Effects of pH Adjustment and Sodium Ions on Sour Taste Intensity of Organic Acids

E.R.D. NETA, S.D. JOHANNINGSMEIER, M.A. DRAKE, AND R.F. MCFEETERS

ABSTRACT: Protonated organic acid species have been shown to be the primary stimuli responsible for sour taste of organic acids. However, we have observed that sour taste may be modulated when the pH of acid solutions is raised using sodium hydroxide. Objectives were to evaluate the effect of pH adjustment on sour taste of equimolar protonated organic acid solutions and to investigate the potential roles of organic anions and sodium ions on sour taste perception. Despite equal concentrations of protonated acid species, sour taste intensity decreased significantly with increased pH for acetic, lactic, malic, and citric acids ($P < 0.05$). Total organic anion concentration did not explain the suppression of sour taste in solutions containing a blend of 3 organic acids with constant concentration of protonated organic acid species and hydrogen ions and variable organic anion concentrations ($R^2 = 0.480$, $P = 0.12$). Sour taste suppression in these solutions seemed to be more closely related to sodium ions added in the form of NaOH ($R^2 = 0.861$, $P = 0.007$). Addition of 20 mM NaCl to acid solutions resulted in significant suppression of sour taste ($P = 0.016$). However, sour taste did not decrease with further addition of NaCl up to 80 mM. Presence of sodium ions was clearly shown to decrease sour taste of organic acid solutions. Nonetheless, suppression of sour taste in pH adjusted single acid solutions was greater than what would be expected based on the sodium ion concentration alone, indicating an additional suppression mechanism may be involved.

Keywords: organic acid, pH, protonated, undissociated

Introduction

Sour taste is the aspect of flavor most commonly associated with the presence of acids in foods. Understanding the mechanisms of sour taste perception and interactions that may occur to suppress the intensity of sour taste contributes to the overall knowledge of food flavor. Sour taste is desirable in some foods, but in other cases, it may contribute to off-flavors. As a result, sour taste is important in many foods including baked goods, beverages, confections, gelatin desserts, jams, jellies, dairy products, processed meats, fats, and oils (Johnson and Peterson 1974; Hartwig and McDaniel 1995).

A considerable amount of research has been conducted to understand the chemical basis of sour taste elicited by organic acids (Neta and others 2007a). Organic acid molecules have one or more carboxyl groups, which can dissociate depending upon the strength of the acid. For a monocarboxylic acid, the 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 in 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. In the case of multiprotic acids such as citric acid, the distribution of organic acid species is determined by multiple dissociation constants, as illustrated in Figure 1. Our laboratory has shown that sour taste is related to both free hydrogen ions and organic acid species that have at least 1 protonated carboxyl group (Neta and others 2007b). For instance, species I, II, and III shown in Figure 1 would be considered active molecules for the sour taste of citric acid.

However, the effect of organic anion species (for example, species IV for citric acid shown in Figure 1) on sour taste perception is not clearly understood. The ability of acids to bind taste receptor sites and elicit sour taste has been linked to their anion composition (Norris and others 1984). Anions may augment sour taste response by decreasing the positive charge of the membrane, and thus favoring the binding of hydrogen ions to receptor molecules (Koyama and Kurihara 1972). Beidler (1971) suggested that the observation of Richards (1898) that acetic acid solution is perceived to be more sour than hydrochloric acid at the same pH could be explained by the presence of anions in the former solution. In another study, Beidler (1967) compared the neural response of rats to acetic acid and to a buffered acetic–sodium acetate solution and found that although they had similar neural responses, the pH of the buffered solution was considerably higher (lower hydrogen ion concentration) than the acetic acid solution. He postulated that in the buffered solution a lower concentration of hydrogen ions was required because acetate ions augmented the binding of hydrogen ions to the receptor sites. In contrast, Lawless (1991) suggested that some large anions may act as masking stimuli to suppress sour taste intensity through contributing tastes of their own.

