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Revisiting Sugar–Fat Mixtures: Sweetness and Creaminess Vary with Phenotypic Markers of Oral Sensation

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Abstract

Genetic variation in oral sensation presumably influences ingestive behaviors through sensations arising from foods and beverages. Here, we investigated the influence of taste phenotype [6-*n*-propylthiouracil (PROP) bitterness, fungiform papillae (FP) density] on sweet and creamy sensations from sugar/fat mixtures. Seventy-nine subjects (43 males) reported the sweetness and creaminess of water or milk (skim, whole, heavy cream) varying in sucrose (0–20% w/v) on the general Labeled Magnitude Scale. Sweetness grew with sucrose concentration and when shifting from water to milk mixtures—the growth was greatest for those tasting PROP as most bitter. At higher sucrose levels, increasing fat blunted the PROP–sweet relationship, whereas at lower levels, the relationship was effectively eliminated. Perceived sweetness of the mixture exceeded that predicted from the sum of components at low sucrose concentrations (especially for those tasting PROP most bitter) but fell below predicted at high concentrations, irrespective of fat level. Creaminess increased greatly with fat level and somewhat with sucrose. Those tasting PROP most bitter perceived greater creaminess in the heavy cream across all sucrose levels. Perceived creaminess was somewhat lower than predicted, irrespective of PROP bitterness. The FP density generally showed similar effects as PROP on sweetness and creaminess, (but to a lesser degree) and revealed potential taste–somatosensory interactions in weakly sweet stimuli. These data support that taste phenotype affects the nature of enhancement or suppression of sweetness and creaminess in liquid fat/sugar mixtures. Taste phenotype effects on sweetness and creaminess likely involve differential taste, retronasal olfactory, and somatosensory contributions to these perceptual experiences.

Key words: data visualization, genetics, individual differences, mixture interaction, psychophysics, taste

Introduction

Due to increasing prevalence of obesity (BRFSS 2003), there is growing interest in the consumption of discretionary sources of energy (USDA 2005), including simple carbohydrates and fats. The oral sensations arising from these components have implications for how much the food is liked as well as consumed, with implications for the energy density of the diet. Although perceptual experiences from these mixtures (e.g., sweetness, creaminess) have been examined previously (Drewnowski et al. 1985), the present study applied modern psychophysical methods and novel statistical approaches to evaluate how taste phenotype influences sweetness and creaminess alone and within liquid sucrose–fat mixtures.

Interactions are frequently observed in simple taste–taste mixtures (Keast and Breslin 2003) and complex stimuli that stimulate taste, touch, smell, and irritation (Delwiche 2004). In simple model systems, these interactions typically result in suppression (Kamen et al. 1961; McBurney and Bartoshuk 1973) but may result in synergy (Ayya and Lawless 1992). Moreover, this suppression may occur in the periphery (Breslin and Beauchamp 1995) or centrally (Lawless 1979). Given the disparate modalities stimulated by foods and beverages, complex mixtures have greater potential to show a range of interactions that may increase or decrease specific sensations. For example, sweetness can be enhanced by odors (Sakai et al. 2001) while odor intensity may track sucrose concentration (Davidson et al. 1999). Conversely, as viscosity and tactile input increase, taste sensations are typically suppressed (Moskowitz and Arabie 1970; Calvino et al. 1993; Hollowood et al. 2002). Regarding sucrose/fat mixtures, increasing sucrose concentration suppresses the perception of fat in solids (Drewnowski and Schwartz 1990; Guinard and Mazzucchelli 1999), whereas in liquids, increasing fat level reportedly suppresses sweetness (Drewnowski et al. 1987, 1989).

Mixtures of sucrose with milk/cream provide a well-characterized system to study sweet–creamy interactions (Drewnowski et al. 1985, 1998; Warwick and Schiffman 1990; Salbe et al. 2004). Milk is a physically and chemically complex mixture of lactose, fat, protein, and salts, all dissolved or suspended in water (McGee 1984; Jensen et al. 1991), as well as numerous volatile compounds. Among the odor-active volatiles, descriptors of green, fruity, and sweet are common (Friedrich and Acree 1998). Because smell and taste are integrated, and because perceptions arise from objects rather than systems (Gibson 1966), sweet and creamy percepts may be produced from the composite of multimodal inputs, not just tastants or fat per se. Odors can add to the perception of sweetness through associative learning (Stevenson et al. 1998), and these associations become more robust with early exposure (Lawless and Engen 1977). As an example, maltol is an odor-active compound found in human milk (Bingham et al. 2003) and human milk is sweet, potentially associating the two. Thus, that maltol is not itself sweet, but it enhances sweet ratings of sucrose in untrained adults (Bingham et al. 1990) is not surprising.

Various models for studying interactions are found in taste (Lawless 1998; Laffort 2006), pharmacology (Hughes et al. 1990; Minto et al. 2000), and toxicology (Feron and Groten 2002). Here, a straightforward algebraic sum of sensations model was used to test for perceptual interactions (Schifferstein and Frijters 1993) in milk samples that varied in the amount of fat and sucrose. Hollowood et al. (2002) recently used low-order polynomial models to explain intensity as function of changes in ingredient level. A similar, albeit linear, approach is used here because of the a priori assumption that intensity increases monotonically.

Sweetness of sugar solutions (Gent and Bartoshuk 1983; Lucchina et al. 1998), sweet foods (Duffy et al. 2003, 2006), alcohol (Lanier et al. 2005), and vegetables (Dinehart et al. 2006) as well as creamy/tactile (Tepper and Nurse 1997; Duffy, Lucchina, Bartoshuk 2004) and complex sensations from fat (Kirkmeyer and Tepper 2003) all vary systematically with 6-*n*-propylthiouracil (PROP) bitterness. Fungiform papillae (FP) density associates with heightened taste and nontaste oral sensations (Prutkin et al. 2000; Prescott, Bartoshuk, Prutkin 2004) and tactile acuity (Essick et al. 2003) because it is a proxy for chorda tympani and trigeminal innervation density. As creaminess is thought to result almost exclusively from fat-dependent changes in viscosity (Mela 1988), FP density would be expected to explain creaminess, as shown previously (Duffy 2004; Duffy, Lucchina, Bartoshuk 2004). Here, sweet–creamy interactions were examined in the context of these phenotypic measures of variation in oral sensation.

