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Sweetness Intensity Enhancement by Pulsatile Stimulation: Effects of Magnitude and Quality of Taste Contrast

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Abstract

Upon stimulation with continuously alternating (pulsatile) taste concentrations, humans report higher average taste intensities than for continuous stimulation with the same average tastant concentration. We investigated the effect of the magnitude of concentration changes (concentration contrast) and the effect of taste quality changes (quality contrast) between alternating tastants on sweet taste enhancement. The perceived sweetness intensity increased with the magnitude of the sucrose concentration contrast: The pulsatile stimulus with the highest concentration difference (average sucrose concentration: 60 g/L) was rated as the sweetest in spite of the fact that the gross sucrose concentrations were identical over stimuli. Moreover, this stimulus was rated equally sweet as a continuous reference of 70 g/L sucrose. On alternation of sucrose with the qualitatively different citric acid, sweet taste enhancement remained at the level observed for alternation with water at citric acid concentration levels up to 3 times its detection threshold. Alternation of a sucrose solution with a citric acid solution at 9 times its threshold concentration, resulted in an attenuation of the pulsation-induced enhancement effect. Upon alternation of citric acid pulses at concentrations around the threshold with water intervals only, no taste enhancement was observed compared with continuous citric acid stimuli of the same net concentration. We propose that the magnitude of pulsation-induced taste enhancement is determined by the absolute rather than relative change of tastant concentration. This explains why 1) pulsation-induced sweet taste enhancement is determined by the magnitude of the sucrose pulse–interval contrast and 2) the alteration of citric acid with water does not enhance taste intensity at detection threshold level.

Key words: pulsatile taste stimulation, sweetness enhancement, taste contrast

Introduction

Oral stimulation with high concentration tastant pulses that are intermitted by low concentration tastant or water intervals (pulsatile stimulation) results in taste intensity ratings that are higher than those observed for continuous stimulation of the same average tastant concentration (Meiselman and Halpern 1973; Busch et al. 2009; Burseg, Brattinga, et al. 2010). Different explanations were suggested for this enhancement (Meiselman and Halpern 1973; Busch et al. 2009; Burseg, Brattinga, et al. 2010). One explanation attributes taste enhancement to taste quality contrast effects with pulse–interval combinations representing qualitative contrasting taste stimuli (Meiselman and Halpern 1973). In that view, the perceived (quality) contrast between pulse and interval invokes a perceptual overestimation of the evaluated taste property leading to an overall taste enhancement. This theory is supported by studies showing the effect of cumulated successive contrasts on taste intensity: After repeated stimulation with one taste quality, the intensity of a successively presented qualitatively contrasting stimulus is perceived as more intense compared with the same stimulus evaluated without preceding contrasting stimuli (Kroeze 1983; Schifferstein and Oudejans 1996). Stimulus contrasts can be achieved by either alternating stimulus qualities or stimulus concentrations (Schifferstein and Oudejans 1996). Supporting the contrast explanation, pulsation studies showed taste enhancement upon alternation of high concentration tastant pulses with low concentration tastant intervals of the same quality (concentration contrasts) (Busch et al. 2009; Burseg, Brattinga, et al. 2010) or by alteration with water intervals (quality contrast) (Meiselman and Halpern,

1973; Burseg, Brattinga, et al. 2010). The water interval is hereby regarded as a separate ''taste quality'' as it differs qualitatively from the target stimulus (Meiselman and Halpern 1973).

In the present work, we investigated the effect of the magnitude and the quality of the pulse–interval taste contrast on sucrose sweet taste enhancement by pulsation. For this aim, the pulse–interval concentration contrast was varied by increasing the pulse/interval sucrose concentration difference in a stepwise manner (Study 1). In a second study, the pulse sucrose concentration was kept constant but pulses were alternated with citric acid at varying concentrations to create taste quality contrasts. In an earlier study, it was shown that contrast-induced taste intensity enhancement is independent of the concentration if the preceding and target stimulus are of different qualities (Schifferstein and Oudejans 1996). In the current study, this was tested by altering the citric acid concentration in the interval. The interval citric acid concentration was varied according to the subject's individual citric acid detection threshold to achieve equal intensities (below, at and above detection threshold). To that end, individual citric acid detection thresholds were determined for continuous and pulsatile citric acid stimulation.

