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The role of congruency in retronasal odor referral to the mouth

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Abstract

Referral of retronasal odors to the mouth is a fundamental phenomenon of flavor perception. A previous study from this laboratory provided evidence that, contrary to prior speculation, taste rather than touch was the primary factor in retronasal odor referral. The present study further investigated this question by studying the role of congruency between taste and odor on retronasal odor referral under conditions that mimicked natural food consumption. Subjects performed odor localization tasks after sampling gelatin stimuli that contained various congruent and incongruent tastes–odor combinations. The results showed that when a congruent taste was added, referral to the oral cavity and tongue were significantly enhanced. In addition, the data also indicate that the degree of congruency between taste and odor may modulate the degree of odor referral to the mouth. These findings suggest that odor referral is maximized when congruent flavor dimensions are combined to trigger perceptual "flavor objects" that represent known or potential foods. The results are discussed in terms of the factors that play a role in the retronasal odor referral as well as the potential neural mechanisms that may underlie it.

Key words: congruency, flavor binding, localization, odor referral, retronasal odor, sensory processing, tactile stimulation, taste

Introduction

Referral of retronasal odors to the mouth has long been recognized as a fundamental phenomenon of flavor perception (Titchener 1909; Hollingworth and Poffenberger 1917). Although little is known about the sensory mechanisms that underlie it, the prevailing hypothesis has always been that retronasal odor referral is mediated by the sense of touch (Hollingworth and Poffenberger 1917; Murphy and Cain 1980; Rozin 1982). For example, Hollingworth and Poffenberger (1917, p. 13–14) suspected that retronasal odors are referred to tastes largely because of "the customary presence of sensations of pressure, temperature, movement, and resistance which are localized in the mouth and in the organ of taste." Murphy and Cain (1980) later refined this speculation by suggesting that "the trigeminal system may serve to bind the anatomically and physiologically distinct olfactory and taste systems into a single perceptual system during eating." Such speculation has been further supported by evidence that tactile stimulation has a special capacity to "capture" the sensations of other modalities, such as warmth or cold (Green 1977, 1978) and taste (Todrank and Bartoshuk 1991; Green 2002; Lim and Green 2008). Despite the long history of speculation about the role of touch, no studies have investigated potential mechanisms of retronasal odor referral to the mouth, in part because the components of a flavor (i.e., taste, retronasal odor, and tactile sensations) cannot be easily separated in a controllable manner.

Recently, we developed psychophysical methods that allowed us to simultaneously deliver retronasal odors in the presence or absence of taste and/or tactile stimulation and further to quantify the perceived locations and degree of referral under such conditions (Lim and Johnson 2011). In that study, subjects were asked to report the location of perceived odors when a vanilla or soy sauce odor was presented retronasally alone or in the presence of water in the mouth or water with various tastants. Interestingly, when perceived "alone" by inhaling the odor through a straw and exhaling through the nose, the odors were localized remarkably often to the oral cavity and the tongue, accounting for about 40–45% of total localizations. This result was surprising given that there was no taste or tactile stimulation that could capture the odor into the mouth. What was even more surprising was that the presence of water (tactile stimulation) in the mouth did not increase the degree of retronasal odor referral to the mouth. This finding suggested that, contrary to the long-standing speculation (Hollingworth and Poffenberger 1917; Murphy and Cain 1980; Rozin 1982), somatosensory stimulation itself may not be sufficient to cause odor referral to the mouth. Instead, the presence of a congruent taste (i.e., a taste that commonly appears with and thus is highly associated with an odor in a food) significantly increased retronasal odor referral to the mouth, primarily to the tongue.

Given the fact that tactile stimulation seems to be able to capture the sensations of other modalities, it is surprising that such an effect does not occur for olfactory stimulation. One potential explanation could be found from the fact that, unlike during natural tasting, in the previous study, the flavor components were teased apart and delivered separately instead of as a single unity (i.e., odorants were presented in vapor phase by inhaling and exhaling the headspace of the odor solution using a straw while water [tactile stimulation] or tastants were pipetted on to the tongue). The present study was conducted, therefore, to further rule out somatosensory stimulation as the primary factor in retronasal odor referral under normal eating conditions, that is, when both tastants and odorants are released from a food matrix that simultaneously produces tactile stimulation. We hypothesized that the presence of a congruent tactile stimulation (i.e., an appropriate food texture) would increase odor referral to the mouth. The current study also provided an opportunity to test further the role of congruency between odors and tastes on retronasal odor referral. Because the previous study used the odorants that are congruent with sweet and salty tastes (vanilla and soy sauce odors; Lim and Johnson 2011), the current study employed odorants which are potentially congruent with sour and savory tastes. Because foods and beverages are often complex, containing more than one taste quality, we also included a binary taste mixture, which closely mimics a familiar food source. We accordingly hypothesized that the degree of retronasal odor referral would vary depending on the degree of congruency between tastes and odors. Thus, the present study aims to further determine the conditions that are necessary for retronasal odor referral to occur and thus to fully understand the underlying mechanisms of flavor integration process.

