Appetite 111 (2017) 158–165

Contents lists available at ScienceDirect

Appetite

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

Higher sensitivity to sweet and salty taste in obese compared to lean individuals

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ARTICLE INFO

Article history:
Received 3 August 2016
Received in revised form
3 November 2016
Accepted 13 December 2016
Available online 14 December 2016

Keywords:
Taste
Obesity
Taste sensitivity
Pleasantness

ABSTRACT

Although putatively taste has been associated with obesity as one of the factors governing food intake, previous studies have failed to find a consistent link between taste perception and Body Mass Index (BMI). A comprehensive comparison of both thresholds and hedonics for four basic taste modalities (sweet, salty, sour, and bitter) has only been carried out with a very small sample size in adults. In the present exploratory study, we compared 23 obese (OB; BMI > 30), and 31 lean (LN; BMI < 25) individuals on three dimensions of taste perception — recognition thresholds, intensity, and pleasantness — using different concentrations of sucrose (sweet), sodium chloride (NaCl; salty), citric acid (sour), and quinine hydrochloride (bitter) dissolved in water. Recognition thresholds were estimated with an adaptive Bayesian staircase procedure (QUEST). Intensity and pleasantness ratings were acquired using visual analogue scales (VAS). It was found that OB had lower thresholds than LN for sucrose and NaCl, indicating a higher sensitivity to sweet and salty tastes. This effect was also reflected in ratings of intensity, which were significantly higher in the OB group for the lower concentrations of sweet, salty, and sour. Calculation of Bayes factors further corroborated the differences observed with null-hypothesis significance testing (NHST). Overall, the results suggest that OB are more sensitive to sweet and salty, and perceive sweet, salty, and sour more intensely than LN.

1. Introduction

The sense of taste is important to detect nutrients and toxins in our foods. According to this notion, sweet indicates carbohydrates, salty indicates sodium, sour indicates acids and potentially spoiled foods, and bitter acts as a warning sign for potentially toxic ingredients (but also healthy compounds found in green vegetables). Impairments in taste perception and/or hedonic experience of taste can cause deviant eating behaviour, which can lead to mal- or super-nutrition, both representing major public health issues.

Overweight and obesity are defined as abnormal or excessive accumulation of body fat to an extent that may lead to negative effects on health. Body Mass Index (BMI, kg/m^2) is a simple and commonly used measure for classifying weight status (underweight, normal weight, overweight, obese etc.). According to the latest global estimates from the World Health Organisation (WHO), worldwide, prevalence of obesity has more than doubled since 1980 (WHO, 2015). WHO has also reported that an increased BMI is a major risk factor for several non-communicable diseases such as type 2 diabetes, heart disease, stroke, and some forms of cancer. Considering that obesity is preventable, it is important to understand the causes and effects of obesity in order to devise prevention and treatment strategies.

The large part of the obesity research in recent years has concentrated on ‘eating behaviour’, and the reward response to food or food cues (e.g. food pictures) rather than the sensory aspects of food intake, i.e. taste sensitivity and preference. Consequently, the link between taste perception and BMI is unclear (Donaldson, Bennett, Baic, & Melichar, 2009). Studies looking at BMI related sensitivity or threshold differences for sweet, salty, sour and bitter tastes have either found no effect (Malcolm, O'Neil, Hirsch, Currey, & Moskowitz, 1980; Martinez-Cordero, Malacara-Hernandez, & Martinez-Cordero, 2015), lower taste sensitivity in obesity (Proserpio, Laureati, Bertoli, Battezzati, & Pagliarini, 2015)

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http://dx.doi.org/10.1016/j.appet.2016.12.017
0195-6663/

or higher taste sensitivity in obesity in some or all tastes in children, adolescents, and older adults (Overberg, Hummel, Krude, & Wiegand, 2012; Pasquet, Frelut, Simmen, Hladik, & Monneuse, 2007; Simchen, Koebnick, Hoyer, Issanchou, & Zunft, 2006). A comprehensive investigation of taste experience in adults, measured with taste thresholds as well as supra-threshold hedonic ratings for the four basic tastes, found no differences between adult-onset obese, juvenile-onset obese, and never-obese women (Malcolm et al., 1980). However, the small sample sizes may have hindered the authors from detecting small differences between groups.

Research on taste perception and weight status has primarily focused on sweet taste (Bartoshuk, Duffy, Hayes, Moskowitz, & Snyder, 2006; Grinker, Hirsch, & Smith, 1972; Pepino, Finkbeiner, Beauchamp, & Mennella, 2010; Rodin, Moskowitz, & Bray, 1976; Thompson, Moskowitz, & Campbell, 1976); while bitter taste has also been investigated, studies have focused on Phenylthiocarbamide (PTC) and 6-*n*-propylthiouracil (PROP) (Goldstein, Daun, & Tepper, 2005; Tepper et al., 2008), bitter compounds that are not commonly found in foods. Salty and sour taste perception has remained largely unexplored (Donaldson et al., 2009). The combined results from these studies are inconclusive. For instance, in spite of the widespread belief that sweet foods contribute greatly to excess weight gain, no clear difference in sweet sensitivity had been seen between obese and lean individuals (Grinker et al., 1972; Rodin et al., 1976; Thompson et al., 1976). A lower sweet intensity perception was first reported in people with obesity when general Labelled Magnitude Scales (gLMS) were used instead of traditional visual analogue scales (VAS), combined with a higher sweet preference (Bartoshuk et al., 2006). GLMS are designed to be more valid than traditional VAS when comparing inter-individual subjective ratings. However, in a later study, no difference was shown between obese and normal weight groups in detection thresholds, preference, discrimination performance or supra-threshold intensity ratings, even when intensity ratings were acquired using a gLMS (Pepino et al., 2010).

