



Taste mixture interactions: Suppression, additivity, and the predominance of sweetness

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ABSTRACT

Most of what is known about taste interactions has come from studies of binary mixtures. The primary goal of this study was to determine whether asymmetries in suppression between stimuli in binary mixtures predict the perception of tastes in more complex mixtures (e.g., ternary and quaternary mixtures). Also of interest was the longstanding question of whether overall taste intensity derives from the sum of the tastes perceived within a mixture (*perceptual additivity*) or from the sum of the perceived intensities of the individual stimuli (*stimulus additivity*). Using the general labeled magnitude scale together with a sip-and-spit procedure, we asked subjects to rate overall taste intensity and the sweetness, sourness, saltiness and bitterness of approximately equi-intense sucrose, NaCl, citric acid and QSO₄ stimuli presented alone and in all possible binary, ternary and quaternary mixtures. The results showed a consistent pattern of mixture suppression in which sucrose sweetness tended to be both the least suppressed quality and the strongest suppressor of other tastes. The overall intensity of mixtures was found to be predicted best by perceptual additivity. A second experiment that was designed to rule out potentially confounding effects of the order of taste ratings and the temperature of taste solutions replicated the main findings of the first experiment. Overall, the results imply that mixture suppression favors perception of sweet carbohydrates in foods at the expense of other potentially harmful ingredients, such as high levels of sodium (saltiness) and potential poisons or spoilage (bitterness and sourness).

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1. Introduction

Most of what is known about taste interactions at suprathreshold levels has come from studies of simple binary mixtures (see Keast and Breslin [1] for review). Although these studies have yielded a great deal of information about how specific tastes and taste stimuli interact, little is known about how these interactions contribute to the perception of complex mixtures like those encountered in foods and beverages. For example, studies of binary mixtures have established that bitterness can be suppressed both by sweet tasting stimuli [2–7] and by sodium salts [6,8], and that sweetness can suppress both sourness [9–11] and saltiness [12,13]. Studies have also shown that sweetness can be suppressed by stimuli that evoke bitterness [2,14], saltiness [13,15] or sourness [16–18]. An obvious question is how these various suppressive interactions (e.g., sweetness vs. bitterness) may be altered when additional taste stimuli (e.g., salts or acids) are present, as they typically are in foods and beverages, and how they contribute to the overall perceived intensity of taste.

To our knowledge there are only two published studies of interactions within heterogeneous ternary or quaternary taste mixtures that are relevant to the first question. Breslin and Beauchamp [19] focused on a specific ternary mixture of sweet, bitter and salty stimuli to investigate the idea that sodium salts act as ‘flavor enhancers’ by suppressing bitterness, which then releases sweetness from suppression by bitterness. The authors found support for their hypothesis when mixtures of urea and sucrose were rated as less bitter and more sweet after sodium acetate was added. An earlier study by Bartoshuk [20] that included both ternary and quaternary mixtures investigated the broader hypothesis that the amount of mixture suppression depends upon the relative slopes of the psychophysical functions of the stimuli in a mixture (i.e., stimuli that have steeper psychophysical functions will tend to suppress stimuli that have shallower psychophysical functions). Some but not all of the results were consistent with this hypothesis, and the conclusion that sour taste dominates in mixtures [20] was not supported by later studies [10,21,22]. The reason for the disagreement between studies is unclear, but the more recent studies used the sip-and-spit method to deliver taste stimuli whereas Bartoshuk used a dorsal flow method. Because these two methods are known to produce different psychophysical functions for taste [23], it is possible

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that mixture interactions are different when stimuli are tasted inside the mouth rather than flowed over just the front of the tongue.

Like mixture suppression, research on how taste stimuli combine to yield total taste intensity has been carried out almost exclusively with binary mixtures. Studies have generally found sub-additivity, i.e., the sum of the perceived intensities of the component stimuli when tasted alone exceeded the perceived intensity of the mixture; total taste intensity was predicted instead by the sum of the perceived intensities of the tastes experienced *within* the mixture [4,11,21,24]. This result suggests the occurrence of *perceptual additivity*, i.e., additivity of taste intensity rather than additivity of stimulus intensity. This hypothesis has logical appeal as it is reasonable to expect that overall intensity would depend on the tastes perceived after any and all peripheral [8,25,26] and central [2,7,27] interactions have occurred. Perceptual additivity had been assumed by researchers in earlier studies that used a form of ratio scaling in which subjects gave estimates of the intensity of individual tastes within mixtures as fractions of the overall intensity of the mixtures [e.g., 20,28].

It is notable that McBride [10,22] argued that sub-additivity in binary and ternary mixtures could be explained by a 'dominant component model' of taste mixture perception in which no integration of taste components occurs and overall taste intensity is determined by the strongest component stimulus. Although McBride's model seems inconsistent with mixture suppression, which he also reported, the ability of the model to predict overall taste intensity has never been tested directly against the perceptual additivity hypothesis, particularly using complex heterogeneous taste mixtures.

