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Our response to the food when we consume is a combination of visual, tactile, thermal, taste and aroma. Frequently our first interaction with a food is visual or to the aroma of the food. When we put it in our mouth we respond to the temperature, texture (tactile) and taste response. In this chapter we will consider the taste and aroma responses. In recent years, the understanding of taste and smell has increased exponentially.

Hall (1968) defined flavor as follows: “Flavor is the sensation produced by a material taken in the mouth, perceived principally by the senses of taste and smell, and also by the general pain, tactile and temperature receptors in the mouth. Flavor denotes the sum of the characteristics of the material which produce that sensation.” More recently, the International Organization for Standardization (2008) characterized flavor as a “complex combination of the olfactory, gustatory and trigeminal sensations perceived during tasting. The flavor may be influenced by tactile, thermal, painful and/or kinaesthetic effects.” Although the senses of taste and smell are the principal systems for distinguishing flavor in foods, other sensory cues contribute to the overall sensation of flavor. For example, texture has a very definite effect on our perception of taste. Smoothness, roughness, granularity, and viscosity can all influence flavor, as can hotness of spices, coolness of menthol, brothiness or fullness of certain amino acids, and the tastes described as metallic and alkaline. In addition,

flavor perception is affected by visual cues (colors and images) as well as auditory cues (background sound and biting/drinking-induced sound) (DuBose et al. 1980; Spence 2012).

The senses of taste and smell give animals or humans the ability to evaluate what they eat and drink. This evaluation helps animals and humans to promote ingestion of nutritious substances and prevent consumption of potential poisons or toxins. Animals, including humans, develop taste and smell preferences, which is the ability to choose certain types of food in *preference* to others. Taste and smell preferences can change with differing body needs and dietary interactions. The senses of taste and smell also motivate us to eat by seeking the nutrients and energy such as fat and sugar. However, likings of sugar and fat vary with genotype, as well as individual experiences and environmental factors. Animals often develop food aversions, particularly if they become ill soon after eating a certain food, even though that food was not the cause of the illness. Food preferences and aversions involve the senses of taste and smell, and these phenomena are almost certainly mediated through the central nervous system. In addition, by sniffing off-odors or tasting bitterness or sourness, the senses of taste and smell help us to avoid ingesting harmful foods containing toxic, microbes, microbial by products, or chemical contamination (Reed and Knaapila 2010).

Traditionally we are taught that there are five basic taste responses on the tongue; salt, acid,

sweet, bitter, and umami. Each taste quality has a specific role in the detection of nutritious as well as poisonous substances; sweet taste for carbohydrate sources of calories, umami for protein and amino acid contents, salty for mineral contents, and sour for fruits ripeness and spoiled foods, and bitter for harmful compounds (Iwata et al. 2014). Many earlier textbooks and journal articles cite the “tongue map” suggesting that different areas of the tongue are sensitive to specific tastes as show in Fig. 7.1. However, all taste qualities are sensitive across the area of tongue.

The interactions of foods with saliva can also have a major influence on our perception of tasting substances. Saliva acts as a solvent for taste substances as well as a diffuser of the solutes to the taste receptor sites. Salivar also acts as a buffer for acidic foods and may bind with bitter taste substances. In addition, some salivary constituents alter taste sensitivity by continuously stimulating the taste receptors, and salivar also protect the taste receptors from dryness, bacterial infection, and disuse atrophy (Matsuo 2000).

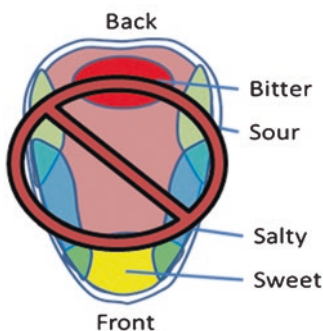
Taste is the response to dissolved molecules and ions called tastants. Taste is detected when tastants interact with taste receptor cells. These cells are clustered in taste buds on the tongue and scattered in other areas of the body, for example the nasal epithelium, the trachea, the stomach, and the intestines (Finger and Kinnamon 2011). Sweet taste receptors (T1Rs) are found in cells of the duodenum. When sugars reach the duodenum, the cells respond by releasing incretins,

causing the pancreas beta cells, located in the islets of Langerhans, to increase the release of insulin (Laffitte et al. 2014). Bitter taste receptors (T2Rs) are found in the cilia of human bronchial and sinonasal epithelial cells where they can serve to cause a response to expel inhaled irritants (Shah et al. 2009).

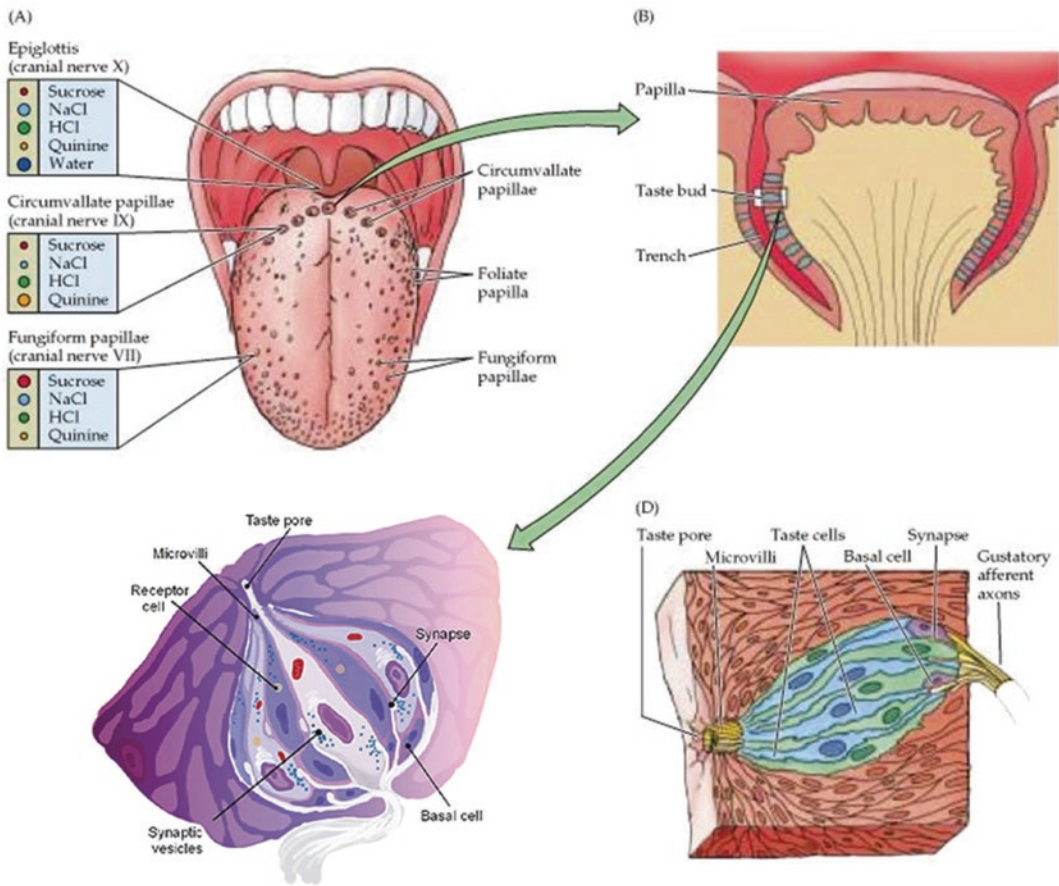
Traditionally various areas of the tongue were considered to be responsible for the perception of the basic tastes. More recent studies have demonstrated that taste buds contain 50–120 taste cells with multiple receptors for all five basic tastes. Each taste cell has receptors on its apical surface that are **transmembrane proteins**. These proteins admit the ions that give rise to the sensations of salty and sour tastes as well as bind to the molecules that elicit the sensations of sweet, bitter, and umami tastes (Engelen 2010).

The various types of taste cells are located within taste buds. These structures are predominantly located on the tongue and soft palate. Most of the taste buds on the tongue are located within tiny projections on the tongue called papillae. The predominant papillae on the tongue are the filiform or threadlike structures that do not contain taste buds. The filiform structures are involved in somatosensory and mechanical functions. The taste buds are found on the fungiform papillae on the anterior two-thirds of the tongue. The fungiform papillae are the most noticeable and typically contain one or more taste buds. The circumvallate papillae are located on the dorsal side of the tongue and the foliate papillae are found in small trenches located on the sides of the rear of the tongue (Fig. 7.2).

Taste buds are onion-shaped structures composed of between 50 and 100 taste cells. Each taste cell has finger-like projection called a microvilli. The microvilli protrude through an opening at the top of the taste bud referred to as the taste pore. Food chemicals called tastants which are dissolved in the saliva contact the taste cells through the taste pore. They then interact with proteins on the surfaces of the cells known as taste receptors or with pore like proteins called ion channels. These interactions cause electrical changes in the taste cells that send chemical signals to adjacent neurons ultimately resulting in



**Fig. 7.1** Misinterpreted tongue map suggesting four basic tastes are sensitive on specific regions of the tongue. The basic tastes are sensitive on every part of the tongue



**Fig. 7.2** Taste buds and the cranial nerves of the tongue. (a) Distribution of taste papillae on the dorsal surface of the tongue. Different responses to sweet, salty, sour, and bitter tastants recorded in the three cranial nerves (VII, IX, and X) that innervate the tongue and epiglottis are indicated at *left* (a). The size of the circles representing sucrose, NaCl, HCl, quinine, and water corresponds to the relative response of the papillae to these stimuli. (b)

Diagram of a circumvallate papilla showing location of individual taste buds. (c) Light micrograph of a taste bud. (d) Diagram of a taste bud, showing various types of taste cells and the associated gustatory nerves. The apical surfaces of the receptor cells have microvilli that are oriented toward the taste pore (reference source of Fig. 7.2 is missing: <http://www.uth.tmc.edu/courses/dental/smell-taste/taste.html?>)

impulses to the brain. The electrical changes in the taste cells that result in signals to the brain are dependent on the concentrations of the ions. Like neurons, taste cells have a net negative charge internally and a net positive charge externally. Tastants bind to the taste cells, the concentration of positive ions inside cells increases, eliminating the net charge differences internally and externally. This depolarization causes the taste cells to release chemical signals called neurotransmitters, which cause neurons connected to the taste cells to transmit electrical messages to the brain.

The responses to bitter and sweet tastes by the taste cells are not always closely correlated with the chemical structure of the tastant molecule. Many carbohydrates, particularly simple sugars are sweet, but others are not sweet at all. Many non-carbohydrate molecules result in a sweet taste response. For example, chloroform, stevaside, saccharin and aspartame all cause sweet responses. None of these molecules has any common structure with sweet sugars. Compounds that result in salty or sour tastes are less diverse because they are generally ions such as hydrogen

ions for sour and sodium for salty taste. The chemicals that produce salty and sour tastes act directly through ion channels, whereas those responsible for sweet and bitter tastes bind to surface of the receptor. The receptors then signal the cells which cause the opening and closing of ion channels. Gustducin is a G-protein that converts the electrical impulse to a signal. Gustducin is referred to as a G-protein, which is found on the underside of many different receptors. The term G-protein is used because the activity of such proteins is regulated by guanosine triphosphate, GTP. When a tastant molecule binds to a taste cell receptor, it prompts the subunits of gustducin to split apart and carry out biochemical reactions that ultimately open and close ion channels and make the cell interior more positively charged.

Within a taste bud, there is a network of dendrites of sensory nerves called “taste nerves.” Taste cells are stimulated by the binding of chemicals to their receptors causing the taste cell to become depolarized, this depolarization is transmitted to the taste nerve fibers resulting in a potential that is ultimately transmitted to the brain. The nerve transmission rapidly adapts after the initial stimulus, and a strong discharge is observed in the taste nerve fibers but within a few seconds. That response diminishes to a steady-state level of much lower amplitude. We know that binding between stimulus and receptor is a weak one because no irreversible effects have been observed. A mechanism of taste stimulation

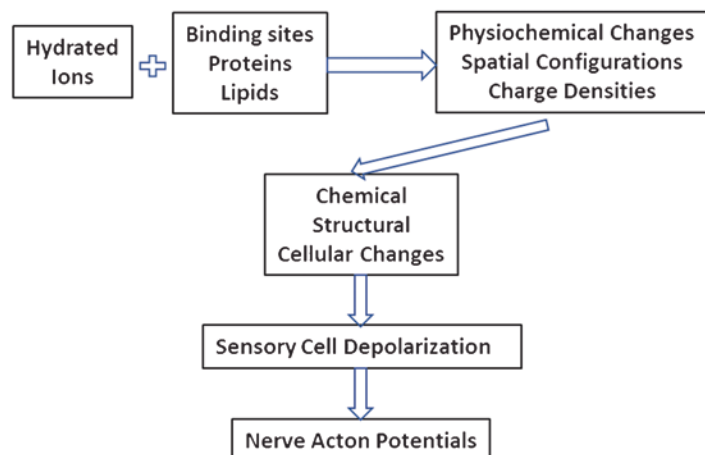
with electrolytes has been proposed by Beidler (1957); it is shown in Fig. 7.3. The time required for taste response to take place is in the order of 25 ms. The taste molecule is weakly adsorbed, thereby creating a disturbance in the molecular geography of the surface and allowing an interchange of ions across the surface. This reaction is followed by an electrical depolarization that initiates a nerve impulse.

The taste receptor mechanism has been more fully described by Kurihara (1987). The process from chemical stimulation to transmitter release is schematically presented in Fig. 7.4. The receptor membranes contain voltage-dependent calcium channels. Taste compounds contact the taste cells and depolarize the receptor membrane; this depolarization spreads to the synaptic area, activating the voltage-dependent calcium channels. Influx of calcium triggers the release of the transmitter norepinephrine.

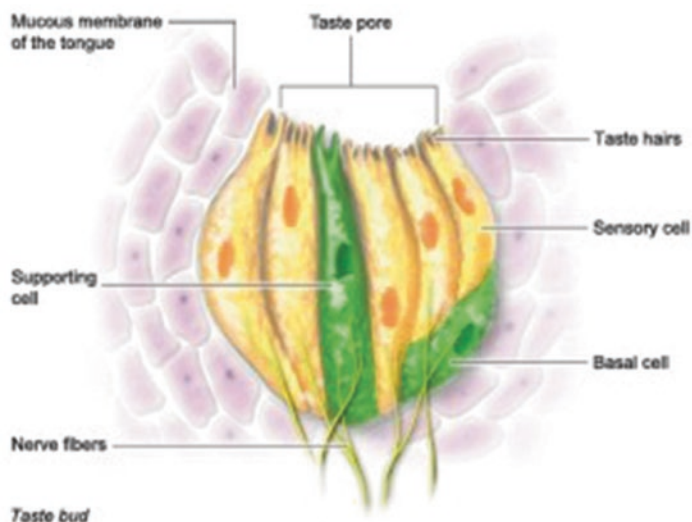
The relationship between stimulus concentration and neural response is not simple. As the stimulus concentration increases, the response increases at a decreasing rate until a point is reached where further increase in stimulus concentration does not produce a further increase in response. Beidler (1954) proposed the following equation relating magnitude of response and stimulus concentration:

$$\frac{C}{R} = \frac{C}{R_s} + \frac{1}{KR_s}$$

**Fig. 7.3** Mechanism of taste stimulation as proposed by Beidler. *Source:* From L.M. Beidler, Facts and Theory on the Mechanism of Taste and Odor Perception, in *Chemistry of Natural Food Flavors*, 1957, Quartermaster Food and Container Institute for the Armed Forces



**Fig. 7.4** Diagram of a taste cell (reference source: <http://scienceinit.in/2016/03/31/how-do-we-taste>)



where

$C$  = stimulus concentration

$R$  = response magnitude

$R_s$  = maximum response

$K$  = equilibrium constant for the stimulus- receptor reaction

$K$  values reported by Beidler for many substances are in the range of 5–15.

It appears that the initial step in the stimulus-receptor reaction is the formation of a weak complex, as evidenced by the small values of  $K$ . The complex formation results in the initiation of the nerve impulse. Because of the decreasing rate of response, we know that the number of receptor sites is finite. The taste response is a function of the proportion of sites occupied by the stimulus compound.

According to Beidler (1957), the threshold value of a substance depends on the equilibrium constant and the maximum response. Since  $K$  and  $R_s$  both vary from one substance to another and from one species to another, the threshold also varies between substances and species. The concentration of the stimulus can be increased in steps just large enough to elicit an increase in response. This amount is called the just noticeable difference (JND).

There appear to be significant age- or sex-related differences in taste sensitivity, and especially heavy smoking (more than 20 cigarettes per day) results in a deterioration in taste responsiveness with age.

Differences in taste perception between individuals seem to be common. Peryam (1963) found that sweet and salt are usually well recognized. However, with sour and bitter taste some difficulty is experienced. Some tasters ascribe a bitter quality to citric acid and a sour quality to caffeine.

Recent studies have demonstrated that taste-signalling molecules are distributed not only in the gustatory epithelium, but also in other tissues, including the gastrointestinal tract, airways, testes and brain. Taste signalling mechanisms in the gastrointestinal tract have been found to participate in detecting sweet, umami and bitter compounds. It has been proposed that tastant/nutrient detection by other systems contributes to the behavioural responses to food intake (Iwatsuki and Torii 2012).

The bitter taste receptor (TAS2R)-family of G-protein-coupled receptors has been identified on the tongue as detectors of bitter taste. In the last few years, they have been discovered in extra-oral tissues, including the airways, the gut, the brain and even the testis. In tissues that contact the exterior, protective functions for

TAS2Rs have been proposed, in analogy to their function on the tongue as toxicity detector. However, TAS2Rs have also been found in internal organs, suggesting other roles for these receptors, perhaps involving as yet unidentified endogenous ligands. The current review gives an overview of the different proposed functions for TAS2Rs in tissues other than the oral cavity; from appetite regulation to the treatment of asthma, regulation of gastrointestinal motility and control of airway innate immunity (Avau and Depoortere 2016).

Once taste signals are transmitted to the brain, several neural pathways are activated that influence digestive function. Tasting food is followed rapidly by increased salivation and by low level secretory activity in the stomach.

## Taste Sensations

The sense of taste is equivalent to excitation of taste receptors. Taste receptors for a large number of specific chemicals have been identified which contribute to the reception of taste. Five basic types of tastes are recognized by humans:

- Sweet—usually indicates energy rich nutrients.
- Bitter—allows sensing of diverse natural toxins.
- Salty—allows modulating diet for electrolyte balance.
- Sour—typically the taste of acids.
- Umami—the taste of amino acids (e.g., meat broth or aged cheese).

None of these tastes are elicited by a single chemical. There are thresholds for detection of taste that differ among chemicals that deliver similar taste. For example, sucrose, 1-propyl-2-amino-4-nitrobenzene and lactose all taste sweet to humans, but the sweet taste is elicited by these chemicals at concentrations of roughly 10 mM, 2  $\mu$ M and 30 mM respectively—a range of potency of roughly 15,000-fold. Substances sensed as bitter typically have very low thresholds. Table 7.1 illustrates the relative threshold concentrations of various types of tastants.

**Table 7.1** Taste thresholds for basic taste sensations

Examples of human taste thresholds		
Taste	Substance	Threshold for tasting
Salty	NaCl	0.01 M
Sour	HCl	0.0009 M
Sweet	Sucrose	0.01 M
Bitter	Quinine	0.000008 M
Umami	Glutamate	0.0007 M

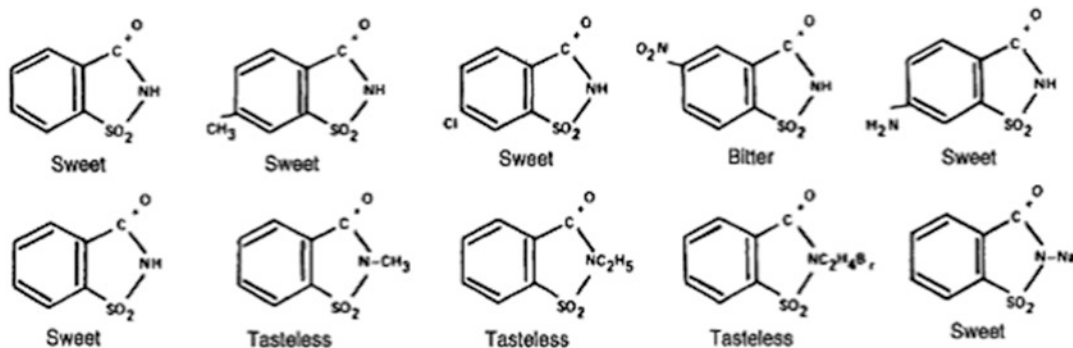
(Source: rbowen@colostate.edu)

The taste cells transduce the stimuli from tastants and provide the identity, concentration, and pleasant or unpleasant quality of the tastant. This information is translated to the gastrointestinal system causing salivation and swallowing (or gagging and regurgitation if the substance is noxious). The temperature and texture of food is relayed from the mouth via somatic sensory receptors from the trigeminal and other sensory cranial nerves to the thalamus and somatic sensory cortices. Food is not simply eaten for nutritional value; taste perception also depends on cultural backgrounds and psychological factors (Purves et al. 2001).

