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Journal

Perception, 16(5)

ISSN

0301-0066 1468-4233

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Publication Date

1987-10-01

DOI

10.1068/p160629

Data Availability

The data associated with this publication are within the manuscript.

Peer reviewed

Interactions between CO₂ oral pungency and taste

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Abstract

Two experiments are reported in which the perceptual interactions between oral pungency, evoked by CO₂, and the taste of each of four tastants—sucrose (sweet), quinine sulfate (bitter), sodium chloride (salty), and tartaric acid (sour)—were explored. In experiment 1 the effect of three concentrations of each tastant on the stimulus-response function for perceived oral pungency, in terms of both rate of change (slope) and relative position along the perceived pungency axis, was determined. In experiment 2 the effect of three concentrations of CO₂ on the stimulus-response function for the perceived taste intensity of each tastant was examined. Results show that the characteristics of the mutual effects of tastant and pungent stimulus depend on the particular tastant employed. Sucrose sweetness and CO₂ oral pungency have no mutual effect; sodium chloride saltiness or tartaric acid sourness and CO₂ oral pungency show mutual enhancement; and quinine sulfate bitterness abates CO₂ oral pungency, whereas CO₂ has a double and opposite effect on quinine sulfate bitterness—at low concentrations of bitter tastant CO₂ enhances bitterness, and at high concentrations of bitter tastant CO₂ abates bitterness. It is suggested that the perceptual attributes of saltiness and sourness are closer, from a qualitative point of view, to oral pungency than are the attributes of bitterness and sweetness.

1 Introduction

The oral cavity is a particularly rich anatomical structure in terms of the number, quality, and properties of the different sensations that can arise from it. Although taste is probably the most specific sensory modality associated with the mouth, the sensations of common chemical sensitivity ('pungency'), pain, temperature, kinesthesia, texture, and tactile sensations in general can also arise there. This enables a large number of perceptual interactions to occur among the different modalities.

Little attention has been given to the study of the interaction between oral pungency and taste, despite the fact that this is a very common and interesting interaction from physiological, psychological, and food-related points of view (Kawamura et al 1968; Rozin et al 1981; Berridge and Fentress 1985). Oral pungency is associated with the stimulation of free nerve endings which are responsible for the chemical sensitivity of the conjunctiva, as well as of the nasal and oral mucosae. These free nerve endings belong primarily to cranial nerve V (trigeminal nerve) (Silver and Maruniak 1981) and they mediate common chemical sensations such as stinging, cooling, irritating, burning, prickling, tingling, etc, which can be generally described as pungent sensations.

Lawless and Stevens (1984) investigated the perceived intensities of two concentrations of each of four tastants after a rinse with emulsifying agents or water compared to after a rinse with capsicum oleoresin or piperine (irritating agents present in red and black pepper, respectively). They found that a prerinse with piperine produced a significant decrease in perceived intensity for the four tastants. A prerinse with capsicum oleoresin reduced significantly the taste intensity of citric acid, quinine hydrochloride, and one concentration of sucrose, but had no effect on sodium chloride (NaCl). Sizer and Harris (1985) studied the effects of various tastants and temperatures on capsaicin pungency threshold perception. Their results suggested that the highest levels of sucrose (concentrations of 10, 60, 150, and 290 mM were tested) produced a masking effect, elevating capsaicin recognition thresholds. Also, there was a trend towards a reduction of recognition thresholds as the temperature was raised (temperatures of 2, 18, and 60 °C were tested). Lawless et al (1985) observed moderate decrements of all four taste qualities after rinses with capsaicin compared to after rinses with ethanol (the capsaicin vehicle). In a more recent paper, Stevens and Lawless (1986) studied the time course of oral irritation evoked by capsaicin and piperine, and how that time course was affected by periodic rinses with solutions of each of four tastants (quinine, sucrose, NaCl, or citric acid), water, or nothing (a 'no-tastant' condition). Subjects rated perceived irritation ('burning') at three different times for each periodic rinse: just before the rinse, during it, and 2 s after it. Results showed that the mean perceived intensity

of burning for both irritants was, in general, significantly higher for the no-tastant condition compared to the other conditions. Also, the perceived intensity of burning for both stimuli, and for all conditions except the no-tastant one, was significantly lower in the 'during' and 'after' intervals compared to the 'before' interval. In the case of the no-tastant condition, for both irritants the ratings for the three intervals were not significantly different.

