Taste-odour interactions in sweet taste perception

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Abstract

1 Introduction

The sense of smell plays a major role in food flavour perception: Individuals who loose their sense of smell often report that food has no taste anymore. Yet, from a neuroanatomical point of view taste and smell are very different senses. Taste is perceived primarily on the tongue whereas odours are perceived in the upper part of the nasal cavity either directly or via the back of the mouth. But does this neuroanatomical dissociation imply that taste and odour perception are independent? Probably not! Indeed, information coming from the gustatory and the olfactory systems are likely to be combined at a higher level of processing in the brain to give rise to a unique perception referred to as "flavour" (1), (28). The question thus is: What is the nature of this combination? Is it an additive combination whereby taste and odour perception are simply added to form an overall perception or can we observe interactions between taste and odours? In this context, taste odour interaction refers to a modification in perceived taste intensity in the presence of an odour. For example, a sweet solution will taste sweeter in the presence of a vanilla aroma even though the vanilla aroma possesses no taste properties. The aim of this chapter is to examine whether such interactions exist for sweet taste perception. We begin with an overview of the literature on the effect of odour

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on sweet taste perception. Then we present the factors that might affect taste-odour interactions and the different underlying mechanisms proposed in the literature. Finally we highlight some implications of taste-odour interactions for food product development.

2 Overview of the literature

Early work suggested that odour and taste were independent. Murphy, Cain and Barthoshuck (1977), for example, examined the perceived odour intensity, taste intensity and overall intensity of mixtures of sodium saccharin and ethyl butyrate. They found that the overall intensity of the mixtures approximate the simple sum of the intensities of the unmixed components (90%). The same pattern of results was also obtained by Murphy and Cain (1980) for sucrose-citral mixtures. However, in both studies, authors indicate that, despite this apparent independency between taste and aroma, participants tend to perceive olfactory stimulation as taste. For example, Murphy and Cain (1980) report that whereas citral had no effect on sweet perception it was judged to 'have taste magnitude when presented alone'. This effect, referred to as 'olfactory referral' by the authors, does not result from the stimulation of receptors in the oral cavity since it can be abolished by pinching the nostrils (Murphy and Cain,1980; Schifferstein and Verlegh, 1996). It was first attributed to trigeminal stimulations (Murphy and Cain ,1980). According to these authors 'the trigeminal system may serve to bind the anatomically and physiologically distinct olfactory and taste systems into a single perceptual system during eating' (see Murphy and Cain ,1980 p. 605). As we shall see in section 5.3, other explanations are proposed to account for this effect. Since these first demonstrations of taste-odour confusion many studies have investigated the effect of odours on sweet taste perception over the past 20 years. Although those studies use different experimental paradigms, the general principle remains the same. Participants are presented with a series of solutions made of a sweetener alone and a sweetener plus an odorant. Their task is to estimate the sweet (and aroma) intensity of each solution. An odour-induced taste enhancement is said to occur if the perceived sweet intensity of the mixture is greater than the perceived sweet intensity of the sweetener alone. And inversely an odour-induced taste suppression is said to occur if the perceived sweet intensity of the mixture is smaller than the perceived sweet intensity of the sweetener alone. The picture emerging from these studies is somewhat confusing (cf. Table 1). However, despite some divergence in the results, most studies showed that sweet intensity can be enhanced by odour. For example, Frank and Byram (1988) reported that the perceived sweetness of whip cream samples increased when a strawberry aroma was added. The same type of effect was obtained by other authors in presence of several aromas including almond, caramel, coffee, lemon, peach and vanilla and for several sweeteners such as sucrose, fructose, aspartame and saccharine. This effect occurs both when subjects swallow the test solutions as well as when they spit it (Frank, Ducheny & Mize, 1989). In addition, Cliff and Noble (1990) using a peach aroma showed that increasing the concentration of aroma increased not only the intensity of perceived sweetness of a glucose solution but also its duration. More striking, Algom, Marks and Cain (1993) indicated that both perceived and mentally imagined mixtures of different concentrations of glucose and orange aroma showed the same patterns of interaction. In other words imagined odours interact with perceived sweetness the same way as perceived odours (Djordjevic, Zatorre and Jones-Gotman , 2004). Schifferstein (1997), however, indicates that in the case of mentally imagined mixtures participants might not base their response on mental images but rather on their knowledge of sensory interaction. Finally, Sakai, Kobayakawa, Gotow, Saito and Imada (2001) found that sweetness enhancement of aspartame by vanilla persists when vanilla is presented simultaneously with, but not dissolved in, the taste stimuli.

So, to summarize it seems that sweet taste perception might be modified in the presence of an odour and that this effect is not due to changes in the physico-chemical properties of tastants in the presence of odorants since it can be observed when odorants and tastants are presented separately. Yet, despite the many studies demonstrating an enhancement of sweet taste in the presence of an odour, the conditions of appearance of such an effect are far from being clear. Indeed, as can be noted on Table 1, all odours do not have the same effect on sweetness perception. Some odours such as strawberry, vanilla, lemon, almond, caramel, maracuja and lychee tend to increase sweetness intensity of sucrose or aspartame. Other odours tend to have no effect (peanut butter, ham, chocolate, mango and wintergreen) or tend to decrease sweetness intensity of sucrose or aspartame (liquorice, almond, damascene, and angelica oil). Moreover, the same odour does not seem to always induce a similar effect. For example lemon seems some times to enhance sweet taste intensity, some times to suppress it and other times to have no effect.

