the concentration 5. Channels such as the K+, potassium, channels, close.III. Part III is the response of the taste cell. 6. This leads to increased levels of Ca+. 7. The neurotransmitters are activated. 8. The signal is sent to the neuron.

Bitterness is the most sensitive of the tastes, and many perceive it as unpleasant, sharp, or disagreeable, but it is sometimes desirable and intentionally added via various bittering agents. Common bitter foods and beverages include coffee, unsweetened cocoa, South American mate, bitter gourd, olives, citrus peel, many plants in the Brassicaceae family, dandelion greens, wild chicory, and escarole. The ethanol in alcoholic beverages tastes bitter, as do the additional bitter ingredients found in some alcoholic beverages including hops in beer and orange in bitters. Quinine is also known for its bitter taste and is found in tonic water.

Bitterness is of interest to those who study evolution, as well as various health researchers since a large number of natural bitter compounds are known to be toxic. The ability to detect bitter-tasting, toxic compounds at low thresholds is considered to provide an important protective function. Plant leaves often contain toxic compounds, yet even amongst leaf-eating primates, there is a tendency to prefer immature leaves, which tend to be higher in protein and lower in fiber and poisons than mature leaves. Amongst humans, various food processing techniques are used worldwide to detoxify otherwise inedible foods and make them palatable. Furthermore, the use of fire, changes in diet, and avoidance of toxins has led to neutral evolution in human bitter sensitivity. This has allowed several loss of function mutations that has led to a reduced sensory capacity towards bitterness in humans when compared to other species.

The threshold for stimulation of bitter taste by quinine averages a concentration of 8 μM (8 micromolar). The taste thresholds of other bitter substances are rated relative to quinine, which is thus given a reference index of 1. For example, Brucine has an index of 11, is thus perceived as intensely more bitter than quinine, and is detected at a much lower solution threshold. The most bitter substance known is the synthetic chemical denatonium, which has an index of 1,000. It is used as an aversive agent (a bitterant) that is added to toxic substances to prevent accidental ingestion. This was discovered in 1958 during research on lignocaine, a local anesthetic, by MacFarlan Smith of Gorgie, Edinburgh, Scotland.

Research has shown that TAS2Rs (taste receptors, type 2, also known as T2Rs) such as TAS2R38 coupled to the G protein gustducin are responsible for the human ability to taste bitter substances. They are identified not only by their ability to taste for certain "bitter" ligands, but also by the morphology of the receptor itself (surface bound, monomeric). The TAS2R family in humans is thought to comprise about 25 different taste receptors, some of which can recognize a wide variety of bitter-tasting compounds. Over 670 bitter-tasting compounds have been identified, on a bitter database, of which over 100 have been assigned to one or more specific receptors. Recently

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it is speculated that the selective constraints on the TAS2R family have been weakened due to the relatively high rate of mutation and pseudogenization. Researchers use two synthetic substances, phenylthiocarbamide (PTC) and 6-n-propylthiouracil (PROP) to study the genetics of bitter perception. These two substances taste bitter to some people, but are virtually tasteless to others. Among the tasters, some are so-called "supertasters" to whom PTC and PROP are extremely bitter. The variation in sensitivity is determined by two common alleles at the TAS2R38 locus. This genetic variation in the ability to taste a substance has been a source of great interest to those who study genetics.

Gustducin is made of three subunits. When it is activated by the GPCR, its subunits break apart and activate phosphodiesterase, a nearby enzyme, which in turn converts a precursor within the cell into a secondary messenger, which closes potassium ion channels. Also, this secondary messenger can stimulate the endoplasmic reticulum to release Ca2+ which contributes to depolarization. This leads to a build-up of potassium ions in the cell, depolarization, and neurotransmitter release. It is also possible for some bitter tastants to interact directly with the G protein, because of a structural similarity to the relevant GPCR.

Umami

Umami is an appetitive taste and is described as savory or meaty. It can be tasted in cheese and soy sauce, and is also found in many other fermented and aged foods. This taste is also present in tomatoes, grains, and beans.