Materials and methods

Participants sampled and rated model taste solutions and milk-based mixtures in a laboratory setting. Participants were characterized phenotypically for PROP bitterness and FP density on the tongue tip via video microscopy.

Subjects

Subjects were recruited into the Taste Genetics and Dietary Behavior Study, a laboratory study designed to assess relationships between variation in oral sensation, sensations from foods and beverages, and dietary behaviors and health, as described previously (Duffy et al. 2003; Duffy, Lucchina, Bartoshuk 2004; Duffy, Peterson, Bartoshuk 2004). Briefly, healthy men and women were recruited to obtain variation in phenotypic markers of oral sensation while controlling for factors that would confound relationships between taste genetics and dietary habits (e.g., severe history of taste-related pathologies, smoking, high level of dietary restraint). Participants visited the laboratory for 3 testing sessions, typically 1 week apart. All procedures were approved by the University of Connecticut Institutional Review Board, and written consent was obtained from subjects, who were paid for their time.

Stimuli

During the second session, participants sampled in duplicate a 4×4 factorial array of sweet–fat mixtures that varied in the level of added sucrose (0%, 5%, 10%, 20% w/v) and fat: water, skim milk (>0.5%), whole milk (3.5%), and heavy cream (36%). Samples were taken from the refrigerator and served cold (5 °C). Participants rinsed between each sample with room temperature deionized (>15 MΩ) water. On the last day of testing, participants also tasted a concentration series (described below) of PROP (Sigma, St Louis, MO). Throughout each session, participants rated the intensity of a series of 1 kHz tones ranging from 50 to 98dB to serve as a cross modal reference.

Data collection

Measuring intensity

Intensity data were collected using the general labeled magnitude scale (gLMS) (Bartoshuk et al. 2003; Bartoshuk, Duffy, Green, et al. 2004), a semantically labeled line scale that generalizes the labeled magnitude scale (LMS) (Green et al. 1993, 1996) by changing the top anchor from "strongest imaginable oral sensation" to "strongest imaginable sensation of any kind." For intensity, gLMS ranges from "no sensation" at the bottom (0) to 100 at the top and has adjectives spaced as follows: "barely detectable" (1.4), "weak" (6), "moderate" (17), "strong" (35), and "very strong" (53). Changing the top anchor is required because all individuals do not use adjective labels to denote the same perceived intensities (Bartoshuk et al. 2003; Dionne et al. 2005). For example, the veridical intensity of burn described by 2 individuals as very strong may differ greatly with experience (Lawless et al. 1985; Stevenson and Prescott 1994) and taste genetics (Karrer and Bartoshuk 1991). Regarding sweet, Lucchina et al. (1998) found that scaling sweetness with a 9-point scale completely obscures the PROP–sweetness relationship observed with the gLMS.

Phenotypic and anthropometric characterization

To avoid contrast and range effects (Helson 1964; Lawless et al. 2000), the PROP solutions were presented at the end of the final session; this is critical because any context biases would vary nonrandomly with PROP response. As described previously (Bartoshuk et al. 1994; Duffy et al. 2003; Dinehart et al. 2006), the protocol involves alternately rating the intensity of multiple randomized blocks of 1 kHz tones (50–98 dB in 12-dB steps), NaCl solutions (10, 32, 100, 320, 1000 mM), and PROP solutions (0.032, 0.1, 0.32, 1, 3.2 mM). The 2 measures of 3.2 mM PROP bitterness were averaged and treated as a continuous variable unless otherwise noted. As a categorical variable, rated bitterness of 3.2 mM PROP allowed classification of subjects as nontasters (NT ≤22), medium tasters (MT >22 but <51), and supertasters (ST ≥51). To measure FP density, the tongue was stained with blue food coloring and imaged using video microscopy (Miller and Reedy 1990) as described previously (Bartoshuk et al. 1994; Duffy, Peterson, Bartoshuk 2004). The videotape was subsequently reviewed, and the number of FP within a 6-mm circular template was counted on the right and left sides of the tip and averaged to obtain a mean density for each individual. Height and weight were measured in the laboratory and used to calculate body mass index (BMI, kg/m^2).

Statistical analysis

The SAS Release 9.1.3 (SAS, Cary, NC) was used to conduct the statistical analyses. Chi-square was used to assess the relationships between the dichotomous measures of interest. Bivariate relationships between sensations (sweet/creamy) and phenotypic measures (bitterness of PROP/FP density) were quantified using Pierson's r and arranged to generate conditioning plots. Multiple linear regression was used to predict sweetness and creaminess of the mixtures using concentration and the phenotypic marker of interest as predictor variables. Because the intensity of a nonoral stimulus should not correlate systematically with oral sensations (Bartoshuk, Duffy, Green, et al. 2004), the average intensity of the 86 dB tone across the sessions was included in the regression models (Duffy et al. 2006) to partition out variability from idiosyncratic scale usage. Interactions between concentration and phenotype were assessed by including a product term in the regression equation, retaining nonsignificant main effects (Allison 1977). These interactions were visualized by plotting the best-fit surface obtained by the regression equation, substituting the across subject mean rating for the 86-dB tone into the equation and constraining the surface boundaries to the range of values observed in the data set.

Mixture suppression is commonly defined as a perceived intensity less than that of the ratings of the component parts with the reverse being true for enhancement. Thus, we expressed the difference between the perceived intensity of each mixtures and the sum of the intensities of the component parts as percent error—[(perceived − sum)/perceived] × 100—and tested for differences across sucrose and fat level using mixed model analysis of variance (ANOVA) via *PROC MIXED*. Subjects fat, and sucrose were handled as random effects, and within subjects factors (the repeated measures at each fat at sucrose level) were allowed to covary (Moser 2004). Overall F values were not generated because PROC MIXED uses maximum likelihood estimation; denominator degrees of freedom were estimated using the Satterthwaite approximation. Higher order interactions were interpreted first, followed by less complicated interactions if the higher order interaction was not significant (Dallal 2001).

