Chem. Senses 29: 199–208, 2004 DOI: 10.1093/chemse/bjh022

Effects of Perceived and Imagined Odors on Taste Detection

J. Djordjevic, R.J. Zatorre and M. Jones-Gotman

McGill University, Montreal Neurological Institute, Montreal, Québec, Canada

Correspondence to be sent to: Jelena Djordjevic, Montreal Neurological Institute, 3801 University Street, Montreal H3A 2B4, Québec, Canada. e-mail: jelena.djordjevic@mail.mcgill.ca

Abstract

We assessed the influence of different odors on detection of a sweet tastant, and the ability of imagined odors to elicit the same effects as perceived odors on taste perception. The tastant used was sucrose, and the two odorants were strawberry and ham. In the first experiment, participants either smelled or imagined one of two odors during taste detection tasks (between-subject design), whereas in the second one, subjects completed both the odor imagery and perception conditions with taste detection tasks (within-subject design). The effect was odorant-specific: detection of sucrose was significantly better when subjects smelled strawberry than when they smelled ham. Furthermore, imagined odors influenced taste perception in the same way as did perceived odors. We concluded that the odor-specific effect on taste perception is an authentic perceptual phenomenon. Our results also support the notion that odor-induced changes in taste perception are mediated centrally. Finally, our findings are in agreement with reports supporting the existence of odor imagery.

Key words: odor imagery, taste–smell interactions

Introduction

Our chemical senses (taste and smell) work together and influence each other in very specific ways. Murphy *et al.* (1977) reported that fruity smelling ethyl butyrate and a sweet tastant sodium saccharin show almost perfect additivity when presented in mixtures. In a subsequent study, Murphy and Cain (1980) showed that congruency or 'harmony' of taste–smell mixtures does not determine the degree of additivity: both the congruent or harmonious mixtures (lemon-smelling citral and sucrose) and the incongruent or dissonant mixtures (citral and sodium chloride) showed the same pattern of results. However, a series of studies that followed demonstrated that certain odors enhance the intensity of particular tastes, and that these changes in taste perception are both odorant- and tastant-specific. Odors such as strawberry (Frank and Byram, 1988; Frank *et al.*, 1989, 1993; Lawless and Clark, 1992; Clark and Lawless, 1994; Schifferstein and Verglegh, 1996; Stevenson *et al.*, 1999; Frank, 2002), vanilla (Sakai *et al.*, 2001), lemon (Schifferstein and Verglegh, 1996; Frank, 2002), almond (Frank *et al.*, 1993), caramel, maracuja and lychee (Stevenson *et al.*, 1999) enhanced the sweetness of sucrose (most quoted studies) or aspartame (Lawless and Clark, 1992; Clark and Lawless, 1994; Sakai *et al.*, 2001; Frank, 2002), whereas other odors—such as peanut butter (Frank and Byram, 1988; Frank, 2002), ham (Schifferstein and Verglegh, 1996), chocolate, and wintergreen (Frank *et al.*, 1993; Frank, 2002)—did not change perceived sweetness.

Odor-induced changes in taste perception (OICTP) are not limited to sweetness enhancement. For example, maltol, angelica oil, and damascone odors can suppress perceived sweetness of sucrose (Stevenson *et al.*, 1999). Furthermore, the effects of odors on taste perception are not limited to sweetness, but have been shown with sourness as well: chocolate (Frank *et al.*, 1993) and caramel (Stevenson *et al.*, 1999) odors were shown to suppress sourness, whereas lemon and strawberry odor enhanced sourness of citric acid (Frank, 2002). Finally, almond, chocolate, lemon, peanut, strawberry and wintergreen were shown to suppress perceived saltiness (Shaffer and Frank, 1990), although the odor-induced effects on saltiness have not been replicated (Frank, 2002).

Besides the group of studies demonstrating OICTP, Dalton *et al.* (2000) showed that particular tastants can alter odor perception. Olfactory sensitivity to benzaldehyde (a cherry–almond odor) was increased by the presence of a sub-threshold concentration of saccharin in the mouth, whereas having water or another tastant in the mouth did not make any difference; simply repeating the benzaldehyde threshold test for a second time did not result in a change of sensitivity either.

Algom *et al.* (1993) used taste–smell interactions to study odor imagery. Participants in their study were either presented tastant–odorant mixtures (sucrose and orange), or asked to construct these mixtures mentally (both groups were previously familiarized with mixture constituents). The task was to rate the intensity of presented or imagined mixtures. The striking finding was that both perceived and mentally constructed mixtures (of different concentrations of sucrose and orange) showed the same, approximately additive pattern of integration. Thus Algom and colleagues showed that imagined smells interact with both imagined and perceived tastants in the same way as real, perceived smells do. Other studies of odor imagery have provided some supportive evidence of its existence, using a variety of approaches (Lyman and McDaniel, 1990; Algom and Cain, 1991; Carrasco and Ridout, 1993; Ahsen, 1995; Gilbert *et al.*, 1998; Levy *et al.*, 1999; Djordjevic *et al.*, 2004), but some did not find such evidence (Schab, 1990; Crowder and Schab, 1995; Elmes and Jones, 1995; Herz, 2000). Therefore, the existence of odor imagery is still an unresolved and controversial issue.

The present study combines the approach of studying odor-induced changes in taste perception with that of comparing effects of perceived and imagined odors on taste perception. Even though OICTP have been demonstrated repeatedly and by different laboratories, findings from two research laboratories have raised questions about the nature of this phenomenon. Namely, Frank and colleagues (Frank *et al.*, 1993; van der Klaauw and Frank, 1996) and Lawless and Clark (Lawless and Clark, 1992; Clark and Lawless, 1994) showed that odor-induced changes in taste perception are unstable: certain odorants enhanced perceived intensity of certain tastants when intensity was the only rated dimension. However, when participants rated several properties of presented stimuli, the phenomenon either disappeared or reversed from enhancement to suppression. One of the limitations of previous studies of OICTP (Murphy *et al.*, 1977; Murphy and Cain, 1980; Frank and Byram, 1988; Frank *et al.*, 1989, 1993; Algom *et al.*, 1993; Schifferstein and Verglegh, 1996; Stevenson *et al.*, 1999) is that they all used intensity ratings as a dependent measure. Therefore it remained unclear whether OICTP are a reliable perceptual phenomenon or a measurement artifact (restricted to a specific choice of rating alternatives), and this was the first question addressed in the present study. In order to answer this question, we examined whether OICTP can be elicited with a measure other than intensity ratings, and we used a more objective measure: accuracy of detecting a weak tastant. If OICTP are an authentic perceptual phenomenon, it ought to be possible to demonstrate it with different experimental paradigms.