A loanword from Japanese meaning "good flavor" or "good taste", umami (??) is considered fundamental to many Eastern cuisines; and other cuisines have long operated under principles that sought to combine foods to produce umami flavors, such as in the emphasis on veal stock by Auguste Escoffier, the pre-eminent chef of 19th century French cuisine, and in the Romans' deliberate use of fermented fish sauce. However, it was only recently recognized in modern science as a basic taste; well after the other basic tastes have been recognized by scientists, in part due to their correspondence with the four tastes of ancient Greek philosophy. Umami, or "scrumptiousness", was first studied with the scientific method and identified by Kikunae Ikeda, who began to analyze kombu in 1907, attempting to isolate its dashi taste. He isolated a substance he called ajinomoto, Japanese for "at the origin of flavor". Later identified as the chemical monosodium glutamate (MSG), and increasingly used independently as a food additive, it is a sodium salt that produces a strong umami taste, especially combined with foods rich in nucleotides such as meats, fish, nuts, and mushrooms.

Some umami taste buds respond specifically to glutamate in the same way that "sweet" ones respond to sugar. Glutamate binds to a variant of G protein coupled glutamate receptors. It is thought that the amino acid L-glutamate bonds to a type of GPCR known as a metabotropic

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glutamate receptor (mGluR4). This causes the G-protein complex to activate a secondary receptor, which ultimately leads to neurotransmitter release. The intermediate steps are not known. (See TAS1R1 and TAS1R3 pages for a further explanation of the amino-acid taste receptor).

Measuring relative tastes

Measuring the degree to which a substance presents one basic taste can be achieved in a subjective way by comparing its taste to a reference substance.

Sweetness is subjectively measured by comparing the threshold values, or level at which the presence of a dilute substance can be detected by a human taster, of different sweet substances. Substances are usually measured relative to sucrose, which is usually given an arbitrary index of 1 or 100. Fructose is about 1.4 times sweeter than sucrose; glucose, a sugar found in honey and vegetables, is about three-quarters as sweet; and lactose, a milk sugar, is one-half as sweet.

The sourness of a substance can be rated by comparing it to very dilute hydrochloric acid (HCl).

Relative saltiness can be rated by comparison to a dilute salt solution.

Quinine, a bitter medicinal found in tonic water, can be used to subjectively rate the bitterness of a substance. Units of dilute quinine hydrochloride (1 g in 2000 mL of water) can be used to measure the threshold bitterness concentration, the level at which the presence of a dilute bitter substance can be detected by a human taster, of other compounds. More formal chemical analysis, while possible, is difficult.

Functional structure

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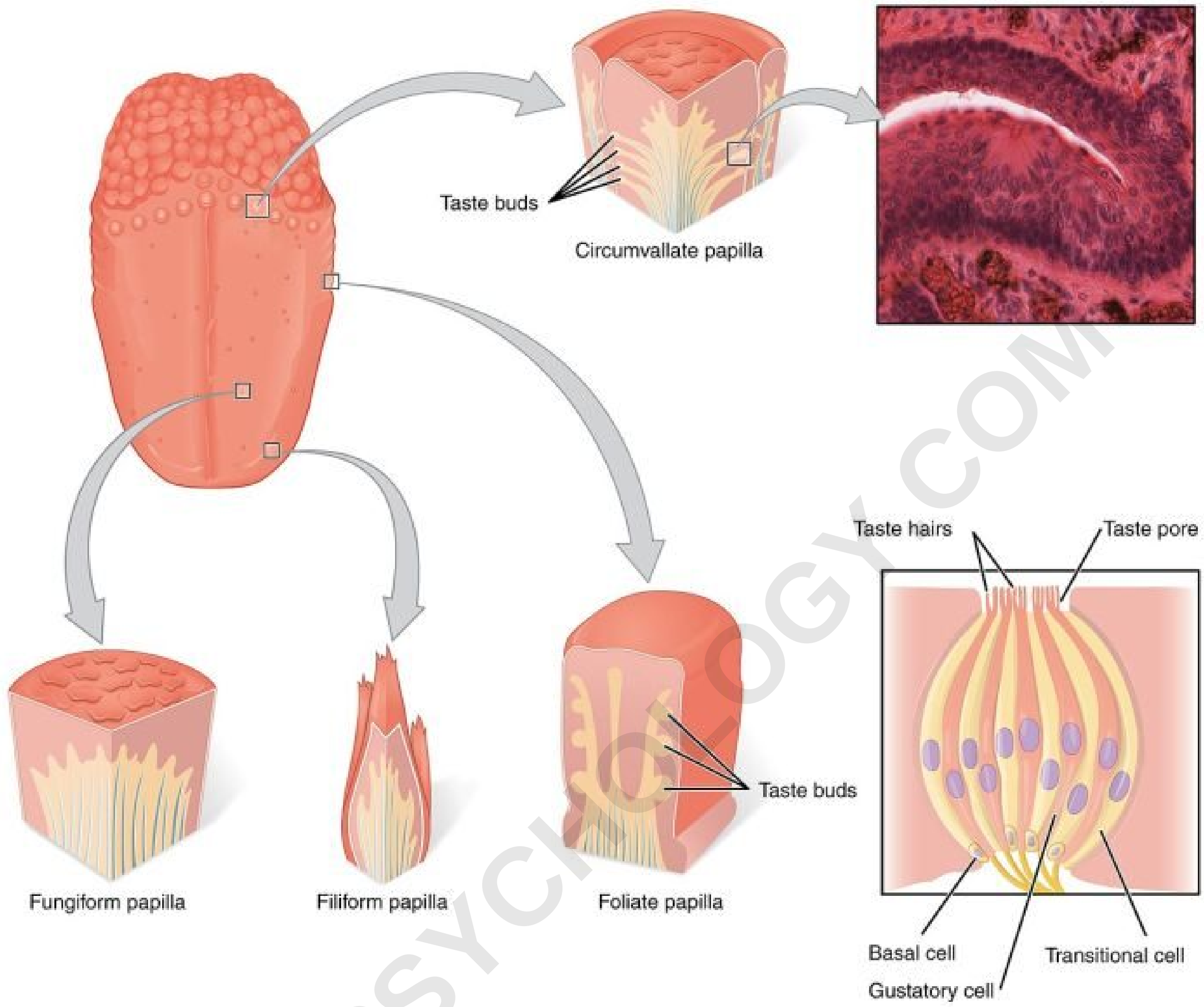