The present study therefore had three main goals: The first was to investigate whether suppressive interactions observed in binary mixtures are predictive of interactions in ternary and quaternary mixtures under conditions that approximate normal, 'active' tasting. The second was to determine if under the same conditions one taste quality (e.g., sweetness or sourness) tends to dominate the perception of mixtures in which they appear. Finally, we sought to provide a direct test of the hypothesis that overall taste intensity equals the sum of the perceived intensities of the tastes within a mixture.

2. Experiment 1

This experiment was designed to address each of the three main goals of the study by using a direct scaling task to measure the perceived intensity of sweetness, saltiness, sourness and bitterness of 4 taste stimuli and their binary, ternary and quaternary mixtures, plus the overall taste intensity of each mixture.

2.1. Methods

2.1.1. Subjects

A total of 35 subjects (23 females and 12 males) between 19 and 42 years of age were recruited from public postings on the Yale University Medical School and Yale College campuses. Each person gave informed consent and was paid for their participation. All subjects were self-reported healthy nonsmokers who had no known taste or smell disorders or deficiencies. The subjects were asked to refrain from eating or drinking foods or beverages for at least 1 h prior to their scheduled session.

2.1.2. Stimuli

The taste stimuli used were aqueous solutions of 0.56 M sucrose, 0.32 M NaCl, 10 mM citric acid, 0.18 mM QSO₄ (4), and all possible binary mixtures (6), ternary mixtures (4), and the quaternary mixture (1). Pilot testing was carried out to choose concentrations of the individual stimuli that produced approximately equi-intense sweetness, saltiness, sourness and bitterness. The sweetness of 0.56 M sucrose was used as a benchmark because it evoked, on average, intensity ratings between 'weak' and 'moderate' on the gLMS. Since

including multiple stimulus concentrations for each stimulus would have made the study of all possible mixtures interactions unwieldy, we chose to measure interactions in the range of mild taste intensities that are most typical in foods and beverages. An umami stimulus was not included because the use of 5 taste stimuli would have significantly increased the total number of stimuli (from 15 to 26) and, more importantly, because the unfamiliarity of the umami taste among most North Americans would have complicated the interpretation of its suppression in complex mixtures. All taste stimuli were prepared weekly in 250-mL samples with deionized water and stored in airtight flasks. The stimuli were delivered using the sip-and-spit method, with subjects receiving 5-mL aliquots. The taste stimuli and a container of deionized water for rinsing between stimuli were heated in circulated water baths to 37 °C to render the stimuli and rinses thermally neutral to the mouth.

2.2. Procedure

2.2.1. Practice session

Prior to the first data collection session, all subjects attended a short practice in which they were instructed in how to use the general version of the labeled magnitude scale (gLMS). The gLMS [29–31] is a category-ratio scale [32] bounded by 'no sensation' at the bottom and 'strongest imaginable sensation of any kind' at the top, with its intermediate intensity labels (i.e., weak, moderate, strong, and very strong) spaced quasi-logarithmically according to their empirically determined semantic magnitudes [30]. The scale was displayed on a computer monitor and subjects used a mouse to move a cursor along the scale to make their ratings. After the instructions were given, the subjects were asked to rate a list of 15 remembered or imagined oral sensations (i.e., the sweetness of cotton candy and the burn of cinnamon gum) to give them experience using the gLMS in the broad context of normal oral perception. Subjects were then instructed to rate the overall taste intensity produced by 4 taste stimuli (0.56 M sucrose, 0.32 M NaCl, 10 mM citric acid, and 0.18 mM QSO₄) as well as a mixture of sucrose, NaCl, and citric acid. The subjects were to hold the stimulus in the mouth for 2 s, expectorate on the experimenter's command, and then rate overall taste intensity on the gLMS.

2.2.2. Experimental session

Subjects attended 2 experimental sessions. In the first session the subjects' task was to rate overall taste intensity with the instructions to base their ratings on the "total impact" of the stimulus. This instruction was intended to encourage subjects to rate their overall impression of the stimuli, as they might do during normal tasting, and to discourage attempts to analyze the sensations into individual taste qualities. In the second session subjects rated the intensity of the individual taste qualities: sweetness, saltiness, sourness, bitterness, and 'other' (in that order). Subjects were told that 'other' referred to any tastes or flavors that did not fall into the typical categories of sweet, salty, sour, or bitter. This category was included because of the possibility that subjects might detect an odor (see below). However, mean ratings of 'other' were below 'barely detectable' for all stimuli, and so were not included in the final data analyses.