Secondly, we addressed a question of whether the effect of odors on taste perception is mediated primarily by peripheral or central gustatory and olfactory structures. Again, previous studies of the phenomenon left this question unanswered, as tastants and odorants were delivered together as mixtures that were sipped by mouth. There were two potential problems with such stimulus delivery. First, there was a possibility that odorants mixed with tastants would change the physico-chemical composition of tastants: if that were the case, OICTP would not be a perceptual, but a chemical effect. By changing the structure of the taste solution, flavorants could affect its taste quality and/or texture (de Wijk *et al.*, 2003). Secondly, even if flavorants do not affect the physico-chemical structure of taste solutions, it still remains unclear whether integration of sensory inputs happens in the periphery, via a taste receptor mechanism, or centrally. In order to address this question (and to rule out the possibility that this is a physico-chemical rather than a perceptual effect), we opted to deliver tastants orally and odorants nasally (rather than in mixtures presented orally). Such delivery precluded any contact between tastants and odorants on the periphery: therefore, demonstration of the effect with a separate stimulus delivery would suggest central integration of olfactory and gustatory sensory inputs. In contrast, the lack of an effect would suggest that previous studies that delivered mixed odorants and tastants reflected either a peripheral mechanism, or a physico-chemical interaction of odorants and tastants.

Lastly, we addressed the question of odor imagery. Previous attempts to study odor imagery could be classified into two broad categories. The first one was to demonstrate that odor, and not some other type of mental imagery, has specific effects on another perceptual or cognitive process (Lyman and McDaniel, 1990; Djordjevic *et al.*, 2004). The second one was to compare the effects of odor imagery and odor perception on another process and to demonstrate that their effects are equivalent (Algom and Cain, 1991; Algom *et al.*, 1993; Carrasco and Ridout, 1993; Levy *et al.*, 1999). The present study used the latter approach: we examined whether imagined odors could elicit the same effect on taste perception as perceived odors, by comparing effects elicited by perceived and imagined odors. A demonstration of an effect elicited by imagined odors on another process (in this case detection of a weak tastant) that would be comparable to the effect elicited by perceived odors, would have implications for the current debate on the existence of olfactory imagery (Crowder and Schab, 1995; Elmes, 1998; Stevenson and Boakes, 2003). Namely, showing that imagined odors influence taste detection in a similar way to perceived odors would be consistent with the notion that imagined odors share common features with olfactory percepts and that odor images have some sensory/perceptual qualities. On the other hand, failure to demonstrate such an effect would be in keeping with the idea that instruction to imagine odors does not evoke a sensory specific type of mental imagery.

We decided to study the effect of two different odorants on detection of a sweet tastant. The reason for choosing the sweet taste was that in previous studies, odor-induced changes of perceived sweetness were demonstrated most consistently. Given that our experimental paradigm introduced a series of methodological modifications, and also given that we were to study the effect of imagined odors, we opted to select a tastant that had been reliably documented to be influenced differently by different odorants. Therefore we examined whether two familiar odorants, one congruent and another incongruent with the sweet taste, would elicit change in detection accuracy of sucrose, and whether imagined odors would bring forth the same effect. We addressed these questions in a between-subject design, and then replicated its main findings in a within-subject experimental design.

Pilot data

In order to select appropriate stimuli for our main experiments, two pilot studies were conducted. The aim of the first pilot study was to establish concentrations of different odorants that would be roughly matched for intensity. We asked nine people to sniff and rate the intensity of strawberry, ham, and peanut butter odorants. Three concentrations of natural strawberry and ham odorants (obtained from Bell Flavors & Fragrances, Brossard, Quebec, Canada) were tested (10, 1 and 0.1% diluted in double-distilled deionized water). In addition, we asked subjects to rate the intensity of a commercially available peanut butter (Yum nature peanut butter, Vicrossano Inc., Montreal, Quebec, Canada) that remained undiluted. Intensity ratings for these seven stimuli were obtained with the Labeled Magnitude Scale (Green *et al.*, 1996). Based on their mean intensity ratings, we selected strawberry 1%, ham 1% and natural peanut butter (undiluted). Their mean intensity ratings were 38.8, 46.0 and 39.6, respectively: there were no statistically significant differences among the mean intensity ratings of these three odorants [$F(2,16) = 0.64$, $P > 0.05$].

In the second pilot study, we examined which of two odorants—peanut butter or ham—would influence detection of weak sucrose solutions differently compared with strawberry. Fourteen normal healthy subjects participated. Each subject was given 90 taste detection tasks—forced-choice between a peri-threshold sucrose stimulus and a blank (water): in 30 trials each they smelled strawberry, ham, or peanut butter (matched for intensity). Results of detection accuracy are expressed as percentage of correct responses (Figure 1). A one-way repeated measures analysis of variance (ANOVA) showed a significant effect of odor [$F(2,26) = 4.22$, $P < 0.05$].

Post-hoc comparisons (with Bonferroni adjustment for multiple comparisons) revealed a tendency for sucrose detection to be more accurate when subjects were smelling strawberry than when they were smelling ham ($P = 0.07$); the other two comparisons (strawberry versus peanut butter and peanut butter versus ham) did not reveal a significant difference ($P = 0.21$ and $P = 0.84$, respectively). Since the effect of strawberry and ham on detection of weak sucrose solutions tended to be different, these two odorants were selected for use in the two main experiments.

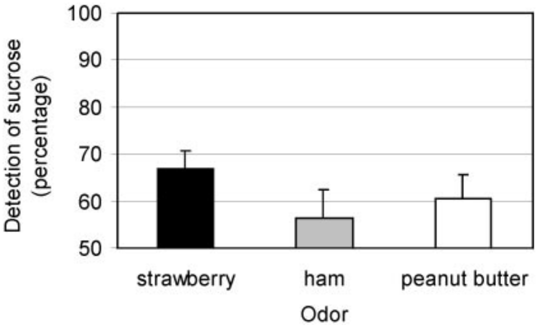

Figure 1 Results of a pilot study ($n = 14$): accuracy of detecting sucrose as a function of odor (strawberry, ham, and peanut butter). Bars show mean detection accuracy of sucrose (%) while smelling each of the three odors, and error bars show standard errors. Note that 50% represents performance at the chance level.

