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Factors affecting detection of a bimodal sour-savory mixture and inter-individual umami taste perception

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ABSTRACT

While basic taste interactions have been the subject of many research studies, there is one combination where data is limited in the literature: sour and umami. This combination is universal in culinary preparations and of key interest to the food industry. Therefore, the primary goal of the present study is to assess how increasing concentrations of acidity (citric acid) affect, if at all, the intensity of a constant concentration of umami (monosodium glutamate, MSG). The secondary goal is to investigate other possible factors in umami taste perception. Here, a crowdsourced cohort of 734 individuals (age range 8–81) tasted and rated the intensity of 50 mM MSG alone, and in combination with citric acid at varying concentrations (1.25 mM, 6.25 mM, 31.25 mM). Participants were also genotyped for the single nucleotide polymorphism rs34160967 in the *TAS1R1* gene. The results show a significant decrease in the intensity perception of umami as sour concentration increases (low: $p = 0.005$, medium: $p < 0.001$, high: $p < 0.001$). Situational factors such as participant hunger level and time since last eating also have a significant effect on umami intensity perception. Neither the biological factors of sex, age, and ancestry appear to play a role in umami perception, nor does variation in gene *TAS1R1* at rs34160967. These new data contribute to the growing field of taste and sensory interaction by giving evidence that sour suppresses umami taste perception in bi-model samples.

1. Introduction

Since its discovery in 1908 by Kikunae Ikeda (Lindemann, Ogiwara, & Ninomiya, 2002), umami has continued to capture the interest of chefs, nutritionists, and taste researchers alike. The taste of umami is associated with foods high in L-glutamate (Chaudhari & Roper, 2010), including cooked meat, seaweed, and vegetables such as tomatoes, mushrooms, and asparagus, in addition to several aged cheeses (Drake et al., 2007). In addition to L-glutamate, there are many additional compounds that can elicit the umami taste, including, inosine monophosphate (IMP), guanosine monophosphate (GMP), adenosine monophosphate (AMP) (Fuke & Ueda, 1996), and monosodium glutamate (MSG), the latter being most commonly used in taste research (e.g., Kemp & Beauchamp, 1994; Keast & Breslin, 2002).

For decades, it was debated if umami was better classified as the fifth basic taste or as a flavor enhancer because its addition to food was known to bring out other flavors and increase palatability (Beauchamp, 2009; Okiyama & Beauchamp, 1998). It was not until researchers discovered the receptors for umami, TAS1R1 and TAS1R3, that umami became more widely accepted as a basic taste (Chaudhari, Pereira, & Roper, 2009; Kim, Wooding, Riaz, Jorde, & Drayna, 2006; Li et al., 2002; Nelson et al., 2002; Zhao et al., 2003). Receptor genetics also played a part in our understanding of umami detection. In 2009, Shigemura and colleagues determined that the single nucleotide polymorphisms (SNPs) rs34160967 (Ala372Thr) in the *TAS1R1 (T1R1)* gene and rs307377 (Arg757Cys) in the *TAS1R3 (T1R3)* gene played a significant role in umami sensitivity (Shigemura, Shirosaki, Sanematsu, Yoshida, & Ninomiya, 2009; reviewed in Hayes, Allen, & Bennett, 2013). Specifically, it was observed that the amino acid substitution −372 T in TAS1R1 created a more sensitive umami receptor than −372A, and that the amino acid substitution −757C in TAS1R3 created a less sensitive umami receptor than −757R (Shigemura et al., 2009). In addition, researchers found that there was a significant association between both rs34160967 and rs307377 with umami recognition thresholds

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(Shigemura et al., 2009). It was advantageous that this work was done with an entirely Japanese cohort because the minor allele for rs34160967, A, is much more prevalent in those with Japanese ancestry (40.9%) than those with European ancestry (12.2%) (Zerbino et al., 2018). Similarly, the minor allele for rs307377, T, is much more prevalent in those with Japanese ancestry (15.4%) compared to those with European ancestry (3.4%) (Zerbino et al., 2018). Studies focusing on predominantly European populations have found it difficult to compare the three genotypes of rs34160967 in their cohorts because of the low prevalence of homozygous A individuals (Raliou, Wiencis, Pillias, Planchais, Eliot, Boucher, Tortier, Montmayeur, & Faurion, 2009; Rawal, Hayes, Wallace, Bartoshuk, & Duffy, 2013). This same difficulty was found when researching the *T1R3* SNP rs307377 in a study done by Chen and colleagues (2009); only 2% of their predominantly European cohort were found to have the minor allele (Chen, Alacron, Tharp, Ahmed, Estrella, Greene, Rucker, & Breslin, 2009). Therefore, this study will focus only on the rs34160967 in *T1R1* because of its higher minor allele frequency and because of the increased possibility of finding all three genotypes.

Given umami's reputation to enhance other tastes and flavors, and its prevalence in "comfort food" ingredients, it is surprising to find that when isolated, most people find the taste of umami unpleasant (Yamaguchi and Takahashi, 1984ab; Fuke & Ueda, 1996; McCabe & Roll, 2007). This incongruity has made the interaction of umami with other basic tastes a subject of much scientific interest. When Kemp and Beauchamp (1994) added MSG (umami) to sweet, salty, and bitter compounds, they found that MSG had concentration specific effects; high concentrations of MSG increased salty taste, while both medium and high concentrations of MSG suppressed sweet and bitter tastes (Kemp & Beauchamp, 1994). The suppression of bitter by umami was later confirmed by Keast and Breslin (2002).

Although a universal culinary pairing (Homes, 2003), few studies have focused on the combination of sour and umami (reviewed in Keast & Breslin, 2003; Wilkie & Capaldi Phillips, 2014). Of the studies that exist, researchers have focused primarily on the impact of umami on sour. The work of Woskow (1969) observed that umami increased the perception of sweetness and saltiness at moderate concentrations, and decreased the taste of sourness and bitterness. Kemp and Beauchamp (1994) concluded that MSG had no impact on the intensity of citric acid (CA), and Yamaguchi and Takahashi (1984a,1984b) observed that adding a low concentration of MSG increased the pleasantness of tartaric acid, however the reported pleasantness was diminished as the MSG concentration increased. No literature could be found that investigated the role of sour on umami perception. In their review of taste interactions, Wilkie and Capaldi Phillips (2014) noted this absence of literature and exhorted researchers to fill this gap. It is surprising that this combination has not been addressed in many years, considering that in meals around the world, acids (sours) are frequently added to meat and fish (umami) dishes in the form of marinades and sauces, side dishes, and toppings, e.g., ceviche, lemon chicken, tamarind curry, lime fajitas, and hot dogs with mustard and relish. In these cases, the amount of umami is constant in the dish and the amount of sour added is adjusted to achieve the desired taste combination.

