# Phenotypic differences in taste hedonics: The effects of sweet liking 

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#### Abstract

Phenotypic differences in sweet liking are well known, but how they relate to actual eating habits and liking for other taste qualities remains unclear. In Experiment One ( 222 participants), we explored if the three sweet-liking phenotypes (extreme sweet-likers, moderate sweet-likers and sweet dislikers) differed in liking for foods and beverages commonly associated with obesogenic westernised diets categorised into three groups (high fat, high sugar, or high fat-sugar) alongside rated liking for foods grouped by five taste qualities (bitter, fatty, salty, spicy and sweet foods). Multiple linear regression models found significant differences between the sweet-liking phenotypes in liking for foods classified as high fat-sugar and high sugar, as well as for sweet foods but not for other taste qualities, with extreme sweet-likers rating liking for these foods significantly higher than sweet dislikers. No other significant differences between the three phenotypes were found. Experiment Two (298 participants) aimed to replicate these findings and investigate if an increased liking for these foods translates into higher intake using a high fat-sugar food frequency questionnaire. Again, extreme sweet-likers rated liking for sweet foods and foods grouped as high fat-sugar significantly higher than sweet dislikers but also disliked bitter foods more. No other significant differences were found, including no differences in the frequency of consumption of these foods. Overall, these data suggest that phenotypic differences in sweet taste liking may be specific to liking for foods high in sweetness only and do not generalise to real-life consumption or liking for other taste qualities unless sweetness is also present.


## 1. Introduction

Taste hedonics have important influences on eating behaviour, informing food preference, selection and, consequently, nutritional intake and health (reviewed in de Graaf \& Boesveldt, 2017). Therefore, a greater understanding of individual differences in sweet liking may help to reveal predispositions to diet-related health outcomes to better support public health strategies and treatments to prevent obesity and noncommunicable diseases (Garcia-Bailo, Toguri, Eny, \& El-Sohemy, 2009; Rauber \& Louzada, 2018). Long considered an innate preference, the seminal work of Pangborn (1970) clearly demonstrated three hedonic responses to sweet taste (illustrated in Fig. 1): extreme sweet likers whose liking increases with sweetness intensity; moderate sweet likers who show a mild liking for moderate levels of sweetness; and sweet dislikers, who show increasing dislike as sweetness increases. Pangborn's observation of consistent individual differences has since been
replicated in numerous studies (reviewed in Iatridi, Hayes, \& Yeomans, 2019b) and has been confirmed in a recent series of studies applying more statistically robust methods for identifying liking patterns across adult populations in the UK, US and Asia (e.g., Garneau, Nuessle, Mendelsberg, Shepard, \& Tucker, 2018; Iatridi, Hayes, \& Yeomans, 2019a; Kavaliauskaite, Thibodeau, Ford, \& Yang, 2023; Kim, Prescott, \& Kim, 2014; Lim, Teo, Tan, \& Forde, 2020; Yang, Kraft, Shen, Macfie, \& Ford, 2019).

It has been argued that taste has two primary functions: to evaluate food for nutrients and toxicity to guide what to ingest and to prepare the body to ingest and metabolise food (Breslin, 2013). Within sensory science, there is general agreement that there are five basic taste qualities, sweet, bitter, salty, sour, and umami taste (Chandrashekar, Hoon, Ryba, \& Zuker, 2006), although the number of taste qualities beyond these is still debated (e.g., starch taste: Lapis, Penner, \& Lim, 2016; fat taste: Running, Craig, \& Mattes, 2015). Liking for sweet taste is

[^0]commonly thought to have developed to identify sources of carbohydrates. Carbohydrates have been part of the human diet since our earliest recorded history (Daniels \& Daniels, 1993). However, on an evolutionary time scale, changes in the modern food landscape towards increased caloric availability being predominantly governed by an abundance of high-fat high-sugar foods are relatively recent (Stein \& Keller, 2015). Current evidence suggests this obesity-promoting food environment influences the physiological crosstalk between brain areas key for the homeostatic regulation of food intake (e.g. hypothalamus) and the so-called hedonic brain (e.g. nucleus accumbens) where pleasure and/or sensory perception navigate intake (Smith \& Hommel, 2022). Since our genome has yet to adapt, that results in ingestive decision making which favours highly palatable food choices independent of our need state (Berthoud, Münzberg, \& Morrison, 2017). In view of this, modern humans have still to cope with neural circuits programmed to protect the body's energy reserves from food scarcity (Carrera-Bastos, Fontes-Villalba, O'Keefe, Lindeberg, \& Cordain, 2011) and, thus, the increased liking for sweet taste orchestrated by the activation of endogenous mechanisms that initially evolved to increase the intake of safe, energy-dense foods may no longer be an asset (Olszewski, Wood, Klockars, \& Levine, 2019).

With global rates of obesity nearly tripling over the last 40 years and with no sign of stopping (Bentham \& Di Cesare, 2022), it is becoming ever-important to understand why regulation mechanisms allow body weight to increase in some but not all individuals. Although the role of genetics (Loos \& Yeo, 2022) and environmental changes will play a significant role in this rapid upward trend (e.g., Grandner, 2018; Kopp, 2019; Ng \& Popkin, 2012), individual differences in taste hedonics may increase susceptibility to consume the energy-dense and nutrient-poor food and beverages found in westernised diets and could therefore play a key role in the obesity epidemic (e.g., Baker \& Friel, 2014; Popkin,

Adair, \& Ng, 2012; Swinburn et al., 2011). This would imply that those with the greatest liking for sweetness, i.e., the extreme sweet-liking phenotype, should have the greatest risk of overconsumption.

However, although individual differences in liking for sweet taste are well known, how they relate to actual eating habits, dietary intake and liking for other taste qualities remains unclear. In sensory science, many researchers have investigated the relationship between liking for various oral sensations (i.e., bitter, salty, astringency and spiciness) with food liking and/or intake. Most have used simple tastants, such as aqueous solutions, to separate the complexity of food perception with a growing body of literature now modelling in real foods (e.g., Hayes, Sullivan, \& Duffy, 2010; Törnwall et al., 2014; Zandstra \& de Graaf, 1998) or using both aqueous solutions and model foods (e.g., Pagliarini et al., 2021; Spinelli et al., 2021). The majority of research has focused on the perceived bitterness of 6-n-propylthiouracil (PROP) and its association with liking and intake of bitter foods (as reviewed in Feeney, O'Brien, Scannell, Markey, \& Gibney, 2011; Garcia-Bailo et al., 2009; Tepper et al., 2009). Despite the considerable interest in sweet preference and liking for sweet tasting foods using aqueous solutions and model foods (e.g., Drewnowski \& Schwartz, 1990; Kim, Prescott, \& Kim, 2014; Mennella, Finkbeiner, Lipchock, Hwang, \& Reed, 2014; Mennella, Finkbeiner, \& Reed, 2012; Methven, Xiao, Cai, \& Prescott, 2016; Tuorila, Keskitalo-Vuokko, Perola, Spector, \& Kaprio, 2017), the literature exploring food liking and intake with the three sweet-liking phenotypes is limited. Only one study previously explored food liking (Kim et al., 2014), who found increased liking for individual sweet and savoury items by extreme sweet likers.

In this work, we present two closely related studies examining how individual differences in liking for sweet taste, as characterised by the three sweet-liking phenotypes, relate to differences in liking for foods grouped by general taste qualities (bitter, fatty, salty, spicy and sweet


Fig. 1. Graphical representation of the three sweet-liking phenotypes identified using Hierarchical Cluster Analysis (modified with permission from Iatridi et al., 2019a). Extreme sweet likers [ESL], whose liking increased with sweetness intensity, moderate sweet likers [MSL], whose liking peaked at around 0.25 M sucrose before decreasing and sweet dislikers [SD], whose liking decreased with sweetness intensity. The suggested liking cut-off at $\pm 15$ for 1.0 M sucrose was based on analysis of the sensitivity and specificity scores for all sucrose concentrations and possible cut-offs ranging from 0 to 20 . The selected cut-offs had the highest combined sensitivity/specificity score for both the prediction of ESL ( $95.6 \%$ ) and SD ( $92.4 \%$ ) phenotypes compared with respective alternative phenotypes across all potential tested cut-of values: see Iatridi et al., 2019 for full specificity and sensitivity data.
foods) and liking for foods implicated in obesogenic westernised diets that are high in saturated fat and refined carbohydrates. Additionally, in Experiment Two, we also investigate differences in dietary intake for foods high in saturated fat and refined carbohydrates using a food frequency questionnaire. Based on the limited evidence linking liking for sweet taste and dietary intake of foods and beverages beyond items high in sweetness as evaluated in our recent review (Armitage, Iatridi, \& Yeomans, 2021) and the differences in food liking found by Kim et al. (2014), we hypothesise that in Experiment One we will see differences in liking for sweet foods but not for foods grouped by the other taste qualities.

## 2. Experiment One

### 2.1. Method

### 2.1.1. Participants

Participants were 261 volunteers, aged 18-34, who were either staff or students at the University of Sussex, UK or residents from the Brighton and Hove area. They were recruited for a 45-minute multi-task session through advertisements in local Facebook groups, flyers distributed in public spaces and on a participant study website. Due to testing restrictions in place due to COVID-19, the first 137 participants took part remotely, and the last 124 took part in the same session at the University of Sussex. Potential participants who had any repository illness, current or recent COVID-19 symptoms or diagnosis, history of diabetes, a prior diagnosis of an eating disorder, took prescription medications (excluding oral contraceptives) or smoked more than five cigarettes a week were excluded. Participants were rewarded either with a small payment (£6) or course credits for undergraduates studying Psychology. The study protocol was approved by the University of Sussex Sciences \&

Technology Cross-Schools Research Ethics Committee (protocol ER/ RA294/7), and conducted per the ethical standards laid down by the British Psychological Society and the Declaration of Helsinki. A summary of participant characteristics can be found in Table 1.