Experiment 1

In the first experiment, participants were randomly assigned to one of two experimental conditions: odor perception or odor imagery. Participants in the odor perception condition smelled odors simultaneously with tasting solutions, whereas those in the odor imagery condition were asked to imagine the odors simultaneously with tasting the solutions.

Method

Subjects

Forty healthy volunteers, all undergraduate students at McGill University, participated in this experiment. All participants reported normal ability to smell and taste. Exclusion criteria were respiratory infections, allergies leading to nasal congestion, history of neurological or psychiatric disease, and other conditions leading to impaired sense of smell and/or taste. Twenty participants were randomly assigned to each condition. The two groups were matched for gender (four men in the perception and five in the imagery condition) and age [mean age of participants was 21.4 and 20.8, respectively, range 18–34, $t(38) = 0.66$, $P > 0.05$]. Mean detection threshold values for sucrose (8.09×10^{-3} and 9.21×10^{-3}) were not different between the two groups [$t(38) = 0.25$, $P > 0.05$].

Stimuli

Two odorants were used in this experiment: strawberry and ham (Bell Flavors & Fragrances Canada). The odorants were presented in 60 ml opaque glass bottles, and each bottle was filled with 9 ml of the odorant. The two stimuli were matched for intensity (see Pilot data): concentrations used were 1% strawberry and 1% ham, both diluted in double-distilled deionized water.

The tastant used in this experiment was sucrose (BDH Inc., Toronto, Ontario, Canada). Sucrose is usually described as a pure tastant and hence odorless. We confirmed its lack of odor in another pilot study with ten participants: they completed 30 forced-choice taste detection tasks between a supra-threshold concentration of sucrose (0.1 M) and double-distilled water. Sucrose could not be discriminated from double-distilled water by active sniffing (binomial $P > 0.05$).

A series of twenty concentrations was used for the taste detection threshold test. Sucrose was mixed with double-distilled deionized water, and concentrations ranged from 5.6×10^{-1} to 1.0×10^{-5} M. Taste stimuli were presented in 10 ml plastic disposable cups: each cup was filled with ~4 ml of a solution containing either tastant (sucrose diluted in water) or water. All stimuli were presented at room temperature.

Procedure

The procedure in the two conditions of the main experiment (odor perception and odor imagery) consisted of three parts: a taste detection threshold test for sucrose, familiarization with the odors, and taste detection tasks with either perceived (odor perception) or imagined (odor imagery) odors.

Detection threshold for sucrose was determined for all subjects, using a modified staircase method. On each trial, two solutions were presented, one containing the tastant (water with sucrose) and the other containing the blank (just water). Subjects sipped one cup, expectorated, rinsed with water, and then sipped the other cup, expectorated, rinsed and responded by indicating which one of the two tasted stronger (two-alternative forced-choice). The two-down/one-up method (Wetherill and Levitt, 1965) was followed. Each change in direction constituted a reversal. Eight reversals were obtained for each subject, and detection threshold was calculated as a mean of the last four reversals.

Following the detection threshold test, subjects were reminded that the two odorants to be used in this experiment would be strawberry and ham. To familiarize them with the odors, they were asked to sniff each one several times. In addition to familiarization with the odors, participants assigned to the imagery condition were given a brief imagery practice. They were told that they would be asked to imagine the two odors in the subsequent part of the experiment and that therefore they should practice imagining them. Odors were presented and then removed, with the request to imagine them. None of the participants reported any problems in imagining these two odors. Following this, each participant was engaged in filling in some questionnaires for ~10 min, in order to make a sufficient time lapse between this and the following part of the session.

The third part involved measurement of detection accuracy for weak sucrose solutions, with simultaneous odor perception or odor imagery. Each participant was given 90 detection trials in which a weak concentration of sucrose paired with water was given, with the task to indicate which one of the two tasted stronger (two-alternative forced-choice). In this part of the experiment, subjects were always presented the concentration of sucrose at their individual threshold level. The purpose was to keep the performance above chance but below ceiling, so that the effect of perceived and/or imagined odors on detection accuracy could be revealed. Olfactory and gustatory stimuli were presented in quick succession: a 'sniff/imagine–sip–spit' method was followed. Participants were asked to sniff or to imagine an odor, and then as soon as possible to sip the taste solution. After that they expectorated and rinsed thoroughly with double-distilled water. Even though olfactory stimuli preceded gustatory, they quickly followed each other and therefore we refer to such stimulus presentation as 'simultaneous' in the rest of the paper. In 30 detection trials, subjects either sniffed or imagined the strawberry odor, and in another 30 trials they either sniffed or imagined the ham odor. Finally, 30 detection trials were given without any presented or imagined odors (in both the perception and the imagery condition these were just two-alternative forced-choice detection tasks). The detection tasks were given in blocks of five so that the instruction to sniff/imagine a particular odor or not to sniff or imagine anything changed after each five trials. The order of blocks was counterbalanced across subjects.

Results

Results were analyzed with a two-way (3 × 2) ANOVA (mixed design). The within-subject variable was odor (strawberry, ham, and no odor); the between-subject factor was condition (perception and imagery). The dependent measure was taste detection, expressed as percent of correct responses on forced-choice tasks.

The two-way ANOVA (Figure 2) showed a significant main effect of odor [$F(2,76) = 12.22$, $P < 0.001$]. The main effect of condition [$F(1,38) = 0.62$, $P > 0.05$] and the interaction between odor and condition [$F(2,76) = 0.19$, $P > 0.05$] were not significant.

Post-hoc comparisons (with Bonferroni adjustment for multiple comparisons) revealed a significant difference

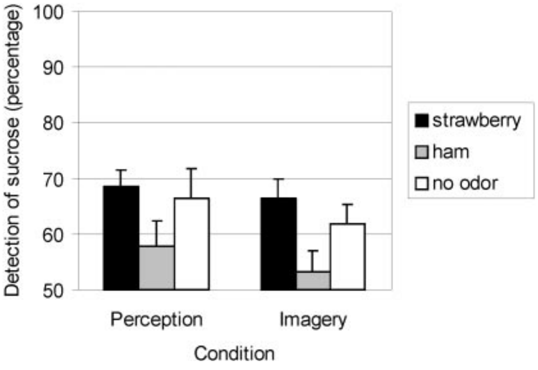

Figure 2 Results of experiment 1: accuracy of detecting sucrose as a function of odor (strawberry, ham, no odor) and condition (perception and imagery). Bars show mean detection accuracy (%), and error bars represent standard error. Note that 50% represents performance at the chance level.

between detection with strawberry versus ham ($P < 0.001$) and between ham versus no odor ($P < 0.01$), but not between strawberry versus no odor ($P > 0.05$).