3 Factors affecting taste-odour interactions

Three major classes of factors that we refer to as 'task-driven', 'stimulus-driven' and 'subject-driven' factors have been proposed to explain the variability of the effect of odour on sweet taste.

3.1 Task-driven factors

A first explanation for the variability of the effects observed in Table 5.1 might be found in differences in the methodology used by the authors. For example, Lawless and Schlegel (1984) found a taste odour interaction in mixtures with variable sucrose and citral concentrations using Thurstonian scale values derived from triangle tests but not using attribute ratings. Inversely, Djordjevic et al. (2004) failed to find an effect of strawberry odour on sweet taste perception with a forced choice detection task whereas other authors found an effect with intensity scaling. These results indicate that the instructions given to the participants as well as the strategy implied by the task performed play an influential role in taste-odour interactions.

3.1.1 Instructions given to the subjects

Most studies of taste-odour interaction use intensity ratings as measurements. Several studies showed that, in this type of experimental set up, the instructions given to the subjects are crucial. In particular, Frank and his collaborators (Frank, Wessel, and Schaffer, 1990; van der Klaauw and Frank, 1996) and Clark and Lawless (1994) showed that sweetness enhancement depend upon the response alternatives given to the subjects. For example in Frank, van der Klaauw and Schifferstein (1993), participants were asked to evaluate either the sweetness of sucrose and sucrose -strawberry mixtures or the sweetness, sourness, and fruitiness of the same mixtures. When sweetness was the only alternative, an enhancement was observed: The sucrose-strawberry mixture was rated as sweeter than the sucrose solution. No such enhancement was observed when participants had to rate simultaneously the sweetness, the fruitiness, sourness and fruitiness of the mixtures. In another condition, participants were asked to first rate the global intensity of the mixture and then separate this global intensity in six ratings (sweet, salty, sour, bitter, fruity and other). A suppression effect was observed: The sucrose-strawberry mixture was rated as less sweet than the sucrose solution. According to Frank, van der Klaauw and Schifferstein (1993), providing participants with alternative scales help them separating their perception in taste and odour perception and thus reduces olfactory referral. Further work by van der Klaauw and Frank (1996) examined if the effect of the instructions given to the subjects was due to the number of alternatives proposed to the participants or to the appropriateness of these alternatives. Six rating conditions were used: 1) sweet only, 2) sweet and bitter, 3) sweet, bitter, and floral, 4) sweet and floral, 5) sweet and fruity, 4) sweet, or fruity or bitter (participants in this condition had to make only one rating per stimulus but were not told before the presentation of the stimulus if this rating was sweet, fruity or bitter). As shown Fig.1, the number of alternatives did not play an important role in determining sweet tasbte enhancement: No decrease in odour-induced enhancement was observed when the number of alternatives increased. In contrast, the appropriateness of alternatives seems to be crucial: Inappropriate alternatives such as bitter did not reduce taste enhancement. Finally, no enhancement was observed in the last condition thus indicating that attending to different components of the overall sensation is more important than actually making multiple ratings.

3.1.2 Strategy implied by the task

As we just saw the number of rating scales available to describe a mixture might affect the appearance of taste-odour interactions. According to Frank and his collaborators this effect can be explain in terms of attentional strategies. Providing participants with multiple scales encourage them to adopt an analytic approach whereas providing them with a single scale encourages them to adopt an integrative or synthetic approach. More specifically Frank (2002) indicates that 'When subjects are asked to attend to multiple stimulus attributes, the instructions encourage them to disentangle the concepts for each of the attributes and this constricts the conceptual boundaries of the attributes and minimizes dimensional interactions' (see Frank, 2002, p. 142). For example, providing only a sweetness scale to evaluate a sucrose-strawberry mixture might lead to a wider interpretation of the sweetness concept including sensation such as fruitiness. By contrast providing both a sweetness and a fruitiness scale might lead to a more narrow sweetness concept excluding fruitiness sensation. An implication of this interpretation is that flavour perception (i.e., the combination of taste and odour) should be analysable into its taste and odour components by individual trained to focus their attention on these components but not by untrained consumers. In agreement with this hypothesis, Bingham, Birch, de Graaf, Behan, and Perring (1990) found that untrained participants rated a mixture of maltol and sucrose as sweeter than an equivalent concentration of sucrose alone but not participants who have been trained to use an analytical tasting strategy. Such effects of training however are not always found. Indeed, Stevenson (2001) and Stevenson and Case (2003) found no difference in the ability of trained and untrained participants to separate an odour-sucrose mixture into its components. In other words, as Stevenson (2001) put it, 'enhancement effects, and thus confusion between odours and tastes, may be more cognitively impenetrable than has sometimes been assumed' (see Stevenson, 2001, p. 242).

