

The Chemistry and Physiology of Sour Taste—A Review

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ABSTRACT: Sour taste is the key element in the flavor profile of food acidulants. Understanding the chemistry and physiology of sour taste is critical for efficient control of flavor in the formulation of acid and acidified foods. After a brief introduction to the main applications of food acidulants, several chemical parameters associated with sour taste are discussed. Special emphasis is given to hydrogen ions, protonated (undissociated) acid species, titratable acidity, anions, molar concentration, and physical and chemical properties of organic acids. This article also presents an overview of the physiology of sour taste and proposed theories for the transduction mechanisms for sour taste. The physiology of sour taste perception remains controversial and significant diversity exists among species with regard to cellular schemes used for detection of stimuli. The variety of mechanisms proposed, even within individual species, highlights the complexity of elucidating sour taste transduction. However, recent evidence suggests that at least one specific sour taste receptor protein has been identified.

Keywords: acids, flavor, receptor, sensory, transduction

Introduction

Acids are found in a wide variety of foods such as baked goods, beverages, confections, gelatin desserts, jams, jellies, dairy products, processed meats, fats, and oils (Jonhson and Peterson 1974; Hartwig and McDaniel 1995). Their main use is to provide and enhance flavor of foods and beverages (Hartwig and McDaniel 1995). In addition to contributing to flavor, acidulants are commonly used for pH control to inhibit microbial growth in food products and aid in gelling properties of gelatin desserts, jams, jellies, and jellied candies (Jonhson and Peterson 1974). Many acidulants also have the ability to chelate trace metal ions and act as a synergist with antioxidants (Jonhson and Peterson 1974). Moreover, food acids have been used to prevent nonenzymatic browning, modify viscosity and melting properties, provide leavening, and act as a curing agent (Gardner 1977; Hartwig and McDaniel 1995). Table 1 shows the main physical and chemical properties of several organic acids commercially used as food ingredients.

Sour taste is the key element in the flavor profile of food acidulants. Understanding sour taste requires information at several levels, including the chemistry of compounds that elicit taste responses, interaction of taste elicitor compounds with taste receptor cells, and the physiological and neurochemical responses that mediate sour taste perception. Significant efforts have been put forth to determine the chemical basis for sour taste. Although it is generally accepted that pH and organic acids are responsible for sour taste, it is not currently possible to accurately predict and modify sour taste intensity in foods. Several studies have also attempted to identify the receptors and transduction mechanisms for sour taste, but as

yet the physiology of sour taste is controversial and not completely understood. The purpose of this article is to present an overview of the literature as it relates to the chemistry and physiology of sour taste perception.

Chemistry of Sour Taste

The chemistry of sour taste appears to be relatively simple in that it has been associated only with acids. In 1898, sour taste was first linked to hydrogen ions (Richards 1898). However, in as early as 1920 it was recognized that sour taste could not be explained solely on the basis of hydrogen ions. It was clear that organic acids could also stimulate a sour taste response. Organic acids all have one or more carboxyl groups, but in addition to carboxyl groups they have a variety of structural features. The carboxyl groups have hydrogen ions that dissociate depending upon the strength of the acid. For an acid with a single carboxyl group this dissociation is determined by the dissociation constant $K_a = [H^+][A^-]/[HA]$, where $[H^+]$ is the concentration of hydrogen ions in solution, $[A^-]$ is the concentration of the acid from which the hydrogen ion has dissociated from the carboxyl group, and $[HA]$ is the concentration of the acid in which a hydrogen ion remains bound to the carboxyl group. A considerable amount of research has attempted to relate the intensity of sour taste perception to properties of organic acids (Kenrick 1931; Beatty and Cragg 1935; Chauncey and others 1963; Moskowitz 1971; Gardner 1980; CoSeteng and others 1989; Siebert 1999) and their ability to bind or release hydrogen ions into water solution (Beidler 1967; Makhlof and Blum 1972; Hartwig and McDaniel 1995; Shallenberger 1996; Richards 1898; Ogiso and others 2000; Lyall and others 2001; Lugaz and others 2005).