Taste buds and papillae of the tongue

In the human body a stimulus refers to a form of energy which elicits a physiological or psychological action or response. Sensory receptors are the structures in the body which change the stimulus from one form of energy to another. This can mean changing the presence of a chemical, sound wave, source of heat, or touch to the skin into an electrical action potential which can be understood by the brain, the body's control center. Sensory receptors are modified ends of sensory neurons; modified to deal with specific types of stimulus, thus there are many different types of sensory receptors in the body. The neuron is the primary component of the nervous system, which transmits messages from sensory receptors all over the body.

Taste is a form of chemoreception which occurs in the specialised taste receptors in the mouth. To date, there are five different types of taste receptors known: salt, sweet, sour, bitter, and umami. Each receptor has a different manner of sensory transduction: that is, of detecting the presence of a certain compound and starting an action potential which alerts the brain. It is a matter of debate whether each taste cell is tuned to one specific tastant or to several; Smith and Margolskee claim that "gustatory neurons typically respond to more than one kind of stimulus, lthough each neuron responds most strongly to one tastant". Researchers believe that the brain interprets complex tastes by examining patterns from a large set of neuron responses. This enables the body to make "keep or spit out" decisions when there is more than one tastant present. "No single neuron type alone is capable of discriminating among stimuli or different qualities, because a given cell can respond the same way to disparate stimuli." As well, serotonin is thought to act as an intermediary hormone which communicates with taste cells within a taste bud, mediating the signals being sent to the brain. Receptor molecules are found on the top of microvilli of the taste cells.

Sweetness

Sweetness is produced by the presence of sugars, some proteins, and a few other substances. It is often connected to aldehydes and ketones, which contain a carbonyl group. Sweetness is detected by a variety of G protein-coupled receptors coupled to a G protein that acts as an intermediary in the communication between taste bud and brain, gustducin. These receptors are T1R2+3 (heterodimer) and T1R3 (homodimer), which account for sweet sensing in humans and other animals.

Sourness

Sourness is acidity, and, like salt, it is a taste sensed using ion channels. Undissociated acid diffuses across the plasma membrane of a presynaptic cell, where it dissociates in accordance with Le Chatelier's principle. The protons that are released then block potassium channels, which depolarise the cell and cause calcium influx. In addition, the taste receptor PKD2L1 has been found to be involved in tasting sour.

Saltiness

Saltiness is a taste produced best by the presence of cations (such as Na^+, K^+ or Li^+) and is directly detected by cation influx into glial like cells via leak channels causing depolarisation of the cell.

Other monovalent cations, e.g., ammonium, NH_4^+, and divalent cations of the alkali earth metal group of the periodic table, e.g., calcium, Ca^{2+}, ions, in general, elicit a bitter rather than a salty taste even though they, too, can pass directly through ion channels in the tongue.