An unambiguous interpretation of the literature on nutritional status and taste is further complicated by the heterogeneity of methods across studies. First of all, the current WHO definitions of weight status are: ‘normal weight’ = 18.5–25 kg/m^2, ‘overweight’ = 25–30 kg/m^2, and ‘obese’ ≥ 30 kg/m^2. But the classification for obese and non-obese groups in studies does not always adhere to these criteria (e.g. Simchen et al., 2006). Secondly, a comparison of thresholds may refer to absolute or detection thresholds, recognition thresholds, or identification thresholds, which may, in turn, be estimated in a variety of ways (Snyder, Sims, & Bartoshuk, 2015). Taste stimuli may be applied in the form of water-based taste solutions, or taste infused paper strips, cotton swabs, or discs (for an overview, see Hummel, Hummel, & Welge-Luessen, 2014). Liquid stimuli can be administered to the tongue as sprays or drops, or as larger aliquots that participants are asked to sip. There is also variability in the chemical compounds (e.g. citric acid or acetic acid for ‘sour’, caffeine or quinine for ‘bitter’)’, concentration ranges, and stimulus amounts used for taste assessment. Sets of taste infused paper often use very few concentration steps (e.g. 4 for taste strips; Mueller et al., 2003) that do not readily allow detection of small differences between groups or across time. It is worth taking into account that differences in taste thresholds do not necessarily reflect differences in supra-threshold sensitivity (Bartoshuk, 1978; Webb, Bolhuis, Cicerale, Hayes, & Keast, 2015). Consequently, it is important to independently estimate supra-threshold sensitivity and preferences for taste, as human food intake generally takes place at a supra-threshold taste level. To date, measures of taste sensitivity and subjective supra-threshold perception have not been systematically assessed and compared between lean and obese individuals.

In the present study, we compared taste perception in lean and obese participants on three dimensions: recognition thresholds as an objective measure of taste sensitivity, as well as subjective intensity and pleasantness for different supra-threshold concentrations of four basic tastes.

2. Materials and methods

2.1. Participants

54 healthy participants between 18 and 35 years of age were recruited into the lean (LN) or obese (OB) group based on BMI of <25 and >30, respectively. The LN group consisted of 31 participants (Mean BMI = 21.88, range = 18.73 to 24.49; 14 women), and the OB group included 23 participants (Mean BMI = 33.8, range = 30.47 to 38.96; 12 women). All women used hormonal contraceptives. Self-report based exclusion criteria were: taste and smell disorders, smoking, substance abuse and other addictions, current or recent oral, nasal or sinus infections, pregnancy, recent (in the last 6 months) childbirth, thyroid disorders, diabetes, or weight loss of more than 10 kg in the last 3 months. All participants gave written informed consent prior to the experiment.

2.2. Stimuli

Tastants were sucrose (Sigma-Aldrich, CAS number: 57-50-1), sodium chloride (NaCl; Sigma-Aldrich, CAS number: 7647-14-5), citric acid (Sigma-Aldrich, CAS number: 77-92-9), and quinine hydrochloride (quinine; Sigma-Aldrich, CAS number: 6119-47-7) dissolved in mineral water (Volvic) creating ‘sweet’, ‘salty’, ‘sour’, and ‘bitter’ taste, respectively. Each stimulus was a 0.2 mL bolus of the tastant administered to the anterior part of the tongue. For threshold estimation, 12 dilution steps, evenly spaced on a decadic logarithmic scale, were prepared for each taste quality. The concentration ranges (Table 1) were derived from the literature, and adjusted according to preliminary testing. Tastants were stored in individual glass bottles with a spray dispenser, presented at room temperature, and kept at 5 °C in the dark for a maximum of three days when not in use.