Materials and methods

Study 1: sucrose concentration contrast

Stimuli

A computer controlled gustometer (Bult et al. 2007) was used to deliver taste stimuli intra-orally at a flow rate of 15 mL/min. Stimuli were produced at desired concentrations by running 4 pumps in parallel, mixing a sucrose solution (15%; 0.438 mol/L; w/v) and water (Evian, Danone) at predefined ratios. In total, 6 stimuli were delivered. To generate continuous stimuli, the sucrose concentration (S; in % [w/v]) was kept constant (c) over 40 s at 6% (Sc6%; 0.175 mol/L) or 7% (Sc7%; 0.204 mol/L). In pulsed stimuli, high concentration sucrose pulses (p) and low concentration sucrose intervals (i) were alternated. Keeping the net sucrose concentration fixed at 6% for all pulsed stimuli, pulse–interval sucrose concentration difference ($\Delta_{p,i} = [S]_p - [S]_i$ in %) were varied between stimuli. The following pulse–interval concentration differences were given: 7.5–4.5 ($\Delta_{p,i}$ = 3%), 9–3 ($\Delta_{p,i}$ = 6%), 10.5–1.5 ($\Delta_{p,i}$ = 9%), and 12–0 ($\Delta_{p,i}$ = 12%). The pulse and interval lengths were 2.5 s each to yield 5-s pulsation periods (pulse + interval in seconds, at these period lengths, we previously observed maximum sweetness enhancement [3]). Periods were repeated 8 times to yield 40-s stimuli. The sucrose concentration of each of the 6 stimuli was verified by refractometry (Jasco polarimeter P 1030; Hg lamp: 365 nm). The polarimeter was calibrated with sucrose solutions of known concentrations.

Subjects

Fourteen subjects (age: 22–52, 4 male) were recruited. They were trained on the gustometer taste delivery method. Subjects were instructed to consume only water 1 h prior to the test. Materials and methods used did not require medical ethical approval under Dutch regulations (retail ingredients, oral delivery). Subjects were paid and gave written informed consent.

Method

Time–intensity analysis: Subjects were instructed to hold a mouthpiece (Teflon tube) in their mouth and keep it gently between their central incisors. During stimulus presentation, subjects rated sweetness intensity over time (time-intensity; scale: 0–100; anchored ''not sweet''–''very sweet'') by moving the control of a vertical rating bar on the computer screen. Subjects evaluated all 6 stimuli (including the continuous reference Sc6% as a blind) 5 times in a block design over 2 independent sessions where stimuli were randomized over subjects and within blocks. Subjects swallowed at will. In one session, 15 stimuli were presented in 3 groups of 5 samples each, separated by 5-min breaks. Before each stimulus group, subjects received the reference for self-calibration. Between samples, a pause of at least 1 min was given to rinse the mouth with water. At the beginning of each session, subjects received 2 warm up stimuli.

Data analysis

Time–intensity analysis: The area under the time–intensity curve (0–40 s) was treated as grouping variable (area under sweetness curve, AUSC; measure for sweetness intensity). Kruskal–Wallis tests (SPSS, Chicago, version 17) were conducted to test for effects of the sucrose pulse–interval contrast ($\Delta_{p,i}$ = 0% [Sp6%], $\Delta_{p,i}$ = 3%, $\Delta_{p,i}$ = 6%, $\Delta_{p,i}$ = 9%, and $\Delta_{p,i}$ = 12%) using the results of all 16 subjects. To test for the effects of stimulus contrast at equal net sucrose concentrations alone, the reference stimulus Sc7% was omitted. Mann–Whitney tests with Bonferroni correction (4 comparisons) and stimulus ''Sp6% [$\Delta_{p,i} = 0$]'' as reference were used to follow up on possible differences. All effects are reported at a 0.0125 level of significance.