In the present investigation our aim was to study, from a perceptual point of view, the effects of presenting a pungent substance and each of four tastants simultaneously to the oral cavity. We were interested to see if the perceived pungency and taste intensities of the mixtures would differ from the perceived intensity of the components when presented individually. We also wanted to explore possible growth rate changes in either pungency or taste perceived intensities when the stimuli were presented mixed compared to when they were presented alone.

CO₂ in water was used as the oral pungent stimulus since it is virtually odorless (Cain and Murphy 1980) and tasteless. CO₂ has been previously chosen as a typical common chemical sense stimulant in investigations that have explored nasal and oral pungency perception (Cometto-Muñiz and Cain 1982; Dunn et al 1982; García-Medina and Cain 1982; Cometto-Muñiz and Noriega 1985). The use of CO₂ allowed us to present the pungent substance and each of the tastants simultaneously, since latency for maximum CO₂ oral pungency (about 5 s; see Cometto-Muñiz and Noriega 1985) is not very different from the latencies for maximum intensities of the four tastants we used (Bujas and Ostojčić 1939; Birch et al 1980).

2 Experiment 1: Effect of various concentrations of four tastants on CO₂ oral pungency perception

2.1 Method

2.1.1 Subjects. All subjects were nonsmokers. The number, sex, and average age $\pm$ SD of subjects who participated in the various tests were:

- (a) Pungency plus sweetness: twenty subjects (eleven males and nine females); 22.9 $\pm$ 3.5 years.
- (b) Pungency plus bitterness: fourteen subjects (six males and eight females); 24.3 $\pm$ 3.9 years.
- (c) Pungency plus saltiness: fourteen subjects (four males and ten females); 21.4 $\pm$ 3.2 years.
- (d) Pungency plus sourness: fourteen subjects (six males and eight females); 20.7 $\pm$ 2.9 years.

Subjects were not informed about the purpose of the experiment. Some of them took part in more than one test, but the time between tests for each subject was in the order of months, thus minimizing any possible experiential factors.

2.1.2 Materials. Different pungency levels were achieved by dilution of an oversaturated solution of CO₂ in distilled and deionized water. The undiluted oversaturated solution was prepared by filling a 2 liter aluminium bottle containing distilled and deionized water with a constant excess pressure of gaseous CO₂ until 4.7 volumes of carbonation were reached. The percentages of this oversaturated solution diluted in distilled and deionized water and used as stimuli were 20, 40, 60, and 80 vol%.

The tastants chosen were: sucrose (sweet), quinine sulfate (bitter), NaCl (salty), and tartaric acid (sour). All were analytical grade reagents except for sucrose, which was commercial grade. The stimuli concentrations in distilled and deionized water were: 88, 175, and 351 mM for sucrose; 17, 33, and 67 μ M for quinine sulfate; 68, 137, and 274 mM for NaCl; and 20, 40, and 80 mM for tartaric acid.

2.1.3 Procedure. In a given session, each subject evaluated the pungency intensity of each of the four CO₂ levels in the presence of each of three different concentrations of a given tastant, plus the 60 vol% CO₂ stimulus without tastant. The total number of different stimuli per session was therefore thirteen [(4 x 3) + 1]. Each subject made four estimates per stimulus in the pungency plus sweetness test, and two estimates per stimulus in the other three tests. Some subjects in the sweetness test made spontaneous comments about the large number of stimuli, so we decided to present the stimuli in the other tests in duplicate rather than in quadruplicate.

Subjects used the magnitude estimation procedure (Stevens 1957, 1975). They assigned any number deemed appropriate to the first stimulus pungency intensity (called the standard or reference) and, thereafter, assigned numbers to the other stimuli that reflected perceived magnitude compared to the standard. Stimuli were presented in an irregular order, i.e., not in a monotonically increasing or decreasing fashion but, also, not completely at random since we avoided presenting a very weak stimulus immediately after a very strong one and vice versa. Subjects were instructed to evaluate only *perceived pungency* (carbonated water type of sensation) and to disregard any associated (sweet, bitter, salty, or sour) taste. Psychophysical functions were obtained using the geometric mean of the average response of each subject.

Participants rinsed their mouths with water before starting the test and after each

stimulus until any previous sensation had disappeared. Subjects had to sip the 25 ml stimulus, keep it in the mouth for 5 s, then expectorate. Cups used to present the stimuli contained the appropriate amount of water for each CO₂ dilution, plus the amount of the particular tastant necessary to reach the desired concentration of that tastant when the corresponding volume of the oversaturated CO₂ solution was finally added. This addition took place a few seconds before the subject sampled the stimulus.