While research on the interaction of sour and umami has been limited, sour has been studied in combination with other taste primaries. Combining sweet and sour appear to be stimuli and concentration dependent as observed by Fabian and Blum (1943). Briefly, it was observed that the sweetness of fructose is suppressed by lactic, malic and tartaric acids, but not by citric acid or hydrochloric acid (HCl); citric, lactic, malic, and tartaric increase the perceived sweetness of sucrose while HCl and acetic acid have no effect (Fabian & Blum, 1943). Fabian & Blum also report that all the sweeteners they investigated suppress the sourness of the acids. This trend of sweeteners to suppress sour has been confirmed by others (e.g., Pangborn, 1960; Prescott, Ripandelli, & Wakeling, 2001; Green, Lim, Osterhoff, Blacher, & Nachtigal, 2010), however these same researchers had differing results when studying the effect of citric acid on sucrose.

Fabian and Blum (1943) also report that all acids except HCl increased the saltiness of NaCl. Other studies have confirmed that sour in combination with either bitter or salty stimuli enhances the taste of both (Bartoshuk & Cleveland, 1977; Kamen, Pilgrim, Gutman, & Kroll, 1961). However, the work of Calviño and García (1998) reports that the addition of sodium citrate, another salty stimulus, has a suppressive effect on the sour perception of citric acid.

As both sour and umami have been extensively studied in combination with other basic taste primaries, this report's primary goal is to partially fill in the gap in the taste literature about how sour and umami interact. Specifically, this work focuses on how the addition of citric acid (sour) changes the taste perception of MSG (umami). In addition, it presents various factors that might impact how strongly one detects the taste of umami (MSG), including: the variation at SNP rs34160967 of the *T1R1* gene, biological factors such as age and sex, hunger level, and time since last eating.

2. Material and methods

2.1. Participants

Guests of the Denver Museum of Nature & Science (Museum) elected to participate as crowdsourced research participants in the Savory and Sour Study, hosted by the Genetics of Taste Lab (Lab), between November 2017 and August 2018. Of the total participants, a subset of unrelated individuals (n = 734; 470 female, with an age range of 8–81) had complete data sets (for taste intensity ratings, genotype data for rs3416097 in *T1R1*, and self-reported age, sex, race, ethnicity, hunger level, and time since last eating) and were therefore included in the final analysis. All procedures were approved by the Colorado Multiple Institutional Review Board (Protocol #: 17-1074) and the study complied with the Declaration of Helsinki for Medical Research involving Human Subjects. The study was open to guests ages 8 and up and was offered in both English and Spanish. Participants 8-17 gave verbal assent and were given permission by a parent or legal guardian who remained present with the child for the duration of the enrollment; participants 18 and older gave verbal consent. All participants volunteered their time.

2.2. Community scientists

Volunteer community scientists (also referred to in the literature as citizen scientists) (Bonney, Cooper, Dickinson, Kelling, Phillips, Rosenberg, & Shirk, 2009; Eitzel, Cappadonna, Santos-Lang, Duerr, West, Virapongse, Kyba, Bowser, Cooper, Sforzi, & Metcalfe, 2017) were trained to collect and process DNA samples and phenotypic data from study participants. Briefly, community scientists completed an ethics course, plus training on internal quality control for data collection, on educational facilitation, and on guest experience. A more in-depth description of the Lab's community science training model can be found in Nuessle, McNamera, and Garneau (2020). Community scientists were also trained on data processing and DNA analysis protocols, including DNA extraction and quantitative polymerase chain reaction (qPCR). All procedures were supervised by the Museum's professional scientific staff.

2.3. TAS1R1 Genotyping

DNA was extracted from Puritan buccal swabs (Puritan 25-1506 1PF TT MC) using the Maxwell 16 Buccal Swab LEV DNA Purification Kit (Promega™ AS1295). The genomic DNA was genotyped for rs34160967 in *TAS1R1* (*T1R1*, NCBI Gene ID #80835) using the TaqMan™ SNP Genotyping Assay (Applied Biosystems, C_225997001_10) and the TaqMan™ Genotyping Master Mix (Applied Biosystems). Amplification was performed and analyzed in triplicate. Amplifications were completed on a CFX96 Real-Time PCR System (Bio-Rad Laboratories) in

96-well plates with an initial step at 95 °C for 10 min, followed by 40 cycles of 95 °C for 15 s and 60 °C for 1 min. The instrument automatically determined the cycle threshold for each sample. Positive controls selected for the assay were confirmed via Sanger Sequencing performed at the University of California Berkeley DNA Sequencing Facility.

2.4. Scale training

Participants trained to use the generalized Visual Analog Scale (gVAS) to rate the intensity of different taste sensations. Briefly, the rating scale is similar to the more commonly used gLMS (Bartoshuk et al., 2004) in that both feature a horizontal line anchored by the labels "no sensation" and "strongest sensation of any kind." While the gLMS contains other word-anchors throughout the scale, the gVAS utilizes only these endpoint anchors (proposed by Snyder, Prescott, & Bartoshuk, 2006 and validated by Hayes, Feeney, & Allen, 2013). Training consisted of a 3-D mockup of the scale to visually demonstrate proper use, and participants were asked to think of the strongest physical sensation they had ever experienced and told that their chosen sensation would be represented by the anchor, "strongest sensation of any kind." Using the mockup, community scientists had participants mark where they would rate the weight of a feather in their hand, the pain of a splinter, and the pain of slamming a car door on their finger, compared to the strongest physical sensation they had ever experienced. This gave community scientists the opportunity to provide further clarification on the scale's usage if it was determined to be needed. Participants were then given three jars of varying weight (1127 g, 499 g, and 53 g; Webb, Bolhuis, Cicerale, Hayes, & Keast, 2015) in descending order and asked to rate the heaviness (intensity) of each jar on the digital version of the scale in the online questionnaire. To prepare for data analysis, ratings were converted to a numerical value (0 to 100; 0 = no sensation, 100 = strongest sensation of any kind). Participants who did not rate the jars in the correct order were assumed to not understand the instrument and were therefore excluded from data analysis.