### 2.1.2. Rating scales and training

Measures of the perceived intensity ("How [sweet/bitter/sour/salty] is [solution number]?" were made using a 100pt horizontal generalised Labelled Magnitude Scales (gLMS), ranging from "No sensation" (0) to "The strongest sensation imaginable" (100). To reduce the possible confound of participants using the labels as anchors (Hayes, Allen, \& Bennett, 2013), they were instructed to make their ratings anywhere on the scale and that the labels were there as a guide. To ensure participants understood the use of this scale, they first completed practice ratings of two non-taste examples recommend in previous studies (Duffy, Peterson, \& Bartoshuk, 2004; Hayes et al., 2013): the perceived intensity of "listening to a heavy metal song with headphones on maximum volume" and "staring at the sun through binoculars". This should have elicited responses close to the maximal "highest sensation imaginable" on the gLMS.

Liking ("How much do you like [solution number]?") was assessed using a horizontal visual analogue scale (VAS) ranging from -50 to +50 and end anchored with "Dislike extremely" $(-50)$ and "Like extremely" $(+50)$. Here, participants were instructed that the middle of the line represented a neutral point, in other words, a stimulus that they 'Neither Like or Dislike'. Again, participants rated four non-taste practice examples: "How much do you like watching your favourite movie?", "How much do you like walking in the rain?", "How much do you like a warm fire on a cold day?" and "How much do you like the sound of a car alarm?".

Participants were trained to correctly use the liking and intensity

Table 1
Summary of characteristics by phenotype for Experiments One and Two.

| Characteristic | Experiment One |  |  |  | Experiment Two |  |  |  |
| :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: |
|  | ESL $(n=85)$ | MSL $(n=91)$ | SD $(n=46)$ | $\begin{aligned} & \text { Overall ( } n= \\ & 222 \text { ) } \end{aligned}$ | ESL ( $n=90$ ) | MSL $(n=140)$ | SD $(n=68)$ | $\begin{aligned} & \text { Overall ( } n= \\ & 298 \text { ) } \end{aligned}$ |
| $\begin{aligned} & \text { Age (years): } M \pm S D \\ & \text { (range) } \end{aligned}$ | $\begin{aligned} & 22.5 \pm 3.7 \\ & (18-35) \end{aligned}$ | $\begin{aligned} & 22.1 \pm 3.2 \\ & (18-34) \end{aligned}$ | $\begin{gathered} 21.1 \pm 2 \\ (18-31) \end{gathered}$ | $\begin{aligned} & 22.1 \pm 3.2 \\ & (18.6-35) \end{aligned}$ | $\begin{aligned} & 21.3 \pm 3.5 \\ & (18-33) \end{aligned}$ | $\begin{aligned} & 21.7 \pm 3.9 \\ & (18-35) \end{aligned}$ | $\begin{aligned} & 21.9 \pm 3.7 \\ & (18-34) \end{aligned}$ | $\begin{aligned} & 21.6 \pm 3.7 \\ & (18-35) \end{aligned}$ |
| $\begin{aligned} & \text { BMI: } M \pm S D \\ & \text { (range) } \end{aligned}$ | $\begin{aligned} & 22.7 \pm 3.9 \\ & (17.1-36.7) \end{aligned}$ | $\begin{aligned} & 22.7 \pm 4 \\ & (14.5-35.6) \end{aligned}$ | $\begin{aligned} & 22.2 \pm 3.5 \\ & (16.9-34.9) \end{aligned}$ | $\begin{aligned} & 22.6 \pm 3.9 \\ & (14.5-36.7) \end{aligned}$ | $\begin{aligned} & 23.1 \pm 4.1 \\ & (17.3-40.9) \end{aligned}$ | $\begin{aligned} & 22.9 \pm 3.8 \\ & (16.6-35.6) \end{aligned}$ | $\begin{aligned} & 22.6 \pm 3.9 \\ & (17.2-38.5) \end{aligned}$ | $\begin{aligned} & 22.9 \pm 3.9 \\ & (16.6-40.9) \end{aligned}$ |
| BMI Class \% of group, $n$ |  |  |  |  |  |  |  |  |
| Underweight | 9\%, 8 | 9\%, 8 | 7\%, 3 | 9\%, 19 | 8\%, 7 | 9\%, 12 | 6\%, 4 | 8\%, 24 |
| Healthy | 71\%, 60 | 62\%, 56 | 76\%, 35 | 68\%, 151 | 63\%, 57 | 66\%, 92 | 74\%, 50 | 67\%, 199 |
| Overweight | 12\%, 10 | 18\%, 16 | 11\%, 5 | 14\%, 31 | 24\%, 22 | 20\%, 28 | 16\%, 11 | 20\%, 61 |
| Obese | 7\%, 6 | 7\%, 6 | 4\%, 2 | 6\%, 14 | 4\%, 4 | 5\%, 7 | 4\%, 3 | 5\%, 14 |
| Unknown ${ }^{\text {a }}$ | $1 \%, 1$ | $5 \%, 5^{\text {b }}$ | $2 \%, 1$ | $3 \% 7$ | , | , | , | , |
| Sex \% of group, $n^{\text {b }}$ |  |  |  |  |  |  |  |  |
| Male | 20\%, 17 | 25\%, 23 | 24\%, 11 | 23\%, 51 | 42\%, 38 | 39\%, 55 | 25\%, 17 | 37\%, 110 |
| Female | 80\%, 68 | 74\%, 67 | 76\%, 35 | 77\%, 170 | 58\%, 52 | 61\%, 85 | 75\%, 51 | 63\%, 188 |
| Ethnicity \% of group, $n^{\text {b }}$ |  |  |  |  |  |  |  |  |
| Caucasian | 62\%, 53 | 66\%, 60 | 67\%, 31 | 65\%, 144 | 69\%, 62 | 66\%, 93 | 68\%, 46 | 67\%, 19 |
| Asian | 20\%, 17 | 19\%, 17 | 17\%, 8 | 19\%, 42 | 13\%, 12 | 19\%, 27 | 16\%, 11 | 17\%, 151 |
| Black | 4\%, 3 | $3 \%$, 3 | 4\%, 2 | 4\%, 8 | 2\%, 2 | 5\%, 7 | $1 \%$, 1 | 3\%, 31 |
| Other | 14\%, 12 | 11\%, 10 | 11\%, 5 | 12\%, 27 | 16\%, 14 | 9\%, 13 | 15\%, 10 | 12\%, 14 |
| Diet \% of group, $n^{\text {b }}$ |  |  |  |  |  |  |  |  |
| Omnivore | 67\%, 57 | 84\%, 76 | 63\%, 29 | 73\%, 162 | 79\%, 71 | 81\%, 114 | 74\%, 50 | 79\%, 235 |
| Pescatarian | 7\%, 6 | 5\%, 5 | 13\%, 6 | 8\%, 17 | 6\%, 5 | 4\%, 6 | $3 \%$, 2 | 4\%, 13 |
| Vegetarian | 15\%, 13 | 8\%, 7 | 15\%, 7 | 12\%, 27 | 13\%, 12 | 11\%, 16 | 15\%, 10 | 13\%, 38 |
| Vegan | 11\%, 9 | 2\%, 2 | 4\%, 2 | 6\%, 13 | 2\%, 2 | $3 \%, 4$ | 9\%, 6 | 4\%, 12 |
| Other | 0\%, 0 | 0\%, 0 | 4\%, 2 | 1\%, 2 | - | - | - | - |

[^1]rating scales based on published protocols (Bartoshuk, 2000; Green et al., 1996) to increase the reliability of between-participant contrasts (see Yeomans, Vi, Mohammed, \& Armitage, 2022 for more information on the specific training).

### 2.1.3. Assessing sweet-liking phenotype status

To determine sweet-liking phenotype status, participants evaluated two samples of 1.0 M sucrose ( $342.3 \mathrm{~g} \mathrm{wt} / \mathrm{vol}$ ), alongside two water blanks, using the Sussex Taste Test (STT) recommended by Iatridi et al. (2019a). Solutions were prepared at least 48 h ahead of testing using a volumetric flask by dissolving food-grade sugar in mineral water and were stored refrigerated at $4{ }^{\circ} \mathrm{C}$ for up to seven days. Four 10 ml samples were decanted into 12.5 ml food-safe screw top plastic bottles and were brought to room temperature at least two hours before the taste test. At the start of the taste test, participants first completed training on the two rating scales (as described above) and a six-question disguised moodappetite questionnaire to allow for controls for appetitive state (as described in Yeomans et al., 2022). Participants first rated hunger using a horizontal VAS followed by five descriptors presented in random order. This included fullness and thirst alongside three mood descriptors (happy, tired and anxious). For the STT, they rated two blocks of two solutions, first water followed by the 1.0 M sucrose, with a 2-minute interval between blocks. Participants were instructed to swill the solution around their mouth for 10 s (controlled by the experimental program) and then swallow the solution, immediately rating each sample on liking then intensity (sweet/bitter/sour/salty) and rinsing their mouth. Instructions, timings and ratings were all presented using Inquisit Version 5.0.11 (Seattle, USA).