According to Keast and Breslin (2002), taste–taste interactions may result from chemical reactions occurring in solution, physiological interactions between chemical compounds at the cellular/epithelial level, or cognitive interactions occurring at the central processing level. Physiological studies have speculated that one of the transduction mechanisms for sour taste perception, the amiloride-sensitive Na^+ channels, may also mediate salty

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taste responses in mammals (Lindemann 1996; Stewart and others 1997). This indicates that sour and salty stimuli may interact with the same receptor site, providing a potential mechanism for competitive inhibition. In fact, Ogawa (1969) reported that rats' neural responses to NaCl solutions were reduced by lowering pH. Sensory studies have shown that suppression of sour taste in sour–salty mixtures may be due to a perceptual phenomenon related to masking of one stimulus by the other. For instance, Keast and Breslin (2002) showed that suppression of sour taste by salts occurred at suprathreshold concentrations. Similarly, Kemp and Beauchamp (1994) reported that increasing the concentration of NaCl from below threshold values to above levels commonly found in foods led to simultaneous increase in salty taste and decrease in sour taste of aqueous solutions containing citric acid.

In a recent publication (Neta and others 2007b), our laboratory proposed a chemical basis for sour taste perception, where protonated organic acid species and hydrogen ions are the chemical entities that elicit sour taste. We concluded that on a molar basis, all protonated acid molecules were equally sour, all protonated species of a given organic acid were equally sour, and hydrogen ions and protonated organic acids were approximately equal in sour taste. However, to demonstrate that these were true, the pH of acid solutions was adjusted with sodium hydroxide resulting in variable organic anion and sodium ion concentrations. We observed that the intensity of sour taste might be influenced by the presence of these species in solution. The objectives of this study were (1) to evaluate the effect of pH adjustment on sour taste intensity of equimolar protonated organic acid solutions and (2) to investigate the ability of organic anions and sodium ions to suppress sour taste of aqueous organic acid solutions.

Materials and Methods

Subjects

Nine, nonsmoking, female students and staff members from the Dept. of Food, Bioprocessing and Nutrition Sciences at North Carolina State Univ. (Raleigh, N.C., U.S.A.), between the ages of 22 and 49 years, served as panel members. Subjects were selected based on availability and ability to distinguish and scale the basic tastes.

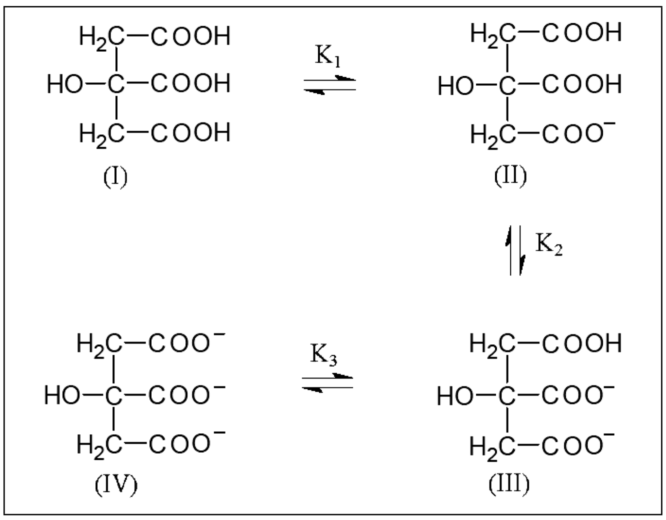

Figure 1—Distribution of organic acid species for citric acid, as determined by its dissociation constants. According to Neta and others (2007b), the protonated organic acid species I, II, and III are the active molecules for the sour taste of citric acid. The anion (species IV) has no ability to elicit sour taste.

Training

The descriptive sensory panel was trained for 40 h in the Spectrum™ method (Meilgaard and others 1991) to evaluate several attributes of aqueous solutions on a 0- to 15-point scale.

