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Odor–Taste Interactions: Effects of Attentional Strategies during Exposure

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Abstract

Through repeated pairings with a tastant such as sucrose, odors are able to take on the tastant's qualities, e.g. by becoming more sweet smelling. When such odors are subsequently experienced with a sweet tastant in solution, the mixture is often given a higher sweetness rating than the tastant alone. Odor-induced taste enhancement appears to be sensitive to whether an odor–taste combination is viewed analytically as a set of discrete qualities, or synthetically as a flavor. The present research attempted to determine if adoption of these different perceptual approaches during co-exposure with sucrose would influence the extent to which an odor would become sweet smelling and subsequently enhance sweetness intensity. In Experiment 1, subjects received multiple exposures to mixtures of sucrose with low sweetness, low familiarity odors or, as a control, the odors and sucrose solutions separately. Two groups that received mixtures made intensity ratings that promoted either synthesis or analysis of the individual elements in the mixtures. The odors became sweeter smelling irrespective of group. Only adopting a synthetic strategy produced odors that enhanced sweetness in solution. However, these effects were also shown with a 'non-exposed' control odor. This could be accounted for if the single co-exposure with sucrose that all odors received in the pre-test was able to produce sweeter odors. A second experiment confirmed this prediction. Thus, while even a single co-exposure with sucrose is sufficient to produce a sweeter odor, the adoption of a synthetic perceptual strategy during the co-exposure is necessary to produce an odor that will enhance sweetness. These data are consistent with associative leaning accounts of how odors take on taste qualities and also support the interpretation that these effects reflect the central integration of odors and tastes into flavors.

Key words: associative learning, odor-induced taste enhancement, perceptual strategy

Introduction

Some odors, when sniffed, elicit descriptions of qualities that are more usually associated with basic tastes (Burdach *et al.*, 1984). For example, in the descriptive analysis of odor characteristics reported by Dravnieks (1985), 65% of assessors gave 'sweetness' as an appropriate descriptor for the odor of vanillin, while 33% described the odor of hexanoic acid as being sour. The possession of taste properties by odors is extremely common, particularly in the case of frequently consumed foods, e.g. the sweet smell of honey and the sour smell of vinegar. In fact, for some odors, taste qualities may represent the most consistent description used (Stevenson and Boakes, 2003).

Frank and Byram (1988) proposed that odors are described in terms of taste qualities as a result of frequent co-occurrence with particular tastes, for example in foods. This associative explanation has been supported by the results of a series of experiments (Stevenson *et al.*, 1995, 1998) in which relatively novel odors, low in smelled sweetness and sourness when sniffed, were repeatedly paired with either sweet (sucrose) or sour (citric acid) tastes in solution. These studies were able to consistently demonstrate that the odors were rated significantly higher in smelled sweetness or sourness, depending on the taste with which they were paired, when sniffed following the exposure phase.

These learning effects appear to represent a change in the perceptual quality of the odor, rather than simply a change in its hedonic value. While odor hedonic changes are known to occur following repeated exposure with sweetness (Zellner *et al.*, 1983), the effects in these studies occurred with no appreciable change in ratings of liking for the odor. Moreover, whether or not the subject was explicitly aware of the specific odor–taste pairing during exposure (based on their estimates of frequency of pairing of the different odors and tastes) did not influence the degree of change in the smelled properties of the odor. This argues against the changes in ratings merely resulting from either the development of an explicit metaphor to describe the odor ('sweet like sugar') or the demand characteristics in the evaluation task.

Odors that are described in terms of taste qualities when sniffed are also able to influence judgements of taste when added to tastants in solution. The most studied example of this effect is the ability of otherwise tasteless food odors such as strawberry or vanilla to enhance sweetness when added to solutions of a sweet tastant (Frank and Byram, 1988; Frank *et al.*, 1989, 1993; Bingham *et al.*, 1990; Cliff and Nobel, 1990; Clark and Lawless, 1994; Prescott, 1999; Stevenson *et al.*, 1999). Rather than resulting from a general sensory summation, the effects are specific to the taste and odor qualities. Hence, Frank and Byram (1988) showed that strawberry, but not peanut butter, odor enhanced the sweetness of sucrose; conversely, saltiness was not enhanced by strawberry odor.

Although smelled sweetness of an odor while sniffing is a significant predictor of the extent to which that odor will enhance sweetness in solution (Stevenson *et al.*, 1999), demonstrating odor induced taste enhancement appears to operate under some constraints. One important influence appears to be how the subject is asked to evaluate the odor–taste mixture. Frank *et al.* (1991, 1993) found that while strawberry odor enhanced the sweetness of sucrose in solution when the subjects were asked to judge only sweetness, the enhancement disappeared when subjects rated the sourness and fruitiness of these mixtures as well. In addition, they found suppression of the sweetness of the strawberry/sucrose mixtures when the subjects rated total intensity of the mixture and then partitioned their responses into sweet, salty, sour, bitter and/or other tastes.

