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Measures of Individual Differences in Taste and Creaminess Perception

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Abstract

Previous reports that the sensitivity to the bitter tasting substance 6-*n*-propylthiouracil (PROP) is related to the sensitivity to other tastes, to chemical irritants, and to fats and oils have led to adoption of PROP as a measure of general oral sensitivity and as a predictor of dietary habits that could impact health. The results, however, have not been consistent. It was recently discovered that the ability to perceive "thermal taste" (i.e., sweetness from thermal stimulation alone) was associated with higher responsiveness to 4 prototypical taste stimuli but not to PROP. This finding implied that individual differences in taste perception are determined in large part by factors other than those related to genetic expression of the PROP receptor. The present study followed up this observation by comparing individual differences in perception of 4 prototypical taste stimuli (sucrose, NaCl, citric acid, and quinine) and PROP under conditions that also enabled assessment of the reliability of individual intensity ratings of taste. Creaminess ratings of 3 milk products that had different fat contents were also collected to investigate further the relationship between taste and oral somatosensory perception. The results showed that intensity ratings across 2 trials were significantly correlated for all 5 taste stimuli and that averaging across replicates led to significant correlations among the 4 prototypical stimuli. In contrast, the bitterness of PROP was correlated only with the bitterness of quinine. None of the taste stimuli, including PROP, was significantly correlated with ratings of creaminess. These results imply 1) that with the exception of PROP, as few as 2 intensity ratings of common taste stimuli can reveal individual differences in overall taste perception and 2) that any relationship between taste and oral sensation is too weak to be detected under the same conditions. Accordingly, the results support other evidence that the genetic factors which determine the ability to perceive PROP do not play a major role in overall taste and oral somatosensory perception.

Key words: central neural process, individual differences, PROP, taste sensitivity, test–retest reliability

Introduction

Taste sensitivity varies greatly among individuals. Because these individual differences could potentially affect food choice and hence influence health, there has been broad interest in understanding the cause of the differences and in finding ways to measure and predict them. Over the past several decades, research on this topic has focused almost exclusively on the sensitivity to the bitter tasting substances phenylthiocarbamide (PTC) and 6-*n*-propylthiouracil (PROP). Blakeslee and Fox (1932) first wrote of the ''different taste world'' produced by genetic variation in sensitivity to PTC. Since then, the ability to taste PTC or its chemical relative PROP has been associated with higher sensitivity to selected bitter substances (Hall et al. 1975; Bartoshuk 1979; Gent and Bartoshuk 1983; Bartoshuk et al. 1986, 1988, 1998; Leach and Noble 1986; Mela 1989; Bartoshuk et al. 1992; Bartoshuk 1993; Drewnowski et al. 1997b; Neely and Borg 1999; Ly and Drewnowski 2001), sweet substances (Bartoshuk 1979; Gent and Bartoshuk 1983; Miller and Reedy 1990; Looy and Weingarten 1992; Lucchina et al. 1998; Bartoshuk et al. 1999), and to chemical irritants (Karrer and Bartoshuk 1991; Bartoshuk et al. 1999; Prescott and Swain-Campbell 2000). The sensitivity to PROP has also been associated with perception of fat and creaminess (Duffy et al. 1996; Tepper and Nurse 1997; Prutkin et al. 1999; Hayes and Duffy 2007) and with tactile acuity on the anterior tongue (Essick et al. 2003). However, numerous studies have also failed to find significant associations between PROP bitterness and other tastes and/or oral tactile sensation (Hall et al. 1975; Gent and Bartoshuk 1983; Schiffman et al. 1985; Leach and Noble 1986; Mela 1989; Schifferstein and Frijters 1991;

Drewnowski et al. 1997a, 1997b, 1997c, 1998, 2007; Delwiche et al. 2001a, 2001b; Kamerud and Delwiche 2007; Keast and Roper 2007).

Although the lack of an association in some of the latter studies has been attributed to procedural differences (e.g., Lucchina et al. 1998), the inconsistency in results across laboratories has raised questions about the strength of the link between the perception of PROP and other gustatory and oral somatosensory stimuli and about what its possible neurophysiological basis could be. Specifically, it is unclear why genetic expression of a particular bitter taste receptor (i.e., *TAS2R38*) should be related to the sensitivity to other taste stimuli that are mediated by different receptors. It would seem more likely that such a specific genetic effect would cause PROP sensitivity to vary independently of other tastes unless other genetic or environmental factors exist that affect the sensitivity to all taste stimuli, including PROP. The factor that has been most often proposed is the density and number of fungiform taste papillae (Bartoshuk et al. 1994; Tepper and Nurse 1997; Prutkin et al. 2000). By virtue of spatial summation of taste (Smith 1971), more taste papillae (and thus possibly more taste receptors) should lead to greater sensitivity to taste. However, the very first study that investigated the association between fungiform papillae density and perceived taste intensity found a stronger relationship for sucrose and NaCl than for PROP (Miller and Reedy 1990). More recently, 2 studies that directly assessed the relationship between papillae density and variation in the *TAS2R38* genotype found no significant association (Duffy et al. 2004; Hayes et al. 2008).

