Chem. Senses 32: 31–39, 2007
doi:10.1093/chemse/bjl033
Advance Access publication October 5, 2006

The Psychophysical Relationship between Bitter Taste and Burning Sensation: Evidence of Qualitative Similarity

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Abstract

Although it has long been studied as a pure sensory irritant, the ability of capsaicin to evoke, mask, and desensitize bitter taste suggests that burning sensations and bitter taste might be closely related perceptually. The current study investigated the psychophysical relationship between bitterness and burning using 2 different approaches. In Experiment 1, spatial discrimination of 4 taste stimuli was measured in the presence or absence of capsaicin. The subjects' task was to report which of 3 swabs, spaced 1 cm apart and presented to the tongue tip, contained a taste stimulus when 1) water was presented on the other 2 swabs or 2) when 10 μM capsaicin was presented on all 3 swabs. The presence of capsaicin did not change performance on the 3 alternative forced-choice (3-AFC) task for sweet, sour, and salty stimuli, while the localization error for 1.8 mM quinine sulfate (QSO_4) increased significantly. In Experiment 2, the perceptual similarity/dissimilarity of taste stimuli and capsaicin was measured directly using pairs of stimuli applied to opposite sides of the tongue tip on swabs separated by 2 cm. Multidimensional scaling analyses showed that capsaicin fell nearer to QSO_4 than to any other taste stimulus. Cluster analysis corroborated this finding: capsaicin was closely linked with QSO_4 and the capsaicin-QSO_4 group was separated from the other taste stimuli. The latter result indicated that bitterness was more similar to burning than to the other tastes. These findings imply that despite being mediated by different sensory modalities, bitterness and burn are qualitatively similar. We speculate that this similarity reflects a common function of these 2 sensations as sensory signals of potentially harmful stimuli.

Key words: bitterness, burning, capsaicin, chemesthesis, spatial discrimination, taste

Introduction

Although long used as a pure chemesthetic stimulus that produces burning sensations, there is evidence that capsaicin can also produce a weak sensation of bitterness (Lawless and Stevens 1984; Green and Schullery 2003; Green and Hayes 2004). Green and Schullery (2003) proposed that capsaicin may produce bitterness by stimulating a subset of gustatory fibers that are sensitive to bitter-tasting substances. In addition to its elicitation of bitterness, capsaicin can inhibit or mask some basic tastes, especially bitterness and sourness (Lawless and Stevens 1984; Lawless et al. 1985; Cowart 1987). Lawless and Stevens (1988) compared taste intensities of 4 stimuli after rinses with capsaicin and after control rinses with emulsifying agents or water and showed that there were significant decrements in taste intensity of QHCl and citric acid following capsaicin. Karrer and Bartoshuk (1995) later reported that desensitization to 100 ppm (but not 10 ppm) capsaicin significantly reduced the perceived bitterness of 0.001 M QHCl and PROP (6-*n*-prophyl-thiouracil). More recently, Green and Hayes (2003) also found that pretreatment with capsaicin significantly reduced the bitterness of QSO_4 and to a lesser extent urea, $MgCl_2$, and PROP.

The fact that capsaicin can elicit, mask, and desensitize bitter taste suggests that there may be a close perceptual and neurophysiological relationship between burning sensations and bitter taste. This hypothesis received informal support when we observed, during preliminary testing, that at certain concentrations the bitterness of QSO_4 appeared difficult to distinguish from weak burning sensations caused by capsaicin. We investigated this possibility in the present study using 2 approaches. In the first experiment we examined the ability of subjects to make spatial discriminations of taste stimuli in the presence or absence of capsaicin. We hypothesized that compared with other taste stimuli, discrimination of QSO_4 would be more difficult in the presence of capsaicin because subjects would sometimes confuse bitterness and burning sensations. We also expected that the sweetness of sucrose should be less vulnerable to confusion, both because of its marked qualitative difference from bitterness and because it has been found to attenuate nociceptive (pain) sensations from oral irritants (Sizer and Harris 1985; Nasrawi and Pangborn 1990; Yau and McDaniel 1992). Because Karrer and Bartoshuk (1995) reported that capsaicin desensitized the bitter taste of QHCl to different degrees depending on concentration, we tested 3 different concentrations of QSO_4.

The purpose of the second experiment was to reexamine the finding from the first study in a more direct way. The perceptual similarity/dissimilarity of bitterness and burn was measured directly, and the results were compared with those for other intensity-matched taste stimuli. We applied multidimensional scaling (MDS) to the similarity/dissimilarity ratings to investigate the psychological or perceptual relationships between sensations without asking for subjective descriptions or ratings on specified attributes. MDS produces a spatial map that reflects the relationships between stimuli in terms of their perceived characteristics (Schiffman et al. 1981). We expected the 4 basic tastes would form a tetrahedron similar to that suggested by Henning (1916), and capsaicin would be located outside of the tetrahedron but situated most closely to QSO_4.

