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Temporal Synchrony and Integration of Sub-threshold Taste and Smell Signals

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Abstract

The importance of stimulus timing and location on the perceptual integration of taste and odour was studied based on a sub-threshold methodology. From a panel of 16 people, 12 showed the integration effect previously reported while 4 showed no effect. The experiment was repeated using retronasal and orthonasal delivery of the odour and with tastant present or absent in the mouth. Integration of taste and odour only occurred when both stimuli were present at the same time. Retro- or orthonasal presentation both produced integration providing that tastant delivery was synchronous but the threshold values for the two presentation methods were different. The relevance of these findings to flavour perception under realistic conditions is considered.

Key words: cross-modal integration, flavour intensity, sensory perception, smell, taste

Introduction

Anatomically, the senses of taste and smell are two separate entities. Taste is stimulated through physical interactions of non-volatile molecules with receptors on the tongue and mouth surfaces, while volatile compounds reaching the receptors in the olfactory epithelium determine smell. At a perceptual level, however, there are many indications that the sensations of taste and smell interact (Delwiche, 2003). Typical manifestations of these taste–smell interactions are rating enhancement and suppression effects. The mere presence of a tastant may affect the perceived intensity of an odour (Bonnans and Noble, 1993; Cayeux and Mercier, 2003), and conversely, the presence of odour volatiles may modulate the rated intensity of tastants (Clark and Lawless, 1994; Frank and Byram, 1988; Frank *et al.*, 1989).

To explain this phenomenon, recent studies have emphasized the central integration of the two modalities (taste and smell). Commonly known as the multi-modal approach, this interpretation relies on the fact that humans are naturally integrative in their sensory perceptions, i.e. that judgement in one sensory modality is frequently affected by information in other sensory dimensions even if they do not physically or physiologically interact (Lavin and Lawless, 1998). This interpretation is supported by some electrophysiological and neuroimaging investigations. Although extensive work has been carried out on the interplay between vision and other modalities, these techniques have only recently been applied to taste–smell integration. Rolls (1997) suggested olfactory and gustatory co-encoding in primates when he reported the detection of bimodal neurons in the orbitofrontal cortex that responded to both taste and odour stimuli. In humans, the orbitofrontal cortex has also been defined as the brain centre creating the psychological notion of flavour, i.e. the region in the brain where taste, smell and trigeminal information can all interact. Recently, De Araujo *et al.* (2003) and Small *et al.* (2004) obtained further evidence to support multi-modal interpretation of flavour perception. Using functional magnetic resonance imaging (fMRI), congruent combinations of taste + odour were found to activate certain areas of the brain (e.g. the orbitofrontal cortex) in a synergistic fashion, i.e. greater activation with the mixture compared to the sum of each stimulus presented alone. While this type of study provides significant evidence on the integration of flavour in the brain, there are some concerns about the reliability of such results, which appear to be highly dependent on the experimental conditions and paradigms used (Calvert, 2001). fMRI studies are also costly and time consuming, and traditional sensory analysis can provide substantial information on the perceptual interactions between taste and smell. The experiment by Dalton *et al.* (2000) is a clear example of taste–odour interaction. To overcome potential problems at supra-threshold levels with panel rating variations, e.g. scale usage and 'dumping', Dalton *et al.* used sub-threshold levels of a tastant

(saccharin) and an odour (benzaldehyde) on the basis that interactions should make the sub-threshold combination perceptible by the panellists. The authors observed that the detection threshold for benzaldehyde, delivered orthonasally via sniffing, was lower when panellists held a sub-threshold solution of saccharin in their mouths compared to simply sniffing the odour alone. Even though it has been presented as one of the most convincing pieces of evidence of cross-modal summation (Delwiche, 2003), to date, there are no other published reports on this phenomenon. The first objective of this study was therefore to replicate the experiment of Dalton *et al.* (2000) to determine whether similar results could be obtained with a different sensory panel.

