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Binary Taste Mixture Interactions in PROP Non-tasters, Medium-tasters and Super-tasters

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Abstract

It is generally assumed that the mutual, but asymmetric, suppression of the components in binary taste mixtures is an invariant property of the human psychophysical response to such mixtures. However, taste intensities have been shown to vary as a function of individual differences in sensitivity, indexed by the perceived bitterness of 6-*n*-propylthiouracil (PROP). To determine if these variations in taste perception influence taste mixture interactions, groups of PROP super-, medium- and non-tasters assessed four binary taste mixtures: sweet–bitter [sucrose/quinine hydrochloride (QHCl)], sweet–sour (sucrose/citric acid), salty–bitter (NaCl/QHCl) and salty–sour (NaCl/citric acid). In each experiment, subjects received factorial combinations of four levels of each of two tastants and rated individual taste intensities and overall mixture intensity. For each taste quality, super-tasters typically gave higher ratings than either medium- or non-tasters, who tended not to differ. There were also group differences in the interactions of the mixtures' components. Super-tasters rated the overall intensity of the mixtures, most likely reflecting integration of the taste components, as greater than medium- and non-tasters, who again showed few differences. In sweet–bitter mixtures, non-tasters failed to show the suppression of sweetness intensity by the highest QHCl concentration that was evident in super- and medium-tasters. These data show that the perception of both tastes and binary taste mixture interactions varies as a function of PROP taster status, but that this may only be evident when three taster groups are clearly distinguished from one another.

Introduction

It is well established that individuals vary in the extent to which they perceive the compounds phenylthiocarbamide (PTC) and 6-*n*-propylthiouracil (PROP) as bitter (Fox, 1932; Bartoshuk *et al*., 1994). Recent research has confirmed the existence of three subgroups, conventionally labelled as non-tasters (NTs), medium-tasters (MTs) and super-tasters (STs), varying in sensitivity to PROP/PTC at either threshold or suprathreshold concentrations (Bartoshuk *et al*., 1992). Variations in PROP/PTC sensitivity appear to arise from underlying anatomical differences, since ratings of PROP intensity are highly correlated with the density of fungiform papillae on the tongue (Miller and Reedy, 1990; Bartoshuk *et al*., 1994). This being the case, it is not surprising that the degree of PROP/PTC sensitivity has also been associated with variations in the perception of a number of other taste compounds.

Although studies to date have not yielded completely consistent results, PROP tasters have been reported as rating urea, sucrose octa-acetate and denatonium benzoate (Mela, 1989), sodium and potassium benzoate, potassium chloride (Bartoshuk *et al*., 1988), quinine (Leach and Noble, 1986) and caffeine (Hall *et al*., 1975) as more bitter than do NTs, and sucrose as sweeter (Gent and Bartoshuk, 1983). Both the bitterness and sweetness of saccharin are rated as more intense by PROP tasters than by NTs (Bartoshuk, 1979). There are also recent reports that the saltiness of NaCl (Bartoshuk *et al*., 1998) and sourness of citric acid (Prutkin *et al*., 1999) are both positively correlated with PROP ratings. These psychophysical differences between taster groups also appear to be reflected in different degrees of liking for tastes (Looy and Weingarten, 1992) and ultimately in different patterns of food preferences (Drewnowski and Rock, 1995).

If there are differences between individuals in their sensitivity to individual tastes, the question arises of how this translates into the experience of taste qualities during the consumption of foods and beverages. Clearly, the most common experience of tastes is in the form of mixtures of two or more different taste qualities such as sweetness and sourness or sweetness and bitterness—both combinations being characteristic of fruit juices, for example. Interactions in taste mixtures have been extensively studied and binary, heterogeneous taste mixtures most commonly exhibit a mutual, but asymmetrical suppression of the different taste

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qualities (Kamen *et al*., 1961; Moskowitz, 1972; McBurney and Bartoshuk, 1973). While these interactions are generally thought to be invariant properties of taste mixtures, the existence of subgroups varying in sensitivity to individual tastants raises the possibility that this may not be the case. In fact, there are reports of exceptions to the typical pattern of suppression. Kroeze (Kroeze, 1989), for example, has noted that up to 20% of subjects in some of his studies failed to show suppression in taste mixtures. McBride (McBride, 1989) presented data that suggested that the magnitude of suppression depends only on the intensity of the suppressor. Clearly, if this component is perceived as less intense by PROP NTs, relative to tasters, then the interactions within the mixture might be expected also to reflect variations in PROP sensitivity.

The role that such individual differences have to play in determining taste mixture interaction has been investigated in two previous studies. Lawless (Lawless, 1979) found PTC NTs failed to show the suppression of sucrose sweetness by PTC that was shown by tasters. However, this study failed to demonstrate differences between the taster groups for another sweet/bitter mixture, that of quinine hydrochloride (QHCl) and sucrose. More recently, Schifferstein and Frijters (Schifferstein and Frijters, 1991) failed to find any differences between PROP taster and non-taster groups in the bitterness, saltiness or overall intensity of a NaCl/QHCl mixture.

Since these studies, there have been a number of changes in the ways in which taste sensitivity is both classified (e.g. subdividing tasters into MTs and STs) and measured. Thus, supra-threshold measurements of PROP sensitivity have recently been examined and found to be a poor reflection of the underlying distribution when certain types of rating scales (e.g. 9-point category scales) are used to measure PROP bitterness. As a result, previous studies using such scales may have underestimated the variability in PROP ratings. Additionally, because tasters, and especially STs, find the bitterness of PROP extremely strong, many of these rating scales compress the scores at the upper end (producing a ceiling effect), effectively reducing the variability of the scores and limiting the chance of finding significant relationships between PROP ratings and the perception of other tastes (Prutkin *et al*., 2000). The recent development of a scale that substantially reduces ceiling effects—the Labelled Magnitude Scale or LMS (Green *et al*., 1993)—has allowed a more accurate reflection of the underlying distribution of sensitivity to PROP (Lucchina *et al*., 1998).

The present research set out to further explore taste mixture interactions as a function of sensitivity to PROP by recognition of the existence of three taster subgroups defined using the LMS. The research examined four taste mixtures—sweet/bitter; sweet/sour; salty/bitter; salty/sour—across a range of concentrations. In addition to the effects of each tastant on the quality of the other tastant, the extent to which the two tastants were integrated to produce an overall mixture intensity was also assessed. It has been suggested that such measures are dependent on a dominant component (Frank and Archambo, 1986; McBride, 1989). If the intensity of this component varies with taster status, it is possible that overall mixture intensity is also sensitive to PROP status.