Aqueous solutions of citric acid, sucrose, NaCl, caffeine, alum, and acetic acid were used as reference stimuli for sour, sweet, salty, and bitter tastes, astringency, and vinegar flavor, respectively. Reference concentrations were selected from the Spectrum method (Meilgaard and others 1991) with the exception of astringency and vinegar flavor, which were developed during training. Alum has been shown to be an appropriate astringency reference standard for descriptive analysis (Wismer and Goonewardene 2003). Concentrations of 0.25, 0.56, 1.1, and 1.5 g/L alum represented 2, 5, 10, and 15 intensities on the astringency scale, respectively. Concentrations of 4.2, 8.8, and 38.5 mM acetic acid anchored the intensities 2, 5, and 10 for vinegar flavor, respectively.

Sample presentation

Samples were presented at room temperature in 2 oz. plastic cups labeled with a 3-digit code. Each sample was evaluated for sour, salty, bitter, and sweet tastes, astringency, vinegar flavor, and "other." The "other" category was an open scale with space allotted for a write-in descriptor to be used when a nonanticipated off-note was observed. Subjects evaluated 5 or 6 samples of acid solutions per session using the sip-and-spit method. The duration of each tasting session was approximately 30 to 45 min. Panelists were instructed to take a comfortable amount of sample into their mouth, swish it around for approximately 5 s and expectorate it into a waste cup. Panelists were also instructed to wait for 1 min between samples. Reference solutions for sour taste, astringency, and vinegar flavor were provided in every session for panelists' calibration. Water and crackers were available as palate cleansers between samples. Also, 5.5% carboxymethylcellulose (CMC) (Aqualon, Wilmington, Del., U.S.A.) and/or Münster cheese were supplied to counteract the drying and puckering sensations of astringency. Between samples, panelists rinsed with CMC or ate a piece of cheese, sipped water, ate a piece of unsalted cracker, and sipped water again. CMC has been previously shown to act as an effective inter-stimulus rinse for astringency in model solutions (Brannan and others 2001).

Sample preparation

Food grade acid solutions were prepared with purified water (Rainbow Water Service, Durham, N.C., U.S.A.) at the beginning of each week of testing and refrigerated between sensory evaluations. Acetic, lactic, adipic, malic, tartaric, succinic, and fumaric acids were obtained from Sigma Aldrich (St. Louis, Mo., U.S.A.). Citric acid, hydrochloric acid, and sodium hydroxide were obtained from Spectrum (Spectrum Chemical & Laboratories Products, Gardena, Calif., U.S.A.). pH adjustments were performed using 2N sodium hydroxide (NaOH).

Aqueous solutions containing a single organic acid were used to investigate the potential sour taste suppression caused by the adjustment of pH with sodium hydroxide. Acid solutions had constant concentrations of protonated organic acid species, and were in the pH range where hydrogen ions have little or no contribution to sour taste perception ($pH \geq 3$) (Neta and others 2007b). Acetic and lactic acids were tested at 10 mM protonated organic acid species, with pH ranging from 3 to 5.5 and 3 to 4.5, respectively. Citric and malic acids were evaluated at 8 mM protonated organic acid species concentration (sum of fully and partially protonated species), with pH ranging from 3 to 6 and 3 to 5.5, respectively.

Table 1 — Aqueous solutions containing a blend of 3 organic acids with constant concentration of protonated organic acid species (sum of fully and partially protonated species = 20 mM) and constant hydrogen ions ([H^+] = 0.1 mM, pH = 4). Solutions pH values were adjusted using NaOH.