Bitterness

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only by their ability to taste certain bitter ligands, but also by the morphology of the receptor itself (surface bound, monomeric).

Umami

The amino acid glutamic acid is responsible for umami, but some nucleotides (inosinic acid and guanylic acid) can act as complements, enhancing the taste.

Glutamic acid binds to a variant of the G protein-coupled receptor, producing an umami taste.

Further sensations and transmission

The tongue can also feel other sensations not generally included in the basic tastes. These are largely detected by the somatosensory system. In humans, the sense of taste is conveyed via three of the twelve cranial nerves. The facial nerve (VII) carries taste sensations from the anterior two thirds of the tongue, the glossopharyngeal nerve (IX) carries taste sensations from the posterior one third of the tongue while a branch of the vagus nerve (X) carries some taste sensations from the back of the oral cavity.

The trigeminal nerve (cranial nerve V) provides information concerning the general texture of food as well as the taste-related sensations of peppery or hot (from spices).

Pungency (also spiciness or hotness)

Substances such as ethanol and capsaicin cause a burning sensation by inducing a trigeminal nerve reaction together with normal taste reception. The sensation of heat is caused by the food's activating nerves that express TRPV1 and TRPA1 receptors. Some such plant-derived compounds that provide this sensation are capsaicin from chili peppers, piperine from black pepper, gingerol from ginger root and allyl isothiocyanate from horseradish. The piquant ("hot" or "spicy") sensation provided by such foods and spices plays an important role in a diverse range of cuisines across the world--especially in equatorial and sub-tropical climates, such as Ethiopian, Peruvian, Hungarian, Indian, Korean, Indonesian, Lao, Malaysian, Mexican, New Mexican, Singaporean, Southwest Chinese (including Szechuan cuisine), Vietnamese, and Thai cuisines.

This particular sensation, called chemesthesis, is not a taste in the technical sense, because the sensation does not arise from taste buds, and a different set of nerve fibers carry it to the brain. Foods like chili peppers activate nerve fibers directly; the sensation interpreted as "hot" results from the stimulation of somatosensory (pain/temperature) fibers on the tongue. Many parts of the body with exposed membranes but no taste sensors (such as the nasal cavity, under the fingernails, surface of the eye or a wound) produce a similar sensation of heat when exposed to hotness agents. Asian countries within the sphere of, mainly, Chinese, Indian, and Japanese

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cultural influence, often wrote of pungency as a fifth or sixth taste.

Coolness

Some substances activate cold trigeminal receptors even when not at low temperatures. This "fresh" or "minty" sensation can be tasted in peppermint, spearmint, menthol, ethanol, and camphor. Caused by activation of the same mechanism that signals cold, TRPM8 ion channels on nerve cells, unlike the actual change in temperature described for sugar substitutes, this coolness is only a perceived phenomenon.

Numbness

Both Chinese and Batak Toba cooking include the idea of ? (má or mati rasa), a tingling numbness caused by spices such as Sichuan pepper. The cuisines of Sichuan province in China and of the Indonesian province of North Sumatra often combine this with chili pepper to produce a ?? mál? , "numbing-and-hot", or "mati rasa" flavor. These sensations although not taste fall into a category of Chemesthesis.

Astringency

Some foods, such as unripe fruits, contain tannins or calcium oxalate that cause an astringent or puckering sensation of the mucous membrane of the mouth. Examples include tea, red wine, rhubarb, some fruits of the Syzygium genus, and unripe persimmons and bananas.

Less exact terms for the astringent sensation are "dry", "rough", "harsh" (especially for wine), "tart" (normally referring to sourness), "rubbery", "hard" or "styptic".

When referring to wine, dry is the opposite of sweet, and does not refer to astringency. Wines that contain tannins and so cause an astringent sensation are not necessarily classified as "dry," and "dry" wines are not necessarily astringent.

In the Indian Ayurvedic tradition, one of the six tastes is astringency (kasaaya). In Sinhala and Sri Lankan English it is referred to as kahata.