Hydrogen ions, protonated acid species, and titratable acidity

For convenience, pH ($-\log [H^+]$) is generally used to indicate hydrogen ion concentration in acid solutions and foods. All acids partially or fully dissociated into anions and protons ($[H^+]$) when they are dissolved in water. Thus one might expect a direct relationship between sour taste and pH. However, human psychophysical and animal physiological studies have shown that organic acids such as

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acetic and citric acids are more sour than hydrochloric acid at the same pH (Pfaffmann 1959; Koyama and Kurihara 1972; Ganzevles and Kroeze 1987a; Richards 1898; Ugawa and others 1998; Ogiso and others 2000; Lyall and others 2001; Richter and others 2003; Lugaz and others 2005). Beidler (1967) showed that solutions of 20 organic and inorganic acids that produced an equivalent neural response to 5 mM HCl in rats had pH values ranging from 2.11 to 3.14. Likewise, Makhlof and Blum (1972) found a poor correlation between sour taste of organic acids and stimulus pH using acid-induced salivary secretion as an index of response. Moreover, the pH of various organic acid solutions is considerably different at their observed threshold concentrations (Berg and others 1955; Amerine and others 1965). Altogether, these results indicate that in addition to hydrogen ions, anions and/or protonated (undissociated) acid species play a role in determining sour taste intensity of organic acids.

Titrateable acidity (also known as total acidity) is a measure of both bound and free hydrogen ions in solution. It is experimentally determined by measuring the amount of sodium hydroxide required to raise the pH to 8.2, where phenolphthalein indicator dye turns pink. In 1920, Harvey (1920) raised the question: "What do we taste in acid solutions, hydrogen ion concentration or total acidity?" Many studies have reported that sour taste intensity increases with increasing titrateable acidity at a given pH (Makhlof and Blum 1972; Plane and others 1980; Norris and others 1984; Lugaz and others 2005). Shallenberger (1996) proposed that sour taste intensity is entirely a function of potential hydrogen ion concentration. The implication of his hypothesis is that acid solutions of equal normality have equal sour taste intensities as they have equivalent titration coefficients. In summary, these studies suggest that the chemical mechanism for sour taste perception may be analogous to a titration of an acid by a base to a neutral end point, the receptor serving as the "base" (Liljestrand 1922; Kenrick 1931; Beatty and Cragg 1935; Makhlof and Blum 1972; Norris and others 1984; Shallenberger 1996). However, Richards (1898) showed that hydrochloric acid solution was more sour than equinormal solutions of tartaric, citric, and acetic acids. Acetic acid was perceived as the least sour among the organic acids, followed by citric and tartaric acids. Likewise, Becker and others (1907) concluded that normality was not sufficient to predict sour taste response, the ranking order being HCl > HNO₃ > lactic > acetic > butyric acid. CoSeteng and others (1989) showed that solutions of

citric, malic, tartaric, lactic, and acetic acids with equivalent pH and titrateable acidity gave significantly different sour taste responses. Likewise, Pangborn (1963) found no relation between pH, titrateable acidity, and relative sour taste intensity of several organic acids at both threshold and suprathreshold concentrations.

Buffer capacity is defined as the molar concentration of strong acid or strong base, which causes variation of the pH of a buffer solution by 1 unit. Early studies suggested that the buffer capacity of an acid solution is an important determinant of sour taste. Beatty and Cragg (1935) and Kenrick (1931) reported that the volume of a phosphate buffer required to bring the pH of various equimolar acids to about 4.5 was proportional to the sour taste intensity. Noble and others (1986) also found a positive correlation between buffer capacity of acid solutions and sour taste in 5 of 6 paired comparisons. The exception was the contrast between malic and succinic acids as the former has greater buffer capacity at the pH tested, but was rated as less sour. However, Ganzevles and Kroeze (1987b) measured the volume of NaOH needed to bring the pH of equimolar solutions of tartaric, citric, formic, lactic, acetic, and propionic acids to 4.4 and reported a titration volume rank-order, which differed from the sour taste response rank order.