Methods

Subjects

A total of 22 subjects (13 females and 9 males) between 20 and 48 years of age (mean = 27 years old) were recruited on the Oregon State University campus and were paid to participate. All were nonsmoking and nonpregnant individuals who were free from deficits in taste and smell by self-report. Subjects were asked to refrain from eating/drinking for at least 1 h prior to their scheduled session and from using menthol products on the morning of testing. They were also asked to avoid eating hot and spicy food for at least 24 h before testing. The experimental protocol was approved by the Oregon State University Institutional Review Board, and subjects gave written informed consent.

Odor and taste stimuli

Two odorants were used in the experiment: 0.00125% (v/v) citral (Alfa-Aesar) and 0.00025% (v/v) chicken odor (Givaudan Flavors Corporation). Each odorant was presented in a gelatin alone, with one of 5 tastants (0.32 M sucrose [J.T. Baker], 5.6 mM citric acid [Sigma-Aldrich], 0.18 M sodium chloride [NaCl, J.T. Baker], 0.1 mM quinine hydrochloride [QHCl, Alfa-Aesar], and 56 mM monosodium glutamate [MSG, Fisher Scientific]) or with a binary taste mixture that was presumed to be the most congruent pair for each odorant (0.32 M sucrose + 5.6 mM citric acid for citral, and 0.18 M NaCl + 56 mM MSG for chicken odor). The concentrations of the stimuli were chosen based upon pilot testing results, which showed that the concentrations of the odorants were sufficient to evoke distinct retronasal odors in a gelatin matrix and that the concentrations of the five tastants were approximately equi-intense. A commercially available peach-flavored gelatin (Jell-O, Kraft Foods) was also used for the practice trial (see below).

Gelatin disks

Gelatin samples were made by dissolving the odorants in the absence or presence of tastants in the gelatin stock solution, which was prepared by mixing 113.4 g of unflavored gelatin powder (Knox gelatin, Kraft Foods) in 1 L of deionized water. For the practice samples, one package of sweetened peach-flavored gelatin powder was dissolved in 1 L of deionized water. The liquid form of the gelatin stimuli were poured in 5-mL aliquots into 1-oz medicine cups, covered with lids, and stored at 4–6 °C to set. The test stimuli were then kept at room temperature (22 ± 1 °C) for an hour prior to the testing session. Gelatin disks (3 cm diameter and 1 cm height) were unmolded prior to delivery to the subject on a per-trial basis by placing the portion cup in a warm water bath (37 ± 0.5 °C) for 5 s.

Experimental procedures

Each subject participated in two 30-min sessions separated by at least 24 h. Prior to the data collection session, all subjects were initially given instructions on the localization task, followed by a practice trial. On each trial, the subject was asked to open his/her mouth and to turn the provided sample cup upside down such that the top of the unmolded gelatin disk would be placed on the top of his/her anterior tongue. Once the gelatin disk was in contact with the tongue, the subject was asked to close his or her mouth and begin to chew the sample for 5 s. The subject was also told not to swallow or to discontinue breathing during this time. After the 5 s, the subject was asked to expectorate the gelatin sample. The subject's task was to verbally report the locations where he or she perceived the "peach" odor by consulting an oral and nasal cavity map (Figure 1) that included 1) the nose, 2) the throat, 3) the oral cavity, 4) the tongue, and 5) the gelatin object. It was emphasized that the peach odor might be perceived at one location, multiple locations, or not at all and that the decision should be made before expectorating the stimulus. It was also emphasized that the task was to report where the peach odor was perceived but not other sensations such as sweet, sour, salty, or bitter taste. However, no specific information was provided regarding the differences between tastes and smells in general and/or how taste and odor stimuli would be delivered during the procedure.