2.3. Recognition thresholds

Recognition thresholds were estimated for each of the four taste qualities independently through an adaptive staircase procedure based on QUEST (Watson & Pelli, 1983), implemented via PsychoPy 1.80.03 (Peirce, 2007). The procedure assumed the relationship between log-transformed stimulus concentrations and perceived taste intensities to follow the shape of a Weibull function with a slope of 3.5, and the threshold as free parameter. Pilot testing showed that participants were highly unlikely to report a stimulus at very low concentrations or when pure water was presented (low false-alarm rate; FAR), and, likewise, would only rarely report not perceiving a stimulus at high concentrations (low lapsing rate). Therefore, we assumed both false-alarm and lapsing rates to be fixed at 0.01. A starting concentration and its standard deviation were provided to QUEST as a prior. These concentrations were chosen after pilot testing in such a way that they would be clearly perceptible to most participants (sucrose: 5.022 g/100 mL, NaCl: 1.615 g/100 mL, citric acid: 0.285 g/100 mL, quinine: 0.0092 g/100 mL) and presented on the first trial of threshold estimation for the respective taste quality. After each response given by the participant, QUEST updates the posterior probability density function for the threshold, and proposes the next concentration to be presented. Since we only had a limited number of stimuli available, if the exact concentration proposed by QUEST was unavailable (which was usually the case), QUEST suggested the closest available concentration for presentation. If the newly selected concentration had already been presented in the immediately preceding trial, the next lower or higher concentration was chosen based on whether the participant had succeeded or failed in detecting it, respectively. The procedure was repeated until the 90% confidence interval of the estimated threshold was less than half (approx. width of the log-step) of the concentration presented last, or after a maximum of 20 trials. Thresholds were estimated separately for the four taste qualities in a counterbalanced order across participants. On each trial, participants were presented with a single stimulus and asked to answer whether they could perceive the target taste or not by stating ‘Yes’ or ‘No’, respectively. They were instructed to respond promptly, and only answer ‘Yes’ if they were certain, thereby enforcing a strict response criterion. After a response was given, participants rinsed their mouth with water, and waited for 30 s before the next presentation.

2.4. Supra-threshold perception

Participants rated four supra-threshold concentrations of each taste quality (16 stimuli) for their intensity and pleasantness using VAS anchored with labels, i.e., “no sensation” (0) and “extremely intense” (100) for intensity, and “extremely unpleasant” (−50), “neutral” (0), and “extremely pleasant” (50) for pleasantness. All participants evaluated an “Absolute High” and “Absolute Low” concentration for each taste to allow for comparison independent of individual taste sensitivity. These concentrations (39.91 and 10.02 g/100 mL for sucrose; 8.8 and 2.84 g/100 mL for NaCl; 1.67 and 0.40 g/100 mL for citric acid; and 0.0151 and 0.0055 g/100 mL for quinine) were the same for all participants. Additionally, participants evaluated a “Relative Low” and “Relative High” concentration of each taste quality. These were one and three concentration steps above the individual threshold, respectively, and thereby adjusted to each participant's individual taste sensitivity. By including both “Absolute” (for all subjects) and “Relative” (threshold adjusted) concentrations, we measured not only how participants rated a given 'high' or 'low' concentration, but also how participants rated high or low concentrations within their individual taste perceptual space.

2.5. Questionnaires

Participants also completed four questionnaires using LimeSurvey (Schmitz, 2012) in a separate session to assess levels of chronic stress (Trier Inventory for Chronic Stress; TICS; Schulz & Schlotz, 1999), depression (Beck Depression Inventory; BDI; Beck, Steer, & Brown, 1996), Inhibition, Drive, Fun-Seeking and Reward Responsiveness (Behavioural Inhibition System/Behavioural Activation System; BIS/BAS; Carver & White, 1994), and Dietary Restraint, Disinhibition and Hunger (Three Factor Eating Questionnaire; TFEQ; Stunkard & Messick, 1985). Questionnaire data from 7 participants (2 LN, 5 OB) for BDI and BIS/BAS, 10 participants (5 LN, 5 OB) for TFEQ, and 11 participants (5 LN, 6 OB) for TICS was missing due to technical difficulties.

Table 1
Taste concentration ranges used for threshold estimation.

Taste	Grams/100 mL		Log-step width
	Lowest	Highest	
Sucrose	0.0100	20.000	0.300
NaCl	0.0100	5.000	0.245
Citric Acid	0.0010	0.900	0.269
Quinine	0.0001	0.025	0.218

2.6. Statistical analyses

Unpaired *t*-tests were performed to compare mean thresholds between groups. Supra-threshold ratings and questionnaire scores were compared using the Mann-Whitney *U* test, as they did not follow a normal distribution (according to Shapiro-Wilk tests).

Along with conventional NHST, Bayes factors (BF) were calculated for taste thresholds as well as supra-threshold ratings via JASP 0.7.5 Beta2 (JASP Team, 2015; https://jasp-stats.org/) using a Cauchy prior width of 0.707. BFs indicate the likelihood ratio that expresses how likely the observed data are under the alternative (H1) hypothesis relative to the null (H0) hypothesis. Thus, a BF10 of 4.5 would mean that the data are 4.5 times more likely to be observed under H1 , whereas a BF10 of 0.3 would mean that the data are 3.3 (i.e., 1/0.3) times more likely to be observed under H0.

Correlations were computed between the first and second subjective rating as a measure of within-subject consistency, and between taste thresholds and supra-threshold ratings to quantify the relation between objective and subjective measures. Pearson's correlation coefficient *r* is reported for data that were normally distributed and Spearman's ρ is calculated for ratings that were not normally distributed.