Total acid concentration (mM)							Anion species (mM)	Sodium ion (mM)
Adipic	Citric	Fumaric	Lactic	Malic	Succinic	Tartaric		
10	5				5.2		0.3	11.4
10					5	8.2	3.4	17.2
	5	10	18				9.5	38.2
3			17	12.5			12.5	23.8
	5	13	18				16.0	36.0
		9.7	15			15	19.7	43.6

The effect of organic anion species in suppressing sour taste intensity was evaluated using mixtures of 3 different organic acids, which were chosen from a group of 8 acids. The concentrations of protonated acid species (sum of fully and partially protonated species) and hydrogen ions were held constant at 20 mM and 0.1 mM (pH = 4), respectively. The acid types and concentrations were chosen based on their pK_a values and by varying mixture compositions using $_{pH}$Tools in MATLAB™ software (The MathWorks, Inc., Natick, Mass., U.S.A.) to obtain an array of samples with increasing concentrations of anions at constant pH and constant concentration of protonated acid species. Table 1 shows the stimulus concentrations used in each acid solution. The effect of sodium ions was also examined in this experiment because each solution required a different amount of sodium hydroxide to achieve the target pH due to differences in their buffer capacities.

The effect of sodium ion concentration in suppressing sour taste intensity was evaluated by adding increasing amounts of sodium chloride (0, 20, 40, 60, and 80 mM) to acid solutions containing mixtures of 3 acids. The concentration of protonated organic acid species and hydrogen ion concentrations were held constant at 9 mM and 2.51 mM (pH = 2.6), respectively. Table 2 shows the stimulus concentrations used in each solution. The concentration of organic anions was kept near zero by choosing a pH that was considerably lower than the pK_a values of the acids. Consequently, the total molar concentrations of the acids were similar to the concentrations of protonated acid species.

Calculation of organic acid species concentration and pH measurements

The distribution of organic acid species was calculated using $_{pH}$Tools, a modeling program implemented in MATLAB, which was previously developed in this laboratory (Dougherty and others 2006). Mathematically, this software adjusts the published pK_a values of the acids for the ionic strength, temperature, and dielectric constant of the medium.

The pH was measured using a pH electrode with a microprocessor pH/mV meter (Accumet Research AR25) equipped with an AcuFet solid-state electrode (Fisher Scientific, Atlanta, Ga., U.S.A.).

Statistical analysis

Aqueous solutions were evaluated in a randomized complete block design with 3 sensory replications. Analysis of variance ($P < 0.05$), followed by means separation using the Duncan's test, as well as linear regression were performed on treatment means using the 9.1.3 version of SAS® software (1987; SAS Inst. Inc., Cary, N.C., U.S.A.).

Results and Discussion

The pH of solutions of acetic, lactic, malic, and citric acids with constant concentrations of protonated organic acid species

Table 2 — Aqueous solutions containing a blend of 3 acids with constant concentration of protonated organic acid species (9 mM), constant hydrogen ions ([H^+] = 2.51 mM, pH = 2.6), and absence of anions. Increasing amounts of NaCl were added to these solutions.

Total acid concentration (mM)							Sodium ion (mM)
Adipic	Citric	Fumaric	Lactic	Malic	Succinic	Tartaric	
3		3		3			0
	4		1		4		20
3				3		3	40
3	3					3	60
			1	4	4		80

was increased by adding NaOH in the range where hydrogen ions have little to no contribution to sour taste (pH $\geq$ 3). According to Neta and others (2007b), these solutions were expected to evoke equivalent sour taste responses. However, sour taste intensity significantly decreased with increasing pH ($P < 0.05$) for each acid tested (Figure 2). Interestingly, the multiprotic citric and malic acids exhibited a greater degree of sour taste suppression than the monoprotic acetic and lactic acids. To maintain the concentration of protonated organic acid species constant in these solutions while varying the pH, 2 variables were inevitably introduced. Sodium ions were incorporated into solutions via addition of sodium hydroxide to increase pH. There was also an increase in the organic anion concentration caused by the higher total acid concentration required to keep the concentration of protonated organic acid species constant at a higher pH. Thus, we hypothesized that sour taste may have been suppressed by the presence of organic anions and/or sodium ions in these acid solutions.