Experiment 1: measurement of perceptual discrimination

Materials and methods

Subjects

A total of 20 subjects (13 females and 7 males) were recruited on the Yale University campus and paid for their participation. Following screening (see *Procedure*), 16 subjects (11 females and 5 males) between 18 and 36 years of age (mean = 25 years) participated in the full experiment. All subjects were nonsmokers and free from deficits in taste or smell by self-report and were asked to refrain from eating, drinking, or using menthol products for at least 1 h prior to their scheduled session. Subjects were also asked to avoid eating hot and spicy food for at least 1 day prior to the experiment.

Stimuli

Taste stimuli included quinine sulfate (QSO_4; 0.32 mM for a practice session; 0.18, 1.0, and 1.8 mM for discrimination sessions; J.T. Baker, Phillipsburg, NJ), NaCl (0.32 M, J.T. Baker, Phillipsburg, NJ), citric acid (17 mM, Pfaltz & Bauer, Inc., Waterbury, CT), and sucrose (0.32 M, J.T. Baker, Phillipsburg, NJ). All taste stimuli were prepared in deionized water and applied to the tip of the tongue using sterile, cotton-tipped swabs. The swabs were saturated just prior to application with the appropriate aqueous solutions, which were kept in individual plastic vials that were partially submerged in a 40 ± 0.2 °C circulated water bath.

Capsaicin (Pfaltz & Bauer, Inc.) was also applied via cotton swabs in concentrations of 3.2, 5.6, 10, and 32 μM for the practice session and 10 μM for the discrimination session. Because of its hydrophobicity, capsaicin stimuli were prepared in ethanol solutions. The ethanol was removed by allowing the cotton swabs saturated in capsaicin-ethanol solution to dry prior to each experimental session (Green and Schullery 2003). Just before application to the tongue, the capsaicin swabs were rewetted by dipping them in deionized water or one of the taste solutions, also at 40 °C. The solutions were warmed to counteract the suppression of capsaicin stimulation caused by cooling (Green 1986). Preliminary testing indicated that using room temperature solutions delayed the onset of burning and transiently suppressed the intensity of ongoing sensations, thus reducing the opportunity for sensory interactions between capsaicin and taste. Heating the solutions eliminated this problem.

Procedure

Screening session. Prior to the first data collection session, all subjects attended a short practice and screening session and were instructed on how to use the general version of the labeled magnitude scale (LMS) (Green et al. 1993, 1996; Bartoshuk et al. 2003). 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, the burn of cinnamon gum) on the LMS to give them experience using the scale in the broad context of normal oral perception (Green and Schullery 2003). Subjects were then instructed to rate the intensity of sweetness, saltiness, sourness, bitterness, and burning or stinging produced by 4 prototypical taste stimuli (0.32 M sucrose, 0.32 M NaCl, 17 mM citric acid, and 0.32 mM QSO_4). Instructions in the practice session required subjects to rate the intensity of each sensation quality separately and to base their ratings on the maximum sensation perceived during stimulus application or immediately afterward.

Following the practice ratings, the subjects were tested for their ability to perceive 10 μM capsaicin, which was used in the discrimination session. They were asked to rate burning or stinging, and all 4 taste qualities (sweetness, saltiness, sourness, and bitterness) for the 4 capsaicin stimuli presented in an ascending concentration series (3.2, 5.6, 10, and 32 μM). The stimuli were applied to the tip of the tongue via cotton swabs for approximately 3 s. After the stimulus was applied, subjects retracted the tongue into the mouth and rated perceived intensities of 5 sensations. During an interstimulus interval of ~30 s, subjects were asked to rinse at least twice with 37 ± 0.2 °C deionized water. Four subjects were disqualified from the experiment because they did not report more than barely detectable burning or stinging from 10 μM capsaicin.

Discrimination session. Subjects attended 2 discrimination sessions in which their task was to identify which of 3 swabs contained a taste stimulus. In one session, the discrimination was made with the other 2 swabs saturated with deionized water (control group), and in another session, all 3 swabs contained 10 μM capsaicin (see Figure 1). The order of the control and capsaicin sessions was counterbalanced across subjects, and the 2 sessions were at least 2 days but no more than 1 week apart. Each session included 18, 3 alternative forced-choice (3-AFC) trials: 1 concentration of NaCl, citric acid, and sucrose, and 3 concentrations of QSO_4, each presented 3 times (once each on the left, middle, or right side of the tongue).

Subjects were asked to rinse at least twice with deionized water kept at body temperature (37 ± 0.2 °C) before beginning the test and between each trial. On each trial, a set of 3 swabs spaced 1 cm apart in a drilled plastic block (3 × 7.5 cm) were applied to the tongue tip in an up and down motion for approximately 3 s (5 strokes). At the beginning of each trial, the experimenter told the subjects which taste quality should be attended, for example, "which of the 3 swabs is most bitter?" The order of stimuli and their swab locations were randomized. However, to prevent either sensitization or adaptation (Cubero-Castillo and Noble 2001) of the bitter response, no more than 2 consecutive QSO_4 stimuli were presented. Because the capsaicin burn takes time to build up to a consistent level during intermittent stimulation, subjects received 3 pretreatment capsaicin (10 μM) stimuli at the beginning of each capsaicin session. The intertrial interval for all stimuli was 30 s.