Results

Participant characteristics

Based on the results in the first session, 8 individuals were excluded—4 had a history of head trauma and/or severe ear infections, 2 were unable to use the scale as instructed, 1 had a history of taste loss and dysgeusia, and 1 had dentures covering the soft palate—leaving 79 subjects [43 males; mean age = 25.9 years, standard deviation (SD) = 4.3] for all analyses. One subject was underweight (BMI < 18.5), 57 were of normal weight (18.5 ≤ BMI < 25), 18 were overweight (25 ≤ BMI < 30), and 3 were obese (BMI ≥ 30). Men were more likely [χ^2 (1) = 8.1, $P < 0.01$] to have a BMI over 25 (e.g., overweight or obese) compared with women. The proportion of individuals with a BMI over 25 did not differ by PROP group [χ^2 (2) = 0.40, $P = 0.81$] or by FP density split at 25 [χ^2 (1) = 0.01, $P = 0.91$].

Variation in PROP bitterness and FP density was observed across the sample, and these measures were positively correlated ($r = 0.36$, $P = 0.001$). There were 17 nontasters, 35 medium tasters, and 27 supertasters; no significant sex differences were found in the mean ($t = 0.57$, $P = 0.57$) or the distribution [χ^2 (2) = 2.05, $P = 0.36$] of PROP bitterness ratings. The number of FP per 6 mm area ranged from 11.75 to 40.25. Although means did not differ between men and women ($t = 1.16$, $P = 0.25$), the men were more likely [χ^2 (1) = 5.17, $P = 0.023$] to have a FP density less than 25 per 6 mm^2 (30 of 43 vs. 16 of 36). Because of this sex difference, sex was controlled in regression models with FP density.

Sweetness

Individuals varied in the degree of sweetness from each stimulus, and mean sweetness increased as sucrose concentration increased. Sweetness also increased when switching from water to skim milk in the 5% and 10% sucrose solutions (rightward shift in Figure 1) but did not continue to increase with fat level. For example, compared with the 5% sucrose–water and the 10% sucrose–water solutions, the milk-containing mixtures were ~2.5 times and ~0.75 times sweeter, respectively. To test for a simple interaction between fat and sucrose, sweetness in the milk samples was predicted via regression using sucrose concentration, fat level, 86-dB tone

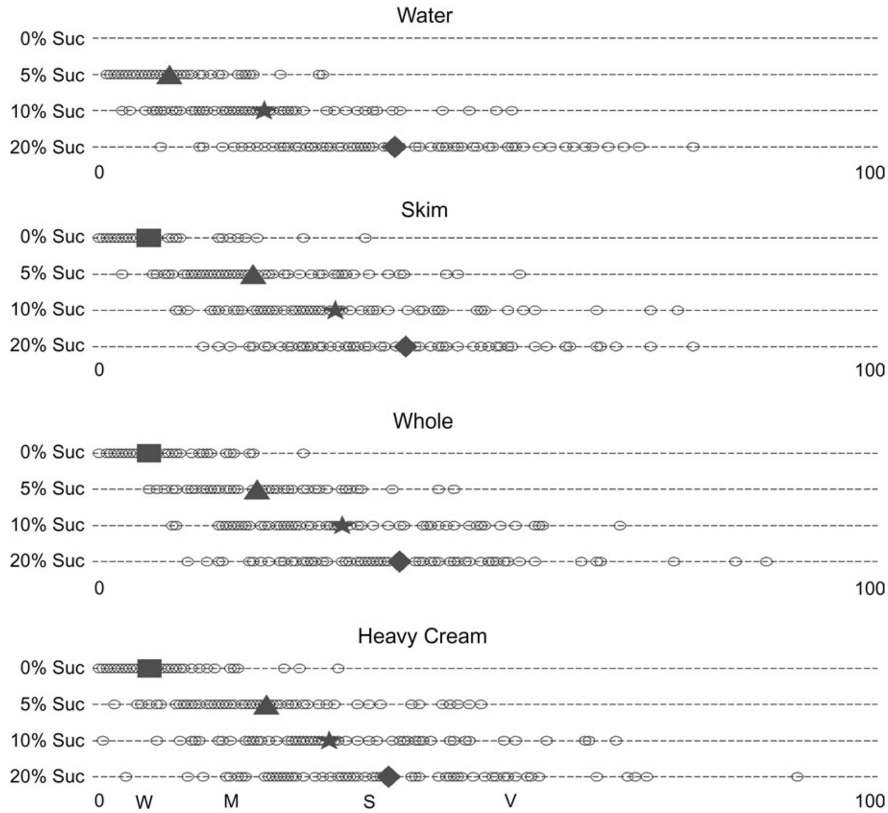

Figure 1 Sweetness. Open circles are individual ratings whereas solid geometric shapes represent means. Possible ratings range from 0 to 100, with adjective labels for weak (W), moderate (M), strong (S), and very strong (V). Sweetness increased when moving from water to milk in 5% and 10% sucrose.

intensity, and a multiplicative sucrose by fat interaction term. The overall model was significant ($P < 0.0001$), explaining 57.9% of the variance in sweetness. The sucrose by fat interaction term was not significant ($P = 0.22$); main effects were observed for sucrose ($P < 0.0001$) and the 86-dB tone ($P < 0.0001$) but not fat ($P = 0.76$).

Likewise, we tested for an interaction between sucrose and PROP via multiple regression. The overall model was significant ($P < 0.0001$), explaining 61.8% of the variation in sweetness. The PROP by sucrose interaction was significant ($P < 0.0001$), and main effects were observed for sucrose ($P < 0.0001$) and the 86-db tone ($P < 0.0001$) but not PROP ($P = 0.95$). PROP bitterness did not influence sweetness in unsweetened milk. In contrast, the 20% sucrose sample was much sweeter for those tasting PROP as more bitter (Figure 2). In comparing 2 hypothetical individuals who tasted PROP bitterness at 10 and 80, the most concentrated sample would be 3.3 times sweeter than the least for the $PROP_{10}$ individual compared with 5.3 times sweeter for the $PROP_{80}$ individual. In terms of isointensity, to reach a rating of 32 (just below strong), the $PROP_{10}$ individual would need a 20% solution compared with only 11% for the $PROP_{80}$ individual.

The next step of the analyses was to determine if fat level modified the relationship between PROP bitterness and sweetness. A conditioning plot was used to visually detect an interaction in the change in slope of *X* (PROP) versus *Y* (sweetness) across additional variables (concentrations of fat and sucrose). Figure 3 shows such a plot, revealing the existence of complex interactions in the sweetened milks. As fat concentration increased, the relationship between PROP and sweetness was either eliminated or blunted. In the 5% sucrose samples, moving from skim to whole milk eliminated the relationship, whereas in the 10% sucrose samples, more fat was needed to attenuate the effect. In milk samples with 20% sucrose, the same pattern was seen.

