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Original Article

Metabolic and Sensory Influences on Odor Sensitivity in Humans

Marielle G. Ramaekers[1], Alard Verhoef[2,3], Gerrit Gort[4], Pieternel A. Luning[1] and Sanne Boesveldt[2]

[1]Food Quality and Design, Wageningen University, Wageningen, the Netherlands,
[2]Division of Human Nutrition, Wageningen University, Wageningen, the Netherlands,
[3]Essensor, Ede, the Netherlands and
[4]Biometris, Wageningen University, Wageningen, the Netherlands

Correspondence to be sent to: Sanne Boesveldt, Division of Human Nutrition, Wageningen University, PO Box 8129, 6700 EV, Wageningen, the Netherlands. e-mail: sanne.boesveldt@wur.nl

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Abstract

Our olfactory sense plays an important role in eating behavior by modulating our food preferences and intake. However, hunger or satiety may also influence how we perceive odors. Albeit speculative, contradictory results found in the past may have resulted from confounding by type of meal that participants ate to induce satiety. We aimed to investigate the influence of hunger state on olfactory sensitivity, comparing hunger to satiety using 2 different types of lunch to control for sensory-specific satiety. Odor detection thresholds were measured in 2 groups of participants (39 per group, 18–40 years), under 3 conditions: when hungry (twice), after a sweet lunch, and after a savory lunch. One group had their detection thresholds tested for a sweet odor, whereas in the other group, sensitivity to a savory odor was measured. Differences in olfactory sensitivity conditions were analyzed using linear mixed models. Participants had higher scores on the odor sensitivity task in a hungry versus satiated state ($P = 0.001$). Within the satiated condition, there was no effect of type of lunch on odor sensitivity. In conclusion, hunger slightly enhances sensitivity to food odors, but did not significantly depend on the type of food participants ate, suggesting no clear influence of sensory-specific satiety.

Key words: detection threshold, hunger, olfaction, savory, sensory-specific satiety, sweet

Introduction

Our olfactory sense plays an important role in eating behavior by shaping our appetite and food choices (e.g., Fedoroff et al. 2003; Gaillet-Torrent et al. 2014; Ramaekers et al. 2014). However, the olfactory system may in turn, be affected by energy homeostasis: hunger or satiety may influence how we perceive odors (e.g., Cabanac and Fantino 1977; Jiang et al. 2008). It is an intuitively appealing concept to be more sensitive to odors that may, among others signal food, when in an energy-deprived state.

Although well-established for animals (e.g., Aimé et al. 2007; Prud'homme et al. 2009), this hypothesis remains subject to debate in humans, despite the many studies that have been done ever since the first studies in the early 20th century (Glaze 1928). Glaze reported on 2 subjects (himself included) who fasted for 5–10 days, and demonstrated an increased sensitivity to various odors during that period. An additional experiment, in which subjects were more sensitive to odors before a meal than after, replicated this finding (Glaze 1928). Since then, discrepant results have been reported in the literature, ranging from an increase in olfactory acuity when hungry (Goetzl and Stone 1947; Goetzl et al. 1950; Hammer 1951; Schneider and Wolf 1955; Guild 1956; Kittel and Reitberger 1970), no change in sensitivity (Janowitz and Grossman 1949; Zilstorff-Pederson 1955;

Furchtgott and Friedman 1960; Turner 1966; Crumpton et al. 1967; Fikentscher et al. 1977; Koelega 1994), to even an increase in acuity after lunch (Berg et al. 1963). Even more recently, results have been contradictory as well (Albrecht et al. 2009; Stafford and Welbeck 2011; Cameron et al. 2012; Hanci and Altun 2015), suggesting that these effects may be subtle or depend on specific methodology or odor type.