Following the practice trials, each subject received 7 test trials for each odorant separated by 2 testing blocks (i.e., citrus and chicken block). The subject's task was again to report the locations where he or she perceived "citrus" or "chicken" odor in the absence and presence of tastes. A gelatin disk containing only the odorant was utilized as a control condition. The subject was asked to rinse with deionized water (37 ± 0.5 °C) at least 3 times during the 1-min intertrial intervals. After completing 7 trials of the localization task for one odorant, there was a 5-min break during which the subjects rinsed vigorously with deionized water. After the 5-min break, another block of 7 trials of the localization task were completed for the other odorant. To obtain replicate measurements, each subject returned to the laboratory for the second session and performed the localization tasks following the same testing procedure but in a different random order. The presenting order of the 2 odorants was counterbalanced across the 2 testing sessions for each subject and the presenting order of the 7 trials under each odorant was completely randomized.

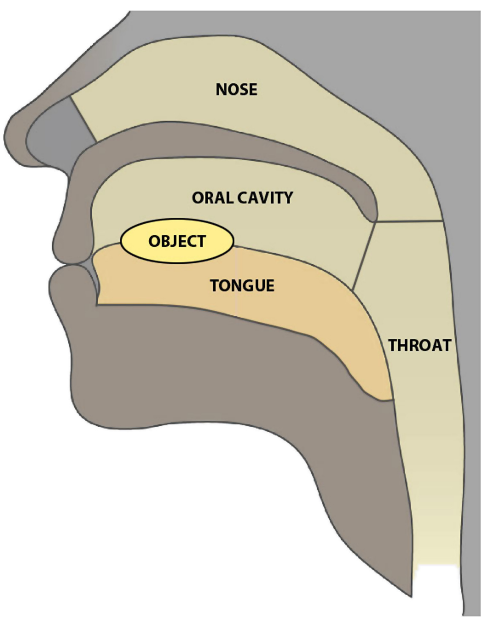

Figure 1 The oral and nasal cavity map. The subjects consulted this diagram while they performed the localization tasks.

Data analysis

Frequency counts of odor localizations to the nose, throat, oral cavity, tongue, and gelatin object were determined for each odor–control and odor–taste pair. Note that total frequency responses varied across odor–control and odor–taste pairs because the subjects were allowed to report multiple locations, a single location, or no location at all for any given test pair. Also note that the odors were rarely localized to the throat and gelatin object (see Tables 1 and 2), and therefore, the frequency counts for these regions were not further considered for the statistical analysis. The frequency responses for the 3 locations (i.e., nose, oral cavity, and tongue) were then analyzed for statistical significance using a 2-tailed chi-square test (O'Mahony 1985). To test the effect of taste stimulation on odor referral, the frequency counts for each odor–taste pair (i.e., the observed values) were compared against those of the odor–control pair (i.e., the expected values). The statistical tests were conducted for the data from each replicate (see Tables 1 and 2) as well as the averaged counts across replicate measurements (see Figures 2 and 3). All statistical analyses were conducted with Statistica 8.0 (StatSoft Inc.).

Table 1 Frequency counts from the odor localization task for each citral-alone and citral–taste pair

	Odor alone	Sucrose[a]	Citric acid[a]	NaCl[a]	QHCl[a]	MSG[a]	Sucrose + CA[a]
Replicate 1							
Throat[b]	0	0	2	1	1	0	2
Gelatin object[b]	0	0	0	0	0	1	0
Nose	13	6	7	9	9	6	5
Oral cavity	7	13	9	7	9	7	14
Tongue	7	15	15	4	10	1	18
Chi square		**18.05**	**12.48**	2.52	3.09	**8.91**	**29.21**
P value		**<0.001**	**<0.01**	0.28	0.21	**<0.05**	**<0.00001**
Replicate 2							
Throat[b]	2	2	2	1	0	2	2
Gelatin object[b]	0	0	0	0	0	0	0
Nose	13	11	8	5	11	6	10
Oral cavity	8	10	9	8	8	5	15
Tongue	6	17	11	5	8	5	21
Chi square		**20.97**	**6.21**	5.09	0.97	5.06	**44.32**
P value		**<0.0001**	**<0.05**	0.08	0.61	0.08	**<0.00001**

[a]The frequency counts for each citral–taste pair were compared with those for citral-alone pair.
[b]The frequency counts for the throat and gelatin object were not included for the chi-square tests due to subject's rare usage.