Intensity scaling session. To make certain the perceived intensities of the 4 taste stimuli were approximately equal and to determine the intensity of the capsaicin burn relative to the taste sensations, 15 out of the original 16 participants (10 females and 5 males) returned for 2 sessions to rate the perceived intensity of the stimuli used in the discrimination task. The experimental procedure was the same as in the discrimination sessions, except the task was intensity rating. The subjects were asked to rate separately the intensity of 5 qualities (sweetness, saltiness, sourness, bitterness, and burning/stinging) produced by the swab that had the strongest taste out of 3 swabs. Ratings were again made using the LMS. Subjects were told that if they could not tell the difference among the 3 swabs, they should nevertheless pick 1 swab and rate its associated taste intensity.

Analysis

Number of correct answers was counted for each case (i.e., 0.18 mM QSO_4 with water control) of each subject separately. Because each subject tested 3 replicates, overdispersion may exist by violating an assumption, the same probability P for all n trials, for the binomial test. Ennis and Bi (1998) suggested using the beta-binomial model, an extension of the binomial distribution, to fit overdispersed binomial data. Therefore, a beta-binomial test was first performed to determine if the binomial assumption was appropriate for the current data using the IFProgram (Institute for Perception, Richmond, VA, 2003). The result shown that the gamma values for all cases were zero, meaning that the beta-binomial model did not fit the data significantly better than the binomial model. The data, hence, were pooled across replicates and subjects and converted to d' values. The d' analysis (Ennis 1993) was further performed in order to measure the significance.

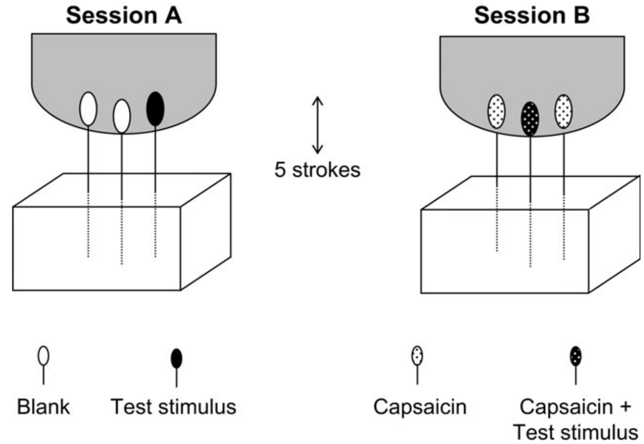

Figure 1 The diagram for the testing conditions.

The arithmetic mean of intensity ratings was calculated across each replicate within subjects. Because responses on the LMS tend to be log-normally distributed across subjects (Green et al. 1993, 1996), the means were log transformed prior to statistical analysis. One-way analysis of variance (ANOVA) and Tukey's HSD post hoc tests were performed to determine whether there were significant differences among perceived intensities of stimuli using Statistica 7.1 (StatSoft Inc., Tulsa, OK).

Results

The d' values for the 3-AFC discrimination task are shown in Table 1. As expected (Shikata et al. 2000), spatial discriminability improved as the concentration of QSO_4 increased when no capsaicin was present. The d' value of 1.93 for the highest concentration of QSO_4 did not differ significantly from the values for the 3 other taste stimuli. However, the addition of capsaicin disrupted spatial discrimination only for the highest concentration of QSO_4.

The narrow effect of capsaicin on discrimination is surprising when the data from the intensity ratings are considered (Figure 2). A 1-way ANOVA revealed that there was a significant effect of stimulus [$F(6,98)=8.46$, $P < 0.0001$], but Tukey's HSD tests ($P < 0.05$) indicated that this was due in large part to the relative weakness of the capsaicin burn, which was significantly less intense than all the tastes except the lowest concentration of QSO_4. Thus a weak burning

Table 1 The d' values from the 3-AFC spatial discrimination task for 4 taste stimuli in the presence or absence of capsaicin

	0.18 mM QSO_4	1.0 mM QSO_4	1.8 mM QSO_4	0.32 M NaCl	17 mM citric acid	0.32 M sucrose
Taste only	0.76	1.52	1.93	2.83	2.56	2.36
Taste + capsaicin	0.49	1.61	1.12*	2.83	2.20	2.20

*P < 0.05 by the d' analysis.

sensation interfered with the localization of a stronger bitter stimulus, the perceived intensity of which equaled or exceeded the intensities of the nonbitter stimuli. This implies that the interference was caused by a mechanism other than masking or inhibition, as weaker stimuli generally cannot mask stronger ones. The results also indicate that spatial discrimination tended to be poorer for QSO_4 than for the other stimuli at an equivalent perceived intensity. NaCl, citric acid, and sucrose yielded significantly higher d' values than 1.0 mM QSO_4, even though all 4 stimuli produced statistically similar perceived intensities.

