A Matter of Taste
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Tell me what you eat, and I shall tell you what you are.
—Jean-Anthelme Brillat-Savarin, 1825

The ability to taste is critical for the survival of most vertebrates and plays a key role in their nutrition and social behavior. The widespread human predilection for sweet- and salty-tasting substances and the equally widespread dislike for things that taste bitter or sour reflect inborn mechanisms of ancient phylogenetic origin. It is generally assumed that these sensibilities developed as protective mechanisms. Thus, many naturally occurring poisons are bitter tasting, while foods that are rich sources of calories are often sweet tasting, and salt is needed to maintain the balance of electrolytes vital to body functions. Inborn preferences and aversions can, however, be markedly altered in omnivorous animals (those that eat both plant and animal foods); the capacity to change these basic preferences is an adaptive advantage that allows for the exploitation of novel foods and diverse habitats, as is sometimes required when seasonal shortages occur in specific food sources. Interestingly, data from animal studies suggest that some taste preferences may be learned in utero or during suckling and can reflect components of the mother’s diet.

**Flavor—taste and smell working together**

Flavor is by far the single most important factor in determining human food choices. For this reason, dysfunction of the gustatory (taste) system can be very debilitating. Indeed, in extreme cases disturbances in taste function can lead to malnutrition and even starvation and death.

Although the senses of taste and smell work together in contributing to flavor sensations, the two sensory systems are anatomically and functionally distinct. In the case of taste, specific chemicals are detected by the taste buds, which are located within the oral cavity; the derived sensations are largely limited to those of sweet, sour, bitter, salty, and perhaps metallic. In the case of olfaction (smell), a much broader range of chemicals can be detected. The olfactory receptors are located within an area of specialized tissue high in the nose; sensations derived through the sense of smell can number in the thousands.

Most flavor sensations commonly referred to as taste actually result from the stimulation of the olfactory receptors by odor-laden air forced during chewing and swallowing from the rear of the oral cavity into the higher recesses of the nose. The list of foods and beverages whose “taste” is olfactory in origin is extensive and includes such flavors as chocolate, vanilla, grape, lemon, coffee, pizza, chicken, peanut butter, onion, cheese, and pineapple. One can make a simple demonstration of the dependence of such sensations on olfaction by holding the nose while eating or drinking a food or beverage containing one of the above flavors; the “taste” readily disappears (because active movement of air from the oral cavity to the rear of the nasal cavity is prevented), even though the characteristic texture, temperature, sweetness, saltiness, sourness, or bitterness remains.

The human taste bud consists of specialized cells that form a budlike structure with a small opening—the taste pore—through which a taste stimulus, or tantant, can enter. Tastants interact with portions of the membrane covering tiny fingerlike extensions (microvilli) of cells located within the taste bud. This physical interaction, in turn, induces biochemical events that ultimately send impulses to the brain via nerve fibers, signaling the taste sensations. Taste buds are dynamic in that their cells undergo birth, maturation, development of sensory responsiveness, old age, and death within the time span of a week or two. Connections between the sensory elements of the bud and the nervous system are also dynamic; nerve branches are continuously sprouting new processes, or extensions, to connect to young taste cells and withdrawing such connections from old taste cells. Taste buds are found
in all vertebrates and in some, for example, the catfish, are located over the entire surface of the body. In human newborns taste buds are found in large numbers on the inside of the lips and cheeks, as well as on the tongue, palate, and oropharynx (area between the mouth and the esophagus). This distribution changes during development so that by adulthood few taste buds are present on the lips or cheeks.