We also looked at whether these taste detection means differed from chance performance (50% in the case of two-alternative forced-choice task). Sucrose detection was significantly different from chance ($P < 0.01$) in all cases except with perceived ham [$t(19) = 1.74$, $P > 0.05$] and with imagined ham [$t(19) = 0.84$, $P > 0.05$].

Experiment 2

Method

In experiment 2, we aimed to replicate the main results of experiment 1 (in which 'condition'—odor perception or odor imagery—was a between-subject variable) in a within-subject experimental design. Twenty subjects (six men), with mean age of 21.3 years (range 18–27 years), participated in this study. Exclusion criteria were the same as in experiment 1. The method was like the one in the first experiment, with two modifications. The first difference was that in experiment 2, each participant completed two sessions, one with smelling (odor perception) and the other with imagining (odor imagery) odors during taste detection trials. The two sessions were always conducted on separate days, and their order was counterbalanced across subjects. The procedure consisted of the same three parts as in experiment 1: detection threshold test for sucrose, familiarization with the odors, and taste detection trials with perceived and imagined odors. The second difference between the two experiments was that taste detection tasks did not include 'no odor' trials. We opted for this change for two reasons: first, the main finding of experiment 1 that we aimed to replicate was the difference elicited on taste detection by the two odors, and the second reason was practical (duration of session). Therefore each participant was given 60 taste detection trials in each session (30 with strawberry and 30 with ham).

Results

Results were analyzed with a two-way (2 × 2) repeated measures ANOVA. The first within-subject variable was odor (strawberry and ham), and the second within-subject variable was condition (perception and imagery). Again, the dependent measure was taste detection, expressed as percent of correct responses on forced-choice tasks.

The two-way ANOVA (Figure 3) showed a significant main effect of odor [$F(1,19) = 17.66$, $P < 0.001$: detection of sucrose was significantly different with strawberry than with ham, $P < 0.001$].

As in experiment 1, the effect of condition [$F(1,19) = 3.04$, $P > 0.05$] and the interaction between odor and condition [$F(1,19) = 1.76$, $P > 0.05$] were not significant.

Again, we looked at whether sucrose detection means differed from chance performance. Sucrose detection was significantly different from chance ($P < 0.01$) in all cases except with perceived ham [$t(19) = 1.96$, $P > 0.05$].

Individual differences in odor imagery ability

The paradigm used in experiments 1 and 2 enabled us to measure odor imagery ability indirectly in individual subjects: the difference between detection of sucrose while imagining strawberry versus ham can be calculated for each individual subject. We will refer to this difference as the odor imagery index (OII). Higher OII scores indicate greater odor imagery ability. Figure 4 shows individual values of OII calculated for all participants who completed the imagery condition in experiment 1 ($n = 20$) and experiment 2 ($n = 20$).

Inspection of individual values of the OII (Figure 4) reveals that not all subjects show the superiority of sucrose detection when imagining strawberry over ham. According to the obtained results, it seems that >50% of people show

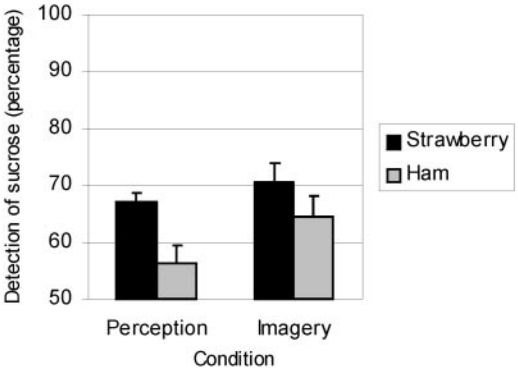

Figure 3 Results of experiment 2: accuracy of detecting sucrose as a function of odor (strawberry, ham) and condition (perception, imagery). Bars show mean detection accuracy (%), and error bars represent standard error. Note that 50% represents performance at the chance level.

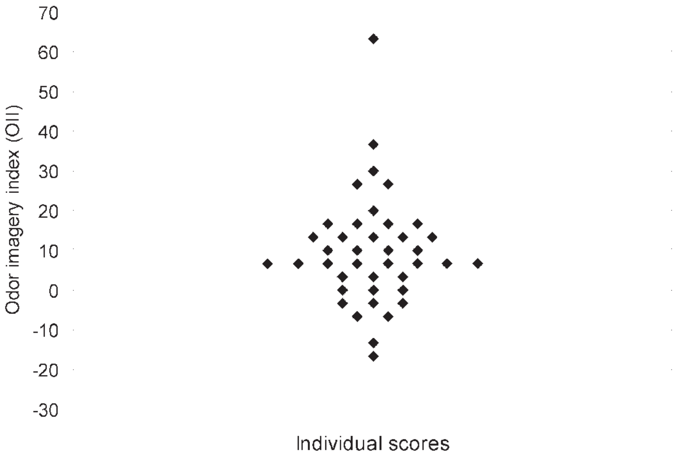

Figure 4 Individual differences in odor imagery ability. Each diamond represents the OII calculated for one subject (by subtracting sucrose detection with imagined ham from sucrose detection with imagined strawberry, expressed as %). The graph illustrates a large variation in participants' ability to imagine odors.

some ability to imagine odors, but also that a smaller portion of subjects can be qualified as 'high odor imagers'. In fact, high odor imagery ability can be defined in different ways. One possibility would be to do a tertiary split of the tested sample and declare that participants in the upper third are 'high odor imagers'. Another option could be to predetermine the cut-off score (for example, 10% difference in taste detection) and to classify all subjects whose score is greater than the cut-off as 'high odor imagers'. In either case, the operational definition is based on a somewhat arbitrary criterion, but the advantage is that it still relies on an objective measure rather than on self report of one's odor imagery ability.

Discussion

Odor-induced changes in taste perception have been shown previously, but this is the first study to demonstrate that this is a reliable perceptual phenomenon (by using an objective measure) that is centrally mediated (as it can be elicited by the separate delivery of odorants and tastants). Detection of sucrose was better when combined with strawberry than with ham odor, and changes of taste perception can be induced not only with physically present (real) odors but with imagined odors as well. We obtained these findings in a between-subject design, and replicated them in a within-subject experiment.