2.5. Taste intensity rating

Kits containing seven taste samples were presented to each participant. All the samples were presented in 2 oz. condiment cups which contained 5 mL of solution; the solutions were prepared in deionized water. The first two samples were reference samples to familiarize participants with the taste of sour (12.5 mM citric acid) and umami (50 mM MSG), as well as train participants on how to rate each sample. The reference samples were labeled "sour" and "umami" respectively. Participants were instructed to swish the sample in their mouth for 5 s and then spit it back out into the cup. Participants were then directed to select all the tastes they detected (sweet, sour, salty, bitter, umami, and none of the above were listed). An individual gVAS appeared for each selected taste which participants then used to rate the taste's intensity. All five of the basic tastes were available as an option to prevent a halo-dumping effect and to ascertain if the participants identified other taste qualities in the reference samples so as not to confound any later data (Clark & Lawless, 1994; Wise & Breslin, 2011).

After familiarizing themselves with the reference solutions, five samples were presented in a randomized, double blinded order. Each sample contained 50 mM MSG, an amount commonly found in food (Kemp & Beauchamp, 1994), and one of the following concentrations of CA: zero (0 mM), low (1.25 mM), medium (6.25 mM), or high (31.25 mM). Each kit was labeled with one of 25 Taste ID codes which were used to decode the sample order during analysis. Participants tasted the samples and followed the same procedure as with the training samples (swish the sample in their mouth for 5 s, spit it out, and select any of the five basic tastes they detected). Bottled water was provided for participants to rinse their mouth and small breaks were given between each sample to prevent taste fatigue.

2.6. Statistical analysis

Analysis was performed on samples from 734 unrelated individuals with complete data sets to assess differences in umami taste perception. Complete data sets included: taste intensity ratings, genotype data for rs3416097 in *T1R1*, and self-reported age, sex, race, ethnicity, hunger level, and time since last eating. From the participants' self-reported race, participants were then grouped into four ancestral categories: African (n = 33), Asian (n = 43), European descent (n = 561), and other (n = 97). A subset of participants (n = 76) rated that they did not perceive any umami taste (score = 0) in the 50 mM MSG sample with no CA: 33 reported all tastes as zero whereas 43 reported perception of another taste. The data of these 76 participants were not included in the final statistical model because we could not be certain if they were taste blind to MSG (Lugaz, Pillias, & Faurion, 2002), were confused by the term umami despite training, or perceived the umami as other tastes, and we did not want to confound the results.

The data was organized in such a way to allow for modeling. Briefly, each participant's data was included in the data set four times, with all factors remaining the same except the corresponding strength of umami taste for the four different levels of citric acid (zero, low, medium, and high). Then the linear mixed model, $Y_{ij} = \beta_0 + \beta_1 x_{ij} + \nu_i + \in_{ij} for i \in \{1, \cdots, n = 734\}, j \in \{1, \cdots, 4\}$, was applied. Here, Y_{ij} is the taste intensity rating of umami taste for the j^{th} citric acid level of the i^{th} subject. $\beta_0 + \beta_1 x_{ij}$, is the fixed effect component and is no different than linear regression. The covariates used in the fixed effect portion of the model were citric acid level, age, sex, genotype (G/G, G/A, A/A), how hungry (not at all, a little bit, moderately hungry, starving), last ate (a substantial beverage [smoothie, blended coffee, milk shake, etc.], a large meal, a small meal, a snack), hours since food (<1 h, between 1 and 2 h, between 2 and 3 h, between 3 and 4 h, greater than 4 h), and continental ancestry (European, Asian, African, Other). The random effect portion of the model, $\nu_i\ N(0, \sigma_\nu^2)$ is used to model visitor ID since four measures were taken for each subject. The random effect models the correlation that occurs by having the same subject present more than 1 time in the data set. $\in_{ij}\ N(0, \sigma_\in^2)$, is the Gaussian error term that models the residuals for the fixed effects.

Backward step-wise selection was done using the likelihood ratio test. Once the model containing all the covariates was fit, the variable with the highest p-value was removed first. The model was refit without the variable and then compared to the full model using the likelihood ratio test. If the new model was considered an improvement based on the Akaike Information Criterion or AIC, then this model was used as the new baseline for comparison. This process continued until no further improvements to AIC were possible. After the backward stepwise selection, the model with only citric acid level, hunger level, and hours since food was found to be the best model. Therefore, the final model used was the linear mixed effects model with fixed effects citric acid level, hunger level and hours since eating, and random effect visitor ID (Table 1).

3. Results

3.1. Changes in umami perception with increasing acidity

In order to understand if umami taste perception changes with increasing concentrations of acidity, we analyzed how participants rated the strength of umami when MSG was presented with zero (0 mM), low (1.25 mM), medium (6.25 mM), or high (31.25 mM) citric acid levels. Ratings from umami with no CA were used as the baseline. The mean intensity score for the baseline umami strength is 39.76. From the final statistical model, we see that each level of citric acid has a significant inverse relationship with umami strength perception (low: $p = 0.005$, medium: $p < 0.001$, high: $p < 0.001$). The low CA samples decrease umami intensity ratings from the baseline by an average of 2.89 points,

Table 1
Summary of the factors included in the final statistical model and their effect on umami taste intensity ratings.