Study 2: sucrose–citric acid quality contrast

Stimuli

Citric acid detection threshold: The gustometer (see Study 1) delivered citric acid stimuli at a flow rate of 15 mL/min. Stimuli were produced by running 2 pumps in parallel, mixing a citric acid solution (1.56 mmol/L) and water (Evian, Danone, France) at predefined ratios. For continuous stimulation, the citric acid concentration decreased between stimuli from 1.20 to 0.36 mmol/L by 0.052 mmol steps. For pulsatile stimulation, citric acid pulses were produced by

running 2 pumps in parallel, mixing a citric acid solution (3.12 mmol/L) and water (Evian, Danone, France) at predefined ratios. Alternating water intervals were delivered by a third pump. The citric acid concentration decreased between stimuli from 2.40 mmol to 0.72 mmol/L by 0.104 mmol steps. Pulse and interval lengths were 2.5 s each. Sweetness intensity rating: The gustometer (see Study 1) delivered alternating sucrose–citric acid stimuli by running 4 pumps in parallel (total flow rate: 15 mL/min). Defined sucrose and citric acid concentrations were achieved by mixing a sucrose solution (0.78 mmol/L) and citric acid solution (1.56 mmol/L) with water at predefined ratios. Six stimuli were defined: a continuous sucrose reference at 3% (Sc3%; 20 s; no citric acid), 5 pulsed stimuli where 6% sucrose pulses (Sp) were alternated by citric acid intervals ($C[i]$). $C[i]$ concentrations were defined individually with respect to the individual C-detection threshold (T) obtained in Study 1. The concentrations were $9 \times T$ ([>>T]), $3 \times T$ ([>T]), T ([=T]), $T/3$ ([<T]), and 0 ([0]). The pulse and interval length was 2.5 s each to yield 5-s pulsation periods. Periods were repeated 4 times to yield 20-s stimuli. All pulsed stimuli, including the continuous reference, yielded an average sucrose concentration of 3% (w/v). This was verified for each of the 6 stimuli by refractometric determination (Jasco polarimeter P 1030; Hg lamp: 365 nm). The polarimeter was calibrated with sucrose solutions of known concentrations.

Subjects

Sixteen subjects (age: 22–52, 5 male) from which 14 subjects also participated in Study 1 were recruited. They were trained on the gustometer taste delivery method. Subjects were instructed to consume only water 1 h prior to the test. Materials and methods used did not require medical ethical approval under Dutch regulations (retail ingredients, oral delivery). Subjects were paid and gave written informed consent.

Method

Detection threshold: Subjects were presented with 2 stimuli, one of them being water, the other being aqueous citric acid solutions either in continuous or pulsed fashion (starting concentration: 0.88 mmol/L for continuous and 1.77 mmol/L for pulsed stimuli). Stimulation duration was 20 s each (corresponding to 4 pulsation periods) with a 3 s break between stimuli. For each stimulus pair, the subject had to identify the solution containing citric acid. Following the staircase procedure (Bartoshuk 1978), the concentration was increased by one step if an incorrect answer was given. After 2 correct answers, the concentration was decreased by one step. The session was terminated after recording of 7 reversals. Detection thresholds for continuous and pulsed citric acid were determined over 2 separate sessions. The order of these sessions was balanced over subjects. Between stimuli, at least 1 min was given to rinse the mouth with water. After every fifth rating, subjects were given a 5 min break. At the beginning of each session, subjects received 2 warm up stimuli. Sweetness intensity rating: Subjects first received the continuous reference Sc3% over 20 s which was denoted "5"on a horizontal line scale (0–10 with 0 = "not sweet at all" and 10 = "very sweet"). After a 3 s break, they received one of the 6 stimuli (the reference was included as blind) and rated the sweetness intensity of the stimuli relative to the reference. Subjects received an auditory signal before presentation of each stimulus to focus their attention. Each stimulus and the blind reference were evaluated 3 times to obtain a total of 18 ratings. Stimuli were given in blocks of 3 with a 5 min break between blocks. Between stimuli, at least 1 min was given to rinse the mouth with water. At the beginning of each session, subjects received 2 warm up stimuli. Subjects rated all stimuli within a 1-h session in a randomized order.