Previously (Cometto-Muñiz and Noriega 1985) we explored the exponent of the psychophysical function for the perceived buccal pungency evoked by CO₂ and found it to be remarkably constant in relation to gender (1.1 for males, 1.2 for females) and scaling method (1.1 for magnitude estimation, 1.2 for magnitude matching). This constancy encouraged us to use one of the concentrations of the previously studied CO₂ range as an anchor to compare the CO₂ oral pungency function to the ones that we would obtain in this investigation with the same CO₂ concentrations but in the presence of three different levels of each of four tastants. In any case, if our extrapolation was not valid because CO₂ buccal pungency was being evaluated in a different context, this would show up in the exponent of the CO₂ function in the presence of any tastant where the results showed no significant interaction with CO₂. In the case where a tastant did not interact with CO₂, the exponent for the CO₂ function in the presence of the tastant would be approximately the same as that obtained for CO₂ alone. If the value of such an exponent were, again, around 1.1, the possibility of the different context modifying the CO₂ exponent could be ruled out and the extrapolation considered valid.

The CO₂ concentration chosen to anchor the previous buccal pungency function in this experiment was 60 vol% in water. Since this stimulus would be used as the standard in each of the four tests, we thought it would be convenient to avoid using either the lowest or the highest concentrations of the range. We thus chose 60%, which is in the middle of the previously studied CO₂ range of concentrations (20, 40, 60, 80, and 100 vol%).

The standard stimulus used in each of the four tests was always the 60 vol% CO₂ solution without added tastant. In this way the relative position along the ordinate of the stimulus-response (psychophysical) functions for the pungent plus each tastant stimuli could be compared to the position of the function for the pungent stimuli alone (20, 40, 60, and 80 vol% CO₂) previously obtained.

To allow the comparison to be made between the oral pungency function for CO₂ alone and the same function in the presence of each tastant, data were treated in the following way: a factor was found which made the average value (geometric

mean) of the intensity of the 60 vol% CO₂ stimulus from the previous experiment (Cometto-Muñiz and Noriega 1985) the same as the average value (geometric mean) of the intensity of the 60 vol% CO₂ without tastant stimulus from this experiment. Then, that same factor was applied to the average values (geometric means) of the remaining stimuli from the function for CO₂ alone previously obtained, i.e., 20, 40, and 80 vol% CO₂. By means of this procedure, functions obtained representing perceived pungency intensity of four CO₂ concentrations in the presence of different concentrations of various tastants can be compared, in terms of relative position along the ordinate, to the functions representing perceived pungency intensity of those same CO₂ concentrations *without* any associated tastant.

2.2 Results

2.2.1 Pungency perception at various background sweetness levels. Figure 1 shows the stimulus-response (psychophysical) functions describing the oral pungency evoked by different CO₂ concentrations in the presence of three sucrose concentrations. Also shown is the pungency function of those same CO₂ concentrations in the absence of any tastant. Functions were compared in terms of rate of change (slope in the logarithmic coordinates of the figure) and in terms of relative position along the ordinate.

The slope of the CO₂ pungency function in the presence of the three sucrose levels averaged ($\pm$ standard deviations, SD) 1.08 (± 0.03), almost the same as the value (1.1) obtained without sucrose. Furthermore, the four functions are almost indistinguishable in terms of relative position along the ordinate.

This was confirmed in a statistical analysis of the data: a two-way analysis of variance (ANOVA) with interaction (on log transformed magnitude estimations) was made over a 4 x 4 factorial design (four CO₂ concentrations and four sucrose concentrations, including zero) with different but proportional numbers of observations per cell (Winer 1971). Main effect for CO₂ was highly significant ($F_{3,334} = 340.48$, $p < 0.001$). Main effect for sucrose and the interaction were not significant.

From the ANOVA results we can say that the CO₂ oral pungency function was not affected at all by the presence of sucrose in the range explored, whereas the average slope of the function, ≈ 1.1 , confirmed our previous observation on slope constancy for CO₂ oral pungency, lending support to the extrapolation made in this experiment.

Figure 1. Perceived oral pungency as a function of CO_2 concentration in the presence of 0 (circles), 88 (squares), 175 (triangles), and 351 (diamonds) mM sucrose. For the function with no added tastant each point represents the geometric mean of the average of four replicates made by each of thirty subjects. For the other functions each point represents the geometric mean of the average of four replicates made by each of twenty subjects. Slopes for increasing sucrose concentration are: 1.11 (circles), 1.07 (squares), 1.06 (triangles), and 1.12 (diamonds), respectively. Coordinates are logarithmic.