Both sessions consisted of two blocks of 15 stimuli with a 5-min break between blocks. In one block the solutions were sipped and tasted normally, with the nose open. In the other block subjects wore a nose clip as they sipped the solutions and made their ratings. The order of 'nose-open' and 'nose-closed' blocks was counterbalanced across subjects. In the 'nose-closed' blocks the subjects removed the nose clip after they made their rating. Note that a nose-closed condition was included in the experiment because preliminary data had indicated that mixtures containing sucrose and citric acid produced an odor that was perceptible to some but not all subjects. Subsequent analyses showed that while there was a slight trend for ratings made with the nose open to be higher than ratings made with

the nose closed, this difference was not significant for any of the 15 stimuli. As a result the data from the 2 conditions were treated as replicates in all subsequent data analyses.

In both blocks the subjects sipped the solutions into the mouth, swished them gently for 2 s, then expectorated the solutions and made normal tasting movements with their mouths as they rated stimulus intensity. Although swallowing was not allowed, the tasting movements were intended to ensure maximum spread of the stimulus throughout the mouth and palate. The instructions were to rate the maximum taste intensity perceived, whether during the initial sipping phase or during normal tasting after expectoration. There was a 60-s inter-trial interval between stimuli, during which subjects rinsed vigorously at least 3 times with 37 °C deionized water. The subjects were randomly assigned to one of four groups, and each group received the stimuli in a different pseudorandom order.

2.2.3. Data analysis

Analyses of the frequency distributions of taste ratings of overall intensity and individual taste qualities showed consistent deviations from normality, with nearly all distributions being skewed to the right, consistent with log-normal distributions. Kolmogorov–Smirnov tests confirmed that the frequency histograms did not deviate significantly from the log-normal distribution. Thus ratings were converted to $\log_{10}$ values before repeated-measures ANOVAs were conducted. Differences between specific stimuli were assessed using Tukey HSD post-hoc tests. Because conversion to logarithms complicates the assessment of taste additivity in mixtures, additivity was evaluated arithmetically using normalized intensity ratings. The data were normalized to ensure that each subject's data had equal weight in the additivity analysis, thus preventing individuals who gave higher taste intensity ratings from having a disproportionate influence on the results. Normalization was achieved by first dividing each subject's overall mean taste intensity rating (calculated across all stimuli) into the grand mean of taste intensity ratings for all subjects. This operation yielded a normalization factor for each individual: subjects whose mean ratings exceeded the group mean had a factor <1 and subjects whose mean ratings were less than the group mean had a factor >1 . The subjects' raw intensity ratings were then multiplied by their individual normalization factor, resulting in all subjects having the same overall mean rating and contributing equally to the additivity analysis.

2.3. Results and discussion

2.3.1. Mixture suppression

The present results support and extend the earlier evidence that suppression dominates interactions between and among suprathreshold tastes in heterogeneous mixtures. Shown in Fig. 1 are the log-mean intensity ratings of the 4 primary taste qualities (sweetness, saltiness, sourness, and bitterness) evoked by each of the 4 taste stimuli alone and in mixture with the other 3 stimuli. The results show that suppression occurred for all 4 tastes but in greatly varying amounts. Repeated-measures ANOVAs with stimulus and replicate as factors were conducted on the intensity ratings for the primary taste quality of each stimulus by itself and in the different mixtures. The analysis confirmed that there was a significant main effect of stimulus for each taste quality [sweetness, $F_{(7,245)} = 6.08$, $p < 0.0001$; saltiness, $F_{(7,245)} = 21.1$, $p < 0.00001$; sourness, $F_{(7,245)} = 9.82$, $p < 0.00001$; and bitterness, $F_{(7,245)} = 16.25$, $p < 0.00001$], indicating that significant mixture suppression occurred for each stimulus. However, post-hoc tests (Tukey HSD, $p < 0.05$) showed that sucrose sweetness was much less susceptible to suppression than were the other tastes. Sweetness was not reduced significantly in any binary mixture, whereas saltiness and sourness were suppressed in 2 binary mixtures and bitterness was suppressed in 1 binary mixture (with sucrose). In addition, sucrose sweetness was maximally suppressed by just 42.7% in the

quaternary mixture, whereas NaCl saltiness, citric acid sourness and QSO₄ bitterness were maximally suppressed by 84.5%, 83.2% and 86.2%, respectively.

As well as being the stimulus most resistant to suppression, sucrose was also the dominant suppressor of other tastes. In binary mixtures sucrose significantly reduced the tastes of each of the other 3 stimuli (Tukey HSD, $p < 0.05$), and for saltiness and sourness the degree of suppression was not significantly less than what occurred in the quaternary mixture. In other words, suppression by sucrose alone could account for the amount of suppression of saltiness and sourness observed in the quaternary mixture. Sucrose was an especially effective suppressor of saltiness, which in binary mixture with NaCl was reduced by 82.6%. Although previous studies had demonstrated that sucrose can suppress saltiness [12,13], sourness [11] and bitterness [2–7] in binary mixtures, no previous study had established its dominance over the other 3 tastes while also being the most resistant taste to suppression.