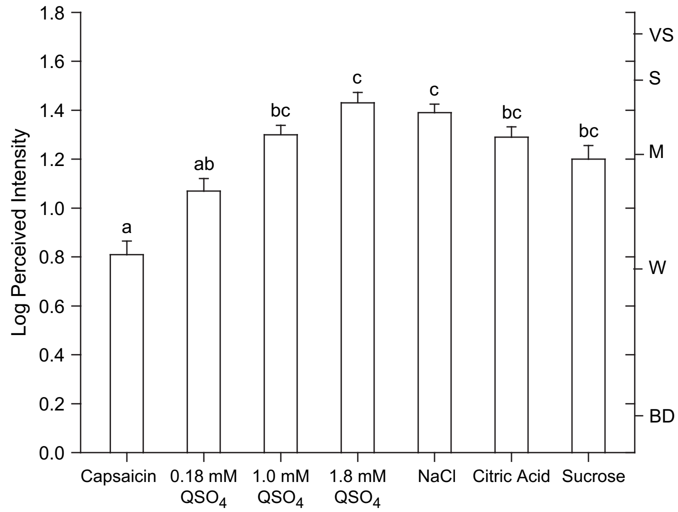

Figure 2 Log means of perceived intensity ± standard error of relevant sensations of the target swab (burning/stinging for capsaicin, bitterness for QSO_4, saltiness for NaCl, sourness for citric acid, and sweetness for sucrose). The different letters indicate significant differences on perceived intensities by the Tukey's HSD test (P < 0.05).

Experiment 2: measurement of perceptual similarity/dissimilarity

The finding that capsaicin disrupted spatial discrimination for the 1.8 mM QSO_4 supported the hypothesis that, under some conditions, bitter taste and burning sensations may be sufficiently similar in quality to be confusable. In the present experiment we tested this hypothesis directly by measuring the perceptual similarity/dissimilarity of the burning sensation from capsaicin to the tastes of QSO_4 and 3 other prototypical taste stimuli using MDS. The intensities of both capsaicin and QSO_4 were varied to investigate the possible effect of concentration on perceived similarity.

Materials and methods

Subjects

A total of 21 subjects (11 females and 10 males) between 18 and 30 years of age (mean = 23 years) were paid to participate. Potential subjects were again screened for their ability to perceive 10 μM capsaicin, and other criteria and constraints for the subjects were the same as Experiment 1.

Stimuli

The taste and capsaicin stimuli used for the screening session were the same as those used in the Experiment 1. A total of 8 test stimuli were used: 10 and 32 μM capsaicin, 1.0 and 1.8 mM QSO_4, 0.32 M NaCl, 17 mM citric acid, 0.32 M sucrose, and a mixture of citric acid and sucrose. Because the perceived intensity of 0.18 mM was quite low for some subjects (d' value: less than 1), only 1.0 and 1.8 mM QSO_4 were used in this experiment. The mixture of citric acid and sucrose was included to provide subjects with a complex sensation that we expected would fall intermediate to its components in multidimensional space. The stimuli were prepared as the Experiment 1. All combinations of test stimuli were applied in pairs to opposite sides of the tongue using cotton-tipped swabs.

Procedure

The experiment was divided into 2 parts: a practice session and 2 sessions of similarity/dissimilarity scaling.

Practice session. Prior to the first test session, all subjects attended a short practice session and were instructed on how to use the similarity scale. The scale was anchored at its ends by the terms "exactly the same" and "completely different" (Schiffman et al. 1981) and was presented horizontally on a computer screen. After instructions were given, the subjects were asked to rate the similarity/dissimilarity of 14 pairs of common food items in terms of oral sensations (i.e., honey and hot sauce, maple syrup and honey). This practice allowed subjects to become familiar with the scale and encouraged them to rate stimuli within the context of everyday life.

Test session. All combinations of the taste stimuli and capsaicin stimuli were compared in 2 separate sessions: one session with 10 μM capsaicin and another session with 32 μM capsaicin. In each session the subjects made a total of 21 ratings. Because burning sensations from capsaicin linger for several minutes, the stimulus pairs were blocked according to the presence or absence of capsaicin in each session. The first block consisted of all the comparisons among taste stimuli (total of 15) in a random order. Comparisons between capsaicin and the taste stimuli were presented in the second block of the session. To ensure that a capsaicin burn was present at the outset of taste testing, 3 capsaicin pretreatment trials (capsaicin on one side and water on another side of the tongue) were presented before the second block of test trials. In addition, capsaicin was always presented on the same side of the tongue, with the side counterbalanced across subjects. The order of presentation of stimulus pairs was randomized, and the order in which the 2 concentrations of capsaicin were presented was counterbalanced across subjects.