2.2.2 Pungency perception at various background bitterness levels. Figure 2 shows perceived oral pungency functions for CO_2 when present with each of three quinine sulfate concentrations. The reference function for CO_2 alone is also shown. Compared to the reference, there seems to be a reduction in the perceived CO_2 pungency at low concentrations of CO_2 (20 and 40%) because of the presence of the bitter tastant. The reduction at those concentrations causes the slope of the functions to steepen and rise from 1.1 for CO_2 alone to 1.39, 1.55, and 1.63 for CO_2 with 17, 33, and 67 μM quinine sulfate, respectively.

Again, a two-way ANOVA with interaction (on log transformed magnitude estimations) was made over a 4 x 4 factorial design with different but proportional number of observations per cell (Winer 1971). Main effect for CO_2 was highly significant ($F_{3,272} = 310.78$, $p < 0.001$), main effect for quinine sulfate was significant ($F_{3,272} = 2.87$, $p < 0.05$), and the interaction was also significant ($F_{9,272} = 2.59$, $p < 0.01$). Subsequent multiple comparisons by the Newman-Keuls procedure revealed that the 20 vol% CO_2 perceived pungency without quinine sulfate was significantly higher ($p < 0.05$) than that same CO_2 concentration with

67 or 33 μM quinine sulfate (see figure 2).

Figure 2. Perceived oral pungency as a function of CO_2 concentration in the presence of 0 (circles), 17 (squares), 33 (triangles), and 67 (diamonds) μM quinine sulfate. For the function with no added tastant, each point represents the geometric mean of the average of four replicates made by each of thirty subjects. For the other functions each point represents the geometric mean of the average of two

replicates made by each of fourteen subjects. Slopes for increasing quinine sulfate concentration are: 1.11 (circles), 1.39 (squares), 1.55 (triangles), and 1.63 (diamonds), respectively. Coordinates are logarithmic. Multiple comparisons (Newman-Keuls test) at each CO_2 level showed that $A \neq B$.

2.2.3 Pungency perception at various background saltiness levels. The influence of each of three NaCl concentrations on the function for CO_2 perceived pungency compared to the function for CO_2 alone can be seen in figure 3. In this case there is almost no variation in the slope of the different functions representing increasing saltiness [average slope ($\pm$ SD) = 1.01 ($\pm$ 0.06)], but there is a shift in the relative position of the functions. As the NaCl concentration rises from 0 to 274 mM, the functions representing perceived buccal pungency move upwards towards higher perceived intensity values, but the rate of change (slope) remains the same.

The ANOVA results showed highly significant effects for CO_2 ($F_{3,272} = 216.03$, $p < 0.001$) and for NaCl ($F_{3,272} = 15.51$, $p < 0.001$), but their interaction was not significant. This outcome gives statistical support to the observed fact that perceived CO_2 pungency in the presence of NaCl increases, maintaining, approximately, the same rate of change. Here again, in the absence of interaction and even in the presence of a significant effect of the tastant, the CO_2 oral pungency slope is still around 1.1, thus adding further support to the validity of the extrapolation made regarding the slope of such a function. Subsequent multiple comparisons by the Newman-Keuls procedure revealed that at 20 and

40 vol% CO₂ the presence of higher NaCl concentrations increased perceived

pungency significantly (see figure 3).

Figure 3. Perceived oral pungency as a function of CO₂ concentration in the presence of 0 (circles), 68 (squares), 137 (triangles), and 274 (diamonds) mM NaCl. For the function with no added tastant each point represents the geometric mean of the average of four replicates made by each of thirty subjects. For the other functions each point represents the geometric mean of the average of two replicates made by each of fourteen subjects. Slopes for increasing NaCl

concentration are: 1.11 (circles), 1.04 (squares), 1.06 (triangles), and 0.94 (diamonds), respectively. Coordinates are logarithmic. Multiple comparisons (Newman-Keuls test) at each CO₂ level showed that: A ≠ D ($p < 0.01$), A ≠ C ($p < 0.05$), B ≠ D ($p < 0.05$), E ≠ H ($p < 0.05$), E ≠ G ($p < 0.05$), F ≠ H ($p < 0.05$), F ≠ G ($p < 0.05$).