The least effective suppressor was citric acid, which in binary mixtures failed to significantly suppress any of the other 3 tastes. Saltiness was the most suppressed taste quality overall, although sourness was also suppressed significantly in all but 1 mixture (with QSO₄). In most binary and ternary mixtures QSO₄ bitterness was more resistant to suppression than were saltiness or sourness, but bitterness was suppressed to a similar degree (to nearly barely detectable) in the quaternary mixture.

The evidence that sweetness is the dominant taste quality in taste mixtures conflicts with Bartoshuk's [20] finding that citric acid sourness was most resistant to suppression. However, data from that study (Table 1, p. 645) also show that sweetness was the strongest taste reported in 5 of the 7 mixtures containing sucrose, including a binary mixture with citric acid in which sweetness was not suppressed at all. Other studies of binary mixtures have also reported that sweetness suppresses sourness more than the reverse [9–11]. The conclusion that sourness was dominant in the Bartoshuk study came from the very high sourness ratings given to 3 ternary mixtures and the quaternary mixture, all of which were rated as more sour than citric acid alone. The complete absence of sourness suppression in ternary and quaternary mixtures is surprising and may have been a byproduct of flowing the stimulus over the anterior dorsum of the tongue. Alternatively, restricting gustatory stimulation to a single taste region, especially with the tongue extended from the mouth, may hamper perceptual analysis of complex mixtures. Several subjects in the present study exhibited negative reactions (e.g., frowns and grimaces) in response to the quaternary mixture, particularly upon initial exposure. Perhaps under the conditions of dorsal flow stimulation the unpleasantness of the complex taste was attributed primarily to sourness, whereas in the present study subjects may have been better able to analyze the percept into its component tastes. Analysis of the mixtures would have been aided in the present study not only by spreading the stimulus throughout the mouth, but also by continuing to actively taste the residual stimulus as subjects made their ratings.

On the other hand the present data are consistent with Bartoshuk's [20] finding that adding NaCl to a mixture of sucrose and quinine deepened the suppression of both sweetness and bitterness. This result is at odds with Breslin and Beauchamp's [19] report that adding Na acetate to a mixture of sucrose and urea decreased bitterness and increased sweetness. A possible explanation for this disagreement is the weaker saltiness of Na acetate compared to NaCl. In an earlier paper Breslin and Beauchamp [8] took advantage of this difference to test the hypothesis that Na salts suppress bitterness primarily via a peripheral effect of sodium on bitter taste transduction rather than a central effect of saltiness. By using Na acetate in their study of salt as a flavor enhancer, Breslin and Beauchamp produced bitterness suppression, and consequently the release of sweetness from suppression by bitterness, without inducing a strong salty taste that could have