3. Results

3.1. Questionnaires

OB and LN yielded similar scores in all questionnaires expect for higher median Hunger scores in the TFEQ (LN = 4, OB = 5; $U = 134$, $p = 0.015$) and higher Fun Seeking in BIS/BAS (LN = 12, OB = 13.5; $U = 154.5$, $p = 0.018$) in OB compared to LN.

3.2. Recognition thresholds

OB had significantly lower thresholds for sweet ($t_{52} = 2.681$, $p = 0.01$) and salty ($t_{52} = 3.072$, $p = 0.003$) than LN, which was further corroborated by moderate evidence for H_1 (a difference in the two groups) for sweet ($BF_{10} = 4.778$), and strong evidence for H_1 for salty ($BF_{10} = 11.008$) thresholds. No significant group difference was found for sour and bitter. Threshold statistics are reported in Table 2 and Fig. 1.

3.3. Supra-threshold perception

For the supra-threshold tastants, OB tended to rate the “Absolute Low” and “Absolute High” concentrations as more intense than LN (Tables 3a and 3b, Fig. 2a and b). This difference was significant for the “Absolute High” sweet ($U = 227.5$, $p = 0.024$), “Absolute Low” sweet ($U = 201.5$, $p = 0.007$), “Absolute Low” salty ($U = 209.5$, $p = 0.01$), and “Absolute Low” sour ($U = 193.5$, $p = 0.004$) concentrations. OB also rated the “Relative High” sweet ($U = 220$, $p = 0.017$) as more pleasant than the LN.

In line, BFs provided moderate evidence for H_1, implying higher intensity ratings in OB compared to LN for the “Absolute Low” sweet ($BF_{10} = 4.689$), “Absolute Low” salty ($BF_{10} = 6.387$), and “Absolute Low” sour ($BF_{10} = 8.075$) concentrations. No significant group differences were found for intensity ratings of “Absolute High” salty, sour or bitter tastants, the “Relative High” and “Relative Low” concentrations of any of the four tastes, the pleasantness ratings “Relative High” salty, sour or bitter tastants, or any of the “Absolute High”, “Absolute Low”, or “Relative Low” concentrations (all $p > 0.055$). For “Absolute High” sweet intensity, and “Relative

Table 2
Unpaired *t*-tests and Bayes factors (log-transformed threshold values (g/100 mL) [a].

Taste	Lean		Obese		NHST		BF	
	Mean	SD	Mean	SD	t_{52}	p	BF_{10}	error %
Sucrose	−0.273 [b]	0.344	−0.554 [c]	0.427	2.681	0.01	4.778	2.341e −6
NaCl	−0.888 [d]	0.295	−1.170 [e]	0.383	3.072	0.003	11.008	1.423e −6
Citric Acid	−1.612 [f]	0.386	−1.711 [g]	0.406	0.905	0.370	0.390	1.586e −4
Quinine	−3.175 [h]	0.604	−3.346 [i]	0.697	0.960	0.342	0.405	1.619e −4

[a] The log threshold values correspond to the following concentrations on a linear scale.
[b] 0.5333 g/100 mL.
[c] 0.2796 g/100 mL.
[d] 0.1294 g/100 mL.
[e] 0.0676 g/100 mL.
[f] 0.0244 g/100 mL.
[g] 0.0195 g/100 mL.
[h] 0.0007 g/100 mL.
[i] 0.0005 g/100 mL.

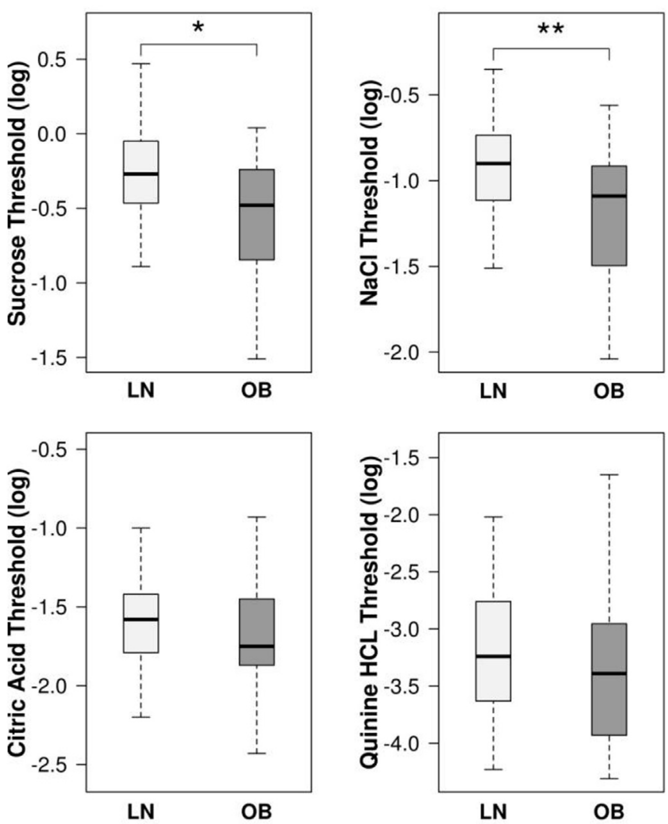

Fig. 1. Boxplots of log-transformed recognition threshold (g/100 mL) distributions for LN and OB groups for sucrose (sweet), sodium chloride (salty), citric acid (sour), and quinine (bitter). *$p \leq 0.05$, **$p \leq 0.01$.