The second objective was to investigate whether spatial coincidence is an important factor for sub-threshold integration of taste and smell. Dalton *et al.* (2000) chose to present the target stimuli from different locations (olfactory stimulus presented to the nostrils and gustatory stimulus presented in mouth), a situation the consumer rarely experiences. Odour perception of foods and beverages is more likely to result from retronasal stimulation, where the volatiles are carried from the back of the oral cavity via the nasopharynx to the olfactory receptors. These two modes of stimulation, retronasal and orthonasal olfaction, have been shown to create different interactions with taste at a cortical level (Small *et al.*, 1997; De Araujo *et al.*, 2003; Small *et al.*, 2004). However, in the above fMRI studies, only a limited amount of volatile can be expected to reach the nasal cavity as no mouth movements or swallowing actions were allowed to avoid motion artefacts. In order to simulate typical consumption of foods, the swallowing event needs to be included. In order to simulate typical consumption of foods, the swallowing event needs to be included. This approach is supported by several physiological studies which strongly indicate that the intensity of retronasally perceived odour compounds is highly dependent on the swallowing action (Burdach and Doty, 1987; Land, 1996). Buettner and colleagues (Buettner and Schieberle, 2000; Buettner *et al.*, 2001; Buettner *et al.*, 2002) clearly showed that transport of molecules through the olfactory cavity did not take place unless swallowing or vigorous mouth movements (mastication) were performed. They reported that it was mainly the exhalation that follows the act of swallowing, termed 'swallow breath' (Land, 1996), that was responsible for transporting volatiles to the upper airways. Using electroglottography, Hodgson *et al.* (2003) calculated the volume associated with the 'swallow breath' and obtained further evidence of its connection with volatile delivery to the nasal cavity. These findings support the statement from Burdach and Doty (1987) that swallowing plays a role in retronasal odour perception analogous to that played by sniffing in orthonasal perception.

Swallowing not only produces a marked retronasal odour transport (and perception), but also introduces a temporal dimension to the stimulus delivery. While there is concordant stimulation in time in the Dalton *et al.* (2000) experiment (subjects were asked to sniff while holding liquid in mouth), the swallowing process creates a temporal asynchrony. Taste receptors are stimulated as soon as liquid comes in contact with the mouth and tongue, whereas the olfactory receptors will be mainly activated by volatiles carried on the 'swallow breath'. Thus the sequence of stimuli is taste first and odour second with a time offset dependent on the mode of retronasal transport, i.e. chewing/swallowing (Hodgson *et al.*, 2003). This offset leads to the question as to whether taste and smell sensations are perceived sufficiently close in time to induce multisensory integration at the neuronal level. In a similar manner to cross-modal processing of visual and auditory inputs (Calvert *et al.*, 1998), temporal factors may also be critical for taste–smell cross-modal integration.

The present study was designed to progress knowledge on the sub-threshold integration of taste and smell signals reported by Dalton *et al.* (2000). The first experiment aimed to replicate part of the original study to determine if the same enhancement effects could be observed with a different, and larger, panel. The second objective was to study the effect of asynchronous taste and odour stimuli on the sensory perception to determine whether integration of taste and smell stimuli was dependent on the mode of stimulation.

Materials and methods

Subjects

Panellists (aged 34–64 years) from the University of Nottingham external sensory panel participated in this study. From the 16 original panellists for experiment 1 (14 females), 13 panellists (11 females) took part in experiment 2. In experiments 3 and 4, 11 (9 females) and 6 panellists respectively (4 females) were selected on the basis of availability and results obtained in experiment 1. Subjects were naïve with respect to the objectives of the experiments but not with respect to the nature of the compounds used (due to concerns about saccharin intake).

Materials

In order to replicate the experiment of Dalton *et al.* (2000), the same materials were employed. Saccharin (99%, Sigma), which elicits a sweet sensation, was used as the taste stimulus, and benzaldehyde (Firmenich, 906707), commonly referred to as having an almond-like odour, was used as the test odour in all four experiments. All solutions were prepared in deionized water. Blanks corresponded to samples containing deionized water only.

Sensory procedure

Detection thresholds for taste and smell stimuli were quantified using a two-alternative, forced choice, transformed up-down staircase procedure (Wetherill and Levitt, 1965). In each trial, a stimulus was paired with a blank and the subjects were instructed to indicate the sample containing the

stimulus (correct identifications were recorded as an X, incorrect ones as an O). Presentation order was randomized within pairs. The 3-down, one-up rule (rule number 7) (Levitt, 1971) was selected to target the 79.4% performance level on the psychometric function. The stimulus level was increased by one step up if one of the following patterns was obtained: O, XO or XXO; and one step down in case of an XXX pattern. To determine an appropriate starting concentration, the procedure described by Wetherill and Levitt (1965) was adopted. Solutions with decreasing benzaldehyde concentration were presented until an incorrect response was obtained. This concentration defined the starting level for the staircase procedure. A run is defined as a decreasing or increasing slope between two numbered peaks. Testing stopped after six runs in experiments 1 and 3, and after four runs in experiments 2 and 4 to minimize the volume of liquid ingested and to avoid problems of motivation with the panellists to carry out further experiments.