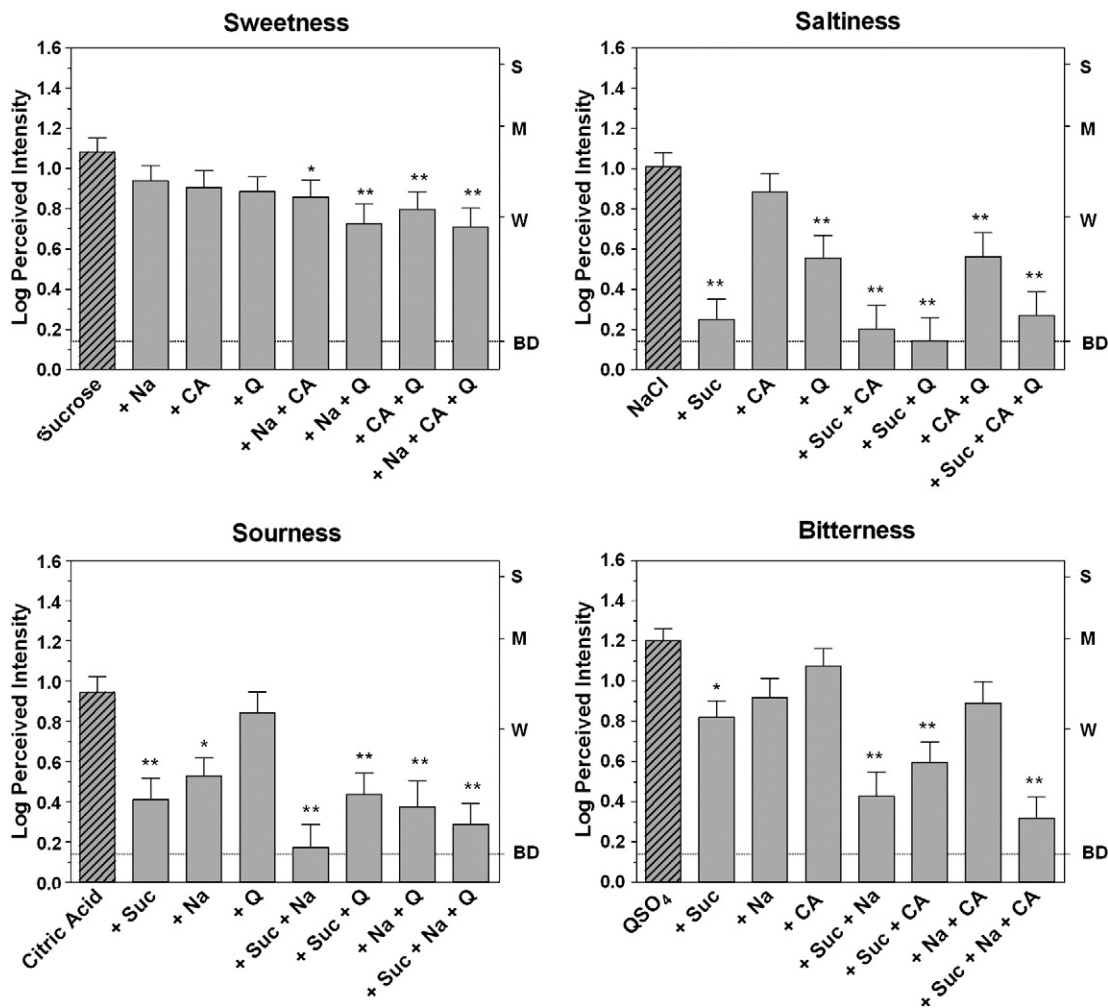


Fig. 1. Shown are the log-mean ratings of perceived intensity of sweetness, saltiness, sourness and bitterness made in response to each of the individual taste stimuli and all stimulus mixtures. For example, the graph in the top left hand corner contains the mean sweetness ratings given to sucrose alone and to each of the mixtures that contained sucrose. Suc = sucrose; CA = citric acid; Na = NaCl; Q = QSO₄. Asterisks indicate statistically significant suppression of the primary taste quality (* <0.05 ; ** <0.01) and vertical bars represent the standard errors of the means (SEMs). Letters on the right y-axis represent semantic labels of the gLMS: BD = barely detectable; W = weak, M = moderate; S = strong.

added its own suppressive effect on sweetness. Note, however, that based on the present results the degree of sweetness suppression by saltiness would not be expected to be large. Although adding NaCl reduced the mean rating of sucrose sweetness in binary mixture, the reduction was not significant (Tukey HSD >0.05).

The question of how NaCl interacts with sweetness and bitterness in a ternary mixture is representative of the larger question of whether interactions in ternary and quaternary mixtures can be predicted from interactions in binary mixtures. Most of the evidence suggests they can. First, based on the resistance of sucrose sweetness to mixture suppression, sweetness should be the dominant taste quality in mixtures of equi-intense tastes that include sucrose. This prediction receives support from the data shown in Fig. 2. For all 7 mixtures that contained sucrose, mean taste intensity ratings were higher for sweetness than for the other taste qualities, and these differences were significant for all except the sucrose + QSO₄ and sucrose + citric acid + QSO₄ mixtures. Second, mixture suppression tends to be additive. The best examples of this tendency are the effects of combining sucrose + NaCl on citric acid and quinine. Indeed, sucrose and NaCl are responsible for virtually all of the suppression of these two taste stimuli. In addition, the fact that sucrose sweetness was significantly suppressed only in ternary and quaternary mixtures also implies additivity of weak suppressive effects between and among the other stimuli.

2.3.2. Additivity

Fig. 3 displays the relationship of the normalized mean ratings of overall taste intensity to the intensities predicted by stimulus additivity, perceptual additivity, and the dominant component hypothesis. The clearest finding is that, consistent with earlier studies [4,11,21,24,33], stimulus additivity (i.e., the sum of the unmixed taste intensities) was by far the poorest predictor, as it greatly overestimated overall taste intensity for all of the mixtures. In contrast, the sum of the perceived intensities of the tastes within the mixtures was a very good predictor of overall intensity, with the estimated means falling within the 95% confidence intervals of the actual means for several of the mixtures [4,11,21,24]. The dominant component hypothesis also yielded much better estimates than did stimulus additivity [22,34]. A dotted horizontal line drawn through the means for perceived sourness and bitterness enables direct comparisons to be made between the intensities of these dominant qualities and the overall intensities of the mixtures in which they appeared. Although the perceived intensities of these two stimuli are close to the overall intensities of some of the mixtures, for many they are clearly poorer predictors than are the estimates that assume perceptual additivity. It is particularly noteworthy that the dominant component hypothesis underestimated the overall intensity of the citric acid + QSO₄ binary mixture, which according to the hypothesis should have equaled the intensity of the QSO₄ stimulus by itself. The present results therefore