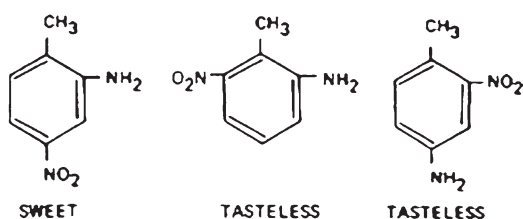
## Chemical Structure and Taste

A first requirement for a substance to produce a taste is that it be water soluble. The relationship between the chemical structure of a compound and its taste is more easily established than that between structure and smell. In general, all acid substances are sour. Sodium chloride and other salts are salty, but as constituent atoms get bigger, a bitter taste develops. Potassium bromide is both salty and bitter, and potassium iodide is predominantly bitter. Sweetness is a property of sugars and related compounds but also of lead acetate, beryllium salts, and many other substances such as the artificial sweeteners saccharin and cyclamate. Bitterness is exhibited by alkaloids such as quinine, picric acid, and heavy metal salts.

Minor changes in chemical structure may change the taste of a compound from sweet to bitter or tasteless. For example, Beidler (1966) has examined saccharin and its substitution compounds. Saccharin is 500 times sweeter than sugar (Fig. 7.5). Introduction of a methyl group or of chloride in the *para* position reduces the



**Fig. 7.5** The effect of substitutions in saccharin on sweetness. *Source:* From L.M. Beidler, Chemical Excitation of Taste and Odor Receptors, in *Flavor Chemistry*, I. Hornstein, ed., 1966, American Chemistry Society



**Fig. 7.6** Taste of nitrotoluidine isomers

sweetness by half. Placing a nitro group in the *meta* position makes the compound very bitter. Introduction of an amino group in the *para* position retains the sweetness. Substitutions at the imino group by methyl, ethyl, or bromoethyl groups all result in tasteless compounds. However, introduction of sodium at this location yields sodium saccharin, which is very sweet.

The compound 5-nitro-*o*-toluidine is sweet. The positional isomers 3-nitro-*o*-toluidine and 3-nitro-*p*-toluidine are both tasteless (Fig. 7.6). Teranishi et al. (1971) provided another example of change in taste resulting from the position of substituent group: 2-amino-4-nitro-propoxybenzene is 4000 times sweeter than sugar, 2-nitro-4-amino-propoxybenzene is tasteless, and 2,4-dinitro-propoxybenzene is bitter (Fig. 7.7). Dulcin (*p*-ethoxyphenylurea) is extremely sweet, the thiourea analog is bitter, and the *o*-ethoxyphenylurea is tasteless (Fig. 7.8).

Just as positional isomers affect taste, so do different stereoisomers. There are eight amino acids that are practically tasteless. A group of three has varying tastes; except for glutamic acid,

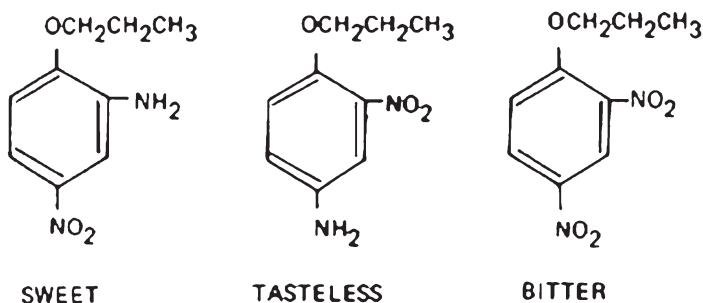
these are probably derived from sulfur-containing decomposition products. Seven amino acids have a bitter taste in the L form or a sweet taste in the D form, except for L-alanine, which has a sweet taste (Table 7.2). Solms et al. (1965) reported on the taste intensity, especially of aromatic amino acids. L-tryptophan is about half as bitter as caffeine; D-tryptophan is 35 times sweeter than sucrose and 1.7 times sweeter than calcium cyclamate. L-phenylalanine is about one-fourth as bitter as caffeine; the D form is about seven times sweeter than sucrose. L-tyrosine is about one-twentieth as bitter as caffeine, but D-tyrosine is still 5.5 times sweeter than sucrose.

Some researchers claim that differences exist between the L and D forms of some sugars. They propose that L-glucose is slightly salty and not sweet, whereas D-glucose is sweet. There is even a difference in taste between the two anomers of D-mannose. The  $\alpha$  form is sweet as sugar, and the  $\beta$  form is bitter as quinine.

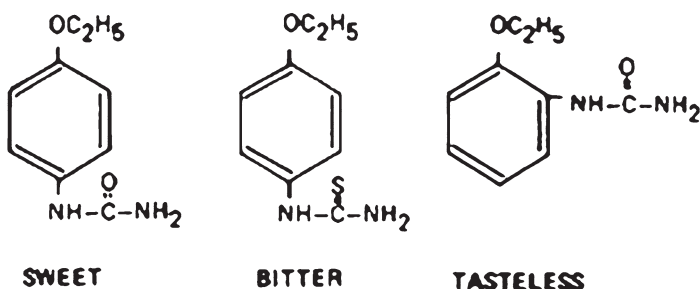
Optical isomers of carvone have totally different flavors. The D+ form is characteristic of caraway; the L- form is characteristic of spearmint.

The ability to taste certain substances is genetically determined and has been studied with phenylthiourea. At low concentrations, about 25% of subjects tested do not taste this compound; for the other 75%, the taste is bitter. The inability to taste phenylthiourea is probably due to a recessive gene. The compounds by which tasters and nontasters can be differentiated all contain the following isothiocyanate group:

**Fig. 7.7** Taste of substituted propoxybenzenes

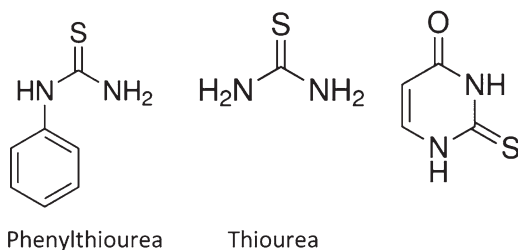


**Fig. 7.8** Taste of substituted ethoxybenzenes

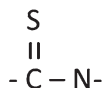


**Table 7.2** Difference in taste between the L- and D-forms of amino acids

Amino acid	Taste of L isomer	Taste of D isomer
Asparagine	Insidid	Sweet
Glutamic acid	Unique	Almost tasteless
Phenylalanine	Faintly bitter	Sweet, bitter aftertaste
Leucine	Flat, faintly bitter	Strikingly sweet
Valine	Slightly sweet, bitter	Strikingly sweet
Serine	Faintly sweet, stale after taste	Strikingly sweet
Histidine	Tasteless to bitter	Sweet
Isoleucine	Bitter	Sweet
Methionine	Flat	Sweet
Tryptophan	Bitter	Very sweet



**Fig. 7.9** Compounds containing the  $\begin{matrix} \text{S} \\ || \\ -\text{C}-\text{N}- \end{matrix}$  group by which tasters and nontasters can be differentiated



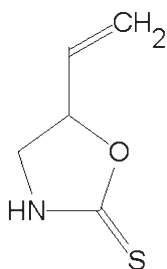
These compounds—phenylthiourea, thiourea, and thiouracil—are illustrated in Fig. 7.9. The corresponding compounds that contain the group,

phenylurea, urea, and uracil, do not show this phenomenon. Another compound containing the isothiocyanate group has been found in many species of the Cruciferae family; this family includes cabbage, turnips, and rapeseed and is well known for its goitrogenic effect. The compound is goitrin, 5-vinylloxazolidine-2-thione (Fig. 7.10).



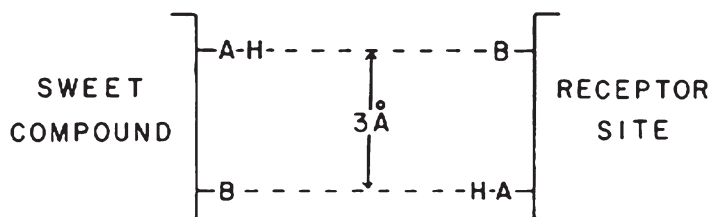
## Sweet Taste

Many investigators have attempted to relate the chemical structure of sweet tasting compounds to the taste effect, and a series of theories have been proposed (Shallenberger 1971). Shallenberger and Acree (1967, 1969) proposed a theory that can be considered a refinement of some of the ideas incorporated in previous theories. According to this theory, called the AH,B theory, all compounds that bring about a sweet taste response possess an electronegative atom A, such as oxygen or nitrogen. This atom also possesses a proton attached to it by a single covalent bond; therefore, AH can represent a hydroxyl group, an imine or amine group, or a methine group. Within a distance of about 0.3 nm from the AH proton, there must be a second electronegative atom B, which again can be oxygen or nitrogen (Fig. 7.11). Investigators have recognized that sugars that occur in a favored chair conformation yield a glycol unit conformation with the proton of one hydroxyl group at a distance of about 0.3 nm from the oxygen of the next hydroxyl group; this unit can be considered as an AH,B system. It was also found that the  $\pi$  bonding cloud of the benzene ring could serve as a B moiety. This explains



**Fig. 7.10** 5-vinylloxazoline-2-thione

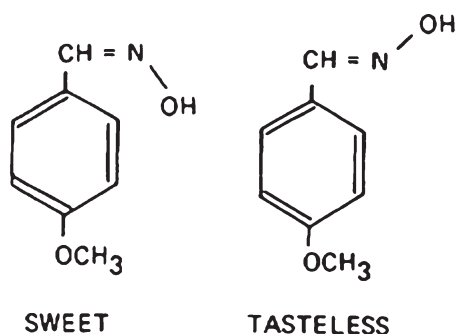
**Fig. 7.11** The AH,B theory of sweet taste perception



the sweetness of benzyl alcohol and the sweetness of the *anti* isomer of anisaldehyde oxime, as well as the lack of sweetness of the *syn* isomer. The structure of these compounds is given in Fig. 7.12. The AH,B system present in sweet compounds is, according to Shallenberger, able to react with a similar AH,B unit that exists at the taste bud receptor site through the formation of simultaneous hydrogen bonds. The relatively strong nature of such bonds could explain why the sense of sweetness is a lingering sensation. According to the AH,B theory, there should not be a difference in sweetness between the L and D isomers of sugars. Experiments by Shallenberger (1971) indicated that a panel could not distinguish among the sweet taste of the enantiomeric forms of glucose, galactose, mannose, arabinose, xylose, rhamnose, and glucoheptulose. This suggests that the notion that L sugars are tasteless is a myth.

Spillane (1996) has pointed out that the AH,B theory appears to work quite well, although spatial, hydrophobic/hydrophilic, and electronic effects are also important. Shallenberger (1998) describes the initiation of sweetness as being due to a concerted intermolecular, antiparallel hydrogen-bonding interaction between the glycopore (Greek *glyks*, sweet; *phoros*, to carry) and receptor dipoles. The difficulty in explaining the sweetness of compounds with different chemical structures is also covered by Shallenberger (1998) and how this has resulted in alternative taste theories. The application of sweetness theory is shown to have important applications in the food industry.

Extensive experiments with a large number of sugars by Birch and Lee (1971) support Shallenberger's theory of sweetness and indicate that the fourth hydroxyl group of glucopyranosides is of unique importance in determining



**Fig. 7.12** *Anti*-anisaldehyde oxime, sweet; and *syn*-anisaldehyde oxime, tasteless

sweetness, possibly by donating the proton as the AH group. Apparently the primary alcohol group is of little importance for sweetness. Substitution of acetyl or azide groups confers intense bitterness to sugars, whereas substitution of benzoyl groups causes tastelessness.

As the molecular weight of saccharides increases, their sweetness decreases. This is best explained by the decrease in solubility and increase in size of the molecule. Apparently, only one sugar residue in each oligosaccharide is involved in the interaction at the taste bud receptor site.

The relative sweetness of a number of sugars and other sweeteners has been reported by Solms (1971) and is given in Table 7.3. These figures apply to compounds tasted singly and do not necessarily apply to sugars in foods, except in a general sense. The relative sweetness of mixtures of sugars changes with the concentration of the components. Synergistic effects may increase the sweetness by as much as 20–30% in such mixtures (Stone and Oliver 1969).

Steroidal alkaloids (SAs) and their glycosylated forms (SGAs) found in the nightshade family are toxic to humans and animals. These compounds are produced by members of the Solanaceae and Liliaceae plant families. In the plants these metabolites serve as a chemical barrier against a broad range of pests and pathogens. In humans and animals, SAs are considered anti-nutritional factors because they affect the digestion and absorption of nutrients from food and in some cases they can cause poisoning (Cardenas et al. 2015).

**Table 7.3** Relative sweetness of sugars and other sweeteners

Compound	Relative sweetness
Sucrose	1
Lactose	0.27
Maltose	0.5
Sorbitol	0.5
Galactose	0.6
Glucose	0.5–0.7
Mannitol	0.7
Glycerol	0.8
Fructose	1.1–1.5
Cyclamate	30–80
Glycyrrhizin	50
Aspartyl-phenylalanine methylester	100–200
Stevioside	300
Naringin dihydrochalcone	300
Saccharin	500–700
Neohesperidin dihydrochalcone	1000–1500

*Source:* From J. Solms, *Nonvolatile Compounds and the Flavor of Foods*, in *Gustation and Olfaction*, G Ohloff and A.F. Thomas, eds., 1971, Academic Press

## Sour Taste

Although it is generally recognized that sour taste is a property of the hydrogen ion, there is no simple relationship between sourness and acid concentration. Acids have different tastes; the sourness as experienced in the mouth may depend on the nature of the acid group, pH, titratable acidity, buffering effects and the presence of other compounds, especially sugars. Organic acids have a greater taste effect than inorganic acids (such as hydrochloric acid) at the same pH. Information on a number of the most common acids found in foods and phosphoric acid (which is also used in soft drinks) has been collected by Solms (1971) and compared with hydrochloric acid. This information is presented in Table 7.4.

According to Beatty and Cragg (1935), relative sourness in unbuffered solutions of acids is not a function of molarity but is proportional to the amount of phosphate buffer required to bring the pH to 4.4. Ough (1963) determined relative sourness of four organic acids added to wine and

**Table 7.4** Properties of some acids, arranged in order of decreasing acid taste and with tartaric acid as reference

Acid	Properties of 0.05 N solutions			Ionization constant	Taste sensation	Found In
	Taste	Total acid (g/L)	pH			
Hydrochloric	+1.43	1.85	1.70	–	–	–
Tartaric	0	3.75	2.45	$1.04 \times 10^{-3}$	Hard	Grape
Malic	–0.43	3.35	2.65	$3.9 \times 10^{-4}$	Green	Apple, pear, prune, grape, cherry, apricot
Phosphoric	–1.14	1.65	2.25	$7.52 \times 10^{-3}$	Intense	Orange, grapefruit
Acetic	–1.14	3.00	2.95	$1.75 \times 10^{-5}$	Vinegar	–
Lactic	–1.14	4.50	2.60	$1.26 \times 10^{-4}$	Sour, tart	–
Citric	–1.28	3.50	2.60	$8.4 \times 10^{-4}$	Fresh	Berries, citrus, pineapple
Propionic	–1.85	3.70	2.90	$1.34 \times 10^{-5}$	Sour, cheesy	–

Source: From J. Solms, *Nonvolatile Compounds and the Flavor of Foods*, in *Gustation and Olfaction*, G. Ohloff and A.F. Thomas, eds., 1971, Academic Press

also preference for these acids. Citric acid was judged the most sour, fumaric and tartaric about equal, and adipic least sour. The tastes of citric and tartaric acids were preferred over those of fumaric and adipic acids.

Pangborn (1963) determined the relative sourness of lactic, tartaric, acetic, and citric acid and found no relation between pH, total acidity, and relative sourness. It was also found that there may be considerable differences in taste effects between sugars and acids when they are tested in aqueous solutions and in actual food products.

Buffering action appears to help determine the sourness of various acids; this may explain why weak organic acids taste more sour than mineral acids of the same pH. It is suggested that the buffering capacity of saliva may play a role, and foods contain many substances that could have a buffering capacity.

Wucherpennig (1969) examined the sour taste in wine and found that alcohol may decrease the sourness of organic acids. He examined the relative sourness of 17 organic acids and found that the acids tasted at the same level of undissociated acid have greatly different intensities of sourness. Partially neutralized acids taste more sour than pure acids containing the same amount of undissociated acids. The change of malic into lactic acid during the malolactic fermentation of wines leads to a decrease in sourness, thus making the flavor of the wine milder.

## Salty Taste

The salty taste is best exhibited by sodium chloride. It is sometimes claimed that the taste of salt by itself is unpleasant and that the main purpose of salt as a food component is to act as a flavor enhancer or flavor potentiator. The taste of salts depends on the nature of both cation and anion. As the molecular weight of either cation or anion—or both—increases, salts are likely to taste bitter. The lead and beryllium salts of acetic acid have a sweet taste. The taste of a number of salts is presented in Table 7.5.

The current trend of reducing sodium intake in the diet has resulted in the formulation of low-sodium or reduced-sodium foods. It has been shown (Gillette 1985) that sodium chloride enhances mouthfeel, sweetness, balance, and saltiness, and also masks or decreases off-notes. Salt substitutes based on potassium chloride do not enhance mouthfeel or balance and increase bitter or metallic off-notes.

Some individuals are sensitive are sensitive and need to reduce the sodium content of their diet. Salt sensitivity individuals experience increases in blood pressure in response to salt intake, Salt sensitive individuals are more likely to have high blood pressure than those who are resistant to salt. Salt-sensitive individuals are at higher risk for high blood pressure, cardiovascular disease and lower survival rate later in life if

**Table 7.5** Taste sensations of salts

Taste	Salts
Salty	LiCl, LiBr, Lil, NaNO <sub>3</sub> , NaCl, NaBr, NaI, KNO <sub>3</sub> , KCl
Salty and bitter	KBr, NH <sub>4</sub> I, KCl
Bitter	CsCl, CsBr, KI, MgSO <sub>4</sub>
Sweet	Lead acetate, <sup>a</sup> beryllium acetate <sup>a</sup>
Taste	Salts

<sup>a</sup>Extremely toxic

**Table 7.6** Percentage of salt-sensitive people in different populations (data from Sullivan 1991)

Blood pressure	Population	
	White (%)	Black (%)
Normal	15	27
Hypertension	29	50

they continuously live an unhealthy lifestyle or have a high-sodium diet (Weinberger et al. 2001). A study by Sullivan (1991), salt-sensitive individuals are more likely to have hypertension, as are blacks more than whites (Table 7.6). Another study reports that approximately 60% of Chinese who have high blood pressure are salt-sensitive (Li 2012).

Sodium homeostasis in the human body is regulated mainly by the renin-angiotensin-aldosterone system. This system operates mainly in the kidney and in vascular smooth muscle cells. Variations in this system, due to genetic background, age, race, gender and medical history, cause the kidney of salt-sensitive individuals to handle excess sodium less efficiently. Asian or African ancestry, older age, female gender, high blood pressure, and kidney disease are all associated with salt-sensitivity.

Salt sensitive individuals exhibit variations in genes involved in the renin-angiotensin-aldosterone system which predispose them to salt sensitivity (Sanada et al. 2011). About 38% of the general population carries an ACE gene variant that causes increased activity of the system leading to blood pressure increase in response to higher sodium levels in the blood. This part of the population becomes salt-sensitive. Two other genes associated with salt sensitivity are the NOS3

gene, and the AGT gene, Table 7.7 lists the frequency of risk variants associated with increased risk for salt sensitivity and hypertension.

To help consumers reduce or control sodium intake, many salt substitutes with low sodium content have been designed to reduce the risk of high blood pressure and cardiovascular disease associated with a high intake of sodium chloride, while delivering similar taste [Scientific Advisory Committee on Nutrition Salt and Health (2003)]. The increase in sodium consumption is considered a potential health threat for some individuals. The Institute of Medicine of the National Academy of Sciences has established adequate daily intakes (AIs) for sodium and potassium and a tolerable upper intake level (UL) for sodium, based on its effects on blood pressure (Table 7.8; IOM 2004). Persons with a greater risk for hypertension (adults who are Black, over 40 years old, or already have hypertension or prehypertension) have been urged to consume no more than the AI level of sodium each day (CDCP 2009; Doyle and Glass 2010). These products are predominantly potassium chloride (KCl). Potassium Chloride's toxicity is similar to Sodium Chloride in healthy individuals; the LD<sub>50</sub> is about 2.5 g/kg. Potassium lactate is frequently used to reduce sodium levels in meat and poultry products. The recommended daily allowance of potassium is higher than that for sodium (Caggiula et al. 1985).