An interaction between FP density and sucrose was also tested using regression. After sex was dropped from the model as a nonsignificant contributor ($P = 0.89$), the final model was significant ($P < 0.0001$), explaining 50.9% of the variance in the sweetness of the milk samples (not shown). The sucrose by FP interaction was significant ($P < 0.0001$), and main effects were observed for sucrose ($P = 0.0004$), the 86-dB tone ($P < 0.0001$), and FP density ($P = 0.0001$). For a low FP individual (mean − 1 SD), the 20% sucrose sample was 3.0 times sweeter than the unsweetened sample, compared with 5.4 times for a high FP individual (mean + 1 SD).

As above, the effect of sucrose and fat on the bivariate relationship between FP density and sweetness was visualized in a conditioning plot (Figure 4). In the milk samples with no

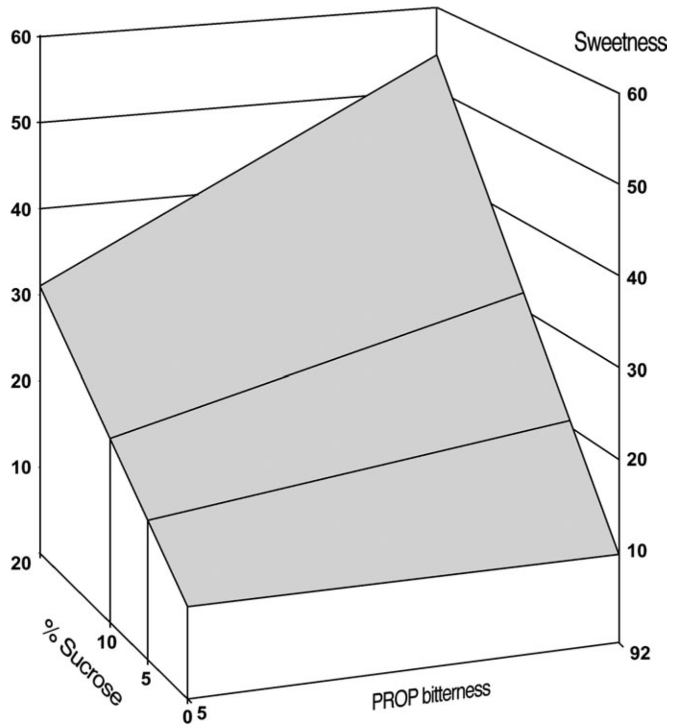

Figure 2 Best-fit surface for sweetness obtained via linear regression. In unsweetened milk, PROP did not predict sweetness. As sucrose level increased (lines at 5%, 10%, and 20%), the relationship between PROP bitterness and sweetness became progressively stronger.

added sucrose (the top row), sweetness was lower in individuals with greater numbers of FP. However, as sucrose concentration increased to 20%, this effect first disappeared and then reversed as correlations trended in the opposite direction. Fat level did not appear to have an effect.

Creaminess

Mean creaminess increased with increases in fat and sucrose concentration, showing variability across the subjects (Figure 5). We tested for a fat–sucrose interaction via multiple regression. The overall model was significant ($P < 0.0001$), explaining 65.6% of the variance in creaminess (not shown). The sucrose by fat interaction term was not significant, yet the main effects of fat ($P < 0.0001$) and sucrose ($P = 0.0006$) were significant. This implies that creamy sensations increased with sucrose level but the effect was additive—visualized as an ANOVA interaction, the plot lines for the milks would be parallel (i.e., vertically separated with similar slopes). As a percentage (mixture vs. unsweetened milk), the relative increases in creaminess from added sugar were more pronounced in skim and whole milk. Creaminess increased about 80% in skim and about 50% in whole milk with minimal increases (<20%) for heavy cream.

The interaction between PROP and fat level in the milk-based samples was tested via regression. The model, shown in Figure 6, was significant ($P < 0.0001$) and explained 69.0% of the variance in creaminess. The PROP by fat interaction term was significant ($P < 0.0001$); main effects were observed for fat level ($P < 0.0001$) and the 86-dB tone ($P < 0.0001$) but not PROP ($P = 0.78$). The heavy cream was 2.3 times creamier than the skim milk for a $PROP_{10}$ individual compared with 3.7 times for a $PROP_{80}$ individual.

In a conditioning plot (not shown), a strong relationship between PROP bitterness and creamy sensations was found but only in the samples with the highest level of fat (r's ranged from 0.40 to 0.47). Increasing amounts of sucrose did not alter the relationship between PROP bitterness and perceived creaminess.

In multiple regression, testing for a FP density by fat interaction generated a significant model ($P < 0.0001$) that explained 61.0% of the variance in creaminess (not shown). The FP by fat interaction term was significant ($P < 0.01$); main effects were observed for fat ($P < 0.0001$) and the 86-dB tone ($P < 0.0001$) but not FP density ($P = 0.11$). For a low FP individual (mean − 1 SD), the heavy cream would be 2.6 times creamier than skim milk, compared with 3 times for a high FP individual (mean + 1 SD). Effects of fat and sucrose levels could not be assessed in a conditioning plot (not shown) as the bivariate relationship between FP and creaminess was less pronounced than that for PROP, only trending toward significance for the heavy cream without added sugar ($r = 0.20$, $P = 0.07$).

Perceived intensity versus predicted intensity

In repeated measures mixed model ANOVA, the perceived intensity of the mixture differed from the predicted intensity based on the sum of the component parts, for sweetness but not creaminess. For sweetness, the 3-way (sucrose × fat × PROP group) interaction was not significant [$F(8,303) = 1.22$, $P = 0.28$]. The 2-way PROP × sucrose [$F(4,152) = 4.12$, $P = 0.003$] was significant (left panel of Figure 7). In medium and supertasters, the perceived intensity exceeded the predicted sweetness at low sucrose concentration and was less than the predicted sweetness at high concentration, and this pattern was essentially linear. In nontasters, the same under- and overprediction was seen at the high and low concentrations, but the pattern was not linear—at 10% sucrose, the perceived sweetness was well below the predicted sweetness.