The majority of human taste buds are located on or around papillae—peglike protuberances distributed across the surface of the tongue. There are different kinds of papillae on different parts of the tongue. Several thousand taste buds are often found distributed among the 200–500 fungiform papillae on the anterior, or forwardmost, part of the tongue. The 8 to 12 circumvallate papillae, located along a chevron-shaped border between the anterior two-thirds of the tongue and the posterior one-third, contain about 250 taste buds apiece. Additional taste buds are located on the soft palate, pharynx, epiglottis (structure that covers the tracheal opening), and upper third of the esophagus. In some humans the foliate papillae, located along the posterior lateral (side) surfaces of the tongue also contain taste buds. Both behavioral and electrophysiological data suggest that the front of the tongue is more sensitive to sweet and salty stimuli, whereas the back of the tongue is more sensitive to sour and bitter stimuli.

### Dysfunctions of taste

A number of diseases and medications are associated with dysfunctions of taste; however, total loss of the ability to detect sweet, sour, bitter, and salty sensations is relatively rare. Unlike the olfactory receptors, which are innervated by the olfactory nerves, the taste buds are innervated on each side of the oral cavity by several cranial nerves, which are much less likely than the olfactory nerves to be damaged by trauma. In recent study of 750 patients evaluated for smell and taste dysfunction at the Smell and Taste Center of the Hospital of the University of Pennsylvania, fewer than 4% had evidence of even partial loss of taste function despite the fact that 67% complained of loss of taste and smell and 10% reported loss of taste unaccompanied by loss of smell. Typically, such reports of loss of taste reflect loss of flavor sensations resulting from decreased olfactory function.

Despite the rarity of true taste loss, about one-third of the patients in the study complained of strange taste sensations (known as dysgeusias), a condition second in frequency only to pain as a sensory symptom in patients seen by dentists and other oral health specialists. Of these individuals, 40% reported that chemosensory stimulation (e.g., that induced by food during eating) was not required for the elicitation of the strange taste. An upper respiratory infection or cough was associated with 23% of these cases, head trauma with 18%, and nasal sinus disease with 8%. Dental procedures (e.g., tooth extraction), medications, and oral exposure to toxic chemicals (usually the result of an occupational accident or the accidental swallowing of acids, cleaning products, and so forth) accounted for about 8% of the cases. The probable causes of the remaining cases were unknown. Although most dysgeusias were reported as producing sour, bitter, salty, or metallic taste sensations, a number of people complaining about a taste problem did not experience any true taste sensations, suggesting that some kind of dysgeusia may actually reflect distortions in smell function misperceived as distortions in taste.

The physiological bases for most cases of dysgeusia and hypogeusia (lessened taste sensitivity) are poorly understood; however, there are straightforward remedies for certain taste problems.

- Vitamin and mineral (e.g., iron) deficiencies, as well as certain medications (e.g., antibiotics, cancer chemotherapy agents, and anticholinergic medications), can result in depapillation of the tongue and can be reversed by the taking of the appropriate vitamin or discontinuation of the medication.
- When an individual has fillings and dental prostheses made of different types of metals, electric currents, perceived as metallic tastes, can be set up in the mouth; this problem can be corrected by replacing the fillings or prostheses with ones composed of only a single type of metal or with nonmetallic substances.
A taste loss is sometimes reported by patients undergoing radiation treatment for head and neck cancer. This is believed to be due to radiation-induced damage to the taste-receptor cells. Usually patients recover their sense of taste within two to four months after the last radiation treatment.

The lessened taste function associated with cigarette smoking or poor oral hygiene can be reversed, to some degree, by cessation of smoking and improved hygienic measures.

Taste alterations are sometimes associated with acute liver disease but usually disappear following recovery from illness.

Fungal infections in the mouth and other oral infections may cause symptoms of lessened or altered taste perception; treatment of the disorder usually restores normal taste function.