3.2 Stimuli-driven factors

A second explanation for the variability of the effects observed in Table 1 might be linked to the nature of the odorants and tastants mixtures. Indeed Frank and Byram (1988), for example, found sweetness to be enhanced by strawberry odour, but not by peanut butter odour.According to Stevenson, Prescott & Boakes (1995; see also Stevenson, Boakes & Prescott, 1998) the degree of association between tastant and odorant is crucial in taste-odour interactions. More specifically, these authors suggest that an interaction will occur when the odour and the taste have previously been experienced conjointly. Other authors mention as a determining factor the nature of the relationship between tastant and odorant. The harmony between tastant and odorant was first studied by Murphy and Cain (1980) who failed to show an effect of this factor on taste-odour interaction. Their results reveal the same pattern of additivity for both a harmonious (citral and sucrose) and an inharmonious (citral and sodium chloride) mixture. However, this result has to be interpreted with some caution because the degree of 'harmony' between tastant and odorant was not estimated by the participants but was based on assumptions from the authors. Later, Frank, Shaffer and Smith (1991) asked subjects to evaluate the similarity of pairs of odorants and tastants. They found that the more similar tastant and odorant pairs yielded the stronger effect of odour on taste. Using a similar method, Schifferstein and Verlegh (1996) examined the effect of the congruency between taste and odour. They found a taste enhancement for congruent mixtures (sucrose-strawberry, sucrose-lemon) but not for incongruent mixtures (sucrose-ham). In agreement with this result, a single cell recording study (Rolls and Bayliss, 1994) indicates that some cells of monkey orbitofrontal cortex respond to both olfactory and gustatory stimuli but mostly for congruent stimuli such as glucose and fruity odours. However, Schifferstein and Verlegh reported that the degree of congruence was not linearly correlated with the amount of odour-induced taste enhancement. They suggested that 'the congruency judgements are not effective in explaining the enhancement because they do not reflect the degree of association between two elements but they reflect how much somebody likes the combination of two elements' (see Schifferstein and Verlegh , 1996, p. 102). A better predictor might be the smelled taste of the odorants (e.g., the sweetness rating of a strawberry aroma) as proposed by Stevenson, Prescott and Boakes (1999). Indeed these authors reported that the degree to which an odour smelled sweet predicted about 60% of odour induced sweetness enhancement or suppression. In this study caramel, maracuja, strawberry and lychee were found to enhance sweet perception whereas angelica oil and damascene suppressed it. To evaluate if the different concepts used in the literature tapped the same aspect of the relationship between odorant and tastant, Nguyen (2000) asked four groups of participants to rate the harmony, the congruency, the similarity and the smelled taste of four mixtures. The four mixtures were chosen based on a free association task whose goal was to evaluate the cognitive association between odours and tastes (Sauvageot, Nguyen, Valentin, 2000). Two of them were associated: sucrose-vanilla and acid-lemon. That is some subjects spontaneously answered acid when prompted with the word 'lemon' and some sweet when prompted with the word 'vanilla'. The two others were not associated. That is no subjects answered acid to vanilla or sweet to lemon. A fifth group of participants had to rate the sweetness or the sourness of the mixtures and two control mixtures made of pure sucrose or acid. Contrast analyses showed that, although the four rating scales were positively correlated, only smelled taste (40%), and similarity (29%), predicted the observed odour-induced taste enhancement. Moreover, a very high correlation was observed between similarity and smelled taste indicating that these two scales measure the same aspect of the odorant-tastant relationship, probably what Stevenson (2001) calls the confusion between odour and taste. The fact that harmony and congruence ratings did not predict taste enhancement is in agreement with previous data by Murphy and Cain (1980) and Schifferstein and Verlegh (1996). These aspects of the relationship between tastants and odorants might be more difficult to estimate and more prone to individual variations than smelled taste and similarity.

Yet, the most surprising aspect of this study is that an odor-induced taste enhancement effect was observed for the acid-vanilla mixture. This mixture was considered as being incongruent, not harmonious and not similar. Furthermore, Sauvageot et al. (2000) study showed that no subjects associated the term 'sour' with the term 'vanilla' even in a forced choice association task in which the possible choices corresponded to the four fundamental tastes (sweet, salty, sour, bitter). Finally, the vanilla aroma was not perceived to smell 'sour'. Thus, the positive effect of vanilla on sourness cannot be explained in terms of relationship, cognitive association, or perceptual similarity between odorant and tastant. This last result indicates rather that the similarity or confusability between odorant and tastant might not be a necessary condition for enhancement to occur. This last point will be discussed later in the chapter.

3.3 Subject-driven factors

Additional constraints for the observation of an effect of odour on sweet taste seem to be subject-driven. We already saw that participants' degree of expertise might play an important role in the ability to separate or integrate olfactory and gustatory components of a mixture. Other factors affecting taste odour interactions include participants' culture and individual differences.