Frank and colleagues (Frank *et al.*, 1993; van der Klaauw and Frank, 1996; Frank, 2003) interpreted such rating scale effects by suggesting that, given perceptual similarity or congruency between an odor and taste (that is, sharing a similar quality such as sweetness), the conceptual 'boundaries' that the subject sets for a given complex stimulus will reflect the task requirements. In the case of an odor–taste mixture in which the elements share a similar quality, integration of perceptually similar dimensions can be determined by the attentional focus demanded in the task. Similarly, McBurney (1986) suggested that flavors reflect the fusion of odors and tastes into a single perception, rather than combining synthetically to form a new sensation (as is found in odor mixtures, for example). He argues that such fusions remain analysable even when perceived as a whole. An implication of this notion is that whether an odor–taste mixture is perceived analytically or synthetically can therefore be determined by the responses required of the subject. Requiring a single rating of a sensory quality that can apply to both the odor and taste (e.g. the tasted sweetness of sucrose and the smelled sweetness of strawberry odor) encourages synthesis of the common quality from both sensory modalities. In contrast, ratings of multiple appropriate attributes forces an analytical approach and taste enhancement is eliminated. Consistent with this, Bingham *et al.* (1990) showed that untrained subjects judged solutions of the odorant maltol plus sucrose as sweeter than a solution of sucrose alone, whereas a panel trained to adopt an analytical approach to sensory properties found no such enhancement.

Another factor that may determine whether or not an odor enhances a taste is the nature of their prior joint exposure. An exposure strategy that emphasizes the distinctiveness of the elements in the odor–taste mixture (an analytical strategy) during their joint exposure may inhibit increases in the taste properties of the odor and the subsequent ability of the odor to influence tastes in solution. In contrast, treating the elements as a synthetic whole is likely to encourage the blurring of the perceptual boundaries, fostering subsequent odor–taste interactions. This issue has been addressed previously, but with mixed and inconclusive results.

Stevenson and Case (2003) compared untrained subjects with subjects trained to distinguish the individual components of mixtures of odors with sucrose or citric acid on the development of smelled taste properties in odors following exposure. Such training had no impact, possibly because both trained and untrained subjects were asked to rate their liking for the new odor–taste mixtures during exposure. This is likely to have encouraged synthesis of these elements, since hedonic responses tend to be global and synthetic, and thus incompatible with an analytical approach. Prescott (1999) examined the impact of strategies that encouraged either synthesis or analysis of odor–taste mixtures during their repeated co-exposure. During exposure, one group rated the overall flavor intensity of the mixtures (a synthetic approach), while an analytical group rated intensity of the mixture components separately. Although the synthetic approach produced greater increases in the smelled sweetness of some odors, there were no differences between groups in the impact of the odor on sweetness in solution following exposure. These data are difficult to interpret, however, since changes following exposure were not compared to an odor–sucrose combination that was not exposed. Moreover, the evaluation of the odors in solution without sucrose during the pre- and post-tests may have also militated against the effectiveness of the synthetic approach by exposing subjects to one of the elements alone. This has been shown to inhibit odor–taste integration (Stevenson and Case, 2003).

The present research was a further test of the notion that interactions of odors and tastes following their exposure together in flavors is influenced by task demands that manipulate the attentional strategy taken during exposure. In the first study reported here, subjects in a synthetic strategy group focused only on overall flavor of odor–taste pairs during exposure and were never exposed to the mixture elements alone. Subjects in an analytic strategy group were not only informed that they were receiving a mixture of an odor and sucrose, but they also received distinct trials during which their attention was directed to only one of these components, thereby ensuring that the elements of the flavor were treated separately. The test of the impact of these differing task demands was the ability of the exposed odors to subsequently influence taste intensities.

Experiment 1

Methods

Subjects

Thirty-six University of Otago staff and students (six male and 30 females; age range 18–27 years) volunteered to participate. Each subject received a small payment for participating.

Odorant selection

A pilot study using eight subjects was conducted to select two odors that were similar in smelled sweetness and familiarity. Using 100 mm visual analog scales [anchors: not at all sweet (0)–extremely sweet (100); not at all familiar (0)–extremely familiar (100)], the odorants prune (0.15 g/100 ml; Firmenich) and waterchestnut (0.6 g/100 ml; Quest) were selected for the main experiment, because they were both low in smelled sweetness (mean ratings of 29 and 37, respectively) and low-moderate in familiarity (58 and 50, respectively).

Procedure

Solutions were prepared from research grade sucrose (SU) at either 9 or 10% w/w, prune (PR) and waterchestnut (WC) odorants and distilled water. All solutions were used as taste samples, with 0.15% PR and 0.20% WC also doubling as odor samples. Solutions were stored at 4°C for a maximum of 6 days. Taste samples (10 ml) were served at ~18°C. Odor samples (50 ml) were poured into flip-top opaque plastic squeeze bottles (250 ml capacity) 1 day prior to testing and stored at room temperature.

Subjects tasted the sample by swishing it around their mouth for 5 s and then expectorating. When they were required to smell a sample, subjects were asked to hold the bottle under their nose and squeeze vigorously while inhaling. Between samples, subjects were instructed to rinse thoroughly with filtered water.

