Food Quality and Preference 34 (2014) 5–13

Contents lists available at ScienceDirect

Food Quality and Preference

journal homepage: www.elsevier.com/locate/foodqual

The role of congruency in taste–odor interactions

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ARTICLE INFO

Article history:
Received 16 July 2013
Received in revised form 23 October 2013
Accepted 9 December 2013
Available online 14 December 2013

Keywords:
Congruency
Enhancement
Flavor
Referral
Retronasal odor
Taste

ABSTRACT

The present study investigated the role that congruency between tastes and odors plays in two types of taste–odor interactions: retronasal odor enhancement by taste and retronasal odor referral to the mouth. In the first experiment, subjects rated (1) the intensities of sweetness, sourness, bitterness, and specific odor of aqueous samples of 3 tastants (sucrose, citric acid, caffeine) and 2 odorants (citral, coffee odor), both alone and in taste–odor mixtures, and (2) the degree of congruency of all possible taste–odor pairs. The results showed that only sucrose significantly enhanced the perceived intensities of citrus and coffee odors (Tukey's test, $p < 0.05$), while citric acid and caffeine failed to enhance or even suppressed the odors. In the second experiment, the returning subjects were asked (1) to report the perceived locations of the odors after inhaling 3 odorants (citral, "sweet" and "bitter" coffee odors) through the mouth alone or in the presence of either water or various tastes in the mouth, and (2) to rate the degree of congruency between tastes and odors. The data showed that a highly congruent taste or taste mixture significantly increased localization of odors to the mouth (χ^2, $p < 0.05$). These findings suggest that taste–odor congruency is a necessary but not sufficient condition for retronasal odor enhancement. In contrast, taste–odor congruency is a critical component for retronasal odor referral, and the degree of congruency modulates the degree of odor referral to the mouth. The results and implications of the study findings are discussed in terms of cognitive and perceptual factors of flavor perception.

1. Introduction

Because gustation and olfaction are anatomically and physiologically distinct entities, taste and smell were considered as two modalities that may process the inputs independently of one another. However, there is mounting evidence that inputs of gustation and olfaction—retronasal olfaction in particular—interact closely with one another (see Delwiche, 2004 for perceptual evidence; Small, 2012 for neural evidence), supporting the existence of a unified perceptual system (Gibson, 1966) for perceiving objects in the mouth, i.e., flavor system. While we have only recently begun to understand the neural basis of taste–odor interactions, psychophysicists have long been searching for perceptual phenomena of and potential conditions for interactions between taste and retronasal odor.

The first psychophysical studies on such interactions can be traced to those of Murphy and Cain (1980), Murphy, Cain, and Bartoshuk (1977), who measured potential supra-additivity of perceived intensities of tastes and retronasal odors. Based on the findings that the intensity of taste–odor mixtures approximated the sum of the intensities of taste and odor alone, they concluded that there is no systematic interaction between the two modalities. The authors also recognized that subjects attributed a considerable degree of taste magnitude to solutions containing odors only. They interpreted this observation as retronasal odors being confused with tastes and thereby being mislocalized to the oral cavity. Murphy and Cain (1980) suggested that such an "illusion" might be mediated through cutaneous stimulation in a manner akin to the illusory referral of thermal sensations to the locus of an accompanying tactile stimulus (Green, 1978). Rozin (1982) later discussed that referral of retronasal odor to the mouth is an essential part of flavor perception. Meanwhile, Frank and Byram (1988) followed up the study of Murphy and Cain (1980) by reporting that certain odors could in fact enhance the intensity of tastes (e.g., sweetness of sucrose was enhanced by a strawberry odor but not by a peanut butter odor). However, Frank and his colleagues later discovered that taste enhancement by retronasal odor was significant only when the psychophysical rating task lacked a suitable response category for odor (Frank & Van der Klaauw, 1992; Frank, van der Klaauw, & Schifferstein, 1993). This finding was confirmed by Clark and Lawless (1994), who dubbed the effect of too few response categories on ratings of perceived intensity as 'dumping.' Taste enhancement by retronasal odor has since been reported by other researchers who explained the phenomenon as a result of perceptual interactions between taste and odor. Those include

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http://dx.doi.org/10.1016/j.foodqual.2013.12.002

perceptual similarity (Schifferstein & Verlegh, 1996), possession of taste-like qualities by odors (Stevenson, Prescott, & Boakes, 1999), and attentional strategy (i.e., synthetic vs. analytical) demanded in the tasks (Prescott, 1999; Prescott, Johnstone, & Francis, 2004; Prescott & Murphy, 2009). However, in most of these studies, subjects were not asked to rate both taste and odor intensity on every trial and thus potentially invited 'dumping.' Independently, other investigators reported enhancement of retronasal odor (often referred to as 'flavor') by tastes (e.g., Bonnans & Noble, 1993; Davidson, Linforth, Hollowood, & Taylor, 1999; McBride & Johnson, 1987), but yet again in nearly all of these experiments subjects were asked to rate only flavor or to rate the taste and flavor on separate trials.