The 2-way fat × sucrose [$F(4,303) = 3.3$, $P = 0.012$] interaction was also significant (right panel of Figure 7). In skim and whole milk, the perceived sweetness exceeded the predicted sweetness at low sucrose concentration and was less than predicted at high concentrations, and the pattern was essentially linear. In heavy cream, the same under- and overprediction was seen at the extreme sucrose concentrations, but again the pattern was not linear—at 10% sucrose, the perceived sweetness was well below the predicted sweetness.

For creaminess, no interactions or main effects were significant. Examining the accuracy of the predicted creaminess

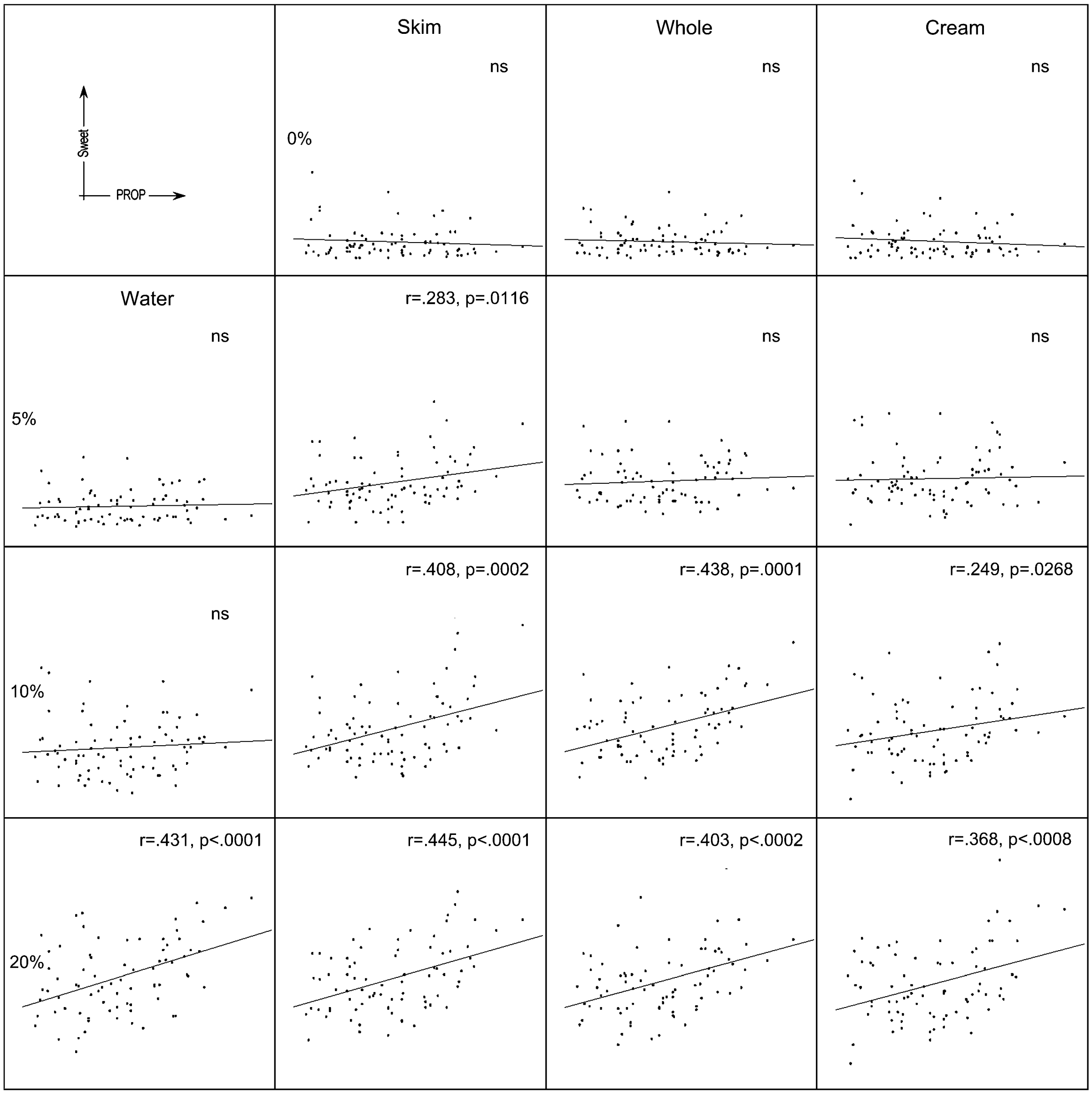

Figure 3 Conditioning plot showing the effect of fat and sucrose levels on the bivariate relationship between sweetness and PROP bitterness. Sweetness is plotted against PROP bitterness in each box. Looking at patterns down the columns and across the rows reveals how fat and sucrose influence the PROP–sweet relationship.

across the individual fat and sucrose levels revealed that the perceived creaminess was consistently less by between 5% and 20% (not shown). That is, the creaminess of the mixture was not as great as would be expected when considering the separate contributions of fat and sucrose levels to creaminess. However, the mixture creaminess never dropped below that of unsweetened milk.

Discussion

The present study found that sweet and creamy sensations from sweetened milk vary with phenotypical measures of oral sensation. Regarding sweet, shifting from water to milk enhanced sweetness, an increase that was greater for those who tasted PROP as more bitter. Although regression analysis suggested fat did not alter the sweetness of the mixtures, a conditioning plot revealed that fat influenced the positive association between PROP and sweetness. As fat level increased, the PROP–sweet relationship was blunted or eliminated, depending on sucrose level. For creaminess, the concentration of fat and sucrose both contributed, however, the effect of one did not depend on the other. PROP was a strong predictor of creaminess in heavy cream, and this was uninfluenced by sucrose level. In general, FP density was less able than PROP to explain variance in sweetness