Apart from the exact threshold test that was conducted, other aspects in study design may have been vital for establishing the effect of hunger on odor sensitivity. For instance, the type of lunch that participants ate to induce satiety may affect odor perception. It is already known that the pleasantness of the taste, smell, and sight of a food that is eaten to satiety decreases relative to uneaten foods, a phenomenon coined *sensory-specific satiety* (Rolls et al. 1981). For example, after consumption of banana, pleasantness ratings for banana as well as for banana smell decreased significantly, compared with the pleasantness of other odors; an equivalent result occurred for chicken (Rolls and Rolls 1997). Similarly, a decrease in the pleasantness of isoamyl-acetate (banana odor), but not *n*-butanol (a chemical solvent), was found after consumption of a breakfast that contained banana (Albrecht et al. 2009). Typically, the sensory characteristics (taste, smell) of a meal reflect its' macronutrient content (van Dongen et al. 2012; Boesveldt and Lundström 2014), and sensory-specific satiety is thus thought to aid in the intake of a variety of foods and macronutrients.

Perhaps, when odor sensitivity is thought to play a role for food intake, this may also be affected by sensory-specific satiety. Though the majority of aforementioned studies on the influence of satiety levels on olfactory thresholds did not specifically report on the food that was eaten, their contradictory results may have been confounded by the congruency of the meal that participants ate to induce satiety with the odor that was tested. Therefore, the aim of the current study was 2-fold: First, to investigate the influence of hunger state on olfactory sensitivity, and secondly, to explore a possible effect of sensory-specific satiety on odor sensitivity, by comparing hunger to satiety using 2 different types of lunch. We hypothesized that odor sensitivity would decrease in a satiated compared with a hunger state, and that this effect would be larger after eating a lunch congruent to the tested odor than after an incongruent lunch.

Materials and methods

Experimental design

Participants were divided over 2 groups: a vanillin odor group and a meat odor group. Per group, a within-subject design was used with 3 experimental conditions. Odor sensitivity of participants was tested once after consumption of a sweet lunch, once after consumption of a savory lunch and twice in a hungry state (to balance the number of tests in a hungry state and in a satiated state). In total, participants took part in 6 separate test sessions, on 6 separate days (see Figure 1 for a schematic overview of the test sessions). The first 2 sessions were considered as training sessions and these data were not used for analysis. All participants were scheduled at the same time of the day as much as possible to exclude a possible effect of diurnal variations on odor sensitivity. The combination of 2 hungry, 1 sweet and 1 savory meal sessions, led to 12 possible orders of conditions over 4 sessions. All 12 orders were assigned to participants, leading to a reasonably (but not completely) balanced design of conditions over sessions. The experiment was executed during 8 weeks, between 11 AM and 3 PM.

Participants

Participants with a self-reported normal sense of smell, aged 18–40 years and BMI 18.5–25 kg/m^2 were recruited in and around the Wageningen area (the Netherlands). Exclusion criteria were: smoking, allergy, or hypersensitivity to any of the food products used in the study, being vegetarian, using medication known to interfere with olfactory function, lack of appetite, following an energy-restricted diet or change in body weight > 5 kg during the last 3 months. Participants were randomly assigned to the sweet or the savory group. Thirty-nine participants (M/F: 4/35, age: 23 ± 4.3 years, BMI: 21 ± 1.8 kg/m^2) participated in the vanillin odor group and 39 participants (M/F: 24/15, age: 23 ± 3.7 years, BMI: 21 ± 1.7 kg/m^2) in the meat odor group. This study was exempt from approval by the Medical Ethical Committee of Wageningen University, because the rules of conduct in the present research were not interventionist, with very little burden to the participants. This study was registered at the Dutch trial register (NTR3830; www.trialregister.nl/trialreg/admin/rctview.asp?TC=3830). All participants gave written informed consent and were paid 50€ upon completion of the study.

Procedure

Participants were requested to avoid wearing odors. Test sessions were rescheduled in case of difficulties with breathing or smelling (e.g., when having a cold).