The effect of organic anions in suppressing sour taste was investigated in solutions containing mixtures of 3 acids with constant concentrations of protonated organic acid species and hydrogen ions. Total organic anion concentration did not correlate well with the suppression of sour taste observed in these solutions (Figure 3; $R^2 = 0.480$, $P = 0.12$). The effect of sodium ions in suppressing sour taste intensity was also investigated in these solutions because they had different buffer capacities, and thus required different amounts of sodium hydroxide to achieve pH = 4. Sour taste intensity decreased ($R^2 = 0.861$, $P = 0.007$) and salty taste intensity increased ($R^2 = 0.752$, $P = 0.02$) as the concentration of sodium ions increased from 10 to 45 mM (Figure 4). Sour taste decreased approximately 2 intensity units, while salty taste increased about 1 intensity unit on a 0- to 15-point universal scale. No significant correlations were observed between sour taste suppression and the other sensory attributes measured in this study ($P < 0.05$).

The effect of sodium ions in suppressing sour taste intensity was further investigated by adding sodium chloride to solutions containing mixtures of 3 organic acids at a constant concentration of protonated organic acid species and hydrogen ions, and in the absence of organic anion species. Addition of 20 mM NaCl resulted in a significant decrease in sour taste intensity of about 2 intensity units (Figure 5, $P = 0.016$). Amiloride-sensitive Na^+ channels in the cell membrane have been proposed to mediate both sour and salty responses, providing a potential mechanism for competitive inhibition (Lindemann 1996; Stewart and others 1997). This could explain the suppression observed when small amounts of sodium ions were present in solution. Sensory studies have indicated that sour taste suppression by salts may also be a perceptual phenomenon. For instance, increasing concentrations of NaCl, from below threshold values to above levels commonly found in foods led to simultaneous increases in salty taste and decreases in sour taste of aqueous solutions containing citric acid (Kemp and Beauchamp 1994). Similarly, Pangborn and Chrisp (1964) showed that the sour taste of citric acid was suppressed by high concentrations of NaCl in canned tomato juice, and Hellemann (1992) reported that NaCl suppressed the sour taste of lactic acid in aqueous solutions. However, in the current study, increasing the concentration of NaCl from 20 to 80 mM resulted in a significant increase in salty taste intensity ($R^2 = 0.980$, $P = 0.012$) but had no additional effect on sour taste (Figure 5). This suggests that suprathreshold perceptual interactions between sour and salty tastes do not appear to be the driving force for the observed sour taste suppression by the low concentration of sodium ions in pH-adjusted mixed acid solutions.

Increasing the sodium ion concentration by addition of NaCl had a higher impact on salty taste intensity compared to NaOH. For instance, increasing sodium ion concentration from about 10 to 45 mM resulted in a 1-point compared to a 4-point increase in salty taste intensity for NaOH and NaCl, respectively (Figure 4 and 5). The simultaneous increase of organic anions with sodium ions in the pH adjusted organic acid solutions (Table 1) may account for their lower salty taste compared to NaCl supplemented solutions. Sodium ions may bind to anions in solution, decreasing the amount of free Na^+ available to induce salty taste perception. Rosett and others (1995) found that, at equivalent NaCl levels, the salty taste