Results

Citrus odor

As shown in Table 1, the statistical results for the 2 replicates were very comparable, indicating that the subjects' responses for the localization task were statistically reliable. The averaged results of the localization task across replicates are shown in Figure 2. When citral was presented alone in a gelatin matrix, the citrus odor was localized 48.1%, 27.8%, and 24.1% (of total frequency counts) in the nose, oral cavity, and on the tongue, respectively. The presence of a congruent taste (sucrose or citric acid), but not an incongruent taste (NaCl, QHCl, or MSG), significantly increased localization of the citrus odor to the oral cavity and tongue (chi square = 17.58 and 9.13 for sucrose and citric acid, respectively; degrees of freedom [df] = 2; $P < 0.05$). The addition of a congruent taste mixture (sucrose + citric acid) to a citrus-flavored gelatin even more dramatically increased localization of the citrus odor to the oral cavity and tongue (chi square = 34.86; df = 2; $P < 0.0001$: percentage localizations were 18.1%, 34.9%, and 47.0% [of total average frequency counts] in the nose, oral cavity, and on the tongue, respectively).

Table 2 Frequency counts from the odor localization task for each chicken-alone and chicken–taste pair

	Odor alone	Sucrose[a]	Citric acid[a]	NaCl[a]	QHCl[a]	MSG[a]	NaCl + MSG[a]
Replicate 1							
Throat[b]	2	1	1	1	1	4	5
Gelatin object[b]	0	0	0	0	0	0	0
Nose	12	7	4	4	4	7	10
Oral cavity	7	6	12	17	7	13	20
Tongue	6	12	15	14	6	16	18
Chi square		**8.23**	**22.41**	**30.29**	5.33	**23.89**	**48.48**
P value		**<0.05**	**<0.0001**	**<0.00001**	0.07	**<0.00001**	**<0.00001**
Replicate 2							
Throat[b]	1	1	1	1	1	3	3
Gelatin object[b]	0	1	0	0	0	0	0
Nose	13	3	8	6	10	8	8
Oral cavity	10	8	5	10	9	12	17
Tongue	4	11	11	16	3	15	20
Chi square		**20.34**	**16.67**	**39.77**	1.04	**32.57**	**70.82**
P value		**<0.0001**	**<0.001**	**<0.00001**	0.59	**<0.00001**	**<0.00001**

[a]The frequency counts for each chicken–taste pair were compared with those for chicken-alone pair.
[b]The frequency counts for the throat and gelatin object were not included for the Chi-square tests due to subject's rare usage.

Chicken odor

Another set of data using chicken as the test odor (see Figure 3) also showed a very similar trend as citral. When the odorant was presented alone in a gelatin disk, the chicken odor was localized 48.1%, 32.7%, and 19.2% (of total frequency counts) in the nose, oral cavity, and on the tongue, respectively. The frequency counts reported for the chicken

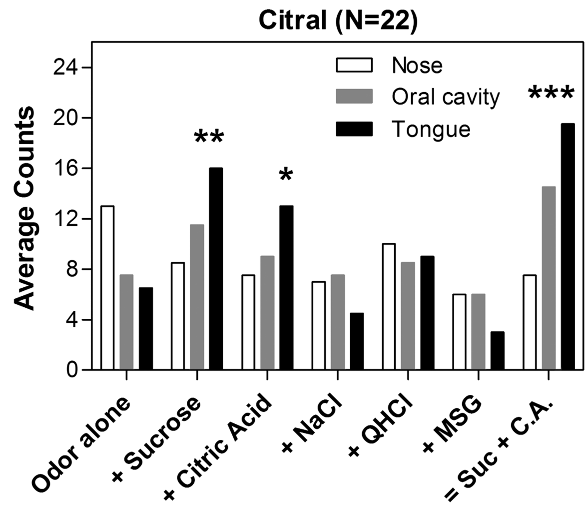

Figure 2 Averaged frequency responses for the odor localization tasks for each citral-blank or citral–taste pair. Note that the subjects were allowed to report none, one location, or multiple locations for each test pair, and thus, the total frequency counts across the test pairs are not exactly the same. The frequency responses for each citral–taste pair were compared with those for citral-blank pair by a 2-tailed chi-square test. The asterisk indicates a significant difference (**P* < 0.05, ***P* < 0.01, ****P* < 0.0001).