Subjects rinsed at least twice with deionized water (37 ± 0.2 °C) before beginning each block and between each trial. On each trial, 2 cotton-tipped swabs spaced 2 cm apart in a plastic block (3 × 7.5 cm) were applied to the tongue tip in an up and down motion for approximately 3 s (5 strokes). Subjects rated the degree of similarity/dissimilarity of each stimulus pair. The stimuli were again presented at 40 ± 0.2 °C to avoid delaying and suppressing the burn at the moment of stimuli application, and the intertrial interval was again 30 s.

Analysis

The data from 2 different sessions with 10 and 32 μM capsaicin were treated separately. Average similarity ratings for each possible stimulus pair were calculated across subjects, and 2 similarity rating matrices were constructed. The data were analyzed using the MDS procedure in Statistica 7.0 (StatSoft). This method has been shown to be useful in providing pictorial representation of the relationships among various chemosensory stimuli (Schiffman and Erickson 1971; Schiffman et al. 1980; Murphy et al. 1981; Kielhorn and Thorngate 1999). Cluster analysis was used to help interpret the groupings in the MDS configurations by a second quantitative method. Several agglomerative techniques, such as complete, single, and Ward's linkage methods were performed on the data, and the results were in good agreement. For economy, only the results from the complete-linkage cluster analyses were presented.

Results

Three-dimensional solutions from the MDS analysis are shown in Figures 3 and 4. A 3-dimensional solution, which can be geometrically conceptualized, was chosen after calculating stress values for different numbers of dimensions. The stress values for the final configurations of 10 and 32 μM capsaicin were 0.06 and 0.00. Dissimilarity is represented by distance: stimuli that are close together were judged to be similar and those that are far apart were judged to be dissimilar. As expected (see Figure 3), the intensity-matched 4 taste stimuli (1.8 mM QSO_4 for the bitter stimulus) were dissimilar from one another and the degrees of difference varied. For example, the average similarity ratings for NaCl versus citric acid and 1.8 mM QSO_4 versus sucrose were 42.7 and 73.4, respectively (0 would mean 2 stimuli were rated exactly the same, and 94.5 would mean they were rated completely different). The sweet and sour mixture was located at approximately equal Euclidian distances from each component stimulus, but a bit closer to sucrose. The most important finding was the closeness of capsaicin to the 2 concentrations of QSO_4. This "bitter-burning" group was clearly separated from the other taste stimuli. Capsaicin also fell outside the

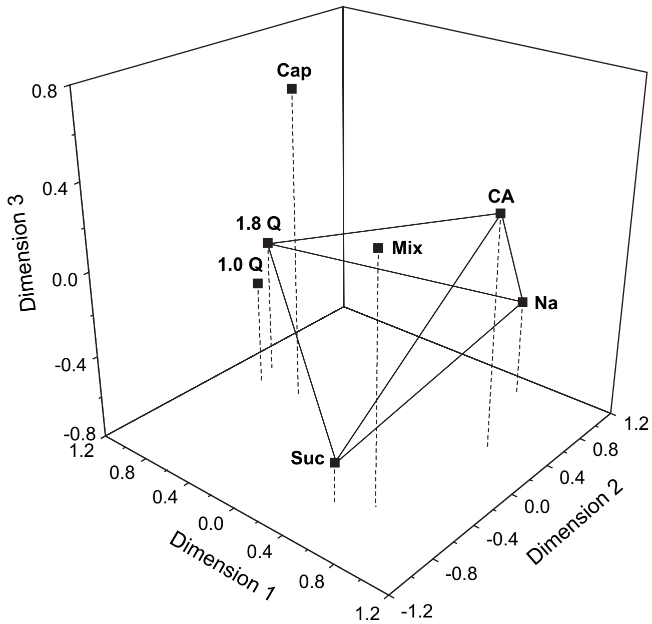

Figure 3 Three-dimensional MDS configuration with 10 μM capsaicin.

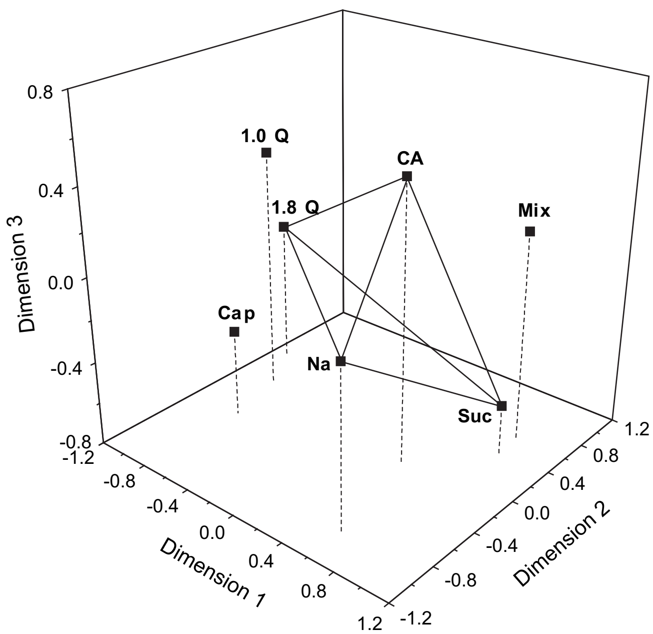

Figure 4 Three-dimensional MDS configuration with 32 μM capsaicin.

area of the space defined by the sweet, sour, salty, and bitter standard.