Inherited taste deficits
Genetically determined deficits in the ability to detect specific types of tastants have been reported, although such insensitivities are rarely recognized as such by individuals experiencing them. The best example of a deficit of this type is the inability to taste a class of bitter-tasting compounds commonly found in edible plants of the *Brassica* genus, including kale, turnips, cabbage, and brussels sprouts. The prototype taste stimulus of this class is the chemical compound phenylthiocarbamide (PTC; also termed phenylthiourea), which may be either bitter or tasteless depending on the genetic makeup of the individual who ingests it. Among Caucasians in Western Europe and North America, about 30% of the population are nontasters. The percentage of nontasters is much lower in other populations that have been tested. Since such bitter-tasting compounds inhibit the synthesis of thyroid hormone and, as a result, permit the pituitary gland to secrete large amounts of thyroid-stimulating hormone, their ingestion can lead to the development of a goiter (enlargement of the thyroid gland). In a study of people in highland Peru, "tasters"—those who experienced the bitter taste—avoided foodstuffs containing these compounds (for example, bread made from a local grain) and therefore did not have goiters; their nontasting counterparts did. The nontasting gene, however, is associated with protection against malaria, a possible reason why it continues to exist in the gene pool. Some data suggest that PTC taster status is associated with the type of thyroid disorder that persons develop.

Another example of a specific taste deficit that has some medical significance is observed in people with diabetes and some of their close relatives. Patients with late-onset diabetes (type II, non-insulin-dependent diabetes mellitus) not only have an abnormality in insulin release in response to the sugar glucose but are also less sensitive than normal to the taste of this sugar. Some first-degree relatives of these individuals with diabetes, none of whom have diabetes themselves, also have decreased taste sensitivity to glucose but not to the closely related sugar fructose. This observation suggests that late-onset diabetes may be caused by a biochemical abnormality that influences both the endocrine and taste systems. Further support for this hypothesis comes from the finding that one form of glucose (alpha-D-glucose), which is known to be more potent in releasing insulin than another form (beta-D-glucose), elicits stronger sweet taste sensations. More research is needed to test the intriguing hypothesis that the nondiabetic relatives who have decreased glucose taste sensitivity will themselves eventually develop late-onset diabetes.

Taste perception and obesity
Obese individuals have great difficulty inhibiting their consumption of calorically dense sweet-tasting foods. The role played by taste in the development of obesity is, at present, poorly understood. Recent data suggest that markedly obese persons show a greater liking than nonobese persons for complex carbohydrate-fat mixtures (milk shakes, for example) and that their taste sensitivity, per se, is not different from that of their nonobese counterparts. However, in studies using simpler, sweeter test substances (e.g., sweetened water), obese patients reported less of a preference for solutions with higher sugar-concentration levels than with lower levels; furthermore, the rated disliking of such solutions correlated directly with the subject's percentage of body fat. Since sugary-sweet test solutions are generally less palatable than milk shakes and other typical high-calorie food items, it is conceivable that, compared with normal-weight people, obese people are more particular about taste and thereby find these simple sweet-tasting solutions to be relatively less pleasant. Another possible interpretation may be that obese individuals are reluctant to rate sweet-tasting liquids as pleasant in experimental settings where the goal is to achieve weight loss.

Salt taste and health
Salt (sodium chloride), the substance that is widely used as a preservative and seasoning agent, provides the sodium essential for basic bodily functions, including nerve conduction, acid-base balance, cardiovascular tone, and muscle contraction. Not surprisingly, there are both behavioral and physiological mechanisms that maintain an appropriate level of sodium in the body. If too much salt is ingested, the kidney compensates by excreting sodium in the urine. If too little sodium is present in bodily fluids, conservation mechanisms come into play to inhibit sodium excretion.

Salt-deficient animals (including those whose requirement for salt is produced by failure or removal of the adrenal glands) search out sources of salt and
show a strong preference for salty-tasting foods or liquids. This is commonly observed in such herbivores as cattle and deer, whose plant diets usually do not contain adequate levels of salt. Similar cravings for salt are observed in human patients whose adrenal glands fail to produce necessary hormones.