Anions

The effect of anionic species on the mechanism of sour taste perception is not clearly understood. Norris and others (1984) suggested that differences in the anion composition of acids in solution affect the binding of the stimuli to the receptor sites. Beidler and Gross (1971), Koyama and Kurihara (1972), and Beidler (1978) speculated that anions influence sour taste response by decreasing the positive charge of the membrane and thus increasing the binding of hydrogen ions to receptor molecules. Beidler (1971) suggested that the observation by Richards (1898) that acetic acid solution was perceived to be more sour than hydrochloric acid at the same pH could be explained by the presence of anions in the acetic acid solution. He also cited a study by Liljestrand (1922), where the pH of acetic acid-sodium acetate solution was significantly higher than acetic acid solutions at their observed threshold concentrations. The higher concentration of anion in the buffer solution was suggested as the major factor for the lower hydrogen ion concentration required to produce an equivalent taste response. Similarly, Beidler (1967) tested the effect of anions on sour taste response by comparing

Table 1 – Chemical and physical properties of organic acids

Acid	MW	pK _a	Solubility (g/100 mL water)	Physical form	Hygroscopicity	Sensory qualities
Acetic	60.05	4.75	Miscible	Clear, colorless liquid	Not applicable	Tart and sour
Adipic	146.14	4.43	1.9 g at 20 °C	Crystalline powder	Low	Smooth lingering tartness
Citric	192.12	5.41	83 g 90 °C	Crystalline powder	Moderate	Tart; delivers a "burst" of tartness
		3.14	Anhydrous: 181 g at 25 °C			
		4.77				
		6.39	Monohydrate: 208 g 25 °C			
Fumaric	116.7	3.03	0.5 g at 20 °C	White granules of crystalline powder	Nonhygroscopic	Tart; affinity for grape flavors
		4.44	9.8 g 100 °C			
Lactic	90.08	3.86	Miscible	Liquid, also available in dry form	Not applicable	Acrid
Malic	134.09	3.40	62 g at 25 °C	Crystalline powder	Nonhygroscopic	Smooth tartness
		5.11				
Succinic	118.09	4.19	7.8 g in cold water	White minute monoclinic prisms	Nonhygroscopic	Tart; slightly bitter in aqueous solutions
		5.50	100 g at 100 °C			
Tartaric	150.09	2.98	147 g at 25 °C	Crystalline powder	Nonhygroscopic	Extremely tart; augments fruit flavors
		4.34				

Adapted from Gardner (1977).

the neural response of rats to acetic acid solution and to a buffered acetic-sodium acetate solution. Although the neural responses were comparable, the pH of the buffered solution was considerably higher (lower hydrogen ion concentration) as compared to the acetic acid solution. He explained the results by suggesting that in the buffered solution a lower concentration of hydrogen ion is needed because acetate ions augment binding of hydrogen ions to the receptor sites.

On the other hand, many studies have theorized that sodium salts of organic acids may inhibit the interaction between taste receptor cells and protonated (undissociated) acids (DeSimone and Price 1976; Ganzevles and Kroeze 1987a). Makhlof and Blum (1972) reported that sodium acetate showed characteristics of competitive inhibition with acetic acid in sour taste perception. Lawless (1991) suggested that some large anions decrease sour taste intensity through contributing tastes of their own, which act as masking stimuli.

Sour taste comparisons based on molar concentrations of acids

Several studies have attempted to rank sour taste intensity based on molar concentration. Makhlof and Blum (1972) reported that sour taste intensity and molar concentration of an acid are described by an equation in the form used for enzyme kinetics and that the order of molar potency is citric > tartaric > succinic > lactic > acetic > propionic. Ganzevles and Kroeze (1987b) by means of a filter-paper method found the molar rank-order for sourness to be HCl > tartaric > citric > formic > acetic > lactic > propionic acid. Lugaz and others (2005) evaluated the time-intensity of sour taste of various organic acids at equal molar concentrations and reported the order of potency to be citric, malic, lactic, and acetic acid from most to least sour. Ough (1963) reported that, when citric, tartaric, fumaric, and adipic acids were added to wine in equimolar concentrations, citric acid was judged as the most sour, followed by tartaric and fumaric acids, which produced equally sour taste responses, and by adipic acid, which was judged as the least sour.

From these studies, it is clear that the molar concentration of acids is not the only governing factor in determining sour taste response. The diversity of results in attempting to rank the sour taste of acids based on molar concentration may be explained by differences in the range of molar concentrations and the pH of the solutions evaluated.