In the absence of direct evidence that the PROP genotype affects the sensitivity of the human taste system in a general way, it seems likely that other taste stimuli, for which there is no evidence of large variations in receptor expression across individuals, might be better predictors of general taste ability. This idea was supported by a study which showed that the ability to perceive "thermal taste" (i.e., sweetness evoked by thermal stimulation alone; Cruz and Green 2000) was associated with relatively higher responsiveness to 5 prototypical taste stimuli (Green and George 2004). Although the authors of the latter study did not attach any special predictive value to the phenomenon of thermal taste itself, they noted that the high correlations among the prototypical taste stimuli implied that response to any one of them could, in principle, be used to predict the responsiveness to all taste stimuli. Because the correlations among the 4 taste stimuli were significant on the back of the tongue as well as on the front of the tongue and because they occurred among stimuli mediated by different gustatory receptors, Green and George (2004) hypothesized that the covariation resulted from a central rather than a peripheral neural mechanism.

The present study tested the hypothesis that taste stimuli other than PROP may serve as better predictors of overall taste perception. Data were collected under conditions that enabled assessment of the reliability of taste intensity ratings obtained from single exposures to each of 4 common taste stimuli and PROP. This was done to evaluate the feasibility of rapid psychophysical assessments of taste phenotype for possible clinical, epidemiological, and basic research applications. In addition, milk products that varied in fat content were included to determine if a relationship between overall taste perception and oral fat perception (i.e., creaminess) could also be detected in a rapid psychophysical test.

Materials and methods

Subjects

A total of 83 subjects (52 females and 31 males) between 19 and 48 years of age (mean = 26 years old) were recruited on the Yale University Campus, none of whom had previously participated in taste experiments. All were nonsmokers and free from deficits in taste or smell by self-report and were asked to refrain from eating or drinking for at least 1 h prior to their scheduled session. Informed consent was obtained, and the subjects were paid for their participation.

Stimuli

Taste stimuli included 0.32 M sucrose (J.T. Baker, Phillipsburg, NJ), 0.56 M NaCl (J.T. Baker), 56 mM citric acid (Pfaltz & Bauer Inc., Waterbury, CT), 1.0 mM QHCl (Fisher Scientific, Pittsburg, PA), and 0.32 mM PROP (Sigma Chemical Co., St Louise, MO). No prototype stimulus was included for umami taste (e.g., MSG) because the need to train the mostly North American subjects to identify its unfamiliar "savory" quality would have required pre-exposure to the test stimulus. The taste and PROP stimuli were prepared weekly from reagent grade compounds using deionized water. Milk stimuli (Garelick Farms Inc., Franklin, MA) used were fat-free milk (0% fat), whole milk (3.25% fat), and half-and-half (10.5% fat). All the stimuli were stored at 4–6 °C prior to use and were allowed to come to room temperature at the time of testing.

Procedure

All subjects were read instructions about how to use the general version of the Labeled Magnitude Scale (gLMS) (Green et al. 1993, 1996; Bartoshuk et al. 2003). The gLMS was displayed on a flat panel computer monitor, and subjects were shown how to use a mouse to make their ratings. After receiving the instructions, subjects were asked to rate a list of 15 remembered or imagined oral sensations (e.g., the sweetness of cotton candy and the bitter taste of black coffee). The use of imagined sensations gave subjects experience using the scale in the broad context of normal oral perception rather than only the experimental stimulus set (Green and Schullery 2003). Although it is standard procedure in this laboratory to administer a small battery of practice taste stimuli prior to

formal testing, none were given in this experiment so that the reliability of ratings made to single exposures to the stimuli could be evaluated. Intensity ratings were collected in blocks of trials according to stimulus category: prototypical taste stimuli and PROP, followed by milk products. Second (replicate) ratings were obtained by repeating the test sequence.