3.3.1 Culture effect

A first demonstration of the effect of culture on odour induced sweetness enhancement resulted from an attempt at replicating Frank and Byram (1988) with French participants (Nguyen, 2000). In both Frank and Byram and Nguyen studies, participants had to rate the sweetness intensity of four whip cream samples containing respectively 0, 0.25, 0.60, and 1.20 M sucrose with and without the presence of a strawberry aroma. Whereas Frank and Byram observed a positive effect of strawberry on sweetness for all sucrose concentrations, Nguyen observed a positive effect only for the second concentration. Moreover, this effect was much smaller than that observed by Frank and Byram (2 vs. 6 points on a 20 points scale). This result can be explained in terms of food consumption habits and cognitive association between odorants and tastants. Whereas the association between strawberry and sweet is very frequent in American food (milk shake, ice cream, yogurts), it is less frequent in French food. This was confirmed in the free association task carried out by Sauvageot et al. (2000): For French subjects, strawberry is more often associated with a sour taste or a red colour than with a sweet taste as it is for American subjects.

A link between food consumption habits and taste odour interaction was also reported in Nguyen, Valentin, Ly Mai, Chrea, and Sauvageot (2001). French and Vietnamese participants were presented with two sets of samples: a sweet set made of a sucrose solution, a sucrose-vanilla mixture and a sucrose-lemon mixture and a sour set made of an acid solution, a acid-vanilla mixture and a acid-lemon mixture They were instructed to swallow the samples and to rate their sweet or sour intensity on a 10 cm unstructured line scale. An analysis of variance revealed a one-way interaction between type of mixtures and cultures. Pairwise comparisons showed that this interaction was mainly due to the sweet mixtures. Whereas for French subjects sweetness enhancement was higher in the presence of vanilla than of lemon, the opposite was observed for Vietnamese subjects. As for strawberry aroma, this cultural effect can be put in perspective with culinary association. Vanilla is very often used in France to flavour sweet dishes but not in Vietnam. In contrast, the association between lemon and sweet is less frequent in France than in Vietnam where lemon soft drinks are very popular.

A study by van der Klaauw and Frank (1994) showed that in addition to cultural differences, individual differences might play a role in odour taste interactions. Participants were given three solutions of sucrose (0.18, 0.30, 0.435 M), a mixture of .30 M sucrose and strawberry aroma, and a mixture of 0.30 M sucrose and coffee aroma. Their task was either to rate the sweet intensity of the five samples or to match each sample with a sucrose solution from a range of nine concentrations going from 0.13 to 0.55 M. While on the whole strawberry aroma and to a lesser degree coffee aroma enhanced the sweetness of sucrose solutions, participants clearly differed in their probability to show an enhancement. Interestingly, these individual differences were consistent across the two tasks. An individual showing an enhancement effect with the scaling method was likely to show the same effect with the matching task. The authors interpreted these individual differences as an indication that some participants are better at separating their perception into olfactory and gustatory components.

4 Mechanisms of taste-odour interactions

Despite the different factors that might intervene the odour-induced taste enhancement or suppression effect seems to be a robust effect. The question that naturally arises, however, is at which level does this effect occurs? It is unlikely it occurs at the receptor level. Since as already mentioned sweet taste enhancement have been observed even in situations in which the odorant and the tastant were presented separately (Sakai et al., 2001; Djordjevic et al, 2004), it is more probable that it occurs at the central processing level. However, the central mechanisms involved in this effect are still controversial and three main views seem to emerge from the literature.

4.1 Response bias

For some authors such as Clark and Lawless (1994), odor-induced taste enhancement could be explained in terms of response biases. These authors base their argumentation on the fact that a taste enhancement is observed only when subjects are provided with a single scale (cf. section 2.1). Clark and Lawless (1994) interpreted this phenomenon as a 'dumping' effect. According to their interpretation, when a participant is not given an appropriate rating scale to express a sensation, he/she 'dumps' this sensation onto the only available scale(s). This behaviour would 'correspond to a general tendency to integrate all information to increase subjective confidence in the judgments' (see Clark and Lawless, 1994, p. 591). For example, when subjects are asked to evaluate the sweetness intensity of an aspartame solution to which a strawberry aroma was added, they 'dump' the strawberry sensation onto the sweetness scale and thus a sweetness overestimation is observed. An opposite effect can also be observed when too many scales are used. For example Clark and Lawless (1994) observed that an aspartame solution without any added aroma was rated as less sweet when participants where asked to rate both the sweetness and the flavour intensity than when they were asked to rate only the sweetness intensity. This suppression effect could be due 'to a tendency to use response category with equal frequency' (p. 592). Within this framework, it is unclear whether taste-odour interactions are a reliable perceptual effect or simply a measurement artefact. Indeed, intensity rating methods indicate that odours might increase sweetness ratings but does that imply that it increases sweetness perception?