For the hungry condition, participants had to restrict their food intake: no snacks after dinner on the evening before the test, consume half a normal breakfast, and additionally fast for 4 h on the morning of the tests. Participants recorded their food intake in a diary. For the satiated conditions, participants were asked to have

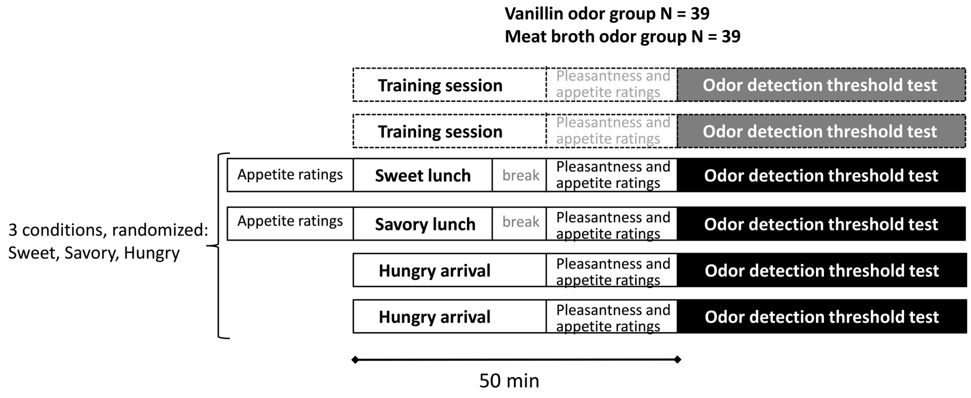

Figure 1. A schematic overview of the experimental procedure and the 3 different test conditions.

a normal breakfast, and received lunch 50 min before the threshold test. Participants were asked to eat until they were pleasantly satiated. The sweet lunch contained vanilla custard (Campina vanille vla, FrieslandCampina; 91 kcal/100 mL), sugar bread and raisin bread (bakery products). Participants had to consume at least 1 bowl (300 mL) of vanilla custard and 1 piece of sugar or raisin bread. The savory lunch consisted of a chicken noodle soup with vegetables (Struik chicken noodle soup; 45 kcal/100 mL) and bread rolls with ham or 40+ Gouda cheese. Participants had to consume at least 1 bowl (300 mL) of soup and 1 bread roll.

Hunger, fullness, desire-to-eat-sweet, desire-to-eat-savory, tiredness, and pleasantness of the odor were measured just before the threshold test, using a 100 mm visual analogue scale (VAS, not at all—very much) in all conditions. In the satiated conditions, the participants additionally rated hunger, fullness, desire-to-eat-sweet, and desire-to-eat-savory just before the lunch on 100 mm VAS (not at all-very much). Subsequently, the odor detection threshold tests were executed.

Odors

The odors that were used for the odor threshold tests were vanillin (4-hydroxy-3-methoxybenzaldehyde; Givaudan, number 9620001) and a savory flavor (Givaudan Schweiz AG, savory BTN flavor number 96900240, 0.05%) which smells like meat broth. Both vanillin and savory flavor were diluted using propylene glycol (1,2-propanediol extra pure, manufacturer: Merck, CAS # 57-55-6). Thirty-two dilution steps were made for both odors. Step 1 contained the highest odor concentration, 0.1% (1 g/kg), and step 32 the lowest concentration, 6.8×10^{-8}% (6.8×10^{-7} g/kg). Both odors were diluted with a dilution ratio of 1:1.6 ($=\sqrt{2.5}$) between steps. Brown 50 mL glass bottles were filled with 10 mL of the odor dilutions. Five sets of all concentrations ("set", see Data analysis) were made to run several threshold tests at the same time.