Taste block

Each subject began by rinsing his/her mouth 3 times with deionized water (37 ± 0.5 °C). The 4 prototypical taste stimuli and PROP were applied by rolling a saturated cotton swab across the tip of the tongue for approximately 3 s. The subjects were asked to retract the tongue into the mouth and then actively taste the stimulus between the tongue and hard palate using normal, gentle "smacking" motions. They then rated the intensity of sweetness, saltiness, sourness, and bitterness using the gLMS. The instructions required subjects to rate the intensity of each taste quality separately and to base their ratings on the maximum sensations perceived during application and active tasting. The order of the 4 taste stimuli was randomized and counterbalanced across subjects, and subjects rinsed at least 3 times with deionized water during each 1-min interstimulus interval. Because exposure to PROP can cause a context effect in sensitive individuals that may interfere with subsequent taste ratings (Bartoshuk 2000), PROP was always presented after the subjects rated the other 4 taste stimuli.

Milk block

After a 3-min break during which subjects rinsed repeatedly to remove any residual bitter taste from PROP, subjects tasted 3 milk products with and without nose clips. Use of nose clips prevented retronasal olfactory stimulation during tasting and allowed analysis of the perception of strictly oral (taste and somatosensory) stimulation. Each subject was presented a series of 10-ml milk stimuli and asked to sip and taste the stimulus in the front of the mouth by gently moving the tongue for approximately 3 s. After spitting out the stimulus, the subjects used the gLMS to rate overall flavor intensity (i.e., the "taste" of the milk product) and creaminess intensity (i.e., the "thickness" of the milk product) sequentially on separate screens. The order of stimuli was randomized and counterbalanced across subjects. Half the subjects received the first 3 stimuli with the nose clip on and then tasted them again without the nose clip. The remaining half received the first 3 stimuli without the nose clip and then tasted them again with the nose clip on. In the nose clip condition, subjects were not allowed to take the clip off until they finished making their ratings.

After completing the overall flavor and creaminess ratings, there was a 5-min break during which subjects cleansed the palate by eating 2 unsalted crackers (Premium unsalted, Nabisco, East Hanover, NJ) and rinsing vigorously with deionized water (37 ± 0.5 °C). To obtain replicate ratings for each stimulus, the testing sequence was then repeated in the same way, beginning with the prototypical taste stimuli.

Data analysis

PROP taster status

Subjects were first classified into 2 groups based on their bitterness ratings for PROP averaged over the 2 replicates. Individuals who gave mean ratings of PROP below "barely detectable" on the gLMS were classified as PROP nontasters ($_P$NT; n = 27), whereas individuals whose mean ratings of PROP were above barely detectable were classified as PROP tasters ($_P$T; n = 56). The $_P$T's were further categorized as PROP medium tasters ($_P$MT) if they rated the bitterness of PROP above barely detectable but below "moderate" (n = 37) and as PROP supertasters ($_P$ST) if they rated the bitterness of PROP above moderate (n = 19). We also classified subjects based on breaks in the distribution of perceived bitterness ratings of PROP that were identified visually. This strategy led to 3 groups that accounted for 32.5%, 44.6%, and 22.9% of the overall sample. This grouping was similar to the arbitrary partitioning based on quartiles (25%, 50%, and 25%) that have been used previously to categorize nontasters, medium tasters, and supertasters (Bartoshuk 2000; Prutkin et al. 2000; Drewnowski et al. 2007).

Statistical analyses

Because responses on the gLMS tend to be log-normally distributed across subjects (Green et al. 1993, 1996), the intensity ratings were log transformed prior to statistical analysis. Repeated-measures analysis of variance (ANOVA) and Tukey's honestly significant difference (HSD) tests were performed on 2 separate sets of data: one for intensity ratings from taste stimuli and PROP and another for the milk products. Arithmetic means of log intensity ratings were calculated across replicates within subjects and were used for further statistical analyses. The Pearson product-moment correlation was also calculated for intensity ratings from all stimuli, and the Bonferroni correction was used to reduce type-I errors. The t-tests for independent samples were carried out to examine the difference between the means of taster status groups (e.g., $_P$NT vs. $_P$T and $_P$MT vs. $_P$ST) for each stimulus. All statistical analyses were performed using Statistica 8.0 (StatSoft Inc., Tulsa, OK).