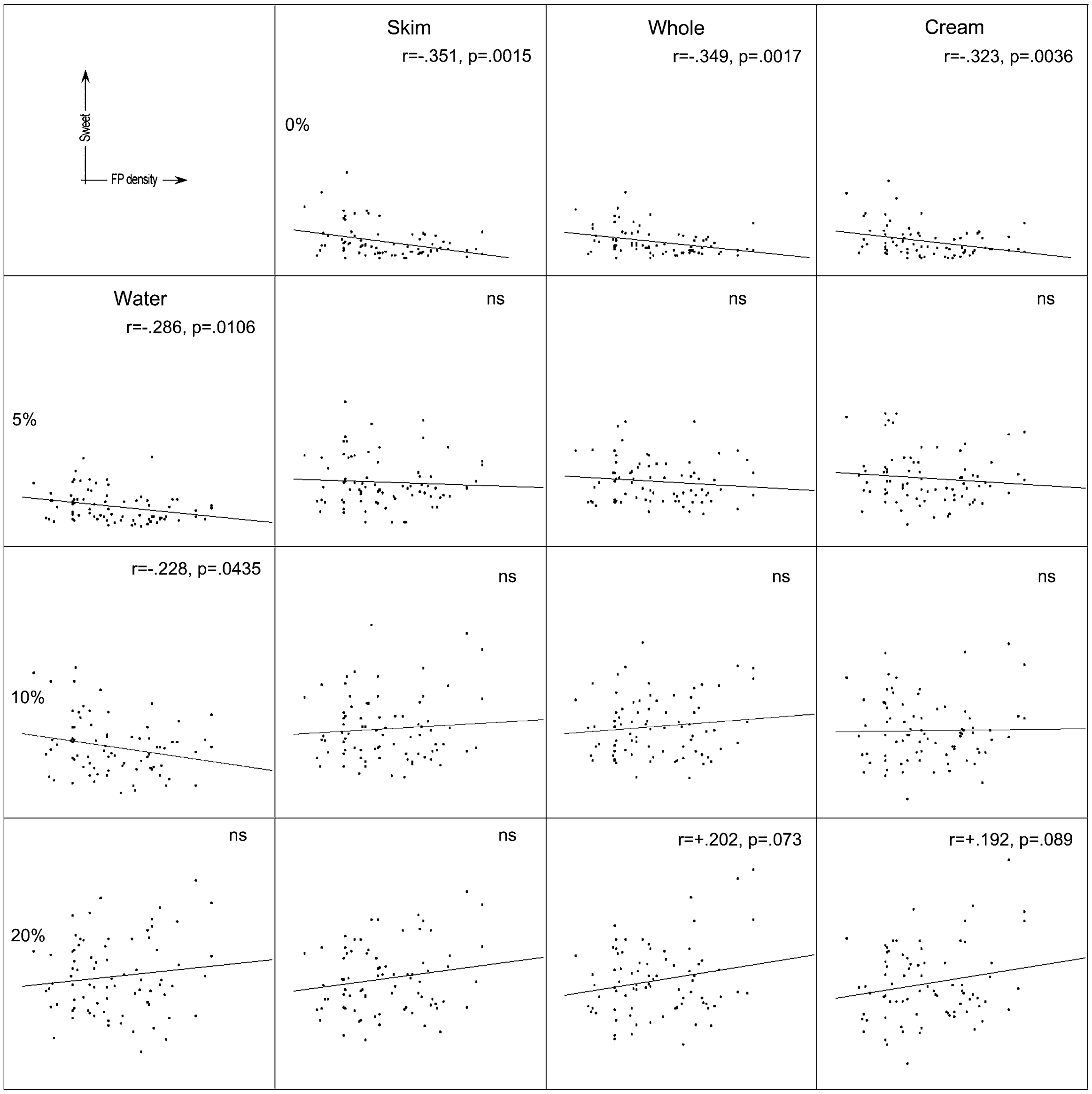

Figure 4 Conditioning plot showing the effect of fat and sucrose levels on the bivariate relationship between sweetness and fungiform papillae. Sweetness is plotted against FP density in each box.

and creaminess of milk samples. When predicting sensations elicited by mixtures from the sum of sensations of their component parts, different patterns were observed for sweet and creamy. For sweetness, the perceived intensity generally exceeded the predicted intensity at low sucrose concentration and was less than the predicted intensity at high concentration. Deviations from this overall pattern were observed across fat level as well as PROP group. For creaminess, the perceived intensity was somewhat lower than the predicted intensity, across all PROP groups and sucrose concentrations.

That ratings of sweetness were higher in those who tasted PROP as more bitter is generally consistent with prior reports with aqueous solutions (Drewnowski et al. 1997; Lucchina et al. 1998) and real foods (Duffy et al. 2003, 2006). Earlier studies that failed to find an association were often hampered by methodological issues—see examples for sweetness in (Bartoshuk 2000). In a forced choice paradigm, Prescott, Soo, et al. (2004) found that, compared with medium and supertasters, nontasters had higher Weber ratios in orange juice and thus appear less sensitive to manipulations in sucrose level. The present work extends past findings in several ways. Rather than use a typical repeated measures ANOVA model, PROP was handled continuously in a multiple regression equation that included a multiplicative interaction term. This allowed testing the PROP–sucrose interaction while avoiding the loss of power associated with categorizing individuals into groups. More importantly, it allowed calculation of isosweet concentrations for individuals