Metallicness

A metallic taste may be caused by food and drink, certain medicines or amalgam dental fillings. It is generally considered an off flavor when present in food and drink. A metallic taste may be caused by galvanic reactions in the mouth. In the case where it is caused by dental work, the dissimilar metals used may produce a measurable current. Some artificial sweeteners are perceived to have a metallic taste, which is detected by the TRPV1 receptors. Blood is considered by many people to have a metallic taste. A metallic taste in the mouth is also a symptom of various medical conditions, in which case it may be classified under the symptoms dysgeusia or

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parageusia, referring to distortions of the sense of taste, and can be caused by various kinds of medication, including saquinavir and zonisamide, and occupational hazards, such as working with pesticides.

Calcium

The distinctive taste of chalk has been identified as the calcium component of that substance. In 2008, geneticists discovered a CaSR calcium receptor on the tongues of mice. The CaSR receptor is commonly found in the gastrointestinal tract, kidneys, and brain. Along with the "sweet" T1R3 receptor, the CaSR receptor can detect calcium as a taste. Whether closely related genes in mice and humans means the phenomenon exists in humans as well is unknown.

Fattiness (oleogustus)

Recent research reveals a potential taste receptor called the CD36 receptor. CD36 was targeted as a possible lipid taste receptor because it binds to fat molecules (more specifically, long-chain fatty acids), and it has been localized to taste bud cells (specifically, the circumvallate and foliate papillae). There is a debate over whether we can truly taste fats, and supporters of our ability to taste free fatty acids (FFAs) have based the argument on a few main points: there is an evolutionary advantage to oral fat detection; a potential fat receptor has been located on taste bud cells; fatty acids evoke specific responses that activate gustatory neurons, similar to other currently accepted tastes; and, there is a physiological response to the presence of oral fat. Although CD36 has been studied primarily in mice, research examining human subjects' ability to taste fats found that those with high levels of CD36 expression were more sensitive to tasting fat than were those with low levels of CD36 expression; this study points to a clear association between CD36 receptor quantity and the ability to taste fat.

Other possible fat taste receptors have been identified. G protein-coupled receptors GPR120 and GPR40 have been linked to fat taste, because their absence resulted in reduced preference to two types of fatty acid (linoleic acid and oleic acid), as well as decreased neuronal response to oral fatty acids.

Monovalent cation channel TRPM5 has been implicated in fattiness taste as well, but it is thought to be involved primarily in downstream processing of the taste rather than primary reception, as it is with other tastes such as bitter, sweet, and umami.

A 2015 study, proposed naming the taste of fat as "oleogustus". The main form of fat that is commonly ingested is triglycerides, which are composed of three fatty acids bound together. In this state, triglycerides are able to give fatty foods unique textures that are often described as creaminess. But this texture is not an actual taste. It is only during ingestion that the fatty acids that make up triglycerides are broken apart and the taste of fat is revealed. The taste is commonly

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related to other, more negative, tastes such as bitter and sour due to how unpleasant the taste is for humans. Richard Mattes, a co-author of the study, explained that low concentrations of these fatty acids can create an overall better flavor in a food, much like how small uses of bitterness can make certain foods more rounded. However, a high concentration of fatty acids in certain foods is generally considered inedible. To demonstrate that individuals can distinguish oleogustus from other flavors, the researchers separated volunteers into groups and had them try samples that also contained the other basic tastes. Volunteers were able to separate the taste of fatty acids into their own category, with some overlap with umami samples, which the researchers hypothesized was due to poor familiarity with both. The researchers note that the usual "creaminess and viscosity we associate with fatty foods is largely due to triglycerides", unrelated to the taste; while the actual taste of fatty acids is not pleasant. Mattes described the taste as "more of a warning system" that a certain food should not be eaten.

There are few regularly consumed foods rich in oleogustus, due to the negative flavor that is evoked in large quantities. Foods whose flavor to which oleogustus makes a small contribution include olive oil and fresh butter, along with various kinds of vegetable and nut oils.

Heartiness (kokumi)

Some Japanese researchers refer to the kokumi of foods. This sensation has also been described as mouthfulness,:290 and appears to be related to a number of γ-L-glutamyl peptides, which activate a calcium-sensing receptor which is also sensitive to glutathione.

Temperature

Temperature can be an essential element of the taste experience. Food and drink that--in a given culture--is traditionally served hot is often considered distasteful if cold, and vice versa. For example, alcoholic beverages, with a few exceptions, are usually thought best when served at room temperature or chilled to varying degrees, but soups--again, with exceptions--are usually only eaten hot. A cultural example are soft drinks. In North America it is almost always preferred cold, regardless of season.

Starchiness

A 2016 study suggested that humans can taste starch (specifically, a glucose oligomer) independently of other tastes such as sweetness. However, no specific chemical receptor has been yet been found for this taste.