Subjects attended five sessions, consisting of a pre-test (session 1), three exposure sessions (sessions 2–4) and a post-test (session 5). The sessions were separated by at least 8 h, but no more than 48 h. In session 1, all subjects tasted and rated four solutions (two 9% SU; 0.15% PR + 9% SU; 0.20% WC + 9% SU) for sweetness and two odors (0.20% WC; 0.15% PR) for sweetness and familiarity, using the scales described in the pilot study. All samples were coded with three-digit numbers and presented in random order.

Following the pre-test, subjects were randomly divided into three groups—synthetic strategy (SS), analytic strategy (AS) and exposure control (EC)—each group containing 12 subjects. The SS and AS groups differed in the instructions that they received when receiving odor–taste pairs, while the EC group received odors and tastes separately.

In each of the three exposure sessions, subjects were presented with 12 solutions, arranged in four sets of three. Each set was labelled with a trial number (1–4). Subjects in each group received solutions containing only one of the two odors assessed in the pre-test—that is, either PR (six subjects/group) or WC (six subjects/group), so that one of the odors was repeatedly exposed, while the other was effectively not exposed. For the SS and AS groups, all solutions also contained SU.

Exposure of the odors and tastes, either jointly or individually, was achieved using a discrimination task, as in previous studies (Stevenson *et al.*, 1995, 1998). On each trial, subjects were asked to taste the three solutions, one at a time, from left to right and pick the 'odd' sample. To give validity to this discrimination task, odorant and SU intensities were varied slightly. In the SS and AS groups, for two of the sets ('Sweet' trials), the amount of odorant was kept constant, but one solution contained a higher SU concentration (10%) than the others in the set (9%). For the remaining two sets ('Flavor' trials), the amount of SU was kept constant (9%), but one solution contained a higher odorant concentration (either 0.20% PR or 0.25% WC) than the others in the set (0.15% PR or 0.20% WC). The EC group performed the same task, except that the solutions contained either SU alone (two sets of three per session) or odorant alone (two sets of three per session). For all groups, the position of the 'odd' solution was balanced across trials, and the order of the Flavor and Sweet trials were counterbalanced across subjects, but kept constant across all three exposure sessions.

On each trial, subjects in the SS group were asked to pick the solution that had the strongest overall flavor intensity. In the AS group, subjects were additionally informed that the solutions were made up of SU and a flavor (odor in solution). In both the AS and EC groups, the task was to pick either the sweetest solution (Sweet trials) or the solution with the strongest flavor (Flavor trials). A schematic of these procedures is shown in Figure 1.

The post-test session was identical to the pre-test, except that the samples were coded with different three-digit numbers and subjects received the samples in a different random order.

Analysis

The sweetness ratings obtained from the four taste samples in the pre-test and post-test sessions (two 9% SU samples; 0.15% PR + 9% SU; 0.20% WC + 9% SU) were measured to the nearest millimeter (from the low anchor) for each subject. Difference scores were calculated by subtracting the mean sweetness rating of the two SU solutions from the sweetness ratings for the odorant + SU mixtures, for both the pre- and post-test. Positive difference scores indicated

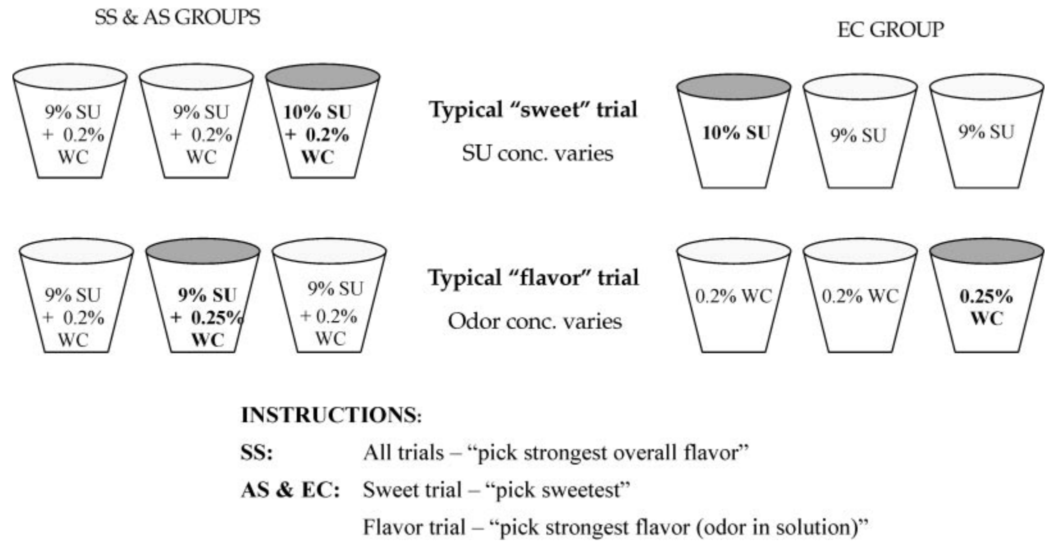

Figure 1 Procedure during the exposure phase in Experiment 1. Typical 'sweet' and 'flavor' trials are shown for one of the odors (water chestnut, WC). In each case, the odd sample is highlighted. In contrast to the AS and EC groups, subjects in the SS group focus only on an overall flavor when making the discrimination.

odor induced sweetness enhancement, whereas negative difference scores indicated odor induced sweetness suppression. Difference scores around zero indicated no effect of the added odorant to the sweetness of the solution. The effect of the odorant on sweetness after the exposure sessions was assessed by subtracting the pre-test difference scores from the post-test difference scores, as follows:

post-test (odorant/SU mixture – SU) – pre-test (odorant/SU mixture – SU).