Numerous studies link excesses in sodium consumption to essential hypertension (high blood pressure of unknown cause), a condition associated with coronary heart disease, stroke, and congestive heart failure. One widely cited estimate of the sodium requirement of humans is 0.25 g per day; however, the average consumption of salt in the United States is from 6 to 18 g per day. Presumably, this high salt intake is a result of the large amounts of salt that are put into processed foods and the widespread popularity of salty "junk" foods.

Recent data suggest that salt preferences, but not sensitivity to salt, are acquired and thus can be altered by dietary factors. Persons placed on a low-sodium diet (which is, nonetheless, above the minimum level required for good health) exhibit, within a time span of two to four months, a preference for lower levels of salt, whereas people whose dietary sodium is increased actually come to prefer higher levels of salt. However, the preference for increased amounts of salt develops only when salt is added directly to the subjects' food. If the intake of salt is increased by administration of a salt tablet, which is swallowed but not tasted, no corresponding preference for saltier-tasting food is observed. This finding suggests that sensory experience is somehow involved in altering the preference for salt.

Scientists speculate that there may be an association between kidney function and salt-taste sensitivity, possibly analogous to the association between diabetes and glucose-taste sensitivity. Thus, when drops of amiloride (a drug that blocks sodium uptake by the kidney) are applied to an individual's tongue, he or she experiences a decrease or block in salt-taste perception, suggesting that blockage of the sodium channels associated with salt-taste function may be involved in altering salt-taste perception. Whether adding or subtracting salt to foods directly influences either the number or responsiveness of these sodium channels is unknown.

Learned taste aversions
As was demonstrated by the Russian physiologist Ivan Pavlov at the turn of the 19th century in his classic experiments with dogs, salivary and gastric secretions are produced as reflexes in the presence of various sensory stimuli. Possibly because of the unconditional nature of the relationship between oral sensory stimulation and oral and gastric secretory activity, tastes are very potent inducers of alterations within the digestive system; indeed, such reflex action may possibly trigger the preingestive (cephalic) period of insulin secretion, which occurs before food has had time to be digested in the stomach or intestines. Clinically, it has long been known that lemon juice is useful for testing salivary reflexes, for increasing the secretion of saliva, and for aiding in the diagnosis of such conditions as xerostomia (dry mouth).

There are important clinical applications for the finding that aversions to specific food items can be conditioned by the pairing of certain tastes and flavors with unpleasant gastric events, such as nausea and vomiting, even though these events may occur long after the ingestion of the food. Studies show that people develop profound distastes for foods coincident with gastrointestinal illness (especially protein-rich foods such as eggs, fish, and meat). In addition, strong food aversions readily develop in children and adults undergoing radiotherapy or chemotherapy for cancer, both of which produce nausea as a common side effect. Research performed at the University of Washington has shown that such conditioning is particularly potent for novel food items and can occur even when (1) the new food is presented only once, (2) a number of chemotherapy treatments have been previously administered, (3) an interval of many hours occurs between the eating of the food and the onset of the gastrointestinal distress, and (4) the patient is aware that the nausea and vomiting are a result of the therapy and not of the ingestion of the newly introduced food. Interestingly, the development of an aversion to a new food can block the development of an aversion to more familiar foods eaten at the same time. This finding has an important clinical application: patients about to undergo chemotherapy can be purposely exposed to new foods, which then serve as "scapegoats," protecting familiar foods from becoming targets of learned taste aversions.

The future of taste research
The diverse phenomena described above illustrate the fact that taste disorders are of clinical significance and suggest that quantitative taste testing may prove to be of use in the early diagnosis of diabetes and other diseases. Formal chemosensory testing will undoubtedly become commonplace in major medical centers in the near future, coincident with the growing realization that taste and smell disorders, like disorders of vision, hearing, and movement, have a significant impact on the well-being of the individual. Future research is likely to focus on factors that (1) influence the development of flavor preference, (2) cause age-related changes in taste and smell perception, and (3) enhance the palatability of beverages and foodstuffs. There will also be significant advances in the understanding of the complex workings of the sensory systems of taste and smell.