Materials and methods

Subjects

Assessment of taster status

A total pool of 119 subjects, predominantly students and staff at the University of Otago, participated. Of these, 37.8% participated in all four experiments, 10.9% in three, 18.5% in two and 32.8% in only one experiment. Subject details are shown in Table 1. Taster status was determined by having each subject rate the intensity of a 10 ml solution of 0.0032 M 6-*n*-propylthiouracil (PROP; Sigma) in deionized water, using an LMS. The top end of this scale uses the descriptor 'strongest imaginable'. In the present study, this was defined in the context of all oral sensations, including painful ones. In the majority of subjects, determination of taster status was carried out after the completion of all taste evaluations. For other subjects, it was completed in a separate session either prior to, or during, their participation in the taste study. Subjects placed the

Table 1 Subject details for each of the four taste mixture experiments

	Taste mixtures			
	SU/QHCl	SU/CA	NA/QHCl	NA/CA
No. of subjects (%F/M):	80 (67.5/32.5)	113 (73.5/26.5)	52 (55.8/44.2)	57 (59.6/40.4)
Mean age (range):	21.4 years (18–40)	21.8 years (18–40)	21.3 years (18–40)	21.5 years (18–40)
n (mean PROP rating)[a]				
STs	23 (127.4)	36 (136.9)	11 (126.4)	12 (124.1)
MTs	36 (60.4)	50 (62.5)	22 (52.9)	25 (54.8)
NTs	21 (5.3)	27 (5.7)	19 (5.8)	20 (5.1)

[a]Mean PROP ratings are in millimetres on a 165 mm LMS.

PROP solution in their mouth, swilled it around for a few seconds, expectorated and then gave their rating. On the basis of these ratings (measured in millimetres from the base of the scale; range 0–165), the different taster groups were defined as follows: STs (rating >100); MTs (ratings 20–100); and NTs (ratings <20). These group definitions are based on the lower and upper 25% of values from the distribution from large data sets (L. Bartoshuk, personal communication).

In the present study, the percentages of STs ranged from 21.1 to 31.9%, MTs from 42.3 to 45% and NTs from 23.9 to 36.5%. Higher percentages of STs, and lower percentages of NTs, in the different experiments were associated with higher percentages of female subjects (range 55.8–73.5%). This is consistent with reports that females are more represented among STs than are males (Bartoshuk *et al.*, 1994).

Taste mixtures

The stimuli were solutions of binary mixtures of sucrose (SU; Sigma), citric acid (CA; Analar), quinine hydrochloride (QHCl; Sigma) and sodium chloride (NA; Sigma) in deionized water. The mixture solutions were prepared at least 24 h before tasting and stored at ~4°C for no longer than 5 days. In each of the experiments, two compounds at each of four concentrations (including 0) were combined factorially, giving a total of 16 taste mixture pairs to be evaluated. The concentrations used in each of the experiments are shown in Table 2. These concentrations were based on values found in the taste mixture literature (Schifferstein and Frijters, 1990, 1992; Schifferstein, 1994) as well as on pilot studies undertaken on each tastant combination to establish levels at which interactions such as suppression were apparent.

Procedure

In each experiment, subjects used the LMS to rate the overall intensity of the mixture, as well as the following qualities: sweetness and bitterness (experiment 1); sweetness and sourness (experiment 2); saltiness and bitterness (experiment 3); and saltiness and sourness (experiment 4). For each sample, the three scales were presented on a single sheet, with the scale order balanced across subjects. At the beginning of each experiment, subjects were presented with the highest concentration of each unmixed tastant and asked to rate that quality plus overall intensity as a means of providing a context, as well familiarizing them with the LMS. As with the assessment of taster status, the highest descriptor—strongest imaginable—referred to any oral sensation and was not restricted to tastes (Green *et al.*, 1993).

Within each experiment, subjects received all combinations in duplicate in a single session. Samples were presented in a random order at 1 min intervals as room temperature (~18°C) solutions (10 ml). Prior to each sample, subjects rinsed twice with deionized water. Samples were taken into the mouth, swilled around for a few seconds and then expectorated. Subjects then provided their ratings of the two taste qualities plus overall intensity. Following presentation of half the solutions, subjects took a 10 min break.

Table 2 Concentrations of the tastants used in each of the four experiments

	Tastant	Concentrations			
Experiment 1	SU (M)	0	0.1	0.25	0.5
	QHCl (μM)	0	10	60	360
Experiment 2	SU (M)	0	0.15	0.3	0.6
	CA (mM)	0	3	6	12
Experiment 3	NA (M)	0	0.15	0.3	0.6
	QHCl (μM)	0	10	60	360
Experiment 4	NA (M)	0	0.15	0.3	0.6
	CA (mM)	0	4.5	9	18

Analysis

Ratings were converted into scores between 0 and 165, and the data submitted to ANOVA (SAS, PROC Mixed) with the model fitted using a maximum likelihood method. Factors were groups (NTs, MTs, STs), tastant concentrations and replicates. The subjects were treated as random effects. Following significant main effects or interactions, *post hoc* comparisons of means were undertaken using Tukey's HSD test, which adjusts for multiple comparisons.

Results

Experiment 1: SU/QHCl mixtures

Figure 1a–c shows the mean ratings of overall intensity, bitterness and sweetness as functions of SU for the different QHCl concentrations, averaged across all taster groups.

Overall intensity

For all groups, overall intensity was strongly influenced by both QHCl [$F(3,1480) = 329.34$, $P < 0.0001$] and SU [$F(3,1480) = 83.12$, $P < 0.0001$]. As shown in Figure 1a, overall intensity was dominated by QHCl at 360 μM, while at lower QHCl concentrations, SU was relatively more influential [QHCl × SU interaction; $F(9,1480) = 35.86$, $P < 0.0001$].

STs gave higher overall intensity ratings of the mixtures than did MTs and NTs, who were not significantly different [$F(2,78) = 4.62$, $P < 0.05$]. These differences were most apparent at 60 and 360 μM QHCl (see Figure 2a), although there was also a difference between STs and MTs at the lowest QHCl level [group × QHCl interaction; $F(6,1480) = 3.17$, $P < 0.005$]. The group × SU [$F(6,1480) = 0.64$] and