Results

Repeated-measures ANOVAs performed on the log intensity ratings for the 4 taste stimuli and PROP (Figure 1) indicated that there were main effects of stimulus ($F_{4,328}$ = 18.54, P < 0.00001) and replicate ($F_{1,82}$ = 10.94, P < 0.002). Tukey's HSD tests (P < 0.05) further confirmed that the effect of stimulus was derived from significantly lower average

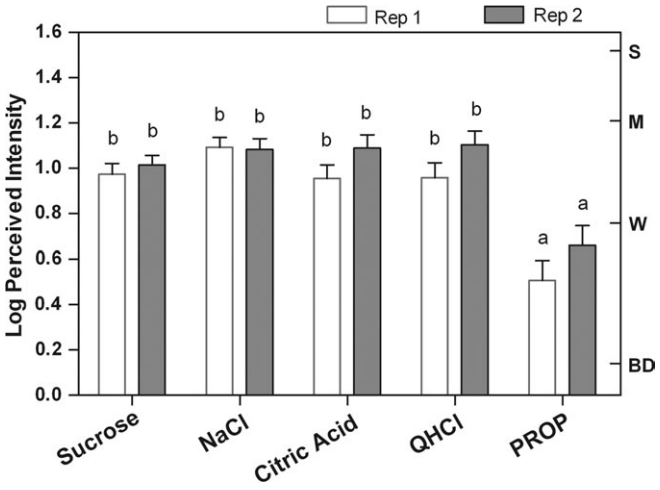

Figure 1 Log means of perceived intensity ± standard error of the relevant taste (sweetness for sucrose, saltiness for NaCl, sourness for citric acid, bitterness for QHCl, and bitterness for PROP). The different letters indicate significant differences on perceived intensities by the Tukey's HSD test ($P < 0.05$).

bitterness ratings of PROP, whereas the perceived intensities of the 4 prototypical taste stimuli did not differ significantly from one another. In addition, although there was a tendency for the replicate ratings to be higher than the initial ratings for all but NaCl, the first and second intensity ratings were not significantly different for any of the 5 stimuli. Pearson product-moment correlation coefficients calculated for the 2 ratings of each stimulus (Table 1) also showed that there was a degree of consistency across replicates (e.g., $r = 0.71$ for sucrose and 0.72 for PROP). However, correlations between different taste stimuli were generally not significant after Bonferroni correction. The sole exception was a significant correlation between bitterness ratings of QHCl and PROP. On the other hand, when taste intensity ratings were averaged across replicates, correlations among all 4 prototypical taste stimuli, excluding PROP, were significant (Table 2). Because the distributions between the bitterness of PROP and other tastes are possibly different (i.e., bimodal vs. normal distribution), we also calculated Spearman's rank-order correlations, which gave results that agreed with those from the Pearson product-moment correlation.

Figure 2 shows the mean log perceived intensity ratings for the primary qualities of the prototypical taste and PROP stimuli grouped by PROP taster status. Analyses revealed no significant group differences between $_{P}$T and $_{P}$NT for the sweetness of sucrose, saltiness of NaCl, and sourness of citric acid, although $_{P}$T's rated the bitterness of QHCl significantly higher than did $_{P}$NT's (Figure 2, the left panel). When the $_{P}$T's were subcategorized as medium vs. supertasters, the taste intensity ratings between groups differed significantly: $_{P}$ST's rated the perceived intensities of all 4 prototypical taste stimuli and PROP significantly higher than did $_{P}$MT's.

Figure 3 shows the mean log intensity ratings for overall flavor (left graph) and creaminess (right graph) of the 3 milk products. Two separate repeated-measures ANOVAs revealed a significant main effect of stimulus for both the perceived intensity of flavor ($P < 0.0001$) and creaminess ($P < 0.0001$). The perceived flavor and creaminess intensities increased with fat content from 0% (fat-free milk) to 10.5% (half-and-half). As expected, the subjects rated overall flavor to be significantly higher ($P < 0.0001$) in the condition without the nose clip. Although creaminess ratings also tended to be higher without the nose clip, Tukey's HSD tests ($P < 0.05$) showed that the main effect of retronasal odor on creaminess ratings was significant only for whole milk.

There was no significant relationship between ratings of creaminess and taste intensity for any of the taste stimuli, including PROP (Table 3). Indeed, for the averaged data, only a single significant correlation was obtained (saltiness of NaCl and creaminess of half-and-half); most other correlation coefficients were less than 0.20. Similarly, correlations between ratings of flavor intensities of the milk products and taste intensity were low (results not shown). After Bonferroni correction, the only significant correlations involved sucrose and NaCl: NaCl saltiness was correlated with the flavor intensity of half-and-half without the nose clip ($r = 0.34$), and sucrose sweetness was correlated with the flavor of whole milk in both the nose open and nose closed conditions ($r = 0.42$ and 0.32, respectively). Ratings of PROP bitterness were not significantly correlated with flavor ratings for any of the milk products in either condition (all $r < 0.22$).