### 2.1.4. Food-liking questionnaire

To classify liking for food implicated in westernised diets and grouped by taste qualities, participants completed a food-liking questionnaire adapted from Pallister et al. (2015) and Vink, Van Hooijdonk, Willemsen, Feskens, and Boomsma (2020) by the UK Biobank. Participants rated 152 items on a 9 -point hedonic scale from 1 (extremely dislike) to 9 (extremely like) with two additional options: "Have never tried it" and "Prefer not to answer". Details of the questionnaire can be found at (https://biobank.ndph.ox.ac.uk/showcase/showcase/docs /foodpref.pdf). We extracted the liking ratings of foods grouped by five taste qualities (bitter, fatty, salty, spicy and sweet foods) alongside food and beverage items also listed in the Dietary Fat and free Sugar Short Questionnaire (DFS; Francis \& Stevenson, 2011) which is a reliable and valid measure of saturated fat and refined sugar, implicated in obesogenic westernised diets. Items were then grouped into the Francis and Stevenson (2011) three subscales: fat, fat-sugar and sugar. However, as there were only six items in the original sugar subscale and additional sweet items collected in the food-liking questionnaire that were not in the original DFS questionnaire (i.e., cake icing, dried fruit and fruit), we added these to increase the size of the category and reflect wider sweet taste liking. For a full list of all items in the original DFS questionnaire and used in our liking for sugar subscale see Table 2.

### 2.1.5. Procedure

The session was split into two sections: sensory ratings of tastes and questionnaires. For this paper, we only look at the STT (described in Sections 2.1.2 and 2.1.3) and select questions extracted from a foodliking questionnaire (described in Section 2.1.4).
2.1.5.1. Remote participants. Participants were recruited to complete a 45-minute online task and questionnaire on their food preferences and sensory experiences. After completing the information sheet and consent form, taste packages were sent to the participant's UK home addresses with instructions on participating and storing the solutions (i.e., upright in the fridge). On the day of testing, participants were instructed to eat their normal breakfast or lunch before removing the solutions from the

Table 2
The full list of all items in the original Dietary Fat and free Sugar Short Questionnaire (DFS; Francis \& Stevenson, 2011) and equivalent items used items in our liking for fat, fat-sugar and sugar subscales from the UK Biobank food liking questionnaire adapted from Pallister et al. (2015) and Vink et al. (2020).

| Francis and Stevenson (2011) Original Items and Groupings | UK Biobank Adapted Food Liking Questionnaire Equivalent Items |
| :---: | :---: |
| DFS Grouping - Fat Subscale |  |
| Beef or pork such as steak, ribs, roasts or in sandwiches | Beef steak |
| Cheese or cheese spread (not low fat) | Hard cheese |
|  | Soft cheese |
| Corn chips, potato chips, popcorn with butter | Potato crisps |
| Eggs (not egg whites alone) | Eggs |
| French fries, fried potatoes | Chips/French fries |
| Fried chicken or chicken burgers | Fried chicken |
| Margarine, butter or oil in cooking | - |
| Mince, beef or lamb e.g. in hamburgers, nachos or bolognese | Burgers |
|  | Bolognese |
| Pizza | Pizza |
| Salad dressings (not low in fat) | Salad dressing |
| Sausages, Frankfurt's or salami | Sausages (meat) |
| Bacon | Bacon |
| Cakes, cookies | Biscuits |
|  | Cake |
|  | Cheesecake |
| Chocolate | Milk chocolate |
| DFS Grouping - Fat-Sugar Subscale |  |
| Doughnuts, pastries, croissants | Croissant |
| Ice cream (not sorbet or low fat) | Ice cream |
| Milk (full fat only). Include milk drunk by itself or in cappuccinos, milkshakes, hot chocolates etc.) | Whole milk <br> Sweet coffee house drinks (e.g. <br> Mocha's, Frappucino's, flavoured Latte's) |
| Pancakes or French toast | - |
| Spreads incl. peanut butter, jam honey | Honey |
|  | Jam |
|  | Peanut butter |
| Takeaways | N/A |
| DFS Grouping - Sugar Subscale |  |
| Lollies | - |
| Other sweetened beverages (e.g. juice with added sugar, cordial, sweetened teas) | Apple juice |
|  | Orange juice |
|  | Tea with sugar |
| Soft drinks (not including diet) | Regular (non- diet) fizzy drinks |
| Sports drinks (e.g. Gatorade) or energy drinks (e.g. Red Bull) | - |
| White bread (White bread only) | White bread |
| Spoonful of sugars | N/A |
| N/A | Cake icing ${ }^{\text {a }}$ |
|  | Dried fruit ${ }^{\text {a }}$ |
|  | Fruit ${ }^{\text {a }}$ |

Note. Three lines ( --- ) denotes the item being unavailable, with two questions on the DFS questionnaire, takeaway usage and spoonful of sugars used, being non-applicable to the liking ratings.
${ }^{\text {a }}$ Additional sweet items included in the sugar subscale of the food liking groupings not in the original DFS questionnaire included due to low number of sweet items in the category and to represent wider liking for associated sweet tastes.
fridge to allow them to come to room temperature. Then for the next two hours, they had to refrain from eating or drinking anything apart from water, smoking, chewing gum or brushing their teeth.

After two hours, using their unique code, they were first directed to Inquisit to confirm they had followed the preparation instructions, were not experiencing signs of COVID-19 and that they or anyone in their social bubble had not tested positive for COVID-19 in the last two weeks. After which, they completed the STT. Participants were then automatically re-directed to Qualtrics (Provo UT, USA), where they entered demographic information and completed a series of eating habits questionnaires. They were then debriefed and compensated for their time.
2.1.5.2. Lab participants. These followed the same recruitment, preparation and procedures described above, but participants completed the study in experimental cubicles at The University of Sussex instead of taking part at home.

### 2.1.6. Classifying sweet-liking phenotype status

Sweet-liking status was determined by the ratings for the two 1.0 M sucrose solutions (Iatridi et al., 2019a). Initial checks confirmed whether participants consistently responded: participants who indicated a $>30 \mathrm{pt}$ difference in liking on the VAS scale and indicated liking for one 1.0 M sucrose solution ( $>0$ ) but disliked the other $(<0)$ were classified as erratic, and their data excluded from the analysis. For the remaining participants, both ratings above a score of +15 classified participants as extreme sweet likers, both below a score of -15 classified as sweet dislikers, and between these scores as moderate sweet likers.

### 2.1.7. Data analysis plan

To test whether sweet-liking phenotypes differed in their liking of foods grouped by the five taste qualities (bitter, fatty, salty, spicy and sweet foods) and diet groupings (fat, fat-sugar and sugar), separate multiple linear regression models were run, and key assumptions of the general linear model were checked. This included checks for outliers and influential cases through visual inspection of the data (i.e., histograms), standardised residuals and Cooks distance (Cook \& Weisberg, 1982); spherical errors by plotting residuals vs. predicted values and normality using Q-Q plots. In the final analysis, robust linear regression models were used with Welch $F$ and Games-Howell post-hoc tests to correct for unequal variance and sample size. These are reported alongside parameter estimates and Eta squared effect sizes $\left(\eta p^{2}\right)$ : small effect $<0.06$; medium effect $>0.06$ and $<0.14$; large effect $>0.14$. For all analyses, significance was set at $p<.05$ and were computed using $R$ Studio Version 4.0.4 (Boston, US). For any significant models follow-up analysis were conducted to ensure these were not driven by differences in sex or BMI following the same procedures as described above. In addition, since the analysed data combined results collected at home and in the lab, we ran additional analyses, following the same procedures as described above, to test if location influenced outcomes. Location was not significant in these analyses, and therefore we only report the outcomes for the combined dataset for the sake of brevity.

### 2.2. Results

Following the phenotyping method from Iatridi et al. (2019a) out of

261 participants who completed the taste test, 39 were excluded as erratic responders, leaving a final sample of 222 participants (extreme sweet likers $=85$; moderate sweet likers $=91$; sweet dislikers $=46$ ).

A significant effect of sweet-liking phenotype on liking for sweet foods was found but not for the other four taste qualities (see Fig. 2 and Table 3). On average extreme sweet likers liked sweet foods 1.1 units higher than did sweet dislikers on the 9pt scale (difference $=-1.1$ $[-2.0,-0.3], t(64.40)=3.22, p=.01)$. In addition, there were also significant effects of phenotype on the fat-sugar and sugar liking subscales but not for the fat liking subscale (see Fig. 3 and Table 3). On average extreme sweet likers liked fat-sugar foods 0.7 units higher than did sweet dislikers (difference $=-0.7[-1.3,-0.2], t(78.46)=3.3, p$ $<.001$ ) and sugar items 0.7 units higher (difference $=-0.7$ [ -1.3 , $-0.1], t(68.56)=2.79, p=.02)$. There was no significant main effect of sex, BMI or any sex/BMI by phenotype interaction for liking for sweet foods, fat-sugar or sugar subscales. No other significant differences were found for the five taste qualities or three food groupings between the

Table 3
Summary of effects of phenotype on liking for taste qualities, food groupings and use of food groupings for Experiment One and Two.

| Subscale | Experiment One |  |  | Experiment Two |  |  |
| :---: | :---: | :---: | :---: | :---: | :---: | :---: |
|  | DF | Welchs F | $\eta p^{2}$ | DF | Welchs F | $\eta p^{2}$ |
| Liking for Taste Qualities |  |  |  |  |  |  |
| Bitter | 2, 188.22 | 0.38 | 0 | 2, 162.09 | 5.06** | 0.03 |
| Fatty | 2, 125.6 | 1.64 | 0.01 | 2, 155.2 | 1.39 | 0.01 |
| Salty | 2, 124.14 | 0.7 | 0.01 | 2, 160.52 | 1.47 | 0.01 |
| Spicy | 2, 121.55 | 0.53 | 0 | 2, 165.6 | 1 | 0.01 |
| Sweet | 2, 107.86 | 5.34** | 0.06 | 2, 160.71 | 10.5*** | 0.06 |
| Liking for Food Groupings |  |  |  |  |  |  |
| Fat | 2, 121.11 | 0.81 | 0.01 | 2, 157.03 | 0.88 | 0.01 |
| Fat-Sugar | 2, 115.59 | 5.76** | 0.05 | 2, 158.22 | 5.29** | 0.03 |
| Sugar | 2, 109.98 | 4.85** | 0.04 | 2, 168.08 | 3.01 | 0.02 |
| Food Frequency Questionnaire Groupings |  |  |  |  |  |  |
| Fat | - | - | - | 2, 162.09 | 2.14 | 0.01 |
| Fat-Sugar | - | - | - | 2, 162.04 | 0.02 | 0 |
| Sugar | - | - | - | 2, 156.96 | 0.01 | 0 |
| Total | - | - | - | 2, 163.22 | 0.55 | 0 |

Note. Welchs $F$ are reported alongside adjusted DF and p-vales. These are reported alongside Eta squared effect sizes $\left(\eta p^{2}\right)$ : small effect $<0.06$; medium effect $>0.06$ and $<0.14$; large effect $>0.14$. *p <.05. **p <.01. ***p <.001.