Detection threshold test

The odor threshold tests were performed in sensory booths with a continuous airflow to prevent odor contamination in the rooms (Restaurant of the Future, Wageningen, the Netherlands). Participants first received a short explanation of the test procedure. Furthermore, participants sniffed from a bottle containing the strongest odor solution (0.1%) to rate the pleasantness of the odor and to familiarize with the odor. They also smelled a bottle with solvent (PG) to be able to distinguish between the odor and the solvent. The odor detection threshold was determined using a 3-alternative forced-choice, 2-up-one-down, staircase procedure (Ehrenstein and Ehrenstein 1999). For each trial, participants were presented with 3 bottles, of which 2 contained no odor (only solvent), and 1 contained the odorant at a certain concentration. Participants had to detect the odd one out. Reversal of the staircase was triggered when the odor was correctly identified in 2 successive trials for a total of 7 reversals. Trials were presented with an interval time of 30 s. Participants were told to smell each bottle about 3–5 s while placing the bottle just under the nose, but without touching it. The average of the last 4 reversal points determined the threshold score. Possible thresholds scores range between 1 and 32, where higher scores correspond to a lower odor detection threshold and thus higher odor sensitivity.

Data analysis

We formulated a linear mixed model (Littell et al. 2006) to analyze odor threshold scores as a function of odor (vanillin or meat broth) and experimental condition (sweet, savory, no lunch) and their interaction, correcting for participants and the experimental factors session, and set ("set", see Odors). Session, odor, condition, and odor–condition interaction entered the model with fixed effects, whereas random effects were assumed for subjects, and set. The variance components for subjects, set, and residual error were allowed to be different for the 2 types of odors, as there was little reason to assume that variabilities of odor threshold scores were equal for vanillin and meat broth odors. Because gender was rather unbalanced over the 2 odor groups (see Participants) and therefore a possible confounder of odor effects, we included it as extra fixed factor, both with main effects and interacting with odor and condition, in the mixed model. If not-significant, it will be removed from the model again for reasons of parsimony. Plots for studentized residuals were made to check for outliers, normality and constant variance. Out of 312 possible data points (78 participants, 4 sessions each), 8 data points were missing due to lack of availability of participants (4 participants missed a single vanillin session; 2 participants missed a single meat session, 1 participant missed 2 meat sessions), and 17 observations were removed before final analysis because of severe suspicions about their validity regarding threshold or appetite scores, leaving 287 observations for final analysis. User-specified contrasts were formulated for odor threshold scores based on our a priori research questions and hypotheses: Does the satiated condition (averaging over sweet and savory condition, and both odors) differ from the hungry condition? Does a congruent condition (sweet lunch/vanillin odor + savory lunch/meat broth odor) differ from the hungry condition? Does an incongruent condition (sweet lunch/meat broth odor + savory lunch/vanillin odor) differ from the hungry condition? Do the congruent and incongruent conditions differ? Furthermore, pairwise comparisons among conditions, separately for the meat broth and vanillin odors groups were made.

Before statistical analysis of the appetite and odor pleasantness ratings, we calculated the mean delta desire-to-eat sweet and mean delta desire-to-eat savory by averaging the delta scores (before ratings minus after ratings). Next, the appetite and odor pleasantness ratings were logit transformed using $\ln[(y/100 + 0.01)/(1 - y/100 + 0.01)]$ to stabilize the variance. We studied the effects of hungry state versus sweet lunch versus savory lunch, on hunger, fullness, desire-to-eat, desire-to-eat sweet, desire-to-eat savory, delta desire-to-eat sweet, delta desire-to-eat savory, and odor pleasantness by using linear mixed models. Session was included as a factor with fixed effects in the model to account for possible effects over sessions.

Statistical analyses were performed by using SAS (version 9.2; SAS Institute Inc.). Two-sided tests were used. Significance was set at $P < 0.05$. Raw data in Table 1 are presented as means ± SD. Results in the text and Figure 2 show least-squares means ± standard error (SE). The latter are estimated means, based on the linear mixed models. All degrees of freedom were calculated according to the method by Kenward and Roger (Kenward and Roger 1997).