Variable	Coefficient estimate	Standard Error	p-value
Intercept	39.756	2.212	< 0.0001 *
Citric Acid Level: High	−20.654	1.028	< 0.0001 *
Citric Acid Level: Medium	−7.211	1.028	< 0.0001 *
Citric Acid Level: Low	−2.886	1.028	0.0051*
How Hungry: A little bit	1.527	1.622	0.3467
How Hungry: Moderately Hungry	4.066	1.858	0.0289*
How Hungry: Starving	12.921	3.353	0.0001*
Hours Since Food: Between 1 and 2 Hours	−8.521	2.342	0.0003*
Hours Since Food: Between 2 and 3 h	−6.636	2.386	0.0056*
Hours Since Food: Between 3 and 4 h	−5.899	2.539	0.0204*
Hours Since Food: More than 4 h	−8.272	2.598	0.0015*
Random effects			
Person ID (Intercept)	Variance = 206.0, Std. Deviation = 14.35		
Residual	Variance = 388, Std. Deviation = 19.70		

* Indicates significant p value with a significance interval at $p \leq 0.05$.

the medium CA decrease from baseline by 7.21 points, and the high CA decrease from baseline by 20.65 points (see Fig. 1).

3.2. Variation in umami intensity ratings

During data collection, participants were asked about their hunger level at the time of their enrollment. The options included were: not at all, a little bit, moderately hungry, and starving. Using the "not at all" hunger level as the baseline, we observe a positive relationship between the taste of umami and participant hunger level, as hunger level increases, umami perception increases (see Fig. 2). There is a statistically significant increase in the intensity rating of umami detected when the baseline is compared to "moderately hungry" and "starving, "4.07 ($p = 0.029$) and 12.92 ($p < 0.001$), respectively. When comparing hunger levels, the umami intensity rating increases by 1.53 from "not at all" hungry to "a little bit" hungry, though this result is not significant ($p = 0.347$).

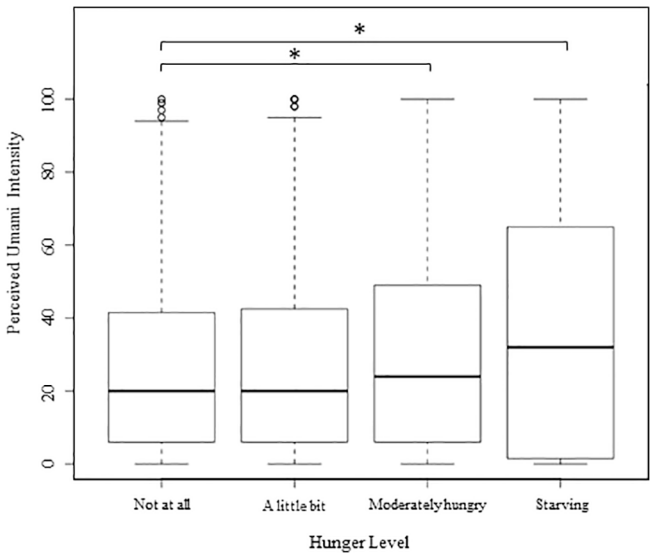

Fig. 2. Boxplot of umami strength at differing hunger levels. Not at all hungry was used as the baseline. As the degree of hunger increases, the perceived umami strength also increases. * indicates significant difference ($p < 0.05$) from baseline.

In addition to hunger level, participants were asked to report how many hours had elapsed since they had last eaten. Participants could select from the following options: <1 h, between 1 and 2 h ago, between 2 and 3 h ago, between 3 and 4 h ago, and more than 4 h ago. Using the "<1 h" category as the baseline, we observe a decrease in umami intensity ratings across the categories tested. Comparing all the categories to the baseline, we see that those who marked "between 1 and 2 h" since eating show a decrease in their umami rating by 8.5 ($p < 0.001$); "between 2 and 3 h" show a decrease in umami ratings by 6.6 ($p = 0.005$); "between 3 and 4 h" and "more than 4 h" show a decrease in umami

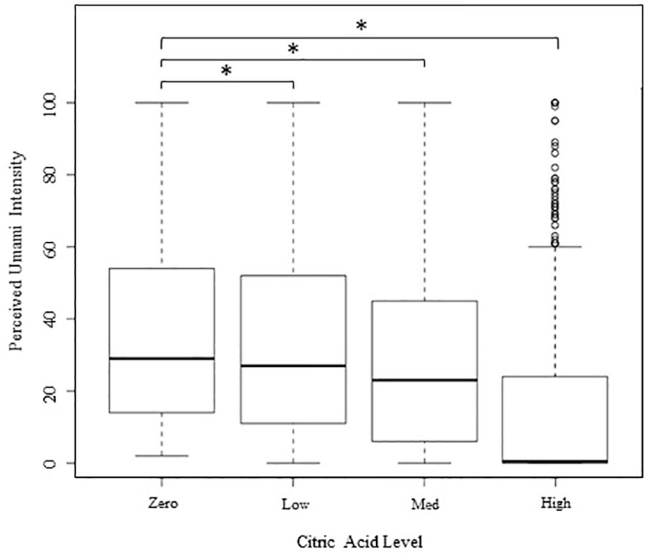

Fig. 1. Boxplot of umami strength at varying citric acid levels. Zero citric acid was used as the baseline level. As the concentration of citric acid increases, the perceived strength of umami decreases. * indicates significant difference ($p < 0.05$) from baseline.

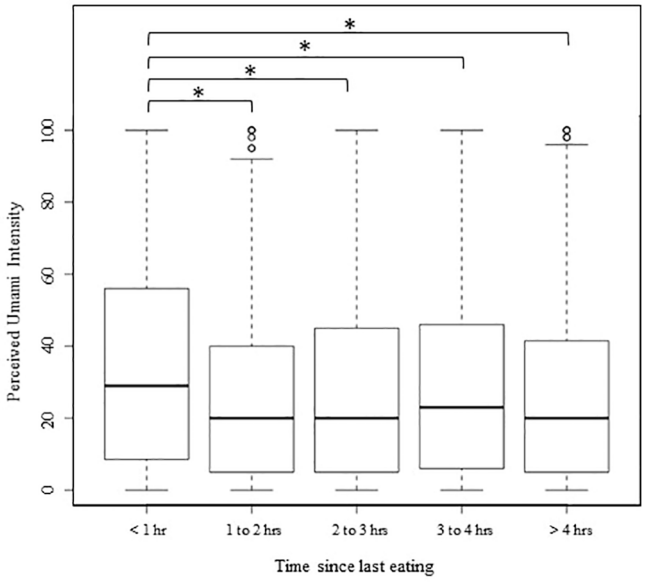

Fig. 3. Boxplot of umami strength and time since last eating. <1 h was used as the baseline. Overall, as the time since last eating increased, the strength of umami decreased. * indicates significant difference ($p < 0.05$) from baseline.

ratings by 5.9 ($p = 0.02$) and 8.3 ($p = 0.001$), respectively (See Fig. 3).