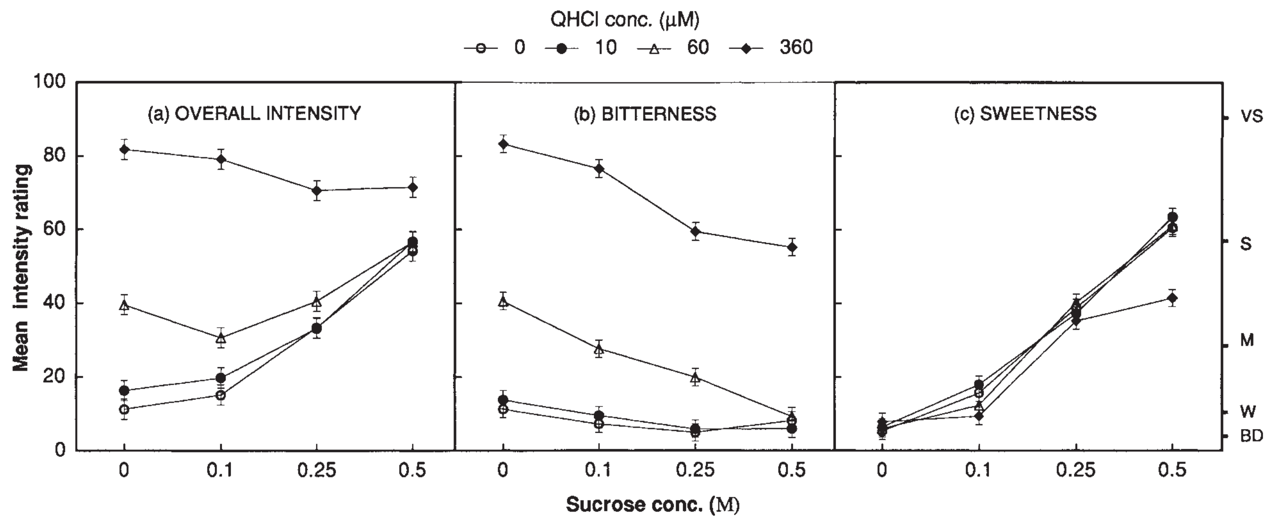

Figure 1 SU/QHCl mixtures: mean (±SEM) ratings of **(a)** overall intensity, **(b)** bitterness and **(c)** sweetness as a function of SU concentration for the different QHCl concentrations, averaged across all taster groups. Also shown on the right-hand edge of (c) are the label abbreviations from the LMS: VS, very strong; S, strong; M, moderate; W, weak; BD, barely detectable.

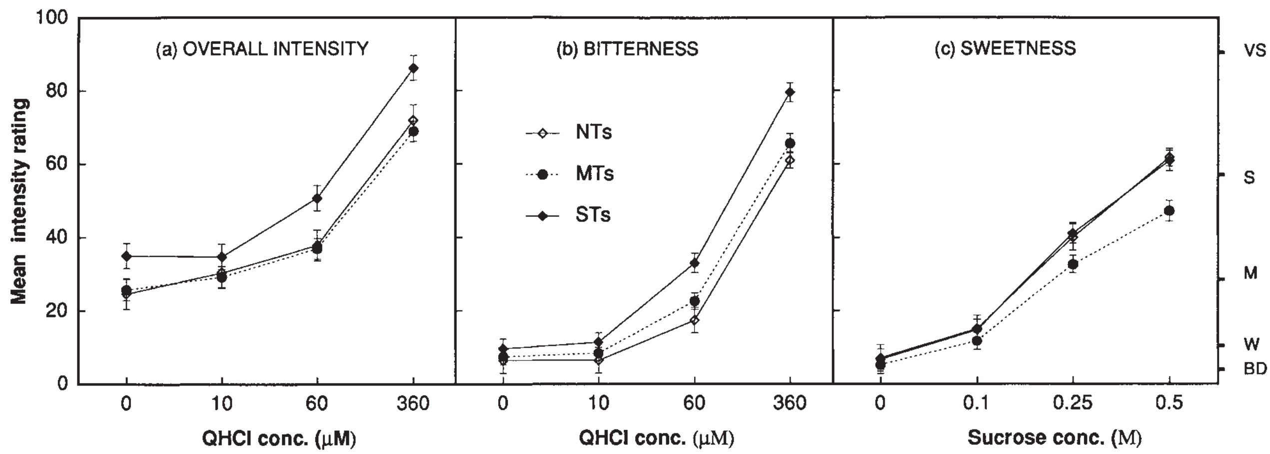

Figure 2 SU/QHCl mixtures: mean (±SEM) ratings of **(a)** overall intensity, **(b)** bitterness and **(c)** sweetness by the different taster groups. These are shown as a function of the tastant for which there was a significant interaction with group.

group × QHCl × SU [$F(18,1480) = 0.65$] interactions were not significant.

Bitterness

Bitterness was primarily determined by QHCl [$F(3,1480) = 635.31$, $P < 0.0001$], although there was also evidence of suppression by SU [SU main effect; $F(3,1480) = 48.51$, $P < 0.0001$; see Figure 1b]. This suppression was clearly greater at higher concentrations of QHCl [QHCl × SU interaction; $F(9,1480) = 12.37$, $P < 0.0001$].

There was an overall difference between groups in ratings of bitterness [$F(2,78) = 5.01$, $P < 0.01$]. As with overall intensity ratings, STs gave higher bitterness ratings than MTs and NTs, who did not differ. Figure 2b shows these differences to be most evident with 60 and 360 μM QHCl [group × QHCl interaction; $F(6,1480) = 5.96$, $P < 0.0001$]. The group × SU [$F(6,1480) = 1.59$] and group × QHCl × SU [$F(18,1480) = 0.52$] interactions were not significant.

Sweetness

Sweetness ratings showed main effects for SU [$F(3,1480) = 492.46$, $P < 0.0001$] and QHCl [$F(3,1480) = 11.59$, $P < 0.0001$]. Sweetness was suppressed by 360 μM QHCl, particularly at 0.5 M SU [QHCl × SU interaction; $F(9,1480) = 8.91$, $P < 0.0001$; see Figure 1c].

There was no overall group difference [$F(2,78) = 2.75$]. A marginal group × QHCl interaction [$F(6,1480) = 2.09$, $P = 0.052$] suggests that the suppression of sweetness by the highest concentration of QHCl (see Figure 1c) was group dependent. *Post-hoc* tests revealed that decrease in ratings of sweetness at the highest concentration of QHCl occurred for STs and MTs, but not for NTs, who showed no significant