Physical and chemical properties of organic acids

Sour taste intensity has been associated with the capacity of the acid to dissociate, which is dependent upon the pK_a values of the acids. Makhlof and Blum (1972) found that the molar potency of several organic acids was inversely related to the 1st pK_a . They concluded that acids having a higher capacity to dissociate (small pK_a) were able to elicit higher sour taste responses. In contrast, Hartwig and McDaniel (1995) reported that organic acids with higher pK_a values (low capacity to dissociate) were perceived to be more sour than those having lower pK_a values. However, the latter study evaluated acids on an equivalent weight percentage basis rather than a molar basis, so comparisons were made with unequal numbers of acid molecules.

A common hypothesis for sour taste perception is that an acid compound must penetrate the cell membrane and release hydrogen ions inside the cell in order to elicit a sour taste response (Taylor and others 1930; Gardner 1980). This hypothesis is supported by the strong correlation found between hydrophobicity of a fatty acid and its ability to elicit sour taste (Taylor and others 1930; Chauncey and others 1963; Greenberg 1980). Gardner (1980) showed that the ability of an acid to penetrate the membrane was enhanced as nonpolar

groups were introduced into the acid structure and reduced with addition of polar groups. Chauncey and others (1963) and CoSeteng and others (1989) assessed the effects of physical and chemical properties of several organic acids on sour taste perception. They found that hydrophobicity was an important factor in sour taste response, and that the intensity of sour taste decreased as the number of carboxyl groups in the molecule increased. CoSeteng and others (1989) reported that sour taste intensity of organic acids increased with molecular weight. Chauncey and others (1963) found that introduction of polar groups on acid molecules led to decreased sour taste response. In contrast, Noble and others (1986) reported that the sour taste of several binary solutions at a constant pH and titratable acidity did not correlate with the degree of hydrophobicity. Likewise, Norris and others (1984) reported that hydrophobicity was not sufficient to predict the relative sour taste response of citric, fumaric, and tartaric acids.

Siebert (1999) applied principal component analysis to 11 properties of 17 organic acids and reported that threshold concentrations were closely predicted in solutions by the number of polar groups, the number of double bonds, molecular size, and the solubility of the acids in nonpolar solvents. Moskowitz (1971) assessed the relationship between sour taste and molar acid concentration as well as sour taste and pH for 24 organic acids in a psychophysical function study. He reported that the relative sour taste intensity of acids differed across a range of molar concentrations and pH and concluded that no simple relationship exists between sour taste intensity and physical-chemical properties of the acids, such as molecular weight, polarity, and optical form.

Although significant efforts have been made to understand the chemistry of sour taste, it is not currently possible to accurately predict and modify sour taste intensity in foods by simply knowing the concentration of acids and pH. Our laboratory recently developed a new hypothesis for the chemical basis of sour taste of organic acids (Johanningsmeier and others 2005), which proposed that sour taste intensity is a linear function of the total molar concentration of all organic acid species that have one or more protonated carboxyl groups plus the concentration of free hydrogen ions. This hypothesis was based on correlations between sour taste intensity and the molar concentrations of protonated organic acid species and hydrogen ions in dill pickles, sauerkraut, and acid solutions analyzed from published datasets (Hartwig and McDaniel 1995; Sowalsky and Noble 1998).

Other flavor characteristics of acids

Sour taste is the aspect of flavor most commonly associated with acids, but they are also able to elicit nonsour taste characteristics such as bitterness, saltiness, and astringency (Meiselman and Dzendolek 1967; McBurney and Shick 1971; Settle and others 1986; Rubico and McDaniel 1992; Siebert 1999). The nature and proportion of nonsour taste qualities are mainly dependent on the type and concentration of the acid as well as the pH. Settle and others (1986) reported that bitterness is the most perceived nonsour taste component of organic acids in a moderate to strong taste intensity range. Hydrochloric acid has been described as having a "faintly bitter taste" (Harvey 1920). Hartwig and McDaniel (1995) used the free-choice profiling method to show that common food acidulants differ widely in sensory qualities at different pHs. Using the same method, Rubico and McDaniel (1992) reported that succinic acid has a bitter note in addition to sour taste. They also observed that Oriental panelists described succinic acid as having a monosodium glutamate taste while Caucasians used the term "savory" and "brothy."