For each group (SS, AS, EC), these difference scores were divided according to whether they had received the odor during the exposure phase (exposed versus non-exposed), regardless of odorant type. The smelled sweetness and familiarity ratings from the two odorant samples (0.15% PR; 0.20% WC) from the pre-test and post-test were also measured to the nearest millimeter (from the low anchor) for each subject. These data were then analysed as specified below, using an α-level of 5%.

Results

Sniffed odorants

Paired *t*-tests (two-tailed) revealed no significant differences between PR and WC in their initial smelled sweetness [$t(35) = -1.0$] or familiarity [$t(35) = -0.2$]. The effect of exposure on the smelled sweetness and familiarity of the exposed and non-exposed odorants was also examined. Here, the pre-test sweetness and familiarity ratings were compared to the equivalent post-test ratings, for exposed and non-exposed odorants in each group.

An exposure (pre-test; post-test) × odor type (exposed; non-exposed) × group (SS; AS; EC) analysis of variance (ANOVA) for sweetness revealed no effect of group [$F(2,33) = 0.10$] or odor type [$F(1,33) = 1.92$]. However, there was a significant effect for exposure [$F(1,33) = 11.40$, $P < 0.01$]. The smelled sweetness of the odorants (regardless of whether they were exposed or not) increased from the pre- to post-test (see Figure 2). There were no significant interactions between any of the three variables.

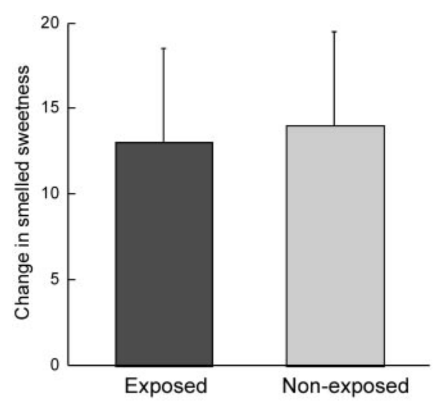

Figure 2 Mean (±SEM) change in smelled sweetness from pre- to post-test for the exposed and non-exposed odors. Data are averaged across groups.

An equivalent ANOVA for familiarity revealed no effect of group [$F(2,33) = 0.44$], odor type [$F(1,33] = 0.26$), or exposure [$F(1,33) = 0.24$], nor any interactions between any of the three variables. Therefore, there was no evidence to suggest that subjects rated either PR or WC as more familiar after exposure.

Odor–taste mixtures

Prior to exposure (session 1), the sweetness of the 9% SU solutions was not significantly changed by the addition of PR or WC. Confidence intervals (95%) for the odor–SU ratings, relative to SU alone, included a zero difference score for both PR (mean = –0.2 ± 6.1) and WC (mean = 1.5 ± 6.2).

Figure 3 shows the mean sweetness ratings of all odors in SU solutions, relative to SU alone, prior to exposure, as well as the mean changes in sweetness of these mixtures with exposed and non-exposed odors following exposure for each group. An odor type × group ANOVA on these scores revealed a significant effect of group [$F(2,33) = 8.78$, $P < 0.01$], but no significant effect of odor type [$F(1,33) = 0.09$], nor any group × odor type interaction [$F(2,33) = 1.23$]. The data were collapsed across odor types for each group in order to assess the change in the ability to modify SU sweetness following exposure. Subjects in the SS group showed a significant increase in sweetness enhancement after exposure [mean increase = 25.2 ± 8.1, 95% confidence intervals (CI)]. In contrast, neither the AS, nor the EC, group showed any change due to exposure (95% CI for both groups included zero; mean AS = –3.8 ± 5.7; mean EC = 4.2 ± 7.3). The lack of significant effects involving odor type indicates that there was no evidence that the exposed and non-exposed odors differed in these effects.