2.2.4 Pungency perception at various background sourness levels. The effect of tartaric acid on the CO₂ buccal pungency psychophysical function is shown in figure 4. The slopes of functions obtained with added tartaric acid average 0.99 (± 0.07), a value which is quite close to the slope of the function for CO₂ alone (1.1). The relative positions of the functions seem to shift upwards with increasing concentrations of tartaric acid. The ANOVA results showed a highly significant effect for CO₂ ($F_{3,272} = 192.18$, $p < 0.001$), a significant effect for tartaric acid ($F_{3,272} = 3.93$, $p < 0.01$), and no significance for their interaction. Thus, increasing concentrations of tartaric acid move the CO₂ oral pungency psychophysical function upwards but maintain, approximately, the same slope. The effect is similar to that obtained with NaCl but is less intense. Subsequent multiple comparisons by the Newman-Keuls procedure revealed that for 20 vol% CO₂ with 80 mM tartaric acid, perceived pungency was significantly higher ($p < 0.05$) than that for the same CO₂ concentration without tartaric acid.

Figure 4. Perceived oral pungency as a function of CO_2 concentration in the presence of 0 (circles), 20 (squares), 40 (triangles), and 80 (diamonds) mM tartaric acid. For the function with no added tastant each point represents the geometric mean of the average of four replicates made by each of thirty subjects. For the other functions each point represents the geometric mean of the average of two replicates made on each of fourteen subjects. Slopes for increasing tartaric acid concentration are: 1.11 (circles), 1.06 (squares), 0.99 (triangles), and 0.93 (diamonds),

respectively. Coordinates are logarithmic. Multiple comparisons (Newman-Keuls test) at each CO_2 level showed that $A \neq B$ ($p < 0.05$).

3 Experiment 2: Effect of CO_2 oral pungency on the perception of each of four tastes

3.1. Method

3.1.1 Subjects. All subjects were nonsmokers. The number, sex, and average age $\pm$ SD of subjects were:

- (a) Sweetness plus pungency: fourteen subjects (six males and eight females); 25.7 ± 3.0 years.
- (b) Bitterness plus pungency: fourteen subjects (six males and eight females); 24.0 ± 3.7 years.
- (c) Saltiness plus pungency: fourteen subjects (four males and ten females); 24.1 ± 3.4 years.
- (d) Sourness plus pungency: fourteen subjects (six males and eight females); 24.2 ± 3.6 years.

Subjects were not informed about the purpose of the experiment. Some of them took part in more than one test, but the time between tests for each subject was in the order of months, thus minimizing any possible experiential factors.

3.1.2 Materials. The four tastants used were the same as those in experiment 1. The concentrations were: 88, 175, 263, and 351 mM for sucrose; 8, 17, 33, and 67 μ M for quinine sulfate; 86, 171, 342, and 685 mM for NaCl; and 10, 20, 40, and 80 mM for tartaric acid.

The pungent stimulus CO₂ was prepared as described for experiment 1 and presented at concentrations of 20, 60, and 80 vol% of the oversaturated solution.

3.1.3 Procedure. In a given session, each subject evaluated the taste intensity of each of the four concentrations of one tastant, both in the absence of CO₂ and in the presence of three different concentrations of it. The total number of different stimuli per session was therefore sixteen (4 x 4). Subjects made two estimates per stimulus.

Participants again used magnitude estimation procedure (Stevens 1957, 1975) to evaluate the *perceived taste intensity* of the stimuli. They were told which particular taste they had to concentrate on (sweet, bitter, salty, or sour) and were asked to disregard any associated pungent sensation. Stimuli were presented in an irregular order, in the way described in section 2.1.3. Psychophysical functions were obtained using the geometric mean of the average response of each subject.

As before, subjects rinsed their mouths with distilled and deionized water before starting the test and after each stimulus until any previous sensation had disappeared. Participants sipped the 25 ml stimulus, kept it in the mouth for about 4 s, and then expectorated. The procedure for making the various CO₂ dilutions was the same as that described in experiment 1.

3.2 Results

3.2.1 Sweetness perception with and without associated buccal pungency. Figure 5 shows the effect of each of the three orally presented concentrations of CO₂ on the psychophysical function for the sweetness of sucrose. Again, functions can be compared in terms of rate of change (slope) and of relative position along the ordinate. The slope for sucrose alone is 1.66, and the slopes for sucrose with 20, 60, and 80 vol% CO₂ are, respectively 1.50, 1.32, and 1.46.