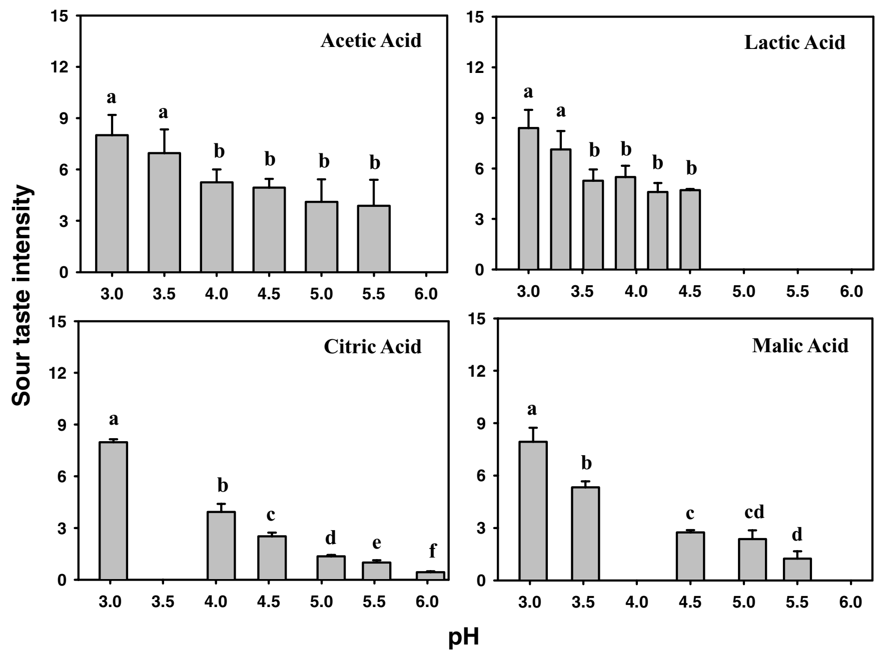

Figure 2—Sour taste intensity of single acid solutions having constant concentration of protonated organic acid species (10 mM for acetic and lactic acids, and 8 mM for citric and malic acids). pH was raised using NaOH in the range where hydrogen ions have little to no contribution to sour taste (pH ≥ 3). Differing lowercase letters indicate means that are significantly different (*P* < 0.05).

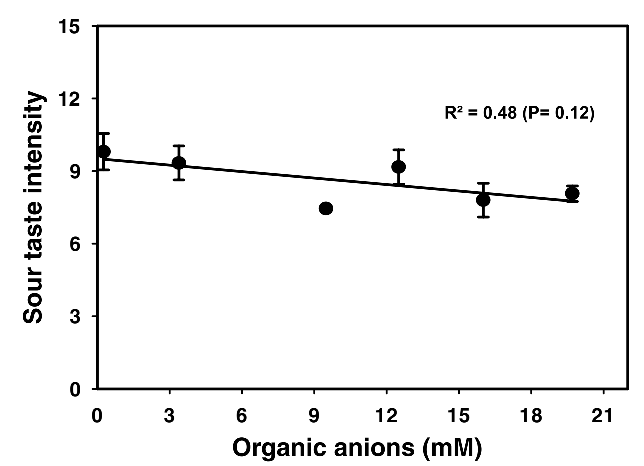

Figure 3—Effect of organic anions on sour taste intensity of mixtures of 3 acids with constant concentration of protonated organic acid species and hydrogen ions (pH).

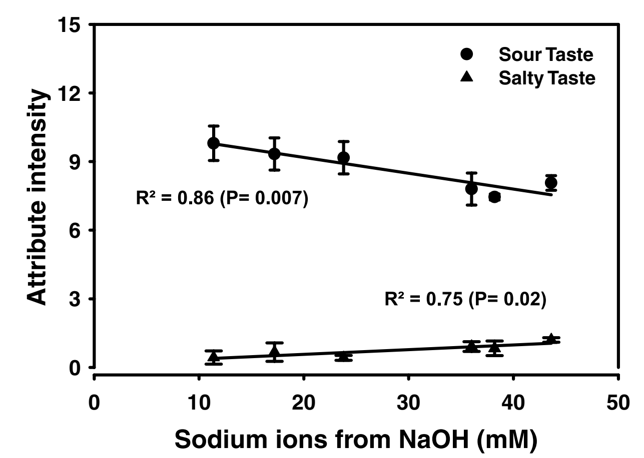

Figure 4—Effect of sodium ions (NaOH) on sour and salty tastes of solutions containing mixtures of 3 acids with constant concentration of protonated organic acid species and hydrogen ions (pH).