Discussion

The results of this experiment indicated that simple pairing with sucrose in solution can be sufficient to produce a sweeter smelling odor. This is in agreement with previous studies that used a discrimination task as a form of exposure, but did not manipulate task requirements (Stevenson *et al.*, 1995, 1998). Given the absence of any group effect in smelled sweetness, and the fact the increase did not vary between exposed and non-exposed odors, it is plausible to suggests that the limited co-exposure with sucrose that all both odors received during the pre-test

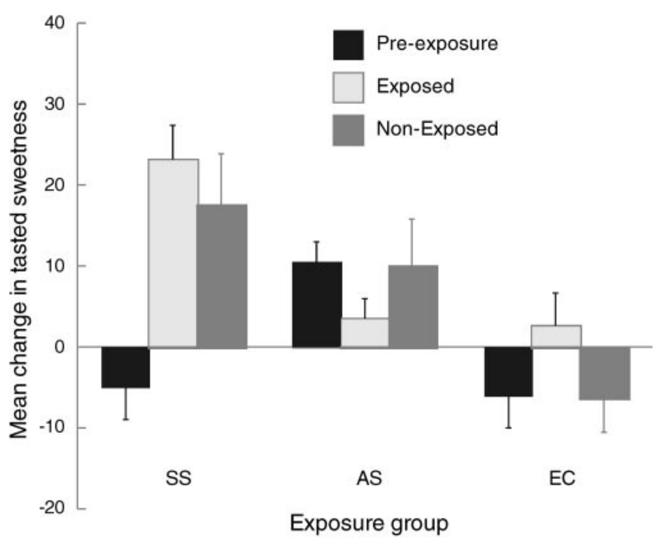

Figure 3 Mean (±SEM) ratings of the sweetness of the odor–SU mixtures, relative to SU alone, for each group, for all odors prior to exposure and for exposed and non-exposed odors following exposure. A significant increase in mixture sweetness was present only for the SS group.

session, common to all groups, was sufficient to facilitate the odor taking on taste qualities. Similar substantial effects of single co-exposures on associative learning have been demonstrated in animal learning studies. Rescorla and Durlach (1981) showed that, with rats, the greatest degree of within-event learning in flavor compounds (analogous to the type of co-exposure studied in the present experiment) occurs with the first exposure to the compound. To date, none of the studies that have addressed the issue of odor–taste learning in humans have assessed the degree of exposure required to produce sweeter odors.

In line with predictions, the present results indicate that, while the associative process (even with relatively little exposure) can lead to sweeter smelling odors, adopting the strategy of treating an odor and taste as a synthetic whole during their joint exposure is necessary in addition to produce enhancement of sucrose sweetness. The present data suggest, therefore, that exposure alone is a necessary, but not sufficient, cause of sweetness enhancement effects.

Finding significant differences in odor-induced sweetness enhancement as a function of perceptual strategy in the present study supports the view that previous failures to find these effects were due to an ineffective manipulations of such strategies. This experiment sought to maximize the synthetic task required by subjects in the SS group by having them attend only to any overall flavor differences between samples and by limiting prior oral exposure to the odors to the odor–SU mixtures. In addition, asking subjects in the AS group to focus on the components in separate trials and to be explicitly aware of the mixture as a combination of an odor and a taste was introduced to make their task more analytical, as was the presentation of the odor and taste trials in separate blocks for the EC group.

The failure to find differences between the exposed and non-exposed odors in sweetness enhancement suggests that the SS group adopted a synthetic strategy during the exposure phase and then applied it during the assessment of mixtures containing either odor, both of which had increased in smelled sweetness. In other words, when subjects adopt a synthetic strategy in relation to a sweet smelling odor, sweetness enhancement results. This is, of course, exactly what has been observed in studies comparing ratings of sweetness alone versus multiple attribute ratings of odor–taste pairs (Frank *et al.*, 1991, 1993). In these latter studies, rating odor–taste mixtures for sweetness only has been sufficient to demonstrate sweetness enhancement with sweet-smelling odors. Since, in the present study, these conditions were also present, taste enhancement should have been expected in all groups. That enhancement was confined to the SS group underlines the fact that the different strategies during exposure were effective in influencing the subjects to perceptually combine or separate the odors and taste. Specifically, these data suggest that the form of exposure received by the AS group inhibited their ability to combine the elements at post-test.

Experiment 2

Because our interpretations of the data from Experiment 1 rely on the assumption that a single co-exposure with sucrose can produce an increase in an odor's smelled sweetness, we conducted an experiment to test this hypothesis. Here we compared sweetness ratings for an unfamiliar, low sweetness odor tasted with sucrose on a single prior occasion with a similar odor that was only sniffed. In addition, we assessed the ability of both odors to enhance sweetness. On the basis of the interpretations above, we expected that only the odor that was experienced in sucrose would become sweeter smelling, but that without a specific integration strategy, this odor would not subsequently enhance sucrose sweetness.

Methods

Subjects

Eighteen University of Otago staff and students (seven males and 11 females; age range 17–29 years) volunteered to participate. Each subject received a small payment for participating. None had participated in Experiment 1.

Procedure

Solutions were prepared from research grade sucrose (SU; 9% w/w), prune (PR) odorant (0.15% w/w; Firmenich), waterchestnut (WC) odorant (0.2% w/w; Quest) and distilled water. Three solutions were used as taste samples (SU; SU + PR; SU +WC) and two solutions (PR; WC) were used as odor samples. Sample preparation and presentation were identical to Experiment 1.