Data analysis

Detection threshold: Detection thresholds were calculated as the geometric mean of the last 5 staircase reversals. Thresholds were measured over 2 independent sessions and both values were correlated (linear regression) to obtain a threshold reliability estimate. Arithmetic means of both sessions were then used as final citric acid detection threshold. This was done separately for continuous and pulsatile stimulation. For pulsatile stimulation, thresholds were calculated from the average concentration of a period. Sweetness intensity rating: The sweetness intensity ratings from the line scales were averaged over replicate and subject. Effects on sweetness by citric acid contrast ([>>T], [>T], [=T]), [<T], and [0]) were tested by nonparametric Kruskal–Wallis tests considering the results of all 16 subjects. Mann–Whitney tests with Bonferroni correction (4 comparisons) were used as pairwise comparison tests between "[0]" as the reference stimulus and each of the 4 citric acid containing pulsatile sucrose stimuli ([>>T], [>T], [=T]), [<T]). All effects are reported at a 0.0125 level of significance.

Results

Study 1: sucrose concentration contrast

Sucrose concentration

The net average sucrose concentration as measured by refractometry was 6.1 ± 0.1% and 7.2 ± 0.1% (mean ± standard deviation [SD]) for the continuous stimuli Sc6% and Sc7%, respectively. It was 6.1 ± 0.1% for pulsed stimuli. *Psychophysical results*: Despite equal net sucrose concentrations, total sweetness (AUSC) differed between stimuli. Pulsatile stimuli were rated sweeter than the continuous reference "Sc6%" (Figures 1 and 2). Ratings increased with the sucrose contrast. Stimulus "$\Delta_{p,i}$ =12%" was rated the most sweet. Kruskal–Wallis tests revealed significant effects of stimulus [$H(4) = 33.4$, $P < 0.0001$] on AUSC. Mann–Whitney tests revealed that differences existed between the continuous

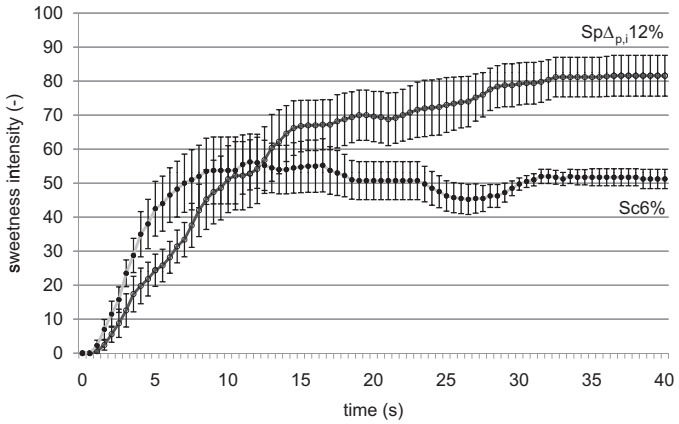

Figure 1 Example of pulsation-induced sweetness enhancement as shown by averaged time–intensity curves (5 replicates) of one subject for stimuli "Sp$\Delta_{p,i}$12%" (2.5 s high concentration sucrose pulses [Sp; 12%; w/v] alternated with 2.5 s water intervals [i] over 40 s) and "Sc6%" (sucrose concentration [S; w/v] was kept constant [c] over 40 s at 6%); the net sucrose concentration was 6% for each stimulus; error: standard error.