High" sweet pleasantness, the BFs provided only anecdotal evidence for the alternative hypothesis ($BF_{10} = 2.757$, and $BF_{10} = 2.867$, respectively).

Notably, participants exhibited a high intra-individual consistency in their ratings as supported by significant correlations between ratings on the first and second trial of all stimuli (Spearman's $\rho = 0.911$, $p < 0.0001$) which was similar for OB ($\rho = 0.9$, $p < 0.0001$) and LN ($\rho = 0.921$, $p < 0.0001$).

Taste thresholds and subjective ratings of intensity for concentrations "Relative" to individual thresholds were positively correlated (two-tailed). These were most pronounced for "Relative High" concentrations of sucrose ($r = 0.689$, $p < 0.0001$), NaCl ($r = 0.487$, $p < 0.0001$), citric acid ($r = 0.293$, $p = 0.031$), quinine ($\rho = 0.607$, $p < 0.0001$), and weaker, yet in part significant, for "Relative Low", sucrose ($\rho = 0.456$, $p = 0.001$), NaCl ($\rho = 0.247$, $p = 0.07$), citric acid ($\rho = 0.163$, $p = 0.239$), and quinine ($\rho = 0.368$, $p = 0.006$).

"Absolute" concentrations, which were chosen independent of individual thresholds, exhibited consistently negative correlations (one-tailed) with individual thresholds; these were strongest for "Absolute Low" sucrose ($r = -0.253$, $p = 0.044$), NaCl ($\rho = -0.308$, $p = 0.012$), citric acid ($r = -0.481$, $p < 0.0001$), and quinine ($\rho = -0.649$, $p < 0.0001$), weaker for "Absolute High" sucrose ($\rho = -0.114$, $p = 0.206$), NaCl ($\rho = -0.274$, $p = 0.022$), and quinine ($\rho = -0.569$, $p < 0.001$), and stronger for "Absolute High" citric acid ($r = -0.536$, $p < 0.0001$).

4. Discussion

In the present study, we compared lean and obese participants on three dimensions of taste perception: recognition threshold as an objective measure of taste sensitivity, and intensity and pleasantness as the subjective measures, for four basic tastes. Our results indicate that obese participants are more sensitive to taste than lean participants. This notion is evidenced by significantly lower recognition thresholds to sweet and salty, indicating a higher sensitivity, and further corroborated by the observation that OB rated the same concentrations of sweet, salty, and sour as significantly more intense than LN. We did not find evidence for a difference in sour and bitter thresholds between OB and LN. It was observed that overall, participants could taste more of the lower concentrations of sour and bitter, and the final threshold estimates for these taste qualities were gathered towards the lower end of the concentration range. These concentration ranges were designed to cover the expected thresholds of the entire population with a limited number of stimuli. For taste qualities with large inter-individual differences, this implies a decrease in the granularity of the threshold estimate, i.e., lowered precision on the single-subject level. Hence, it is possible that even more narrow dilution steps are required to detect potential group differences for these tastes.

In line with lower thresholds, OB participants reported significantly higher subjective taste intensity for "Absolute Low" sweet, salty, and sour and "Absolute High" sweet, compared to LN. Notably, this group difference did not manifest in the concentrations that were adjusted to individual thresholds (i.e., "Relative Low" and "Relative High") corroborating our threshold estimates. The group differences in sweet and salty taste are of particular interest for eating behaviour and energy intake, and with that for obesity research, as these taste qualities provide information

Table 3a
Intensity ratings for supra-threshold concentrations.

Taste	Conc.	Lean	Obese	Mann-Whitney *U*		Bayes factor	
		Median (IQR)	Median (IQR)	*U*	p	BF_{10}	error %
Sucrose	Absolute High	84 (71–90.5)	94.5 (80.5–98.5)	227.5	0.024	2.757	1.019e –7
	Absolute Low	67 (56–77.5)	81 (70–89)	201.5	0.007	4.689	2.306e –6
	Relative High	45 (32–60)	36 (14.5–61)	279	0.175	0.667	7.549e –5
	Relative Low	18 (7–40)	8.5 (3–22.5)	247	0.055	1.305	3.152e –5
NaCl	Absolute High	90 (81–97.5)	93.5 (89–99)	259.5	0.089	0.935	6.086e –5
	Absolute Low	81 (66.5–85.5)	91 (77–95.5)	209.5	0.01	6.387	2.397e –6
	Relative High	55 (34.5–61.5)	45 (26–54.5)	273.5	0.146	0.690	7.556e –5
	Relative Low	20 (8–35)	16 (8–29)	321	0.535	0.359	1.527e –4
CitricAcid	Absolute High	93 (77.5–98)	95 (85.5–99.5)	274.5	0.151	0.793	7.183e –5
	Absolute Low	71 (61.5–79)	86 (76–90)	193.5	0.004	8.075	2.035e –6
	Relative High	44 (32.5–63)	47 (33–69)	325	0.582	0.296	1.459e –4
	Relative Low	14.5 (10–31)	15.5 (4–34)	339	0.759	0.286	1.459e –4
Quinine	Absolute High	79.5 (70–86)	85 (75–95)	258	0.085	0.510	1.813e –4
	Absolute Low	58 (40.5–76)	67.5 (43.5–86.5)	306.5	382	0.357	1.523e –4
	Relative High	39.5 (15–71)	36.5 (14–68.5)	319	0.512	0.297	1.459e –4
	Relative Low	18.5 (10.5–36.5)	15.5 (7.5–21.5)	308.5	0.401	0.375	1.557e –4

Table 3b
Pleasantness ratings for supra-threshold concentrations.