Fig. 2. Mean liking values and boxplots for the five taste qualities, bitter, fatty, salty, spicy and sweet from left to right, by the three sweet-liking phenotypes in Experiment One and Experiment Two. Note the abbreviations for the three phenotypes: Extreme Sweet Likers [ESL.]; Sweet Dislikers [SD]; Moderate Sweet Likers [MSL].


Fig. 3. Mean liking values and boxplots for the three food liking groupings (liking for fat, fat-sweet and sweet items) by the three sweet-liking phenotypes in Experiment One (left) and Experiment Two (right). Note the abbreviations for the three phenotypes: Extreme Sweet Likers [ESL.]; Sweet Dislikers [SD]; Moderate Sweet Likers [MSL].
three phenotypes (see Table 3). For descriptive statistics of all outcomes by phenotype see Table 4.

### 2.3. Discussion

The data in Experiment One suggests that phenotypic differences in sweet taste liking based on evaluation of a 1.0 M sucrose solution did translate to liking of actual sweet foods, with extreme sweet likers rating higher liking for sweet foods than sweet dislikers. This effect was also seen when grouping individual food items by their sensory properties, with extreme sweet likers rating higher liking than sweet dislikers for foods high in fat and sweetness and when taking into account a larger variety of sweet items. This suggests that this effect does not generalise to foods grouped by other taste qualities unless high levels of sweetness is also present. However, Experiment One did not collect consumption data, therefore we cannot see how an increased liking for food high in sweetness by extreme sweet likers translates into actual dietary intake.

Research in this area, exploring how increased liking for sweetness translates into dietary differences, is limited. A review by Tan and Tucker (2019) explored sweet taste as a predictor of dietary intake and included studies with a wider variety of psychophysical tests for sweet taste liking (i.e., liking, preference, intensity and taste sensitivity). They found only a small proportion of available studies reported significant associations between taste sensitivity, intensity, and hedonics with dietary intake, where hedonics seemed to still be the best predictor of overall energy intake. But notably few of those studies had analysed data taking sweet-liking phenotypes into account.

As part of our recent review exploring how sweet-liking phenotypes specifically relate to obesity (Armitage et al., 2021), we reviewed the literature on if the sweet-liking phenotypes differed in dietary intake. We found no differences in intake in many of the foods implicated in obesity (foods high in sugar, salt and fat) but did find increased use of purely sweet products (e.g., sugar-sweetened beverages) by extreme
sweet likers. This implies that sweet dislikers may tolerate sweetness when consumed alongside fat but tend to avoid purely sweet products (Iatridi, 2021). The current literature therefore only provides limited support for the idea that sweet liking per se drives overconsumption. However, relatively few studies used this approach at the time of publication (Garneau et al., 2018; Holt, Cobiac, Beaumont-Smith, Easton, \& Best, 2000; Iatridi, Armitage, Yeomans, \& Hayes, 2020; Methven et al., 2016; Turner-Mcgrievy, Tate, Moore, \& Popkin, 2013).

Therefore, Experiment Two had two aims. Firstly, to try and replicate the effects found in the Experiment One in a separate sample and secondly to test whether increased liking for food high in sweetness by extreme sweet likers translates into actual dietary intake assessed through a food frequency questionnaire following the same grouping as used for liking in Experiment One. As we were predicting differences between the phenotypes in liking for real foods high in sweetness and sweetness and fat, but only differences in consumption for sweet products without fat, we recruited a larger sample to reduce risks of misinterpretation of non-significant findings.

## 3. Experiment two

### 3.1. Method

### 3.1.1. Participants

Participants were 318 volunteers, aged 18-34, who were either staff or students at the University of Sussex, UK or residents from the Brighton and Hove area. They were recruited for a two-part 'Taste, Genetics and Body Composition' lab study at the University of Sussex through advertisements in local Facebook groups, flyers distributed in public spaces and on a participant study website. The same exclusion criteria applied as for Experiment One with the addition of a women needing to report a regular menstrual cycle due to additional anthropometric assessments (not analysed in this paper). Participants were screened to

Table 4
Descriptive statistics of all outcomes by phenotype for Experiment One and Two.

| Subscale | Experiment One |  |  | Experiment Two |  |  |
| :---: | :---: | :---: | :---: | :---: | :---: | :---: |
|  | $\begin{aligned} & \text { ESL }(n \\ & =85) \end{aligned}$ | MSL <br> ( $n=$ <br> 91) | $\begin{aligned} & \mathrm{SD}(n \\ & =46) \end{aligned}$ | $\begin{aligned} & \text { ESL ( } n= \\ & 90 \text { ) } \end{aligned}$ | $\begin{aligned} & \text { MSL ( } n= \\ & 140 \text { ) } \end{aligned}$ | $\begin{aligned} & \text { SD }(n= \\ & 68) \end{aligned}$ |
| Liking for Taste Qualities: $M \pm$ SD |  |  |  |  |  |  |
| Bitter | $\begin{aligned} & 3.76 \pm \\ & 1.8 \end{aligned}$ | $\begin{aligned} & 3.91 \\ & \pm 1.99 \end{aligned}$ | $\begin{aligned} & 3.61 \pm \\ & 1.95 \end{aligned}$ | $\begin{aligned} & 3.53 \pm \\ & 1.94^{\mathrm{d}^{* *}} \end{aligned}$ | $\begin{aligned} & 3.98 \pm \\ & 1.97 \end{aligned}$ | $\begin{aligned} & 4.54 \pm \\ & 2^{\mathrm{d}^{* *}} \end{aligned}$ |
| Fatty | $\begin{aligned} & 6.02 \pm \\ & 1.93 \end{aligned}$ | $\begin{aligned} & 5.67 \\ & \pm 2,2 \end{aligned}$ | $\begin{aligned} & 5.43 \pm \\ & 1.76 \end{aligned}$ | $\begin{aligned} & 5.94 \pm \\ & 1.9 \end{aligned}$ | $\begin{aligned} & 5.95 \pm \\ & 1.85 \end{aligned}$ | $\begin{aligned} & 5.46 \pm \\ & 2.21 \end{aligned}$ |
| Salty | $\begin{aligned} & 6.82 \pm \\ & 1.78 \end{aligned}$ | $\begin{aligned} & 6.52 \\ & \pm 2.17 \end{aligned}$ | $\begin{aligned} & 6.87 \pm \\ & 1.72 \end{aligned}$ | $\begin{aligned} & 6.57 \pm \\ & 1.61 \end{aligned}$ | $\begin{aligned} & 6.69 \pm \\ & 1.72 \end{aligned}$ | $\begin{aligned} & 7.04 \pm \\ & 1.85 \end{aligned}$ |
| Spicy | $\begin{aligned} & 5.98 \pm \\ & 2.58 \end{aligned}$ | $\begin{aligned} & 6.25 \\ & \pm 2.41 \end{aligned}$ | $\begin{aligned} & 5.85 \pm \\ & 2.32 \end{aligned}$ | $\begin{aligned} & 6.22 \pm \\ & 2.63 \end{aligned}$ | $\begin{aligned} & 6.29 \pm \\ & 2.42 \end{aligned}$ | $\begin{aligned} & 6.71 \pm \\ & 2.21 \end{aligned}$ |
| Sweet | $\begin{aligned} & 7.32 \pm \\ & 1.34^{\mathrm{a}^{*}} \end{aligned}$ | $\begin{aligned} & 6.99 \\ & \pm 1.74 \end{aligned}$ | $\begin{aligned} & 6.2 \pm \\ & 2.15^{\mathrm{a}^{\star}} \end{aligned}$ | $\begin{aligned} & 7.54 \pm \\ & 1.37^{\mathrm{e} / \mathrm{f}^{* * *}} \end{aligned}$ | $\begin{aligned} & 6.79 \pm \\ & 1.66^{\mathrm{e}^{\text {e** }}} \end{aligned}$ | $\begin{aligned} & 6.51 \pm \\ & 1.81^{\mathrm{f}^{\mathrm{f**}}} \end{aligned}$ |
| Liking for Food Groupings: $M \pm$ SD |  |  |  |  |  |  |
| Fat | $\begin{aligned} & 6.26 \pm \\ & 1.62 \end{aligned}$ | $\begin{aligned} & 6.23 \\ & \pm 1.58 \end{aligned}$ | $\begin{aligned} & 5.92 \pm \\ & 1.51 \end{aligned}$ | $\begin{aligned} & 6.63 \pm \\ & 1.17 \end{aligned}$ | $\begin{aligned} & 6.46 \pm \\ & 1.23 \end{aligned}$ | $\begin{aligned} & 6.37 \pm \\ & 1.44 \end{aligned}$ |
| FatSugar | $\begin{aligned} & 6.61 \pm \\ & 1.07^{\mathrm{b}^{* *}} \end{aligned}$ | $\begin{aligned} & 6.27 \\ & \pm 1.31 \end{aligned}$ | $\begin{aligned} & 5.88 \pm \\ & 1.3^{b^{* *}} \end{aligned}$ | $\begin{aligned} & 6.53 \pm \\ & 0.855^{g^{* *}} \end{aligned}$ | $\begin{aligned} & 6.26 \pm \\ & 0.98 \end{aligned}$ | $\begin{aligned} & 6.03 \pm \\ & 1.14^{\mathrm{g}^{* *}} \end{aligned}$ |
| Sugar | $\begin{aligned} & 6.2 \pm \\ & 1.06^{\mathrm{c}^{*}} \end{aligned}$ | $\begin{aligned} & 5.82 \\ & \pm 1.28 \end{aligned}$ | $\begin{aligned} & 5.49 \pm \\ & 1.54^{\mathrm{c}^{*}} \end{aligned}$ | $\begin{aligned} & 6.26 \pm \\ & 1.09 \end{aligned}$ | $\begin{aligned} & 5.97 \pm \\ & 1.07 \end{aligned}$ | $\begin{aligned} & 5.88 \pm \\ & 0.94 \end{aligned}$ |
| Food Frequency Questionnaire Groupings: $M \pm$ SD |  |  |  |  |  |  |
| Fat | - | - | - | $\begin{aligned} & 27.93 \pm \\ & 5.57 \end{aligned}$ | $\begin{aligned} & 28.04 \pm \\ & 5.77 \end{aligned}$ | $\begin{aligned} & 26.32 \pm \\ & 5.91 \end{aligned}$ |
| FatSugar | - | - | - | $\begin{aligned} & 17.6 \pm \\ & 4.52 \end{aligned}$ | $\begin{aligned} & 17.69 \pm \\ & 4.09 \end{aligned}$ | $\begin{aligned} & 17.72 \pm \\ & 4.03 \end{aligned}$ |
| Sugar | - | - | - | $\begin{aligned} & 11.4 \pm \\ & 3.8 \end{aligned}$ | $\begin{aligned} & 11.44 \pm \\ & 3.25 \end{aligned}$ | $\begin{aligned} & 11.5 \pm \\ & 3.51 \end{aligned}$ |
| Total | - | - | - | $\begin{aligned} & 56.93 \pm \\ & 11.12 \end{aligned}$ | $\begin{aligned} & 57.16 \pm \\ & 10.81 \end{aligned}$ | $\begin{aligned} & 55.54 \pm \\ & 10.6 \end{aligned}$ |