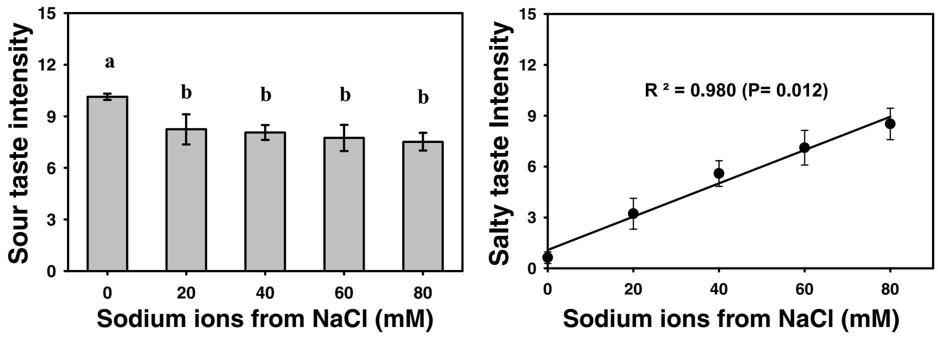

Figure 5—Effect of sodium ions (NaCl) on sour and salty tastes of solutions containing mixtures of 3 organic acids with constant concentration of protonated organic acid species and hydrogen ions, and in the absence of organic anion species. Differing lowercase letters indicate means that are significantly different ($P < 0.05$).

of ionic xanthan gum solution was lower than a nonionic gum (locust bean) solution due to higher ionic binding sites for Na^{+}, thus concluding that less free sodium ions were available to induce salty taste. Differences in salty taste obtained from NaOH or NaCl may also be explained by the type of anions present. Previous studies have proposed that sodium ions are the active stimuli for salty taste and that anions modulate the perceived saltiness intensity, with larger anions having a greater effect than smaller anions (Schiffman and others 1980; Bartoshuk 1988; Miller and Bartoshuk 1991; Delwiche and others 1999). The salty taste associated with calcium chloride has been shown to be largely suppressed when combined with larger organic ions such as lactate and gluconate, which suggests anionic inhibition (Lawless and others 2003). van der Klaauw and Smith (1994) showed that on a molar basis, NaCl is perceived as more salty than organic sodium salts, and Ye and others (1991) proposed that larger anions such as organic anions resulted in a lower salty taste response because they have lower permeability in tight junctions between taste receptor cells compared to small anions such as chloride.

Conclusions

In theory, organic anions and sodium ions may suppress sour taste by physiological interactions at the cellular/epithelial level or cognitive interactions occurring at the central processing level. However, the suppression of sour taste observed in aqueous solutions having constant pH and protonated organic acid species was not clearly related to the total concentration of organic anions. Suppression of sour taste seemed to be more closely related to the amount of sodium ions added in the form of NaOH. Addition of small amounts of NaCl to acid solutions in the absence of anions and at constant pH and protonated organic acid species resulted in a significant decrease in sour taste intensity. Sour taste intensity was unaffected by higher concentrations of NaCl although these solutions had a significant increase in salty taste. Results from this study suggest that sodium ions influence sour taste of organic acids, even though they did not account for the total suppression of sour taste that was observed in the pH-adjusted solutions. Neither sodium ion concentration alone nor total anion concentration accounted for the differential sour taste suppression between monoprotic and multiprotic organic acids that was shown in single acid pH adjusted solutions. This indicated that an additional mechanism of sour taste inhibition by organic anions may be involved.

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References

Bartoshuk LM. 1988. Taste. In: Atkinson RC, Herrnstein RJ, Lindzey G, Luce RD, editors. Steven's handbook of experimental psychology. New York: Wiley. p 461–99.

Beidler LM. 1967. Anion influences in taste receptor response. In: Hayashi T, editor. Olfaction and taste II. New York: Pergamon Press. p 509–34.

Beidler LM. 1971. Taste receptor stimulation with salts and acids. In: Beidler LM, editor. Handbook of sensory physiology IV. Chemical senses 2. New York: Springer-Verlag. p 200–20.

Brannan GD, Setser CS, Kemp KE. 2001. Effectiveness of rinses in alleviating bitterness and astringency residuals in model solutions. J Sens Stud 16:261–75.

Delwiche JF, Halpern BP, DeSimone JA. 1999. Anion size of sodium salts and simple taste reaction times. Physiol Behav 66:27–32.