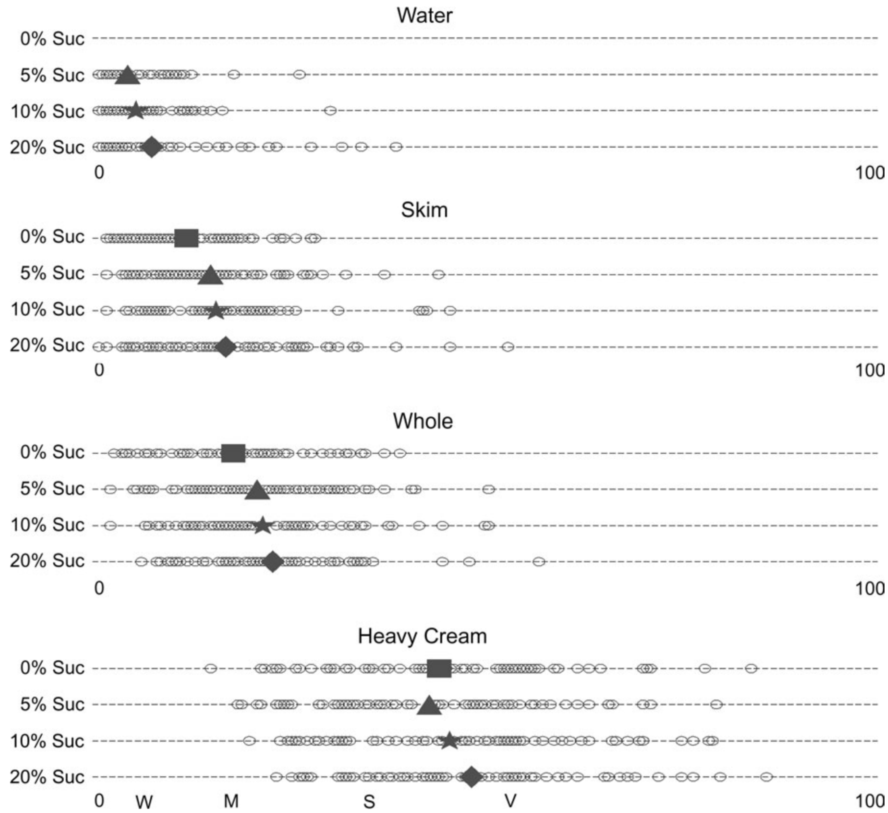

Figure 5 Creaminess. Open circles are individual ratings whereas solid geometric shapes represent means.

who differed in PROP bitterness. An individual with low PROP bitterness would require double the sucrose concentration to achieve strong as compared with an individual with high PROP bitterness. Additionally, a cross-modal rating (e.g., sound) was included in the regression to control for differential scale usage, which supports that the differences observed are not merely a scaling artifact.

At the same sucrose concentration, the milk samples were rated as sweeter than water-based samples. This finding was initially surprising because increasing viscosity (Moskowitz and Arabie 1970; Pangborn et al. 1978) and fat level (Drewnowski et al. 1989) reportedly decrease sweet intensity. Enhancement seen here is probably not due to endogenous carbohydrate; milk only contains 4.6% lactose, and lactose is only a third as sweet as sucrose. Instead, this may reflect a perceptual enhancement of sweet taste by a nontaste modality that is stimulated by the milk samples. Valentin et al. (2006) present a model for taste–odor interactions that includes perceptual enhancement [via associative learning (Prescott, Johnstone, Francis 2004)] and response bias [via dumping (Clark and Lawless 1994)]. Because our subjects were able to rate multiple qualities for each stimulus, we believe present data are best explained via enhancement. Enhancement occurs for congruent, odor–taste pairs—in both scaling paradigms that prevent dumping (Valentin et al. 2006) and in criterion free paradigms (Dalton et al.

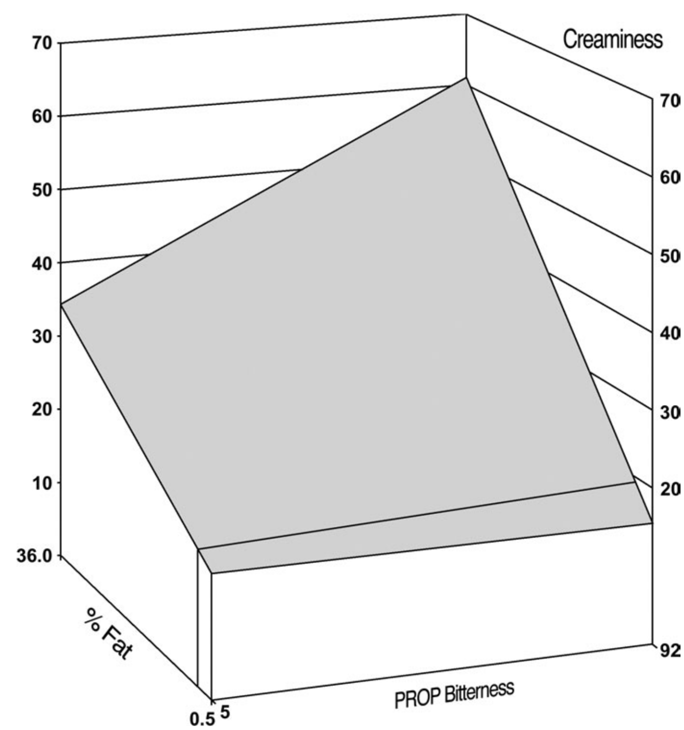

Figure 6 Best-fit surface for creaminess obtained via linear regression. In skim and whole milk (lines at 0.5% and 3.5% fat), PROP had minimal influence. In heavy cream (36% fat), a strong PROP effect was seen.

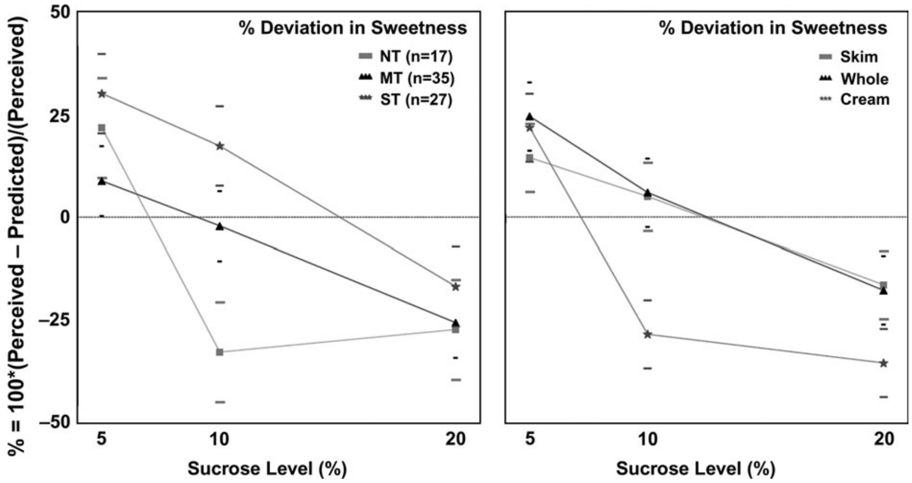

Figure 7 ANOVA interaction plots showing the percent deviation between perceived sweetness and sweetness predicted from the component parts. The left panel shows the interaction with PROP group; the interaction across fat level is shown on the right. Above the dashed line, perceived is greater than predicted, with the reverse being true below.

2000; White and Prescott 2001). Regarding milk, adding a dairy flavor enhances sweetness (Frøst et al. 2001).