The results for 32 μM capsaicin (Figure 4) were similar to those for 10 μM capsaicin. The primary difference was that 32 μM capsaicin was rated somewhat more dissimilar from the nonbitter taste stimuli than was 10 μM capsaicin. The distance between bitter stimuli and other taste stimuli was also stretched. The relationship among the other taste stimuli was similar in both cases, except the direction of dimension 2 was swapped.

The hierarchical dendrogram of the complete-linkage cluster analysis for 10 μM capsaicin is shown in Figure 5. The cluster analysis objectively confirmed the finding that burning sensation is perceptually similar to bitter taste by clustering capsaicin with QSO_4. Among the other taste stimuli, sucrose was first grouped with the mixture of sucrose and citric acid. This sweet grouping was then aggregated with the citric acid/NaCl grouping at the next level. The dendrogram produced by 32 μM capsaicin (data not shown) indicated the same stimulus groupings and similar linkage distances among stimuli as that produced by the 10 μM capsaicin.

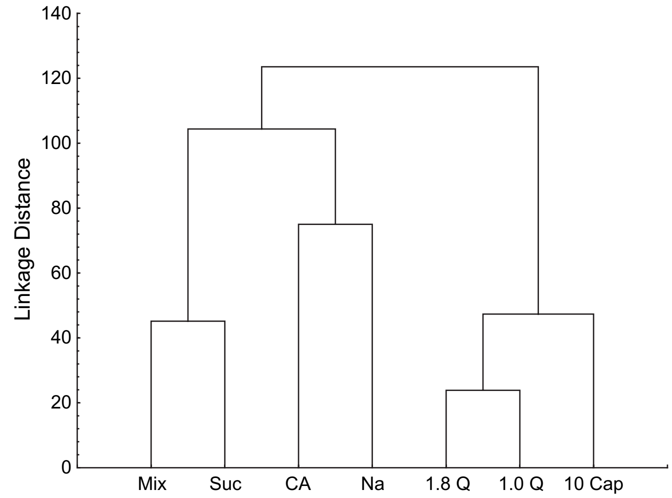

Figure 5 Dendrogram produced by hierarchical cluster analysis of the 3-dimensional coordinates in the MDS solutions of Figure 3 using the complete-linkage method.

Discussion

The present results show that the bitter taste of QSO_4 and the burning sensation from capsaicin are perceptually similar and, under some conditions, even confusable. This is a surprising result given that QSO_4 and capsaicin are considered prototypical stimuli for different sensory modalities. Indeed, capsaicin is best known and most extensively studied as a pain stimulus (e.g., Tominaga and Julius 2000; Green et al. 2005).

We believe that there are 2 possible explanations for our findings: 1) the ability of capsaicin to induce bitterness in some individuals can lead to a judged similarity or confusion with purely bitter stimuli, or 2) burning and bitterness are inherently perceptually similar. Regarding the first possibility, Green and Schullery (2003) reported that capsaicin produces a bitter taste in some individuals, although its bitterness tends to be more pronounced on the back of the tongue than on the front of the tongue (Green and Hayes 2003), where the present study was conducted. Nevertheless, it is plausible that in Experiment 1, the ability to discriminate which swab contained QSO_4 may have been more difficult when capsaicin was perceived to have a bitter taste as well as a burn.

Similarly, in Experiment 2, stimulation of bitterness by capsaicin may have resulted in a compound sensation of bitterness and burning, which would be expected to increase ratings of similarity between capsaicin and QSO_4. However, the compound sensation hypothesis fails to explain why capsaicin did not interfere with localization of the 2 lower concentrations of QSO_4 in Experiment 1. A weak bitter sensation accompanying the capsaicin burn would be expected to have its greatest impact on perception of other weak bitter stimuli. Although it might be argued that the poor localization of 0.18 mM QSO_4 in the control condition left little room for detection of an effect by capsaicin, the same cannot be said of 1.0 mM QSO_4. The latter stimulus was localized in the water control condition (d' value = 1.52) to a degree similar to 1.8 mM QSO_4 (d' value = 1.93), yet the addition of capsaicin led to a nonsignificant increase in performance (d' value = 1.61). We therefore conclude that any bitter taste of capsaicin itself was unlikely to have caused the worsening of performance for the strongest bitter stimulus.