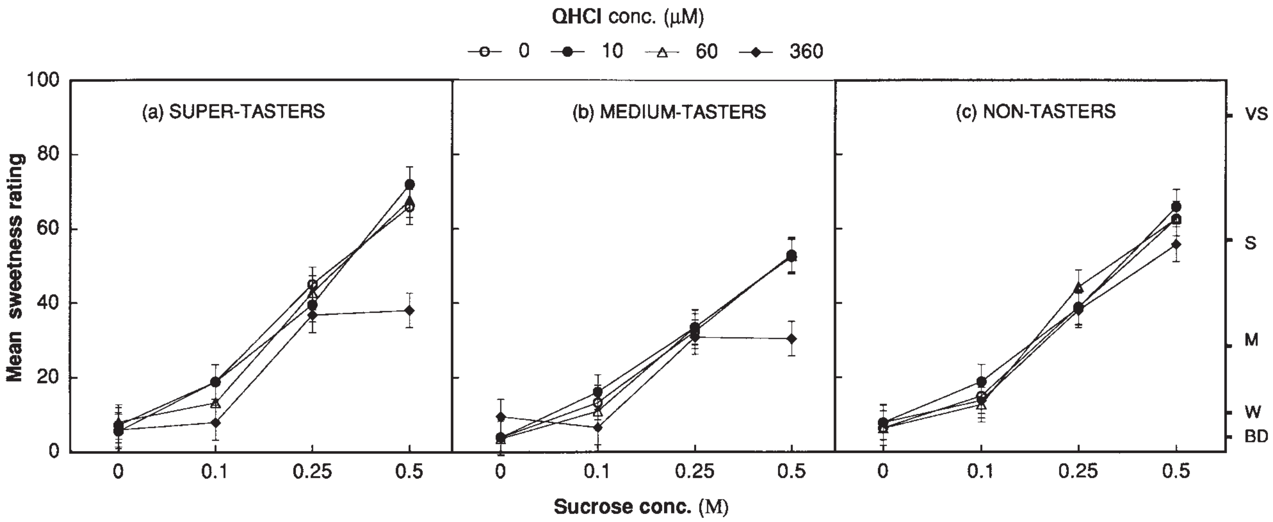

Figure 3 SU/QHCl mixtures: mean (±SEM) ratings of sweetness by the different taster groups as a function of SU concentration for the different QHCl concentrations.

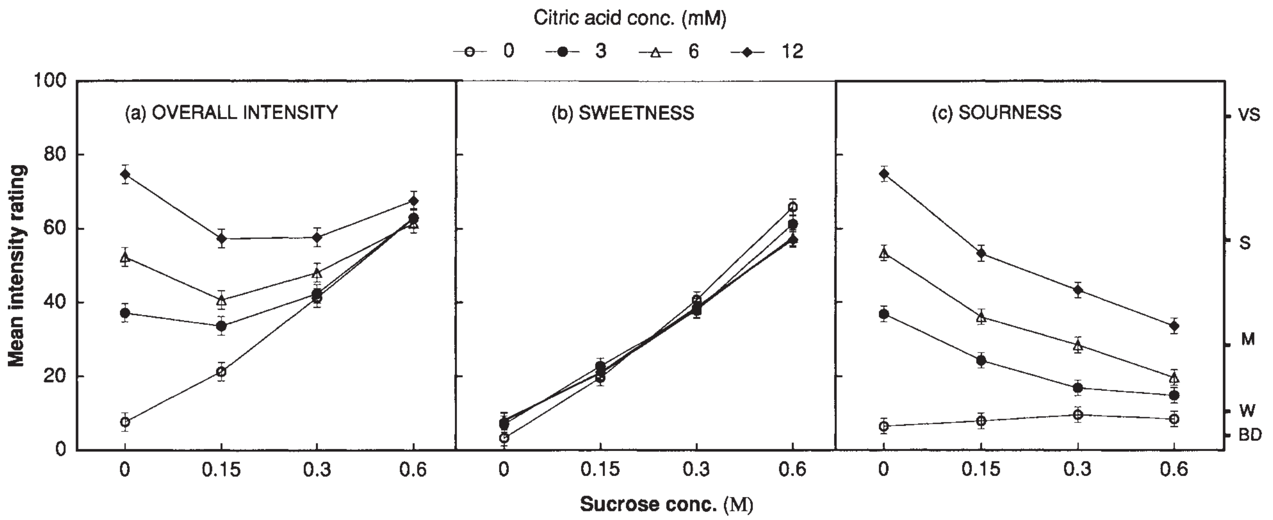

Figure 4 SU/CA mixtures: mean (±SEM) ratings of **(a)** overall intensity, **(b)** sweetness and **(c)** sourness as a function of SU concentration for the different CA concentrations, averaged across all taster groups.

differences in sweetness ratings for the different concentrations of QHCl (see Figure 3). There was also a significant group × SU interaction [$F(6,1480) = 6.12$, $P < 0.0001$], shown in Figure 2c. Here, there were no significant differences between STs and NTs at any SU level. However, both groups had higher sweetness ratings than MTs at 0.5 M SU and STs also had higher ratings than MTs at 0.25 M SU. The group × SU × QHCl interaction [$F(18,1480) = 1.00$] was not significant.

Experiment 2: SU/CA mixtures

Figure 4a–c shows the mean ratings of overall intensity, sweetness and sourness as functions of SU for the different CA concentrations, averaged across all taster groups.

Overall intensity

There were strong main effects for both CA [$F(3,2419) = 208.63$, $P < 0.0001$] and SU [$F(3,2419) = 150.7$, $P < 0.0001$]. Although overall intensity was primarily determined by CA concentration at low SU concentrations (see Figure 4a), at 0.3 and 0.6 M SU, there was clearly much less influence of CA [CA × SU interaction; $F(9,2419) = 50.23$, $P < 0.0001$].

There was no overall difference in overall intensity ratings between groups [$F(2,110) = 0.32$], nor any interaction with CA [$F(6,2419) = 1.05$]. However, Figure 5a shows that, while all groups gave similar ratings over the three lower levels of SU, at the highest level, STs gave significantly higher overall intensity ratings than MTs [group × SU interaction; $F(6,2419) = 2.5$, $P < 0.05$]. The three-way interaction with CA and SU [$F(18,2419) = 1.06$] was not significant.

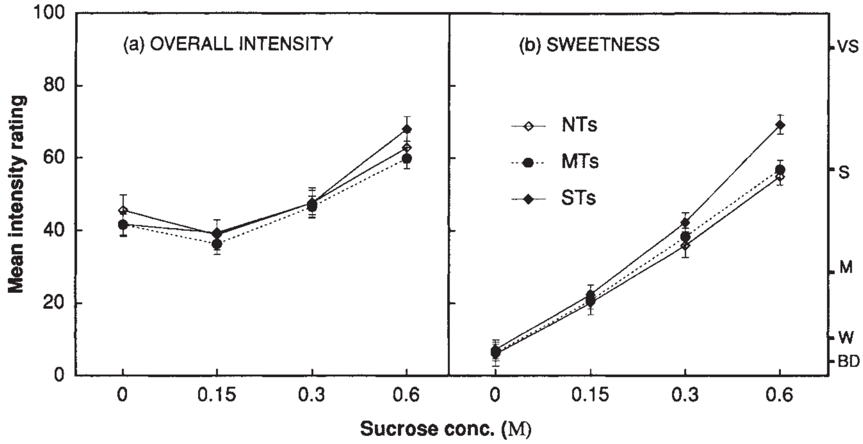

Figure 5 SU/CA mixtures: mean (±SEM) ratings of **(a)** overall intensity and **(b)** sweetness by the different taster groups. These are shown as a function of the tastant for which there was a significant interaction with group.

There was a significant replicate × CA interaction [$F(3,2419) = 9.32$, $P < 0.0001$] produced by higher ratings being given to the high CA levels in the first test.