Odor-induced changes in taste perception: a perceptual phenomenon or a measurement artifact

The first question addressed in this study was whether OICTP are a stable perceptual phenomenon or a measure-specific effect. Notably, all previous studies demonstrating OICTP used intensity ratings of presented stimuli as a dependent measure (Murphy *et al.*, 1977; Murphy and Cain, 1980; Frank and Byram, 1988; Frank *et al.*, 1989, 1993; Schifferstein and Verglegh, 1996; Stevenson *et al.*, 1999; Sakai *et al.*, 2001; Frank, 2002). However, two independent research groups raised a possibility that OICTP were a measurement artifact. Namely, OICTP seemed to depend on the number and/or appropriateness of attributes subjects were asked to judge (Frank *et al.*, 1990, 1993; Lawless and Clark, 1992; Clark and Lawless, 1994; van der Klaauw and Frank, 1996). Sweetness enhancement was demonstrated when sweetness was the only judged attribute, but the effect disappeared when several different attributes were rated, and especially when fruitiness was included. Therefore the OICTP did not appear to be a stable phenomenon, or at least not when judgments were made using intensity ratings.

Our results clearly show that odor-specific effects on taste perception can be demonstrated with a measure other than intensity rating, which in this case was accuracy of detecting a peri-threshold tastant. Thus the results of the present study are in agreement with an experiment conducted by van der Klaauw and Frank (1994). They demonstrated this phenomenon using a sweetness-matching procedure: participants consistently matched strawberry-sucrose mixtures with plain sucrose solutions in which the sucrose was significantly more concentrated than in the mixture. Taken together, van der Klaauw and Frank's and the present study show that OICTP are not an artifact of measurement, but a robust perceptual phenomenon.

Odor-induced changes in taste perception: a peripheral or a central phenomenon

The second question addressed here was whether this effect is primarily mediated by peripheral or central mechanisms. Previous studies of taste–smell interactions delivered taste and smell (flavorant) stimuli together in mixtures. Again, there were some exceptions (Small *et al.*, 1997a; Dalton *et al.*, 2000; Sakai *et al.*, 2001). A strong argument for presenting taste and smell stimuli together is that this is the way we perceive smells and tastes when we consume food. This method of stimulus presentation is hence ecologically valid, but it does not exclude the possibility of flavorants (odorants) having some taste as well, and that in fact the taste of the 'odorant', rather than its smell, might be causing the change in taste perception. For example, maltol was one of the odors found to suppress sweetness, but it was also found to have a bitter taste; therefore it is not clear whether the sweetness suppression effect was induced by its smell or by its bitter taste (Stevenson *et al.*, 1999). In order to exclude this confound, some authors have used the 'pinched nose' method (Murphy *et al.*, 1977; Murphy and Cain, 1980) to examine whether a pure tastant could be discriminated from a tastant-flavorant mixture when olfactory input is precluded. We took one step further and demonstrated that taste–smell interactions can be revealed with separate delivery of odorants and tastants. By using separate delivery, the physical contact between olfactory and gustatory system on the periphery was minimized. There was no reason to assume any retronasal olfactory sensations generated by the presence of peri-threshold sucrose in the mouth, as basic tastants including sucrose have no smell, which we confirmed to be the case for the sucrose used in this study (see the Stimuli subsection of experiment 1). In addition, odorants were sniffed rather than sipped. Even though it may be possible that some odorant molecules could end up in the oral cavity by vigorous sniffing, the likelihood that a sufficient amount would enter the mouth and interact with the tastant and/or taste receptors is very low.

Therefore, the results of the present study are consistent with the idea that OICTP are a centrally rather than peripherally mediated phenomenon. As such, our results are consistent with findings reported by Sakai *et al.* (2001) who found enhancement of sweetness (measured by intensity ratings) induced by vanilla odor presented either by the retronasal or by the orthonasal route. In addition, they are consistent with our own findings from a previous experiment in which we also used intensity ratings as a measure of taste perception: even though olfactory and gustatory stimuli were presented separately, sucrose solutions received higher sweetness ratings when presented with strawberry than with soy sauce or no odor, and sodium chloride solutions were rated as tasting saltier with soy sauce than with strawberry or no odor (J. Djordjevic *et al.*, submitted for publication). Finally, Dalton *et al.* (2000) demonstrated integration of subthreshold tastants and odorants using a separate delivery of the two types of stimuli.

Separate delivery of odorants and tastants proved to be a crucial aspect of our study that enabled us to examine the effect of imagined odors. The existence of the effect with such stimulus delivery implies a central rather than peripheral locus of interaction between taste and smell. Had the taste–smell interactions been based on a peripheral mechanism, we could not expect that imagined odors would induce the same changes in taste receptors as perceived odors, and the study of odor imagery would have been rendered infeasible.

Are we humans able to imagine odors?

Last but not least, our results show that odors imagined in minds' noses have an effect on taste perception that is comparable to the effect elicited by odors that come through real noses. The similar pattern of results obtained with perceived and imagined odors was striking in the two experiments reported here. We showed that accuracy of detecting weak sucrose is better when the odor imagined during the detection task is strawberry than when it is ham, and that this pattern parallels the one observed when the actual odors are presented.

We chose two odors that are familiar to the general population, assuming that they would be equally imaginable. Another possible approach to study odor imagery might be to select relatively unfamiliar odors that are difficult to name. For example, lychee has been shown to be relatively unfamiliar and yet rated as a sweet-smelling odorant (Stevenson *et al.*, 1998); in the same way it would be possible to find an unfamiliar non-sweet-smelling odorant. Such stimuli would enable an equivalent experimental exposure to novel odorants, and make a strong case that odor images rather than semantic constructs can account for the results. However, one potential difficulty with this approach would be the fact that the effect of unfamiliar odors on taste perception does not seem to be consistent: Stevenson *et al.* (1999) reported that lychee elicited a sweetness-enhancing effect in their first experiment, but no such effect was observed in their second experiment. In addition, only one (the lowest) concentration of this odorant induced changes in taste perception, whereas four other concentrations did not. Since it seems that the effects that unfamiliar odorants induce on taste perception may be unstable, we opted to use familiar odors whose effects on taste perception have been reliably documented before.

We recognize that some form of semantic mediation is likely to occur in association with any type of mental imagery, including odor imagery. In fact, it is questionable whether generation of a purely sensory mental image without any additional semantic associations is possible. Furthermore, Schifferstein (1997) and Stevenson and Prescott (1997) argued that participants have explicit knowledge of sensory interactions, and that such knowledge plays a significant role when people are asked to create chemosensory mixtures mentally. However, the dependent measure in our experiment (accuracy of detecting a weak tastant measured by a forced-choice task) was such that semantic mediation and explicit knowledge cannot fully explain the observed results. In most cases, participants were not aware that they were detecting sucrose, since the tastants were presented at each individual's detection threshold level, which is below the quality recognition level (Small *et al.*, 1997b). This finding reported by Small *et al.* was consistent with our own observations: most participants in the present study were unable to describe the taste, or gave a wrong description, after completing the threshold test. Therefore, it would be difficult to defend the position that two different verbal labels (strawberry and ham) would differently alter detection of an unknown peri-threshold tastant. Similarly, having explicit knowledge that strawberry and ham would change perceived sweet taste differently would not be sufficient to explain the observed difference in performance, given that taste perception was measured as a forced-choice detection of stimuli whose concentration did not permit quality recognition.