Discussion

The present results support earlier evidence (Green and George 2004) that perception of PROP is a poorer predictor of general taste sensitivity than is perception of prototypical stimuli such as sucrose, NaCl, citric acid, and QHCl. In addition, neither the perceived intensity of PROP nor the perceived intensities of the prototypical taste stimuli were significantly correlated with the rated creaminess of milk products. These findings do not support the practice of using PROP as an indicator of general taste or oral tactile perception and thus do not support the assumption that the gene responsible for the expression of the PROP receptor (*TAS2R38*) influences the ability to perceive other taste or oral tactile stimuli.

Correlations among taste intensities

The superiority of the 4 prototypical taste stimuli as measures of taste perception is evident in the finding that ratings of each of the 4 stimuli were significantly correlated with one another, whereas ratings of the bitterness of PROP were significantly correlated only with the bitterness of QHCl. This result is consistent with those from a previous study in our

Table 1 Correlation coefficients (*r*) between replicate taste intensity ratings

	Sucrose replicate 2	NaCl replicate 2	Citric acid replicate 2	QHCl replicate 2	PROP replicate 2
Sucrose replicate 1	**0.71, *P* = 0.000**[a]	0.31, *P* = 0.005	0.32, *P* = 0.004	**0.35, *P* = 0.001**	0.03, *P* = 0.799
NaCl replicate 1	0.24, *P* = 0.032	**0.46, *P* = 0.000**	0.30, *P* = 0.007	0.25, *P* = 0.024	−0.00, *P* = 0.997
Citric acid replicate 1	0.23, *P* = 0.037	0.23, *P* = 0.034	**0.60, *P* = 0.000**	0.18, *P* = 0.099	0.01, *P* = 0.961
QHCl replicate 1	0.24, *P* = 0.031	0.23, *P* = 0.039	0.22, *P* = 0.046	**0.56, *P* = 0.000**	**0.34, *P* = 0.002**
PROP replicate 1	0.27, *P* = 0.016	0.24, *P* = 0.028	0.26, *P* = 0.017	**0.43, *P* = 0.000**	**0.72, *P* = 0.000**

[a]Correlations are significant at an adjusted alpha level of 0.05 after Bonferroni correction ($P < 0.002$).

Table 2 Correlation coefficients (*r*) between stimuli after averaging across replicates

	Sucrose	NaCl	Citric acid	QHCl
NaCl	**0.39, *P* = 0.000**[a]			
Citric acid	**0.35, *P* = 0.001**	**0.43, *P* = .000**		
QHCl	**0.34, *P* = 0.002**	**0.34, *P* = 0.001**	**0.33, *P* = 0.001**	
PROP	0.20, *P* = 0.070	0.18, *P* = 0.100	0.17, *P* = 0.131	**0.46, *P* = 0.000**

[a]Correlations are significant at an adjusted alpha level of 0.05 after Bonferroni correction ($P < 0.005$).