Nerve supply and neural connections

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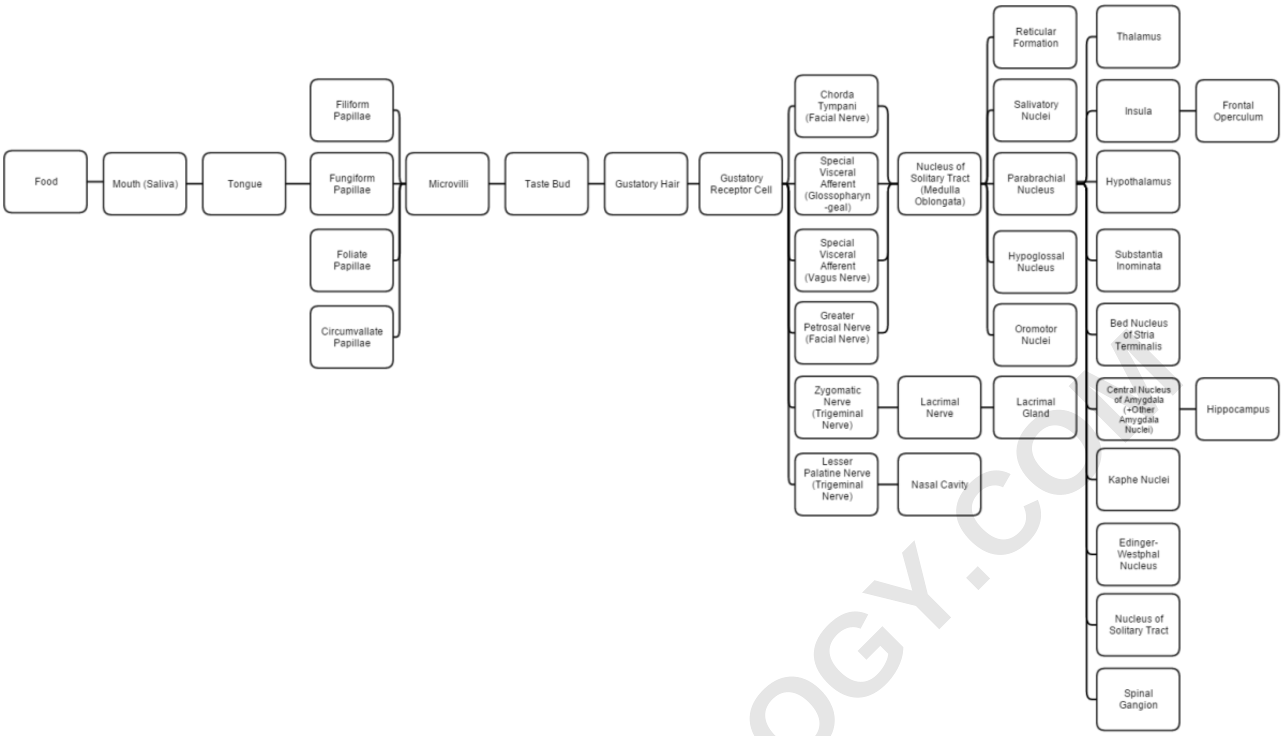

This diagram linearly (unless otherwise mentioned) tracks the projections of all known structures that allow for taste to their relevant endpoints in the human brain.

The glossopharyngeal nerve innervates a third of the tongue including the circumvallate papillae. The facial nerve innervates the other two thirds of the tongue and the cheek via the chorda tympani.

The pterygopalatine ganglia are ganglia (one on each side) of the soft palate. The greater petrosal, lesser palatine and zygomatic nerves all synapse here. The greater petrosal, carries soft palate taste signals to the facial nerve. The lesser palatine sends signals to the nasal cavity; which is why spicy foods cause nasal drip. The zygomatic sends signals to the lacrimal nerve that activate the lacrimal gland; which is the reason that spicy foods can cause tears. Both the lesser palatine and the zygomatic are maxillary nerves (from the trigeminal nerve).

The special visceral afferents of the vagus nerve carry taste from the epiglottal region of the tongue.

The lingual nerve (trigeminal, not shown in diagram) is deeply interconnected with chorda tympani in that it provides all other sensory info from the ? of the tongue. This info is processed separately (nearby) in rostal lateral subdivision of nucleus of the solitary tract (NST).