An alternative explanation might be that some other form of mental imagery, such as visual imagery of the two targets, may account for the present results. We did not explicitly exclude such a possibility in the present study. However, we can offer two arguments against this interpretation of our results. First, it would not be parsimonious to conclude both that instruction to imagine odors would elicit visual but not odor imagery and that visual imagery would influence taste perception in the same way as odor perception. Secondly, in our previous study of odor imagery, we explicitly demonstrated that the effects of a condition in which subjects were instructed to imagine smells were specific and could not be elicited by exactly the same experimental condition in which participants were instructed instead to imagine the same items visually (Djordjevic *et al.*, 2004). We recently replicated this finding (J. Djordjevic, unpublished data). For these two reasons, we believe that a visual imagery interpretation cannot fully explain our results.

We also recognize that our findings and conclusions could be characterized as 'reliance on a null result': we demonstrated a lack of difference between odor perception and odor imagery, rather than a significant difference between odor imagery and a control condition. Even though demonstration of a lack of difference is a less convincing way of providing a basis for firm conclusions, there are two points that need to be considered here. First, we did not merely demonstrate a lack of difference between perception and imagery; rather, we showed the presence of the same significant difference (i.e. between sucrose detection with strawberry versus ham odor) in both conditions. Secondly, we believe that such a demonstration of similar patterns is very informative in the area of mental imagery: comparing imagery and perception within the same sensory modality and demonstrating that they are equivalent or comparable is a valuable way of advancing our understanding of mental imagery (Finke, 1980, 1985). This approach has been successfully used not only in the area of olfactory imagery (Algom and Cain, 1991; Algom *et al.*, 1993; Carrasco and Ridout, 1993; Levy *et al.*, 1999), but numerous studies have reported equivalence between mental images and percepts in vision (Farah *et al.*, 1988), audition (Halpern, 1988) and motion (Roure *et al.*, 1998). Therefore we hold that finding specific commonalities between imagery and perception within the same modality continues to provide a valuable contribution to the area of mental imagery.

In summary, our findings show that imagined and perceived odors elicit similar effects on taste perception, suggesting that they might rely on similar perceptual features. It would be difficult to explain how semantic knowledge, verbal or visual codes would change sensitivity to weak tastants, and particularly in the context in which it is not known what the tastants are.

One of our observations was that there seems to be a large individual variation in people's ability to imagine odors. Again, this is consistent with the results from our previous study on odor imagery (Djordjevic *et al.*, 2004). Individual differences in imagery ability seem to be prominent in other areas of mental imagery as well (Kosslyn *et al.*, 1984). It is possible that this individual variability may account for the apparent difference in the imagery effect in our two experiments. Namely, results for perceived odors are nearly identical in experiments 1 and 2, whereas the effect of imagined odors appears somewhat smaller in experiment 2 than in experiment 1. However, our statistical analysis indicates exactly the same pattern of results in both experiments: a highly significant effect of odor, no effect of condition, and no interaction between odor and condition.

Taken together, our previous (Djordjevic *et al.*, 2004) and the present study show that requesting people to imagine odors can influence perception of chemosensory stimuli. Even thought we measured effects of imagined odors on two different processes (i.e. odor detection in the previous, and taste detection in the present study) and used different odors (rose and lemon in the previous, and strawberry and ham in the present study), the results of these two studies complement each other. They support the idea that it may be possible to imagine odors in our mind's noses (rather than only think of them in verbal format). In addition, we are now able to measure the strength of these imaginary odors. Both our paradigms (effect of odor imagery on odor detection and effect of odor imagery on taste detection) enable classification of subjects into 'high' and 'low odor imagers'. The present findings are also accordant with previous studies that had provided experimental evidence supporting the existence of odor imagery (Lyman and McDaniel, 1990; Algom and Cain, 1991; Algom *et al.*, 1993; Carrasco and Ridout, 1993; Gilbert *et al.*, 1998; Levy *et al.*, 1999). Finally, our findings are consistent with evidence for mental images obtained for other sensory modalities, such as images in vision (Farah *et al.*, 1988; Kosslyn *et al.*, 1995), audition (Farah and Smith, 1983; Zatorre and Halpern, 1993) and movement/motor performance (Roure *et al.*, 1999). However, the neural correlates of visual (Kosslyn *et al.*, 2001), auditory (Zatorre *et al.*, 1996; Halpern and Zatorre, 1999), and motor imagery (Jeannerod, 1994; Parsons *et al.*, 1995) are relatively well understood, whereas we know very little about the brain regions engaged in creating and maintaining odor images. We hope to address this important question in future studies.

Other considerations

An incidental finding of the present study permits some reflection about the direction of the odor-induced changes in taste perception. When we compared taste detection while smelling or imagining odorants with detection in the absence of odorants, we found that detection of a weak sucrose solution while smelling or imagining strawberry odor did not differ from detection without any odors, but that sucrose detection with ham odor was worse than detection without any odors. Therefore our results are consistent with interference or suppression rather than enhancement as the direction of taste–smell interactions, at least when taste detection is measured with a forced-choice task. This finding is partially inconsistent with previous studies from several independent laboratories that clearly showed that OICTP are based to a large degree on sweetness enhancement (Murphy and Cain, 1980; Frank and Byram, 1988, 1989; Frank *et al.*, 1993; Schifferstein and Verglegh, 1996; Stevenson *et al.*, 1999; Frank, 2002; J. Djordjevic *et al.*, submitted for publication). In particular, several authors have reported that strawberry odor enhanced the intensity of perceived sweetness (Frank and Byram, 1988; Schifferstein and Verglegh, 1996; Stevenson *et al.*, 1999; J. Djordjevic *et al.*, submitted for publication). It seems that the direction of taste–smell interactions (enhancement or interference) may depend on a variety of factors, and one of them may be specific procedural aspects of the experimental paradigm. Our own findings showed that odors enhanced taste perception when intensity ratings were used (J. Djordjevic *et al.*, submitted for publication), whereas they interfered with taste detection measured with forced-choice tasks (present study). Teasing out the role of different factors that determine the direction of taste–smell interactions remains a question to be addressed by future studies.