The second possibility, that the poorer localization of 1.8 mM QSO_4 may have resulted from a true qualitative similarity between capsaicin and QSO_4, received support from Experiment 2. The MDS configuration and the dendrogram from the cluster analysis are both consistent with this hypothesis. Capsaicin was more closely related to QSO_4 than to the other 3 taste stimuli, and more surprising, QSO_4 was more closely related to capsaicin than to any other taste stimulus. This is not the first time that capsaicin has been found to cluster close to bitter stimuli: Kielhorn and Thorngate (1999) compared oral sensations produced by catechin and epicatechin (which are known as bitter and astringent stimuli) with diverse compounds representing a wide range of tastes and oral sensations. In that study, capsaicin clustered first with a group of bitter stimuli and secondarily with the astringent cluster and less strongly with sour stimuli. Thus, the Kielhorn and Thorngate study indicates that the relationship between capsaicin and bitter stimuli is not a special circumstance limited to QSO_4.

It might be argued that the rated similarity between QSO_4 and capsaicin in Experiment 2 was influenced more by the low palatability of the 2 stimuli than by their qualitative similarity. Although a contribution of palatability to the present results cannot be ruled out, subjects were specifically instructed to base their judgments on "the oral sensations" produced by the stimuli. The poorer discrimination in Experiment 1 at the higher concentration of QSO_4 is also more consistent with a qualitative confusion than with a perceived hedonic similarity. In addition, the motivation for the study grew out of the introspective observation that bitterness and burn were sufficiently similar in quality to make them difficult to rate independently in an intensity scaling task. Nevertheless, an experiment in which palatability could somehow be manipulated independently of sensation quality would be helpful for determining to what extent, if at all, palatability may affect ratings of the perceived similarity of bitterness and burn.

The most puzzling aspect of the present results is the finding in Experiment 1 that capsaicin was able to disrupt spatial discrimination only at the highest concentration of QSO_4. That finding implies that the similarity between bitterness and burning may increase with the intensity of bitterness and that differences in perceived intensity between the 2 sensations mattered less than their qualitative similarity. The simplest explanation would be that bitterness of QSO_4 becomes more "burn-like" in quality as its intensity increases, which could result either from a change in quality of bitterness per se or from the induction of a burning sensation by QSO_4. Indirect support for the latter possibility comes from evidence that in high concentrations, QHCl was found to stimulate trigeminal neurons in rats (Liu and Simon 1998). However, a more recent electrophysiological study (Simons et al. 2003) failed to find evidence of trigeminal stimulation by QHCl, and not even "barely detectable" burning or stinging was reported for QSO_4 in a psychophysical study in which subjects rated taste and chemesthetic sensations for several bitter-tasting stimuli (Green and Hayes 2003). In addition, the hypothesis that higher concentration of QSO_4 might evoke burning sensations is complicated by the absence of a significant concentration effect for QSO_4 in the MDS results of Experiment 2. In that experiment, 1.0 and 1.8 mM QSO_4 were located at almost equal distances from capsaicin in multidimensional space.

The lack of agreement between the 2 experiments regarding an effect of concentration might be explained by differences in the 2 psychophysical procedures. Whereas discrimination or difference tests are designed for determining the presence and extent of fine differences between stimuli, MDS is intended to help understand more general relationships within a set of stimuli. Thus, the sensitivity of the 2 methods are different: whereas the similarity rating task encourages subjects to make judgments based on overall sensory characteristics, the forced-choice procedure of the discrimination task encourages subjects to look for any discernable differences between or among sensations. In the current study, the difference in sensitivity between tasks was exaggerated by the stark qualitative differences among the "primary" taste sensations (e.g., sweet vs. bitter). The broad perceptual context produced by these diverse sensations worked against detection of smaller or more subtle qualitative differences. Another study including a small number of stimuli that produce only bitterness and/or burning of various intensities might improve the resolution of the MDS procedure. By testing a sufficient number of capsaicin bitter tasters and nontasters, the correlation between capsaicin bitterness and the perceived similarity of QSO_4 and capsaicin could be calculated. A high correlation would imply that similarity ratings were determined in part by the bitter taste of capsaicin rather than by an intrinsic similarity between bitterness and burn.

The possible role of taste referral

Another factor that may have influenced the results of the spatial discrimination task is the phenomenon of "taste referral," in which taste sensations are referred to the location of accompanying tactile stimulation (Todrank and Bartoshuk 1991; Green 2002). Presenting the stimuli on cotton swabs that were moved vertically (up and down) against the front edge of the tongue created conditions of tactile stimulation conducive to referral. If referral did occur, subjects perceived some degree of taste sensation from each of the 3 swabs. However, to account for the results, referral would have to have occurred more strongly for bitterness than for the other tastes and to have been more pronounced at higher concentrations. There are no published data to support either possibility definitively. A slight tendency for greater referral for bitterness compared with other tastes was observed in a study that investigated the mislocalization of tastes under conditions similar to the present experiment (Green 2002), but the trend was not significant. An experiment that will measure referral in a discrimination task that includes multiple concentrations of QSO_4 and at least one other taste stimulus, is being planned to address this issue.