To answer this question a few authors examined taste-odour interactions to see if they can be shown with paradigms different from intensity ratings. Djordjevic et al. (2004) for example used a sweet taste detection task. Participants were given pairs of samples made of a weak sucrose solution and a blank solution. They were asked to sip each solution immediately after having sniffed or imagined a strawberry or a ham odour and to indicate which of the two solutions tasted stronger. In both perceived and imagined conditions, detection of sucrose was poorer when combined with a ham odour than with no odour. No difference was observed with strawberry odour. This result clearly shows that taste-odour interaction can be obtained with a paradigm free of the response biases described by Clark and Lawless (1994). Nguyen, Dacremont and Valentin (2000) proposed another bias free method to measure the effect of vanillin on sucrose. This method, based on Garner (1974) filtering paradigm, evaluates if a categorization task performed on sweetness perception is affected by changes in vanilla aroma. Participants had to make categorization judgments according to the level of the perceived sweetness intensity of samples made of two concentrations of sucrose and two concentrations of vanillin. Results show that categorization performance was systematically lower when the concentration in vanillin changed in addition to the concentration of sucrose. This indicates that participants were unable to ignore the olfactory component when categorizing the solutions according to the gustatory component. Taken together the Djordjevic et al. (2004) and Nguyen et al. (2000) results suggest that taste-odour interactions cannot be explained solely in terms of responses biases.

4.2 Learned synesthesia

For other authors such as Stevenson et al. (1998), the effect of odour on sweet taste perception could be explained in terms of learned synesthesia. Synesthesia is defined as a systematic association between two sensations corresponding to two different sensory modalities. A classical example of synesthesia can be found in Cytowic (1993). For the patient described in this book, each different taste had a different feel. Mint for instance felt like ‘smooth, cool columns of glass’. Stevenson et al. (1998, see also Stevenson et al., 1995) showed that synesthesia can be learned through a combined exposure to two sensations. Especially, they showed that repeated pairing of a previously neutral odorant with sucrose results in an increased perceived sweetness of the odorant. Participants attended five sessions, one session of pre-test, three sessions of conditioning and a session of post-test. During pre-test, participants had to rate among other ratings (liking, overall intensity, sourness, familiarity) the sweetness of lychee and water chestnut odours. During each conditioning session participants performed six triangle tests among which one consisted of water chestnut (or lychee) paired with sucrose (conditioning trial) and one of lychee (or water chestnut) and water (control condition). The other triangle tests served as fillers. During the post-test, participants had to rate again the sweetness of lychee and water chestnut odours and to answer an awareness test on the same odours. Results indicated that sweetness perceived intensity increased between pre-and post-tests for the odour paired with sucrose (water chestnut or lychee) but not for that paired with water. This increase in perceived sweetness occurred independently of participants' awareness that the odour was paired with sucrose during the conditioning test and did not disappear after 24h of delay. More recently, Prescott, Johnstone and Francis (2004), using a similar paradigm, found that even a single co-exposure with sucrose was sufficient to enhance the perceived sweetness of a prune and a water chestnut odour. However they also found that a synthetic perceptual strategy during the co-exposure was necessary to observe a taste enhancement in the presence of the same odours. Indeed, participants instructed to evaluate the overall flavour of sweet-prune (or water chestnut) flavoured solutions during the conditioning phase showed an enhancement whereas participants instructed to evaluate separately the sweetness and the aroma of the same solutions did not. Prescott et al. (2004) concluded that 'exposure alone is a necessary, but not sufficient, cause of sweetness enhancement effects' (see Prescott et al, 2004, p. 335).

Both Stevenson et al. (1998) and Prescott et al. (2004) results emphasize the role of associative learning in odour-induced sweetness enhancement. However, can we really interpret this effect in terms of learned synesthesia as proposed by Stevenson et al. (1998)? Synesthesia is the involuntary physical experience of a cross-modal association. It is characterized by idiosyncratic, vivid and irrepressible perceptions and does not seem to rely on any form of learning (Cytowic and Wood, 1982). In contrast, taste-odour interactions seem to result from perceptual learning and to be culture-dependent rather than idiosyncratic. An interpretation in terms of central integration as proposed by Prescott et al (2004) seems more appropriate. Consistent with this interpretation, White and Prescott (2002) showed that an odour can prime the cognitive system to expect a particular type of taste based on past flavour experiences. More specifically, reaction time to identify a taste in the presence of an orthonasally delivered odour decreases if the taste and the odour have been encountered conjointly in a previous conditioning phase. Likewise, White and Prescott (2001) found that participants identified faster a sweet taste in the presence of a congruent odour such as strawberry than in presence of an incongruent odour such as grapefruit.

4.3 Central integration

Integration between odour and taste could occur in a brain region called the orbitofrontal cortex (Rolls, 2004). This brain structure receives projections from the olfactory cortex and the gustatory cortex. As already mentioned, Rolls and Bayliss (1994) found in the orbitofrontal cortex of monkeys some neurons that respond to both olfactory and gustatory inputs. Among these bimodal neurons, some responded to odours and tastes that occur together in food. For example, a given neuron will respond preferentially to a sweet taste in a taste discrimination task and to a fruit odour in an odour discrimination task. Moreover, Rolls, Critchley, Mason, and Wakeman (1996) showed that the response of some olfactory neurons in the monkey orbitofrontal cortex depends upon the taste with which the odour is associated. Rolls (1997) suggested that bimodal neurons would develop from unimodal neurons through associative learning of tastes and odours occurring naturally together in food.