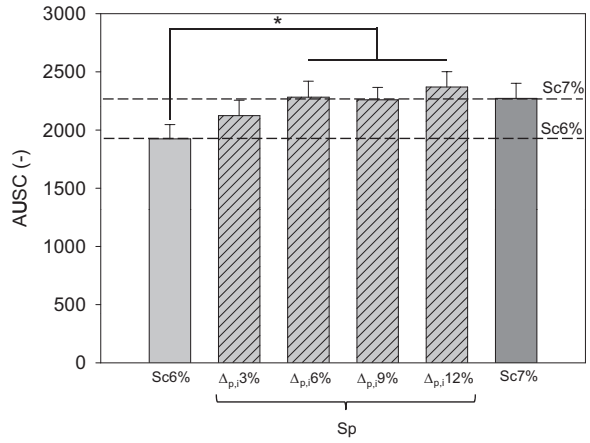

Figure 2 Comparison of average areas under sweetness curves (AUSC; measure of sweetness intensity) for continuous (Sc) and pulsed stimuli (Sp); in pulsed stimuli, pulse–interval sucrose concentrations varied to increase the pulse–interval sucrose concentration difference ($\Delta_{p,i}$; 3–12%); pulsed stimuli are of the same net sucrose concentration (6%) as the continuous reference Sc6%; the 7% continuous sucrose reference (Sc7%) was evaluated to express the gain in sweetness intensity for pulsed stimuli; error bars: standard error; *pulsatile stimuli that are significantly different from the continuous reference SC6% ($P < 0.0125$).

reference and pulsed stimuli "$\Delta_{p,i} = 12\%$ [$U = 1258$; $z = -4.97$, $P < 0.0001$], $\Delta_{p,i} = 9\%$ [$U = 1402$; $z = -4.37$, $P < 0.0001$], and $\Delta_{p,i} = 3\%$ [$U = 1492$; $z = -4.00$, $P < 0.0001$]," if compared to. There was a trend for stimulus "$\Delta_{p,i} = 1.5\%$" [$U = 1867$; $z = -2.43$; $P = 0.015$].

Study 2: sucrose–citric acid contrast

Sucrose concentration

The net average sucrose concentration as measured by refractometry was 3.1 ± 0.1% (mean ± SD) for the continuous stimulus Sc3% (continuous delivery of a 3% sucrose solution) and 3.0 ± 0.13% for pulsed stimuli.

Psychophysical results

Detection Threshold: Average citric acid detection thresholds differed between subjects but not between stimulation mode (continuous vs. pulsatile; Figure 2). The median citric acid threshold for all subjects was 0.71 mmol/L (range: 0.36–1.13 mmol/L) for continuous stimulation and 0.75 mmol/L (range: 0.53–1.05 mmol/L) for pulsatile stimulation (Figure 3). For pulsatile stimulation, threshold concentrations were defined as geometric average of a period. Hence, for all subjects, the median detection threshold of citric acid pulses was 1.50 mmol/L. Threshold correlation analysis revealed a sufficient correlation for both continuous (R: 0.77) and pulsatile stimulation (R: 0.62). The method used to determine citric acid detection thresholds was therefore of adequate reliability.

Sweetness intensity: Despite their equal average sucrose concentrations, stimuli were rated different in sweetness intensity [$H(4) = 18.9$; $P = 0.001$] (Figure 4). Pulsatile stimuli were rated sweeter than the continuous reference "Sc3%" if the interval citric acid concentration was equal or smaller than 3 times the citric acid threshold (Figure 4). At concentrations up to 3 times the citric acid threshold, no difference was found between stimulus "SpC[0]" and stimuli "SpC[$<T$] ($U = 1039$; $z = -0.84$, $P = 0.403$); SpC[$=T$] ($U = 1120$; $z = -0.24$, $P = 0.809$) and SpC[$>T$] ($U = 999$; $z = -1.14$, $P = 0.255$). Hence, the presence of citric acid at concentrations up to 3 times the citric acid threshold did not affect the pulsation effect on sweetness intensity. Stimulus "Sp[$C >> T$]" was rated less sweet than stimulus "SpC[0]" ($U = 746$; $z = -3.00$, $P = 0.003$). This stimulus was rated as sweet as the continuous reference (Figure 4).

Discussion

Confirming earlier results, pulsatile taste stimuli were perceived as sweeter than a continuous reference at the same net sucrose concentration. Furthermore, as expected, sweetness ratings of pulsatile stimuli increased with the magnitude of the pulse–interval sucrose contrast (Study 1). Alternating sucrose pulses with citric acid concentrations up to 3 times, the citric acid detection threshold did not alter sweetness ratings compared with those observed for sucrose–water combinations (Study 2). Only at supra-threshold concentrations of 9 times the citric acid detection threshold concentration, citric acid attenuated the sweetness enhancement observed for other stimuli. Sweetness intensities for this pulsed stimulus were similar to the intensity of the continuous sucrose reference.