In an effort to elucidate whether taste and retronasal odor interact, and if so, to what extent, we have recently followed up on the above-mentioned studies and reported conditions that produced two perceptual phenomena of taste–odor interaction: retronasal odor enhancement by taste (Fujimaru & Lim, 2013; Green, Nachtigal, Hammond, & Lim, 2012) and retronasal odor referral to the mouth (Lim & Johnson, 2011, 2012) (Note: for orthonasal odor referral, see Stevenson, Mahmut, & Oaten, 2011; Stevenson, Oaten, & Mahmut, 2011). To test the potential for enhancement, both taste by odor and odor by taste, we used a psychophysical procedure which offered subjects all possible response categories on every test trial (Green et al., 2012). The results showed that retronasal odor enhancement by taste was consistent and statistically significant, while taste enhancement by odor was inconsistent and generally weak. More interestingly, all test odor stimuli (i.e., citral, vanillin, furaneol, cherry odor) were selectively enhanced by sucrose but not by other tastes (i.e., citric acid, sodium chloride), suggesting that the presence of a congruent, nutritive taste might be a necessary condition for odor enhancement to occur. Concurrently, we also investigated the long-standing speculation that retronasal odor referral was mediated by tactile stimulation in the mouth (Murphy & Cain, 1980; Rozin, 1982) by employing a psychophysical method that allowed us to simultaneously deliver retronasal odors in the presence and absence of gustatory and/or tactile stimulation (Lim & Johnson, 2011). Our findings were rather surprising in that, contrary to the long-standing hypothesis, tactile stimulation itself did not seem to contribute to retronasal odor referral to the mouth. Instead, it was again the presence of a congruent, nutritive taste (i.e., sucrose for vanillin and sodium chloride for soy sauce odor) that increased the degree of odor referral to the mouth. These findings were confirmed by our follow-up study (Lim & Johnson, 2012), which tested the same hypothesis under normal eating conditions using an actual food matrix: the presence of an appropriate food texture did not increase retronasal odor referral, but a congruent taste or taste mixtures (e.g., sucrose, citric acid, and their mixtures for citral) significantly enhanced the degree of odor referral to the oral cavity and tongue.

Combined together, our recent findings suggest that the temporal and spatial co-occurrence of perceptually congruent tastes and odors (i.e., tastes and odors that are commonly experienced together in foods and thus have become associated) is a necessary condition for both retronasal odor enhancement by taste and retronasal odor referral to the mouth. Equally important, our most recent referral study (Lim & Johnson, 2012) suggested that the degree of congruency between tastes and odors might modulate the degree of odor referral to the mouth. However, in none of our studies was the degree of taste–odor congruency directly measured but the assumption was made that some pairs were congruent while others were not. The present study was therefore designed to test the congruency hypothesis by measuring the degree of congruency between taste and odor and directly comparing it to the degree of odor enhancement and odor referral to the mouth. The current study also provided an opportunity to further test the role of the nutritive status of taste on both phenomena. The fact that sucrose was the only taste stimulus which significantly enhanced retronasal odors (Fujimaru & Lim, 2013; Green et al., 2012) suggests that "nutritive" status of tastes (i.e., tastes that signal the presence of macronutrients) might also play an important role in the taste–odor interactions. This hypothesis was partially supported in the referral paradigm: in our first referral study (Lim & Johnson, 2011), subjects localized vanilla and soy sauce odors significantly more often when a congruent and nutritive taste (sucrose and sodium chloride, respectively) was delivered to the mouth. On the other hand, in the second referral study (Lim & Johnson, 2012) a non-nutritive taste (i.e., citric acid) was able to significantly increase odor referral to the mouth, albeit to a lesser degree than a nutritive taste (i.e., sucrose). Because our previous studies mostly used odors that are primarily congruent with a nutritive taste (sweet or salty), for the present study we used odors (citral and coffee odor) that are congruent with a non-nutritive taste, sour and bitter, respectively. Thus, the current study aims to determine the roles of congruency and nutritive vs. non-nutritive tastes in the interactions between taste and retronasal odor and to fully understand the underlying mechanisms of flavor integration process. Due to the inherent differences in the experimental schemes, the two perceptual phenomena were studied in two separate experiments.

2. Experiment I: odor enhancement

2.1. Materials and methods

2.1.1. Subjects

A total of 29 subjects (17 females and 12 males) between 18 and 45 years of age (mean = 25 years old) were recruited from the Oregon State University campus and the surrounding community. Individuals who were interested in participating in a flavor perception study were asked to fill out a screening questionnaire, which consisted of questions about general health and the consumption of various beverages. Subject inclusion criteria were: individuals who are (1) free from deficits in taste and smell; (2) not on any prescription medication; (3) not pregnant; (4) non-smokers; (5) free from food allergies; (6) fluent English speakers; and (7) familiar with coffee/coffee-flavored and lemon-flavored foods and beverages. Respondents who met all of the above criteria were invited to participate in the study. The subjects were further asked to refrain from consuming foods and beverages and using menthol products (e.g., toothpaste, mouthwash, chewing gums) for at least 1 h prior to their scheduled sessions. The experimental protocol was approved by the Oregon State University Institutional Review Board. Subjects gave informed consent and were compensated for their participation.

2.1.2. Stimuli

The experiment included a total of 11 test stimuli: 3 taste stimuli [0.56 M sucrose (Mallinckrodt Baker), 10 mM citric acid (Sigma–Aldrich), 5.6 mM caffeine (Sigma–Aldrich)], 2 odor stimuli [0.00006% citral (Alfa-Aeser), 0.0004% coffee odor (Givaudan Flavors Corporation)], and all possible 6 taste–odor mixtures. The concentrations of the taste stimuli were chosen to produce approximately equal intensity. The concentrations of the odor stimuli were selected to produce clearly perceivable, but rather weak olfactory sensation without evoking any oral sensations. It is known that odor stimuli often elicit an off taste (e.g., bitterness) and/or oral irritation at medium to high concentrations (e.g., Cometto-Muniz, 1981). The taste stimuli were prepared weekly from reagent grade compounds using deionized water and stored in airtight glass containers at 4–6 °C. In order to prevent the loss