Results

Appetite and odor pleasantness ratings

Participants were more hungry, less full, and had more desire to eat (sweet and savory) in the hungry than in the satiated condition (Table 1; all $P < 0.001$). After consumption of the sweet lunch, appetite for sweet decreased more than appetite for savory, and vice versa (Table 1; both $P < 0.001$).

A comparison of odor pleasantness ratings between the sessions revealed lower pleasantness for vanillin odor after eating a sweet lunch versus a savory lunch ($P = 0.018$), but no significant difference

Table 1. Mean values ± SD of appetite and odor pleasantness ratings (100 mm VAS)

	Vanillin odor group					Meat odor group				
	Hungry	Sweet lunch[a]		Savory lunch		Hungry	Sweet lunch		Savory lunch[a]	
		Before	After	Before	After		Before	After	Before	After
Hunger	83 ± 12	62 ± 21	13 ± 11	68 ± 17	13 ± 11	78 ± 18	67 ± 21	14 ± 16	64 ± 22	8 ± 7
Fullness	12 ± 12	28 ± 18	79 ± 13	30 ± 21	78 ± 17	12 ± 11	26 ± 24	77 ± 17	26 ± 19	82 ± 15
Desire-to-eat	84 ± 12	67 ± 17	16 ± 14	70 ± 16	18 ± 17	79 ± 18	67 ± 20	17 ± 15	66 ± 21	11 ± 9
Desire-to-eat sweet	66 ± 23	55 ± 19	12 ± 16	46 ± 25	27 ± 21	58 ± 28	51 ± 29	13 ± 16	40 ± 29	23 ± 22
Desire-to-eat savory	78 ± 22	67 ± 16	30 ± 28	66 ± 23	18 ± 22	75 ± 22	67 ± 21	36 ± 31	72 ± 19	11 ± 15
Odor pleasantness	75 ± 18		68 ± 22		72 ± 19	52 ± 27		46 ± 24		46 ± 25

[a]Lunch congruent with odor.

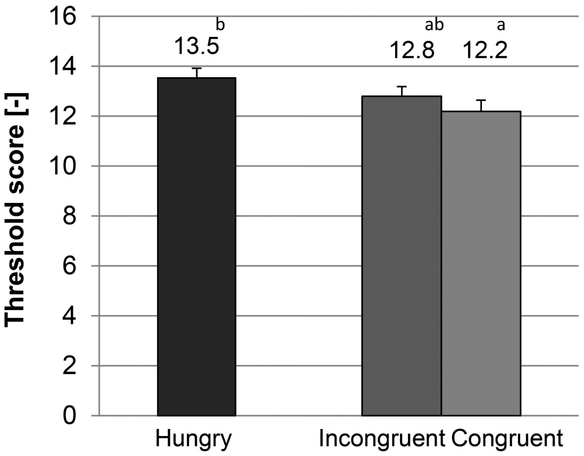

Figure 2. Estimated mean values of the odor detection threshold scores ± SE, in hungry and satiated conditions; the satiated conditions are split per congruent and incongruent combination of odor and lunch. Means without a common letter differ, *P* < 0.05.

in (decrease of) pleasantness ratings for the meat broth odor between the 2 types of lunch (*P* = 0.471).

Olfactory sensitivity

No main effect of gender (*P* = 0.26), nor of its interaction with odor (*P* = 0.21) or condition (*P* = 0.33) was found. Gender was therefore removed from the model.

The mean odor threshold score was 1.0 ± 0.3 higher in the hungry than in the satiated conditions (*P* = 0.001), indicating an increased odor sensitivity in the hunger state.

When the satiated conditions were split per (in)congruent condition (depending on the combination of type of lunch and odor), threshold scores in the hungry condition were higher than the scores in the congruent condition (*P* < 0.001) and borderline significant as compared with an incongruent lunch (*P* = 0.052). There was no significant difference in odor threshold scores between congruent versus incongruent lunch (*P* = 0.16). Figure 2 shows the least square means of odor detection threshold scores combined over the 2 odors.