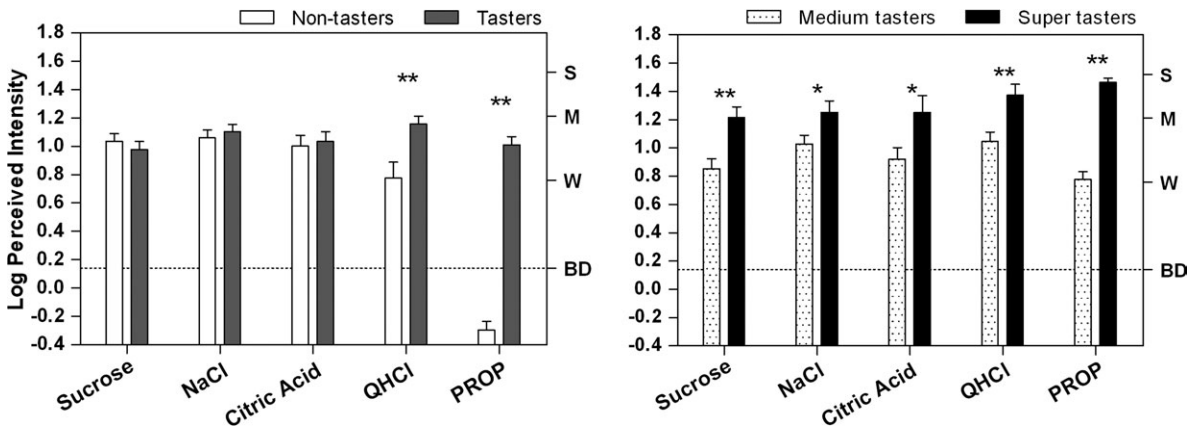

Figure 2 Log means of perceived intensity ± standard error for sweetness of sucrose, saltiness of NaCl, sourness of citric acid, bitterness of QHCl, and bitterness of PROP grouped by PROP taster status. The left panel shows the comparison between the PROP nontasters ($n = 27/83$) versus the PROP tasters ($n = 56$) and the right panel shows the comparison between the PROP medium tasters ($n = 37/83$) versus the PROP supertasters ($n = 19/93$). Asterisk indicates significant differences on perceived intensities by the *t*-test (1-tailed, independent sample *t*-test, $*P < 0.05$, $**P < 0.005$).

laboratory of the association between individual differences in perception of prototypical taste stimuli and PROP (Green and George 2004) and with other studies that failed to find significant correlations between PROP bitterness and other tastes (Hall et al. 1975; Gent and Bartoshuk 1983; Schiffman et al. 1985; Leach and Noble 1986; Mela 1989; Schifferstein and Frijters 1991; Drewnowski et al. 1997a, 1997b, 1997c, 1998, 2007; Delwiche et al. 2001a; Kamerud and Delwiche 2007; Keast and Roper 2007). Indeed, in the earliest study of the relationship between the sensitivity to PROP and other taste stimuli, Fischer and Griffin (1963) reported that although thresholds for the PROP and quinine tended to covary, individuals who were ''nontasters'' of PROP were sometimes very sensitive to quinine. However, the present results are inconsistent with numerous studies in which individual differences in taste and oral somatosensory perception have been reported to be correlated with PROP bitterness (Gent and Bartoshuk 1983; Bartoshuk et al. 1992, 1993, 1994, 1999; Looy and Weingarten 1992; Bartoshuk 1993; Duffy et al. 1996; Tepper and Nurse 1997; Drewnowski et al. 1998; Lucchina et al. 1998; Prutkin et al. 1999; Ly and Drewnowski 2001).

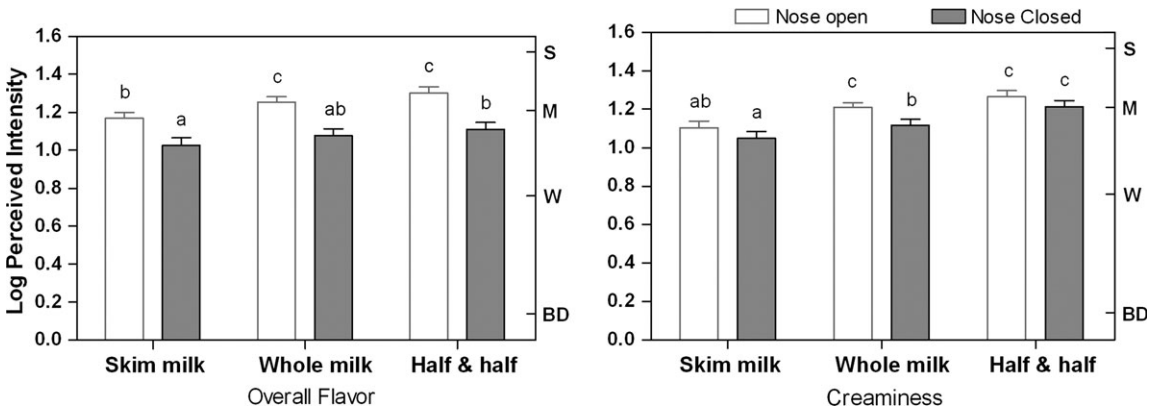

Figure 3 Log mean intensity ratings ± standard error for overall flavor and creaminess intensity ratings for the 3 milk stimuli varying in fat content for the nose-open and nose-closed conditions. Error bars represent standard errors. The different alphabets indicate significant differences on perceived intensities by the Tukey's HSD test ($P < 0.05$).

Table 3 Correlation coefficients (*r*) between taste intensities and creaminess ratings in nose-closed condition

	Sucrose	NaCl	Citric acid	QHCl	PROP
Skim milk	0.24, $P = 0.027$	0.21, $P = 0.062$	0.14, $P = 0.207$	0.14, $P = 0.205$	0.19, $P = 0.093$
Whole milk	0.24, $P = 0.028$	0.22, $P = 0.044$	0.17, $P = 0.117$	0.14, $P = 0.206$	0.15, $P = 0.185$
Half-and-half	0.28, $P = .012$	**0.34, $P = 0.002$**[a]	0.26, $P = 0.019$	0.08, $P = 0.449$	0.21, $P = 0.062$

[a]Correlations are significant at an adjusted alpha level of 0.05 after Bonferroni correction ($P < 0.003$).