Taste	Conc.	Lean	Obese	Mann-Whitney *U*		Bayes factor	
		Median (IQR)	Median (IQR)	*U*	p	BF_{10}	error %
Sucrose	Absolute High	26.5 (10–36)	24 (8.5–42.5)	353.5	0.958	0.277	1.462e –4
	Absolute Low	19.5 (13.5–32)	14.5 (6.5–29.5)	281.5	0.189	0.564	1.866e –4
	Relative High	13.5 (5.5–24.5)	6 (0–14.5)	220	0.017	2.867	3.342e –8
	Relative Low	2 (0–8)	0 (0–2)	251.5	0.064	1.078	4.845e –5
NaCl	Absolute High	−36 (−42.5–−16)	−31 (−45–−15)	329	0.630	0.298	1.459e –4
	Absolute Low	−20 (−31.5–−4)	−24.5 (−34–−7)	293	0.267	0.465	1.741e –4
	Relative High	−3.5 (-14–3)	−1 (-7–2)	294.5	0.278	0.482	1.771e –4
	Relative Low	−1 (-4–0)	0 (−2.5–1.5)	292	0.255	0.277	1.462e –4
Citric Acid	Absolute High	−21 (−34–−1)	−9 (-43–5.5)	337	0.733	0.306	1.462e –4
	Absolute Low	−11 (-22–0.5)	−12 (−36.5–7)	341	0.786	0.317	1.469e –4
	Relative High	−2 (-6–5)	−4.5 (-13–2)	279	0.175	0.819	7.010e –5
	Relative Low	0 (-2–2)	0 (−3.5–0)	285	0.205	0.846	6.814e –5
Quinine	Absolute High	−33 (−41–−24)	−41.5 (−45–−28)	278	0.170	0.452	1.717e –4
	Absolute Low	−20 (−27–−15)	−27.5 (−39–−9)	294	0.274	0.420	1.651e –4
	Relative High	−10 (−24–−2)	−9 (−28–−1.5)	344.5	0.512	0.306	1.462e –4
	Relative Low	−2 (-10–0)	−5.5 (−9.5–0)	346	0.853	0.286	1.459e –4

regarding the nutritional value of food. In that sense, sweet taste indicates calories from certain carbohydrates, and salty taste signals the availability of sodium and/ or minerals. Beyond this traditional view, saltiness can be associated with the availability of energy from fat, particularly in processed foods in the Western diet. High amounts of fat are also more likely to be consumed in processed sweet foods.

The findings on subjective perception are consistent with the group difference found for taste thresholds: more sensitive participants reported “Absolute” taste concentrations, i.e. those concentrations that were identical for all participants irrespective of their threshold, as more intense than less sensitive participants. Whereas “Relative” taste concentrations, i.e. concentrations that were aligned to individual threshold levels, yielded no group differences in intensity. Previous studies have investigated the link between different - objective and subjective - measures of taste perception including detection and recognition thresholds, ratings of supra-threshold tastants, and density of fungiform papillae. While detection and recognition thresholds are commonly correlated (e.g. Webb et al., 2015; Wise & Breslin, 2013), thresholds have seldom been found to be related to supra-threshold intensity rating (Webb et al., 2015). Webb et al. (2015) concluded that these individual measures characterize different facets of the taste experience rather than providing a measure of overall taste function, and suggested that this explains conflicting data pertaining to taste function and sensitivity and its link with dietary intake. We observed consistently strong positive correlations between thresholds and intensity ratings that were aligned “Relative” to individual thresholds as expected, because the concentrations were only few concentration-steps above individual thresholds and provide a similar perceptual frame for participants. Correlation between thresholds and intensity ratings for concentrations that were chosen independent of thresholds were consistently negative, weaker, and only partially significant. Together our findings suggest a systematic link between taste thresholds and supra-threshold intensity ratings if these are aligned to individual taste sensitivity.