NST receives input from the amygdala (regulates oculomotor nuclei output), bed nuclei of stria terminalis, hypothalamus, and prefrontal cortex. NST is the topographical map that processes gustatory and sensory (temp, texture, etc.) info.

Reticular formation (includes Raphe nuclei responsible for serotonin production) is signaled to

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release serotonin during and after a meal to suppress appetite. Similarly, salivary nuclei are signaled to decrease saliva secretion.

Hypoglossal and thalamic connections aid in oral-related movements.

Hypothalamus connections hormonally regulate hunger and the digestive system.

Substantia innominata connects the thalamus, temporal lobe, and insula.

Edinger-Westphal nucleus reacts to taste stimuli by dilating and constricting the pupils.

Spinal ganglion are involved in movement.

The frontal operculum is speculated to be the memory and association hub for taste.

The insula cortex aids in swallowing and gastric motility.

Other concepts

Taste as a philosophical concept

Taste can be objective in terms of the five tastes (sweet, salt, sour, bitter, and umami) but it can also be subjective in terms of what we deem "good" and "bad." Taste is "subjective, objective, and qualitative". In terms of it being a philosophical concept, taste is hard to define because it is essentially subjective when pertaining to the personal preferences of individuals i.e. "'de gustibus non est disputandum' (there is no disputing taste)". We cannot tell someone they do not think something tastes good because we do not agree, and vice versa. In order to evaluate taste in this context, we must explore all the ways in which taste can be defined. According to Alan Weiss, taste fulfills the purpose of six functions: taste is the tool in which we use to define flavor; it is also flavor and how we categorize flavor (sweet or salty); it is the preference, we as the tastemakers, place on specific flavors and our demand for those flavors; it is whether we choose to like or dislike a certain taste and therefore allow it into our general society of acceptable tastes or exile it; it is the value in which we place on certain taste (one might believe one's taste in Bach or Rothko earns one capital); and lastly, with good judgement comes good taste and therefore, one with expressively good taste are expected to have good judgement, just as those in bad taste are expected to be in bad judgement.

Supertasters

A supertaster is a person whose sense of taste is significantly more sensitive than average. The cause of this heightened response is likely, at least in part, due to an increased number of fungiform papillae. Studies have shown that supertasters require less fat and sugar in their food to get the same satisfying effects. However, contrary to what one might think, these people actually tend to consume more salt than the average person. This is due to their heightened sense of the taste of bitterness, and the presence of salt drowns out the taste of bitterness. (This also explains why supertasters prefer salted cheddar cheese over non-salted.)

Aftertaste

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Aftertastes arise after food has been swallowed. An aftertaste can differ from the food it follows. Medicines and tablets may also have a lingering aftertaste, as they can contain certain artificial flavor compounds, such as aspartame (artificial sweetener).

Acquired taste

An acquired taste often refers to an appreciation for a food or beverage that is unlikely to be enjoyed by a person who has not had substantial exposure to it, usually because of some unfamiliar aspect of the food or beverage, including a strong or strange odor, taste, or appearance.

Clinical significance

Patients with Addison's disease, pituitary insufficiency, or cystic fibrosis sometimes have a hyper-sensitivity to the five primary tastes.

Disorders of taste
ageusia (complete loss of taste)
hypogeusia (reduced sense of taste)
dysgeusia (distortion in sense of taste)
hypergeusia (abnormally heightened sense of taste)

History

In the West, Aristotle postulated in c. 350 BCE that the two most basic tastes were sweet and bitter. He was one of the first to develop a list of basic tastes.

Ayurveda, an ancient Indian healing science, has its own tradition of basic tastes, comprising sweet, salty, sour, pungent, bitter & astringent.

Similarly, the Ancient Chinese regarded spiciness as a basic taste.

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Research

The receptors for the basic tastes of bitter, sweet and umami have been identified. They are G protein-coupled receptors. The cells that detect sourness have been identified as a subpopulation that express the protein PKD2L1. The responses are mediated by an influx of protons into the cells but the receptor for sour is still unknown. The receptor for amiloride-sensitive attractive salty taste in mice has been shown to be a sodium channel. There is some evidence for a sixth taste that senses fatty substances.

In 2010, researchers found bitter taste receptors in lung tissue, which cause airways to relax when a bitter substance is encountered. They believe this mechanism is evolutionarily adaptive because it helps clear lung infections, but could also be exploited to treat asthma and chronic obstructive pulmonary disease.

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