Sweetness

Sweetness ratings showed a main effect for SU [$F(3,2420) = 704.41$, $P < 0.0001$], but not for CA [$F(3,2420) = 0.52$], although there was a significant CA × SU interaction [$F(9,2420) = 3.04$, $P < 0.005$], reflecting sweetness suppression by all three CA concentrations at 0.6 M SU (see Figure 3b).

There was no overall difference in sweetness ratings between groups [$F(2,110) = 1.68$], nor any interaction with CA [$F(6,2420) = 0.18$]. The significant group × SU interaction [$F(6,2420) = 5.93$, $P < 0.0001$], shown in Figure 5b, reflects the higher sweetness ratings given by STs than by NTs and MTs at 0.6 M SU. The three-way interaction with SU and CA [$F(18,2420) = 0.67$] was not significant.

Sourness

Sourness ratings had main effects for both CA [$F(3,2420) = 460.83$, $P < 0.0001$] and SU [$F(3,2420) = 144.11$, $P < 0.0001$]. Figure 4c shows the overall suppressive effect of SU on sourness, as well as the increase in suppression with increasing SU levels [CA × SU interaction; $F(9,2420) = 28.08$, $P < 0.0001$].

There was no overall difference in sourness ratings between groups [$F(2,110) = 0.39$], nor any interaction with CA [$F(6,2420) = 1.03$] or SU [$F(6,2420) = 1.36$]. The three-way interaction with CA and SU [$F(18,2420) = 1.08$] was also not significant.

Experiment 3: NA/QHCl mixtures

Figure 6a–c shows the mean ratings of overall intensity, bitterness and saltiness as a function of QHCl for the different NA concentrations, averaged across all taster groups.

Overall intensity

Both QHCl [$F(3,1527) = 311.12$, $P < 0.0001$] and NA [$F(3,1527) = 121.86$, $P < 0.0001$] strongly contributed to overall intensity of the mixture. As shown in Figure 6a, however, while overall intensity is determined primarily by NA concentration at the two lowest QHCl levels, as QHCl increased in concentration, it had a greater impact. Thus, at 360 μM QHCl, there was much less effect of NA concentration [QHCl × NA interaction; $F(9,1527) = 30.46$, $P < 0.0001$].

STs gave significantly higher overall intensity ratings than either MTs or NTs, who did not differ [$F(2,48) = 7.24$, $P < 0.002$]. There was also a significant group × QHCl interaction [$F(6,1527) = 11.96$, $P < 0.001$]. As can be seen in Figure 7a, all groups showed increased overall intensity ratings with increasing QHCl concentrations, except from 0 to 10 μM. ST ratings were greater than those of NTs at 10, 60 and 360 μM QHCl, and greater than those of MTs at 60 and 360 μM QHCl. There were no differences between NTs and MTs at any QHCl level. A significant group × QHCl × NA interaction [$F(18,1527) = 2.06$, $P < 0.01$] appears to relate to differences between groups in the role of NA and QHCl in determining overall intensity (see Figure 8). At 360 μM QHCl, ratings of overall intensity for STs were determined primarily by bitterness, since overall intensity is reduced by the two highest NA levels, as is bitterness produced by QHCl (see below). In contrast, for both MTs and NTs, either high bitterness (0 NA) or high saltiness (0.6 M NA) produced increased overall intensity ratings.

Bitterness

Figure 6b shows bitterness ratings as a function of QHCl level. The effects of both QHCl level [$F(3,1527) = 608.29$, $P < 0.0001$] and NA level [$F(3,1527) = 34.13$, $P < 0.0001$] are apparent, the latter particularly in the suppression of the high levels of bitterness once NA at any concentration is

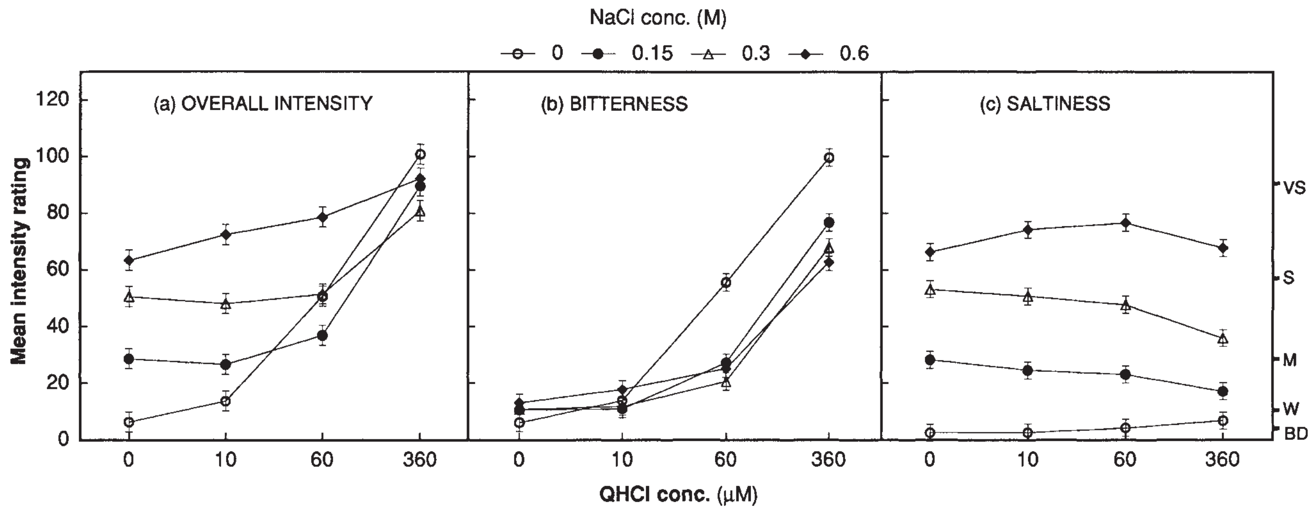

Figure 6 NA/QHCl mixtures: mean (±SEM) ratings of **(a)** overall intensity, **(b)** bitterness and **(c)** saltiness as a function of QHCl concentration for the different NA concentrations, averaged across all taster groups.