In addition to other taste qualities, acids can impart olfactory and tactile sensations. It has been shown that solutions of lactic, citric,

malic, tartaric, sulfuric, hydrochloric, and phosphoric acids at high concentrations can be detected by nasal inhalation, apparently by the trigeminal nerve (Settle and others 1986). Hartwig and McDaniel (1995) reported that acetic acid has a distinct vinegar flavor character. Meilgaard (1975) described several odors associated with organic acids such as "cheesy," "sweaty," "vegetable oil," "citrus," and "tallowy." Inorganic acids such as hydrochloric and phosphoric acids have been reported to be more astringent than sour (Rubico and McDaniel 1992; Corrigan and Lawless 1995). Fumaric and adipic acids have been described as metallic and chalky, respectively (Jonhson and Peterson 1974). Gardner (1977) described the sour taste of several acids as follows: malic (green), citric (fresh), succinic (salty and bitter notes), lactic (sourish but tart), and tartaric (hard).

Lugaz and others (2005) investigated the effect of chemical properties of acids and subject salivary flow rate on the temporal response of sour taste. They reported that pH, type of acid, and group of subjects (high compared with low salivary flow rate) had a significant effect on the time-intensity profiles of acidulants. Likewise, Arnold (1975) proposed that the intensity and duration of sour taste differed among acids.

Astringency is an important sensory attribute of both organic and inorganic acids. Astringency is developed over time and grows in intensity with repeated stimulation (Joslyn and Goldsten 1964; Guinard and others 1986). It is strongly dependent on pH, with the intensity of perception increasing with decreasing pH (Lawless and others 1996; Sowalsky and Noble 1998). Sierbert and Chassy (2003) proposed that acids evoke the astringency sensation by intensifying the interaction between salivary proteins and polyphenols already present in the saliva. Another hypothesis suggests that salivary proteins are denatured by acids due to low pH exposure, causing loss of their lubricating and protective functions (Lawless and others 1996).

Physiology of Sour Taste

Anatomy of the taste system

A taste bud contains a group of 30 to 100 taste cells and is located on special folds and protrusions of the lingual epithelium called papillae (Stewart and others 1997). There are 3 types of gustative papilli: fungiform, foliate, and vallate. Fungiform papilli are mushroom-shape structures located at the front of the tongue. They typically consist of 3 to 5 taste buds. Foliate and vallate papilli contain hundreds of taste buds and are found, respectively, at the sides and rear of the tongue (Gilbertson and others 2000).

Taste receptors are bipolar cells having a short lifetime, approximately 10 d (Beidler 1971). They occur either lightly or densely packed in taste buds. Taste receptor cells are oriented perpendicularly to the surface in contact with the stimuli in a roughly parallel arrangement with apical and basolateral regions. The apical region is composed of microvilli, which have contact with the oral cavity, while the basolateral region contains synapses with the sensory nerve fibers (Lindemann 1996, 2001). Taste buds are innervated by the glossopharyngeal nerve (posterior tongue), the chorda tympani branch of the facial nerve (anterior tongue), and the vagal nerve (laryngeal buds) (Gilbertson and others 2000). Taste perception is initiated by the interaction of the chemical stimulus with receptor sites located on microvilli. The stimuli may bind to a membrane receptor or protein, it may pass through a channel, or it may activate or block an ion channel (Lindemann 1996). The receptors then activate the synapses by releasing neurotransmitters, which cause excitation of the nerve fibers. The signals are carried to the brain stem where the central nervous system processes the information, resulting in taste perception (Lindemann 2001).

Sour taste transduction

Significant efforts have been put forth to determine the transduction mechanisms underlying sour taste perception. Numerous animal species such as frog, rat, hamster, mudpuppy, mouse, and chimpanzee have been used in physiological studies of sour taste. However, there are several limitations to development of a single model for sour taste transduction. Differences in chemical sensitivity of taste receptors occur across animal species (Beidler and Gross 1971; Lyall and others 2001). Thus, one should be cautious when extrapolating conclusions from 1 species to another. The existence of multiple transduction pathways within a given species also represents a challenge (Lindemann 1996). Another difficulty is the fact that lowering the pH may affect several ion channels and transport systems (Liu and Simon 2001). Furthermore, it is crucial to consider the influence of adjacent structures such as nonsensory epithelial tissue and paracellular diffusional pathways in determining sour transduction mechanisms (Lindemann 1996).