We also investigated if variation in umami taste ratings is due to age, sex, and/or variation in *T1R1* at SNP rs34160967. The full model (Supplementary Table 1) shows that neither sex ($p = 0.085$), nor age ($p = 0.186$) affect umami intensity ratings. While the statistical model shows that *G/A* heterozygotes and *G/G* homozygotes taste umami less intensely than *A/A* homozygotes, the difference in ratings is not significant ($p = 0.342$ and $p = 0.258$, respectively).

4. Discussion

The purpose of the Savory and Sour Study presented here is to fill in the gaps in the bi-modal taste interaction literature for sour and umami. Specifically, we sought to understand how the addition of increasing concentrations of citric acid (sour) might alter the perception of a consistent concentration of MSG (umami). The primary results from the present study show that as the concentration of citric acid increases, the perceived intensity of umami decreases. This result is not surprising considering that many people find the taste of umami unpleasant in isolation (Fuke & Ueda, 1996; McCabe & Roll, 2007), and that sour is one the tastes regularly added to savory dishes to enhance flavor (Marcus, 2019); it may be that sour is masking the taste of the umami. Another possibility is that the addition of citric acid to MSG causes acidification and thus changes the MSG to glutamic acid, eliciting both a sour and umami taste (Schiffman & Sennewald, 1981); this chemical change may result in both an increased sour perception and a decreased umami perception. Both hypotheses limit the ability for one to detect umami, though the mechanism varies. More research should be done to determine if either of these theories is correct.

In addition, more research is needed to investigate if other acidic stimuli also suppress MSG as we observed for citric acid; findings suggest that sour is complex (Chang, Waters, & Liman, 2010; Ye et al., 2016; Zhang et al., 2019) and that citric acid might not be representative of all organic acids (Miranda, Nuessle, Wilson, Datta, & Garneau, 2020). The taste field would benefit from studying a variety of sour and umami stimuli in conjunction with each other both in terms of intensity and preference. This research was limited to assessing sour's role on umami; however, previous studies have found that the addition of umami (MSG) increases the palatability and acceptance of many foods (Chi & Chen, 1992; Yamaguchi & Ninomiya, 2000; Yamaguchi & Takahashi, 1984a). Therefore, umami's influence on sour also warrants further investigation.

Another benefit to considering a multitude of umami stimuli is that some people may be taste blind to MSG (Chen et al., 2009; Lugaz et al., 2002; Pepino, Finkbeiner, Beauchamp, & Mennella, 2010; Raliou et al., 2009; Singh, Schuster, & Seo, 2010). This finding is based on studies with participants of either a European or Japanese background. Indeed, in our predominantly European descent cohort, 9.38% of participants ($n = 76$) did not detect umami when tasting MSG alone. However, it should be noted that the majority of those participants indicated perceiving another taste in the sample, predominantly salty or bitter. Previous studies have shown similar findings of MSG taste blindness among study populations. Work performed by Lugaz et al. (2002) found that approximately 3.5% of their predominantly French cohort was blind to MSG. Similarly, Singh et al. (2010) found that 3.2% of their German participants and 4.6% of their Norwegian participants were potential MSG non-tasters. Therefore, it could be hypothesized that race/ancestry plays a role in the ability to detect umami in MSG. Future research including a more diverse population may help determine if MSG taste blindness is due to genetic variation and/or other factors such as ancestry and ethnicity.

As we also wanted to assess what factors affect umami perception, we found that neither age nor sex play a role. In terms of sex, this result aligns with previous findings (Barragan, Coltell, Portolés, Asensio, Sorlí, Ortega-Azorín, González, Sáiz, Fernández-Carrión, & Ordovas, 2018; Mojet et al., 2001, 2003). With regards to age, the results from this study conflict with previously published data by Barragán et al. (2018) and Methven, Allen, Withers, and Gosney (2012), which both report that age has a significant effect on umami intensity perception. It is possible that our results did not align with those reporting a correlation between age and umami perception because our study includes children and has a larger age range overall. Our results do, however, support findings from Fischer et al. (2014) who reported that age does not play a role in the detection of four of the basic tastes, but the study did not test an umami stimulus, making it difficult to claim that age does not affect overall taste perception. Overall, it is difficult to draw definitive conclusions about the role of age and sex in umami taste perception from this study, and the studies mentioned, as all of the studies used different methods for data collection, had different population backgrounds, and may have used different stimuli.

Much like age and sex, we did not see a significant association between umami perception and the *T1R1* SNP rs34160967. We did observe a pattern where participants who are homozygous *A/A* rate the taste of umami higher than either *G/A* heterozygotes or *G/G* homozygotes, however it was not significant. This pattern is supported by previous work showing that the *A* allele is associated with increased umami taste sensitivity in a predominantly Japanese population, and that the missense mutation may play a role in creating a more sensitive umami receptor for MSG (Shigemura et al., 2009). Two separate studies conducted on a predominantly French population also showed that the *A* allele was also associated with increased MSG sensitivity (Raliou et al., 2009, 2011). Rawal et al. (2013) found in a reanalysis of a study with only Japanese participants, that there was an association between *G/A* heterozygotes and higher MSG thresholds. Out of the entire cohort ($n = 734$) for this study, only 11 participants were homozygous *A/A*, 164 were heterozygous *G/A*, and the remaining 559 were homozygous *G/G*. In order to test if the *A* allele is associated with increased umami perception in the general American population, perhaps a larger study population is needed in order to increase the number of participants with the minor allele and the homozygous A/A genotype.