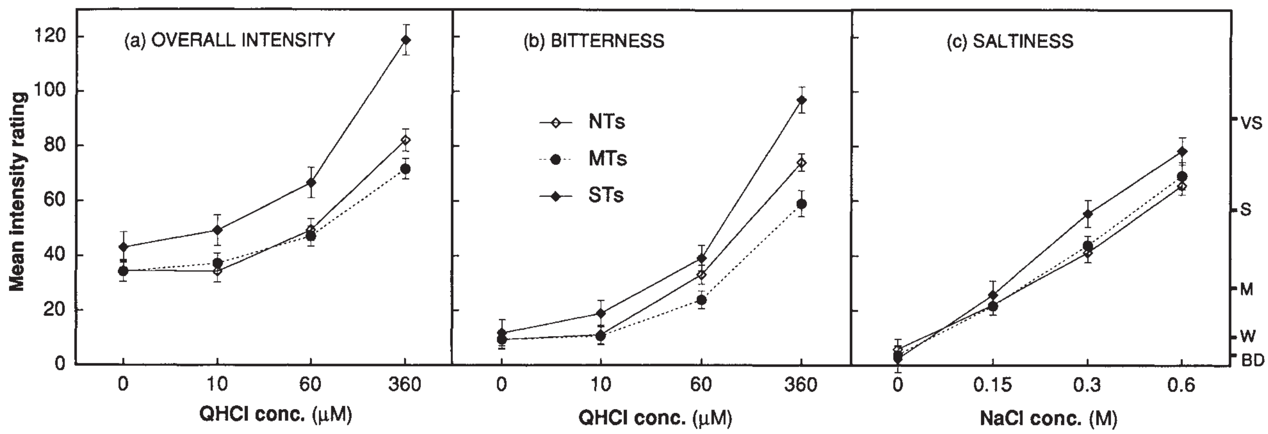

Figure 7 NA/QHCl mixtures: mean (±SEM) ratings of **(a)** overall intensity, **(b)** bitterness and **(c)** saltiness by the different taster groups. These are shown as a function of the tastant for which there was a significant interaction with group.

included in the mixture [QHCl × NA interaction; $F(9,1527) = 17.66$, $P < 0.0001$].

Overall ratings of bitterness differed between the groups [$F(2,48) = 5.17$, $P < 0.01$]. Although NTs and MTs were not significantly different from one another, MTs gave slightly lower ratings. As a result, STs ratings were significantly higher than those of MTs, but not NTs. Differences between STs and MTs at the two highest QHCl levels are evident in Figure 7b [group × QHCl interaction; $F(6,1527) = 12.67$, $P < 0.0001$]. At 360 μM QHCl, STs were also significantly different from NTs who, in turn, gave higher ratings than MTs. The group × NA [$F(6,1527) = 1.19$] and group × NA × QHCl [$F(18,1527) = 1.17$] interactions were not significant.

Saltiness

Figure 6c shows that saltiness was most strongly determined by NA levels [$F(3,1525) = 734.7$, $P < 0.0001$], although there was some suppression by QHCl [$F(3,1525) = 7.66$, $P < 0.0001$], particularly as QHCl levels increased [QHCl × NA interaction; $F(9,1525) = 5.29$, $P < 0.0001$].

While there were no differences between groups in overall saltiness ratings [$F(2,48) = 0.78$], or in the group × QHCl interaction [$F(6,1525) = 1.44$], there was a significant group × NA interaction [$F(6,1525) = 4.34$, $P < 0.0005$]. All groups gave increasing saltiness ratings as a function of NA level (see Figure 7c). However, at 0.3 and 0.6 M NA, STs gave significantly higher saltiness ratings than NTs. The group × NA × QHCl interaction was not significant [$F(18,1525) = 0.67$].

Experiment 4: NA/CA mixtures

Figure 9a–c shows the ratings of overall intensity, saltiness and sourness as a function of CA for the different NA concentrations, averaged across all taster groups.

Overall intensity

As shown in Figure 9a, overall intensity increased as a

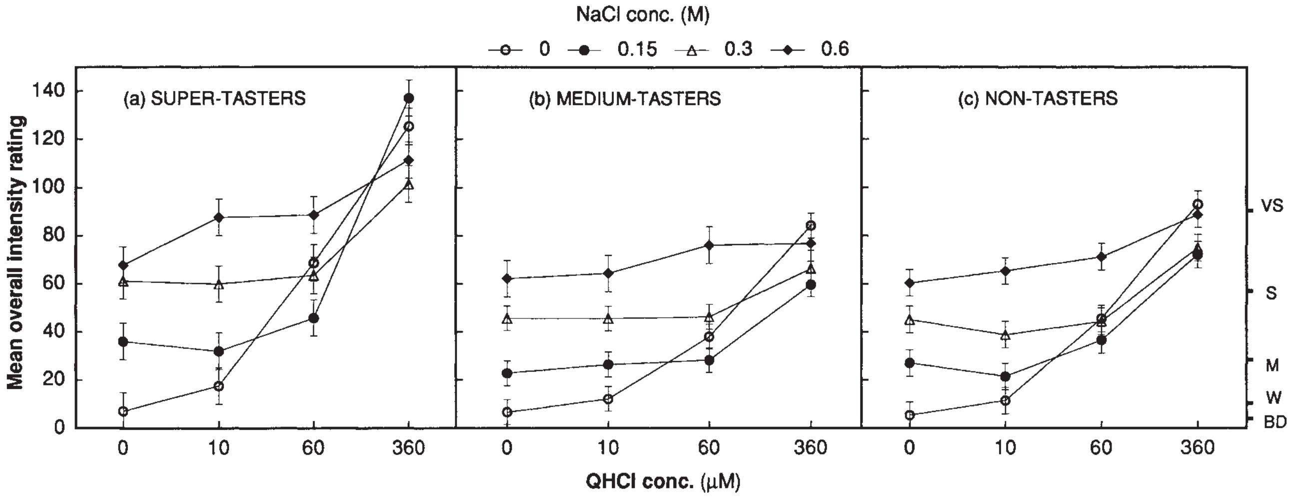

Figure 8 NA/QHCl mixtures: mean (±SEM) ratings of overall intensity by the different taster groups as a function of QHCl concentration for the different NA concentrations.

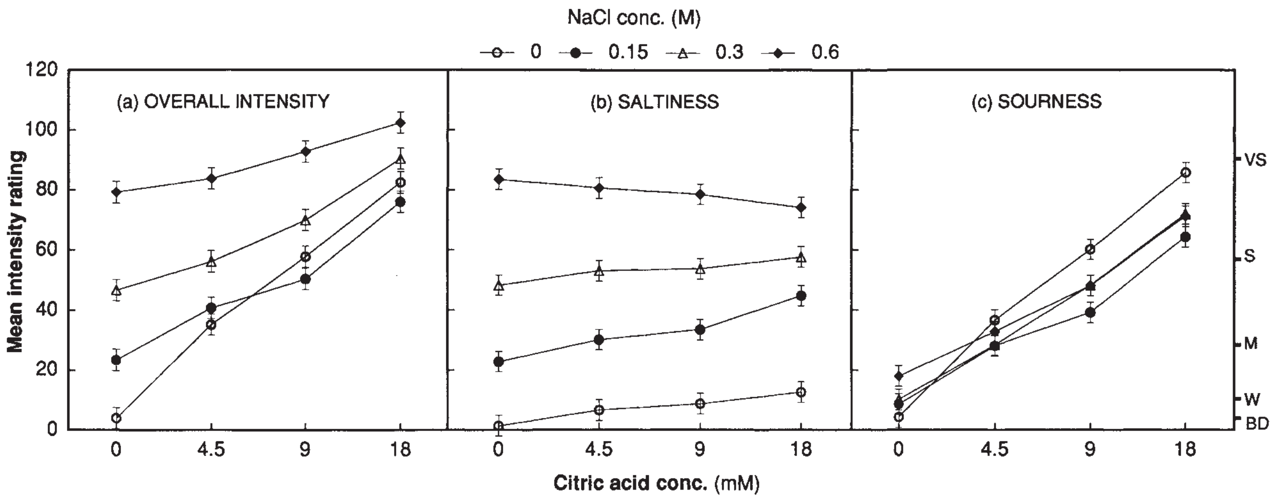

Figure 9 NA/CA mixtures: mean (±SEM) ratings of **(a)** overall intensity, **(b)** saltiness and **(c)** sourness as a function of CA concentration for the different NA concentrations, averaged across all taster groups.