It is generally accepted that activation of sour taste receptors causes depolarization of acid-sensitive taste receptor cells (Lyall and others 2001). Each cell of the body has an electrical potential difference across its plasma membrane due to differences in ion concentrations between the inside and outside of the cell (Beidler 1978). In nerve cells, this difference is mainly determined by the membrane permeability of sodium, potassium, and chloride ions (Beidler 1967; Myamoto and others 1998). At resting potential, the cell is negatively charged inside relative to the outside. As the cell is stimulated, an electrical gradient is established across the membrane, causing cell depolarization. Thus, the cell becomes positive inside relative to the outside (Beidler 1967; Lindemann 1996). The activation of receptors by acidic stimuli is usually accompanied by decreased intracellular pH and release of transmitters, which initiate excitation of afferent nerve fibers to the brain cortex, ultimately leading to sour taste perception (Lyall and others 2001).

A number of methods, including electrophysiological measurements, have been applied to investigate the cellular mechanisms of sour taste transduction in animal models. A common approach has been the use of microelectrodes to record the cell depolarizing potential caused by acids (Kinnamon and others 1988; Myamoto and others 1998). Electrical recordings from the human chorda tympani nerve have been shown to correlate well with subjective intensity of sour taste (Borg and others 1967). Loose-patch recording and micro methods such as patch clamping and microscopic fluorescence imaging have also been applied (Kinnamon and others 1988; Lindemann 1996; Miyamoto and others 1998). In addition, measuring the intracellular pH has been a valuable technique (Lyall 2001). Recent studies have benefited from genetic and molecular methodologies, which have provided advanced tools for elucidating the molecular interactions governing the transduction of sour taste (Ugawa and others 1998).

Acid stimuli primarily elicit a sour taste response at low concentrations, which is transduced by the chorda tympani. However, at high concentrations, acids may also evoke an irritation sensation, which is transduced by the trigeminal nerve (Nagy and others 1982; Yamasaki and others 1984). Two general hypotheses exist as to the mechanism of sour taste perception. The first assumes extracellular adsorption of acidic stimuli, while the second presumes penetration of sour taste stimuli into the cell. Early studies proposed that sour taste perception is induced by binding of hydrogen ions to a phosphate group on phospholipids in the gustatory receptor membrane (Koyama and Kurihara 1972). It has been hypothesized that the chemical nature of the sour taste receptor is essentially like a lipid rather than a protein since lengthening the alkyl chain structure of an acid favors its diffusion through the membrane, while

introducing polar groups decreases the acid's permeability (Taylor 1927, 1930; Taylor and others 1930). In contrast, Beidler (1971) suggested that proteins are the most likely candidates for taste receptors and proposed that carboxyl groups on the protein are the specific receptor sites for sour stimuli.

It has also been speculated that fully protonated (undissociated) organic acid molecules induce sour taste perception by entering the apical membrane of taste receptor cells, dissociating inside the cell, and thus causing cytoplasmic acidification (Taylor and others 1930; Gardner 1980; Ogiso and others 2000; Lyall and others 2001). This hypothesis is supported by the evidence that weak acids acidify taste cells to a greater extent than do strong acids at a fixed pH (Koyama and Kurihara 1972; Ugawa and others 1998; Ogiso and others 2000; Lyall and others 2001; Richter and others 2003). Lyall and others (2001) studied the effect of weak and strong acids on intracellular pH and chorda tympani nerve stimulation in rats. They found that nerve responses were positively correlated with a decrease in intracellular pH and that weak acids were more effective than strong acids in acidifying the cell. They suggested that fully protonated acids passively diffuse into taste receptor cells across the membrane.

Different receptor systems are possibly implicated for sour taste transduction of hydrogen ions and protonated acid species (Ganzevles and Kroeze 1987a, 1987b). Studies of self- and cross-adaptation of weak and strong acids have attempted to confirm this hypothesis. It is generally believed that if adaptation to 1 stimulus does not reduce the response to another stimulus, the mechanisms responsible for transducing the 2 stimuli are different (McBurney and others 1972). Ganzevles and Kroeze (1987a) proposed that the mechanisms involved in sour taste perception from protonated organic acid species and hydrogen ions are different because acetic acid and hydrochloric acid behave differently in self and cross-adaptation studies.