That retronasal olfactory components of milk added to sweetness are also supported by the deviation of perceived sweetness from predicted sweetness in the mixtures. Perceived exceeded predicted at the lowest sucrose concentration regardless of fat level when the sweetness is not predominated by a high level of sucrose. The magnitude of these deviations was also influenced by PROP group and fat level. At the 10% sucrose level, the supertasters experience sweet enhancement on the order of 20%, whereas the nontasters experience suppression of almost 30%. This differential enhancement could be related to intensity of retronasal sensations in supertasters (Bartoshuk, Duffy, Chapo, et al. 2004; Pickering et al. 2006). The retronasal effects on sweetness may not be due to PROP tasting per se. Recently, Green and George (2004) reported sweetness differences between "thermal tasters" who also report heightened bitterness from PROP and thermal nontasters who report low bitterness from PROP. Thermal tasters gave higher sweet ratings to sucrose during retronasal presentation of the odorant vanillin. Consistent with our findings, the enhancement of sweetness in these "tasters" during concurrent odor presentation was greater at lower sucrose concentration. Given Gibson's (1966) distinction between sensory modalities and perceptual systems, learning processes that allow odors to enhance sweetness likely apply to other modalities involved in flavor (for reviews, see Delwiche 2004; Small and Prescott 2005). Primate recording and human imaging both suggest the orbitalfrontal cortex is a likely site for this associative learning to occur (Rolls et al. 1996; Small et al. 2004).

Complex interactions between taste, somatosensory, and olfactory sensations may explain the apparent suppression of sweetness. By comparing perceived versus predicted sweetness, heavy cream suppressed the sweetness of 10% and 20% added sucrose, presumably because of the viscosity effects on sweetness (Moskowitz and Arabie 1970; Pangborn et al. 1978). Similarly, sweetness in the unsweetened milks was lower in individuals with greater numbers of FP. Increased innervation density and resultant increased tactile input may explain this suppressed sweetness. As more sucrose is added, the increased sweet input may first offset and eventually overtake the suppressive tactile effect. Such a tactile effect may explain the patterns seen in the PROP–sweetness conditioning plot (Figure 3). Each successive level of sucrose required more fat to attenuate the PROP–sweet relationship, which is consistent with competing tactile and taste inputs. Similar suppression of PROP–sweet effects in mixtures with trigeminal stimuli has been reported previously (Prescott, Soo, et al. 2004). The reason why low FP individuals taste greater sweetness for 5% and 10% sucrose in water is not fully understood. Competing taste/tactile effects, even in the absence of fat, may potentially explain this observation. Present findings continue to support that FP and PROP capture separate but overlapping amounts of variation in human orosensory experiences.

For creaminess, the predicted intensity of the sugar–fat mixtures was consistently greater than the perceived creaminess for all subjects, as might be expected with a signal saturation effect. If the overall contribution of sucrose to the total viscosity of the milk solutions was too small (i.e., is below the just noticeable difference), the predicted creaminess should exceed the perceived creaminess in the mixtures, as was observed. The observation that the relative increase in creaminess was much greater in thinner mixtures is also supportive of the relatively small contribution of sucrose to the overall viscosity.

That PROP bitterness is predictive of creamy sensations is also consistent with earlier work (Duffy et al. 1996; Tepper and Nurse 1998) and is related to increased tactile input via the trigeminal nerve and possibly retronasal input. Regarding tactile input, Prutkin found that the 2-point gap threshold for supertasters was half that of nontasters and that the gap threshold was correlated with FP density (reported in Prescott, Bartoshuk, Prutkin 2004), whereas Essick et al. (2003) reported spatial acuity on the tongue was highly correlated with PROP bitterness and FP density. Although FP density was predictive of creaminess in heavy cream, it was less predictive than was PROP bitterness. FP may be an especially good marker of oral somatosensory sensations when taste input is altered. Somatosensory sensations are enhanced when taste is depressed, either experimentally (via anesthesia) or clinically (via pathology), especially in individuals with high density of FP (Bartoshuk et al. 2005). In the present study, individuals with significant reported history of taste damage were excluded, which may explain the inability of FP density to explain creaminess at lower fat levels.

Additionally, the ability of PROP to better explain variation in creaminess compared with FP implies that the creaminess is not merely a tactile event. Previously, Mela (1988) suggested that creamy sensations result almost exclusively from fat-dependent differences in viscosity. However, when Drewnowski and Greenwood (1983) instructed subjects to give ratings for both ''fat'' and ''creamy,'' they found that the power functions have different slopes and intercepts, suggesting there are subtle distinctions in these concepts. Several observations support that creamy has an odor component: ratings drop when olfactory input is excluded using nose clips (Weenen et al. 2005), creaminess includes an aroma component (Richardson-Harman et al. 2000), and the addition of dairy volatiles moves a lower fat sample toward the high fat sample in a multidimensional space (Tepper and Kuang 1996). If volatiles contribute to the creamy percept, an increased response via heightened retronasal olfaction (Bartoshuk, Duffy, Chapo, et al. 2004; Pickering et al. 2006) would be expected. Indeed, we report here that in heavy cream, PROP was strongly correlated with creamy ratings. Kirkmeyer and Tepper (2003) found that PROP supertasters used a more complex set of descriptors and relied more heavily on flavor and texture cues than did nontasters.

Limitations of the study should be noted. Individuals with potential taste damage were excluded, so present findings may not generalize to other groups, including the elderly. Moreover, these findings may not generalize to solid foods as the oral cues of fat content differ between liquid and solid foods (Drewnowski et al. 1989). Other sources of genetic variation may also influence perception of fats (e.g., Abumrad 2005). Additionally, a simple sum of sensations model was used to test for suppression and enhancement. Future work may benefit from more sophisticated models, like isobolographic analysis (Gessner 1995), although care needs to be taken to account for variation in oral sensations.

Summary

Prior work (Prescott et al. 2001; Lanier et al. 2005; Dinehart et al. 2006), along with the data presented here, emphasize that researchers studying mixture interactions—whether they be in binary mixtures, model systems, or complex foods—need to account for effects of genetic variation in taste. Although mixtures of fat and sweet may exhibit hedonic synergy, the only interaction seen here between sucrose and fat was the apparent suppression of sweetness at high levels of fat, which occurred irrespective of PROP phenotype. Increasing fat also blunted or eliminated the expected PROP-sweet relationship. Separate from fat effects on sweetness, we found evidence that the volatile components of milk may enhance sweetness, and this enhancement was greater in those for whom PROP was most bitter.

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