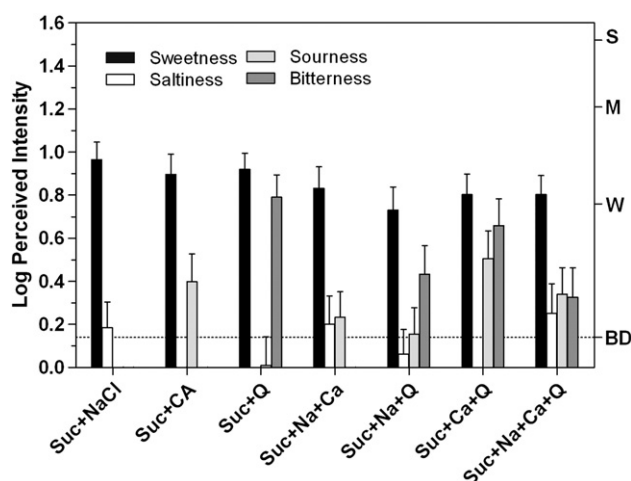


Fig. 2. Log-means of ratings of the perceived intensity of sweetness (black bars), saltiness (white bars), sourness (light gray bars) and bitterness (dark gray bars) for the mixtures shown. The data are replotted from Fig. 1. Vertical bars = SEMs.

support the perceptual additivity model and extend it to ternary and quaternary taste mixtures.

3. Experiment 2

Although the dominance of sucrose sweetness in the present study is consistent with results from studies of binary mixtures, the large difference between sweetness and the other tastes, particularly sourness, led us to assess our psychophysical procedure for possible sources of bias that may have favored this outcome. One potential source was the order in which subjects rated the four taste qualities: sweetness was rated first on every trial, followed by saltiness, sourness and bitterness. It was possible that attending to sweetness first on every trial favored rating sweetness over the other taste qualities, which may have begun to adapt by the time their intensities were rated. Focusing attention on sweetness first may also have increased the probability that sweetness would be perceived in the ternary and quaternary mixtures, since it has been argued that cognitive factors can limit the number of taste qualities perceived in complex mixtures

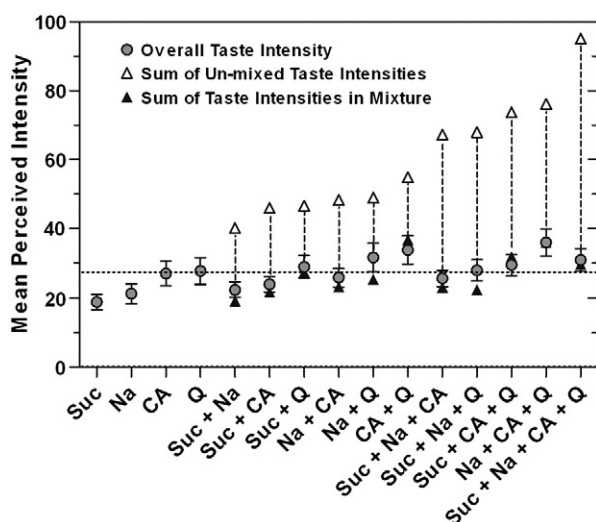


Fig. 3. Shown are the arithmetic means of the ratings of overall perceived intensity for the individual taste stimuli and taste mixtures (gray circles), compared to the sum of the perceived intensities of the primary taste quality of the individual taste stimuli when they were perceived alone (open triangles) and to the sum of the rated intensities of the individual taste qualities as perceived within each mixture (filled triangles). The dashed horizontal line represents the prediction of the dominant component hypothesis. Vertical bars indicate SEMs.

[35,36]. Finally, because no prior studies of taste mixtures had tested solutions warmed to 37 °C in order to be thermally neutral in the mouth, and because sweetness is known to be enhanced by warming [37,38], it was important to rule out temperature as a possible contributing factor to the predominance of sweetness. Thus we conducted a second experiment in which the order of taste ratings was counterbalanced and both room temperature and warmed stimuli were used.

3.1. Methods

3.1.1. Subjects

A total of 28 subjects (16 females and 12 males) between 18 and 36 years of age were recruited from public postings on the Yale University College and Medical School campuses. Each person gave informed consent and was paid for their participation. Inclusion criteria and constraints on eating and drinking were the same as in Experiment 1.

3.1.2. Stimuli

Taste stimuli were the same as those used in Experiment 1. However, the stimuli were placed in 2 circulated water baths prior to the beginning of each session to enable presentation at the same temperature used in Experiment 1 (37 °C) and at room temperature (unregulated, ≈21 °C).

3.2. Procedure

3.2.1. Practice session

Subjects served in a practice session identical to that of Experiment 1.

3.2.2. Experimental session

There were 2 experimental sessions in which subjects rated the intensity of the individual taste qualities of the 15 stimuli on the gLMS. Taste qualities were rated in the sequence 'sweet', 'salty', 'sour', 'bitter', and 'other' in one session and in the reverse sequence in the other session. The order of the 2 rating sequences was counterbalanced across subjects. As in Experiment 1, mean other ratings were below 'barely detectable' for all stimuli, and so were not included in the final data analyses. Both sessions consisted of 2 blocks of the 15 stimuli with a 5-min break during which they rinsed with deionized water and ate an unsalted cracker to clear the palate. In one block the solutions were sipped and tasted at room temperature, and in the other block they were tasted at 37 °C. The order of the temperature blocks was counterbalanced across subjects. Additionally, to reduce the likelihood of stimulus order effects, each subject received the 15 stimuli in 2 different orders during the 2 blocks. Other tasting procedures were the same as Experiment 1.