Rankin and Marks (1991) described that when low ranges of intensities of a stimulus are combined with high ranges of stimuli of a different quality, intensity ratings within each

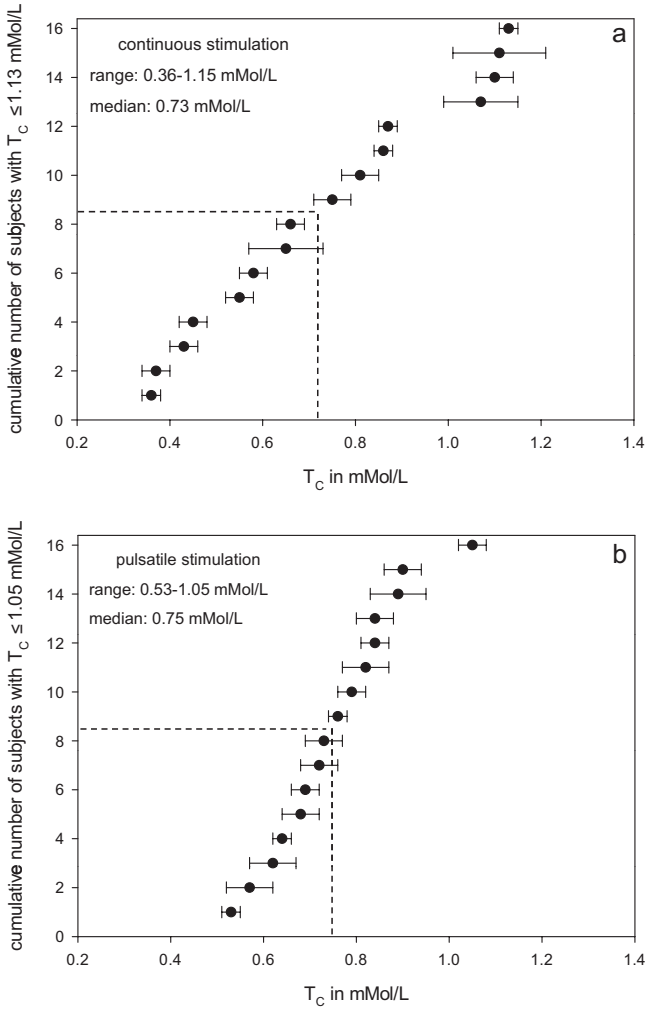

Figure 3 Individual citric acid detection thresholds (T_C in millimoles per liter) as measured for 16 subjects upon continuous **(a)** or pulsatile stimulation **(b)**; dashed lines indicate median T_C in millimoles per liter; error bars: standard error Figure 4. Comparison of sweetness intensity for the continuous reference (Sc3%) and pulsed stimuli (SpC[*i*]); in pulsed stimuli, sucrose pulses (Sp) were alternated with citric acid intervals (*C*[*i*]) of different concentrations (*C*[0]: not present; *C*[<*T*]: 3 times below the individual detection threshold (*T*); *C*[=*T*]: at *T*; *C*[>*T*]: 3 times above; or *C*[>>*T*]: 9 times above *T*); *pulsatile stimulus that is significantly different from remaining pulsatile stimuli ($P < 0.0125$).