To consider the possible reasons for these inconsistencies, it is helpful to return to the assumptions that underlie the use of PROP as an indicator of taste and oral sensation. As mentioned earlier, the link between PROP taste and general taste sensitivity has been explained in terms of variation in the number and density of fungiform taste papillae on the anterior tongue (Reedy et al. 1993; Bartoshuk et al. 1994; Hosaka-Haito et al. 1996; Tepper and Nurse 1997). It has been inferred that if PROP tasting is associated with the number of taste papillae, then by virtue of spatial summation of taste (Smith 1971), PROP medium tasters and supertasters should also perceive all other tastes more intensely. However, this has not always been found. For example, the bitterness of quinine has been reported to vary only modestly across PROP taster groups (Ly and Drewnowski 2001), and data on the relationship between the bitterness of PROP and the saltiness of NaCl are particularly confusing. Differences in saltiness across PROP taster groups have been reported to range from moderate to nonexistent (Bartoshuk et al. 1994, 1998; Drewnowski et al. 1997a, 2007), and the assumption that perception of NaCl is independent of perception of PROP has led to the use of saltiness ratings as a way to standardize ratings of PROP bitterness across subjects (Bartoshuk et al. 1994; Kirkmeyer and Tepper 2003). In addition, the first study of the relationship between fungiform taste pore density and perceived taste intensity found a stronger relationship for NaCl and sucrose than for PROP (Miller and Reedy 1990). Recall, too, that direct tests of the hypothesis that PROP genotype was related to fungiform papillae density yielded no significant association in one study (Duffy et al. 2004; Hayes et al. 2008). Finally, Delwiche et al. (2001a) reported a significant relationship between the number of fungiform papillae stimulated and the bitterness of both PROP and quinine but found no evidence that individual differences in quinine bitterness were related to differences in papillae number. These divergent results can be explained if it is assumed that 1) papillae density affects taste perception via spatial summation, but 2) it is not genetically linked to PROP sensitivity, and that 3) other neurophysiological factors also affect general taste sensitivity. Together these assumptions predict that subjects who perceive PROP (or any taste stimulus) very strongly are more likely to have larger numbers of taste papillae than are less-sensitive subjects, but that additional factors combine to complicate this relationship in any given individual or group of individuals.

The results of the present study are consistent with this explanation. When subjects were divided into groups of pT's and pNT's, a significant difference in mean perceived intensity between groups was found only for QHCl (Fig. 2, left panel). Whereas intensity ratings of PROP bitterness varied between these 2 groups by a factor of nearly 20 to 1, there was no difference in perception of sucrose sweetness, NaCl saltiness, or citric acid sourness. Because we used a very stringent criterion for classifying subjects as pNT's (i.e., average bitterness ratings below barely detectable on the gLMS), we

can assume that the differences between these 2 groups depended heavily, if not entirely, on the *TAS2R38* genotype (Kim and Drayna 2004; Bufe et al. 2005; Behrens et al. 2007). Yet, pNT's perceived sucrose, NaCl, and citric acid just as strongly as pT's. Furthermore, when pT's were classified as either pMT's or pST's, the pST's gave significantly higher taste ratings not only to PROP but also to the other 4 prototypical taste stimuli (Fig. 2, right panel). This implies that factors other than PROP genotype contribute to the differences in taste perception between pMT's and pST's and that these factors affect the perception of "all" tastes.

To explain their finding that individuals who perceived taste from thermal stimulation also perceived prototypical taste stimuli to be more intense, Green and George (2004) suggested that a CNS mechanism might influence the general responsiveness to taste. Because those authors measured taste perception on the back of the tongue and soft palate as well as on the front of the tongue, they were able to rule out fungiform papillae density as the primary source of the individual differences: Miller and Reedy (1990) had previously found no association between the number of taste buds per papillae or the overall number of taste buds in the fungiform, foliate, and circumvallate regions of the tongue. Green and George (2004) speculated instead that gustatory responsiveness may be influenced by a central "gain" mechanism that determines the responsiveness of the gustatory (and possibly the flavor) system to peripheral stimulation. Individual variation in a central gain mechanism could explain the wide range of slopes in PROP bitter taste functions that have been reported for subjects who have different haplotypes of the *TAS2R38* gene (Bufe et al. 2005); steep slopes would be consistent with a high central gain, whereas low slopes might reflect a low central gain. Individual variation in slope was so great in Bufe et al. (2005) that some subjects who had categorically different *TAS2R38* genotypes had indistinguishable suprathreshold PROP phenotypes. Thus, individual differences in central gain may complicate the use of suprathreshold PROP phenotypes to make inferences about *TAS2R38* genotypes.