Note. Abbreviations: Extreme Sweet Likers [ESL.]; Sweet Dislikers [SD]; Moderate Sweet Likers [MSL]. Significant Games Howell Post Hoc tests between phenotypes denoted by letters.
*p <.05. **p <.01. ***p <.001.
ensure they not take part in Experiment One and were rewarded either with a small payment ( $£ 10$ ) or course credits for undergraduates studying Psychology. The study protocol was approved by the University of Sussex Sciences \& Technology Cross-Schools Research Ethics Committee (protocol ER/RA294/12) and was conducted per the ethical standards laid down by the British Psychological Society and the Declaration of Helsinki. A summary of participant characteristics can be found in Table 1.

### 3.1.2. Procedure and materials

Experimental sessions were held in the Human Psychopharmacology Lab at the University of Sussex on the same day with three hours between the start of the two sessions. The first 25 -minute session was an anthropometric assessment conducted between 08:00-11:00 followed by the Dietary Fat and free Sugar Short Questionnaire (Francis \& Stevenson, 2011) administered on Qualtrics (Provo UT, USA). The second session was 35-minutes, held between 11:00-14:00, starting with the STT followed by the UK Biobank adapted food liking questionnaire (see 2.1.4). After which all participants were compensated for their time and debriefed. Materials, procedures and ratings scales for the STT, including the preparation instructions (i.e., to refrain from eating and drinking flavoured beverages, smoking, chewing gum, or brushing their teeth for two hours) and food liking questionnaire remain the same as Experiment One.

### 3.1.3. Food frequency questionnaire

The Dietary Fat and free Sugar Short Questionnaire (DFS; Francis \& Stevenson, 2011) is a reliable and valid measure of saturated fat and refined sugar implicated in obesogenic westernised diets (Francis \&

Stevenson, 2013). This 26 -item questionnaire requires participants to recall the number of times they consumed certain foods and drinks over the preceding 12 months, with each item scored on a scale of $1-5$, with 1 the least frequent (less than once a month) and 5 the most frequent ( $5+$ times a week). Scoring of the DFS generates both an overall total score (FFQ-total) as well as measures for frequency of use of items high in fat (FFQ-fat), sugars (FFQ-sugar), and both fat and sugar (FFQ-fat-sugar). DFS overall scores can range from 26 to 130 with higher scores indicating a poorer quality diet that is higher in saturated fat and added sugar.

### 3.1.4. Analysis plan

Analysis followed that of Experiment One with the same corrections of unequal variance and sample size (see Section 2.1.7) but with the addition of multiple linear regression models to assess whether sweetliking phenotypes differed in their consumption of foods implicated in obesogenic westernised diets that are high in saturated fat and refined carbohydrates as classed by the DFS (Francis \& Stevenson, 2011) described in Section 3.1.3.

### 3.2. Results

Following the phenotyping method from Iatridi et al. (2019a), as used in Experiment One, out of 318 participants who completed the taste test, 22 were excluded as erratic responders, leaving a final sample of 298 participants (extreme sweet likers $=90$; moderate sweet likers $=$ 140; sweet dislikers $=68$ ).

A significant effect of sweet-liking phenotypes were found for liking for sweet food and bitter foods, but not for the other taste qualities (see Fig. 2 and Table 3). On average extreme sweet likers liked sweet foods 1 point higher than sweet dislikers on a 9pt scale (difference $=-1[-1.7$, $-0.4], t(120.47)=3.92, p<.001)$ and 0.8 points higher than moderate sweet likers (difference $=-0.8[-1.2,-0.3], t(214.36)=3.74, p<.001$; see Fig. 2). In addition, extreme sweet likers liked bitter foods 1.0 points less than did sweet dislikers on a 9 pt scale (difference $=1.0[0.3,1.8], t$ $(141.87)=3.18, p<.001)$, although sweet dislikers mean response still fell at the neutral rating (see Fig. 2 and Table 3).

There were also a significant effect of phenotype on the fat-sugar liking subscale but not for the fat liking subscale or, once robust estimation was applied, the sugar liking subscale ( $p=.052$; see Fig. 3 and Table 3). On average extreme sweet likers liked fat-sugar foods 0.5 units higher than did sweet dislikers (difference $=0.5[-0.9,-0.1], t$ $(119.64)=3.07, p=.01)$. There was no significant main effect of sex, BMI or any sex/BMI by phenotype interaction for liking for sweet foods or liking for the fat-sugar subscale, but there was a significant main effect of sex for bitter foods $\left(F(5,100.93)=6.92, p<.001, \eta p^{2}=0.04\right)$ with females rating bitter foods as 0.8 point less pleasant than males on a 9pt scale (difference $=-0.8[-1.2,-0.3], t(251.19)=3.28, p<.001$ ). However, as this did not interact with phenotypes this has no impact on the current findings.

There were no significant differences between the three phenotypes for the food frequency groupings (see Fig. 4 and Table 3). In addition, no other significant differences were found for the five taste qualities, liking food groupings or food frequency groupings between the three phenotypes (see Table 3). For descriptive statistics of all outcomes by phenotype see Table 4.

## 4. General discussion

In this paper, through two closely related experiments, we aimed to investigate how individual differences in liking for sweet taste as defined by the three sweet-liking phenotypes related to participants own perception of their broader liking for taste qualities generalised across all contexts (bitter, fatty, salty, spicy and sweet foods) and for foods implicated in obesogenic westernised diets (foods high in fat, sugar or a combination). In addition, in Experiment Two, we sought to replicate


Fig. 4. Mean scores and boxplots for DFS questionnaire food frequency questionnaire subscales (FFQ fat, FFQ fat-sweet, FFQ sweet and FFQ total), by the three sweet-liking phenotypes in Experiment Two. Note the abbreviations for the three phenotypes: Extreme Sweet Likers [ESL.]; Sweet Dislikers [SD]; Moderate Sweet Likers [MSL].
the findings in Experiment One and to investigate how differences in liking for sweet taste translates into actual dietary intake, as assessed through a food frequency questionnaire (foods high in fat, high in sugar or a combination).

The data in both experiments suggest that phenotypic differences in sweet taste liking based on evaluation of a 1.0 M sucrose solution did translate to differences in liking for sweet foods, with extreme sweet likers giving higher liking ratings for sweet foods than did sweet dislikers. This effect was also seen when grouping individual food items which are characteristic of obesogenic westernised diets by their sensory properties: compared to sweet dislikers, extreme sweet likers rated liking for foods high in fat and sweetness in both experiments higher than did sweet dislikers. This was also observed when a larger variety of sweet tasting items were taken into account as part of Experiment One, and that pattern replicated in Experiment 2, although there the overall effect of phenotype on liking for sweet items was only close to significant once a robust model was applied. Overall, these results clearly suggest that phenotypic differences in liking for a pure sweet taste do predict wider liking for sweetness in the diet, but as these effects are relatively small, it implies that other factors also influence real-life food choice beyond simple taste hedonics. These findings are consistent with the wider conclusions of Adam Drewnowski and colleagues that while sensory responses to taste is an important contributor to food choice, wider factors, including genetic, physiological, and metabolic variables alongside demographic, economic and sociocultural variables all also contribute to food choice (e.g., Drewnowski, 1995; Drewnowski, 1997). In Experiment Two, we also sought to investigate if an increased liking for foods high in sweetness by extreme sweet likers translated into eating foods high in saturated fat and sugar more frequently. No significant differences between the three phenotypes in intake were found. However, this is not surprising since liking for fat rather than sweet taste has been long shown to have the greater influence on food preference and intake (i.e., Drewnowski, Brunzell, Sande, Iverius, \& Greenwood, 1985).