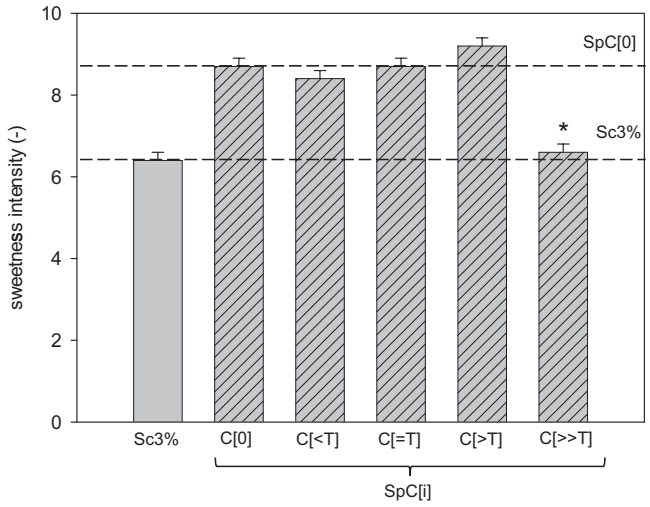

Figure 4 Comparison of sweetness intensity for the continuous reference (Sc3%) and pulsed stimuli (SpC[i]); in pulsed stimuli, sucrose pulses (Sp) were alternated with citric acid intervals (*C*[*i*]) of different concentrations (*C*[0]: not present; *C*[<*T*]: 3 times below the individual detection threshold (*T*); *C*[=*T*]: at *T*; *C*[>*T*]: 3 times above; or *C*[>>*T*]: 9 times above *T*); *pulsatile stimulus that is significantly different from remaining pulsatile stimuli ($P < 0.0125$).

quality category will be biased toward the intensity range of the contrasting stimuli. If such global stimulus context effect would also apply to the fast-alternated taste pulses in our study, we would expect an increase in sweetness enhancement with citric acid concentration. Interestingly, in the present study, sweet taste enhancement did not increase with citric acid concentration up to 3 times its detection threshold. And even at the highest citric acid concentrations (9 times the citric acid detection threshold concentration), sweetness ratings were attenuated compared with the regular sweetness enhancement observed for stimuli containing less citric acid.

With the exception of the pulsed stimuli containing the highest citric acid concentration, these findings are more in line with studies showing the effect of cumulated successive contrasts on taste intensity: When taste solutions with contrasting taste qualities are evaluated sequentially, the taste quality of the primary stimulus enhances the perceived intensity of the subsequent stimulus (Schifferstein and Oudejans 1996). As observed in the present study, the quality contrast-induced taste intensity enhancement is independent of the concentration if the preceding and target stimulus are of different qualities (Schifferstein and Oudejans 1996).

Mixing tastants with contrasting taste qualities (e.g., sweet and sour stimuli) generally results in an attenuation of their main taste qualities (Pangborn 1961; Schifferstein and Frijters 1990; Schifferstein 1994; Prescott et al. 2001; Pelletier et al. 2004). Although sucrose pulses and citric acid intervals were never really mixed, mixture suppression may explain why, for the most intense citric acid concentration, sweetness ratings were attenuated with respect to the other pulsatile stimuli. In this study, the temporal proximity of sucrose and citric acid stimuli in combination with the physical separation of these on the tongue can be well compared with the spatially separated, simultaneous stimuli in split-tongue studies for which mixture suppression was also observed (Lawless 1979; Kroeze and Barthoshuk 1985). Because receptor based interaction is ruled out due to either temporal (current study) or spatial separation, the suppression observed in both studies is attributed to perceptual interactions occurring at late integrative stages of stimulus processing.

Citric acid thresholds for continuous and pulsed citric acid stimuli revealed that the pulsed citric acid concentration had to be twice as large as the citric acid concentration in

continuous stimuli to be detectable. As the individual detection threshold concentration for pulsed stimuli was the averaged tastant concentration over citric acid pulses and water intervals of equal lengths (period threshold), equal citric acid detection thresholds for pulsed and continuous stimuli imply 1) equal responses for pulsed and continuous citric acid solutions and 2) no taste enhancement by pulsation of citric acid concentrations around threshold level. Because the absolute pulse–interval concentration difference cannot be larger than the detection threshold level, it may be that a minimum pulse–interval concentration difference is required to allow for a pulsation-induced enhancement. This implies that pulsation-induced taste enhancement is most likely caused by the absolute concentration difference (which is small in this case) rather than by the relative concentration difference (which is large for stimuli at peri-threshold concentrations). This is supported by the sweet taste enhancement dependency on pulse–interval sucrose contrast (Study 1) and the equal enhancement observed for pulsed stimuli consisting of 12% sucrose pulses and 0% sucrose intervals, in spite of their variable citric acid concentrations (Study 2).