Sodium is an essential micronutrient and, via salt taste, appetitive. High consumption of sodium is, however, related to negative health effects such as hypertension, cardiovascular diseases and stroke. In industrialized countries, about 75% of sodium in the diet comes from processed foods and foods eaten away from home. Reducing sodium in processed foods will be, however, challenging due to sodium's specific functionality in terms of flavor and associated palatability of foods (i.e., increase of saltiness, reduced bitterness, enhancement of sweetness and other congruent flavors). Salt has many beneficial properties for both preservation and multiple culinary benefits. Salt improves the sensory properties of nearly all foods. The principle reason for adding salt to food is that enhances the positive sensory attributes of foods. Salt makes

**Table 7.7** Percentage gene variants associated with salt sensitivity in different populations

Gene symbol	All (%)	African (%)	American (%)	Asian (%)	European (%)
ACE	38	17	40	31	56
ADD1	27	17	19	50	20
ADRB1	30	40	21	21	34
AGT	66	88	64	83	41
AGTR1	16	3	23	7	27
CYP11B2	36	17	43	31	49
GNB3	48	79	42	47	31
NOS3	26	50	50	20	50

(Source: <http://www.gbhealthwatch.com/Trait-Salt-Sensitivity.php?>)

ALL general population, AFR Africans, AMR Americans, ASN Asians, EUR Europeans. Data are from 1000 genome project

**Table 7.8** Daily sodium and potassium intakes and recommended intakes in the U.S. (IOM 2004)

	Sodium	Sodium chloride (g)	Potassium
AI (adequate intake): 19–50 years	1.5 g/d (65 mmol)	3.8	4.7 g/d (120 mmol)
AI: 51–70 years	1.3 g/d (55 mmol)	3.3	4.7 g/d (120 mmol)
AI: >71 years	1.2 g/d (50 mmol)	3	4.7 g/d (120 mmol)
UL: tolerable upper intake level	2.3 g/d (95 mmol)	5.8	Not established
Median intake (males)	4.2 g (183 mmol)	10.6	2.9–3.2 g/d (74–82 mmol)
Median intake (females)	3.3 g (142 mmol)	8.3	2.1–2.3 g/d (54–59 mmol)
AI (adequate intake): 19–50 years	1.5 g/d (65 mmol)	3.8	4.7 g/d (120 mmol)

(Source: IOM 2004)

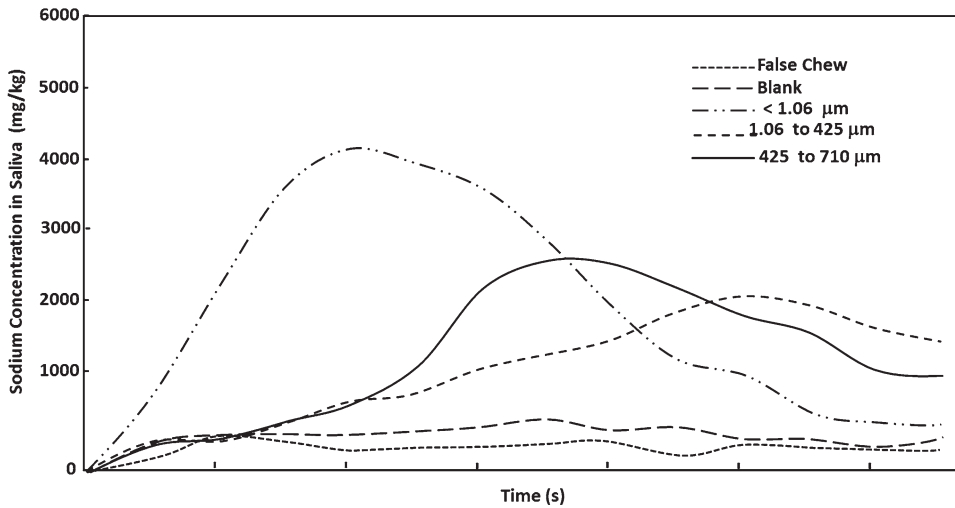
foods “taste” better. Consumers who are accustomed to higher levels of salt in their foods find foods without salt unpalatable. Reductions in levels of salt in their food therefore must be gradual. In order to lower salt consumption in the population as a whole, it will be necessary to reduce salt levels in the human food supply with careful attention to their flavor-enhancing properties (Liem et al. 2011).

Rama et al. (2013) demonstrated that salt crystal size impacted upon the rate of initial response and perceived saltiness. They studied three different sizes of salt crystals on potato crisps to measure the rate of solubilisation of the salt crystals. A single sample of salt was ground in a mortar and pestle and mechanically sieved to produce three sizes of salt particles: S1 (<106  $\mu\text{m}$ ), S2 (106–425  $\mu\text{m}$ ), S3 (425–710  $\mu\text{m}$ ). The smallest crystal size salt dissolved and diffused throughout the mouth to the tongue saliva faster than the medium and the larger crystals ones; the smallest crystal size delivered the highest maximum concentration and greatest total

sodium in the saliva. The results correlated with the sensory perceived saltiness, where the smallest crystal size fraction resulted in the fastest salty perception, highest maximum saltiness intensity and maximum total saltiness. The different delivery rates can be explained by differential dissolution kinetics and enhanced mass transfer of sodium into the saliva. The sodium concentration in the saliva from the various crystal sizes salt are shown in Fig. 7.13.

The results demonstrate that when salt is placed on the surface of foods the total salt added can be reduced by using smaller crystal size salt. Salt substitutes offer alternatives to enhance flavor while reducing sodium content of the food. Frequently low-sodium products have been formulated with a blend of sodium and potassium chlorides, but potassium causes bitter and metallic tastes. Many methods have been developed to improve foods made with low or reduced sodium.

Some food manufacturers have reduced sodium in foods like salty snacks. AkzoNobel ([www.akzonobel.com/saltspecialties](http://www.akzonobel.com/saltspecialties)) developed



**Fig. 7.13** Salivary sodium concentration after chewing crisps with differing salt crystal fractions, S1 ( $<106 \mu\text{m}$ ), S2 ( $106\text{--}425 \mu\text{m}$ ), and S3 ( $425\text{--}710 \mu\text{m}$ ), Blank (no salt)

and false chew ( $n = 8$ ). Error bars indicate standard deviation. (Adapted from: Rama et al. 2013)

its OneGrain technology to combine regular salt, a salt replacer, and taste-enhancing flavors in single salt grains to achieve up to 50% sodium reduction. Suprasel Loso OneGrain, produced using the technology, can provide a one-for-one replacement for regular salt, and the company says that the ingredient is a genuine replacement for salt in terms of taste and functionality (Nachay 2013).

Reducing sodium in baked goods is challenging because of the important roles that sodium plays. Innophos ([www.innophos.com](http://www.innophos.com)) offers calcium phosphates and sodium aluminum phosphates that can be used to reduce sodium in chemically leavened bakery products. These ingredients like Cal-Rise<sup>®</sup> calcium acid pyrophosphate, Regent 12XX<sup>®</sup> monocalcium phosphate, monohydrate, Levair<sup>®</sup> sodium aluminum phosphate, and more replace some or all of the traditional leavening agents in a variety of baked goods applications. Each ingredient has its own benefits, some of which are improved texture, resilient crumb structure, and better stability (Nachay 2013).

Morton Salt ([www.mortonsalt.com](http://www.mortonsalt.com)) offers Morton<sup>®</sup> LiteSalt<sup>™</sup> Mixture, a blend of sodium chloride and potassium chloride that contains 50% less sodium than regular salt, and Morton Salt Balance<sup>®</sup> Salt Blend, a blend of sodium chlo-

ride and potassium chloride with 25% less sodium than regular salt (Nachay 2013).

Tate & Lyle ([www.tateandlyle.com](http://www.tateandlyle.com)) offers SODA-LO<sup>™</sup>, which is manufactured using proprietary technology that turns salt crystals into free-flowing crystalline microspheres. The benefit of this ingredient, according to the company, is that the smaller crystals optimize saltiness perception in foods by maximizing the surface area relative to volume, allowing for an up to 50% reduction in sodium in some applications. The company also emphasizes that since the ingredient is made from salt, it does not impart any off-tastes. It functions well in breads, breadings, and coatings, and salty snacks (Nachay 2013).

## Bitter Taste

Bitter taste is characteristic of many foods and can be attributed to a great variety of inorganic and organic compounds. Many substances of plant origin are bitter. Although bitter taste by itself is usually considered to be unpleasant, it is a component of the taste of many foods, usually those foods that are sweet or sour. Inorganic salts can have a bitter taste (Table 7.5). Some amino acids may be bitter (Table 7.2). Bitter peptides

**Table 7.9** Taste of some selected peptides

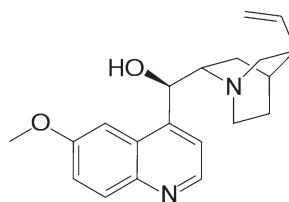
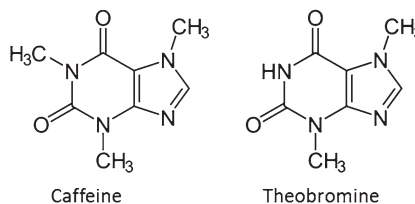
Taste	Composition of peptides
Flat	L-Lys-L-Glu, L-Phe-L-Phe, Gly-Gly-Gly-Gly
Sour	L-Ala-L-Asp, $\gamma$ -L-Glu-L-Glu, Gly- L-Asp-L-Ser-Gly
Bitter	L-Leu-L-Leu, L-Arg-L-Pro, L-Val- L-Val-L-Val
Sweet	L-Asp-L-Phe-OMe, L-Asp-L- Met-OMe
Biting	$\gamma$ -L-Glutamyl-S-(prop-1-enyl)-L-cysteln

Source: From J. Solms, *Nonvolatile Compounds and the Flavor of Foods*, in *Gustation and Olfaction*, G. Ohloff and A. F. Thomas, eds., 1971, Academic Press

may be formed during the partial enzymic hydrolysis of proteins—for example, during the ripening of cheese. Solms (1969) has given a list of peptides with different taste sensations (Table 7.9).

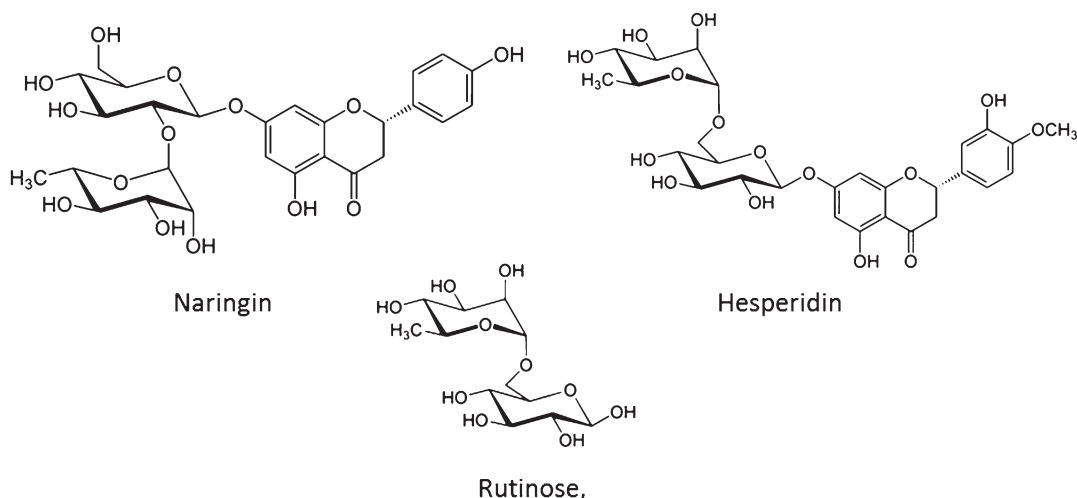
Bitter taste is an important evolutionary system that helps prevent mammals from ingesting food containing bitter-tasting toxins, which include a wide range of structurally diverse molecules. Bitter taste mediated by a family of heptahelical G protein-coupled receptors, called taste 2 receptors or TAS2Rs or T2Rs. The ability of TAS2Rs to recognize a broad range of bitter compounds provides us with the ability to detect the wide range of bitter substances in foods and beverages. Individual TAS2Rs possess only one binding site, in which they accommodate their ligands by contacting different but overlapping sets of amino acids on the protein in the transmembrane portion of the cell. There is a large genetic variability in TAS2Rs in humans including single nucleotide polymorphisms, variations in copy numbers and receptor functionally which cause variability in the sensitivity to the bitterness of specific compounds (Meyerhof et al. 2011).

Food preferences are influenced by many factors including personal experiences, cultural adaptations and perceived health benefits. Taste is the most important determinant effecting whether a food is liked or disliked. Based on the response to bitter-tasting compounds, such as phenylthiocarbamide (PTC) or 6-n-propylthiouracil (PROP), individuals can be classified as supertasters, tasters, or nontasters. Genetic differences in bitter taste perception may account for many individual differences in food preferences. Other factors such as age, sex and ethnicity may also modify the

**Fig. 7.14** Structure of quinine. This has an intensely bitter taste**Fig. 7.15** Caffeine and theobromine

response to bitter-tasting compounds (Bartoshuk et al. 1994). There are several members of the TAS2R receptor gene family that encode taste receptors on the tongue, and genetic polymorphisms of TAS2R38 have been associated with differences in the perception of PTC and PROP (El-Sohemy et al. 2007; Hayes and Keast 2011).

Alkaloids and glycosides are the most common bitter compounds in foods. Alkaloids are basic nitrogen-containing organic compounds that are derived from pyridine, pyrrolidine, quinoline, isoquinoline, or purine. Quinine is often used as a standard for testing bitterness (Fig. 7.14). The bitterness of quinine hydrochloride is detectable in a solution as dilute as 0.00004 M, or 0.0016%. If 5-mL of this solution is tasted, the amount of substance a person detects would be 0.08 mg (Moncrieff 1951). Our sensitivity to bitterness is more extreme than our sensitivity to other tastes; the order of sensitivity is from bitter to sour to salty and our least sensitivity is to sweet taste. Threshold values reported by Moncrieff are as follows: sour—0.007% HCl; salt—0.25% NaCl; and sweet—0.5% sucrose. If the artificial sweeteners such as saccharine are considered, the sweet sensitivity is second to bitter. Quinine is used as a component of some soft drinks to produce bitterness. Other alkaloids occurring as natural bitter constituents of foods are caffeine and theobromine (Fig. 7.15), which are derivatives of purine.



**Fig. 7.16** Naringin, hesperidin, rutinose, 6-O-α-L-rhamnopyranosyl-D-glucopyranose

Another naturally occurring bitter substance is the glycoside naringin, which occurs in grapefruit and some other citrus fruits. Naringin in pure form is more bitter than quinine and can be detected in concentrations of less than 0.002%. Naringin (Fig. 7.16) contains the sugar moiety rutinose (L-rhamnose-D-glucose), which can be removed by hydrolysis with boiling mineral acid. The aglycone is called naringenin, and it lacks the bitterness of naringin. Since naringin is only slightly soluble in water (0.05% at 20 °C), it may crystallize out when grapefruit is subjected to below-freezing temperatures. Hesperidin (Fig. 7.16) occurs widely in citrus fruits and is also a rutinose glycoside. It occurs in oranges and lemons. Dried orange peel may contain as much as 8% hesperidin. The aglycone of hesperidin is called hesperetin. The sugar moiety is attached to carbon 7. Horowitz and Gentili (1969) have studied the relationship between bitterness and the structure of 7-rhamnoglucosides of citrus fruits; they found that the structure of the disaccharide moiety plays an important role in bitterness. The point of attachment of rhamnose to glucose determines whether the substance will be bitter or tasteless. Thus, neo-hesperidin contains the disaccharide neohesperidose, which contains rhamnose linked 1 → 2 to glucose; therefore, the sugar moiety is 2-O-α-L-rhamnopyranosyl-D-glucose. Glycosides containing this sugar, including neo-hesperidin, have a bitter taste. When the linkage between rhamnose

and glucose is 1 → 6, the compound is tasteless as in hesperidin, where the sugar part, rutinose, is 6-O-α-L-rhamnopyranosyl-D-glucose.

Bitterness occurs as a defect in dairy products as a result of casein proteolysis by enzymes that produce bitter peptides. Bitter peptides are produced in cheese because of an undesirable pattern of hydrolysis of milk casein (Habibi-Najafi and Lee 1996). According to Ney (1979), bitterness in amino acids and peptides is related to hydrophobicity. Each amino acid has a hydrophobicity value ( $\Delta f$ ), which is defined as the free energy of transfer of the side chains and is based on solubility properties (Table 7.10). The average hydrophobicity of a peptide,  $Q$ , is obtained as the sum of the  $\Delta f$  of component amino acids divided by the number of amino acid residues. Ney (1979) reported that bitterness is found only in peptides with molecular weights below 6000 Da when their  $Q$  value is greater than 1400. These findings indicate the importance of molecular weight and hydrophobicity. In a more detailed study of the composition of bitter peptides, Kanehisa (1984) reported that at least six amino acids are required for strong bitterness. A bitter peptide requires the presence of a basic amino acid at the N-terminal position and a hydrophobic one at the C-terminal position. It appears that at least two hydrophobic amino acids are required in the C-terminal area of the peptide to produce intense bitterness. The high hydrophobicity of leucine and the number of



leucine and possibly proline residues in the peptide probably play a role in the bitterness.

Flavan-3-ols and their condensation products are the most common flavonoids consumed in the American diet. The flavan-3-ols and their polymeric condensation products, the proanthocyanidins, are regarded as functional ingredients in various beverages, whole and processed foods, herbal remedies and supplements. They are present in food influence several taste parameters including astringency, bitterness, sourness, sweetness, salivary viscosity, aroma, and color formation. Some foods contain only monomeric flavan-3-ols [(–)-epicatechin predominates] and dimeric proanthocyanidins, most foods contain oligomers of d.p. values ranging from 1 to 10 or greater than 10. Flavan-3-ols have been reported to exhibit several health beneficial effects by acting as antioxidant, anticarcinogen, cardiopreventive, antimicrobial, anti-viral, and neuro-protective agents Aron and Kennedy (2008).

Beer flavonoids such as the flavan-3-ols and their condensed products, the proanthocyanidins are easily oxidized. As a result they are capable of hindering or preventing the oxidation of other components present in beer. Flavan-3-ols and proanthocyanidin improve oxidative stability in food systems, and thus they also can function as beer

flavor modifiers and/or stabilizers. The polyphenols can also bind with protein contributing to haze in beer (Aron and Shellhammer 2010).

The antioxidant capacity of polyphenols from green tea, grape juice, and chocolate, as well as a wide range of fresh fruits and vegetables is well established. Fresh produce is a good source of polyphenols which influence the sensory and nutritional qualities of produce. The astringency and bitterness of foods and beverages are largely due to their polyphenolic content. Considerable variation is found in measuring the polyphenolic content of produce. The polyphenolic content of produce seems to be primarily influenced by genetics, but numerous other factors including degree of ripeness, climate, storage and processing can also influence phenolic content (Hughes 2010).

## Other Aspects of Taste

The basic sensations—sweet, sour, salty, and bitter—account for the major part of the taste response. However, it is generally agreed that these basic tastes alone cannot completely describe taste. In addition to the four individual tastes, there are important interrelationships among them. One of the most important in foods is the interrelationship between sweet and sour. The sugar-acid ratio plays an important part in many foods, especially fruits. Kushman and Ballinger (1968) have demonstrated the change in sugar-acid ratio in ripening blueberries (Table 7.11). Sugar-acid ratios play an important role in the flavor quality of fruit juices and wines

**Table 7.10** Hydrophobicity values ( $\Delta f$ ) of the side chains of amino acids

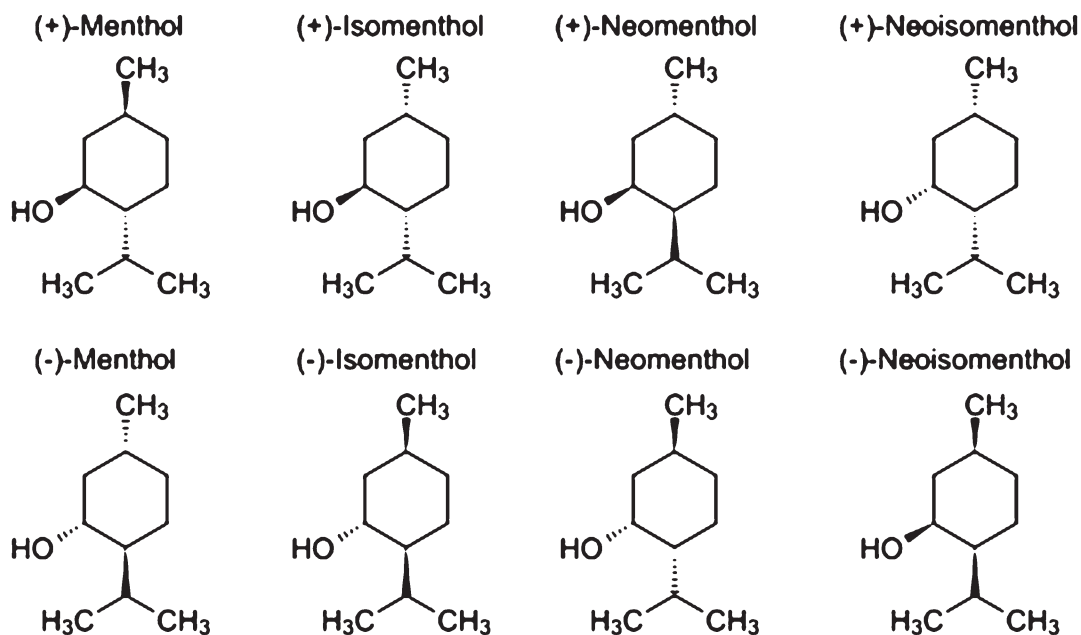
Amino acid	Abbreviation	$\Delta f$ (cal/mol)
Glycine	Gly	0
Serine	Ser	40
Threonine	Thr	440
Histidine	His	500
Aspartic acid	Asp	540
Glutamic acid	Glu	550
Arginine	Arg	730
Alanine	Ala	730
Methionine	Met	1300
Lysine	Lys	1500
Valine	Val	1690
Leucine	Leu	2420
Proline	Pro	2620
Phenylalanine	Phe	2650
Tyrosine	Tyr	2870
Isoleucine	Ile	2970
Tryptophan	Trp	3000

**Table 7.11** Change in sugar-acid ratio during ripening of blueberries<sup>a</sup>

	Unripe	Ripe	Overripe
Total sugar (%)	5.8	7.9	12.4
pH	2.83	3.91	3.76
Titrateable acidity	23.9	12.9	7.5
Sugar-acid ratio	3.8	9.5	25.8

Source: From L.J. Kushman and W.E. Ballinger, *Acid and Sugar Changes During Ripening in Wolcott Blueberries*, *Proc. Amer. Soc. Hort. Soc.*, Vol. 92, pp. 290–295, 1968

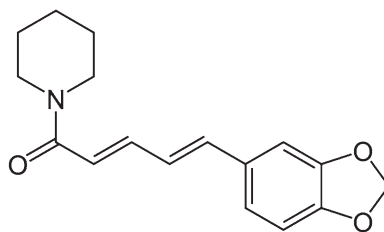
<sup>a</sup>The sugars are mainly glucose and fructose, and the acidity is expressed as citric acid



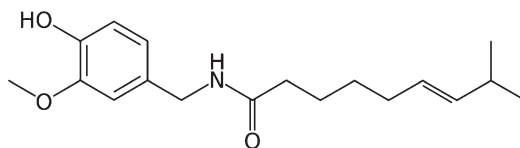
**Fig. 7.17** Isomeric forms of menthol

(Ough 1963). Alkaline taste has been attributed to the hydroxyl ion. Caustic compounds can be detected in solutions containing only 0.01% of the alkali. Probably the major effect of alkali is irritation of the general nerve endings in the mouth. Another effect that is difficult to describe is astringency. Borax is known for its ability to produce this effect, as are the tannins present in foods, especially those that occur in tea. Even if astringency is not considered a part of the taste sense, it must still be considered a feature of food flavor.