To our knowledge, only five studies have previously investigated the relationship between dietary intake and liking for sweet taste in adults taking into account classification into distinct sweet-liking phenotypes (Garneau et al., 2018; Holt et al., 2000; Iatridi et al., 2020; Methven et al., 2016; Turner-Mcgrievy et al., 2013). However, none have explored liking and intake concurrently, with Garneau et al. (2018), Holt et al. (2000), Iatridi et al. (2020) and Methven et al. (2016) using food frequency questionnaires to assess dietary intake and TurnerMcgrievy et al. (2013) using two 24-hour dietary recalls. Of those studies, three used dichotomous phenotyping with just the two extreme phenotypes (sweet likers and dislikers), which would have misclassified moderate sweet likers (Iatridi et al., 2019b) and, therefore, could have masked the potential effects of the phenotypes on dietary intake. Of these three studies, two reported some significant differences in dietary intake. In Turner-Mcgrievy et al. (2013) sweet likers had a higher intake of sugar-sweetened beverages (SSB) and reduced intake of dietary fibre whilst Holt et al. (2000) reported higher intake of refined sugars by
sweet likers. The third study by Methven et al. (2016) did not find any significant differences between the two phenotypes in total carbohydrate and sugar intake or in sugar consumption as a percentage of total energy intake but noted that this might be due to a lack of power ( $N=$ 36).

Interestingly, Iatridi et al. (2020) who classified participants based on the more robust hierarchical cluster analysis into the three sweetliking phenotypes, used the same dietary assessment as Methven et al. (2016), the EPIC-Norfolk food frequency questionnaire (Bingham et al., 2001) but had greater power $(N=148)$. However, like Methven et al. (2016), they found no significant differences in intake of individual food items between the phenotypes using this measure. Likewise, when, in the same participant group, phenotypic differences in intake of macronutrients were examined using dietary recall data (two weekday- and one weekend day-24-hour recalls), no significant effect of phenotype on energy, fats, carbohydrates, or sugars was revealed (Iatridi, 2021). Iatridi et al. (2020) did, however, report some links between sweetliking phenotypes and habitual use of beverages assessed in two samples: via the relevant EPIC-Norfolk questions $(N=148)$ in the UK and a validated beverage intake questionnaire (BEVQ-15: Hedrick et al., 2012) in the US $(N=126)$. In particular, in participants identified with a higher exposure to the obesogenic environment, intake of sweetened fruit beverages was a significant predictor of the effect of sweet-liking phenotype on both body mass index and waist circumference; in that subpopulation, extreme sweet likers were presented with significantly higher BMI and waist circumference than sweet dislikers (Iatridi et al., 2020).

Overall, this may support the earlier findings of Garneau et al. (2018), who used the BEVQ-15 questionnaire with the three phenotypes across a broader range of ages (18-92 years; $M=42$ ) and found that extreme sweet likers had significantly higher energy intake from SSB. Taken with our findings, these data provide minimal support for the idea that sweet liking per se drives overconsumption since no differences in intake in many of the foods implicated in obesity (foods high in sugar, salt and fat) were found. However, it seems that consistent differences for the intake of SSB only, a highly sweet product whereby its flavour profile is not influenced by other taste qualities.

The literature exploring food liking with the three sweet-liking phenotypes is extremely limited, although some have explored sweet preference and liking for sweet tasting foods using aqueous solutions and model foods (e.g., Mennella, Finkbeiner, Lipchock, Hwang, \& Reed, 2014; Mennella, Finkbeiner, \& Reed, 2012; Tuorila, Keskitalo-Vuokko, Perola, Spector, \& Kaprio, 2017), only one study has previously exploring food liking. Kim et al. (2014) investigated differences in liking ratings for common sweet and savoury foods and for milk and dark chocolate samples, tasted in the lab. Extreme sweet likers consistently rated a higher liking for a range of sweet and savoury food items and a greater preference for sweet milk chocolate compared to the other two phenotypes. However, these items were not grouped by their sensory or macronutrient profile but analysed as separate items instead, where the
influence of broader sensory properties of the food and/or cultural norms (Leng et al., 2017) may have masked wider differences in eating habits. Here we found some support for their findings, with extreme sweet likers also rating higher liking for sweet items and sweet-fat items but not when rating liking for fat items, which were predominantly savoury, when assessed alone.

In addition, in Experiment Two, when rating liking for taste qualities, sweet dislikers also showed a preference for bitter foods over extreme sweet likers. Bitter taste sensitivity is commonly investigated based on the perceived bitterness intensity of the compounds phenylthiocarbamide (PTC) and 6-n-propylthiouracil (PROP) with well-established genetic differences, partly attributed to the TAS2R38 gene (e.g., Bartoshuk, 2000; Bartoshuk, Duffy, \& Miller, 1994; Dinehart, Hayes, Bartoshuk, Lanier, \& Duffy, 2006). As summarised in a recent systematic-review by Diószegi, Llanaj, and Adany (2019) it seems that the variations in the TAS2R38 bitter-taste gene, and not genes encoding the oral detection of sweetness, were significant predictors of sweet preference and intake. This suggests a link between individual differences in sweet-liking and bitter-taste sensitivity. However, most of the studies reviewed by Diószegi et al. (2019) treated sweet-liking as a continuous variable rather than as discrete phenotypes, with no studies to our knowledge investing the possible inter-relationship between sweet liking phenotypes and the three PROP taster status (super-tasters; medium tasters; and non-tasters) alongside dietary habits. Although differences in PROP taster status have been associated with differences in liking for a range of sensory experiences and foods, with those having higher bitter taste sensitivity disliking bitter tasting food and beverages (as reviewed in Feeney et al., 2011; Garcia-Bailo et al., 2009; Tepper et al., 2009).

Yang et al. (2019) and Yeomans et al. (2022) both recently investigated the association between PROP taster status and the three sweetliking phenotypes and found all three sweet-liking phenotypes were represented in all three PROP taster groups. However, Yang et al. (2019) found a tendency for sweet dislikers to have the lowest bitter sensitivity (PROP non-taster group) whereas in contrast Yeomans et al. (2022) found the opposite: sweet dislikers were more likely to be PROP supertasters. This was noted to be likely due to differences in methodology and classification of PROP taster status. Our findings would suggest support for Yang et al. (2019), as you would expect greater liking for bitter foods in those who are non-tasters. However, it is important to note that this effect did not replicate across both studies presented in this paper and although significantly different from extreme sweet likers, responses from sweet dislikers still did not represent a liking response, whose mean response still fell at the neutral rating (see Table 4).

It is important to recognise that preference and intake of sweet foods may depend on oral sensations beyond sweetness (e.g., retronasal flavour components and creamy sensations of high-fat foods: Duffy et al., 2004) and chemosensory learning mechanisms (Prescott, 2012; Yeomans, 2006; Yeomans, 2012). This includes flavour-flavour learning, where pairing a flavour with a sweet taste would result in increased liking for that flavour for extreme sweet likers and a decrease in liking or no increase for sweet dislikers (Yeomans, Prescott, \& Gould, 2009). Therefore, focusing on the intake of sweet tasting products alone may underestimate the broader impact of sweet taste liking on food and drink intake. Considering we found increased liking for foods high in sweetness and fat by extreme sweet likers across both studies, it may also be that those who like sweet taste may differ in wider liking for a range of sweet associated flavours and have a more varied diet (Armitage et al., 2021). However, as we collected habitual intake data for foods high in saturated fat and sugar only, we are unable to investigate this, although we have found preliminary evidence that sweet dislikers seem to tolerate sweetness when consumed with fat (Iatridi, 2021), which could explain why we, and others discussed earlier, did not find differences in intake for the sensory-based groupings we had. Although, promising results from suprathreshold measures published since the Tan and Tucker (2019) review have suggested the potential importance of gustatory
suprathreshold measures, including to sucrose, in predicting dietary carbohydrate composition (Abeywickrema et al., 2023) and ad libitum snack choices (e.g., Abeywickrema, Ginieis, Oey, \& Peng, 2022).

Here, we used a statistically robust method to classify participants into groups of distinct sweet-liking patterns, and after finding promising results in Experiment One, we sought to explore if these would replicate in a larger sample, testing for the first time if the sweet-liking phenotypes differed in liking and intake of food concurrently, focusing on foods commonly associated with obesogenic westernised diets. However, it should also be noted that other methods exist to identify sweet liking phenotypes (as reviewed in Iatridi et al., 2019b), and while no gold standard currently exists, issues with subjective approaches, arbitrary definitions and differences in protocols undermine consistency across prior studies. The method used here, the 'Sussex Taste Test', was designed to resolve these issues and create a less time-consuming, accessible and statistically robust sweet taste liking phenotype discrimination method (Iatridi et al., 2019a). In addition, we must recognise the limitation of using FFQ, as opposed to more in-depth dietary recalls and that the liking and intake questionnaires used were not designed with the exact same food items, only cover a small portion of the diet, and did not specifically allow sensory, macronutrient and sensory macronutrient profiles to be examined. Future research would benefit from combining broader FFQ with dietary recalls that have been designed to evaluate wider dietary patterns and components.

Furthermore, we cannot but acknowledge that our sample might not perfectly reflect the characteristics of the general adult population. Although, in Experiment Two it seems that participants followed a comparable diet to others of their age group (mean age of 21), with similar DFS mean scores as reported elsewhere (i.e., Experiment Two: $56.72 \pm 10.84$; Francis and Stevenson (2013): $59.11 \pm 12.05$; and Mantzios, Egan, Hussain, Keyte, and Bahia (2018): $57.29 \pm 11.71$ ), while still slightly higher than some studies (e.g., Attuquayefio, Stevenson, Oaten, \& Francis, 2017: 53.6 $\pm$ 5.7; Fromm \& Horstmann, 2019: $53.62 \pm 10.29)$. In addition, across both studies, the mean BMI was $<0.9$ units different than the mean BMI in 16-24-year-olds in England (23.5 $\pm 0.25$ : NatCen Social Research, 2022).