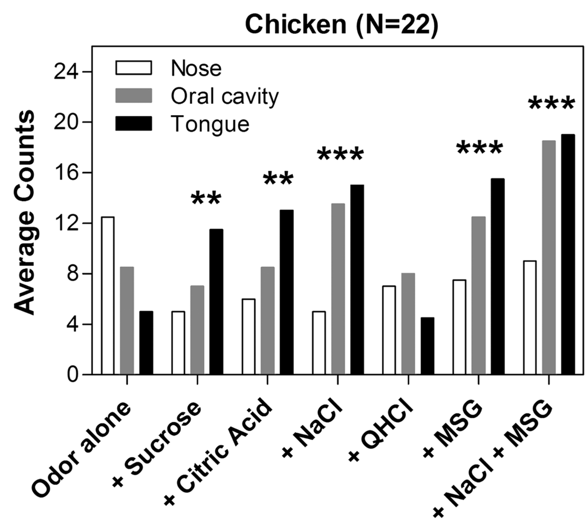

Figure 3 Averaged frequency responses for the odor localization tasks for each chicken-blank or chicken–taste pair. Note that the subjects were allowed to report none, one location, or multiple locations for each test pair, and thus the total frequency counts across the test pairs are not exactly the same. The frequency responses for each chicken–taste pair were compared with those for chicken-blank pair by a 2-tailed chi-square test. The asterisk indicates a significant difference (**P* < 0.05, ***P* < 0.01, ****P* < 0.0001).

odor in the presence of QHCl, an incongruent taste, were not significantly different (chi square = 2.50; df = 2; $P > 0.05$) from when no taste was presented in the gelatin disc (the tactile control). However, the presence of other tastes significantly increased localization of the chicken odor to the oral cavity and tongue to varying degrees (chi square = 13.21, 16.18, 27.44, and 25.93 for sucrose, citric acid, NaCl, and MSG, respectively; df = 2; $P < 0.01$). The results also indicated that when a congruent taste mixture (NaCl + MSG) was added to the chicken odor in a gelatin, the chicken odor was reported to be perceived significantly more in the oral cavity and on the tongue (19.3%, 39.8%, and 40.9% of total average counts for nose, oral cavity, and tongue, respectively). Again, note that the statistical results for each replicate were also comparable (see Table 2). Combined together, these results suggest that when flavor components (i.e., taste, odor, and tactile stimulation) are congruent to each other, the specific food odor is referred more often to the oral cavity and especially to the tongue and that the degree of referral to the mouth depends on the degree of congruency between the odor and taste.

Discussion

The role of congruent tastes on retronasal odor referral

The present results reinforce and extend our recent findings (Lim and Johnson 2011), which indicated that the congruency between tastes and odors plays an important role in retronasal odor referral to the mouth. In the previous study, subjects performed odor localization tasks when food odors were inhaled through a straw and exhaled through the nose in the absence and the presence of water or various tastants in the mouth. The results showed that vanilla and soy sauce odors were localized on the tongue significantly more often when sucrose and NaCl, respectively, but not other tastes, were presented simultaneously in the mouth. The results of the present study, which employed a more natural food tasting condition, also indicate that the presence of a congruent taste significantly augments retronasal odor referral to the mouth. When sampled with citric acid, sucrose, or the mixture of sucrose and citric acid, citrus odor was localized on the tongue 2, 2.5, and 3 times more often than when it was sampled alone in a gelatin matrix (see Figure 2). In the case of chicken-flavored gelatin (see Figure 3), the presence of all single tastants (sucrose, citric acid, NaCl, and MSG) with the exception of quinine, as well as the binary mixture of NaCl and MSG, significantly increased odor referral to the tongue. Although we did not expect that the addition of sucrose or citric acid would increase the referral of chicken odor to the tongue, some subjects reported that sweet- and sour-tasting gelatin reminded them of consuming honey and sour chicken dishes. More interestingly, the degree of odor localization to the tongue varied considerably across the odor–taste pairs. For example, 19 out of 22 (86%) subjects reported the chicken odor being received on the tongue when the mixture of NaCl and MSG was added to a chicken gelatin. In contrast, only 11–13 out of 22 (52–59%) subjects localized chicken odor to the tongue when they sampled sweet- or sour-tasting chicken gelatin (see Figure 3). In addition, the localization of odors in the oral cavity was also significantly augmented for some odor–taste combinations—primarily those that contained the binary taste mixtures which closely mimic a familiar food source (e.g., a lemony gelatin dessert, a piece of chicken). Together, these results confirm the earlier finding (Lim and Johnson 2011) that retronasal odor referral to the mouth depends strongly on the presence of a congruent taste. Moreover, the current data suggest that the degree of congruency between tastes and odors modulates the degree of retronasal odor referral to the oral cavity and tongue. This hypothesis is currently being investigated by directly comparing congruency ratings between tastes and odors to the degree of odor referral to the mouth.