Our findings of heightened taste sensitivity in obese participants stand in contrast to existing literature which presents a rather diverse picture that nevertheless points to reduced taste abilities in obesity. Previous reports have suggested either no difference on sweet and salty taste sensitivity between obese and lean participants (Bertoli et al., 2014; Pepino et al., 2010; Simchen et al., 2006), or even lower sensitivity in obesity for salty (Skrandies & Zschieschang, 2015) for sour (Bertoli et al., 2014), sour and bitter (Simchen et al., 2006), or for sweet, salty, sour and bitter (Proserpio et al., 2015). An improvement of taste detection rates has also been reported after weight loss (Altun et al., 2016). However, it cannot be excluded that the choice of methods and the resolution of the

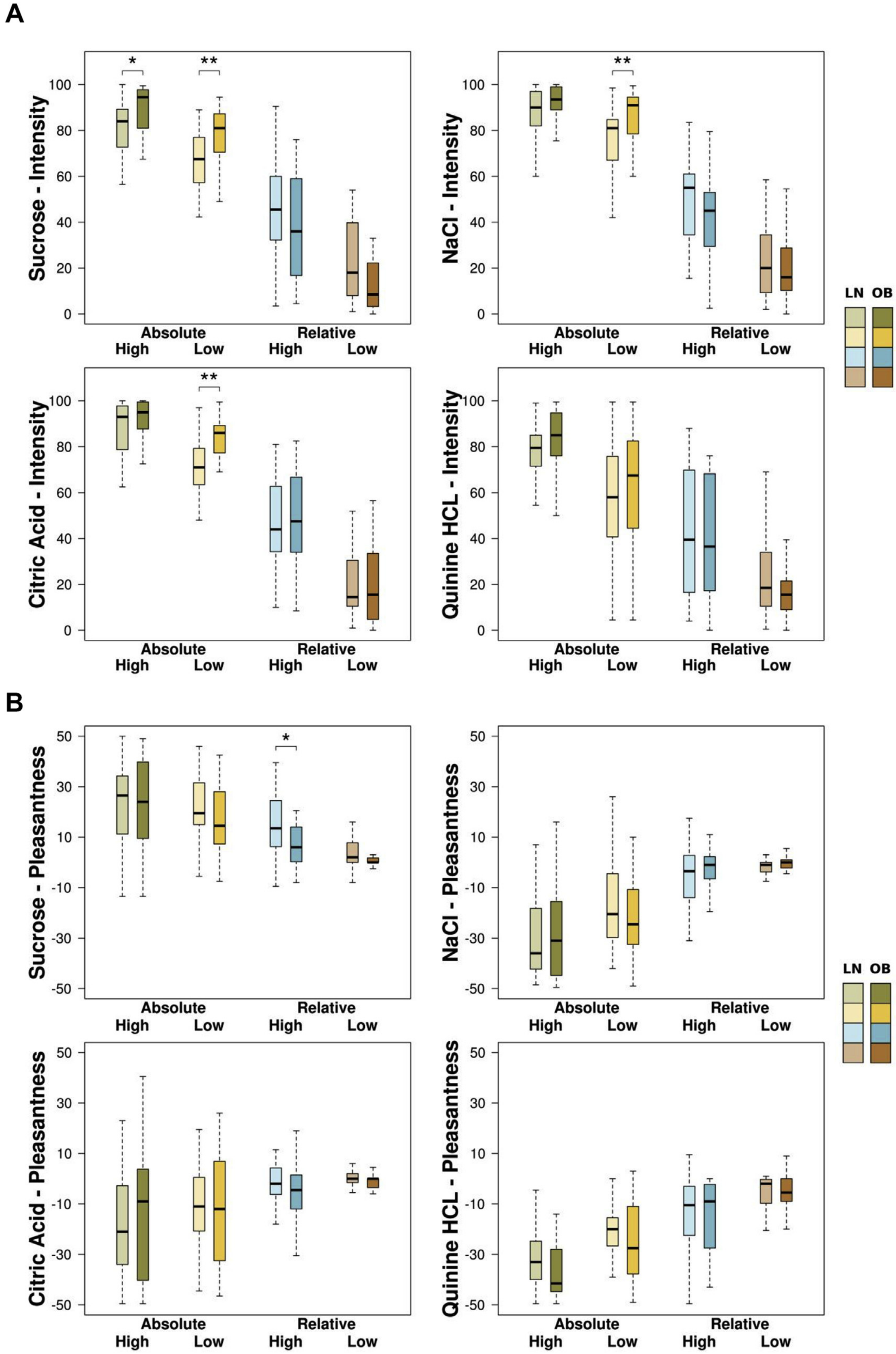

Fig. 2. (A) Boxplots showing distributions of the intensity of four concentrations of sucrose (sweet), sodium chloride (salty), citric acid (sour), and quinine (bitter), for LN and OB. $^{*}p \le 0.05$, $^{**}p \le 0.01$. (B) Boxplots showing distributions of the pleasantness of four concentrations of sucrose (sweet), sodium chloride (salty), citric acid (sour), and quinine (bitter), for LN and OB. $^{*}p \le 0.05$.

measure (i.e. number of dilution steps) to assess taste sensitivity contributed to this discrepancy.