In conclusion, these findings suggest that phenotypic differences in sweet taste liking may be specific to liking for foods high in sweetness only and do not generalise to real-life intake or liking for other taste qualities unless high levels of sweetness is also present. This may mean that those who like sweet taste may differ in wider liking for a range of sweet associated flavours and have a more varied diet. Thus, future research should look at the relationship between the three sweet-liking phenotypes and more detailed dietary data. This should include evaluations of tasted foods and should categorise wider food liking and use data concurrently into groups based on sensory, macronutrient and sensory macronutrient profiles to further elucidate these differences.

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## CRediT authorship contribution statement

Rhiannon Mae Armitage: Conceptualization, Methodology, Resources, Investigation, Data curation, Formal analysis, Writing - original draft, Visualization, Project administration. Vasiliki Iatridi: Conceptualization, Validation, Writing - review \& editing. Chi Thanh Vi: Software, Resources, Investigation. Martin Richard Yeomans: Supervision, Validation, Funding acquisition.

## Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence
the work reported in this paper.

## Data availability

Data and analysis scripts will be made available on request.

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## References

Abeywickrema, S., Ginieis, R., Oey, I., \& Peng, M. (2022). Olfactory and Gustatory SupraThreshold Sensitivities Are Linked to Ad Libitum Snack Choice. Foods, 11(6). https:// doi.org/10.3390/foods11060799
Abeywickrema, S., Ginieis, R., Oey, I., Perry, T., Keast, R. S. J., \& Peng, M. (2023). Taste but not smell sensitivities are linked to dietary macronutrient composition. Appetite, 181, Article 106385. https://doi.org/10.1016/j.appet.2022.106385
Armitage, R. M., Iatridi, V., \& Yeomans, M. R. (2021). Understanding sweet-liking phenotypes and their implications for obesity: Narrative review and future directions. Physiology \& Behavior, 235, Article 113398. https://doi.org/10.1016/j. physbeh.2021.113398
Attuquayefio, T., Stevenson, R. J., Oaten, M. J., \& Francis, H. M. (2017). A four-day Western-style dietary intervention causes reductions in hippocampal-dependent learning and memory and interoceptive sensitivity. PLoS ONE, 12(2), Article e0172645. https://doi.org/10.1371/journal.pone. 0172645
Baker, P., \& Friel, S. (2014). Processed foods and the nutrition transition: Evidence from Asia. Obesity Reviews, 15(7), 564-577. https://doi.org/10.1111/obr. 12174
Bartoshuk, L. M. (2000). Comparing sensory experiences across individuals: Recent psychophysical advances illuminate genetic variation in taste perception. Chemical Senses, 25(4), 447-460. https://doi.org/10.1093/chemse/25.4.447
Bartoshuk, L. M., Duffy, V. B., \& Miller, I. J. (1994). PTC/PROP tasting: Anatomy, psychophysics, and sex effects. Physiology \& Behavior, 56(6), 1165-1171. https://doi. org/10.1016/0031-9384(94)90361-1
Bentham, J., \& Di Cesare, M. (2022). Obesity: A long-term global challenge. In G. GarciaAlexander \& J. Poston, D.L. (Eds.), International handbook of the demography of obesity (Vol. 12, pp. 15-37). Springer. [https://doi.org/10.1007/978-3-031-10936-2_2](https://doi.org/10.1007/978-3-031-10936-2_2).
Berthoud, H.-R., Münzberg, H., \& Morrison, C. D. (2017). Blaming the brain for obesity: Integration of hedonic and homeostatic mechanisms. Gastroenterology, 152(7), 1728-1738. https://doi.org/10.1053/j.gastro.2016.12.050
Bingham, S. A., Welch, A. A., McTaggart, A., Mulligan, A. A., Runswick, S. A., Luben, R., ... Day, N. E. (2001). Nutritional methods in the European prospective investigation of cancer in Norfolk. Public Health Nutrition, 4(3), 847-858. https://doi.org/ 10.1079/phn2000102

Breslin, P. A. S. (2013). An evolutionary perspective on food and human taste. Current Biology, 23(9), R409-R418. https://doi.org/10.1016/j.cub.2013.04.010
Carrera-Bastos, P., Fontes-Villalba, M., O'Keefe, J. H., Lindeberg, S., \& Cordain, L. (2011). The western diet and lifestyle and diseases of civilization. Research Reports in Clinical Cardiology, 2, 15-35. https://doi.org/10.2147/RRCC.S16919
Chandrashekar, J., Hoon, M. A., Ryba, N. J., \& Zuker, C. S. (2006). The receptors and cells for mammalian taste. Nature, 444(7117), 288-294. https://doi.org/10.1038/ nature05401
Cook, R. D., \& Weisberg, S. (1982). Residuals and influence in regression. New York: Chapman and Hall.
Daniels, J., \& Daniels, C. (1993). Sugarcane in prehistory. Archaeology in Oceania, 28(1), 1-7. https://doi.org/10.1002/j.1834-4453.1993.tb00309.x
de Graaf, C., \& Boesveldt, S. (2017). The chemical senses and nutrition: The role of taste and smell in the regulation of food intake. In B. Tepper \& M. Yeomans (Eds.), Flavor, satiety and food intake (pp. 35-56). <https://doi.org/10.1002/9781119044970. ch3>.
Dinehart, M. E., Hayes, J. E., Bartoshuk, L. M., Lanier, S. L., \& Duffy, V. B. (2006). Bitter taste markers explain variability in vegetable sweetness, bitterness, and intake. Physiology \& Behavior, 87(2), 304-313. https://doi.org/10.1016/j. physbeh.2005.10.018
Diószegi, J., Llanaj, E., \& Adany, R. (2019). Genetic background of taste perception, taste preferences, and its nutritional implications: A systematic review. Frontiers in Genetics, 10, 1272. https://doi.org/10.3389/fgene.2019.01272
Drewnowski, A. (1995). Energy intake and sensory properties of food. The American Journal of Clinical Nutrition, 62(5), 1081S-1085S. https://doi.org/10.1093/ajcn/ 62.5.1081S

Drewnowski, A. (1997). Taste preferences and food intake. Annual Review of Nutrition, 17, 237-253. https://doi.org/10.1146/annurev.nutr.17.1.237
Drewnowski, A., Brunzell, J. D., Sande, K., Iverius, P., \& Greenwood, M. (1985). Sweet tooth reconsidered: Taste responsiveness in human obesity. Physiology \& Behavior, 35 (4), 617-622. https://doi.org/10.1016/0031-9384(85)90150-7

Drewnowski, A., \& Schwartz, M. (1990). Invisible fats: Sensory assessment of sugar/fat mixtures. Appetite, 14(3), 203-217. https://doi.org/10.1016/0195-6663(90)90088$\stackrel{p}{p}$
Duffy, V. B., Peterson, J. M., \& Bartoshuk, L. M. (2004). Associations between taste genetics, oral sensation and alcohol intake. Physiology \& Behavior, 82(2-3), 435-445. https://doi.org/10.1016/j.physbeh.2004.04.060

Feeney, E., O'Brien, S., Scannell, A., Markey, A., \& Gibney, E. R. (2011). Genetic variation in taste perception: Does it have a role in healthy eating? Proceedings of the Nutrition Society, 70(1), 135-143. https://doi.org/10.1017/s0029665110003976
Francis, H., \& Stevenson, R. (2013). Validity and test-retest reliability of a short dietary questionnaire to assess intake of saturated fat and free sugars: A preliminary study. Journal of Human Nutrition and Dietetics, 26(3), 234-242. https://doi.org/10.1111/ jhn. 12008
Francis, H. M., \& Stevenson, R. J. (2011). Higher reported saturated fat and refined sugar intake is associated with reduced hippocampal-dependent memory and sensitivity to interoceptive signals. Behavioral Neuroscience, 125(6), 943. https://doi.org/ 10.1037/a0025998

Fromm, S. P., \& Horstmann, A. (2019). Psychometric evaluation of the German version of the dietary fat and free sugar-short questionnaire. Obesity Facts, 12(5), 518-528. https://doi.org/10.1159/000501969
Garcia-Bailo, B., Toguri, C., Eny, K. M., \& El-Sohemy, A. (2009). Genetic variation in taste and its influence on food selection. OMICS A Journal of Integrative Biology, 13 (1), 69-80. https://doi.org/10.1089/omi.2008.0031

Garneau, N. L., Nuessle, T. M., Mendelsberg, B. J., Shepard, S., \& Tucker, R. M. (2018). Sweet liker status in children and adults: Consequences for beverage intake in adults. Food Quality and Preference, 65, 175-180. https://doi.org/10.1016/j. foodqual.2017.10.005
Grandner, M. A. (2018). The cost of sleep lost: Implications for health, performance, and the bottom line. American Journal of Health Promotion, 32(7), 1629-1634. https:// doi.org/10.1177/0890117118790621a
Green, B. G., Dalton, P., Cowart, B., Shaffer, G., Rankin, K., \& Higgins, J. (1996). Evaluating the 'Labeled Magnitude Scale' for measuring sensations of taste and smell. Chemical Senses, 21(3), 323-334. https://doi.org/10.1093/chemse/21.3.323
Hayes, J. E., Allen, A. L., \& Bennett, S. M. (2013). Direct comparison of the generalized visual analog scale (gVAS) and general labeled magnitude scale (gLMS). Food Quality and Preference, 28(1), 36-44. https://doi.org/10.1016/j.foodqual.2012.07.012
Hayes, J. E., Sullivan, B. S., \& Duffy, V. B. (2010). Explaining variability in sodium intake through oral sensory phenotype, salt sensation and liking. Physiology \& Behavior, 100 (4), 369-380. https://doi.org/10.1016/j.physbeh.2010.03.017