An initial training session was dedicated to familiarize panellists with the odour and the taste stimuli, the test procedure and to aid determination of the appropriate concentration ranges. As variation was expected between thresholds obtained for benzaldehyde when experienced orthonasally or retronasally, another session was used as a 'range finder' before conducting experiment 2. The results from these pretesting sessions were disregarded.

All four experiments were conducted in a similar manner; each consisted of three different trials. First, thresholds for benzaldehyde and for saccharin were determined separately for each panellist. The order of presentation, i.e. assessing saccharin or benzaldehyde first, was randomized across the panel. A threshold for benzaldehyde was then obtained a second time in the presence of saccharin at sub-threshold level, although the way in which the stimuli were combined was specific to each experiment (Figure 1). The panellists were instructed to keep their mouth closed during each sample assessment. Total session time was between 2 and 3 h, including 15 min breaks between trials. All testing was performed at room temperature (~20°C) in an air-conditioned room, under northern hemisphere daylight and in individual booths.

Experiment 1: orthonasal presentation of aroma

Saccharin threshold was determined through a sip and spit procedure. Aliquots (10 ml) of stimulus/blank pairs were presented in 30 ml glass bottles. For each pair, the panellist was instructed to take all the first sample into the mouth, swirl it around, spit it out, rinse the mouth with deionized water, then perform the same process with the second sample. Benzaldehyde threshold was obtained by sniffing 50 ml aliquots of odour stimuli or blanks which were presented in wide-necked 100 ml glass bottles sealed with low-odour plastic screw lids. This type of bottle was especially chosen as it allows a close contact of both nostrils with the sample headspace. It was assumed that this method, by keeping an overall constant flow rate to the nose, would carry a constant olfactory signal to the brain (Sobel *et al.*, 1999). Panellists were told to open the first sample bottle, sniff the headspace once, put the lid back on to reduce loss of headspace over time, and then proceed to the second sample. The bottles were regularly shaken between presentations to re-establish equilibrium for the volatile in the headspace. Two sets of bottles were used for each concentration to enable time for equilibrium to be established.

The combination of the two stimuli consisted of holding a 10 ml solution of saccharin in a closed mouth whilst sniffing the benzaldehyde sample (Figure 1). The concentration of saccharin was equal to 50% of the particular panellist's saccharin threshold determined earlier in the session. Panellists rinsed with deionized water after each sample to remove any tastant from the mouth. No swallowing was allowed during the entire session. Subjects participated in three replicated sessions.

As a control experiment, experiment 1 was repeated, except that panellists simply held water, not saccharin solution, in the mouth to rule out the effect of somatosensory cues.

Experiment 2: retronasal presentation of aroma

Experiment 2 was performed in the same way as Experiment 1, except that instead of sniffing the benzaldehyde solution, the volatile was delivered in a solution taken orally so that retronasal delivery was achieved. Thresholds for saccharin and for benzaldehyde in the single and the combination conditions were determined by presenting pairs of stimulus/blank in 10 ml aliquots in 30 ml glass bottles. For each pair, the panellist was instructed to take the first sample in mouth, swirl it around and swallow it, rinse the mouth with deionized water and swallow the liquid to remove potentially lingering volatiles from the pharyngeal part of the tongue. The panellist then assessed the second sample. The swirling served to ensure that the tastant was in contact with taste receptors whereas the swallowing action was crucial to deliver the volatile via the retronasal route (Figure 1). Subjects participated in two replicated sessions.

Experiment 3: orthonasal presentation of aroma with temporal asynchrony

Individual saccharin and benzaldehyde thresholds were determined using the same procedure described in Experiment 1. The combination trial, however, consisted of spitting out the solution of saccharin before sniffing the benzaldehyde sample, to create a temporal delay (Figure 1). Timing between the two tasks was especially important and the subjects were therefore told to unscrew (but not remove) the lid of the benzaldehyde sample while swirling the liquid in their mouths to reduce time between the spit and sniff steps. Panellists were particularly instructed to keep the delay between steps as consistent as possible. Panellists rinsed after