The experimental procedure is shown in Table 1. Each subject attended two sessions, which were separated by 24 h on average. In session 1, each subject first rated the two odor samples (PR; WC) for smelled sweetness. Subjects then rated the sucrose solution and either a SU + PR solution (nine subjects) or a SU + WC solution (nine subjects) for tasted sweetness. This constituted an exposure for that odor only. In session 2, all subjects again rated the two odors for smelled sweetness, followed by all three taste solutions (SU; SU + PR; SU + WC) for sweetness. Therefore, in session 2, subjects rated a SU + odor mixture that had been exposed in session 1 and another that had not been exposed. Sweetness ratings for all samples in both sessions were made on 100 mm visual analog scales with the anchors 'not at all sweet' (0 mm) and 'extremely sweet' (100 mm). All samples were coded with unique three-digit numbers.

Table 1 Design and sample details for Experiment 2

Subjects	Session 1		Session 2	
	Sniffed	Tasted	Sniffed	Tasted
n = 9	PR, WC	SU, SU/PR	PR, WC	SU, SU/PR, SU/WC
n = 9	PR, WC	SU, SU/WC	PR, WC	SU, SU/PR, SU/WC

The two groups of subjects differ in which odor is tasted together with SU in session 1.

Results and discussion

The sweetness ratings obtained from the two odor and two taste samples in session 1 and the two odor and three taste samples in session 2 were measured to the nearest millimeter (from the low anchor) for each subject.

Odor sweetness

The smelled sweetness of the two odors was compared over the two sessions by subtracting the smelled sweetness ratings from session 1 from those obtained in session 2. Figure 4A shows the mean sweetness difference ratings for the exposed odor (paired with sucrose in session 1) and non-exposed odor (no previous sucrose pairing). Confidence intervals (95%) revealed a significant increase in smelled sweetness for the exposed odor (mean = 20.1 ± 6.6), but no evidence of any

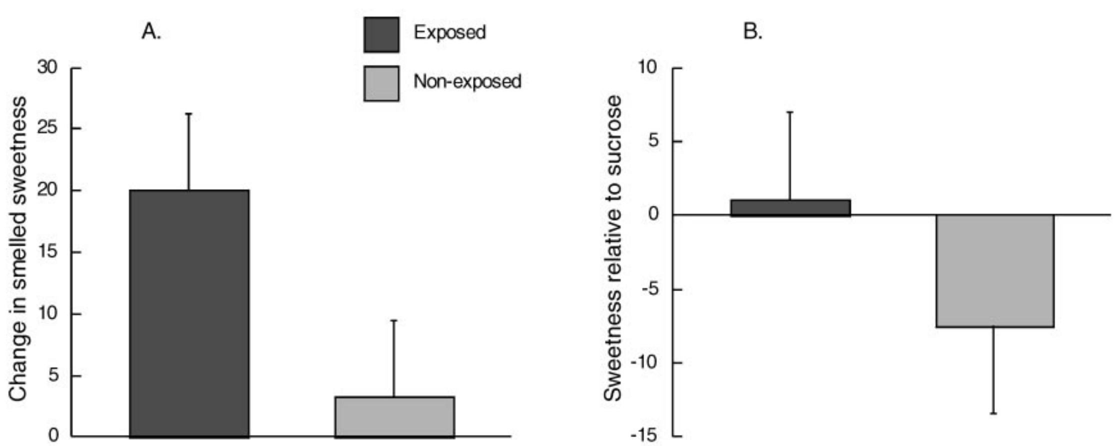

Figure 4 **(A)** Mean (±SEM) change in smelled sweetness from session 1 to session 2 for the exposed (one previous sucrose pairing) and non-exposed (no previous sucrose pairing) odors. **(B)** Mean (±SEM) tasted sweetness of the odor–SU mixtures, relative to SU alone, for both exposed and non-exposed odors in session 2.

change in the smelled sweetness of the non-exposed odor (mean = 3.4 ± 6.2).

Sweetness enhancement

In order to examine whether, over the two sessions, SU + odor combinations changed in sweetness compared to SU alone, the sweetness rating for SU alone was subtracted from the SU + odor sweetness ratings in sessions 1 and 2. A 2 × 2, repeated measures ANOVA with session as a within-subjects variable, and odor (PR; WC) as a between-subjects variable was carried out on these difference ratings. This analysis revealed no change in the ability of the odors to modify SU sweetness [main effect of session; $F(1,16) = 0.72$] and no overall effect of odor on the difference ratings [$F(1,16) = 3.19$]. There was no interaction between session and odor [$F(1,16) = 0.17$].

Subjects also evaluated the sweetness of a SU/odor combination in session 2 that had not been previously paired in session 1 (Non-exposed). An unpaired, two-tailed *t*-test revealed no evidence of a difference in sweetness relative to SU alone between the non-exposed and exposed SU + odor combinations [$t(17) = 1.52$; see Figure 4B].

The data from this experiment support the hypothesis that a single co-exposure with sucrose is sufficient to produce an enhancement of smelled sweetness, at least for an odor that is low in familiarity and initial sweetness. This exposure was not sufficient, however, to produce an odor which would then enhance SU sweetness. We cannot definitively rule out that this was due to insufficient co-exposure with SU, but these results, combined with those from Experiment 1, support an argument for the importance of attentional strategies in determining whether a sweeter odor will then produce sweetness enhancement.