Similarly, the supra-threshold findings of higher intensity differ from previous studies where obese individuals were reported to have perceived supra-threshold sweet and salty tastants as less intense (Sartor et al., 2011), or no different from lean individuals (Malcolm et al., 1980; Pepino et al., 2010). In our sample, taste pleasantness was significantly higher in OB compared to lean for "Relative High" sweet only. Although OB tended to rate all concentrations of sweet taste as less pleasant than LN, this model was moderately favoured by the BF calculation only for the "Relative High" sweet. Previously, there have been isolated reports of obese individuals reporting higher pleasantness for higher concentrations of sucrose (Rodin et al., 1976), reports of obese adults consuming more energy in salty foods (Cox, Perry, Moore, Vallis, & Mela, 1999), and also a correlation of BMI with liking for salty-fatty foods (Deglaire et al., 2014). One may speculate that increased liking and perceived pleasantness may therefore be an indicator of actual food intake, and liking of sweet and salty taste may foster overweight as processed foods with that taste commonly contain lots of calories.

As mentioned earlier, a comparative interpretation of existing findings is hampered by the methodological differences present across studies. These involve particularly the differences in threshold algorithms (e.g. ascending versus adaptive methods), tasks (e.g. 2- or 4- alternative forced choice; AFC), modes of stimulation (e.g. whole mouths versus localised stimulation), concentration ranges and number of dilution steps, and also the type of concentration scale (linear versus log-linear). Our use of broad concentration ranges together with the adaptive, Bayesian approach has enabled us to detect minute threshold differences that may have been missed in previous studies. Our threshold measurement procedure was specifically designed for a rapid estimation of taste thresholds. While spatial and temporal AFC tasks are typically used for that purpose, we employed a yes-no paradigm because the total time required for the procedure is greatly reduced as only a single stimulus is presented on each trial. Furthermore, this approach avoids memory effects and interval biases typically associated with AFC tasks in naïve participants, who might be more inclined to pick one interval over the other, regardless of actual stimulation (see e.g. Klein, 2001). Two major problems specific to the chemical senses are persistent habituation and carry-over effects from one stimulus to the next. To avoid these, each stimulation is followed by rinsing and a long inter-stimulus interval (ISI; typically 10s–30s). However, experiments with long ISIs are known to prevent participants from directly comparing two or more stimuli (Kaernbach, 1990), thereby introducing a major memory-related confound in gustatory AFC tasks. Presenting one stimulus per trial bypasses this problem, and allows the processing of stimuli independently from one another. Additionally, King-Smith et al. (1994) stated that for the estimation of an approximate absolute threshold, a yes-no method similar to the one used here is preferable to an AFC task, mainly because of its greater speed while still providing accurate results.

It is known that the outcome of threshold estimation procedures might not entirely reflect participants' true sensory sensitivity due to individual response criteria, specifically the decision as to how strongly a stimulus has to be perceived to elicit a "Yes" response. Commonly, stimulations with pure water (blanks) are used as control and allow for the estimation of false alarm rate (FAR), i.e., a "Yes" responses when no tastant is presented. However, adding blanks to derive a meaningful FAR inflates the number of trials required. Instead, based on pilot testing, we assumed a fixed FAR of almost zero (0.01). While we cannot rule out the possibility that LN and OB in the present study employed different response criteria on population average, any such difference should not be selective of one or more taste qualities within an individual, leaving the reported group effects for different tastes unaffected by this cognitive confound.

Another practical argument builds on observations that forced-choice procedures are unsuitable for some participants, especially in a clinical setting, as participants might be reluctant to guess the target interval when feeling unsure (Green, 1993). As extensive "practice" sessions cannot usually be performed with these populations (Jones, Moore, & Amitay, 2015), directly asking the participants whether or not they perceived a stimulus might be more suitable for naïve subjects (Green, 1993). Because the method presented here does not require any practice, doesn't strain the memory, has a very short testing duration, relies on portable stimulus material, and can even be easily adapted to allow for non-verbal responses (e.g. indicating the perceived taste by pointing out a related food item on a response chart), we suggest it is suitable also for children, elderly, and clinical populations. Future studies will have to confirm this claim of applicability.

5. Conclusion

Together, our findings suggest that higher body mass is associated with higher sensitivity to, and subjective strength experience of salty and sweet taste. While sour and bitter taste showed a similar pattern of results, this was markedly less pronounced and not statistically significant. Given that our understanding of the aetiology of obesity is in its infancy, any interpretation of the results along those lines would be highly speculative. Accordingly, the current findings are presented and discussed within the context of the existing literature on gustatory perception and BMI. Notably, these findings contradict some of the previous reports suggesting a reduced sensitivity and/or ability to detect different tastes in obese compared to lean. We believe that the discrepancies are grounded in methodological but also conceptual differences in measuring taste sensitivity. Comparisons of taste perception in lean and obese groups have also continually suffered from the drawback of small sample sizes. It should be recognised that BMI is a population level measure of obesity (WHO), and may only have a small effect compared to the total effect of other factors such as age, health, socio-economic status, current eating habits, hormone levels etc., in small samples. We have tried to control for some of these by limiting our sample to young men and women without known chronic illness, and women who use contraceptives. While we deem understanding the role of taste sensitivity in the development of obesity crucial, ascertaining the extent to which differences in supra-threshold taste experience modulate eating behaviour and weight status remains equally important.

Acknowledgements

This work was supported by the German Research Foundation within CRC 1052 "Obesity Mechanisms" (A01).

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