The role of tactile stimulation on retronasal odor referral

The current data also confirm and extend the previous finding that the presence of somatosensory stimulation itself is not sufficient to cause retronasal odor referral to the mouth (Lim and Johnson 2011). The results from the earlier study showed that the frequency counts for a retronasal odor when it was perceived alone were not significantly different from those when water (tactile stimulus) was in the mouth. This finding was in conflict with the long-standing speculation that odor referral may be mediated through tactile stimulation (Hollingworth and Poffenberger 1917; Murphy and Cain 1980; Rozin 1982). However, no concrete conclusions could be made based on the earlier finding because the psychophysical paradigm used in the earlier study did not represent a normal eating/drinking circumstance, that is, the components of the flavors were teased apart and presented separately. In the current study, we hypothesized that the presence of natural tactile stimulation in a food would enhance the degree of retronasal odor referral to the mouth. In addition, we anticipated that some subjects might even localize the odor to the ‘‘gelatin object’’ placed in the mouth (see Figure 1). Yet again, however, the data did not support our hypotheses: almost no subjects localized retronasal odors to the gelatin object (see Tables 1 and 2). Furthermore, the retronasal odors were localized in the nose at a similar rate (~50% of total localization) when tasteless tactile stimulation was presented simultaneously, whether it was presented as a separate entity (water in the previous study) or as a food substance (a tasteless gelatin disk in the current study). Overall, these 2 sets of data imply that tactile stimulation itself is not a primary factor in retronasal odor referral to the mouth. Nevertheless, the fact that gustatory stimulation cannot be achieved without touch raises the possibility that tactile stimulation may contribute indirectly to retronasal odor referral to the mouth. This possibility is supported by the evidence that taste sensations can be referred to accompanying tactile stimulation (Todrank and Bartoshuk 1991; Green 2002; Lim and Green 2008). It is yet to be seen whether variations in tactile stimulation can affect the degree of retronasal odor referral and more broadly whether incongruent tactile stimulation can disrupt or circumvent integrative mechanisms between tastes and odors.

Potential mechanisms of flavor binding

The evidence that retronasal odor referral to the mouth is significantly enhanced by the presence of a congruent taste raises the fundamental question of how sensory inputs from the 2 anatomically distinct organs of mouth and nose are integrated to cause such an "illusion" (Murphy et al. 1977; Murphy and Cain 1980; Rozin 1982; Prescott 1999). Although the neural mechanisms for the integration process are largely unknown, the results from the current study in conjunction with those from the previous study (Lim and Johnson 2011) provide compelling evidence that the congruency between tastes and odors plays an important role in so-called "flavor binding" (Stevenson 2009; Small and Green 2011). It has been proposed that when flavor components are congruent, the qualities of taste and smell fuse (McBurney 1986; Auvray and Spence 2008) into a unified, harmonious percept. This higher order, presumably cortical binding mechanism may be based upon the proximity of the encoded neural pattern to the pattern of a known flavor object, which may also include its tactile and thermal dimensions. In other words, perceptual binding would occur when the encoding of neural activities of a test stimulus match with that of a known flavor object. Thus, the more congruent the flavor components are (or the more similar the flavor percept to a known flavor concept) the more readily flavor binding may occur. In support of this view, several authors have proposed the existence of an object-based flavor system (Gibson 1966; Small and Prescott 2005; Auvray and Spence 2008; Small and Green 2011), although the hypothesized system or mechanisms have not been directly tested. Also consistent with this view is the evidence that congruency between tastes and odors is learned (Stevenson et al. 1995, 1998; Prescott 1999; Prescott et al. 2004), which means associative learning may play an important role in the development and thus the recognition of a flavor object. A series of experiments that address the latter question is underway. Whether the hypothesis about associative learning turns out to be true or not, the notion of odor referral to the mouth demonstrates that as much as olfaction and gustation are anatomically separate systems, they are functionally united to perform their shared role of detecting and selecting potential foods (Gibson 1966).