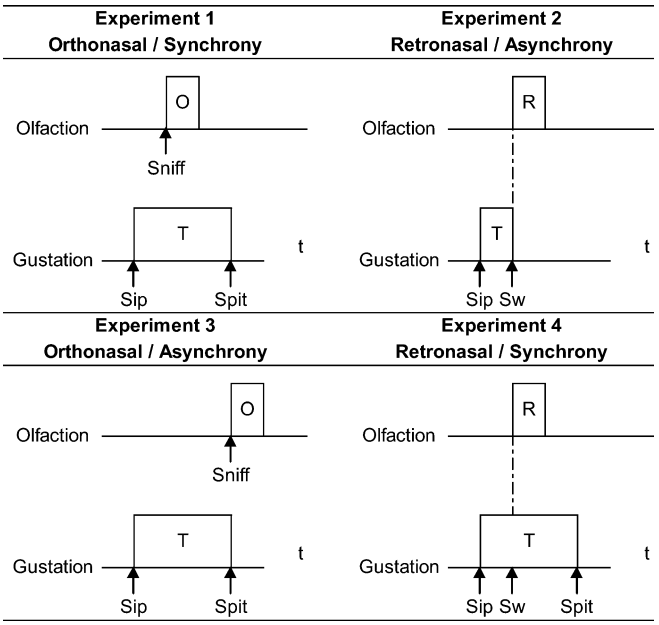

Figure 1 Summary of protocols used in Experiments 1–4. Combination conditions are represented as a function of time (t) where T = taste delivery, O = orthonasal odour delivery and R = retronasal delivery via swallowing (Sw).

each sample. No swallowing was allowed during the entire session. Subjects participated in two replicated sessions.

Experiment 4: retronasal presentation of aroma with temporal synchrony

Saccharin and benzaldehyde thresholds were determined using the procedure described in experiment 2 with the exception that stimulus/blank pairs were presented in aliquots of 20 ml, twice as much as in the last three experiments. Double the amount of liquid was chosen to make the combination trial possible in this experiment. The procedure for the combination trial consisted of taking the whole 20 ml sample in the mouth and then swallowing approximately half of the solution to deliver the benzaldehyde retronasally, while keeping the other half in the mouth. This was done to maintain the presence of saccharin on the tongue throughout the experiment (Figure 1) and had been practised by the panel prior to the experiment. The liquid was subsequently expectorated. Subjects participated in three replicated sessions.

Preparation of samples

Experiments 1 and 3

Series of solutions were prepared using 75% decreasing dilution steps for the odour stimulus and 10 μmol decreasing steps for the taste stimulus. The highest concentrations for benzaldehyde and saccharin were 18 and 95 μmol respectively. Additional solutions were prepared for the last trial (combination trial) of each session and for each panellist containing saccharin at a concentration corresponding to 50% of their respective threshold value determined earlier during that particular session.

Experiments 2 and 4

Series of solutions were prepared using 75% decreasing dilution steps for the odour stimulus and 10 μmol decreasing steps for the taste stimulus. The highest concentrations for benzaldehyde and saccharin were 56 and 95 μmol respectively. For the last trial of each session, a second series of benzaldehyde was prepared for each panellist but in addition contained saccharin at a concentration corresponding to 50% of each panellist's threshold value determined earlier during that particular session.

Data analysis

The data analysis was conducted similarly for the four experiments. For each sequence obtained, the panellist's threshold was obtained by averaging the concentration level at the peaks and valleys (Wetherill and Levitt, 1965). Ratios, expressed as percentages between benzaldehyde threshold values obtained in the combination condition and obtained individually, were calculated for each panellist replicates. Ratios lower than 100% would therefore indicate that the combination with saccharin had a positive effect on the detection of benzaldehyde. One way analysis of variance (ANOVA) was conducted on these ratios to check for significant differences within the panel and in experiments 1 and 2, panellists with ratios above and below 100% identified to determine which individuals demonstrated an integration effect. Threshold means for benzaldehyde alone and in combination with saccharin were calculated. Paired-sample *t*-tests ($\alpha = 0.05$) were subsequently conducted to assess for significant difference between these thresholds.

Results

Experiment 1

Figure 2 highlights the overall results for experiment 1 which was a repeat of the original Dalton experiment with synchronous taste and orthonasal smell delivery. ANOVA indicated significant differences between panellists ($P < 0.001$). There were significant differences between the mean threshold values obtained for benzaldehyde alone and in combination with saccharin but for some panellists there was a decrease and for others there was an increase. For 12 panellists the presence of saccharin increased the sensitivity to benzaldehyde ($P < 0.001$), (50% average decrease in threshold), whereas for four panellists the threshold was higher when saccharin was present in solution ($P = 0.01$). The range of ratios across the three sessions was 31–70% and 110–161% for the two groups respectively and the direction of change in threshold was consistent across replicates.