An alternative explanation for the observation that pulse–interval concentration differences predict sweetness enhancement (Study 1) may be that it is not the concentration difference that drives enhancement but the mere pulse sucrose concentration. In that case, subjects would have rated the stimuli according to the pulse sucrose concentration rather than averaging sweetness intensity over periods. This seems plausible if subjects were not aware of sucrose concentration alternations and pulsatile stimuli were perceived as continuous taste sensation of subsequent higher intensity than the continuous reference. Their ratings then reflect the intensity of the high concentration sucrose pulses.

Citric acid detection thresholds for continuous and pulsatile stimulation correlated poorly (data not shown). In other words, subjects with a low citric acid detection threshold for continuous stimulation did not necessarily fall in the same threshold category with responses to pulsatile stimulation. Hence, the detection threshold for one stimulation mode is a poor predictor for a person's detection threshold in the other stimulation mode. Moreover, the panel's threshold range obtained for pulsatile stimulation was a factor 2 smaller than the observed threshold range observed for continuous stimulation, even though the median threshold concentrations were the same for both stimulation modes. These observations suggest that taste information is processed differently for pulsatile and continuous stimulation. A physiological observation that may explain that difference is that responses to taste stimulation recorded in the taste periphery (chorda tympani) already show remarkable burst pattern differences between intermittent (pulsed) and continuous taste stimulation (Halpern and Marowitz 1973; Hallock and Di Lorenzo 2006). These chorda tympani recordings show an extraordinary increase in transient chorda tympani burst counts after pulse onset, whereas continuous stimulation invokes sustained burst trains at much lower frequencies. The elevated chorda tympani output that result from trains of transient burst peaks for pulsatile stimulation then explains the increase in taste intensity upon pulsatile stimulation. The involvement of 2 intrinsically different stimulus encoding modes (transient chorda tympani responses in the case of pulsatile stimuli and sustained chorda tympani responses in the case of continuous stimuli) offers then an explanation for the observed poor correlation between citric acid detection thresholds for pulsed and continuous stimuli and the observed difference in range of detection thresholds for these stimuli.

Like the taste fusion period (TFP) and detection thresholds for continuous stimuli, subjects seem to vary with respect to the minimum pulse–interval concentration difference required to induce a pulsation effect (as manifested by interindividual differences in the detection threshold for pulsed stimuli). This may be explained by individual differences in the processing of both pulsatile and continuous taste stimuli. This also includes the moment and frequency of swallow as subjects were instructed to swallow at-will. Moreover, retaining a certain stimulus volume prior to swallowing may result in mixing of pulse and interval and hence alter the pulse–interval profile after delivery in-mouth. This may, for example, account for differences in the detection threshold of pulsatile stimuli as well as TFP. Despite interindividual differences, were subjects consistent in the way they processed (pulsatile) stimuli. This is shown by the size of errors upon determination of the detection threshold of pulsatile citric acid stimuli and the repeatability of the pulsation effect across different studies (Burseg, Brattinga, et al. 2010; Burseg, Camacho, et al. 2010).

In conclusion, we propose that the magnitude of pulsation-induced taste enhancement is determined by the absolute stimulus concentration contrast. This is based on the findings that 1) pulsation-induced sweet taste enhancement is determined by the magnitude of the sucrose pulse–interval concentration contrast and 2) the alteration of citric acid with water does not enhance taste intensity at detection threshold level. The latter case also suggests the requirement for a minimum pulse–interval concentration difference to induce taste enhancement. Pulsatile sucrose stimulation with a qualitatively altered stimulus (here: citric acid) equally results in sweet taste enhancement. Enhancement is independent of the citric acid concentration if presented at levels up to 3 times the detection threshold. At levels clearly above detection threshold, perceptual suppression between citric acid and sucrose reduced the pulsation effect.

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