3.3. Results and discussion

The results supported the main findings of Experiment 1. Sucrose was again the dominant taste in most mixtures and was most resistant to suppression. These trends, and the key findings regarding possible effects of stimulus temperature and order of rating, can be seen in Fig. 4. A repeated-measures ANOVA (with factors solution temperature, rating order, and stimulus) conducted on the sweetness ratings of sucrose and its mixtures with other taste stimuli found no significant main effects or interactions involving either solution temperature or order of rating. However, post-hoc tests identified a single specific effect of the order of taste quality rating on perceived sweetness in the binary mixture of sucrose + QSO₄ (Tukey HSD, $p < 0.05$). In that case sweetness was perceived to be weaker when rated last than when rated first. It is possible the delay in rating sweetness allowed sweetness to decay over time, rendering it more vulnerable to suppression by bitterness. However, if this explanation

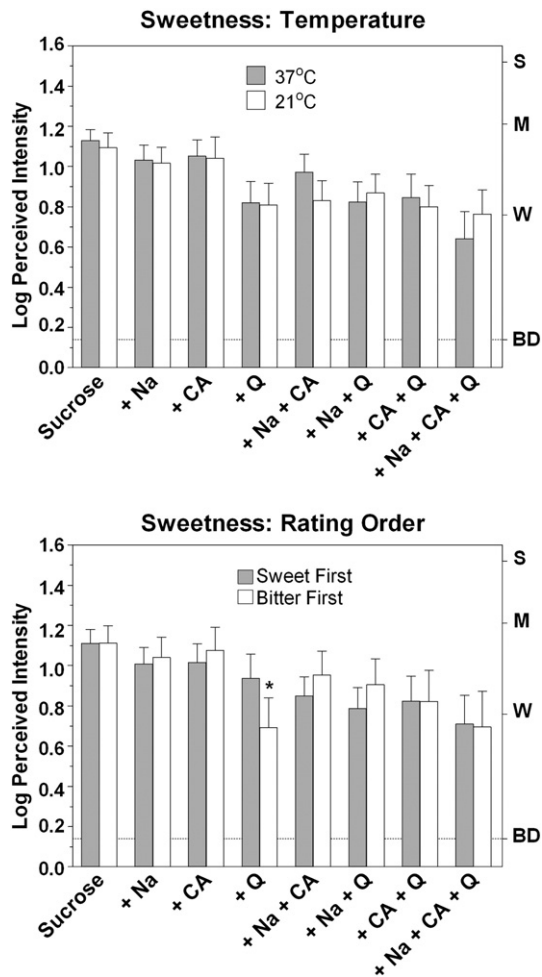


Fig. 4. Shown are the log-mean ratings of perceived sweetness in response to sucrose and its mixture with other stimuli. Top: when the solutions were warmed to 37 °C (gray bars) or left at room temperature (≈ 21 °C) (open bars); Bottom: when subjects rated in the order of sweetness, saltiness, sourness, and bitterness (gray bars) and in the order of bitterness, sourness, saltiness, and sweetness (open bars) on every trial. Vertical bar indicate SEMs.

were correct, lower sweetness ratings might also be expected for the other 3 mixtures that contained QSO₄, but no such trend is evident in the data (Fig. 4).

Separate repeated-measures ANOVAs conducted on the ratings of perceived saltiness of NaCl, sourness of citric acid and bitterness of QSO₄ also found no main effects of solution temperature or order of rating (data not shown). A single significant interaction was found between solution temperature and stimulus for the bitterness of QSO₄ [$F_{(7, 182)} = 3.2$, $p < 0.005$], but in no case did the bitterness of any mixture that contained QSO₄ differ significantly for the two solution temperatures (Tukey HSD test, $p > 0.05$). Instead, the source of the interaction was a combination of slightly higher and lower bitterness ratings across mixtures. For example, the bitterness of the sucrose-QSO₄ mixture was slightly lower at 21 °C whereas the bitterness of the citric acid-QSO₄ mixture was slightly higher at 37 °C. This combination of non-significant differences led to a significant difference in the bitterness of these two mixtures for the 21 °C solutions that was not present for the 37 °C solutions (Tukey HSD, $p < 0.05$). There is no obvious explanation for why this difference occurred.