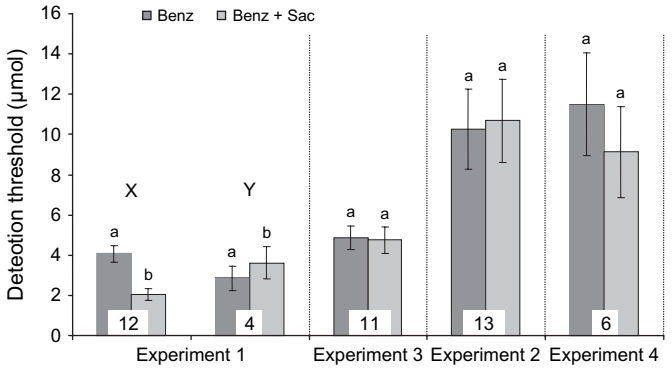

Figure 2 Grand means and standard errors of the detection thresholds for benzaldehyde obtained in the single (Benz) and combination condition (Benz + Sac) in experiments 1 (orthonasal presentation of aroma), 2 (retronasal presentation of aroma), 3 (orthonasal presentation of aroma with temporal asynchrony) and 4 (retronasal presentation of aroma with temporal synchrony). For experiment 1 group X represent subjects demonstrating a decrease in threshold. Group Y represents subjects demonstrating an increase in threshold. Numbers in bars indicate number of the panellists. Within a pair, different letters denote a significant difference ($P < 0.05$) between threshold means.

No significant difference in orthonasal benzaldehyde thresholds was observed when holding water in the mouth, ruling out the effect of any other stimuli other than the presence of saccharin.

Experiment 2

Due to availability, three panellists from the original panel did not take part in this experiment. Delivery in this experiment was asynchronous with first taste and then retronasal stimulus delivery (Figure 1). Figure 2 highlights the overall results and it is notable that detection thresholds were higher when determined retronasally (compare with experiment 1). The ANOVA revealed that there was no significant difference within the panel ($P = 0.11$) and the *t*-test indicated that no significant difference between grand means of threshold obtained for benzaldehyde alone and in combination with saccharin ($P = 0.45$).

Experiment 3

Only panellists demonstrating an enhancement effect in experiment 1 participated in this experiment. Delivery in this experiment was asynchronous with taste first followed by orthonasal stimulus delivery (Figure 1). Overall results for experiment 3 are highlighted in Figure 2. The ANOVA revealed that there was no significant difference within the panel ($P = 0.69$) and *t*-test indicated that there was no significant difference between grand means of thresholds obtained for benzaldehyde alone or in combination with saccharin ($P = 0.41$).

Experiment 4

Delivery in this experiment was synchronous but with retronasal odour delivery (Figure 1). Panellists were selected from those demonstrating enhancement effects in experiment 1. The results from experiment 4 are highlighted in Figure 2 alongside experiment 2 for comparison. ANOVA indicated some significant differences between panellists ($P = 0.04$). No significant difference existed between the two benzaldehyde thresholds. However, looking at the ratios four of the six panellists did show a significant reduction ($P = 0.002$) in benzaldehyde threshold in the presence of 50% of threshold saccharin solution. This reduction (and lack of a reduction in the remaining panellists) was consistent across replicates.

Discussion

Using specific spatial and temporal manipulations, this study investigated the role of location and timing on the integration of taste and odour inputs. Variations in detection threshold for a volatile compound (benzaldehyde) when experienced alone or with a sub-threshold solution of a tastant (saccharin) were compared as a function of combination mode. This approach is particularly suitable to understand the mechanisms underlying perceptual taste–odour interactions. Some researchers have suggested that taste-induced odour enhancement may often be due to the response context and the strategy adopted by the panellists (Frank *et al.*, 1993; Clark and Lawless, 1994). When the panellists are presented with a complex stimulus eliciting various sensory sensations and asked to rate only one of these attributes, they may include the intensity of other stimulus components in their intensity judgement. The panellist's estimate may also be influenced by confusion between senses (Rozin, 1982). Because the panellists are unable to attend to the taste stimulus (presented at sub-threshold level), the present testing methodology rules out these response biases. The results obtained are more likely to suggest that the interaction happens at an involuntary level.