Another important taste sensation is coolness, which is a characteristic of menthol. The cooling effect of menthol is part of the mint flavor complex and is exhibited by only some of the possible isomeric forms. Only (–) and (+) menthol show the cooling effect, the former to a higher degree than the latter, but the isomers isomenthol, neomenthol, and neoisomenthol do not give a cooling effect (Fig. 7.17) (Kulka 1967). Hotness is a property associated with spices and is also referred to as pungency. The compound primarily responsible for the hotness of black pepper is piperine (Fig. 7.18). In red pepper or capsicum, non-volatile amides are responsible for the heat effect. The heat effect of spices and their constituents



**Fig. 7.18** Piperine, responsible for the hotness of pepper



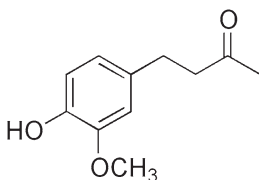
**Fig. 7.19** Capsaicin, the pungent principle of red pepper

can be measured by an organoleptic threshold method (Rogers 1966) and expressed in heat units. The pungent principle of capsicum is capsaicin. The structure of capsaicin is given in Fig. 7.19. Capsaicin shows similarity to the compound zingerone, the pungent principle of ginger (Fig. 7.20).

Govindarajan (1979) has described the relationship between pungency and chemical struc-

ture of pungent compounds. There are three groups of natural pungent compounds—the capsaicinoids, piperine, and the gingerols. These have some common structural aspects, including an aromatic ring and an alkyl side chain with a carbonyl function (Figs. 7.19 and 7.20). Structural variations in these compounds affect the intensity of the pungent response. These structural variations include the length of the alkyl side chain, the position of the amide group near the polar aromatic end, the nature of the groupings at the alkyl end, and the unsaturation of the alkyl chain.

The metallic taste has been described by Moncrieff (1964). There are no receptor sites for this taste or for the alkaline and meaty tastes. However, according to Moncrieff, there is no doubt that the metallic taste is a real one. It is observable over a wide area of the surface of the tongue and mouth and, like irritation and pain, appears to be a modality of the common chemical sense. The metallic taste can be generated by salts of metals such as mercury and silver (which are most potent) but normally by salts of iron, copper, and tin. The threshold concentration is in the order of 20–30 ppm of the metal ion. In canned foods, considerable metal uptake may occur and the threshold could be exceeded in such cases. Moncrieff (1964) also mentions the possibility of metallic ion exchange between the food and the container. The threshold concentration of copper is increased by salt, sugar, citric acid, and alcohol. Tannin, on the other hand, lowers the threshold value and makes the copper taste more noticeable. The metallic taste is frequently observed as an aftertaste. The lead salt of saccharin gives an impression of intense sweetness, followed by a metallic aftertaste. Interestingly, the metallic taste is frequently associated with oxidized products. Tressler and Joslyn (1954) indicate that 20 ppm of copper is detectable by taste



**Fig. 7.20** Zingerone, the pungent principle of ginger

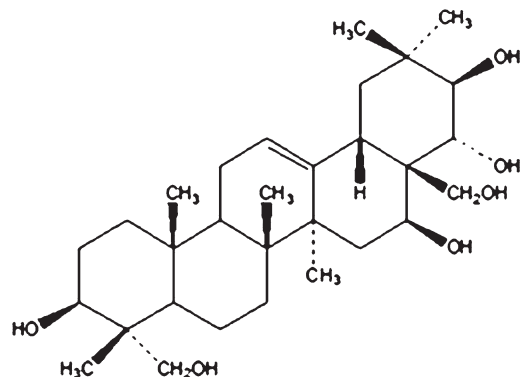
in orange juice. Copper is well known for its ability to catalyze oxidation reactions. Stark and Forss (1962) have isolated and identified oct-1-en-3-one as the compound responsible for the metallic flavor in dairy products.

## Taste Inhibition and Modification

Some substances have the ability to modify our perception of taste qualities. Two such compounds are gymnemagenin, which is able to suppress the ability to taste sweetness, and the protein from miracle fruit, which changes the perception of sour to sweet. Both compounds are obtained from tropical plants.

The leaves of the tropical plant *Gymnema sylvestre*, when chewed, suppress the ability to taste sweetness. The effect lasts for hours, and sugar seems like sand in the mouth. The ability to taste other sweeteners such as saccharin is equally suppressed. There is also a decrease in the ability to taste bitterness. The active principle of leaves has been named gymnemic acid and has been found (Stöcklin et al. 1967) to consist of four components, designated as gymnemic acids, A<sub>1</sub>, A<sub>2</sub>, A<sub>3</sub>, and A<sub>4</sub>. These are D-glucuronides of acetylated gymnemagenins. The unacetylated gymnemagenin is a hexahydroxy pentacyclic triterpene; its structure is given in Fig. 7.21.

The berries of a West African shrub (*Synsepalum dulcificum*) contain a substance that has the ability to make sour substances taste sweet. The berry, also known as miracle fruit, has been shown



**Fig. 7.21** Structure of gymnemagenin

to contain a taste-modifying protein (Kurihara and Beidler 1968, 1969). The protein is a basic glycoprotein with a molecular weight of 44,000. It is suggested that the protein binds to the receptor membrane near the sweet receptor site. The low pH changes the conformation of the membrane so that the sugar part of the protein fits into the sweet receptor site. The taste-modifying protein was found to contain 6.7% of arabinose and xylose.

These taste-modifying substances provide an insight into the mechanism of the production of taste sensations and, therefore, are a valuable tool in the study of the interrelationship between taste and chemical structure.

### Flavor Enhancement—Umami

A number of compounds have the ability to enhance or improve the flavor of foods. It has often been suggested that these compounds do not have a particular taste of their own. Evidence now suggests that there is a basic taste response to amino acids, especially glutamic acid. This taste is sometimes described by the word *umami*, derived from the Japanese for deliciousness (Kawamura and Kare 1987). It is suggested that a primary taste has the following characteristics:

- The receptor site for a primary taste chemical is different from those of other primary tastes.
- The taste quality is different from others.
- The taste cannot be reproduced by a mixture of chemicals of different primary tastes.

From these criteria, we can deduce that the glutamic acid taste is a primary taste for the following reasons:

- The receptor for glutamic acid is different from the receptors for sweet, sour, salty, and bitter.
- Glutamic acid does not affect the taste of the four primary tastes.
- The taste quality of glutamic acid is different from that of the four primary tastes.
- Umami cannot be reproduced by mixing any of the four primary tastes.

Monosodium glutamate has long been recognized as a flavor enhancer and is now being considered a primary taste, umami. The flavor potentiation capacity of monosodium glutamate in foods is not the result of an intensifying effect of the four primary tastes. Glutamate may exist in the L and D forms and as a racemic mixture. The L form is the naturally occurring isomer that has a flavor-enhancing property. The D form is inert. Although glutamic acid was first isolated in 1866, the flavor-enhancing properties of the sodium salt were not discovered until 1909 by the Japanese chemist Kikunae Ikeda. Almost immediately, commercial production of the compound started and total production for the year 1954 was estimated at 13000,000 pounds. The product as first described by Ikeda was made by neutralizing a hydrolysate of the seaweed *Laminaria japonica* with soda. Monosodium glutamate is now produced from wheat gluten, beet sugar waste, and soy protein and is used in the form of the pure crystallized compound. It can also be used in the form of protein hydrolysates derived from proteins that contain 16% or more of glutamic acid. Wheat gluten, casein, and soy flour are good sources of glutamic acid and are used to produce protein hydrolysates. The glutamic acid content of some proteins is listed in Table 7.12 (Hall 1948). The protein is hydrolyzed with hydrochloric acid, and the neutralized hydrolysate is used in liquid form or as a dry powder. Soy sauce,

**Table 7.12** Glutamic acid content of some proteins

Protein source	Glutamic acid (%)
Wheat gluten	36.0
Corn gluten	24.5
Zein	36.0
Peanut flour	19.5
Cottonseed flour	17.6
Soybean flour	21.0
Casein	22.0
Rice	24.1
Egg albumin	16.0
Yeast	18.5

Source: From L.A. Hall, Protein Hydrolysates as a Source of Glutamate Flavors, in *Monosodium Glutamate—A Symposium*, 1948, Quartermaster Food and Container Institute for the Armed Forces

which is similar to these hydrolysates, is produced wholly or partially by enzymic hydrolysis. This results in the formation of ammonia from acid amides; soy sauce contains ammonium complexes of amino acids, including ammonium glutamate.

The flavor of glutamate is difficult to describe. It has sometimes been suggested that glutamate has a meaty or chickeny taste, but it is now generally agreed that glutamate flavor is unique and has no similarity to meat. Pure sodium glutamate is detectable in concentrations as low as 0.03%; at 0.05% the taste is very strong and does not increase at higher concentrations. The taste has been described as a mixture of the four tastes (Crocker 1948). At about 2 threshold values of glutamate concentration, it could be well matched by a solution containing 0.6 threshold of sweet, 0.7 of salty, 0.3 of sour, and 0.9 of bitter. In addition, glutamate is said to cause a tingling feeling and a marked persistency of taste sensation. This feeling is present in the whole of the mouth and provides a feeling of satisfaction or fullness. Apparently glutamate stimulates our tactile sense as well as our taste receptors. The presence of salt is required to produce the glutamate effect. Glutamate taste is most effective in the pH range of 6–8 and decreases at lower pH values. Sugar content also affects glutamate taste. The taste in a complex food, therefore, depends on a complex interaction of sweet, sour, and salty, as well as the added glutamate.

Monosodium glutamate improves the flavor of many food products and is therefore widely used in processed foods. Products benefiting from the addition of glutamate include meat and poultry, soups, vegetables, and seafood.

For many years glutamate was the only known flavor enhancer, but recently a number of compounds that act similarly have been discovered. The 5'-nucleotides, especially 5'-inosinate and 5'-guanylate, have enhancement properties and also show a synergistic effect in the presence of glutamate. This synergistic effect has been demonstrated by determining the threshold levels of the compounds alone and in mixtures. The data in Table 7.13 are quoted from Kuninaka (1966). The 5'-nucleotides were discovered many years ago in Japan as components of dried bonito (a

**Table 7.13** Threshold levels of flavor enhancers alone and in mixtures in aqueous solution

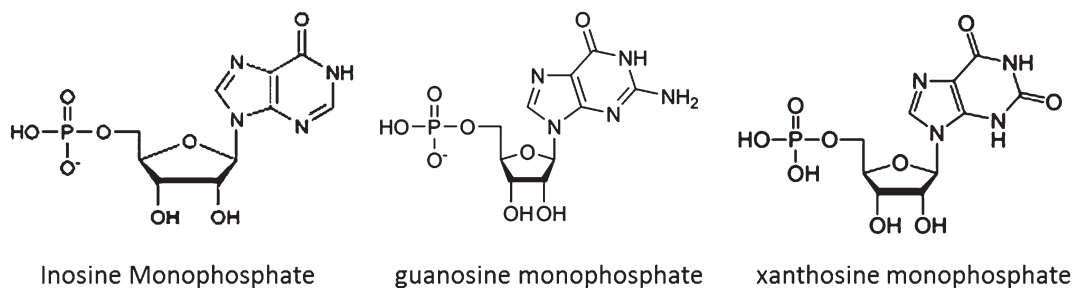
Solvent	Threshold level (%)		
	Disodium 5'-inosinate	Disodium 5'-guanylate	Monosodium L-glutamate
Water	0.012	0.0035	0.03
0.1% glutamate	0.0001	0.00003	–
0.01% inosinate	–	–	0.002

*Source:* From A. Kuninaka, Recent Studies of 5'-Nucleotides as New Flavor Enhancers, in *Flavor Chemistry*, I. Hornstein, ed., 1966, American Chemical Society

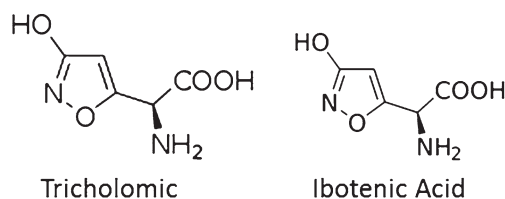
kind of fish). However, they were not produced commercially and used as flavor enhancers until recently, when technical problems in their production were solved. The general structure of the nucleotides with flavor activity is presented in Fig. 7.22. There are three types of inosinic acid, 2'-, 3'-, and 5'-isomers; only the 5'-isomer has flavor activity. Both riboside and 5'-phospho-ester linkages are required for flavor activity, which is also the case for the OH group at the 6-position of the ring. Replacing the OH group with other groups, such as an amino group, sharply reduces flavor activity but this is not true for the group at the 2-position. Hydrogen at the 2-position corresponds with inosinate and an amino group with guanylate; both have comparable flavor activity, and the effect of the two compounds is additive.

The synergistic effect of umami substances is exceptional. The subjective taste intensity of a blend of monosodium glutamate and disodium 5'-inosinate was found to be 16 times stronger than that of the glutamate by itself at the same total concentration (Yamaguchi 1979).

5'-nucleotides can be produced by degradation of ribonucleic acid. The problem is that most enzymes split the molecule at the 3'-phosphodiester linkages, resulting in nucleotides without flavor activity. Suitable enzymes were found in strains of *Penicillium* and *Streptomyces*. With the aid of these enzymes, the 5'-nucleotides can be manufactured industrially from yeast ribonucleic acid. Another process produces the nucleoside inosine by fermentation, followed by chemical phosphorylation to 5'-inosinic acid (Kuninaka 1966).



**Fig. 7.22** Structure of nucleotides with flavor activity



**Fig. 7.23** Tricholomic and ibotenic acid

The search for other flavor enhancers has brought to light two new amino acids, tricholomic acid and ibotenic acid, obtained from fungi (Fig. 7.23). These amino acids have flavor activities similar to that of monosodium glutamate. Apparently, the flavor enhancers can be divided into two groups; the first consists of 5'-inosinate and 5'-guanylate with the same kind of activity and an additive relationship. The other group consists of glutamate, tricholomic, and ibotenic acid, which are additive in action. Between the members of the two groups, the activity is synergistic.

A different type of flavor enhancer is maltol, which has the ability to enhance sweetness produced by sugars. Maltol is formed during roasting of malt, coffee, cacao, and grains. During the baking process, maltol is formed in the crust of bread. It is also found in many dairy products that have been heated, as a product of decomposition of the casein-lactose system. Maltol (Fig. 7.24) is formed from di-, tri-, and tetrasaccharides including isomaltose, maltotetraose, and panose but not from maltotriose. Formation of maltol is brought about by high temperatures and is catalyzed by metals such as iron, nickel, and calcium.

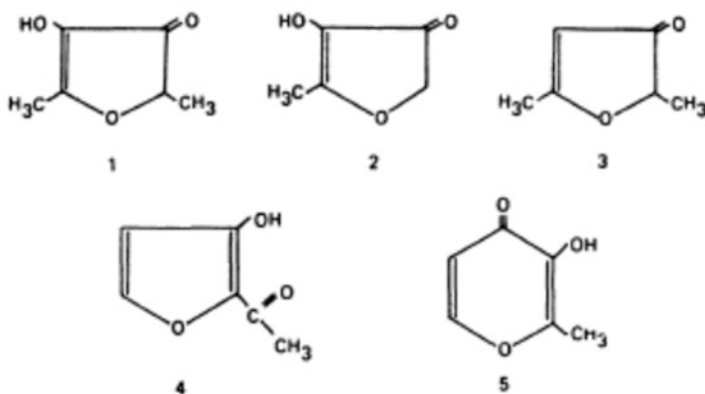
Maltol has antioxidant properties. It has been found to prolong storage life of coffee and roasted cereal products. Maltol is used as a flavor enhancer in chocolate and candies, ice cream, baked products, instant coffee and tea, liqueurs, and flavorings. It is used in concentrations of 50–250 ppm and is commercially produced by a fermentation process.

## Odor

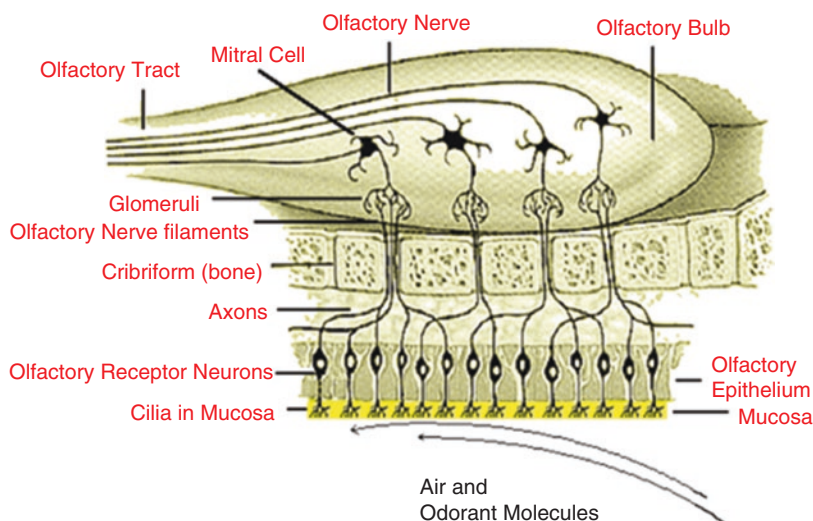
The olfactory mechanism is both more complex and more sensitive than the process of gustation. Olfaction, the sense of smell is a primal sense for all humans and animals. Olfaction helps both vertebrates and other organisms with olfactory receptors to identify food, mates, and predators. It also can provide sensual pleasure (the odor of flowers and perfume) or threats from spoiled food or chemical dangers. Thus, olfaction is one of our principal means to communicate with our environment. There are thousands of odors, and the sensitivity of the smell organ is about 10,000 times greater than that of the taste organ.

Odorants are volatile chemical compounds that are carried by inhaled air to the Regio olfactoria (olfactory region) which are located in the roof of the two nasal cavities of the human nose (Fig. 7.25). The molecular properties of an odorant determine the sensory properties of the compound. The odorant must be at least partially water solubility, have a sufficiently high vapor pressure, low polarity, some ability to dissolve in fat (lipophilicity), and surface activity

**Fig. 7.24** Some furanones (1,2,3), isomaltol (4), and maltol (5)



**Fig. 7.25** Structure of olfactory cells and olfactory bulb (Leffingwell 2001). The diagrams of the “Olfactory Region” and the “Olfactory Bulb” are adapted from a drawing that appears at <http://www.sciencenet.org.uk/database/Social/Senses/s00122b.html>



(Leffingwell 2001; Greenman and Benkara Mostefa Saad 2009).

The olfactory sense is able to distinguish among numerous chemical compounds at very low concentrations (Ohloff 1994). The olfactory region in the two nasal passages of humans is a small area (about 2.5 cm<sup>2</sup>) containing approximately 50 million primary sensory receptor cells. The olfactory region consists of cilia projecting out of the olfactory epithelium into a layer of mucous which is about 60 μ thick. This mucous layer is a lipid-rich secretion that bathes the surface of the receptors at the epithelium surface. The mucous layer is produced by the Bowman’s glands which reside in the olfactory epithelium. The mucous lipids assist in transporting the odorant molecules as only volatile materials that are

soluble in the mucous can interact with the olfactory receptors and produce the signals that our brain interprets as odor. Each olfactory receptor neuron has 8–20 cilia that are whip-like extensions 30–200 μ in length. The olfactory cilia are the sites where molecular reception with the odorant occurs and sensory transduction (i.e., transmission) starts (Leffingwell 2001).