Another observation made in this study was that the overall detection accuracy was kept above chance performance for most but not all subjects, even though measures were taken to achieve detection above chance (by establishing the sucrose detection threshold for each participant). Namely, in both experiments we observed that a minority of participants had overall detection accuracy below chance even though the tastant to be detected was given at their threshold level (we observed eight such cases in experiment 1 and five in experiment 2). The pattern of results was the same with and without these subjects, so we kept them in our sample. As a result, some taste detection means failed to reach significance when compared with chance performance. However, this affected only group means with the ham odorant, either perceived or imagined. Overall, in the case of individual subjects, detection not different from chance was restricted to a small minority of participants, and in the case of group means it was restricted to detection levels associated with only one odorant. Therefore we do not consider that a failure to keep detection levels above chance in a few instances changes the interpretation of our findings.

Finally, we wish to comment on another aspect of taste–smell interactions. The notion that taste–smell interactions are both odorant- and tastant-specific is becoming increasingly accepted, and there are more and more empirical findings that support it. Odor-induced changes in taste perception have been demonstrated with some taste–smell combinations as predicted, whereas other combinations did not show the expected pattern of results. For example, strawberry, almond, and lemon were shown both to enhance perceived sweetness (Frank and Byram, 1988; Frank *et al.*, 1989, 1993; Schifferstein and Verglegh, 1996; Stevenson *et al.*, 1999) and to suppress perceived saltiness (Shaffer and Frank, 1990). Similarly, caramel enhanced sweetness and suppressed sourness (Stevenson *et al.*, 1999). However, such opposite effects of odorants on perception of different taste qualities were not always demonstrated as predicted. For example, chocolate and wintergreen did not change perceived sweetness (Frank *et al.*, 1993), but they did suppress perceived saltiness (Shaffer and Frank, 1990). Similarly, the sour-smelling odorant angelica oil suppressed sweetness of sucrose, but did not enhance sourness of citric acid (Stevenson *et al.*, 1999). Frank (2002) found that lemon and strawberry odors enhanced sweetness of aspartame, but also that the same odors enhanced sourness of citric acid. In other words, it remains uncertain why clear-cut dissociations can be demonstrated with some odorants and tastants but not others. In such a context, it would be interesting to explore whether strawberry and ham odorants would influence detection of a salty tastant differently than they influenced sucrose detection. Thus the topic of taste–smell interactions remains an active area of research with many questions waiting to be tackled.

Acknowledgements

The authors would like to thank Bell Flavors & Fragrances Canada for donating the strawberry and ham odorants used in this study. We are grateful to Julie Boyle and Kaajal Abrol for their help in testing participants. This study was supported in part by grant MOP 57846, awarded to MJG and RJZ by the Canadian Institutes of Health Research.

References

Ahsen, A. (1995) *Self-report questionnaires: new directions for imagery research*. J. Ment. Imag., 19, 107–123.

Algom D. and **Cain W.S.** (1991) *Remembered odors and mental mixtures: Tapping Reservoirs of Olfactory Knowledge*. J. Exp. Psychol. Hum. Percept. Perform., 17, 1104–1119.

Algom, D., Marks, L.E. and **Cain, W.** (1993) *Memory psychophysics for chemosensation: perceptual and mental mixtures of odor and taste*. Chem. Senses, 18, 151–160.

Carrasco, M. and **Ridout, J.B.** (1993) *Olfactory perception and olfactory imagery: a multidimensional analysis*. J. Exp. Psychol. Hum. Percept. Perform., 19, 287–301.

Clark, C.C. and **Lawless, H.T.** (1994) *Limiting response alternatives in time–intensity scaling: an examination of the halo dumping effect*. Chem. Senses, 19, 583–594.

Crowder, R.G. and **Schab F.R.** (1995) *Imagery for odours*. In Crowder, R.G. and Schab, F.R. (eds), Imagery for Odors. Lawrence Erlbaum Associates, Mahwah, NJ, pp. 93–107.

Dalton, P., Doolitle, N. Nagata, H. and **Breslin, P.S.** (2000) *The merging of the senses: integration of subthreshold taste and smell*. Nat. Neurosci., 3, 431–432.

de Wijk, R.A., Prinz, J.F., Polet, I.A., van Doorn, J.M. and **Weenen, H.** (2003) *Effects of flavorants on oral texture sensations*. Chem. Senses, 28, 77.

Djordjevic, J., Zatorre, R.J., Petrides, M. and **Jones-Gotman, M.** (2004) *The mind's nose: effects of odor and visual imagery on odor detection*. Psychol. Sci., 15, 143–148.

Elmes, D.G. (1998) *Is there an inner nose?* Chem. Senses, 23, 443–445.

Elmes, D.G. and **Jones, S.R.** (1995) *Ineffective odor images*. Abstract, 36th Annual Meeting of the Psychonomic Society, Los Angeles.

Farah, M.J. and **Smith, A.F.** (1983) *Perceptual interference and facilitation with auditory imagery*. Percept. Psychophys., 33, 475–478.

Farah, M.J., Peronnet, F., Gonon, M.A. and **Giard, M.H.** (1988) *Electrophysiological evidence for a shared representational medium for visual images and visual percepts*. J. Exp. Psychol. Gen., 3, 248–257.

Finke, R.A. (1980) *Levels of equivalence in imagery and perception*. Psychol. Rev., 87, 113–132.

Finke, R.A. (1985) *Theories relating mental imagery to perception.* Psychol. Bull., 98, 236–259.

Frank, R.A. (2002) *Response context affects judgments of flavor components in foods and beverages*. Food Qual. Prefer., 14, 139–145.

Frank R.A. and **Byram, J.** (1988) *Taste–smell interactions are tastant and odorant dependent*. Chem. Senses, 13, 445–455.

Frank, R.A., Ducheny, K. and **Mize, S.J.S.** (1989) *Strawberry odor, but not red color, enhances the sweetness of sucrose solutions*. Chem. Senses, 14, 371–377.

Frank, R.A., Wessel, N. and **Shaffer, G.** (1990) *The enhancement of sweetness by strawberry odor is instruction-dependent*. Chem. Senses, 15, 576.

Frank, R.A., Van Der Klaauw, N.J. and **Schifferstein, H.N.J.** (1993) *Both perceptual and conceptual factors influence taste–odor and taste–taste interactions*. Percept. Psychophys., 54, 343–354.