Experiment 1 yielded comparable results to that of Dalton *et al.* (2000) and in our experiment, for 12 of the panellists, the benzaldehyde threshold with a 50% threshold level saccharin solution in mouth was 50% lower than the threshold obtained alone, thus demonstrating complete additivity. For 4 panellists, the presence of saccharin had no significant effect on the sensitivity to benzaldehyde. Although the latter could reflect random variation, it is also possible that other factors may influence the occurrence of the integration effect. Taste–odour interactions are highly dependent on learned associations which are acquired as a result of repeated pairing of a taste and an odour when experiencing foods and beverages (Kuo *et al.*, 1993; Stevenson *et al.*, 1995, 1999). Dalton *et al.* (2000) showed that, as opposed to almond and sweetness, integration between non-congruent pairs (almond and umami taste) did not occur. However, Breslin *et al.* (2003), using the same protocol, further observed that congruency and integration might be achieved through

repeated exposure. Therefore the lack of any integration effect could be due to unfamiliarity with this taste aroma pair. The difficulty of the task could be a disrupting factor but it should pointed out that the panellists have been similar experiences of a range of different sensory tests over the past four years.

In experiment 2 significantly higher odour threshold values were obtained retronasally. This is in agreement with Voirol and Daget (1986) who observed higher thresholds retronasally compared to sniffing the headspace from solution, and more recently with Heilmann and Hummel (2004) who obtained analogous results using precise control of the retronasal odour presentation. This supports the concept that significant differences exist between ortho- and retronasal perception of odours, an idea first expressed by Rozin (1982). In parallel, these two modes of stimulation also differ in the manner they interact with gustatory signals. In the combination condition, no improvement in sensitivity to benzaldehyde was found when the odour was delivered retronasally. This cannot be explained by the difficulty of the task as swallowing is easier and more natural for the panellist than holding/sniffing. There is evidence that spatial concordance is a key factor determining whether or not taste and smell cues are integrated. Inhibition in cortical sensory areas has been found when presenting odours orthonasally with tastants in mouth (Small *et al.*, 1997); however, an increase in brain activity in the sensory areas of the cortex was obtained with retronasal olfaction (De Araujo *et al.*, 2003). This indicates that the brain may process information from ortho- and retronasal routes differently in the presence of a tastant. Our first experiment showed that integration was achieved when presenting the stimuli from two separate locations (mouth and nose). Therefore it could have been assumed that similar, or even better results, would be obtained when presenting both stimuli in the mouth. However, in fMRI studies, the effect of swallowing is not taken into account. It is more likely that the temporal asynchrony induced by swallowing eliminated the enhancement effect. Consequently, we postulated that the delay between the odour and the taste sensations would prohibit the formation of the necessary brain pattern for an integration of the two signals.

Experiments 3 and 4 were designed to further investigate this hypothesis by removing or generating temporal synchrony between the taste and the smell sensations. The modifications did not create a major disturbance to the panel's performance as the same range of threshold values was obtained for experiments 1 and 3 and for experiments 2 and 4. The enhancement effect obtained in Experiment 1 was eliminated when the panellists spat out the saccharin solution before sniffing (Experiment 3, 11 panellists). Although, no overall effect was observed in Experiment 4, an enhancement effect was observed for four of the six assessors when swallowing half of the solution (odour sensation) and keeping the other half in mouth (taste sensation) allowing simultaneous timing. This was consistent across replicates. With such a small panel firm conclusions are not possible but a comparison of results from Experiments 1 and 3 and from Experiments 2 and 4 illustrates that temporal coincidence is a factor for multisensory integration in flavour perception. If the tastant signal is not presented simultaneously in combination with the odour signal, no taste-induced odour enhancement occurs.

The phenomenon described by Dalton *et al.* (2000) either appears or disappears depending on the particular consumption condition applied. In a real-life situation (e.g. consuming a beverage) taste–odour interactions will only occur if there is residual tastant in-mouth after swallowing at a concentration that is sufficient to elicit a taste–aroma interaction. Careful attention is needed before the generalization of taste–odour interactions observed in experiments such as Dalton *et al.* (2000) to the investigation of taste–aroma interactions under standard eating conditions. The combined data from these experiments clearly illustrates that temporal synchrony represents the main constraint. It is possible that there is a specific temporal window for the achievement of taste–smell integration. However, although temporal coincidence is a necessary condition for some panellists, for others (who show no integration) it is irrelevant. This may suggest that taste–odour interactions are dependent on the subject's previous experience. The structure of the neural network leading to multisensory integration may be closely linked to repetitive exposure to the co-occurrence of taste/smell combinations.

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