Dougherty DP, Neta ERD, McFeeters RF, Lubkin SR, Breidt F Jr. 2006. Semi-mechanistic partial buffer approach to modeling pH, the buffer properties, and the distribution of ionic species in complex solutions. J Agric Food Chem 54:6021–9.

Hartwig P, McDaniel MR. 1995. Flavor characteristics of lactic, malic, citric, and acetic acids at various pH levels. J Food Sci 60(2):384–8.

Hellemann U. 1992. Perceived taste of NaCl and acid mixtures in water and bread. Int J Food Sci Technol 27:201–11.

Johnson AH, Peterson MS. 1974. Acidulants. In: Encyclopedia of food technology. Westport, Conn.: Avi Publishing Co. p 1–6.

Keast RSJ, Breslin PAS. 2002. An overview of binary taste-taste interactions. Food Qual Pref 14:111–24.

Kemp SE, Beauchamp GK. 1994. Flavor modification by sodium chloride and monosodium glutamate. J Food Sci 59(3):682–6.

Koyama N, Kurihara K. 1972. Receptor site for sour stimuli. Nature 239(5373):459–60.

Lawless HT. 1991. Taste and odor. In: Hui YH, editor. Wiley encyclopedia of food science and technology. New York: John Wiley and Sons. p 2509–25.

Lawless HT, Rapacki F, Horne J, Hayes A. 2003. The taste of calcium and magnesium salts and anionic modifications. Food Qual Pref 14:319–25.

Lindemann B. 1996. Taste reception. Phys Rev 76(3):719–59.

Meilgaard MC, Civille GV, Carr BT. 1991. Sensory evaluation techniques. 2nd ed. Boca Raton, Fla.: CRC Press.

Miller IJ, Bartoshuk LM. 1991. Taste perception, taste bud distribution, and spatial relations. In: Getchell TV, Doty RL, Bartoshuk LM, Snow JB Jr, editors. Smell and taste in health and disease. New York: Raven Press. p 205–33.

Neta ERD, Johanningsmeier SD, McFeeters RF. (2007a). The chemistry and physiology of sour taste: a review. J Food Sci 72(2):R33–8.

Neta ERD, Johanningsmeier SD, Drake MA, McFeeters RF. (2007b). A Chemical basis for sour taste perception of acid solutions and fresh-pack dill pickles. J Food Sci 72(6):S352–9.

Norris MB, Noble AC, Pangborn RM. 1984. Human saliva and taste responses to acids varying in anions, titratable acidity, and pH. Physiol Behav 32:237–44.

Ogawa H. 1969. Effects of pH on taste responses in the chorda tympani nerve of rats. J Physiol 19:670–81.

Pangborn RM, Chrisp RB. 1964. Taste interrelationships. VI Sucrose, sodium chloride, and citric acid in canned tomato juice. J Food Sci 29:490–8.

Richards TW. 1898. The relation of the taste of acids to their degree of dissociation. J Am Chem Soc 20:121–6.

Rosett TR, Wu Z, Schmidt SJ, Ennis DM, Klein BP. 1995. KCl, $CaCl_2$, Na^{+} binding and salt taste of gum systems. J Food Sci 60(4):849–53.

Schiffman SS, McElroy AE, Erickson RP. 1980. The range of taste quality of sodium salts. Physiol Behav 24:217–24.

Stewart RE, DeSimone JA, Hill DL. 1997. New perspectives in gustatory physiology: transduction, development, and plasticity. Am J Physiol Cell Physiol 272:C1–26.

van der Klaauw NJ, Smith DV. 1994. Taste quality profiles for fifteen organic and inorganic salts. Physiol Behav 58(2):295–306.

Wismer WV, Goonewardene LA. 2003. Selection of an astringency reference standard for the sensory evaluation of black tea. J Sens Stud 19:119–32.

Ye Q, Heck GL, DeSimone JA. 1991. The anion paradox in sodium taste reception: resolution by voltage-clamp studies. Science 254:726–42.