The base olfactory epithelium consists partially of basal cells located in the lowest cellular layer of the olfactory epithelium just above the mucous layer. These basal cells undergo mitotic cell division to form olfactory receptor neurons. Olfactory receptor neurons turnover approximately every 40 days. The olfactory receptor neurons extend through the epithelium to contact odorants in the atmosphere. Within the

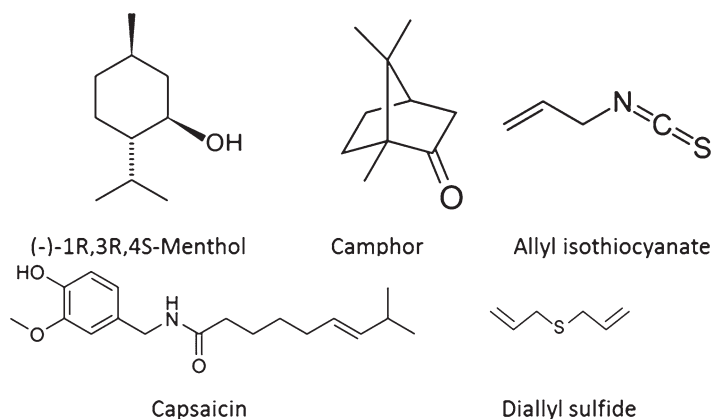
epithelium, the neuronal cells form axons that are bundled in groups of 10–100 and these bundles penetrate the bone, ending in the olfactory bulb of the brain. In the olfactory bulb of the brain, the neurons converge and terminate with post-synaptic cells to form synaptic structures called glomeruli. The glomeruli are connected in groups that converge into mitral cells. In rabbits, there are 26,000 receptor neurons that converge onto 200 glomeruli, which then converge at 25:1 onto each mitral cell. The total convergence is estimated to be about 1000:1. From the mitral cells, the message is sent directly to the higher levels of the central nervous system in the corticomedial amygdala portion of the brain (via the olfactory nerve tract) where the signaling process is decoded and olfactory interpretation and response occurs (Leffingwell 2001).

The olfactory epithelium contains another sensory system in the form of “trigeminal nerve” receptors. Some chemicals are trigeminal stimulants that produce sensations described as hot, cold, tingling or irritating. For example, levo-menthol or (–)-menthol produces the trigeminal feeling of cold at moderate concentrations and “hot” at high concentrations in the nasal cavity. Similarly, camphor which possesses markedly more aroma than menthol, also produces the “cold” sensation via interaction with trigeminal receptors. Other commonly encountered trigeminal stimulants include the chemicals allyl isothiocyanate (mustard, mustard oil), capsaicin (hot chile powder, mace spray) and Diallyl sulfide (onion) (Leffingwell 2001). See Fig. 7.26.

Most odorous compounds are soluble in a variety of solvents, but it appears that solubility is less important than type of molecular arrangement, which confers both solubility and chemical reactivity (Moncrieff 1951). Some degree of water solubility does appear to contribute.

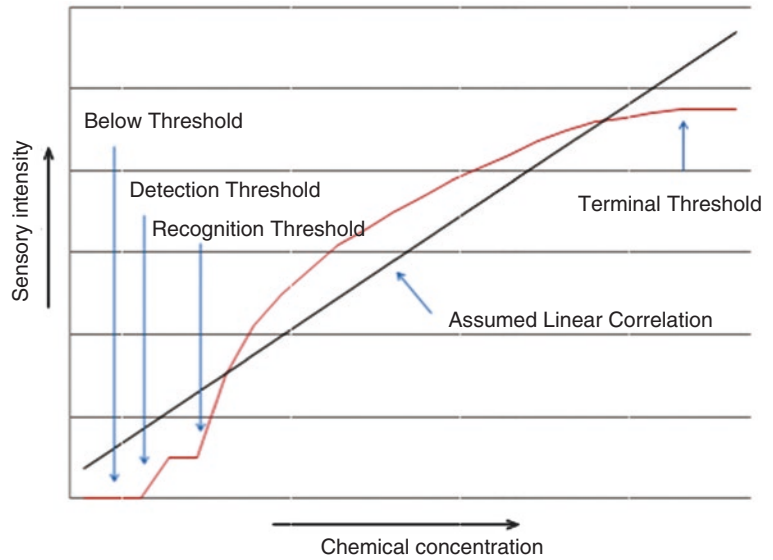
There are two common ways to establish relationships between a sample odor and a chemical. One is to find statistical associations between the data obtained from sensory analysis and GC-MS analysis for the specific sample or volatile compounds. The other is to use trained panelists sniffing at GC-MS ports to detect and identify volatile compounds that are also identified by sensors and computer programs (GC-MS Olfactometry). Moreover, direct relationships to identify an odor compound can be done by comparing the sample odor to a number of volatile compounds that may have a similar odor description, which may require knowledges of odorous volatile compounds. Instrumental measurements are useful when detecting and identifying specific compounds. GC-MS may be used in combination with the sensory aromatic profile analysis to identify the volatile compounds present in the sample. More specifically, GC-MS sniff ports may be used to identify volatile compounds that have an odor detectable by the human nose. In this way, compounds identified by GC-MS can be related to the sensory aromatic results. Drawing correlations is frequently complicated since perceived intensity and aroma concentration are rarely linear. Frequently the detection or recognition thresholds are rapidly reached and

**Fig. 7.26** Common food compounds that are trigeminal stimulants





**Fig. 7.27** Schematic diagram of potential relationships between chemical concentration and sensory intensity (from Chambers and Koppel 2013)



at higher levels the perceived intensity levels off reaching a terminal threshold as shown in Fig. 7.27 (Chambers and Koppel 2013).

The number of volatile compounds occurring in foods is very high. Maarse (1991) has given the following numbers for some foods: beef (boiled, cooked)—486; beer—562; butter—257; coffee—790; grape—466; orange—203; tea—541; tomato—387; and wine (white)—644. Not all of these substances may be essential in determining the odor of a product. Usually, the relative amounts of a limited number of these volatile compounds are important in establishing the characteristic odor and flavor of a food product.

The sensitivity of the human olfactory organ is inferior to that of many animals. Dogs and rats can detect odorous compounds at threshold concentrations 100 times lower than man. When air is breathed in, only a small part of it is likely to flow over the olfactory epithelium in the upper nasal cavity. When a smell is perceived, sniffing may increase the amount reaching the olfactory tissue. When foods are eaten, the passage of breath during exhalation reaches the nasal cavity from the back. Döving (1967) has quoted the threshold concentrations of odorous substances listed in Table 7.14. Apparently, it is possible to change odor thresholds by a factor of 100 or more by stimulating the sympathetic nervous system

**Table 7.14** Odor threshold concentrations of odorous substances perceived during normal inspiration

Compound	Threshold concentration (molecules/cc)
Allyl mercaptan	$6 \times 10^7$
Sec. butyl mercaptan	$1 \times 10^8$
Isopropyl mercaptan	$1 \times 10^8$
Isobutyl mercaptan	$4 \times 10^8$
Tert. butyl mercaptan	$6 \times 10^8$
Thiophenol	$8 \times 10^8$
Ethyl mercaptan	$1 \times 10^9$
1,3-Xylen-4-ol	$2 \times 10^{12}$
$\mu$ -Xylene	$2 \times 10^{12}$
Acetone	$6 \times 10^{13}$

Source: From K.B. Döving, Problems in the Physiology of Olfaction, in *Symposium on Foods: The Chemistry and Physiology of Flavors*, H.W. Schultz et al., eds., 1967, AVI Publishing

so that more odors can reach the olfactory tissue. What is remarkable about the olfactory mechanism is not only that thousands of odors can be recognized, but that it is possible to store the information in the brain for retrieval after long periods of time. The ability to smell is affected by several conditions, such as colds, menstrual cycle, and drugs such as penicillin. Odors are usually the result of the presence of mixtures of several, sometimes many, different

odorous compounds. The combined effect creates an impression that may be very different from that of the individual components. Many food flavors, natural as well as artificial, are of this compound nature.

## Odor and Molecular Structure

M. Stoll wrote in 1957: "The whole subject of the relation between molecular structure and odor is very perplexing, as there is no doubt that there exist as many relationships of structure and odor as there are structures of odorous substances." In 1971 (referring to Stoll 1957), Teranishi wrote: "The relation between molecular structure and odor was perplexing then. It is now." We can observe a number of similarities between the chemical structure of compounds and their odors. However, the field of food flavors, as is the field of perfumery, is still very much an art, albeit one greatly supported by scientists' advancing ability to classify structures and identify the effect of certain molecular configurations. The odor potency of various compounds ranges widely. Table 7.15 indicates a range of about eight orders of magnitude (Teranishi 1971). This indicates that volatile flavor compounds may be present in greatly differing quantities, from traces to relatively large amounts.

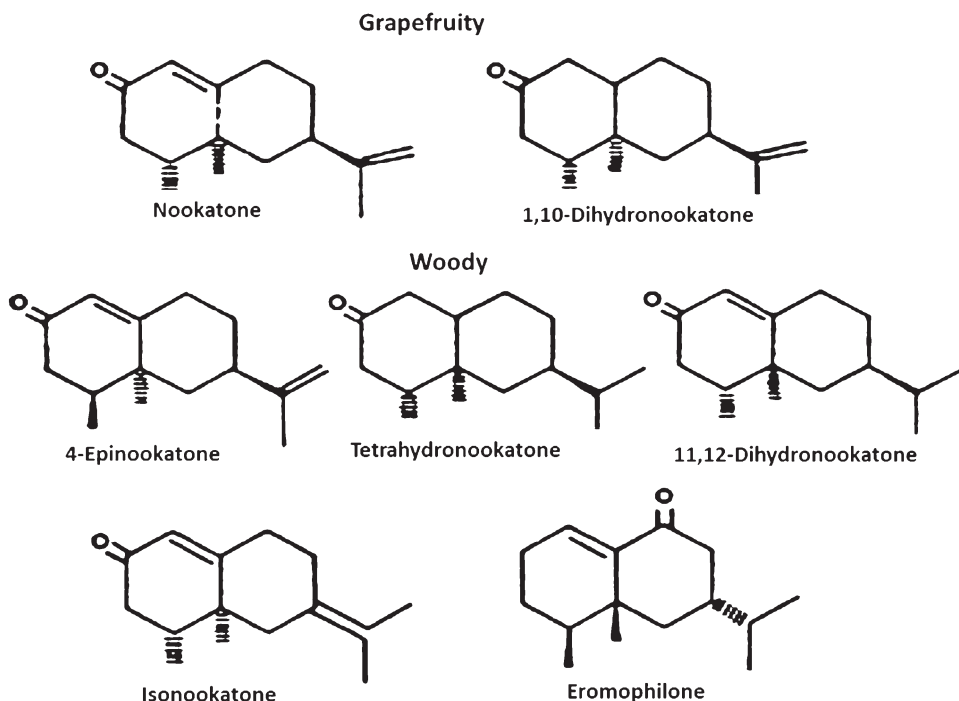
**Table 7.15** Odor thresholds of compounds covering a wide range of intensity

Odorant	Threshold ( $\mu\text{g/L}$ of water)
Ethanol	100,000
Butyric acid	240
Nootkatone	170
Humulene	160
Myrcene	15
<i>n</i> -Amyl acetate	5
<i>n</i> -Decanal	0.0
$\alpha$ - and $\beta$ -Sinensal	0.05
Methyl mercaptan	0.02
$\beta$ -Ionone	0.007
2-methoxy-3- isobutylpyra- zine	0.002

Source: From R. Teranishi, *Odor and Molecular Structure*, in *Gustation and Olfaction*, G. Ohloff and A.F. Thomas, eds., 1971, Academic Press

The musks are a common illustration of compounds with different structures that all give similar odors. These may include tricyclic compounds, macrocyclic ketones and lactones, steroids, nitro-cyclohexanes, indanes, tetrahydronaphthalenes, and acetophenoses. Small changes in the structure of these molecules may significantly change in potency but will not affect quality, since all are musky. There are also some compounds that have similar structures and very different odors, such as nootkatone and related compounds (Teranishi 1971). Nootkatone is a flavor compound from grapefruit oil. This compound and 1,10-dihydronootkatone have a grapefruity flavor (Fig. 7.28). Several other related compounds have a woody flavor. The odor character of stereoisomers may be quite different. The case of menthol has already been described. Only menthol isomers have peppermint aroma. The iso-, neo-, and neoisomenthols have an unpleasant musty flavor. Naves (1957) describes the difference between the *cis*- and *trans*- forms of 3-hexenol ( $\text{CH}_2\text{OH}-\text{CH}_2-\text{CH}=\text{CH}-\text{CH}_2\text{CH}_3$ ). The *cis*-isomer has a fresh green odor, whereas the *trans*-isomer has a scent reminiscent of chrysanthemum. The 2-*trans*-6-*cis* nonadienal smells of cucumber and is quite different from the smell of the 2-*trans*-6-*trans* isomer (nonadienal,  $\text{CHO}-\text{CH}=\text{CH}-(\text{CH}_2)_2-\text{CH}=\text{CH}-\text{CH}_2-\text{CH}_3$ ). Lengthening of the carbon chain may affect odorous properties. The odor of saturated acids changes remarkably as chain length increases. The lower fatty acids, especially butyric, have very intense and unpleasant flavors, because an increased chain length changes flavor character (Table 7.16) and lessens intensity. The fatty acids with 16 or 18 carbon atoms have only a faint flavor.

Another example is given by Kulka (1967). Gamma-nonalactone has a strong coconut-like flavor;  $\gamma$ -undecalactone has a peach aroma. As the chain length is increased by one more carbon atom, the flavor character becomes peach-musk. The lactones are compounds of widely differing structure and odor quality and are found as components of many food flavors. Gamma- and  $\delta$ -lactones with 10–16 carbon atoms have been reported (Jurriens and Oeje 1965) as flavor components of butter, contributing to the butter flavor



**Fig. 7.28** Odor character of nootkatone and related compounds

**Table 7.16** Flavor character of some N-carboxylic acids

Acid	Flavor character
Formic	Acid, pungent
Acetic	Acid, vinegary, pungent
Propionic	Acid, pungent, rancid, cheesy
Butyric	Acid, rancid
Hexanoic	Sweaty, goaty
Octanoic	Rancid
Decanoic	Waxy
Lauric	Tallowy
Myristic	Soapy, cardboard
Palmitic	Soapy

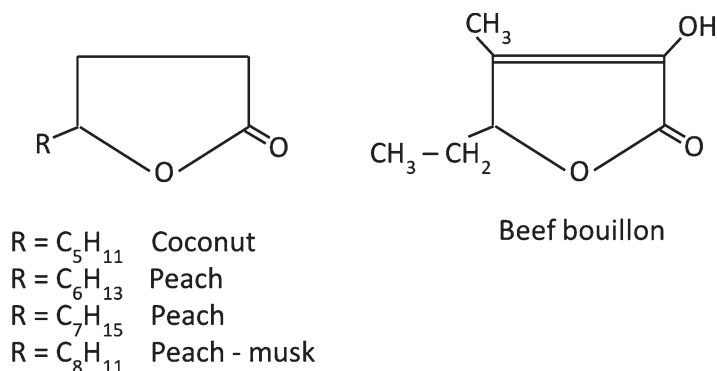
in concentrations of only parts per million. The flavor character and chemical structure of some  $\gamma$ -lactones as reported by Teranishi (1971) are shown in Fig. 7.29. One of these, the  $\gamma$ -lactone with a total chain length of 10 carbons, has peach flavor. The  $\alpha$ -hydroxy- $\beta$ -methyl- $\gamma$ -carboxy- $\Delta^{\alpha-\beta}$ - $\gamma$ -hex-eno-lactone occurs in protein hydrolysate and has very strong odor and flavor of beef bouillon. Gold and Wilson (1963) found that the volatile flavor compounds of celery contain a number

of phthalides (phthalides are lactones of phthalic acid, lactones are internal esters of hydroxy acids). These include the following:

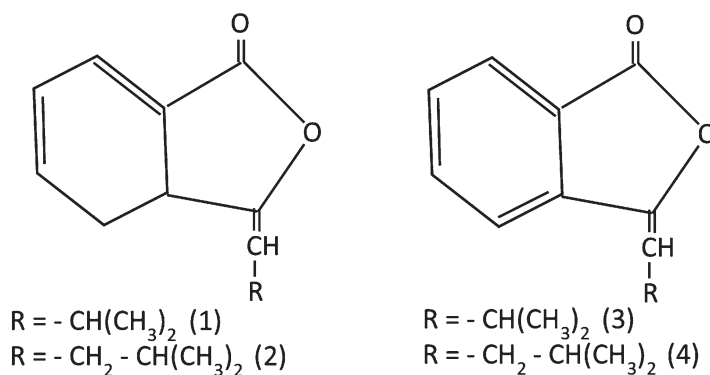
- 3-isobutyliden-3a,4-dihydrophthalide (Fig. 7.30).
- 3-isovalidene-3a,4-dihydrophthalide.
- 3-isobutylidene phthalide.
- 3-isovalidene phthalide.

These compounds exhibit celery-like odors at levels of 0.1 ppm in water. Pyrazines have been identified as the compounds giving the characteristic intense odor of green peppers (Seifert et al. 1970). A number of pyrazine derivatives were tested and, within this single class of compounds, odor potencies showed a range of eight orders of magnitude equal to that of the widely varying compounds listed in Table 7.15. The compounds examined by Seifert et al. (1970) are listed in Table 7.17. 2-methoxy-3-isobutylpyrazine appears to be the compound responsible for the green pepper odor. Removal of the methoxy- or alkyl-groups reduces the odor potency by  $10^5$ –

**Fig. 7.29** Flavor character of some lactones. *Source:* From R. Teranishi, *Odor and Molecular Structure*, in *Gustation and Olfaction*, G. Ohloff and A.F. Thomas, eds., 1971, Academic Press



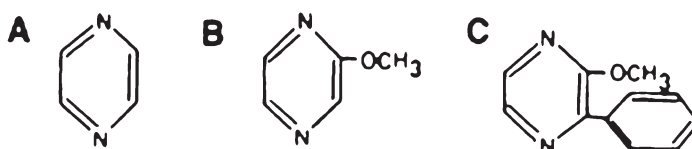
**Fig. 7.30** Phthalides of celery volatiles



$10^6$  times, as is the case with 2-methoxypyrazine, 2-isobutylpyrazine, and 2,5-dimethylpyrazine. Thus, small changes in molecular structure may greatly affect flavor potency. The odors of isobutyl, propyl, and hexyl methoxypyrazines are similar to that of green peppers. The isopropyl compound is moderately similar to peppers and its odor is somewhat similar to raw potato. The ethyl compound is even more similar to raw potato and less to pepper. In fact, this compound can be isolated from potatoes. The methyl compound has an odor like roasted peanuts. The structure of some of the pyrazines is shown in Fig. 7.31. Pyrazines have been identified as flavor components in a number of foods that are normally heated during processing. Rizzi (1967) demonstrated the presence of seven alkyl-substituted pyrazines in chocolate aroma. These were isolated by steam distillation, separated by gas-liquid chromatography, and identified by

mass spectrometry. The components are methyl pyrazine; 2,3-dimethylpyrazine; 2-ethyl-5-methyl-pyrazine; trimethylpyrazine; 2,5-dimethyl-3-ethylpyrazine; 2,6-dimethyl-3-ethylpyrazine; and tetramethylpyrazine. Other researchers (Flament et al. 1967; Marion et al. 1967) have isolated these and other pyrazines from the aroma components of cocoa. Pyrazines are also aroma constituents of coffee. Goldman et al. (1967) isolated and identified 24 pyrazines and pyridines and revealed the presence of possibly 10 more. Bondarovich et al. (1967) isolated and identified a large number of pyrazines from coffee aroma and drew attention to the importance of pyrazines and dihydropyrazines to the flavor of roasted or otherwise cooked foods. These authors also drew attention to the instability of the dihydropyrazines. This instability not only makes their detection and isolation difficult, but may help explain why flavors such as that of

**Fig. 7.31** (a) Pyrazine, (b) 2-methoxypyrazine, and (c) 2-methoxy-3-hexylpyrazine



**Table 7.17** Odor threshold of pyrazine and derivatives

Compound	Odor threshold (parts per $10^{12}$ parts of water)
2-methoxy-3-hexylpyrazine	1
2-methoxy-3-isobutylpyrazine	2
2-methoxy-3-propylpyrazine	6
2-methoxy-3-isopropylpyrazine	2
2-methoxy-3-ethylpyrazine	400
2-methoxy-3-methylpyrazine	4000
2-methoxypyrazine	700,000
2-isobutylpyrazine	400,000
2-5-dimethylpyrazine	1,800,000
Pyrazine	175,000,000

Source: From R.M. Seifert et al., Synthesis of Some 2-Methoxy-3-Alkylpyrazines with Strong Bell Pepper-Like Odors, *J. Agric. Food Chem.*, Vol. 18, pp. 246–249, 1970, American Chemical Society

roasted coffee rapidly change with time. Another roasted product from which pyrazines have been isolated is peanuts. Mason et al. (1966) found methylpyrazine; 2,5-dimethylpyrazine; trimethylpyrazine; methylethylpyrazine; and dimethylethylpyrazine in the flavor of roasted peanuts. The pyrazines appear to be present in unprocessed as well as in heated foods. The thresholds of some pyrazines in water are found in Table 7.17.

Another group of compounds that have been related to the aroma of heated foods is the furanones. Teranishi (1971) summarized the findings on several of the furanones (see Fig. 7.24). The 4-hydroxy-2, 5-dimethyl-3-dihydrofuranone (1) has a caramel or burnt pineapple odor. The 4-hydroxy-5-methyl-3-dihydrofuranone (2) has a roasted chicory root odor. Both compounds may contribute to beef broth flavor. The 2,5-dimethyl-3-dihydrofuranone (3) has the odor of freshly baked bread. Isomaltol (4) and maltol (5) are products of the caramelization and pyrolysis of carbohydrates.