General discussion

Consistent with the results from previous studies (Stevenson *et al.*, 1995, 1998; Prescott, 1999), data from both experiments reported here show that an odor will take on the characteristics of a taste with which it is paired, even with as little as a single co-exposure. Additionally, when a strategy that promotes perceptual synthesis of the odor and taste during their joint exposure was used, these odors acquired a capacity to subsequently influence taste intensities in solution. These data therefore show that both associative learning and cognitive processes are relevant to explaining odor-induced taste enhancement.

While these data appear consistent with a process of odor–taste integration, facilitated by a specific perceptual strategy, an alternative explanation of odor-induced taste enhancement interprets this phenomenon as an example of 'halo-dumping' (Lawless and Clark, 1992; Clark and Lawless, 1994). In order to explain the impact of rating scales on enhancement, it is proposed that, when subjects are unable to rate sensory qualities that may be present in a sample (for example, fruitiness in a fruit odor–sweet taste mixture), they 'dump' these odor qualities onto ratings of other qualities that are rated, such as sweetness, thereby producing enhancement. Under conditions where multiple, appropriate scales are provided, enhancement is not seen since, it is argued, the subject is able to rate all qualities. In other words, enhancement is a function of the number of scales used influencing the subject's rating strategy (Clark and Lawless, 1994).

Although such an interpretation was initially plausible, several more recent studies have provided data that are more compatible with a perceptual account of odor-induced taste enhancement than they are with 'halo-dumping'. Thus, van der Klaauw and Frank (1996) were able to eliminate taste enhancement by directing subjects' attention to the appropriate attributes in a taste–odor mixture, even when they were only required to rate sweetness. The demonstration by Stevenson *et al.* (1999) of an odor's ability to either enhance or suppress tastes in solution was explained primarily by the sniffed taste properties that the odor possessed and did not depend on varying the number of rating scales used. Most convincingly, Nguyen *et al.* (2002) tested the impact of varying the number of scales on the ability of two odors differing in the degree of congruence with sour taste to produce taste enhancement. They found that a general tendency to integrate sensory information, as shown by an enhancement effect of vanilla on sourness when sourness only was rated, was in fact eliminated when multiple scales were used. However, the enhancement seen with the more congruent pair—sourness plus lemon odor—remained, even if somewhat reduced in amplitude. They concluded that enhancement in the latter case reflected perceptual integration of the odor and taste arising from prior co-exposure.

In addition, odors with smelled taste properties can be shown to influence responses to tastes using measures other than rating scales. In a study of reaction times to name taste qualities during the simultaneous presentation of an odor, faster naming times were observed when the odor and taste were congruent (e.g. sweetness/strawberry), as compared to presentation of incongruent pairs (sweetness/grapefruit; White and Prescott, 2001). Dalton *et al.* (2000) showed that the detection threshold for a sweet-smelling odor was reduced by the concurrent presence of a sweet taste at sub-threshold levels. A subsequent study has shown that this effect can be dependent on prior supra-threshold pairing of the odor and taste (Breslin *et al.*, 2003).

The research reported here was not designed as a direct test of halo-dumping as an explanation for odor-induced taste enhancement and, as such, does not definitively rule it out as a contributor to such enhancement. However, since the manipulation of attentional task demands in Experiment 1 altered the extent to which odors would influence tastes in solution, while the response task used to assess odor-induced taste enhancement remained constant across groups, we believe that the potential contribution of halo-dumping was probably minor. Nevertheless, the definitive test of whether responses processes like halo-dumping do play a role would be to compare the effects of these differing task requirements when subjects were also able to rate multiple flavor qualities, rather than only sweetness, during the post-test, when the ability of an odor to produce enhancement is assessed.

We argue that the most parsimonious explanation for the results is that the perceptual strategy induced by the differing task demands was primarily responsible for variations in enhancement. The data from the present studies are therefore consistent with a process in which, due to co-exposure and the adoption of a synthetic perceptual strategy, tastes and odors are integrated into a functionally distinct flavor perception. Such an interpretation is consistent with both theoretical accounts of flavor perception, as well as evidence from a variety of physiological and behavioural studies of sensory integration across multiple sensory modalities. Gibson (1966), for example, argued that the physiological origin of sensations is less important than that the sensations can be used to identify objects that, in the case of odors and tastes, are biologically crucial. This view necessarily entails that input from different sensory systems will be integrated. Rozin (1982) has suggested that retronasal olfaction, which occurs during food consumption, can be seen as functionally distinct from orthonasal olfaction (sniffing). While these two 'senses' physiologically differ perhaps only in efficiency of delivery of odors to the olfactory epithelium (Voirol and Daget, 1986; Pierce and Halpern, 1996), the information delivered by each may differ in its cognitive impact. The importance of the olfactory component of flavors lies in the fact that, in association with tastes and other sensory properties, they uniquely identify foods located in the mouth. It is therefore understandable that tastes and odors are integrated as flavors, rather than coded as distinct elements.