Bitterness-burn similarity and modality

The evidence that bitterness is more perceptually similar to burn than to sweetness, sourness or saltiness revives longstanding questions about what constitutes a taste quality and what defines a taste modality (Bartoshuk 1978; McBurney 1978). These questions have remained unresolved because, unlike vision and hearing, taste quality does not vary along a physical continuum such as frequency or wavelength. The absence of both a physical continuum of taste stimulation and a corresponding qualitative continuum of taste sensation gave rise historically to 2 divergent views of taste: one which asserted that taste is a collection of separate modalities and another which held that it is a single modality by virtue of the shared function of detecting and identifying chemical stimuli (Bartoshuk 1978). The bitterness-burning relationship uncovered here could be accommodated by either view but may be more meaningfully included in the latter, functional definition of taste. It has been proposed that the primary function of taste is to motivate ingestion of safe and nutritious substances while avoiding ingestion of potentially harmful (toxic) ones, and that bitter taste is the most reliable predictor of dangerous substances (Scott and Mark 1987; Glendinning 1994). In this view taste quality drives palatability, and palatability is linked fundamentally to healthfulness.

The relationship of palatability to taste quality was first addressed quantitatively in a MDS study (Schiffman and Erickson 1971) in which it was found that palatability was 1 of the 3 dimensions that best defined the taste space. The same study showed that palatability was not determined solely by the classically defined gustatory pathway. In a comparison of similarity spaces derived from human MDS ratings and from neural recordings from the nucleus of the solitary tract in rats, the most notable disagreement was the location of NaOH, which was described by human subjects as having a ''causticity'' in addition to a bitter-salty-sweet taste. It was concluded that a ''trigeminal'' quality had affected the perception of taste by reducing the palatability of a ''taste'' stimulus. The present results indicate that the distinction between trigeminal (i.e., chemesthetic) and taste qualities is not always clear, which reinforces the notion that both sources of stimulation contribute to palatability.

Both inside and outside the mouth, burning sensations can be evoked by potentially dangerous temperatures or by caustic chemicals, particularly those having a low pH (Tominaga et al. 1998; Schmelz et al. 2000), and these sensations are mediated through stimulation of the nociceptive (pain) system (Schmelz et al. 2000; Caterina and Julius 2001). In the mouth, the perceptual similarity of the 2 sensations may be an adaptive consequence of their shared function as detectors of potentially toxic and caustic substances. From a functional standpoint, burning might be considered a taste quality that arises from another independent modality that is sensitive to chemical irritants. Indeed, the functional integrality of the oral sensory systems is manifest in normal parlance, whenever individuals refer to the hot or burning taste of spicy foods. Whereas such terminology may be discounted in the context of the classically defined oral senses, its origin and descriptive utility may reflect the multimodal integration of oral sensory stimulation that is essential for food perception and selection.

Other lines of evidence also support a close functional and perceptual relationship between bitterness and burning: capsaicin can induce (Green and Hayes 2003, 2004; Green and Schullery 2003), mask (Simons et al. 2002), and desensitize (Lawless and Stevens 1984; Karrer and Bartoshuk 1995; Green and Hayes 2003) bitter taste; other common irritants such as ethanol (Mattes and DiMeglio 2001) and nicotine (Dessirier et al. 1997, 1999) can also stimulate bitterness; and some bitter tastants such as caffeine and QHCl have been reported to stimulate trigeminal ganglion neurons in rats (Liu and Simon 1998). In addition, bitterness and burn have a similar psychophysical relationship to sweetness, which lies at the opposite pole of palatability. The well-known reciprocal inhibition between sweetness and bitterness (Lawless 1979; Schiffman et al. 1994; Green 2002) is paralleled by the ability of sucrose to decrease nociceptive sensations from oral irritants (Sizer and Harris 1985; Nasrawi and Pangborn 1990), by the ability of capsaicin to mask or reduce the perception of sweetness (Prescott and Stevenson 1995; Simons et al. 2002), and by the ability of sucrose to have palliative and analgesic effects in animals and human infants (Roane and Martin 1990; Blass and Shide 1994; Blass and Watt 1999; Fernandez et al. 2003).

Summary and conclusion

The present study indicates that the bitter taste from QSO_4 and the burning sensations from capsaicin are judged to be perceptually similar and, under certain stimulus conditions, even confusable. Surprisingly, subjects rated the bitterness of QSO_4 more similar to the burning of capsaicin than to the tastes of 3 other protypical taste stimuli. Although more studies are needed to determine fully the perceptual relationship between bitterness and burning, we speculate that the qualitative similarity of these 2 sensations may derive from their common function as sensory signals of potentially dangerous stimuli.

Acknowledgement

This work was supported by National Institutes of Health grant DC005002.

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Accepted September 11, 2006