4. General discussion

The two main findings of the present study were that the perceived intensities of taste qualities within complex mixtures are

additive, and that sucrose sweetness was the dominant taste quality in binary, ternary and quaternary mixtures with citric acid, NaCl, and QSO₄. The evidence that overall taste intensity equals the sum of the perceived intensities of the component stimuli in ternary and quaternary mixtures is consistent with prior evidence of perceptual additivity from studies of binary mixtures [4,11,21,24,33]. Extending this finding to complex mixtures demonstrates that it is a general property of taste mixtures. Perceptual additivity could theoretically result from a cognitive process in which subjects consciously add the intensity of individual taste qualities together, or from a perceptual process in which the tastes are integrated and perceived as a whole. Although it is impossible to determine with certainty which of these explanations is correct, we favor the second possibility because the experiment was designed such that subjects had to make ratings of overall intensity ('impact') before they were asked to rate individual taste qualities. Without experience analyzing complex mixtures, and with the instruction to rate overall impact, it seems unlikely subjects would have adopted an analytical strategy to arrive at their ratings.

With respect to the dominance of sweetness, we found that sucrose sweetness was both more resistant to suppression by other tastes and was also the strongest suppressor of other tastes. Experiment 2 showed that this dominance was robust to the order of taste quality rating and to the temperature of the solution. From a functional standpoint, the ability to perceive sweet carbohydrates in foods, which are a vital source of energy, provides a clear adaptive advantage, and the resistance of sweetness to suppression by other tastes, via either peripheral or central inhibitory interactions [2,7,39,40], appears to contribute to this advantage. However, it is also thought that bitterness serves to signal the presence of potential poisons [41], which seems inconsistent with the strong suppression of bitterness we observed, particularly in mixtures that contained sucrose (Fig. 1). This finding seems to imply that the ability to find high-energy food sources is of greater survival value than is detecting potentially deadly toxins. However, most bitter compounds can be perceived at much lower concentrations than sweet carbohydrates, as is shown by the fact that 0.18 mM QSO₄ produced a bitter taste approximately equal in magnitude to the sweetness of 0.56 M sucrose—yielding a concentration ratio between sweet and bitter stimuli of 31:1. Viewed in this way the gustatory system may have evolved to effectively balance the risk of consuming small quantities of potential toxins against the need to find and consume high-energy foods.

A similar logic may apply to the ability of sodium salts to suppress bitterness [8,19,42]. Indeed, NaCl and sucrose together were the primary sources of bitterness suppression. Like sweet carbohydrates, consumption of sodium salts is also critical for health because of the need to maintain proper hydration and electrolyte levels. But unlike sweetness, the taste of NaCl was subject to strong suppression, particularly by sucrose. This experimental finding is consistent with the common experience that high levels of salt are often masked in foods. It is difficult to identify an adaptive advantage of suppression of saltiness by sweetness in the natural environment, and in the modern built environment the abundance of processed foods leads to the unwitting consumption of high levels of salt, which heightens the risk of hypertension [43,44].

A more general adaptive function of mixture suppression may be to decouple the complexity of foods from their overall taste intensity [20]. As is graphically illustrated in Fig. 3, for most taste mixtures overall taste intensity was not very much greater than the strongest component of the mixture. This means that the taste intensity of foods is driven more by the concentration of the sapid substances it contains than by its gustatory complexity. Such a mechanism would serve the need to accurately identify high-energy foods by working hand-in-hand with the perceptual dominance of sweet taste to optimize the accuracy of the sweet signal as an indicator of the sugar content of foods.

Although we were able to replicate the main findings of the study in 2 experiments, it is important to keep in mind that the generalizability of the results to other stimulus concentrations, other modes of stimulation, and other types of flavor stimuli, cannot be assumed. With respect to stimulus concentration, there is evidence that nearer the threshold for detection, sucrose and NaCl exhibit additive rather than suppressive interactions, with NaCl tending to increase the sweetness of the mixture [11,24]. The latter is an interesting result given other evidence that taste stimulation is additive at and below the threshold for detection [45]. With respect to the mode of stimulation, the need for caution is evident in the disagreement between these results and those reported for ternary and quaternary mixtures based on the dorsal flow procedure [20]. Although the sip-and-spit procedure is closer to natural tasting, it does not include swallowing, which more strongly recruits taste areas innervated by the superior petrosal (soft palate) and glossopharyngeal (back of the tongue) nerves. Greater contributions by these areas may change the relative amounts of suppression that occur among taste stimuli and qualities. In particular, studies need to be done that include MSG and related glutamates, which are perceived most strongly in these posterior regions of the mouth [46]. Evidence from studies of binary mixtures indicate that at moderate-to-high concentrations [1,47], MSG can suppress sweetness, saltiness and bitterness, and thus may be another example of a gustatory signal of an energetic food source that remains salient in complex mixtures.

It is also unclear whether the effects found here with aqueous solutions hold for actual foods and beverages, which may be encoded and perceived differently. Indeed, it is arguable that perception of tastes in aqueous solutions may relate more to the perception of impurities in water than to perception of sapid substances in foods, which are often accompanied by complex somatosensory and chemesthetic stimulation and are always accompanied by retronasal olfactory stimulation. Nevertheless, the present data provide significant new information about interactions that take place within the human gustatory system and so provide the basis for testable hypotheses about how the taste components of flavor interact in the perception of foods and beverages.

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