Unlike the biological factors that do not play a role in umami perception, situational factors such as hunger level and time since last eating do appear to alter how strongly one perceives umami. In our crowdsourced cohort, participants who reported moderate to extreme hunger levels rated the taste of umami higher than those who reported a lack of hunger or only minor hunger levels. This finding is not unexpected as previous work has shown that the perception of umami may play an important role in protein intake and metabolism (Beauchamp, 2009; Mori, Kawada, Ono, & Torii, 1991), as well as trigger the desire for food intake (Han, Keast, & Roura, 2018), and therefore when hungry, participants may be more sensitive to umami and perceive it more intensely. In the literature, there has been some debate over whether hunger level affects taste sensitivity. Pangborn (1959) and Pasquet, Monneuse, Simmen, Marez, and Hladik (2006) found no significant difference in taste thresholds for sweet, salty, and bitter, in either hungry or satiated participants. In contrast, Zvrev (2004) found that participants had decreased recognition thresholds for sweet and salty— but not bitter— when fasting compared to the same participants in a satiated state. Hanci and Altun (2016) also found that participants in a hunger state had increased sensitivity to sweet, sour, and salty tastes. Further investigation is needed to assess the role of hunger state and time since last eating on taste perception of not just umami, but all five of the basic tastes.

Finally, it is important to note that there are several limitations and caveats to this study. First, because this study was conducted in a museum setting, researchers cannot require fasting for any length prior to participating, and rely on self-reported information concerning duration since last eating. As a result of not being able to control for duration since the last meal, we found that the more time that had elapsed since the participant last ate, the lower the umami rating. This finding seems discordant to the rest of our findings about a participant's hunger state and may have resulted because of our first study limitation.

Second, only one SNP within *T1R1* was analyzed. It is possible that other SNPs within *T1R1* or other known umami genes, such as *T1R3* and *GRM4,* influenced the variation in the umami taste ratings observed. Third, we used monosodium glutamate as the taste stimulus for umami. By using MSG, we had a sizable portion of the study population who reported no umami taste in the samples and were thus not included in the analysis for this study. Previous studies have successfully used monopotassium glutamate (Chen et al., 2009) or MSG in combination with inosine monophosphate (Shigemura et al., 2009) to bring out the umami taste which might overcome any taste blindness. A final caveat of this study is that the majority of the crowdsourced participants were of European descent (76.4%), thus making it difficult to apply these results more broadly. Including a more diverse group of participants introduces increased genetic diversity and could result in a higher frequency of the minor allele, making the results more generalizable.

4.1. Conclusions

The data presented here as part of the Savory and Sour Study provides evidence that sour suppresses umami detection. We also found evidence that many circumstantial factors such as hunger state and time since last eating affect umami perception, while biological factors like age, sex, ancestry, and ethnicity may not.

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CRediT authorship contribution statement

Anjelica M. Miranda: Methodology, Investigation, Data curation, Writing - original draft, Project administration. **Michael Ingram:** Formal analysis, Writing - review & editing. **Tiffany M. Nuessle:** Conceptualization, Methodology, Investigation, Data curation, Writing - original draft, Project administration. **Stephanie A. Santorico:** Writing - review & editing, Formal analysis. **Nicole L. Garneau:** Conceptualization, Writing - review & editing, Supervision, Project administration, Funding acquisition.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Appendix A. Supplementary data

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References

Barragan, R., Coltell, O., Portolés, O., Asensio, E.M., Sorlí, J.V., Ortega-Azorín, C., González, J.I., Sáiz, C., Fernández-Carrión, R., Ordovas, J.M., et al. (2018). Bitter, sweet, salty, sour and umami taste perception decreases with age: sex-specific analysis, modulation by genetic variants and taste-preference associations in 18 to 80 year-old subjects. Nutrients, 10(10), 1539.

Bartoshuk, L. M., & Cleveland, C. T. (1977). Mixtures of substances with similar tastes. A test of a psychophysical model of taste mixture interactions. *Sensory Processes, 1*(3), 176–186.

Bartoshuk, L. M., Duffy, V. B., Green, B. G., Hoffman, H. J., Ko, C.-W., Lucchina, L. A., Marks, L. E., Snyder, D. J., & Weiffenbach, J. M. (2004). Valid across-group comparisons with labeled scales: The gLMS versus magnitude matching. *Physiology & Behavior, 82*(1), 109–114. https://doi.org/10.1016/j.physbeh.2004.02.033

Beauchamp, G.K. (2009). Sensory and receptor responses to umami: an overview of pioneering work. American Journal of Clinical Nutrition, 90(3), 723S-727S.

Bonney, R., Cooper, C.B., Dickinson, J., Kelling, S., Phillips, T., Rosenberg, K.V., Shirk, J. (2009). Citizen science: a developing tool for expanding science knowledge and scientific literacy. BioScience, 59(11), 977–984.9.

Calviño, A. M., & García, M. (1998). Perceived intensity and persistence of heterogeneous taste mixtures: Intensidad y persistencia percibida en mezclas gustativas heterogeneas. *Food Science and Technology International, 4*(4), 277–284. https://doi.org/10.1177/108201329800400406

Chang, R. B., Waters, H., & Liman, E. R. (2010). A proton current drives action potentials in genetically identified sour taste cells. *Proceedings of the National Academy of Sciences, 107*(51), 22320–22325. https://doi.org/10.1073/pnas.1013664107

Chaudhari, N., Roper, S.D. (2010). The cell biology of taste. The Journal of Cell Biology, 190(3), 285-296.

Chaudhari, N., Pereira, E., Roper, S.D. (2009). Taste receptors for umami: the case for multiple receptors. The American Journal of Clinical Nutrition, 90(3), 738S-742S.

Chen, Q.Y., Alacron, S., Tharp, A., Ahmed, O.M., Estrella, N.L., Greene, T.A., Rucker, J., Breslin, P.A.S. (2009). Perceptual variation in umami taste and polymorphisms in TAS1R taste receptor genes. The American Journal of Clinical Nutrition, 90(3), 770S-779S.

Chi, S. P., & Chen, T. C. (1992). Predicting optimum monosodium glutamate and sodium chloride concentrations in chicken broth as affected by spice addition. *Journal of Food Processing and Preservation, 16*(5), 313–326. https://doi.org/10.1111/j.1745-4549.1992.tb00212.x

Clark, C. C., & Lawless, H. T. (1994). Limiting response alternatives in time-intensity scaling: An examination of the halo-dumping effect. *Chemical Senses, 19*(6), 583–594. https://doi.org/10.1093/chemse/19.6.583

Drake, S. L., Carunchia Whetstine, M. E., Drake, M. A., Courtney, P., Flinger, K., Jenkins, J., et al. (2007). Sources of umami in cheddar and Swiss cheeses. *Journal of Food Science, 72*(6), S360–S366.