There was no significant interaction between condition and odor (*P* = 0.10), indicating the effect of hunger state was similar on both odor thresholds. However, when exploring sensitivity for both odors separately, threshold scores were higher in the hungry condition than after the sweet (*P* = 0.007) or the savory lunch (*P* < 0.001) for the meat broth odor, but not for the vanillin odor (all *P* > 0.15). Odor sensitivity after sweet versus savory lunch did not differ significantly, for meat broth odor (*P* = 0.24) or vanillin odor (*P* = 0.39).

Discussion

The present study set out to determine the influence of hunger state on olfactory sensitivity, and comparing 2 different types of lunch to induce satiety that were either congruent or incongruent to the odor tested. Our results indicate that hunger indeed enhanced sensitivity to food odors, but this did not directly depend on the type of food participants ate, suggesting no clear influence of sensory-specific satiety.

Despite much effort on this topic, previous research remained inconclusive regarding the effect of satiety levels on odor sensitivity (Hammer 1951; Schneider and Wolf 1955; Zilstorff-Pederson 1955; Guild 1956; Furchtgott and Friedman 1960; Berg et al. 1963; Turner 1966; Crumpton et al. 1967; Kittel and Reitberger 1970; Fikentscher et al. 1977; Koelega 1994). Most of those studies differed in their methodology or odor selection, rendering it difficult to compare their outcomes. Though the current data are not in line with recent studies that specifically used food-related odors and demonstrated higher sensitivity for a food odor in the satiated state (Albrecht et al. 2009; Stafford and Welbeck 2011), the results confirm our a priori hypothesis: When hungry, it may be beneficial to be better able to detect cues that signal food, thus, that participants were more sensitive to food-related odors in a hungry compared with a satiated state. Consistent with this, modulation of olfactory behavior by feeding state has been well established in a variety of animal species, exhibiting greater olfactory sensitivity and food-odor exploration behavior for rodents in a fasted versus a satiated state (e.g., Aimé et al. 2007; Prud'homme et al. 2009). Indeed, the olfactory system is intimately linked with the endocrine system that regulates energy balance, and a plethora of animal studies have shown that olfaction is modulated in response to changing levels of various hormones and peptides, such as ghrelin, orexin, insulin, and leptin, that are implicated in appetite regulation (e.g., Mousley et al. 2006; Julliard et al. 2007; Root et al. 2011; Tong et al. 2011). Animal, as well as more recently, human work has demonstrated that even the first levels of olfactory signal processing, the olfactory mucosa and the olfactory bulb, are targets for these regulatory metabolic factors (for a comprehensive review, see Palouzier-Paulignan et al. 2012), but also regions associated with higher-order olfactory information processing (such as the orbitofrontal cortex) can be modified by hunger or satiety (Critchley and Rolls 1996). To summarize, a decrease in olfactory sensitivity can be seen as part of the food intake control mechanism, where appetite regulation hormones may be able to shift olfactory sensitivity to achieve nutritional homeostasis.

Though we initially hypothesized that the inconsistency in human literature regarding metabolic influences on odor sensitivity could perhaps be explained by differences in meal type used to satiate participants, we could not confirm this based on our results. We did not find a significant influence of type of lunch (congruent/incongruent) on subsequent odor detection thresholds, suggesting that sensory-specific satiety does not play an important role here. Because sensory-specific satiety is typically related to either food intake or pleasantness (Rolls et al. 1981), and not to sensitivity, this may not seem surprising. Though in the current study we did ask for pleasantness of the odors, this was only assessed once in every test session. Hence we cannot directly compare pleasantness ratings before and after lunch and cannot draw any real conclusions related to sensory-specific satiety-effects on odor pleasantness. Moreover, although sensory-specific satiety is typically assessed by pleasantness ratings, this does not always predict subsequent intake.