**Table 7.18** Primary odors for humans and compounds eliciting these odors

Primary odor	Odor compounds
Camphoraceous	Borneol, <i>tert</i> -butyl alcohol <i>d</i> -camphor, cineol, pentamethyl ethyl alcohol
Pungent	Allyl alcohol, cyanogen, formaldehyde, formic acid, methylisothiocyanate
Ethereal	Acetylene, carbon tetrachloride, chloroform, ethylene dichloride, propyl alcohol
Floral	Benzyl acetate, geraniol, $\alpha$ -ionone, phenylethyl alcohol, terpineol
Pepperminty	<i>tert</i> -butylcarbinol, cyclohexanone, menthone, piperitol, 1,1,3-trimethyl-cyclo-5-hexanone
Musky	Androstan-3 $\alpha$ -ol (strong), cyclohexadecanone, ethylene cebacate, 17- methylandrostan-3 $\alpha$ -ol, pentadecanolactone
Putrid	Amylmercaptan, cadaverine, hydrogen sulfide, indole (when concentrated, floral when dilute), skatole

Source: From J.E. Amoore et al., The Stereochemical Theory of Odor, *Sci. Am.*, Vol. 210, No. 2, pp. 42–49, 1964

Amoore (Amoore et al. 1964; Amoore 1967) compared the various odor qualities that have been used to characterize odors and concluded that seven primary odors would suffice to cover them all: camphoraceous, pungent, ethereal, floral, pepperminty, musky, and putrid. Table 7.18 lists some of the chemical compounds that can be used to demonstrate these primary odors. The theory is based on the assumption that all odorous compounds have a distinctive molecular shape and size that fit into a socket on the receptor site. This would be similar to the “lock-and-key” concept of enzyme action.

The suggestion that odorous character is related to vibrational specificity of odor molecules has led to the vibrational theory of olfaction

(Wright 1957). Vibrational energy levels can be derived from the infrared or Raman spectra. The spectral area of greatest interest is that below  $700\text{ cm}^{-1}$ , which is related to vibrations of chains and flexing or twisting of bonds between groups of atoms in the molecule. Wright and others have demonstrated that correlations exist between spectral properties and odor quality in a number of cases, but inconsistencies in other cases have yet to be explained.

Obviously, none of the many theories of olfaction proposed so far have been entirely satisfactory. It might be better to speak of hypotheses rather than of theories. Most of these theories deal with the explanation of odor quality and do not account for the quantitative aspects of the mechanism of olfaction. The classification of odor and the correlation of chemical structure and odor remain difficult to resolve.

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## Description of Food and Beverage Flavors

The flavor impression of a food is influenced by compounds that affect both taste and odor. The analysis and identification of many volatile flavor compounds in a large variety of food products have been assisted by the development of powerful analytical techniques. Gas-liquid chromatography was widely used in the early 1950s when commercial instruments became available. Introduction of the flame ionization detector increased sensitivity by a factor of 100 and, together with mass spectrometers, gave a method for rapid identification of many components in complex mixtures. These methods have been described by Teranishi et al. (1971). As a result, a great deal of information on volatile flavor components has been obtained in recent years for a variety of food products. The combination of gas chromatography and mass spectrometry can provide identification and quantitation of flavor compounds. However, when the flavor consists of many compounds, sometimes several hundred, it is impossible to evaluate a flavor from this information alone. It is then possible

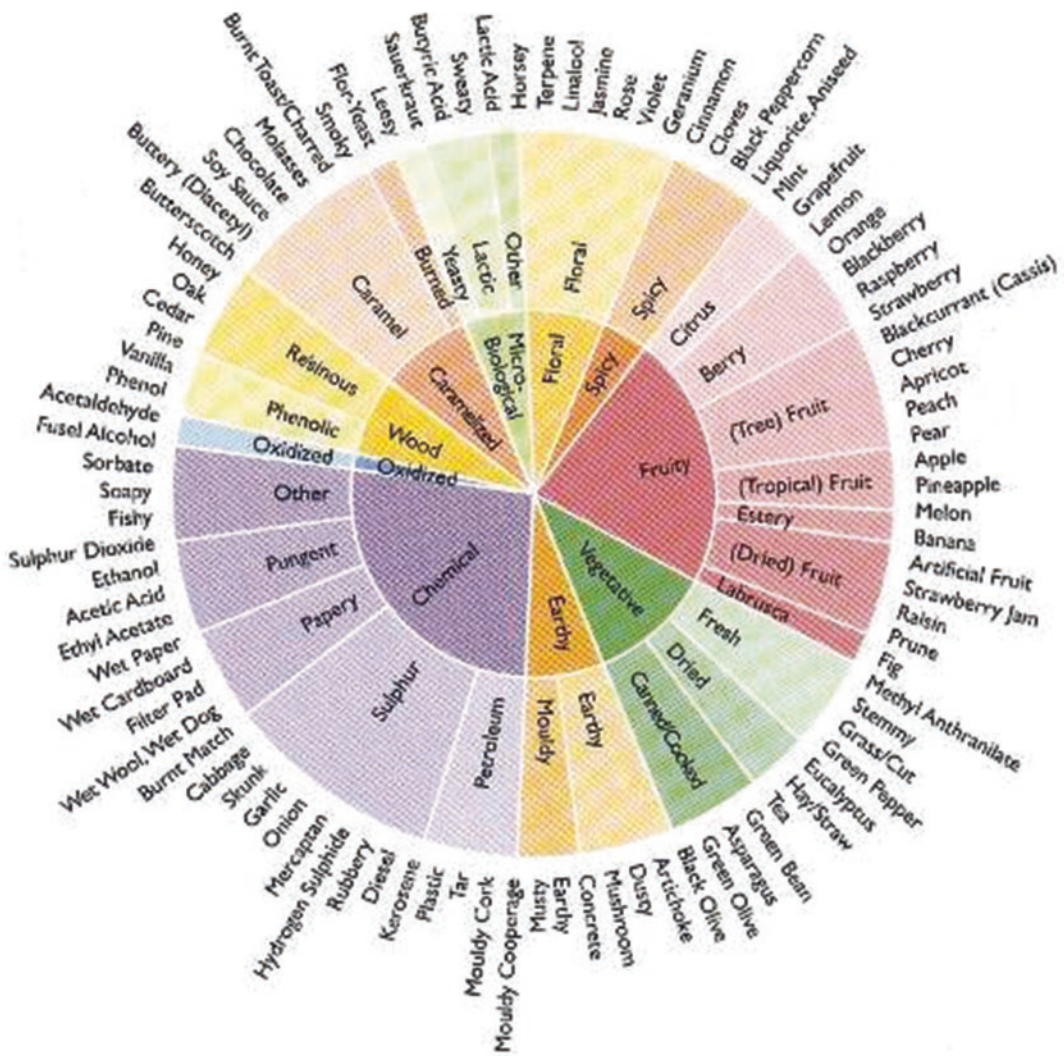
to use pattern recognition techniques to further describe the flavor. The pattern recognition method involves the application of computer analysis of complex mixtures of compounds. Computer multivariate analysis has been used for the detection of adulteration of orange juice and Spanish sherries (Maarse et al. 1987).

Flavors are often described by using the human senses on the basis of widely recognized taste and smell sensations. A proposed wine aroma description system is shown in Fig. 7.32 (Noble et al. 1987). Such systems attempt to provide an orderly and reliable basis for comparison of flavor descriptions by different tasters.

The aroma is divided into first-, second-, and third-tier terms, with the first-tier terms in the center. Examination of the descriptors in the aroma wheel shows that they can be divided into two types, flavors and off-flavors. Thus, it would be useful to divide the flavor wheel into two tables—one for flavors and one for off-flavors, as shown in Tables 7.19 and 7.20.

The difficulty in relating chemical composition and structure to the aroma of a food that contains a multitude of flavor compounds is evident from the work of Meyboom and Jongenotter (1981). They studied the flavor of straight-chain, unsaturated aldehydes as a function of double-bond position and geometry. Some of their results are presented in Table 7.21. Flavors of unsaturated aldehydes of different chain length and geometry may vary from bitter almond to lemon and cucumber when tasted separately.

A method of flavor description, developed by researchers at A.D. Little Inc. (Sjöström 1972), has been named the flavor profile method. The flavor profile method uses the recognition, description, and comparison of aroma and flavor by a trained panel of four to six people. Through training, the panel members are made familiar with the terminology used in describing flavor qualities. In addition to describing flavor quality, intensity values are assigned to each of the quality aspects. The intensity scale is threshold, slight, moderate, and strong, and these are represented by the symbols), (, 1, 2, and 3, respectively.



**Fig. 7.32** Modified wine aroma wheel for the description of wine aroma. *Source:* From A.C. Noble et al., Modification of a Standardized System of Wine Aroma

Terminology, *Am. J. Enol. Vitic.*, Vol. 38, pp. 143–146, 1987, American Society of Enology and Viticulture

With the exception of threshold value, the units are ranges and can be more precisely defined by the use of reference standards. In the panel work, the evaluation of aroma is conducted first because odor notes can be overpowered when the food is eaten. This is followed by flavor

analysis, called “flavor by mouth,” a specialists’ description of what a consumer would experience eating the food. Flavor analysis includes such factors as taste, aroma, feeling, and after-taste. A sample flavor profile of margarine is given in Table 7.22.

**Table 7.19** Aroma description of wine as listed in the aroma wheel, listing only the flavor contribution

First tier	Second tier	Third tier	First tier	Second tier	Third tier		
Floral	Floral	Geranium		Canned/	Green beans		
		Violet		cooked	Asparagus		
		Rose			Green olive		
		Orange blossom			Black olive		
		Linalool			Artichoke		
Spicy	Spicy	Licorice anise Black pepper Cloves		Dried	Hay/straw Tea Tobacco		
Fruity	Citrus	Grapefruit Lemon	Nutty	Nutty	Walnut Hazelnut		
		Blackberry				Almond	
		Raspberry	Caramelized	Caramelized	Honey		
		Strawberry				Butterscotch	
		Black currant			Diacetyl (butter)		
		Tree fruit	Cherry Apricot Peach			Soy sauce Chocolate Molasses	
			Apple	Woody	Phenolic	Phenolic	
		Tropical fruit	Pineapple			Vanilla	
			Melon		Resinous	Cedar	
			Banana			Oak	
	Dried fruit	Strawberry jam Raisin Prune Fig		Burned	Smoky Burnt toast/charred Coffee		
		Artificial fruit Methyl anthranilate					
Vegetative		Fresh	Stemmy Grass, cut green Bell pepper Eucalyptus Mint				

## Astringency

The sensation of astringency is considered to be related more to touch than to taste. Astringency causes a drying and puckering over the whole surface of the mouth and tongue. This sensation is caused by interaction of astringent compounds with proteins and glycoproteins in the mouth. Astringent compounds are present in fruits and beverages derived from fruit (such as juice, wine, and cider), in tea and cocoa, and in beverages matured in oak casks. Astringency is caused by tannins, either those present in the food or extracted from the wood of oak barrels. The astringent reaction involves a bonding to proteins

in the mouth, followed by a physiological response. The astringent reaction has been found to occur between salivary proteins that are rich in proline (Luck et al. 1994). These proline-rich proteins (PRPs) have a high affinity for polyphenols. The effect of the structure of PRP is two-fold: (1) proline causes the protein to have an open and flexible structure, and (2) the proline residue itself plays an important role in recognizing the polyphenols involved in the complex formation. The complex formation between PRP and polyphenol has been represented by Luck et al. (1994) in pictorial form (Fig. 7.33). The reaction is mediated by hydrophobic effects and hydrogen bonding on protein sites close to prolyl



**Table 7.20** Aroma description of wine as listed in the aroma wheel, listing only the off-flavors

First tier	Second tier	Third tier
Earthy	Moldy	Moldy cork Musty (mildew)
	Earthy	Mushroom Dusty
Chemical	Petroleum	Diesel Kerosene Plastic Tar
	Sulfur	Wet wool, wet dog Sulfur dioxide Burnt match Cabbage Skunk Garlic Mercaptan Hydrogen sulfide Rubbery
	Papery	Wet cardboard Filterpad
	Pungent	Sulfur dioxide Ethanol Acetic acid Ethyl acetate
	Other	Fusel alcohol Sorbate soapy Fishy
Pungent	Cool	Menthol
	Hot	Alcohol
Oxidized	Oxidized	Acetaldehyde
Microbiological	Yeasty	Leesy Flor yeast
	Lactic	Lactic acid Sweaty Butyric acid Sauerkraut
	Other	Mousey Horsey

residues in the PRP. The resulting cross-linking, aggregation, and precipitation of the PRP causes the sensation of astringency.

Some anthocyanins are both bitter and astringent. Bitter compounds such as quinine and caffeine compete with the tannins in complexing with buccal proteins and thereby lower the astringent response. Astringency is caused by higher molecular weight tannins, whereas the lower molecular weight tannins up to tetrameres are associated with bitterness (Macheix et al. 1990).

**Table 7.21** Flavor description of unsaturated aldehydes dissolved in paraffin oil

Aldehyde	Flavor description
<i>trans</i> -3-hexenal	Green, odor of pine tree needles
<i>cis</i> -3-hexenal	Green beans, tomato green
<i>trans</i> -2-heptenal	Bitter almonds
<i>cis</i> -6-heptenal	Green, melon
<i>trans</i> -2-octenal	Nutty
<i>trans</i> -5-octenal	Cucumber
<i>cis</i> -5-octenal	Cucumber
<i>trans</i> -2-nonenal	Starch, glue
<i>trans</i> -7-nonenal	Melon

Source: From P.W. Meyboom and G.A. Jongenotter, Flavor Perceptibility of Straight Chain, Unsaturated Aldehydes as a Function of Double Bond Position and Geometry, *J. Am. Oil Chem. Soc.*, Vol. 58, pp. 680–682, 1981

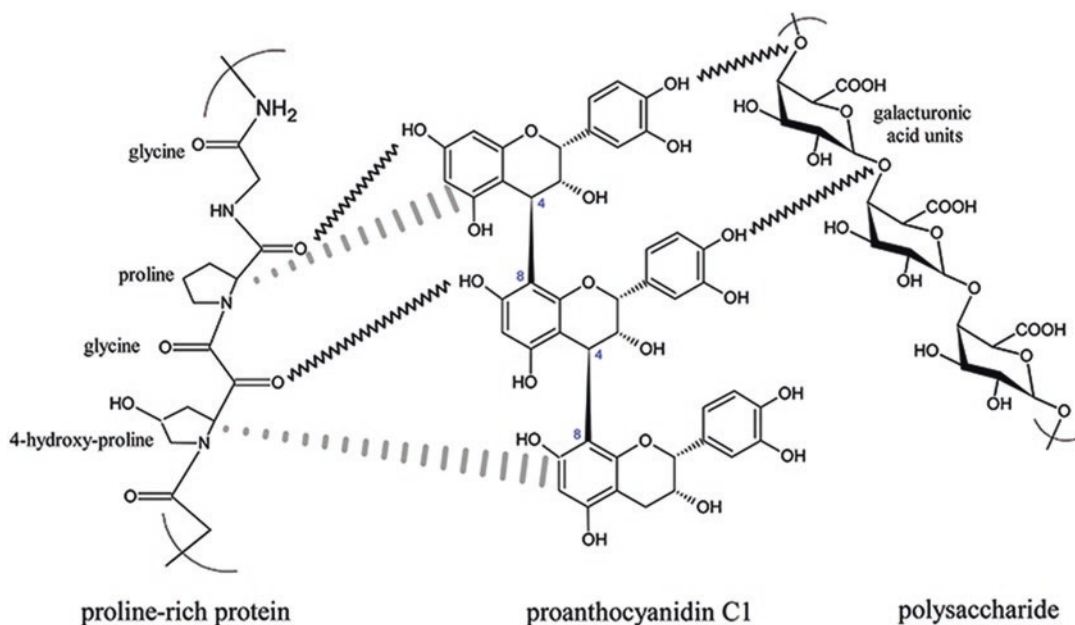
**Table 7.22** Flavor profile of margarine

Aroma		Flavor by mouth	
Amplitude	2	Amplitude	2½
Sweet cream	½	Sweet cream	1½
Oil	) (	Oil	½
Sour	½	Salt	1½
Vanillin sweet	) (	Butter mouthfeel	2
		Sour	1

Note: ) ( = threshold; 1 = slight; 2 = moderate; 3 = strong. Source: Reprinted with permission from L.B. Sjöström, *The Flavor Profile*, © 1972, A.D. Little, Inc.

## Flavor and Off-Flavor

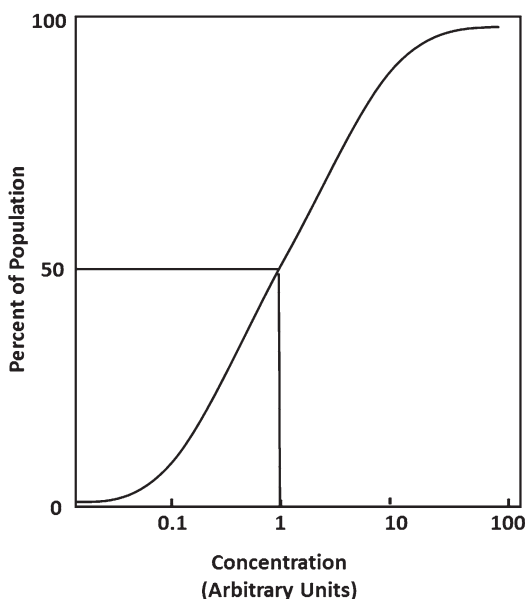
It is impossible to deal with the subject of flavor without considering off-flavors. In many cases, the same chemical compounds are involved in both flavors and off-flavors. The only distinction appears to be whether a flavor is judged to be pleasant or unpleasant. This amounts to a personal judgment, although many unpleasant flavors (or off-flavors) are universally found to be unpleasant. A distinction is sometimes made between off-flavors—defined as unpleasant odors or flavors imparted to food through internal deteriorative change—and taints—defined as unpleasant odors or flavors imparted to food through external sources (Saxby 1996). Off-flavors in animal products, meat and milk, may be caused by transfer of substances from feed. Off-flavors in otherwise sound foods can be caused by heat, oxidation, light, or enzymic



**Fig. 7.33** Complex formation between proline-rich proteins and polyphenols L. Federico Casassa (2017). *Flavonoid Phenolics in Red Winemaking, Phenolic Compounds - Natural Sources, Importance and Applications*, Prof. Marcos Soto-Hernández (Ed.),

InTech, DOI: <https://doi.org/10.5772/67452>. Available from: <https://www.intechopen.com/books/phenolic-compounds-natural-sources-importance-and-applications/flavonoid-phenolic>

action. The perception of taste and flavor can be defined for a given group of people by the International Standards Organization (ISO) 5492 standard (ISO 1992) as follows: The odor or taste threshold is the lowest concentration of a compound detectable by a certain proportion (usually 50%) of a given group of people. A graphic representation of this relationship has been given by Saxby (1996). The graph in Fig. 7.34 relates the percentage of people within a given group to the ability to detect a substance at varying concentrations. Of the population, 50% can detect the compound at the concentration of one unit. At a concentration of the compound 10 times greater than the mean threshold, about 10% of the population is still not able to detect it. At the other end of the spectrum, 5% of the population can still detect the compound at a concentration 10 times less than the mean threshold. These findings have important consequences for the presence of compounds causing off-flavors. Even very low levels of a chemical that produces off-flavors may cause a significant number of people to complain.



**Fig. 7.34** Variation of taste threshold within a given population. Adapted from M.J. Saxby, *Food Taints and Off-Flavors*, p. 43, © 1996, Aspen Publishers, Inc.

Certain flavor compounds may appear quite pleasant in one case and extremely unpleasant in another. Many examples of this can be cited. One of the well-known cases is that of short-chain free fatty acids in certain dairy products. Many cheese flavors contain volatile fatty acids as flavor contributors (Day 1967). Yet, the same fatty acids in very low concentrations in milk and other dairy products cause a very unpleasant, rancid off-flavor (Patton 1964). Forss (1969) has drawn attention to the compound non-2-enal. During studies of dairy product off-flavor, this compound was isolated as a component of the oxidation off-flavor and was found to have an odor reminiscent of cucumbers. The same compound was isolated from cucumbers, and the cucumber-like flavor was assigned to the molecular structure of a 2-*trans*-enal with 9 or 10 carbon atoms. Further unsaturation and conjugation to give a 2,4-dienal produces flavors reminiscent of cardboard or linoleum. Lactones were isolated by Keeney and Patton (1956) and Tharp and Patton (1960) and were considered to be the cause of stale off-flavors in certain dairy products. The same lactones, including  $\delta$ -decalactone and  $\delta$ -dodecalactone, were subsequently recognized as contributors to the pleasant aroma of butter (Day 1966). Dimethylsulfide is a component of the agreeable aroma of meat and fish but has also been found to cause an off-flavor in canned salmon (Tarr 1966). Acetaldehyde occurs naturally in many foods, especially fruits, and is reported to be essential for imparting the taste of freshness (Byrne and Sherman 1984). The same compound is responsible for a very unpleasant oxidized flavor in wine. Sinki (1988) has discussed the problems involved in creating a universally acceptable taste, and has stated that most individual flavor chemicals are either repugnant or painful outside their proper formulations. This complex interaction between flavor chemicals, and between flavors and the individual, makes the creation of a flavorful product both a science and an art, according to Sinki. The subject of pleasantness and unpleasantness of flavors is the basis of a chapter in *Odour Description and Odour Classification* by Harper et al. (1968) and is the main subject of Moncrieff's *Odour Preferences* (1966).

## Flavor of Some Foods

As indicated previously, the two main factors affecting flavor are taste and odor. In a general way, food flavors can be divided into two groups. The first consists of foods whose flavor cannot be attributed to one or a few outstanding flavor notes; their flavor is the result of the complex interaction of a variety of taste and odor components. Examples include bread, meat, and cheese. The second group consists of foods in which the flavor can be related to one or a few easily recognized components (contributory flavor compounds). Examples include certain fruits, vegetables, and spices. Another way of differentiating food flavors is by considering one group in which the flavor compounds are naturally present and another group in which the flavor compounds are produced by processing methods.