A related question is why the retronasal odor is perceived as though it is sensed in the mouth instead of in the nose. As mentioned above, it has long been speculated that odor referral may be mediated through cutaneous stimulation (Hollingworth and Poffenberger 1917; Murphy and Cain 1980; Rozin 1982) in a way similar to the illusory referral of warmth and cold to the locus of an accompanying tactile stimulus (Green 1977, 1978). However, our data suggest that tactile stimulation does not capture retronasal odors. It appears instead that when perceptual components approximate a known food, they are recognized as a coherent, unitary percept and further that the unified flavor percept is projected to the mouth area. In support with the latter view, the data from a neuroimaging study by Small et al. (2005) showed indirect evidence that flavor binding may occur in the somatomotor mouth area of the cortex. In that study, odorants were delivered as vapors via both ortho- and retronasal routes and brain response was measured using functional Magnetic Resonance Imaging. Comparison of ortho- versus retronasal delivery produced preferential activity during retronasal delivery at the base of the central sulcus, a brain region which is responsive to oral cavity somatosensory stimulation in humans (Pardo et al. 1997; Yamashita et al. 1999; Boling et al. 2002). Although the neural mechanisms of flavor binding need to be investigated further, the current data suggest that flavor binding depends strongly on the congruency between flavor components.

Related studies to be considered

It is notable that parallel to our studies on retronasal odor referral to the mouth, Stevenson, Mahmut, and Oaten (2011) and Stevenson, Oaten, and Mahmut (2011) have reported conditions in which the origin of orthonasally perceived odors can be confused. In their studies, they found that somatosensory stimulation alone, instantiated by changes in viscosity and oral movement, is rather ineffective at generating the confusion of odor sources but that the presence of a taste in the mouth causes confusion of the origin of orthonasally perceived odors. Although these results seem to be broadly in line with our previous (Lim and Johnson 2011) and current findings, there are substantial differences between the studies from the 2 laboratories. First, because Stevenson and others were interested in understanding the factors that govern what they termed "location binding" of orthonasal olfaction, the subject's task in their studies was to identify the "source" of the odor (i.e., 1, odor jar; 4, unsure; 7, mouth) rather than the "perceived location" of odor sensations in the oronasal cavity. Second, whereas our results have clearly demonstrated that congruency between tastes and odors is the key factor that causes retronasal odor referral to the mouth, their results suggest that congruency has no impact on identification of the odor source. Instead, they concluded that any salient feature of taste—often unpleasant or irritating in nature—commands "attention" to the mouth at the expense of olfaction; similarly, when an odor component becomes more attention demanding (e.g., judged as less pleasant than a taste in the mouth), this serves to attract attention to the olfactory channel with reduced confusion of the odor source. Finally, the implications of these 2 phenomena are different; although retronasal odor referral is a fundamental feature of flavor perception during eating and drinking, it is unclear how confusing the source of orthonasally smelled odors in the presence of any taste in the mouth contributes to normal flavor perception.

Summary

In conclusion, our previous study (Lim and Johnson 2011) and the present one together provide compelling evidence of the key sensory and cognitive factors that underlie retronasal odor referral to the oral cavity and tongue. First, whether taste and tactile stimulation are present in the mouth or not, odors are referred to the mouth area when food odors reach the olfactory epithelium via the retronasal route (Lim and Johnson 2011). This result is consistent with a prior study (Small et al. 2005) that varied only the direction of airflow (ortho- vs. retronasal stimulation) in the nose. Second, the presence of tactile stimulation itself is not sufficient to enhance the retronasal odor referral. Instead, it is the congruency of flavor components (principally the tastes and odors) that significantly augments odor referral to the mouth. These findings, coupled with neuroimaging data (Pardo et al. 1997; Yamashita et al. 1999; Boling et al. 2002; Small et al. 2005), lead to the conclusion that odor referral is a product of a flavor-binding mechanism, which occurs when taste and retronasal olfactory components approximate known foods. When flavor binding occurs, the resulting unified percept is projected to the mouth area, leading to the well-known sensory confusion between taste and retronasal olfaction (Titchener 1909; Murphy and Cain 1980; Rozin 1982). In this sense, odor referral to the mouth may be seen as a manifestation of flavor integration and further that the degree of odor referral may be considered as the proximity to a flavor object.