Recently, it has been established that cell depolarization caused by the interaction between protons and ion channels mediates sour taste transduction (Myamoto and others 1998; Ugawa and others 1998; Herness and Gilbertson 1999; Stevens and others 2001; Richter and others 2003). Many studies have attempted to identify the specific channel molecules that function as receptors for sour tastants. In the mudpuppy, blockage of voltage-sensitive K^+ channels located in the apical membrane has been suggested to mediate sour taste transduction (Kinnamon and Roper 1988; Kinnamon and others 1988; Cummings and Kinnamon 1992). In the mouse, basolaterally located chloride channels as well as apically located proton-activated cation channels have been associated with acid-induced cell depolarization (Miyamoto and others 1998, 2000). In the hamster, amiloride-blockable epithelial sodium channels (EnaC) also engaged in the taste of organic salts have been proposed to contribute to sour taste transduction (Gilbertson and others 1992). In frogs, depolarization occurs through a proton-gated cation channel and an apical proton pump (Lauger 1991; Myamoto and others 1998). Ugawa and others (1998) and Lin and others (2002) proposed that acid-sensing ion channels (ASICs) located on the apical and basolateral membranes are involved in sour taste transduction in rats. Stevens and others (2001) proposed that hyperpolarization-activated cyclic nucleotide-gated (HCN) channels are gated by extracellular protons and may act as receptors for sour taste stimuli in rats. In addition, proton movement through paracellular pathways may contribute to sour taste transduction (DeSimone and others 1995; Herness and Gilbertson 1999; Lyall and others 2001). It has been proposed that tight junctions in the basolateral membrane are permeable to hydrogen ions, which may cause a decrease in the intracellular pH, contributing to sour taste transduction (DeSimone and others 1995; Lindemann 2001). In humans, there is evidence that

neither apical epithelial Na^+ channels nor apical Na^+/H^+ exchangers are involved in sour taste transduction (DeSimone and others 2001). Independent investigations of sour taste receptor proteins of the mouse have concluded that PKD2L1, a polycystic-kidney-disease-like ion channel, is specifically involved in sour taste perception (Huang and others 2006; Ishimaru and others 2006). In the 2 studies, several lines of evidence supported this conclusion. The results of Huang and others (2006) were particularly compelling in that taste buds from mice genetically modified so they lacked PKD2L1 had a complete loss of response to acids, while at the same time showing normal responses to sweet, bitter, umami, and salty taste stimuli. Both studies concluded that the sour taste receptor function in the circumvallate papilla and foliate papilla is a result of the interaction between the PKD2L1 and PKD1L3 transient receptor potential ion channels. However, they pointed out that in the fungiform papillae and the palate PKD2L1 may require a different partner for functional expression, as PKD1L3 is absent in these areas. Ishimaru and others (2006) observed a greater response to citric acid solutions compared to HCl solutions at the same pH of the test solution, which is consistent with perception of the relative sour taste intensity of these stimuli. It has not been determined, however, whether the sour taste response requires that hydrogen ions and organic acid molecules enter the receptor cells or operate from the surface of the cells.

Conclusions

Sour taste perception is a complex event from both chemical and physiological standpoints. Before efficient control of flavor in the formulation of acid and acidified foods can be done, a clear understanding of the chemistry and physiology of sour taste is needed. It is evident that no simple relationship exists between sour taste intensity and hydrogen ions. Likewise, sour taste intensity of acids cannot be entirely explained by other variables, including titratable acidity, buffer capacity, molar concentration, physical and chemical structure, and so on. The recent hypothesis that sour taste intensity is directly related to the total molar concentration of all organic acid species that have one or more protonated carboxyl groups plus the concentration of free hydrogen ions may provide a basis for predicting sour taste in the formulation of foods. The physiology of sour taste perception remains controversial and significant diversity among species exists with regard to cellular schemes used for detection of stimuli. The variety of mechanisms proposed, even within individual species, highlights the complexity of elucidating sour taste transduction. However, recent evidence suggests that at least 1 specific sour taste receptor protein has been identified.

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