A two-way ANOVA with interaction (on log transformed magnitude estimations) was made over a 4 x 4 factorial design (four sucrose concentrations and four CO₂ concentrations, including zero) with an equal number of observations per

cell (Winer 1971). Main effect for sucrose was highly significant ($F_{3,208} = 311.07$, $p \ll 0.001$), but main effect for CO_2 , as well as the interaction term, did not reach significance.

Figure 5. Perceived sweetness as a function of sucrose concentration in the presence of 0 (circles), 20 (squares), 60 (triangles), and 80 (diamonds) vol% CO_2 . Each point represents the geometric mean of the average of two replicates made by each of fourteen subjects. Slopes for increasing CO_2 concentration are: 1.66 (circles), 1.50 (squares), 1.32 (triangles), and 1.46 (diamonds), respectively. Coordinates are logarithmic.

3.2.2 Bitterness perception with and without associated buccal pungency. The influence of each of the three CO_2 concentrations on the stimulus-response function for quinine sulfate bitterness is shown in figure 6. The presence of associated buccal pungency seems to have opposite effects at low and high concentrations of quinine sulfate. At the lowest concentrations of the tastant perceived bitterness increases with increased associated buccal pungency, whereas at the highest concentrations of quinine sulfate perceived bitterness abates with associated oral pungency. These effects are reflected in the slopes of the bitterness functions, which show a continuous tendency to flatten with increasing CO_2 . In the presence of 0, 20, 60, and 80 vol% CO_2 the bitterness slopes are, respectively, 1.02, 0.70, 0.63, and 0.50.

ANOVA results showed highly significant effects for quinine sulfate ($F_{3,208} = 134.54$, $p \ll 0.001$) and the interaction ($F_{9,208} = 3.68$, $p < 0.001$), but no significance for main effect of CO_2 . Subsequent multiple comparisons by the Newman-Keuls procedure revealed that, at low quinine sulfate concentrations, CO_2 enhanced perceived bitterness: perceived bitterness of 8 μM quinine sulfate with 80 vol% CO_2 was significantly higher than the perceived bitterness of 8 μM quinine sulfate alone. Conversely, at high tastant concentrations, CO_2 decreased perceived bitterness: perceived bitterness of 33 μM quinine sulfate with 20 vol%

CO₂ was significantly lower than the perceived bitterness of 33 μ M quinine sulfate alone; also, perceived bitterness of 67 μ M quinine sulfate with 60 or 80 vol% CO₂ was significantly lower than the perceived bitterness of 67 μ M quinine sulfate alone (see figure 6).

Figure 6. Perceived bitterness as a function of quinine sulfate concentration in the presence of 0 (circles), 20 (squares), 60 (triangles), and 80 (diamonds) vol% CO₂. Each point represents the geometric mean of the average of two replicates made by each of fourteen subjects. Slopes for increasing CO₂ concentration are: 1.02 (circles), 0.70 (squares), 0.63 (triangles), and 0.50 (diamonds), respectively. Coordinates are logarithmic. Multiple comparisons (Newman-Keuls test) at each quinine sulfate concentration showed that: A $\neq$ B ($p < 0.01$), C $\neq$ D ($p < 0.05$), E $\neq$ F ($p < 0.05$)

3.2.3 Saltiness perception with and without associated buccal pungency. Figure 7 shows the psychophysical function for NaCl saltiness presented alone or mixed with each of the three CO₂ concentrations. Results indicate that CO₂ tends to increase the perceived saltiness of low concentrations (86 and 171 mM) of NaCl but has practically no effect on the higher concentrations (342 and 685 mM). Consequently, the NaCl saltiness function slope of 1.45 drops to 1.02, 1.10, and 1.16 in the presence of 20, 60, and 80 vol% CO₂, respectively.

The ANOVA results showed highly significant effects for NaCl ($F_{3,208} = 259.22$, $p < 0.001$), and significant effects for CO₂ ($F_{3,208} = 4.98$, $p < 0.005$) and the interaction ($F_{9,208} = 2.11$, $p < 0.05$). Subsequent multiple comparisons by the Newman-Keuls procedure revealed that perceived saltiness of the lowest NaCl concentration (86 mM) in the presence of 20, 60, or 80 vol% CO₂ was significantly higher ($p < 0.01$) than the perceived saltiness for that concentration of NaCl alone (see figure 7).