Relationship between taste perception, creaminess, and flavor of milk

The present study found no significant relationship between perceived taste intensity ratings and the perceived creaminess of the milk products for any of the taste stimuli, including PROP (Table 3). In addition, no significant group differences were found when creaminess ratings for the 3 milk products were compared across PROP taster groups (results not shown). These findings are in agreement with the results of some studies (Drewnowski et al. 1998; Yackinous and Guinard 2001) but disagree with the results from several others (Duffy et al. 1996; Tepper and Nurse 1997; Prutkin et al. 1999; Hayes and Duffy 2007). Once again, studies that have found a positive association between PROP taste and creaminess have usually attributed the effect to fungiform papillae density. For example, Tepper and Nurse (1997) reported that papillae densities differed significantly among supertasters, medium tasters, and nontasters and that tasters and supertasters could discriminate differences in fat content for Italian salad dressings, whereas nontasters could not. On the other hand, there was no difference in ratings of fat content or oiliness between tasters and supertasters. Relationships between PROP bitterness and fat perception in other previous studies (Duffy et al. 1996; Tepper and Nurse 1997; Hayes and Duffy 2007) were found only in samples that had a very high level of fat (mostly over 35%). An effect of PROP taster status only between stimuli having large differences in fat content is consistent with the low average correlations between PROP ratings and creaminess ($r = 0.18$) in the present study (Table 3) and suggests that any underlying association is not strong. The factor most likely to be responsible for the link between taste and tactile perception is fungiform papillae density, not PROP genotype. In addition to containing taste buds, fungiform papillae are heavily innervated by the trigeminal nerve (Farbman and Mbiene 1991; Whitehead and Kachele 1994) and are assumed to be important for tactile perception. Consequently, associations between taste and touch should be highest when both forms of stimulation are limited to the front of the tongue and lower when stimulation extends to other parts of the mouth, for example, during whole-mouth stimulation. Support for a close association on the front of the tongue comes from a study conducted on a group of female subjects in which a high correlation ($r = 0.84$) was found between fungiform papillae number and tactile acuity on the tip of the tongue (Essick et al. 2003). The same study also found a high correlation between PROP bitterness and papillae number, which would be expected based on spatial summation of taste.

In contrast, it is likely that the lower correlations between perceived taste intensity ratings and creaminess ratings found in the present study were due in part to delivery of the milk products to the whole mouth. A lesser role of fungiform papillae in whole-mouth stimulation would allow other factors to complicate the relationship between taste and predominantly mechanically mediated sensations like creaminess. Similarly, the low correlations that we found between perceived taste intensity ratings and overall milk flavors might also be attributable in part to the mode of stimulation. Although the hypothesized central gain would be expected to affect taste perception during both localized and whole-mouth stimulation, it is not at all clear that the response to taste stimulation predominantly on the tongue tip should accurately reflect the response to food stimuli that evoke complex taste and somatosensory sensations throughout the mouth.

Test–retest reliability in the assessment of individual differences

Compared with intraindividual variations in odor sensitivity (Punter 1984; Rabin and Cain 1986; Stevens et al. 1988;

Lawless et al. 1995), relatively little is known about how measurements of suprathreshold taste perception vary over time. We were able to find only 2 studies that addressed this question directly: Mattes (1988) reported poor retest reliability using the method of magnitude estimation to collect multiple ratings over days, and in a study designed primarily to evaluate context effects in a magnitude matching task, Marks (1991) found substantial variation across days even though 5 replicate ratings were obtained each day. Because one purpose of the present study was to evaluate the feasibility of quick tests of taste and oral texture perception, our subjects rated each test stimulus just twice. As shown in Table 1, the replicate ratings for each stimulus were significantly correlated (coefficients ranged from 0.46 to 0.72), indicating a fair degree of reliability. However, correlations across taste stimuli were generally not significant after Bonferroni correction, with the exception of an association between the bitterness ratings of QHCl and PROP. However, when taste intensity ratings were averaged across replicates, the correlations among all 4 prototypical taste stimuli (but not PROP) were significant (Table 2). This implies that at least 2 taste intensity ratings are necessary to achieve reliable estimates of individual taste responsiveness when using the gLMS. Although more extensive testing would likely lead to significant correlations with PROP as well, the present results indicate that such correlations would remain low compared with those among the prototypical taste stimuli.

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