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References

Auvray M, Spence C. 2008. The multisensory perception of flavor. Conscious Cogn. 17:1016–1031.

Boling W, Reutens DC, Olivier A. 2002. Functional topography of the low postcentral area. J Neurosurg. 97:388–395.

Gibson JJ. 1966. The senses considered as perceptual systems. Boston: Houghton Mifflin.

Green BG. 1977. Localization of thermal sensation: an illusion and synthetic heat. Percept Psychophys. 22:331–337.

Green BG. 1978. Referred thermal sensations: warmth versus cold. Sens Processes. 2:220–230.

Green BG. 2002. Studying taste as a cutaneous sense. Food Qual Prefer. 14:99–109.

Hollingworth HL, Poffenberger AT. 1917. The sense of taste. New York: Moffat, Yard and Company.

Lim J, Green BG. 2008. Tactile interaction with taste localization: influence of gustatory quality and intensity. Chem Senses. 33:137–143.

Lim J, Johnson MB. 2011. Potential mechanisms of retronasal odor referral to the mouth. Chem Senses. 36:283–289.

McBurney DH. 1986. Taste, smell and flavor terminology: taking the confusion out of confusion. In: Meiselman HL, Rivkin RS, editors. Clinical measurement of taste and smell. New York: Macmillan. p. 117–124.

Murphy C, Cain WS. 1980. Taste and olfaction: independence vs interaction. Physiol Behav. 24:601–605.

Murphy C, Cain WS, Bartoshuk LM. 1977. Mutual action of taste and olfaction. Sens Processes. 1:204–211.

O'Mahony M. 1985. Sensory evaluation of food: statistical methods and procedures. New York: Marcell Dekker, Inc.

Pardo JV, Wood TD, Costello PA, Pardo PJ, Lee JT. 1997. PET study of the localization and laterality of lingual somatosensory processing in humans. Neurosci Lett. 234:23–26.

Prescott J. 1999. Flavour as a psychological construct: implications for perceiving and measuring the sensory qualities of foods. Food Qual Prefer. 10:349–356.

Prescott J, Johnstone V, Francis J. 2004. Odor-taste interactions: effects of attentional strategies during exposure. Chem Senses. 29:331–340.

Rozin P. 1982. "Taste-smell confusions" and the duality of the olfactory sense. Percept Psychophys. 31:397–401.

Small DM, Gerber JC, Mak YE, Hummel T. 2005. Differential neural responses evoked by orthonasal versus retronasal odorant perception in humans. Neuron. 47:593–605.

Small DM, Green BG. 2011. A proposed model of a flavor modality. In: Murray MM, Wallace TW, editors. The neural bases of multisensory processes (frontiers in neuroscience). Boca Raton (FL): CRC Press. p. 717–738.

Small DM, Prescott J. 2005. Odor/taste integration and the perception of flavor. Exp Brain Res. 166:345–357.

Stevenson RJ. 2009. The psychology of flavour. New York: Oxford University Press.

Stevenson RJ, Boakes RA, Prescott J. 1998. Changes in odor sweetness resulting from implicit learning of a simultaneous odor-sweetness association: an example of learned synesthesia. Learn Motiv. 29:113–132.

Stevenson RJ, Mahmut MK, Oaten MJ. 2011. The role of attention in the localization of odors to the mouth. Atten Percept Psycho. 73:247–258.

Stevenson RJ, Oaten MJ, Mahmut MK. 2011. The role of taste and oral somatosensation in olfactory localization. Q J Exp Psychol. 64:224–240.

Stevenson RJ, Prescott J, Boakes RA. 1995. The acquisition of taste properties by odors. Learn Motiv. 26:433–455.

Titchener EB. 1909. A textbook of psychology. New York: Macmillan.

Todrank J, Bartoshuk LM. 1991. A taste illusion: taste sensation localized by touch. Physiol Behav. 50:1027–1031.

Yamashita H, Kumamoto Y, Nakashima T, Yamamoto T, Inokuchi A, Komiyama S. 1999. Magnetic sensory cortical responses evoked by tactile stimulations of the human face, oral cavity and flap reconstructions of the tongue. Eur Arch Otorhinolaryngol. 256(Suppl 1):S42–S46.