function of both CA [$F(3,1710) = 334.53$, $P < 0.0001$] and NA [$F(3,1710) = 322.91$, $P < 0.0001$] concentrations. Overall intensity was determined mainly by NA at lower levels of CA. However, as CA concentration increased, both NA and CA influenced overall intensity, as indicated by both the increasing compression and continued separation of the NA functions at 18 mM CA [CA × NA interaction; $F(9,1710) = 18.79$, $P < 0.0001$].

Although there was no main effect for taster group [$F(2,54) = 1.92$], there was a significant group × NA interaction [$F(6,1710) = 3.32$, $P < 0.005$]. STs gave higher ratings than both MTs and NTs at 0.3 M NA and NTs only at 0.6 M NA (see Figure 10a). There were no significant differences between MTs and NTs. The group × CA [$F(6,1710) = 1.78$] and group × CA × NA [$F(18,1710) = 0.73$] interactions were not significant.

Saltiness

There were main effects for both NA [$F(3,1712) = 592.91$, $P < 0.0001$] and CA [$F(3,1712) = 7.38$, $P < 0.0001$]. Overall, increasing CA concentration also increased saltiness ratings, perhaps because of perceptual confusion between the two qualities (see Figure 9b). This was not evident at the highest NA level, however, where there was a decrease in ratings at 18 mM CA, relative to NA alone [CA × NA interaction; $F(9,1712) = 4.74$, $P < 0.0001$].

Figure 10b shows that all groups increased their saltiness ratings linearly with NA level. Although there was no overall group difference [$F(2,54) = 0.78$], STs gave higher mean ratings at the higher NA levels [group × NA interaction; $F(6,1712) = 3.87$, $P < 0.001$], with significant differences between STs and MTs at 0.3 M NA and between STs and NTs at 0.6 M NA. The group × CA [$F(6,1712) = 0.26$] and

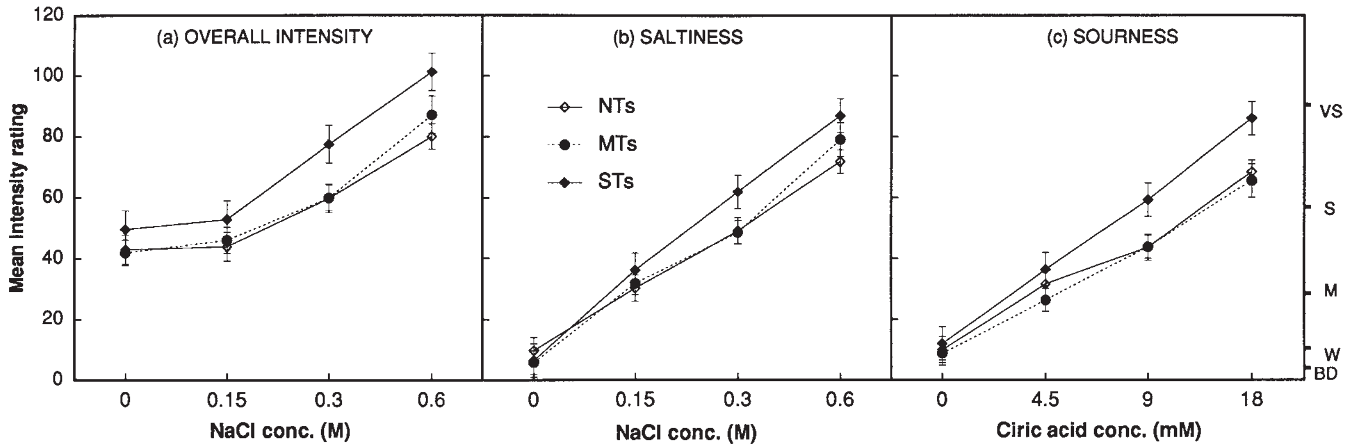

Figure 10 NA/CA mixtures: mean (±SEM) ratings of **(a)** overall intensity, **(b)** saltiness and **(c)** sourness by the different taster groups. These are shown as a function of the tastant for which there was a significant interaction with group.

group × CA × NA [$F(18,1712) = 0.81$] interactions were not significant.

Sourness

As shown in Figure 9c, although sourness ratings increased linearly with CA concentration [$F(3,1712) = 447.25$, $P < 0.0001$], NA exerted a suppressive effect [$F(3,1712) = 15.07$, $P < 0.0001$], particularly at the two highest CA levels [CA × NA interaction; $F(9,1712) = 5.61$, $P < 0.0001$].

There was no overall group main effect [$F(2,54) = 2.12$]. All groups increased sourness ratings with increasing CA concentration (see Figure 10c); however, STs gave higher ratings than MTs and NTs at the two highest CA levels [group × CA interaction; $F(6,1712) = 3.54$, $P < 0.005$]. The group × NA [$F(6,1712) = 1.22$] and group × NA × CA [$F(18,1712) = 0.75$] interactions were not significant.

Discussion

These studies have shown that, using the LMS and classifying subjects into three taster groups based on the rating of a single PROP solution, there was clear evidence of a relationship between PROP sensitivity and the perceived intensity of tastants representing four taste qualities. In addition, differences in the perception of individual tastes were demonstrated in the context of binary mixtures of the type seen within foods and beverages, although almost always confined to the higher tastant concentrations. This is in contrast to some previous findings using saccharin (Bartoshuk, 1979), urea and caffeine (Hall *et al.*, 1975) where taster group differences were found at only lower concentrations, but is consistent with previous ratings of PROP itself, where differences between groups were most obvious at higher intensities (Bartoshuk *et al.*, 1994).