Eitzel, M., Cappadonna, J., Santos-Lang, C., Duerr, R., West, S.E., Virapongse, A., Kyba, C., Bowser, A., Cooper, C., Sforzi, A., Metcalfe, A. (2017). Citizen science terminology matters: Exploring key terms. Citizen Science: Theory and Practice, 2 (1), 1-20.

Fabian, F. W., & Blum, H. B. (1943). Relative taste potency of some basic food constituents and their competitive and compensatory action. *Food Science, 8*(3), 179–193. https://doi.org/10.1111/j.1365-2621.1943.tb16560.x

Fischer, M. E., Cruicshanks, K. J., Schubert, C. R., Pinto, A., Klein, B. E. K., Klein, R., et al. (2014). Taste intensity in the beaver dam offspring stud. *Laryngoscope, 123*(6), 1399–1404.

Fuke, S., & Ueda, Y. (1996). Interactions between umami and other flavor characteristics. *Trends in Food Science & Technology, 7*(12), 407–411. https://doi.org/10.1016/S0924-2244(96)10042-X

Green, B. G., Lim, J., Osterhoff, F., Blacher, K., & Nachtigal, D. (2010). Taste mixture interactions: Suppression, additivity, and the predominance of sweetness. *Physiology & Behavior, 101*(5), 731–737.

Han, P., Keast, R., Roura, E. (2018). TAS1R1 and TAS1R3 Polymorphisms Relate to Energy and Protein-Rich Food Choices from a Buffet Meal Respectively. Nutrients, 10(12), 1906.

Hanci, D., & Altun, H. (2016). Hunger state affects both olfactory abilities and gustatory sensitivity. *European Archives of Oto-Rhino-Laryngology, 273*(7), 1637–1641. https://doi.org/10.1007/s00405-015-3589-6

Hayes, J. E., Allen, A. L., & Bennett, S. M. (2013). Direct comparison of the generalized visual analog scale (gVAS) and general labeled magnitude scale (gLMS). *Food Quality and Preference, 28*(1), 36–44. https://doi.org/10.1016/j.foodqual.2012.07.012

Hayes, J. E., Feeney, E. L., & Allen, A. L. (2013). Do polymorphisms in chemosensory genes matter for human ingestive behavior? *Food Quality and Preference, 30*(2), 202–216. https://doi.org/10.1016/j.foodqual.2013.05.013

Better Homes and Gardens (2003). America's ethnic cuisines: 150 best-loved recipes plus 40 menus. Ed. Chuck Smothermon. Des Moines: Meredith Corporation. Print.

Kamen, J. M., Pilgrim, F. J., Gutman, N. J., & Kroll, B. J. (1961). Interactions of suprathreshold taste stimuli. *Journal of Experimental Psychology, 62*(4), 348–356.

Keast, R. S. J., & Breslin, P. A. S. (2002). Modifying the bitterness of selected oral pharmaceuticals with cation and anion series of salts. *Pharmaceutical Research, 19*(7), 1019–1026.

Keast, R. S. J., & Breslin, P. A. S. (2003). An overview of binary taste–taste interactions. *Food Quality and Preference, 14*(2), 111–124. https://doi.org/10.1016/S0950-3293(02)00110-6

Kemp, Sarah. E., & Beauchamp, GARY. K. (1994). Flavor modification by sodium chloride and monosodium glutamate. *Journal of Food Science, 59*(3), 682–686. https://doi.org/10.1111/j.1365-2621.1994.tb05592.x

Kim, U., Wooding, S., Riaz, N., Jorde, L. B., & Drayna, D. (2006). Variation in the human *TAS1R* taste receptor genes. *Chemical Senses, 31*(7), 599–611.

Li, X., Staszewski, L., Xu, H., Durick, K., Zoller, M., & Adler, E. (2002). Human receptors for sweet and umami taste. *Proceedings of the National Academy of Sciences, 99*(7), 4692–4696. https://doi.org/10.1073/pnas.072090199

Lindemann, B., Ogiwara, Y., & Ninomiya, Y. (2002). The discovery of umami. *Chemical Senses, 27*(9), 843–844.

Lugaz, O., Pillias, A. M., & Faurion, A. (2002). A new specific aguesia: Some humans cannot taste L-glutamate. *Chemical Senses, 27*(2), 105–115.

Marcus, J. B. (2019). Chapter 6 – Flavor Enhancement Ingredients. In *Aging, nutrition and taste: Nutrition, food science and culinary perspectives for aging tastefully* (pp. 173–206). London: Academic Press.

McCabe, C., Roll, E.T. (2007). Umami: a delicious flavor formed by convergence of taste and olfactory pathways in the human brain. European Journal of Neuroscience, 25 (6), 1855-1864.

Methven, L., Allen, V. J., Withers, C. A., & Gosney, M. A. (2012). Ageing and taste. *Proceedings of the Nutrition Society, 71*(4), 556–565. https://doi.org/10.1017/S0029665112000742

Miranda, A. M., Nuessle, T. M., Wilson, C. E., Datta, M., & Garneau, N. L. (2020). Like it or not: Sour taste preference is driven by intensity in most-but not all-acids. *[Manuscript submitted for publication]. Health Sciences Department*. Denver Museum of Nature & Science.

Mojet, J., Heidema, J., & Christ-Hazelhof, E. (2001). Taste perception with age: Generic or specific losses in threshold sensitivity to the five basic tastes? *Chemical Senses, 26*(7), 847–860.

Mojet, J., Heidema, J., & Christ-Hazelhof, E. (2003). Taste perception with age: Generic or specific losses in supra-threshold intensities of five taste qualities? *Chemical Senses, 28*(5), 397–413.