Figure 7. Perceived saltiness as a function of NaCl concentration in the presence of 0 (circles), 20 (squares), 60 (triangles), and 80 (diamonds) vol% CO₂. Each point represents the geometric mean of the average of two replicates made by each of fourteen subjects. Slopes for increasing CO₂ concentration are: 1.45 (circles), 1.02 (squares), 1.10 (triangles), and 1.16 (diamonds), respectively. Coordinates are logarithmic. Multiple comparisons (Newman-Keuls test) at each NaCl concentration showed that A $\neq$ B ($p < 0.01$).

3.2.4 Sourness perception with and without associated buccal pungency. The effect of various CO₂ concentrations on the tartaric acid sourness stimulus response function can be seen in figure 8. At the lowest concentrations of the tastant (10 and 20 mM) perceived sourness increases with increasing CO₂ concentration, but at the highest concentrations (40 and 80 mM) the presence of CO₂ has no apparent effect on perceived sourness. This is reflected in the flattening of the slope of the function for perceived sourness versus concentration, which falls from 1.19 for tartaric acid alone to 1.04, 0.93, and 0.83 for tartaric acid with 20, 60, and 80 vol% CO₂, respectively.

The ANOVA results showed a highly significant effect for tartaric acid ($F_{3,208} = 195.42$, $p < 0.001$), a significant effect for CO₂ ($F_{3,208} = 3.98$, $p < 0.01$), and no significance for the interaction. Subsequent multiple comparisons by the Newman-Keuls procedure revealed that the perceived sourness of 10 mM tartaric acid with 60 or 80 vol% CO₂ was significantly higher than the sourness of 10 mM tartaric acid alone; also, perceived sourness of 20 mM tartaric acid with 20, 60, or 80 vol% CO₂ was significantly higher than the sourness of 20 mM tartaric acid alone (see figure 8).

Figure 8. Perceived sourness as a function of tartaric acid concentration in the presence of 0 (circles), 20 (squares), 60 (triangles), and 80 (diamonds) vol% CO_2 . Each point represents the geometric mean of the average of two replicates made by each of fourteen subjects. Slopes for increasing CO_2 concentration are: 1.19 (circles), 1.04 (squares), 0.93 (triangles), and 0.83 (diamonds), respectively. Coordinates are logarithmic. Multiple comparisons (Newman-Keuls test) at each tartaric acid concentration showed that: $A \neq C$ ($p < 0.01$), $B \neq C$ ($p < 0.05$), $D \neq E$ ($p < 0.05$).

4 Discussion and conclusions

The results summarized in figures 1 to 8 indicate that the mutual perceptual interactions between oral pungency and taste depend on the particular tastant employed.

Figures 1 and 5 reveal that sucrose sweetness and CO_2 oral pungency do not interfere perceptually with each other when presented in mixtures. The presence of sucrose, in the concentration range studied, does not alter either perceived buccal pungency rate of change, which maintains its typical exponent of about 1.1 (Cometto-Muñiz and Noriega 1985), or the relative position of the stimulus-response function on the perceived pungency axis. The same holds for the presence of CO_2 in sucrose sweetness evaluation: CO_2 is unable to modify significantly the sweetness psychophysical function exponent or its relative position.

There is, however, a considerably strong mutual interaction between CO_2 and tartaric acid or NaCl. Figures 4 and 8 show that tartaric acid enhances oral pungency, pushing the oral pungency function upwards along the ordinate, and that CO_2 is also able to enhance sourness, moving the function towards higher sourness values. Although the ANOVA results showed that in both cases the interaction term was not significant, the a posteriori multiple comparisons by the

Newman-Keuls test confirmed the tendencies seen in figures 4 and 8 in the sense that mutual enhancement is stronger at the lowest than at the highest concentrations of the chemical stimulus being scaled.

Figure 3 shows that NaCl enhances oral pungency throughout the CO₂ range used, leaving the slope of the pungency function virtually unaffected (confirmed by the lack of significance of the ANOVA interaction term). CO₂, however, enhances saltiness only at the lowest NaCl concentrations used, producing the converging functions of figure 7 (as opposed to the almost parallel functions of figure 3). This was confirmed by the significance of the ANOVA interaction term. It is worthwhile noting that oral pungency enhancement by NaCl (figure 3) corresponds to the NaCl range 68 to 274 mM, a range that contains only the two lowest concentrations of figure 7, i.e., 86 and 171 mM. These two lowest concentrations are precisely the ones that, according to figure 7, tend to enhance oral pungency. It might be that NaCl saltiness and CO₂ oral pungency mutual enhancement could be observed up to a certain NaCl concentration, around 250-300 mM. This possibility awaits further testing.