Imaging techniques have been used recently to assess the role of central brain structures in flavour perception by humans. Small, Jones-Gotman, Zatorre, Petrides, and Evans (1997) used positron emission tomography (PET) to compare cerebral blood flow (CBF) changes due to the processing of olfactory (e.g. strawberry), gustatory (e.g sucrose), and combined olfactory gustatory stimuli (e.g. strawberry, sucrose). They found that bimodal processing of taste and odours produces significant CBF decreases relative to unimodal processing of identical tastes and odours. This decrease in CBF can be related to suppression effects observed in psychophysical experiments. More recently de Araujo, Rolls, Kringelbach, McGlone, and Phillips (2003), using an event-related functional magnetic resonance imaging (fMRI) study, reported an activity in the orbitofrontal cortex when a tastant (sucrose or monosodium glutamate) and a retronasally delivered odorant (strawberry or chicken-like) were presented simultaneously. This activity was greater than the sum of the activities obtained when tastant or odorant were presented separately, thus indicating that an interaction occurred. A similar finding was also reported by Small et al. (2004) thus indicating that orthonasal and. retronasal olfaction might interact differently with taste. Indeed, Small et al. (1997) found a taste suppression effect with orthonasally delivered odours. This differential effect of orthonasal and retronasal olfaction on taste was not, however, always found in psychophysical studies (Sakai et al., 2001).

Small et al. (2004) also showed that superadditive responses were observed only when the taste-odour pair was congruent (sucrose-vanillin as opposed to NaCl-vanillin). Such patterns of superadditivity seem to be the physiological correlate of psychophysical data by Dalton, Doolittle, Nagata and Breslin (2000). These authors found that participants could detect the presence of benzaldhyde at 30% below its detection threshold when the odorant was combined with sodium saccharin at 30% below its detection threshold. In a second study, Breslin, Doolittle and Dalton (2001) failed to find a superadditivity effect when benzaldehyde was presented in combination with monosodium glutamate.

4.4 Toward a dual model

The literature reviewed so far indicates that two different cognitive mechanisms might be involved in taste-odour interactions. The first one would not require any previous association between odorants and tastants and would give rise to small amplitude effects. It would correspond to a general tendency to integrate all information into a total intensity impression (dumping effect) and thus would be sensitive to the number of rating scales. In contrast, because it acts more like a response bias than a perceptual enhancement, it is would not be sensitive to subjects' history and thus would not be mixture dependent. The second one would correspond to a real perceptual enhancement and give rise to high amplitude effects. It would result from the co-encoding of an odorant and a tastant and thus would be mixture and culture dependent (Nguyen, 2000). To test this dual mechanism hypothesis, Valentin and Nguyen (2001) evaluated the effect of lemon and vanilla aroma on sourness ratings. The experiment consisted of two intensity tasks. In the first intensity task (1 question condition) subjects had to indicate the sourness of an acid solution, a vanilla-acid solution and a lemon-acid solution. In the second intensity task (3 questions condition) subjects were given the same solutions but were instructed to rate the sour, vanilla, and lemon intensity of the mixtures on three different scales. As illustrated on Fig. 2, student t-tests revealed a significant odour-induced taste enhancement for both vanilla and lemon in the 1 question condition with a higher amplitude effect for lemon than for vanilla. In the 3 questions condition, the effect of vanilla on sourness was not significant whereas the effect of lemon is significant. This result indicates that providing several scales to subjects does not have the same effect on odor-induced taste enhancement depending on the association between tastants and odorants. Subjects seem to be able to separate taste and odour sensations only for taste-odour mixtures in which the components are not cognitively associated, similar, harmonious, congruent, and familiar (e.g. acid-vanilla). For other mixtures (e.g. acid-lemon), subjects seem to be able to separate only partially their sensations: Providing several scales decreases the odour-induced taste enhancement effect but does not suppress it.

5 Implications for food product development

Odour-induced sweet taste enhancement or suppression appear to be a robust effect albeit not a strong one. Indeed, while odour and taste sensation in the mouth can, to some extent, be analyzed, sensory integration might be more frequent in natural eating conditions. This is reflected by the spontaneous use of the term "sweet" to describe food related odours (Dravnieks, 1985). The question thus is can we use this natural tendency to integrate sensations to enhance the sweetness of a food product via its aromas? The answer is yes, but the result will depend on several factors. First, all odours will not be equally useful to enhance sweet taste. Odours confusable with sweet taste because they have been experienced often in conjunction with a sweet taste are the best candidates to enhance sweet taste. Second, the ability of an odour to enhance sweet taste does not seem to be universal: An efficient sweet taste enhancer in a given culture might not be as useful in another one. Finally interactions between sweet taste and odours might vary as a function of individual sensitivity and strategy in food tasting. Individuals trained to analyse their sensations might be less prone to taste odour interactions than other individuals.

Taste odour interactions have also broad implications for descriptive analyses in which multiple attributes of complex foods are rated. For some time scientists in sensory evaluation thought that panellists can be trained to separate their sensations. The data presented here show that this is not always the case. For example, it is quite possible that even for a trained panellist the sweetness produced by a fruity aroma cannot be separated from the sweetness produced by sucrose. This raises the question of what do we want to measure when we ask panellists to rate the sweetness of a food product? The overall sweetness of the product or the sweetness yielded by the taste component? According to Prescott (1999), 'this distinction might be artificial [] since the sweetness of the flavour components may be represented cognitively, and even perhaps neurally, as equivalent. They may be functionally equivalent as well' (Prescott, 1999, p. 355). In other words, in some cases, such as understanding consumer preferences, it might be preferable to measure the overall perceived sweetness of a food product. In other cases, where it is necessary to estimate only the sweetness produced by the taste component of a food, the rating scales provided to the panellists should be chosen with care to help them separating their sensations. Indeed instructing a panellist to focus only on taste perception will not be enough to avoid odour induced taste enhancement.