### Bread

The flavor of white bread is formed mainly from the fermentation and baking processes. Freshly baked bread has a delightful aroma that is rapidly lost on cooling and storage. It has been suggested that this loss of flavor is the result of disappearance of volatile flavor components. However, it is well known that the aroma may be at least partially regenerated by simply heating the bread. Schoch (1965) suggested that volatile flavor compounds may become locked in by the linear fraction of wheat starch. The change in texture upon aging may be a contributory factor in the loss of flavor. During fermentation, a number of alcohols are formed, including ethanol, *n*-propanol, isoamyl and amyl alcohol, isobutyl alcohol, and  $\beta$ -phenol alcohol. The importance of the alcohols to bread flavor is a matter of controversy. Much of the alcohols are lost to the oven air during baking. A large number of organic acids are also formed (Johnson et al. 1966). These include many of the odd and even carbon number saturated aliphatic acids, from formic to capric, as well as lactic, succinic, pyruvic, hydrocinnamic, benzilic, itaconic, and levulinic acid. A large number of carbonyl compounds have been

identified in bread, and these are believed to be important flavor components. Johnson et al. (1966) list the carbonyl compounds isolated by various workers from bread; this list includes 14 aldehydes and 6 ketones. In white bread made with glucose, the prevalent carbonyl compound is hydroxymethylfurfural (Linko et al. 1962). The formation of the crust and browning during baking appear to be primary contributors to bread flavor. The browning is mainly the result of a Maillard-type browning reaction rather than caramelization. This accounts for the presence of the carbonyl compounds, especially furfural, hydroxymethylfurfural, and other aldehydes. In the Maillard reaction, the amino acids are transformed into aldehydes with one less carbon atom. Specific aldehydes can thus be formed in bread crust if the necessary amino acids are present. The formation of aldehydes in bread crust is accompanied by a lowering of the amino acid content compared to that in the crumb. Johnson et al. (1966) have listed the aldehydes that can be formed from amino acids in bread crust as a result of the Strecker degradation (Table 7.23).

Grosch and Schieberle (1991) reported the aroma of wheat bread to include ethanol, 2-methylpropanal, 3-methylbutanal, 2,3-butanedione, and 3-methylbutanol. These compounds contribute significantly to bread aroma, whereas other compounds are of minor importance.

**Table 7.23** Aldehydes that can be formed from amino acids in bread crust as a result of the strecker degradation

Amino acid	Aldehyde
Alanine	Acetaldehyde
Glycine	Formaldehyde
Isoleucine	2-Methylbutanal
Leucine	Isovaleraldehyde
Methionine	Methional
Phenylalanine	Phenylacetaldehyde
Threonine	2-Hydroxypropanal
Serine	Glyoxal

Source: From J.A. Johnson et al., *Chemistry of Bread Flavor*, in *Flavor Chemistry*, 1. Hornstein, ed., 1966, American Chemical Society

## Meat

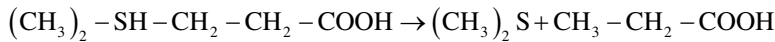
Meat is another food in which the flavor is developed by heating from precursors present in the meat; this occurs in a Maillard-type browning reaction. The overall flavor impression is the result of the presence of a large number of non-volatile compounds and the volatiles produced during heating. The contribution of nonvolatile compounds in meat flavor has been summarized by Solms (1971). Meat extracts contain a large number of amino acids, peptides, nucleotides, acids, and sugars. The presence of relatively large amounts of inosine-5'-monophosphate has been the reason for considering this compound as a basic flavor component. In combination with other compounds, this nucleotide would be responsible for the meaty taste. Living muscle contains adenosine-5'-triphosphate; this is converted after slaughter into adenosine-5'-monophosphate, which is deaminated to form inosine-5'-monophosphate (Jones 1969). The volatile compounds produced on heating can be accounted for by reactions involving amino acids and sugars present in meat extract. Lean beef, pork, and lamb are surprisingly similar in flavor; this reflects the similarity in composition of extracts in terms of amino acid and sugar components. The fats of these different species may account for some of the normal differences in flavor. In the volatile fractions of meat aroma, hydrogen sulfide and methyl mercaptan have been found; these may be important contributors to meat flavor. Other volatiles that have been isolated include a variety of carbonyls such as acetaldehyde, propionaldehyde, 2-methylpropanal, 3-methylbutanal, acetone, 2-butanone, *n*-hexanal, and 3-methyl-2-butanone (Moody 1983).

## Fish

Fish contains sugars and amino acids that may be involved in Maillard-type reactions during heat processing (canning). Proline is a prominent amino acid in fish and may contribute to sweetness.

The sugars ribose, glucose, and glucose-6-phosphate are flavor contributors, as is 5'-inosinic acid, which contributes a meaty flavor note. Volatile sulfur compounds contribute to the flavor of fish; hydrogen sulfide, methylmercaptan, and dimethylsulfide may contribute to the aroma of fish. Tarr (1966) described an off-flavor problem in

canned salmon that is related to dimethylsulfide. The salmon was found to feed on zooplankton containing large amounts of dimethyl-2-carboxyethyl sulfonium chloride. This compound became part of the liver and flesh of the salmon and in canning degraded to dimethylsulfide according to the following equation:



The flavor of cooked, fresh fish is caused by the presence of sugars, including glucose and fructose, giving a sweet impression as well as a umami component arising from the synergism between inosine monophosphate and free amino acids. The fresh flavor of fish is rapidly lost by bacterial spoilage. In fresh fish, a small amount of free ammonia, which has a pH level of below seven, exists in protonated form. As spoilage increases, the pH rises and ammonia is released. The main source of ammonia is trimethylamine, produced as a degradation product of trimethyl-amineoxide.

The taste-producing properties of hypoxanthine and histidine in fish have been described by Konosu (1979). 5'-inosinate accumulates in fish muscle as a postmortem degradation product of ATP. The inosinate slowly degrades into hypoxanthine, which has a strong bitter taste. Some kinds of fish, such as tuna and mackerel, contain very high levels of free histidine, which has been postulated to contribute to the flavor of these fish.

## Milk

The flavor of normal fresh milk is probably produced by the cow's metabolism and is comprised of free fatty acids, carbonyl compounds, alkanols, and sulfur compounds. Free fatty acids may result from the action of milk lipase or bacterial lipase. Other decomposition products of lipids may be produced by the action of heat. In addition to lipids, proteins and lactose may be precursors of flavor compounds in milk (Badings 1991). Sulfur compounds that can be formed by heat from  $\beta$ -lactoglobulin include dimethyl sulfide, hydrogen sulfide, dimethyl disulfide, and methanethiol.

Some of these sulfur compounds are also produced from methionine when milk is exposed to light. Heterocyclic compounds are produced by nonenzymatic browning reactions. Bitter peptides can be formed by milk or bacterial proteinases.

The basic taste of milk is very bland, slightly sweet, and salty. Processing conditions influence flavor profiles. The extent of heat treatment determines the type of flavor produced. Low heat treatment produces traces of hydrogen sulfide. Ultra-high temperature treatment results in a slight fruity, ketone-like flavor. Sterilization results in strong ketone-like and caramelization/sterilization flavors. Sterilization flavors of milk are caused by the presence of 2-alkanones and heterocyclic compounds resulting from the Maillard reaction. Because of the bland flavor of milk, it is relatively easy for off-flavors to take over.

## Cheese

The flavor of cheese largely results from the fermentation process that is common to most varieties of cheese. The microorganisms used as cultures in the manufacture of cheese act on many of the milk components and produce a large variety of metabolites. Depending on the type of culture used and the duration of the ripening process, the cheese may vary in flavor from mild to extremely powerful. Casein, the main protein in cheese, is hydrolyzed in a pattern and at a rate that is characteristic for each type of cheese. Proteolytic enzymes produce a range of peptides of specific composition that are related to the specificity of the enzymes present. Under certain conditions bitter peptides may be

formed, which produce an off-flavor. Continued hydrolysis yields amino acids. The range of peptides and amino acids provides a “brothy” taste background to the aroma of cheese. Some of these compounds may function as flavor enhancers. Breakdown of the lipids is essential for the production of cheese aroma since cheese made from skim milk never develops the full aroma of normal cheese. The lipases elaborated by the culture organisms hydrolyze the triglycerides to form fatty acids and partial glycerides. The particular flavor of some Italian cheeses can be enhanced by adding enzymes during the cheese-making process that cause preferential hydrolysis of short-chain fatty acids. Apparently, a variety of minor components are important in producing the characteristic flavor of cheese. Carbonyls, esters, and sulfur compounds are included in this group. The relative importance of many of these constituents is still uncertain. Sulfur compounds found in cheese include hydrogen sulfide, dimethylsulfide, methional, and methyl mercaptan. All of these compounds are derived from sulfur-containing amino acids. The flavor of blue cheese is mainly the result of the presence of a number of methyl ketones with odd carbon numbers ranging in chain length from 3 to 15 carbons (Day 1967). The most important of these are 2-heptanone and 2-nonanone. The methyl ketones are formed by  $\beta$ -oxidation of fatty acids by the spores of *P. roqueforti*.

## Fruits

The flavor of many fruits appears to be a combination of a delicate balance of sweet and sour taste and the odor of a number of volatile compounds. The characteristic flavor of citrus products is largely due to essential oils contained in the peel. The essential oil of citrus fruits contains a group of terpenes and sesquiterpenes and a group of oxygenated compounds. Only the latter are important as contributors to the citrus flavor. The volatile oil of orange juice was found to be 91.6 mg per kg, of which 88.4 was hydrocarbons (Kefford 1959). The volatile water-soluble constituents of orange juice consist mainly of acetaldehyde, ethanol, methanol, and acetic acid. The

hydrocarbons include mainly D-limonene,  $\beta$ -myrcene, and a compound of composition  $C_{15}H_{24}$ . The esters include isovalerate, methyl alphaethyl-*n*-caproate, citronellyl acetate, and terpinyl acetate. In the group of carbonyls, the following compounds were identified: *n*-hexanal, *n*-octanal, *n*-decanal, and citronella; and in the group of alcohols, linalool,  $\alpha$ -terpineol, *n*-hexane-1-ol, *n*-octan-1-ol, *n*-decan-1-ol, and 3-hexen-1-ol were identified. The flavor deterioration of canned orange juice during storage results in stale off-flavors. This is due to reactions of the nonvolatile water-soluble constituents. As in the case of citrus fruits, no single compound is completely responsible for any single fruit aroma. However, some organoleptically important compounds characteristic for particular fruits have been found. These include amyl esters in banana aroma, citral in lemon, and lactones in peaches. The major flavor component of Bartlett pears was identified by Jennings and Sevenants (1964) as ethyl *trans*-2-*cis*-4-decadienoate.

## Vegetables

Vegetables contain an extensive array of volatile flavor compounds, either in original form or produced by enzyme action from precursors. Maarse (1991) has reviewed these in detail. Onion and garlic have distinctive and pungent aromas that result mostly from the presence of sulfur-containing compounds. A large number of flavor compounds in vegetables are formed after cooking or frying. In raw onions, an important compound is thio-propanal *s*-oxide—the lachrymatory factor. The distinctive odor of freshly cut onions involves two main compounds, propyl methane-thiosulfonate and propyl propanethiosulfonate. Raw garlic contains virtually exclusively sulfur compounds: four thiols, three sulfides, seven disulfides, three trisulfides, and six dialkylthio-sulfonates.

## Tea

The flavor of black tea is the result of a number of compounds formed during the processing of green tea leaves. The processing involves wither-

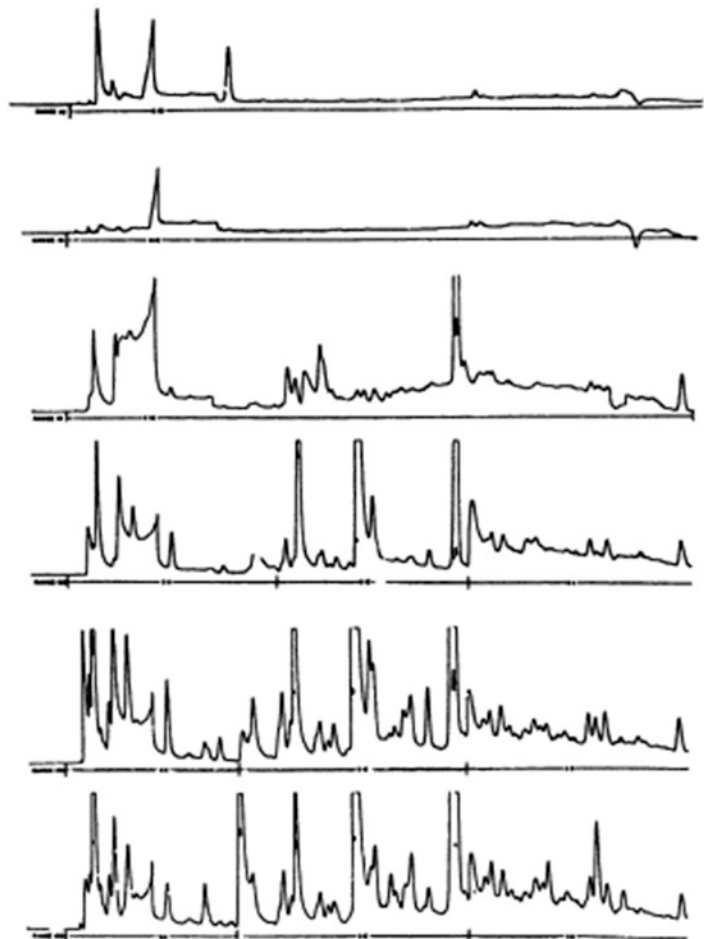
ing, fermentation, and firing. Bokuchava and Skobeleva (1969) indicate that the formation of the aroma occurs mainly during firing. Aromatic compounds isolated and identified from black tea include acrolein, *n*-butyric aldehyde, ethanol, *n*-butanol, isobutanol, hexanal, pentanal, 2-hexanol, 3-hexen-1-ol, benzaldehyde, linalool, terpenol, methylsalicylate, benzyl alcohol,  $\beta$ -phenylethanol, isobutyric aldehyde, geraniol, and acetophenone. The flavor substances of tea can be divided into the following four fractions: a carbonyl-free neutral fraction including a number of alcohols, a carbonyl fraction, a carboxylic acid fraction, and a phenolic fraction. A compilation (Maarse 1991) identifies a total of 467 flavor constituents in tea. The distinctive flavor of tea is due

to its content of lactones, aldehydes, alcohols, acids, and pyridines.

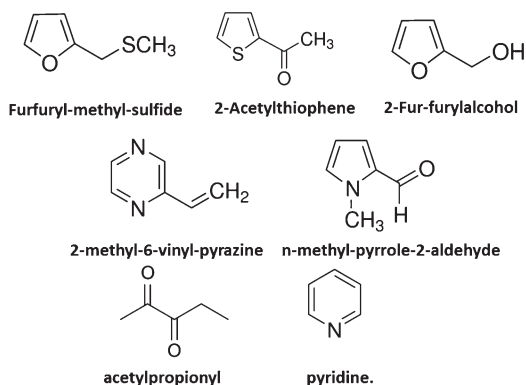
## Coffee

The flavor of coffee is developed during the roasting of the green coffee bean. Gas-liquid chromatography can be used to demonstrate (Fig. 7.35) the development of volatile constituents in increasing amounts as intensity of roasting increases (Gianturco 1967). The total number of volatile compounds that have been isolated is in the hundreds, and many of these have been identified. To determine the flavor contribution of each of these is a Herculean task. Many compounds result from the pyrolytic decomposition

**Fig. 7.35** Development of volatile constituents during roasting of coffee. From top to bottom: green coffee after 2, 6, 8, 11, and 15 min of roasting. The gas chromatograms show increasing concentrations of volatile compounds. Source: From M.A. Gianturco, Coffee Flavor, in *Symposium on Foods: The Chemistry and Physiology of Flavors*, H.W. Schultz et al., eds., 1967, AVI Publishing Co.



of carbohydrates into units of 2, 3, 4, or 5 carbons. Other compounds of carbohydrate origin are 16 furanic compounds, cyclic diketones, and maltol. Roasting of the proteins of the coffee bean can yield low molecular weight products such as amino acids, ammonia, amines, hydrogen sulfide, methyl mercaptan, dimethylsulfide, and dimethyl disulfide. A series of furanic and pyrrolic compounds identified include the following: furan, furfural, acetylfuran, 5-methylfuran, 5-methylfurfural, 5-methyl-2-acetylfuran and pyrrole, 2-pyrrolaldehyde, 2-acetylpyrrole, *N*-methylpyrrole, *N*-methyl-2-pyrrolaldehyde, and *N*-methyl-2-acetylpyrrole. Differences in the aroma of different coffees can be related to quantitative differences in some of the compounds isolated by gas chromatography, and ratios and amounts of these compounds may be different. Pyrazines, furanes, pyrroles, and thiophen derivatives are particularly abundant in coffee aroma. Furfuryl-methyl-sulfide and its homologs are important contributors to the aroma of coffee. The structures of some of the important aroma contributors are presented in Fig. 7.36. The compounds identified in coffee aroma are listed and differentiated on the basis of functional groups in Table 7.24. It is, of course, impossible to compare the aroma of different coffees on the basis of one or a few of the flavor constituents. Computer-generated histograms can be used for comparisons after selection of important regions of gas-liquid chromatograms by using mathemati-



**Fig. 7.36** Structure of some important constituents of the aroma of coffee

cal treatments. Biggers et al. (1969) differentiated the beverage quality of two varieties of coffee (arabica and robusta) on the basis of contributions of flavor compounds.

Recent studies have identified 655 compounds in the flavor of coffee, the principal ones being furans, pyrazines, pyrroles, and ketones (Maarse 1991). The distinctiveness of coffee flavor is related to the fact that it contains a large percentage of thiophenes, furans, pyrroles, as well as oxazoles, thiazoles, and phenols.

## Alcoholic Beverages

In distilled beverages, one of the major flavor compounds is acetaldehyde. Acetaldehyde represents about 90% of the total aldehydes present in beverages like whiskey, cognac, and rum. Together with other short-chain aliphatic aldehydes, it produces a pungent odor and sharp flavor, which is masked by other flavor components in cognac, fruit brandies, rum, and whiskey. In vodka the presence of acetaldehyde may result in an off-flavor. Propanol and 2-methylpropanol, as well as unsaturated aldehydes, are also present in distilled beverages. The aldehydes are very reactive and can form acetals by reacting with ethanol. This reaction results in a smoother flavor profile. Another important flavor compound in distilled beverages is the diketone, 2,3-butanedione (diacetyl), which is a product of fermentation. Depending on fermentation and distillation conditions, the level of diacetyl varies widely in different beverages.

Fusel alcohols, which are present in most distilled beverages, influence flavor. They are formed during fermentation from amino acids through decarboxylation and deamination, and include 1-propanol, 2-methylpropanol, 2-methylbutanol, 3-methylbutanol, and 2-phenylethanol.

Distilled beverages also contain fatty acids—from acetic acid (which is one of the major fatty acids) to long-chain unsaturated fatty acids.

Maturation in oak barrels has a major effect on flavor of distilled beverages. Maturing fresh distillates in oak barrels can transform a raw-tasting



**Table 7.24** Volatile compounds in roasted coffee aroma

Compound Type	None	—OH	—O—	$\begin{array}{c} \text{C=O} \\ \diagdown \\ \text{OH} \end{array}$	Functional Group		$\begin{array}{c} \text{C=O} \\ \diagdown \\ \text{OR} \end{array}$	—S—	Other
					C=O	—C—C—			
Aliphatic	17	19	—	13	30	10	16	9	25
Isocyclic	3	1	—	—	6	6	—	—	—
Benzenic	20	—	6	4	5	1	5	2	16
Furanic	15	1	4	3	13	4	11	7	3
Thiophenic	6	1	—	2	6	2	3	20	—
Pyrolic	10	—	—	8	5	1	—	—	—
Pyrazinic	27	—	—	—	—	—	—	—	—
Other	5	2	8	—	7	—	1	5	13
Total number	103	24	18	30	72	24	36	43	57

product into a mellow, well-rounded beverage. The reactions that take place during maturation involve reactions between components of the distillate and reactions between distillate components and compounds present in the oak wood. The alcoholic solution in the barrel extracts lignin from the oak to form an alcohol-soluble ethanol-lignin. Alcoholysis converts this to coniferic alcohol and then by oxidation to coniferaldehyde. Similarly, sinapic alcohol is converted to sinapaldehyde. These aldehydes then produce syringaldehyde and vanillin. The latter compound is important in the flavor of cognac and whiskey. A similar process occurs in the aging of wines in oak barrels to produce the distinctive smoothness of oak-aged wines.