This type of integration of information from physiologically distinct sensory modalities appears to be a general property of the mammalian nervous system (Gibson, 1966; Marks, 1991; Stein and Meredith, 1993). Its purpose may be to enhance the detection of, and reduce ambiguity associated with, external stimuli, particularly in those cases where a single sensory modality fails to supply all the necessary information about the stimulus (Calvert *et al.*, 1998). Physiological evidence for integration across sensory modalities is found in the presence of multimodal neurons that respond specifically to combinations of different sensory inputs, as well as sensory-specific neurons responsive to modulation by other sensory modalities (Meredith and Stein, 1983; Stein and Meredith, 1993; Calvert *et al.*, 1998). Moreover, studies of coincident visual and auditory stimuli (e.g. Stein *et al.*, 1988) find over-additive enhancement in both physiological (e.g. cell firing rate in the superior colliculus) and behavioural (e.g. response accuracy; reaction time) indices.

In the processing of olfactory and gustatory stimuli, multimodal neurons in the orbitofrontal cortex of the monkey have been shown to respond specifically to qualities that occur together in flavors, e.g. the sweetness of glucose and fruit odors, rather than to incongruous combinations such as saline and these same odors (Rolls and Bayliss, 1994; Rolls, 1997). It is thought that these neurons develop from unimodal neurons that originally responded to olfactory information, through learning of appropriate combinations of signals during repeated co-exposure of particular tastes with odors. Distinct patterns of neural activity reflecting flavor perception have also been demonstrated in humans. Using positron emission tomography (PET) to examine cerebral blood flow during flavor perception, Small *et al.* (1997) found distinct patterns of neural activity in primary gustatory and secondary gustatory and olfactory cortices associated with the simultaneous presentation of odors and tastes as flavors compared to patterns produced by independent presentations of identical stimuli.

Behavioural evidence of odor–taste integration as flavors comes from animal learning studies. Rescorla (see Rescorla, 1980; Rescorla and Durlach, 1981) describes within-event learning in which the simultaneous presentation of distinct qualities (either taste–taste or taste–odor) can lead to the encoding of a compound stimulus to which the individual elements become to be perceived as similar (as assessed by the ability of the elements to elicit behaviors conditioned to the compound stimulus). He notes also that the presentation of each element may also activate the whole compound stimulus. This clearly has parallels with the ability of a sniffed odor to activate a previously encoded odor–taste compound in humans.

Cross-modal sensory integration appears to depend on spatial and/or temporal contiguity (Calvert *et al.*, 1998; Driver and Spence, 2000). Rescorla (1980) suggested that simultaneous presentation of odors and tastes 'discourages the formation of individual representations', which may act to inhibit learning. Contiguity of the odor and taste may also be a crucial determinant of their integration in humans. Central to this process may be the well-known olfactory location illusion, in which retronasal perception of odors is universally interpreted as originating in the mouth, rather than the nose. Mediated by concurrent taste or tactile stimulation (or both), this illusion appears to depend on the temporal contiguity of the discrete sensory inputs. Von Bekesy (1964) showed that the perceived location of an odor (mouth versus nose) and the extent to which an odor and taste were perceived as one sensation or two could be manipulated by varying the time delay between the presentation of the odor and taste. This principle seems to be also critical for odor-induced taste enhancement. Sakai *et al.* (2001) demonstrated that enhancement can occur with orthonasal, as well as retronsal, odors, providing that the odor and taste are presented simultaneously.

Both temporal synchrony (Engel *et al.*, 1992) and focused attention (Triesman, 1999) have been implicated in the binding together of visual features to form recognizable objects. Similarly, these behavioral and physiological data, interpreted in the light of the ecological view of perception described by Gibson (1966), suggest that flavor is represented centrally as a functionally distinct sense which is 'constructed' from the integration of distinct physiologically defined sensory systems (olfaction, taste and other sensory inputs) in order to perceive and identify critical objects—typically, foods. The present data implicate optional perceptual processes, specifically whether attention is directed towards individual stimulus features or the whole 'object' as an important determinant of the extent to which this integration occurs.

Stevenson *et al.* (1995) proposed a mechanism by which such odor–taste integration produce enhancement of tastes by odors. They suggested that when an odor component of a familiar is experienced, the taste component may also be evoked. For example, sniffing caramel odor activates memorial representations of caramel flavors which includes a significant sweet component. This results either in perceptions of smelled taste properties or, in the case of an odor–taste mixture, a perceptual combination of both real and evoked taste properties, leading to enhancement. Such an explanation is consistent with data showing that memorial representations of chemosensory qualities can combine with physically present stimuli to produce mixtures that show very similar interactions to those of combinations of identical, but physically present qualities (Algom *et al.*, 1993; Stevenson and Prescott, 1997). The perceptual strategy, perhaps determined by the instructions provided during the evaluation of odor–taste mixtures, will be influential in determining whether the odor is perceived distinctly or as part of a synthetic flavor.

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