Interestingly, the above-mentioned effect of hunger on odor sensitivity appears to be somewhat smaller, albeit in the same direction, for the vanillin odor compared with the meat broth odor. The vanillin threshold scores showed a larger variation, and perhaps vanillin can also be associated with nonfood products, such as air fresheners or shower gels, that may be less affected by level of satiation, whereas meat broth is very typically food-related. On the other hand, the significant effect for the savory (meat broth) odor may be indicative of our body's tight regulation of protein intake (Simpson et al. 2003). Protein is an indispensable component within the human diet, and when protein-deprived, food intake and preferences may shift toward high-savory foods (Griffioen-Roose et al. 2012), and brain reward responses to odor and visual cues of savory foods are modulated (Griffioen-Roose et al. 2014). Although still speculative at this point, this suggests that it is perhaps more important to regulate our detection ability for savory than for sweet food cues, depending on our internal state. In the present study, we only used 1 sweet and 1 savory odor, limiting the ability to generalize our findings to fully represent the sweet and savory category. Future studies could focus on further determining specific effects of odor categories.

Though our findings are significant, the effect of hunger on odor sensitivity is rather small (approximately 1 dilution step, 1.6× difference in odor concentration), which could account for the inconsistent results in previous studies. It is commonly accepted that the olfactory system is mainly involved in identification and recognition of stimuli, and has low discriminative abilities when it comes to intensity perception or concentration difference (e.g., Stevens 1957; Doty 1975). A 1.6× increase in odor concentration may not always be noticeable, as few studies on difference thresholds or just-noticeable-differences have reported (Stone et al. 1962; Jacquot et al. 2010), but could under certain conditions, such as hunger, become relevant. It may be easier to study these phenomena in animals, because human eating behavior studies are typically complex and it is difficult to have complete control over the experimental conditions, that is, standardize meals and so forth for a longer period of time, to truly regulate metabolic state. Additionally, the olfactory system in animals may be more relevant for food intake regulation, because they have to rely more on their nose to detect foods in their environment than we humans nowadays, where food is abundantly available in the Western world. It could be interesting to perform a similar study in cultures where people still have to actively search for food (e.g., nomadic hunter-gatherer societies), and where the sense of smell has a more prominent role (Majid and Burenhult 2014), hypothesizing that olfactory sensitivity may then be more prone to changes in internal state.

It can be seen as a limitation of the study that we did not include a nonfood odor as control. That way, it could have been established whether satiety selectively influences olfactory sensitivity for food odors, or whether our results reflect a reduction in sensitivity to odors in general. However, because we hypothesized that hunger state modulates the ability to detect food cues, as well as were interested in a possible sensory-specific satiety effect, we opted to only measure detection thresholds for food odors, congruent to the type of lunch (sweet, savory) chosen to induce satiety. To assert whether these results are specific for the olfactory system, or more generally related to attention or arousal in different levels of satiation, it can also be suggested to include a nonodor control task for future studies.

Furthermore, although we set dietary restrictions for participants in the hungry state, this was not equivalent for the satiated state. This variance in breakfast may have led to larger interindividual variation in satiation levels and could have influenced our results. However, participants' appetite ratings matched the condition they were in (hungry vs. satiated).

Lastly, although gender was unbalanced over the 2 odor groups (vanillin 4M/35F; meat 24M/15F), this did not significantly impact any of the results regarding odor sensitivity.

Conclusion

In conclusion, hunger appears to enhance sensitivity to food odors, but did not significantly depend on the type of food participants ate, suggesting no clear influence of sensory-specific satiety. Even though our sense of smell is important in shaping our food preferences and appetite, when taking into account the inconsistency in results from previous studies, it seems that effects of hunger on olfactory sensitivity in humans may be small.

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