6 Future trends

One potentially interesting line of research will be to further examine the effect of the degree of cultural experience with particular combinations of tastants and odorants in odour-induced sweet taste enhancement. Cultural factors are one of the most powerful determinants of which food we consume. Nevertheless, there has been surprisingly little research on how perception of, and preference for food might vary across cultures. To understand how odour induced sweet enhancement as a function of cultural experience may provide some new insights in the understanding of cultural differences in preferences for sweet foods. A second line of research will be to extend the study of odour-taste interactions to multiple interactions in sweet taste perception. It is well known that when eating food, sensations such as somatosensory, visual or auditory sensations influence food perception and preference (Delwiche, 2004). This may be particularly relevant also from a neuroatomical point of view to evaluate how the different sensory inputs interact with each others and how they are integrated in the brain. In this perspective, imaging techniques will be very useful. Finally, focus should be given to a more general consequence of sweet taste enhancement: the improvement of palatability and the compensation for chemosensory losses in populations such as the elderly. Recently, it has been demonstrated that the addition of a flavour enhancer can improve a number of nutritional and immune parameters such as increasing the number of lymphocyte cells or increasing secretion rate of specific antibodies (Schiffman, 2002). As flavour enhancement can be achieved in several ways, in addition to further investigations the contribution of neural integration of sensory inputs, it is crucial to examine also other sources of sweet taste enhancement such as modification of receptor mechanisms.

7 Sources of further information and advice

Reviews

A few reviews are of interest to acquire further information and advice on taste-odour interactions. Prescott (1999) provides a broad body of literature on taste-odour interactions, and also raises the question of the different origins of odour-taste interactions and provides evidence that taste enhancement is a psychological construct. Frank (2002), based on a large number of studies from his laboratory, proposes a model that attempts to characterize taste-odour interactions when making judgements about the sensory magnitude of complex chemosensory stimuli. Recommendations are furthermore made based on studies of response context and flavour research. Delwiche (2004) provides a large scope of investigations on flavour perception. This paper reviews studies that look at the impact of different sensory cues on the perception of taste, odour and taste-odour mixtures, as well as the impact of certain physical interactions on these perceptions such as influence of irritation, temperature, colour, texture and sound. Readers interested in neuroanatomical issues of odour-taste interactions will find some thorough information in Rolls (1999).

Current research and interest groups

The Monell Chemical Senses Center in Philadelphia (USA) and the Sensory Science Research Centre at the University of Otago (New Zealand) are the main references in terms of research groups investigating taste-odour interactions.

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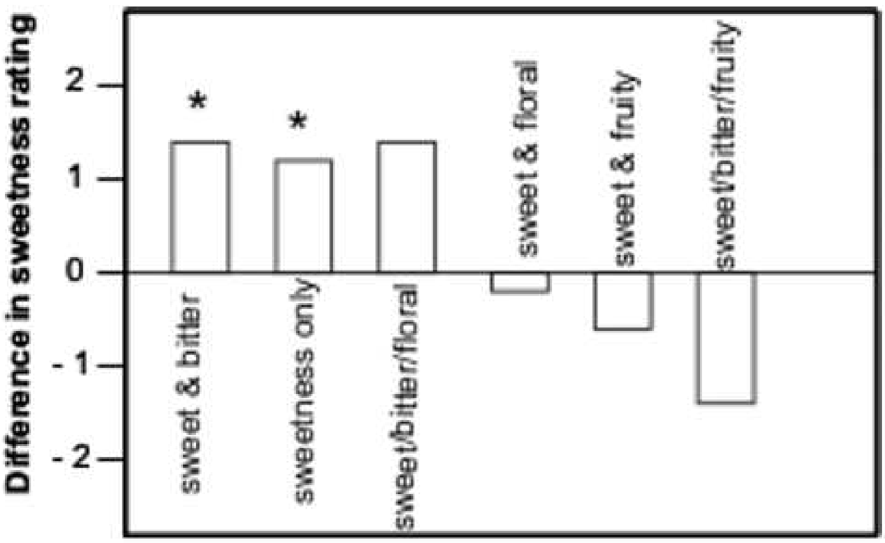

Fig. 1. Changes in sweetness perception (sweetness rating for the mixture minus sweetness rating for sucrose alone) for strawberry sucrose mixtures under six ratings condition. * p>0.05 (adapted from van der Klaauw and Frank (1996).