Mori, M., Kawada, T., Ono, T., & Torii, K. (1991). Taste preference and protein nutrition and L-amino acid homeostasis in male Sprague-Dawley rats. *Physiology & Behavior, 49*(5), 987–995. https://doi.org/10.1016/0031-9384(91)90212-7

Nelson, G., Chandrashekar, J., Hoon, M. A., Feng, L., Zhao, G., Ryba, N. J., et al. (2002). An amino-acid taste receptor. *Nature, 416*(6877), 199–202.

Nuessle, T. M., McNamera, P. A., & Garneau, N. L. (2020). Planning and executing scientifically-sound community science in a public-facing institution. *Citizen Science: Theory and Practice, 5*(1), 1–12.

Okiyama, A., & Beauchamp, G. K. (1998). Taste dimensions of monosodium glutamate (MSG) in food system: Role of glutamate in young American subjects. *Physiology & Behavior, 65*(1), 177–181.

Pangborn, R. M. (1960). Taste interrelationships. *Journal of Food Science, 25*(2), 245–256. https://doi.org/10.1111/j.1365-2621.1960.tb00328.x

Pangborn, R.M. (1959). Influence of hunger on sweetness preferences and taste thresholds. The American Journal of Clinical Nutrition, 7(3), 280-286.

Pasquet, P., Monneuse, M.-O., Simmen, B., Marez, A., & Hladik, C.-M. (2006). Relationship between taste thresholds and hunger under debate. *Appetite, 46*(1), 63–66. https://doi.org/10.1016/j.appet.2005.09.004

Pepino, M.Y., Finkbeiner, S., Beauchamp, G.K., Mennella, J.A. (2010). Obese women have lower monosodium glutamate taste sensitivity and prefer higher concentrations than do normal-weight women. Obesity, 18(5), 959-965.

Prescott, J., Ripandelli, N., & Wakeling, I. (2001). Binary Taste Mixture Interactions in PROP Non-tasters, medium-tasters and Super-tasters. *Chemical Senses, 26*(8), 993–1003. https://doi.org/10.1093/chemse/26.8.993

Raliou, M., Wiencis, A.M., Pillias, A., Planchais, A., Eliot, C., Boucher, Y., Tortier, D., Montmayeur, J.P., Faurion, A. (2009). Nonsynonymous single nucleotide polymorphisms in human tas1r1, tas1r3, and mGluR1 and individual taste sensitivity to glutamate. The American Journal of Clinical Nutrition, 90(suppl), 789S-99S.

Raliou, M., Grauso, M., Hoffmann, B., Schlegel-Le-Poupon, C., Nespoulous, C., Débat, H., et al. (2011). Human genetic polymorphisms in T1R1 and T1R3 receptor subunits affect their function. *Chemical Senses, 36*(6), 527–537.

Rawal, S., Hayes, J. E., Wallace, M. R., Bartoshuk, L. M., & Duffy, V. B. (2013). Do polymorphisms in the *TAS1R1* gene contribute to broader differences in human taste intensity? *Chemical Senses, 38*(8), 719–728. https://doi.org/10.1093/chemse/bjt040

Schiffman, S. S., & Sennewald, K. (1981). Comparison of taste qualities and thresholds of D- and L-amino acids. *Physiology & Behavior, 27*(1), 51–59.

Shigemura, N., Shirosaki, S., Sanematsu, K., Yoshida, R., & Ninomiya, Y. (2009). Genetic and molecular basis of individual differences in human umami taste perception. *PLoS ONE, 4*(8), Article e6717.

Singh, P. B., Schuster, B., & Seo, H. S. (2010). Variation in umami taste perception in the German and Norwegian population. *European Journal of Clinical Nutrition, 64*(10), 1248–1250.

Snyder, D. J., Prescott, J., & Bartoshuk, L. M. (2006). Modern psychophysics and the assessment of human oral sensation. *Advances in Oto-Rhino-Laryngology, 63*, 221–241.

Webb, J., Bolhuis, D. P., Cicerale, S., Hayes, J. E., & Keast, R. (2015). The relationships between common measurements of taste function. *Chemosensory Perception, 8*(1), 11–18.

Wilkie, L. M., & Capaldi Phillips, E. D. (2014). Heterogeneous binary interaction of taste primaries: Perceptual outcomes, physiology, and future directions. *Neuroscience & Biobehavioral Reviews, 47*, 70–86.

Wise, P. M., & Breslin, P. A. S. (2011). Relationships among taste qualities assessed with response-context effects. *Chemical Senses, 36*(7), 581–587.

Woskow, M. H. (1969). Selectivity in flavor modification by 5'-ribo-nucleotides. *Food Technology, 23*, 32–37.

Yamaguchi, S., & Ninomiya, K. (2000). Umami and food palatability. *The Journal of Nutrition, 130*(4), 921S–926S.

Yamaguchi, S., & Takahashi, C. (1984a). Interaction of monosodium glutamate and sodium chloride on saltiness and palatability of a clear soup. *Journal of Food Science, 49*(1), 82–85.

Yamaguchi, S., & Takahashi, C. (1984b). Hedonic function of monosodium glutamate and four basic taste substances used at various concentration levels in single and complex systems. *Agricultural and Biological Chemistry, 48*(4), 1077–1081.

Ye, W., Chang, R. B., Bushman, J. D., Tu, Y. H., Mulhall, E. M., Wilson, C. E., et al. (2016). The K+ channel KIR2.1 functions in tandem with proton influx to mediate sour taste transduction. *Proceedings of the National Academy of Sciences, 113*(2), E229–E238.

Zerbino, D. R., Achuthan, R., Akanni, W., Amode, M. R., Barrell, D., Bhai, J., et al. (2018). *Nucleic Acids Research, 46*(D1), D754–D761.

Zhang, J., Jin, H., Zhang, W., Ding, C., O'Keeffe, S., Ye, M., et al. (2019). Sour sensing from the tongue to the brain. *Cell, 179*(2), 392–402.

Zhao, G., Zhang, Y., Hoon, M., Chandrashekar, J., Erlenbach, I., Ryba, N., et al. (2003). The receptors for mammalian sweet and umami taste. *Cell, 115*(3), 255–266.

Zvrev, Y. P. (2004). Effect of caloric deprivation and satiety on sensitivity of the gustatory system. *BMC Neuroscience, 5*(1), 5.