The mutual influence of the pair quinine sulfate and CO₂ is not as uniform as in the other three cases, in the sense that the effect of tastant on the oral pungency function is quite different from the effect of CO₂ on the bitterness psychophysical function (figures 2 and 6). Quinine sulfate, unlike tartaric acid and NaCl, abates oral pungency. This abatement takes place at low CO₂ concentrations (figure 2), and is strong enough to alter significantly the oral pungency function slope (raising it from 1.1 to 1.6), as revealed by the significance of the ANOVA interaction term. But when looking at the effect of CO₂ on the scaling of quinine sulfate bitterness the picture is different. At low concentrations of bitter tastant CO₂ significantly enhances bitterness, at high concentrations of tastant it significantly abates bitterness (figure 6). This gives rise to a highly significant ANOVA interaction term, which means that the effect of CO₂ on perceived bitterness is not the same along the whole concentration range of quinine sulfate. These concentration-dependent effects cancel each other in the ANOVA, rendering the main effect of CO₂ not significant.

Based on results from experiments 1 and 2 it can be concluded that for the tastants sucrose, NaCl, and tartaric acid the effect of the tastant on the oral pungency stimulus response function is in the same direction as that of the effect of the pungent substance on the taste stimulus-response function. For quinine sulfate, however, this does not hold. In other words, the absence of an effect of sucrose on oral pungency is paralleled by the absence of an effect of CO₂ on sweetness; oral pungency enhancement by NaCl and tartaric acid is paralleled by saltiness and sourness enhancement by CO₂ (although the intensity and

range of enhancement might not be of the same magnitude). Oral pungency abatement by quinine sulfate, however, is not paralleled by a simple bitterness abatement by CO₂. Instead, CO₂ can enhance or abate perceived bitterness depending on the quinine sulfate concentration.

It would be of interest to test the generality of these results by studying the oral pungency - taste interaction with other tastants with the same taste qualities as we tested here (e.g., citric acid, lithium chloride, urea, and glucose). The oral pungent substance could also be changed. This might prove more difficult, however, since there are not many relatively harmless substances that are able to evoke oral pungency without an associated taste or odor, and that are also comparable in terms of latency for maximum intensity to the latencies of the four tastes so that simultaneous presentation of both stimuli can be carried out.

In summary we can say that sucrose sweetness and CO₂ oral pungency simultaneous perception is characterized by a lack of mutual influence; NaCl saltiness or tartaric acid sourness and CO₂ oral pungency simultaneous perception is characterized by mutual enhancement; and quinine sulfate bitterness and CO₂ oral pungency simultaneous perception presents a nonuniform picture.

Previous electrophysiological studies (Beidler 1953) have shown that the lingual nerve (a branch of the trigeminal nerve) is activated by very concentrated salt or acid solutions. Kawamura et al (1968) found that medium and high concentrations of NaCl and high concentrations of tartaric acid are able to elicit responses from the lingual nerve, but that sucrose, even in a saturated solution, does not elicit any response.

We have confirmed the lack of effect of sucrose on perceived oral pungency, but also found that relatively low concentrations of NaCl and tartaric acid are able to enhance CO₂ perceived oral pungency. Probably, these low tastant concentrations are not pungent per se, but rather their perceptual attributes of saltiness and sourness are close enough to oral pungency to potentiate the already existing pungent sensation evoked by CO₂. In relation to this, Sizer and Harris's (1985) results show an apparent capsaicin pungency enhancement (shown by a threshold diminution) by NaCl and citric acid, which did not, however, achieve statistical significance.

This concept of perceptual proximity is reinforced by the fact that CO₂ is also able to enhance the already existing saltiness and sourness evoked by, respectively, NaCl and tartaric acid. The reduction of perceived oral pungency of low concentrations of CO₂ by quinine sulfate might be associated with the characteristic negative hedonic quality that quinine sulfate bitterness has, even at

low concentrations, which could make this tastant a better distractor stimulus than, for example, sucrose sweetness. In addition, the results imply that, from the qualitative point of view, bitterness and sweetness are more distant from oral pungency than saltiness and sourness.

Acknowledgements. This work was supported by a grant to project 9082-03 and by fellowships to MRGM, AMC, and GN from the Consejo Nacional de Investigaciones Científicas y Técnicas (CONICET), República Argentina.

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This is a pre-copyedited, author-produced version of an article accepted for publication in *Perception* following peer review. The version of record *Perception* **16**:629-640, 1987 is available online at: <http://journals.sagepub.com/doi/10.1068/p160629> - DOI: 10.1068/p160629