While a number of studies have shown differences between PROP/PTC taster groups in the perception of bitterness and other taste qualities (Hall *et al.*, 1975; Bartoshuk, 1979; Gent and Bartoshuk, 1983; Leach and Noble, 1986; Bartoshuk *et al*, 1988, 1998; Prutkin *et al.*, 1999), other studies have failed to demonstrate any differences. For example, Schifferstein and Frijters (Schifferstein and Frijters, 1991), studying responses to KCl, QHCl, NaCl plus QHCl/NaCl mixtures, and Smagghe and Louis-Sylvestre (Smagghe and Louis-Sylvestre, 1998) studying NaCl, sucrose, saccharin, caffeine and Naringin, both failed to find PROP taster/non-taster differences in the perception of other taste intensities. Yet other studies have found group differences for some tastants but not others. Hall *et al.* (Hall *et al.*, 1975) found PTC taster/non-taster differences for urea and caffeine, but not QHCl, while Bartoshuk (Bartoshuk, 1979) found differences for saccharin and sucrose, but neither QHCl nor NaCl. Mela (Mela, 1989) failed to find significant taster/non-taster differences for QHCl and caffeine, despite apparent differences in the mean values and significant group differences for urea, sucrose octa-acetate and denatonium benzoate.

The inability to find relationships between PROP tasting and perceived intensity of other tastes may be due in some studies to a failure to discriminate between MTs and STs—in other words, only discriminating between tasters and non-tasters. The present data suggest that the key group differences would have been diluted to a large extent in previous studies by combining MTs and STs, since the overall pattern of differences shows that STs were most clearly distinct in their responses from the other two groups. At least in the context of mixtures with other tastes, STs perceived the bitterness of QHCl, the sweetness of SU, the saltiness of NA and the sourness of CA to be more intense than did MTs and NTs. This pattern of group differences is perhaps counter-intuitive, in that it might be expected that NTs of PROP would differ most from the two taster groups. In fact, only in ratings of the bitterness of QHCl in NA/QHCl mixtures did MTs give clearly higher ratings than NTs. The distinctiveness of STs in these studies also provides further evidence, albeit indirect, for a tri-modal distribution of PROP sensitivity within the population (Bartoshuk *et al.*, 1994).

Many previous studies, including those cited above, have adopted *a priori* distinctions between tasters and non-tasters without consideration of further taster divisions. However, Prutkin *et al.* (Prutkin *et al.*, 2000) have recently pointed out that failure to discriminate between taster groups can also result from defining groups using measures, for example category scales, which act to compress the ratings of tasters at the top end of the scale, effectively reducing discrimination between MTs and STs. For example, Kaminski *et al.* (Kaminski *et al.*, 2000), using a nine-point category scale to measure suprathreshold PROP intensity, found a bimodal distribution of scores, but with the highest rating (9) being the most frequent. This suggests that a more extended scale would have allowed for finer discrimination, and perhaps a different distribution, of intensity ratings. The recent adoption of the LMS to classify PROP taster groups has provided a way of reducing the risk of such ceiling effects and subsequent compression, since the top end of the scale can refer to non-taste (as in the present studies) or even non-oral sensations and hence be unrelated to sensations associated with PROP sensitivity (Bartoshuk *et al.*, 2000; Prutkin *et al.*, 2000).

In addition to showing a relationship between PROP tasting and the intensity of individual taste qualities, there is also evidence of group differences in the perception of mixture interactions. The most apparent of these is with measures of overall intensity of the mixtures. McBride (McBride, 1989) proposed that overall intensity of a heterogeneous taste mixture is determined by a dominant component. He showed, for example, that the total intensity of a mixture containing 0.05 M CA was uninfluenced by the concentration of SU added (up to 0.8 M). While similar patterns of interaction were seen in experiment 1 with SU/QHCl mixtures, in ratings of the overall intensity of NA/CA mixtures (experiment 4), both mixture components contributed. The maximum intensity was greater at the highest concentrations of both NA and CA than for any other concentrations of either CA or NA, alone or in combination. A degree of integration was also evident in the overall intensity ratings of NA/QHCl and SU/CA mixtures. Hence, these data suggest that the dominant-component hypothesis for overall intensity does not hold for all taste mixtures. This has also been suggested by other studies. In both NA/QHCl and SU/CA mixtures, Schifferstein and Fritjers (Schifferstein and Fritjers, 1990, 1992) found that overall intensity could be predicted from the sum of both saltiness and bitterness, or sweetness and sourness. As in the present study, this occurred even though the two tastants in each mixture were unequal in exerting suppression, with saltiness and sweetness being much more effective. This suggests that while one taste quality may be highly effective in suppressing another in a mixture, the two different qualities can be perceptually integrated when subjects are asked to evaluate overall intensity.

Here, for the SU/QHCl and NA/QHCl mixtures, STs gave greater overall intensity ratings than did MTs and NTs, suggesting differences in the perception of the integrated mixture. However, despite such integration, the interactions with tastant intensities in each of the experiments (QHCl in experiments 1 and 3, SU in experiment 2 and NA in experiment 4) showed that certain tastants were more influential in determining overall intensity and, hence, in demonstrating group differences.

For NA/QHCl mixtures, there were also taster group differences in the way in which different taste qualities determined the overall intensity of the mixture. For STs, consistent with their much greater ratings of overall intensity as a function of QHCl intensity, the bitterness of QHCl seemed to determine overall intensity to a greater extent than it did for MTs and NTs, who were equally influenced by both QHCl and NA. One implication of these data is that whether the components in a mixture are integrated to produce overall intensity, or overall intensity is dominated by one component, may be a function of the subject's sensitivity to the individual tastants.

There were also some complex interactions between the individual taste components that suggest that taster groups do not always perceive such interactions equivalently. The present mixture data showed patterns of mutual, but asymmetric, suppression. This is consistent with previous studies of NA/QHCl (Schifferstein and Fritjers, 1990, 1991, 1992; Breslin and Beauchamp, 1995) and SU/CA (McBride, 1989; Schifferstein and Fritjers, 1990) mixtures, which have shown that NA and SU are more effective in suppressing the bitterness and sourness of QHCl and CA, respectively, than vice versa. Here, the sweetness of 0.6 M SU in the SU/QHCl mixtures showed suppression by 360 μM QHCl, but primarily only for STs and MTs. This is certainly consistent with NTs perceiving a lower level of bitterness from QHCl and consistent with previous data showing that the magnitude of suppression depends primarily on the intensity of the suppressor (McBride, 1989). It suggests, as hypothesized, that taste mixture suppression may vary according to taster status and perhaps may explain some examples of failure to find suppression in previous studies. Taster group differences in these interactions may also explain the anomalous finding that both STs and NTs gave higher ratings than MTs for the sweetness of these same mixtures at high SU levels (see Figure 2c). Since NTs perceive QHCl as less bitter, then the higher ratings of sweetness may reflect the lack of a suppressive effect by QHCl.

In summary, these data provide evidence that, at least in some complex taste systems, genetic differences in taste sensitivity determine the degree of interaction which takes place, with the implication that the different taster groups may perceive the taste qualities foods and beverages differently. In addition, however, they suggest that group differences may only begin to be evident at high tastant intensities, and also primarily when STs are discriminated from other taster groups.

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