Gilbert, A.N., Crouch, M. and **Kemp, S.E.** (1998) *Olfactory and visual mental imagery*. J. Ment. Imag. 22, 137–146.

Green, B.G., Dalton, P., Cowart, B. and **Shaffer, G.** (1996) *Evaluating the 'labeled magnitude scale' for measuring sensations of taste and smell*. Chem. Senses, 21, 323–334.

Halpern, A.R. (1988) *Perceived and imagined tempos of familiar songs*. Music Percept., 6, 193–202.

Halpern, A.R. and **Zatorre, R.J.** (1999) *When that tune runs through your head: a PET investigation of auditory imagery for familiar melodies*. Cereb. Cortex, 9, 697–704.

Herz, R. (2000) *Verbal coding in olfactory versus nonolfactory cognition*. Mem. Cognit., 28, 957–964.

Jeannerod, M. (1994) *The representing brain: neural correlates of motor intention and imagery*. Behav. Brain Sci., 17, 187–245.

Kosslyn, S.M., Brunn, J.L., Cave, K.R. and **Wallach, R.W.** (1984) *Individual differences in mental imagery ability: a computational analysis*. Cognition, 18, 195–243.

Kosslyn, S.M., Behrmann, M. and **Jeannerod, M.** (1995) *The cognitive neuroscience of mental imagery*. Neuropsychologia, 33, 1335–1344.

Kosslyn, S.M., Ganis, G. and **Thompson, W.L.** (2001) *Neural foundations of imagery*. Nat. Neurosci., 2, 635–642.

Lawless, H.T. and **Clark, C.C.** (1992) *Psychological biases in time–intensity scaling*. Food Technol., 46, 81–90.

Levy, L.M., Henkin, R.I., Lin, C.S., Hutter, A. and **Schellinge, D.** (1999) *Odor memory induces brain activation as measured by functional MRI*. J. Comput. Assist. Tomogr., 23, 487–498.

Lyman, B.J. and **McDaniel, M.A.** (1990) *Memory for odors and odor names: modalities of elaboration and imagery*. J. Exp. Psychol. Learn. Mem. Cogn., 16, 656–664.

Murphy, C. and **Cain, W.S.** (1980) *Taste and olfaction: independence vs. interaction*. Physiol. Behav., 24, 601–605.

Murphy, C. Cain, W.S. and **Bartoshuk, L.M.** (1977) *Mutual action of taste an olfaction.* Sens. Processes, 1, 204–211.

Parsons, L.M., Fox, P.T., Downs, J.H., Glass, T. Hirsch, T.B., Martin, C.C., Jarabek, P.A. and **Lancaster, J.L.** (1995) *Use of implicit motor imagery for visual shape discrimination as revealed by PET*. Nature, 375, 54–58.

Roure, R., Collet, C., Deschaumes-Molinaro, C., Dittmar, A., Rada H., Delhome, G. and **Vernet-Maury, E.** (1998) *Autonomic nervous system responses correlate with mental rehearsal in volleyball training.* Eur. J. Appl. Physiol., 78, 99–108.

Roure, R., Collet, C., Deschaumes-Molinaro, C., Delhome, G., Dittmar, A. and **Vernet-Maury, E.** (1999) *Imagery quality estimated by autonomic response is correlated to sporting performance enhancement*. Physiol. Behav., 66, 63–72.

Sakai, N., Kobayakawa, T., Gotow, N., Saito, S. and **Imada, S.** (2001) *Enhancement of sweetness ratings of aspartame by a vanilla odor presented either by orthonasal or retronasal routes*. Percept. Motor Skills, 92, 1002–1008.

Schab, F.R. (1990) *Odors and the remembrance of things past*. J. Exp. Psychol. Learn. Mem. Cogn., 16, 648––655.

Schifferstein, H.N.J. (1997) *Perceptual and imaginary mixtures in chemosensation*. J. Exp. Psychol. Hum. Percept. Perform., 23, 278–288.

Schifferstein, H.N.J. and **Verglegh, P.W.J.** (1996) *The role of congruency and pleasantness in odor-induced taste-enhancement*. Acta Psychol., 94, 87–105.

Shaffer, G. and **Frank, R.** (1990) *An investigation of taste–smell interactions across four tastants and six odorants*. Chem. Senses, 15, 638.

Small, D. M., Jones-Gotman, M., Zatorre, R.J., Petrides, M. and **Evans, A.** (1997a) *Flavor processing: more than the sum of its parts*. Neuroreport, 8, 3913–3917.

Small, D.M., Jones-Gotman, M., Zatorre, R.J., Petrides, M. and **Evans, A.C.** (1997b) *A role for the right anterior temporal lobe in taste quality recognition*. J. Neurosci., 17, 5136–5142.

Stevenson, R.J. and **Boakes, R.A.** (2003) *A mnemonic theory of odor perception*. Psychol. Rev., 110, 340–364.

Stevenson, R.J. and **Prescott, J.** (1997) *Judgments of chemosensory mixtures in memory.* Acta Psychol., 95, 195–214.

Stevenson, R.J., Boakes, R.A., and **Prescott, J.** (1998) *Changes in odor sweetness resulting from implicit learning of a simultaneous odor–sweetness association: an example of learned synesthesia*. Learn. Mot., 29, 113–132.

Stevenson, R.J., Prescott, J. and **Boakes, R.A.** (1999) *Confusing tastes and smells: how odours can influence the perception of sweet and sour tastes*. Chem. Senses, 24, 627–635.

van der Klaauw, N.J. and **Frank, R.A.** (1994) *Matching and scaling of taste–smell mixtures: Individual differences in sweetness enhancement by strawberry odor*. Chem. Senses, 19, 567**.**

van der Klaauw, N.J. and **Frank, R.A.** (1996) *Scaling component intensities of complex stimuli: The influence of response alternatives*. Environ. Int., 22, 21–31.

Wetherill, G.B. and **Levitt, H.** (1965) *Sequential estimation of points on a psychometric function*. Br. J. Math. Statist. Psychol., 18, 1–10.

Zatorre, R.J. and **Halpern, A.R.** (1993) *Effect of unilateral temporal-lobe excision on perception and imagery of songs*. Neuropsychologia, 31, 221–232.

Zatorre, R.J., Halpern, A.R., Perry, D.W., Meyer, E. and **Evans, A.C.** (1996) *Hearing in the mind's ear: a PET investigation of musical imagery and perception*. J. Cogn. Neurosci., 8, 29–46.

Accepted December 10, 2003