## References

- Amoore, J. (1967). Stereochemical theory of olfaction. In H. W. Schultz et al. (Eds.), *Symposium on foods: The chemistry and physiology of flavors*. Westport: AVI Publishing Co.
- Amoore, J., Johnston, J. W., Jr., & Rubin, M. (1964). The stereochemical theory of odor. *Scientific American*, 210(2), 42–49.
- Aron, P. M., & Kennedy, J. A. (2008). Flavan-3-ols: Nature, occurrence and biological activity. *Molecular Nutrition & Food Research*, 52(1), 79–104.
- Aron, P. M., & Shellhammer, T. H. (2010). A discussion of polyphenols in beer physical and flavour stability. *Journal of the Institute of Brewing*, 116(4), 369–380.
- Avau, B., & Depoortere, I. (2016). The bitter truth about bitter taste receptors: Beyond sensing bitter in the oral cavity. *Acta Physiologica (Oxford, England)*, 216(4), 407–420.
- Badings, H. T. (1991). Milk. In *Volatile compounds in foods and beverages*. New York: Marcel Dekker.
- Bartoshuk, L. M., Duffy, V. B., & Miller, I. J. (1994). PTC/PROP tasting: Anatomy, psychophysics, and sex effects. *Physiology & Behavior*, 56, 1165–1171.
- Beatty, R. M., & Cragg, L. H. (1935). The sourness of acids. *Journal of the American Chemical Society*, 57, 2347–2351.
- Beidler, L. M. (1954). A theory of taste stimulation. *The Journal of General Physiology*, 38, 133–139.
- Beidler, L. M. (1957). Facts and theory on the mechanism of taste and odor perception. In *Chemistry of natural food flavors*. Chicago: Quartermaster Food and Container Institute for the Armed Forces.
- Beidler, L. M. (1966). Chemical excitation of taste and odor receptors. In I. Hornstein (Ed.), *Flavor chemistry*. Washington: American Chemical Society.
- Biggers, R. E., Hilton, J. J., & Gianturco, M. A. (1969). Differentiation between *Coffea arabica* and *Coffea robusta* by computer evaluation of gas chromatographic profiles: Comparison of numerically derived quality predictions with organoleptic evaluations. *Journal of Chromatographic Science*, 7, 453–472.
- Birch, G. G., & Lee, C. (1971). Chemical basis of sweetness in model sugars. In G. G. Birch (Ed.), *Sweetness and sweeteners*. London: Applied Science Publishers, Ltd.
- Bokuchava, M. A., & Skobeleva, N. I. (1969). The chemistry and biochemistry of tea and tea manufacture. In E. M. Mrak & G. F. Stewart (Eds.), *Advances in food research* (Vol. 17). New York: Academic Press.
- Bondarovich, H. A., Fridel, P., Krampl, V., Renner, J. A., Shephard, F. W., & Gianturco, M. A. (1967). Volatile constituents of coffee: Pyrazines and other compounds. *Journal of Agricultural and Food Chemistry*, 15, 1093–1099.
- Byrne, B., & Sherman, G. (1984). Stability of dry acetaldehyde systems. *Food Technology*, 38(7), 57–61.
- Caggiola, A. W., Wing, R. R., Nowalk, M. P., Milas, N. C., Lee, S., & Langford, H. (1985). The measurement of sodium and potassium intake. *The American Journal of Clinical Nutrition*, 42(3), 391–398.

- Cardenas, P. D., Sonawane, P. D., Heinig, U., Bocobza, S. E., Burdman, S., & Aharoni, A. (2015). The bitter side of the nightshades: Genomics drives discovery in Solanaceae steroidal alkaloid metabolism. *Phytochemistry (Elsevier)*, *113*, 24–32.
- Casassa, L. F. (2017). *Flavonoid phenolics in red wine-making, phenolic compounds—Natural sources, importance and applications*. Prof. Marcos Soto-Hernández (Ed.), InTech. doi:<https://doi.org/10.5772/67452>. <https://www.intechopen.com/books/phenolic-compounds-natural-sources-importance-and-applications/flavonoid-phenolic>.
- Chambers, E., IV, & Koppel, K. (2013). Associations of volatile compounds with sensory aroma and flavor: The complex nature of flavor. *Molecules*, *18*, 4887–4905.
- Crocker, E. C. (1948). Meat flavor and observations on the taste of glutamate and other amino acids. In *Monosodium glutamate—A symposium*. Chicago: Quartermaster Food and Container Institute for the Armed Forces.
- Day, E. A. (1966). Role of milk lipids in flavors of dairy products. In I. Hornstein (Ed.), *Flavor chemistry*. Washington: American Chemical Society.
- Day, E. A. (1967). Cheese flavor. In H. W. Schultz et al. (Eds.), *Symposium on foods: The chemistry and physiology of flavors*. Westport: AVI Publishing Co.
- Döving, K. B. (1967). Problems in the physiology of olfaction. In H. W. Schultz et al. (Eds.), *Symposium on foods: The chemistry and physiology of flavors*. Westport: AVI Publishing Co.
- Doyle, M. E., & Glass, K. A. (2010). Sodium reduction and its effect on food safety, food quality, and human health. *Comprehensive Reviews in Food Science and Food Safety*, *9*, 55–56.
- DuBose, C. N., Cardello, A. V., & Maller, O. (1980). Effects of colourants and flavourants on identification, perceived flavour intensity, and hedonic quality of fruit-flavoured beverages and cake. *Journal of Food Science*, *45*, 1393–1399.
- El-Sohehy, A., Stewart, L., Khataan, N., Fontaine-Bisson, B., Kwong, P., Ozsungur, S., & Cornelis, M. C. (2007). Nutrigenomics of taste—impact on food preferences and food production. *Forum of Nutrition*, *60*, 176–182.
- Engelen, L. (2010). Oral receptors. In J. Chen & L. Engelen (Eds.), *Food oral processing: Fundamentals of eating and sensory perception*. West Sussex: Blackwell Publishing Ltd.
- Finger, T. E., & Kinnamon, S. C. (2011). Taste isn't just for taste buds anymore. *F1000 Biology Report*, *3*, 20.
- Flament, I., Willhalm, B., & Stoll, M. (1967). Research on flavor: Cocoa aroma III. *Helvetica Chimica Acta*, *50*, 2233–2243. (French).
- Forss, D. A. (1969). Role of lipids in flavors. *Journal of Agricultural and Food Chemistry*, *17*, 681–685.
- Gianturco, M. A. (1967). Coffee flavor. In H. W. Schultz et al. (Eds.), *Symposium on foods: The chemistry and physiology of flavors*. Westport: AVI Publishing Co.
- Gillette, M. (1985). Flavor effects of sodium chloride. *Food Technology*, *39*(6), 47–52. 56.
- Gold, H. J., & Wilson, C. W. (1963). The volatile flavor substances of celery. *Journal of Food Science*, *28*, 484–488.
- Goldman, I. M., Seibl, J., Flament, L., Gautshi, F., Winter, M., Willhalm, B., & Stoll, M. (1967). Research on flavor. Coffee aroma II. Pyrazines and pyridines. *Helvetica Chimica Acta*, *50*, 694–705. (French).
- Govindarajan, V. S. (1979). Pungency: The stimuli and their evaluation. In J. C. Boudreau (Ed.), *Food taste chemistry*. Washington: American Chemical Society.
- Greenman, J., & Benkara Mostefa Saad, S. (2009). Relating breath malodour to food constituents and oral health. In M. Wilson (Ed.). Boca Raton: Woodhead Publishing Co.
- Grosch, W., & Schieberle, P. (1991). Bread. In *Volatile compounds in foods and beverages*. New York: Marcel Dekker.
- Habibi-Najafi, M. B., & Lee, B. H. (1996). Bitterness in cheese: A review. *Critical Reviews in Food Science and Nutrition*, *36*, 397–411.
- Hall, L. A. (1948). Protein hydrolysates as a source of glutamate flavors. In *Monosodium glutamate—A symposium*. Chicago: Quartermaster Food and Container Institute for the Armed Forces.
- Hall, R. L. (1968). Food flavors: Benefits and problems. *Food Technology*, *22*, 1388–1392.
- Harper, R., Bate Smith, E. C., & Lad, D. G. (1968). *Odour description and odour classification*. London: J.A. Churchill, Ltd.
- Hayes, J., & Keast, R. S. J. (2011). Two decades of super-tasting: Where do we stand? *Physiology & Behavior*, *104*(5), 1072–1074.
- Horowitz, R. M., & Gentili, B. (1969). Taste and structure in phenolic glycosides. *Journal of Agricultural and Food Chemistry*, *17*, 696–700.
- International Standards Organization. (1992). *Standard 5492: Terms relating to sensory analysis*. International Organization for Standardization. Vienna: Austrian Standards Institute.
- International Standards Organization. (2008). *Standard 5492: Terms relating to sensory analysis*. International Organization for Standardization. Vienna: Austrian Standards Institute.
- Iwatsuki, K., & Torii, K. (2012). Peripheral chemosensing system for tastants and nutrients. *Current Opinion in Endocrinology, Diabetes, and Obesity*, *19*(1), 19–25.
- Iwata, S., Yoshida, R., & Ninomiya, Y. (2014). Taste transductions in taste receptor cells: Basic tastes and moreover. *Current Pharmaceutical Design*, *20*(16), 2684–2692.
- Jennings, W. G., & Sevenants, M. R. (1964). Volatile esters of Bartlett pear III. *Journal of Food Science*, *29*, 158–163.
- Johnson, J. A., Rooney, L., & Salem, A. (1966). Chemistry of bread flavor. In I. Hornstein (Ed.), *Flavor chemistry*. Washington: American Chemical Society.

- Jones, N. R. (1969). Meat and fish flavors: Significance of ribomononucleotides and their metabolites. *Journal of Agricultural and Food Chemistry*, 17, 712–716.
- Jurriens, G., & Oelej, J. M. (1965). Determination of hydroxyacid triglycerides and lactones in butter. *Journal of the American Oil Chemists' Society*, 42, 857–861.
- Kanehisa, H. (1984). Studies of bitter peptides from casein hydrolyzates. VI. Synthesis and bitter taste of BPIC (Val-Tyr-Pro-Phe-Pro-Gly-Ile-Asn-His) and its analog and fragments. *Bulletin of the Chemical Society of Japan*, 57, 301–308.
- Kawamura, Y., & Kare, M. R. (1987). *Umami: A basic taste*. New York: Marcel Dekker.
- Keeney, P. G., & Patton, S. (1956). The coconut-like flavor defect of milk fat I. Isolation of the flavor compound from butter oil and its identification as  $\delta$ -decalactone. *Journal of Dairy Science*, 39, 1104–1113.
- Kefford, J. F. (1959). The chemical constituents of citrus fruits. In E. M. Mrak & G. F. Stewart (Eds.), *Advances in food research* (Vol. 9). New York: Academic Press.
- Konosu, S. (1979). The taste of fish and shell fish. In J. C. Boudreau (Ed.), *Food taste chemistry*. Washington: American Chemical Society.
- Kulka, K. (1967). Aspects of functional groups and flavor. *Journal of Agricultural and Food Chemistry*, 15, 48–57.
- Kuninaka, A. (1966). Recent studies of 5'-nucleotides as new flavor enhancers. In I. Hornstein (Ed.), *Flavor chemistry*. Washington, DC: American Chemical Society.
- Kurihara, K. (1987). Recent progress in the taste receptor mechanism. In Y. Kawamura & M. R. Kare (Eds.), *Umami: A basic taste*. New York: Marcel Dekker.
- Kurihara, K., & Beidler, L. M. (1968). Taste-modifying protein from miracle fruit. *Science*, 161, 1241–1243.
- Kurihara, K., & Beidler, L. M. (1969). Mechanism of the action of taste-modifying protein. *Nature*, 222, 1176–1179.
- Kushman, L. J., & Ballinger, W. E. (1968). Acid and sugar changes during ripening in Wolcott blueberries. *Proceeding of the American Society for Horticultural Science*, 92, 290–295.
- Laffitte, A., Neiers, F., & Briand, L. (2014). Functional roles of the sweet taste receptors in oral and extraoral tissues. *Current Opinion in Clinical Nutrition and Metabolic Care*, 17(4), 379–385.
- Leffingwell, J. C. (2001). *Olfaction—II*. Leffingwell Reports, 1(4), September 2001.
- Li, Y. (2012).  $\alpha$ -Adducin Gly460Trp gene mutation and essential hypertension in a Chinese population: A meta-analysis including 10,960 subjects. *PLoS One*, 7(1), e30214.
- Liem, D. J., Miremadi, F., & Keas, R. S. J. (2011). Reducing sodium in foods: The effect on flavour. *Nutrients*, 3, 694–711.
- Linko, Y., Johnson, J. A., & Miller, B. S. (1962). The origin and fate of certain carbonyl compounds in white bread. *Cereal Chemistry*, 29, 468–476.
- Luck, G., Liao, H., & Murray, N. J. (1994). *The cup that cheers: Polyphenols and the astringency of tea, Lecture Paper No. 0030*. London: Society of Chemical Industry.
- Maarse, H. (1991). *Volatile compounds in foods and beverages*. New York: Marcel Dekker.
- Maarse, H., Tas, A. C., & Slump, P. (1987). Characterization of Spanish medium sherries. In M. Martens, G. A. Dalen, & H. Russwurm Jr. (Eds.), *Flavour science and technology* (pp. 115–118). New York: Wiley.
- Macheix, J.-J., Fleuriot, A., & Billot, J. (1990). *Fruit phenolics*. Boca Raton: CRC Press.
- Marion, J. P., Muggler-Chavan, F., Viani, R., Bricout, J., Reymond, D., & Egli, R. H. (1967). Sur la composition de l'arome de cacao. *Helvetica Chimica Acta*, 50, 1509–1516.
- Mason, M. E., Johnson, B., & Hamming, M. (1966). Flavor components of roasted peanuts: Some low molecular weight pyrazines and a pyrrole. *Journal of Agricultural and Food Chemistry*, 14, 454–460.
- Matsuo, R. (2000). Role of saliva in the maintenance of taste sensitivity. *Critical Reviews in Oral Biology and Medicine*, 11(2), 216–229.
- Meyboom, P. W., & Jongenotter, G. A. (1981). Flavor perceptibility of straight chain, unsaturated aldehydes as a function of double bond position and geometry. *Journal of the American Oil Chemists' Society*, 58, 680–682.
- Meyerhof, W., Born, S., Brockhoff, A., & Behrens, M. (2011). Molecular biology of mammalian bitter taste receptors. A review. *Flavour and Fragrance Journal*, 26(4), 260–268.
- Moncrieff, R. W. (1951). *The chemical senses*. London: Leonard Hill, Ltd.
- Moncrieff, R. W. (1964). The metallic taste. *Perfumery and Essential Oil Record*, 55, 205–207.
- Moody, W. G. (1983). Beef flavor—A review. *Food Technology*, 37(5), 227–232. 238.
- Nachay, K. (2013). Moving forward on sodium reduction. *Food Technology*, 67(5), 35–38. 40, 42–45.
- Naves, Y. R. (1957). The relationship between the stereochemistry and odorous properties of organic substances. In *Molecular structure and organoleptic quality*. London: Society of Chemical Industry.
- Ney, K. H. (1979). Bitterness of peptides: Amino acid composition and chain length. In J. C. Boudreau (Ed.), *Food taste chemistry*. Washington, DC: American Chemical Society.
- Noble, A. C., Arnold, R. A., Buechsenstein, J., Leach, E. J., Schmidt, J. O., & Stern, P. M. (1987). Modification of a standardized system of wine aroma terminology. *American Journal of Enology and Viticulture*, 38, 143–146.
- Ohloff, G. (1994). *Scent and fragrances* (p. 6). Berlin Heidelberg: Springer-Verlag.
- Ough, C. S. (1963). Sensory examination of four organic acids added to wine. *Journal of Food Science*, 28, 101–106.

- Pangborn, R. M. (1963). Relative taste intensities of selected sugars and organic acids. *Journal of Food Science*, 28, 726–733.
- Patton, S. (1964). Flavor thresholds of volatile fatty acids. *Journal of Food Science*, 29, 679–680.
- Peryam, D. R. (1963). Variability of taste perception. *Journal of Food Science*, 28, 734–740.
- Purves, D., Augustine, G. J., Fitzpatrick, D., Katz, L. C., LaMantia, A.-S., McNamara, J. O., & Williams, S. M. (2001). Neuroscience. In *The organization of the taste system* (2nd ed.). Sunderland: Sinauer Associates. Available from: <http://www.ncbi.nlm.nih.gov/books/NBK11018/>.
- Rama, R., Chiu, N., Carvalho, D. A., Silva, M., Heweson, L., Hort, J., & Fisk, I. D. (2013). Impact of salt crystal size on in mouth sodium delivery of sodium and saltiness perception from snack foods. *Journal of Texture Studies*, 44, 338–345.
- Reed, D. R., & Knaapila, A. (2010). Genetics of taste and smell: Poisons and pleasures. *Progress in Molecular Biology and Translational Science (Genes and Obesity)*, 94, 213–240.
- Rizzi, G. R. (1967). The occurrence of simple alkylpyrazines in cocoa butter. *Journal of Agricultural and Food Chemistry*, 15, 549–551.
- Rogers, J. A. (1966). Advances in spice flavor and oleoresin chemistry. In I. Hornstein (Ed.), *Flavor chemistry*. Washington: American Chemical Society.
- Sanada, H., Jones, J. E., & Jose, P. A. (2011). Genetics of salt-sensitive hypertension. *Current Hypertension Reports*, 13(1), 55–66.
- Saxby, M. J. (1996). *Food taints and off-flavors*. London: Blackie Academic and Professional.
- Scientific Advisory Committee on Nutrition Salt and Health (SCAN). (2003). <https://www.gov.uk/government/publications/sacn-salt-and-health-report>
- Schoch, T. J. (1965). Starch in bakery products. *Baker's Digest*, 39(2), 48–57.
- Seifert, R. M., Buttery, R. G., Guadagni, D. G., Black, D. R., & Harris, J. G. (1970). Synthesis of some 2-methoxy-3-alkylpyrazines with strong bell pepper-like odors. *Journal of Agricultural and Food Chemistry*, 18, 246–249.
- Shah, A. S., Ben-Shabar, Y., Moninger, T. O., Kline, J. N., & Welsh, M. J. (2009). Motile cilia of human airway epithelia are chemosensory. *Science*, 325(5944), 1131–1134.
- Shallenberger, R. S. (1971). Molecular structure and taste. In G. Ohloff & A. G. Thomas (Eds.), *Gustation and olfaction*. New York: Academic Press.
- Shallenberger, R. S. (1998). Sweetness theory and its application in the food industry. *Food Technology*, 52, 72–76.
- Shallenberger, R. S., & Acree, T. E. (1967). Molecular theory of sweet taste. *Nature*, 216, 480–482.
- Shallenberger, R. S., & Acree, T. E. (1969). Molecular structure and sweet taste. *Journal of Agricultural and Food Chemistry*, 17, 701–703.
- Sinki, G. S. (1988). Finding the universally acceptable taste. *Food Technology*, 42(7), 90–93.
- Sjöström, L. B. (1972). *The flavor profile*. Cambridge: A.D. Little Inc..
- Spence, C. (2012). Auditory contributions to flavour perception and feeding behaviour. *Physiology & Behavior*, 107, 505–515.
- Solms, J. (1969). The taste of amino acids, peptides and proteins. *Journal of Agricultural and Food Chemistry*, 17, 686–688.
- Solms, J. (1971). Nonvolatile compounds and the flavor of foods. In G. Ohloff & A. F. Thomas (Eds.), *Gustation and olfaction*. New York: Academic Press.
- Solms, J., Vayutaz, L., & Eoli, R. H. (1965). The taste of L and D amino acids. *Experientia*, 21, 692–694.
- Spillane, W. J. (1996). Molecular structure and sweet taste. In T. H. Grenby (Ed.), *Advances in sweeteners*. London: Blackie Academic and Professional.
- Stark, W., & Forss, D. A. (1962). A compound responsible for metallic flavor in dairy products I. Isolation and identification. *The Journal of Dairy Research*, 29, 173–180.
- Stöcklin, W., Weiss, E., & Reichstein, T. (1967). Gymnemic acid, the antisaccharic principle of *Gymnema sylvestre* R. Br. Isolation and identification. *Helvetica Chimica Acta*, 50, 474–490. (German).
- Stoll, M. (1957). Facts old and new concerning relationships between molecular structure and odour. In *Molecular structure and organoleptic quality*. London: Society of Chemical Industry.
- Stone, H., & Oliver, S. M. (1969). Measurement of the relative sweetness of selected sweeteners and sweetener mixture. *Journal of Food Science*, 34, 215–222.
- Sullivan, J. M. (1991). Salt sensitivity. Definition, conception, methodology, and long-term issues. *Hypertension*, 17(1 Suppl), I61–I68.
- Tarr, H. L. A. (1966). Flavor of fresh foods. In I. Hornstein (Ed.), *Flavor chemistry*. Washington: American Chemical Society.
- Teranishi, R. (1971). Odor and molecular structure. In G. Ohloff & A. F. Thomas (Eds.), *Gustation and olfaction*. New York: Academic Press.
- Teranishi, R., Hornstein, I., Issenberg, P., & Wick, E. L. (1971). *Flavor research—Principles and techniques*. New York: Marcel Dekker.
- Tharp, B. W., & Patton, S. (1960). Coconut-like flavor defect of milk fat IV. Demonstration of  $\delta$ -dodecalactone in the steam distillate from milk fat. *Journal of Dairy Science*, 43, 475–479.
- Tressler, D. K., & Joslyn, M. A. (1954). *Fruit and vegetable juice production*. Westport: AVI Publishing Co.
- Weinberger, M. H., Fineberg, N. S., Fineberg, S. E., & Weinberger, M. (2001). Salt sensitivity, pulse pressure, and death in normal and hypertensive humans. *Hypertension*, 37(2 Pt 2), 429–432.
- Wright, R. H. (1957). Odor and molecular vibration. In *Molecular structure and organoleptic quality*. London: Society of Chemical Industry.
- Wucherpennig, K. (1969). Acids: A quality determining factor in wine. *Deutsche Wein-Zeitung*, 30, 836–840.
- Yamaguchi, S. (1979). The umami taste. In J. C. Boudreau (Ed.), *Food taste chemistry*. Washington: American Chemical Society.