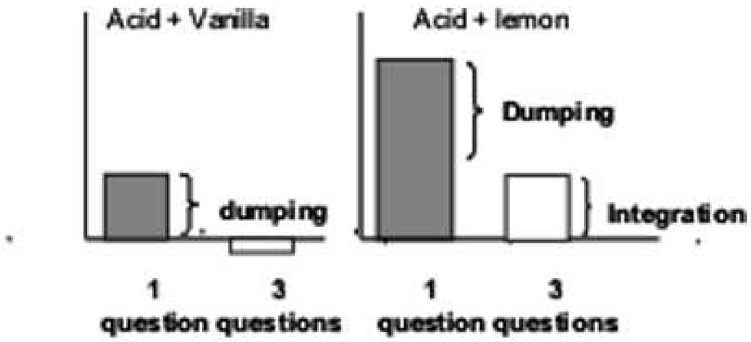

Fig. 2. Changes in sour perception (sourness rating for the mixture minus sourness rating for citric acid alone) for vanilla citric acid and lemon citric acid mixtures under two rating conditions (adapted from Valentin and Nguyen, 2001)

Authors	odorant	tastant	SS	MS	MAT	DET
De Araujo et al. (2003)	strawberry	sucrose	...	+	...	...
Djordjevic et al. (2004)			...	...	...	=
Frank & Byram (1988)			+	...	...	...
Frank et al. (1989)			+	...	...	...
Frank et al. (1990)			+	=	...	...
Frank et al. (1993)			+	=,–	...	...
Nguyen (2000)			=	...	...	...
Schifferstein & Verlegh (1996)			+	...	...	...
Stevenson (2001)			+	...	+	...
Stevenson et al. (1999)			...	+	...	...
van der Klaauw & Frank (1994)			+	...	+	...
van der Klaauw & Frank (1996)			+	+	...	...
van der Klaauw & Frank (1996)			=	=	...	...
van der Klaauw & Frank (1993)		fructose	+	–	...	...
van der Klaauw & Frank (1993)		saccharine	+	–	...	...
Clark & Lawless (1994)		aspartame	+	=	...	...
Frank et al. (1991)			+	...	...	...
van der Klaauw & Frank (1993)			+	–	...	...
Frank et al. (1993)	wintergreen	sucrose	=	=	...	...
van de Klaauw & Frank (1993)		fructose	=	=	...	...
van de Klaauw & Frank (1993)		saccharine	=	=	...	...
Frank et al. (1991)		aspartame	...	=	...	...
van de Klaauw & Frank (1993)		aspartame	=	=	...	...
Lawless & Schlegel (1984)	lemon	sucrose	=	...	...	+
Nguyen (2000)			+	...	...	...
Schifferstein & Verlegh (1996)			+	...	...	...
Frank et al. (1991)		aspartame	...	+	...	...
Clark & Lawless (1994)	vanilla	sucrose	+	...	...	...
Nguyen (2000)			+	...	...	...

Fig. 3. *
Table 1a. Overview of the impact of odours on sweet taste perception. SS=Single scale ratings, MS=multiple scale ratings D= detection, M=matching. + indicates an enhancement effect, - a suppression effect, = no effect, not applicable.

Authors	odorant	tastant	SS	MS	MAT	DET
Prescott (1999)	waterchestnut	sucrose	=	...	...	...
Prescott et al. (2004)			=	...	...	...
Stevenson et al. (1995)			...	=	...	...
Stevenson et al. (1999)			...	=	...	...
Djordjevic et al. (2004)	ham	sucrose	...	...	...	–
Schifferstein & Verlegh (1996)			=	...	...	...
Stevenson et al. (1995)	lychee	sucrose	...	=	...	...
Stevenson et al. (1999)			...	=	...	...
Bingham et al. (1990)	maltol	sucrose	+	=	...	...
Stevenson et al. (1999)			...	–	...	...
Frank & Byram (1988)	peanut butter	sucrose	=	=	...	...
Prescott (1999)			–	...	...	...
Frank et al. (1991)	peanut	aspartame	...	=	...	...
Stevenson et al. (1999)	acetyl methyl carbamol	sucrose	...	=	...	...
Frank et al. (1993)	almond	sucrose	+	=,–	...	...
Stevenson et al. (1999)	angelica oil	sucrose	...	–	...	...
Stevenson et al. (1999)	caramel	sucrose	...	+	...	...
Frank et al. (1991)	chocolate	aspartame	...	=	...	...
van der Klaauw & Frank (1994)	coffee	sucrose	+	...	+	...
Stevenson et al. (1999)	damascone	sucrose	...	–	...	...
Stevenson et al. (1999)	eucalyptol	sucrose	...	=	...	...
Stevenson et al. (1999)	mango	sucrose	...	=	...	...
Stevenson et al. (1999)	maracuja	sucrose	...	+	...	...
Prescott (1999)	olong tea	sucrose	–	...	...	...
Algom et al. (1993)	orange	sucrose	+	...	...	...
Cliff & Noble (1990)	peach	sucrose	+	...	...	...
Prescott et al. (2004)	prune	sucrose	=	...	...	...
Prescott (1999)	raspberry	sucrose	+	...	...	...

Fig. 4. *
Table1b. Overview of the impact of odours on sweet taste perception. SS=Single scale ratings, MS=multiple scale ratings D= detection, M=matching. + indicates an enhancement effect, - a suppression effect, = no effect, not applicable.