Hedrick, V. E., Savla, J., Comber, D. L., Flack, K. D., Estabrooks, P. A., Nsiah-Kumi, P. A., ... Davy, B. M. (2012). Development of a brief questionnaire to assess habitual beverage intake (BEVQ-15): Sugar-sweetened beverages and total beverage energy intake. Journal of the Academy of Nutrition and Dietetics, 112(6), 840-849. https:// doi.org/10.1016/j.jand.2012.01.023
Holt, S. H. A., Cobiac, L., Beaumont-Smith, N. E., Easton, K., \& Best, D. J. (2000). Dietary habits and the perception and liking of sweetness among Australian and Malaysian students: A cross-cultural study. Food Quality and Preference, 11(4), 299-312. https://doi.org/10.1016/S0950-3293(99)00076-2
Iatridi, V. (2021). Understanding sweet liking and disliking: Re-evaluating sweet taste as a driver of overconsumption. [Doctoral dissertation, University of Sussex]. <http://sro. sussex.ac.uk/id/eprint/101563/>.
Iatridi, V., Armitage, R. M., Yeomans, M. R., \& Hayes, J. E. (2020). Effects of sweet-liking on body composition depend on age and lifestyle: A challenge to the simple sweet-liking-Obesity hypothesis. Nutrients, 12(9), 2702. https://doi.org/10.3390/ nu12092702
Iatridi, V., Hayes, J., \& Yeomans, M. (2019a). Quantifying sweet taste liker phenotypes: Time for some consistency in the classification criteria. Nutrients, 11(1), 129. https:// doi.org/10.3390/nu11010129
Iatridi, V., Hayes, J. E., \& Yeomans, M. R. (2019b). Reconsidering the classification of sweet taste liker phenotypes: A methodological review. Food Quality and Preference, 72, 56-76. https://doi.org/10.1016/J.FOODQUAL.2018.09.001
Kavaliauskaite, G., Thibodeau, M., Ford, R., \& Yang, Q. (2023). Using correlation matrices to standardise sweet liking status classification. Food Quality and Preference, 104, Article 104759. https://doi.org/10.1016/j.foodqual.2022.104759
Kim, J.-Y., Prescott, J., \& Kim, K.-O. (2014). Patterns of sweet liking in sucrose solutions and beverages. Food Quality and Preference, 36, 96-103. https://doi.org/10.1016/j. foodqual.2014.03.009
Kopp, W. (2019). How western diet and lifestyle drive the pandemic of obesity and civilization diseases. Diabetes, Metabolic Syndrome and Obesity: Targets and Therapy, 12, 2221-2236. https://doi.org/10.2147/dmso.s216791
Lapis, T. J., Penner, M. H., \& Lim, J. (2016). Humans can taste glucose oligomers independent of the hT1R2/hT1R3 sweet taste receptor. Chemical Senses, 41(9), 755-762. https://doi.org/10.1093/chemse/bjw088
Leng, G., Adan, R. A. H., Belot, M., Brunstrom, J. M., De Graaf, K., Dickson, S. L., Smeets, P. A. M. (2017). The determinants of food choice. Proceedings of the Nutrition Society, 76(3), 316-327. https://doi.org/10.1017/s002966511600286x
Lim, A. J., Teo, P. S., Tan, V. W. K., \& Forde, C. G. (2020). Associations between psychohedonic responses to sweet and savoury tastes with diet and body composition in a sample of Asian females. Foods, 9(9), 1318. https://doi.org/10.3390/foods9091318
Loos, R. J., \& Yeo, G. S. (2022). The genetics of obesity: From discovery to biology. Nature Reviews Genetics, 23(2), 120-133. https://doi.org/10.1007/s11892-010-0153-z
Mantzios, M., Egan, H., Hussain, M., Keyte, R., \& Bahia, H. (2018). Mindfulness, selfcompassion, and mindful eating in relation to fat and sugar consumption: An exploratory investigation. Eating and Weight Disorders - Studies on Anorexia, Bulimia and Obesity, 23(6), 833-840. https://doi.org/10.1007/s40519-018-0548-4
Mennella, J. A., Finkbeiner, S., Lipchock, S. V., Hwang, L.-D., \& Reed, D. R. (2014). Preferences for salty and sweet tastes are elevated and related to each other during childhood. PLoS ONE, 9(3), Article e92201. https://doi.org/10.1371/journal. pone. 0092201

Mennella, J. A., Finkbeiner, S., \& Reed, D. R. (2012). The proof is in the pudding: Children prefer lower fat but higher sugar than do mothers. International Journal of Obesity, 36(10), 1285-1291. https://doi.org/10.1038/ijo.2012.51
Methven, L., Xiao, C., Cai, M., \& Prescott, J. (2016). Rejection thresholds (RjT) of sweet likers and dislikers. Food Quality and Preference, 52, 74-80. https://doi.org/10.1016/ j.foodqual.2016.03.012

NatCen Social Research, U. C. L. (2022). Department of epidemiology and public health. Health survey for england, 2021.[data collection]. UK Data Service. SN: 7260.
Ng, S. W., \& Popkin, B. M. (2012). Time use and physical activity: A shift away from movement across the globe. Obesity Reviews, 13(8), 659-680. https://doi.org/ 10.1111/j.1467-789x.2011.00982.x

Olszewski, P. K., Wood, E. L., Klockars, A., \& Levine, A. S. (2019). Excessive consumption of sugar: An insatiable drive for reward. Current nutrition reports, 8(2), 120-128. https://doi.org/10.1007/s13668-019-0270-5
Pagliarini, E., Proserpio, C., Spinelli, S., Lavelli, V., Laureati, M., Arena, E., .. Dinnella, C. (2021). The role of sour and bitter perception in liking, familiarity and choice for phenol-rich plant-based foods. Food Quality and Preference, 93, Article 104250. https://doi.org/10.1016/j.foodqual.2021.104250

Pallister, T., Sharafi, M., Lachance, G., Pirastu, N., Mohney, R. P., MacGregor, A., ... Menni, C. (2015). Food preference patterns in a UK twin cohort. Twin Research and Human Genetics, 18(6), 793-805. https://doi.org/10.1017/thg.2015.69
Pangborn, R. M. (1970). Individual variation in affective responses to taste stimuli. Psychonomic Science, 21(2), 125-126. https://doi.org/10.3758/BF03335798
Popkin, B. M., Adair, L. S., \& Ng, S. W. (2012). Global nutrition transition and the pandemic of obesity in developing countries. Nutrition Reviews, 70(1), 3-21. https:// doi.org/10.1111/j.1753-4887.2011.00456.x
Prescott, J. (2012). Chemosensory learning and flavour: Perception, preference and intake. Physiology \& Behavior, 107(4), 553-559. https://doi.org/10.1016/j. physbeh.2012.04.008
Rauber, F., Louzada, M. L. d. C., Steele, E. M., Millett, C., Monteiro, C. A., \& Levy, R. B. (2018). Ultra-processed food consumption and chronic non-communicable diseasesrelated dietary nutrient profile in the UK (2008-2014). Nutrients, 10(5), 587. [https://doi.org/10.3390/nu10050587](https://doi.org/10.3390/nu10050587).
Running, C. A., Craig, B. A., \& Mattes, R. D. (2015). Oleogustus: The unique taste of fat. Chemical Senses, 40(7), 507-516. https://doi.org/10.1093/chemse/bjv036
Smith, A. E., \& Hommel, J. D. (2022). Neuroanatomical integration of homeostatic and hedonic brain regions to regulate consummatory behavior.
Neuropsychopharmacology, 47(1), 417. https://doi.org/10.1038/s41386-021-011655
Spinelli, S., Prescott, J., Pierguidi, L., Dinnella, C., Arena, E., Braghieri, A., ... Monteleone, E. (2021). Phenol-rich food acceptability: The influence of variations in sweetness optima and sensory-liking patterns. Nutrients, 13(3), 866. https://doi.org/ 10.3390/nu13030866

Stein, W. M., \& Keller, K. L. (2015). The modern food environment: Changes in food quantity and quality and their impact on hedonic eating. In N. Avena (Ed.), Hedonic
eating: How the pleasurable aspects of food can affect our brains and behavior (pp. 0). Oxford University Press. <https://doi.org/10.1093/med/ 9780199330454.003.0009>.

Swinburn, B. A., Sacks, G., Hall, K. D., McPherson, K., Finegood, D. T., Moodie, M. L., \& Gortmaker, S. L. (2011). The global obesity pandemic: Shaped by global drivers and local environments. The Lancet, 378(9793), 804-814. https://doi.org/10.1016/ S0140-6736(11)60813-1
Tan, S.-Y., \& Tucker, R. M. (2019). Sweet taste as a predictor of dietary intake: A systematic review. Nutrients, 11(1), 94. https://doi.org/10.3390/nu11010094
Tepper, B. J., White, E. A., Koelliker, Y., Lanzara, C., D’Adamo, P., \& Gasparini, P. (2009). Genetic variation in taste sensitivity to 6-n-propylthiouracil and its relationship to taste perception and food selection. Annals of the New York Academy of Sciences, 1170(1), 126-139. https://doi.org/10.1111/j.1749-6632.2009.03916.x
Törnwall, O., Silventoinen, K., Hiekkalinna, T., Perola, M., Tuorila, H., \& Kaprio, J. (2014). Identifying flavor preference subgroups. Genetic basis and related eating behavior traits. Appetite, 75, 1-10. https://doi.org/10.1016/j.appet.2013.11.020
Tuorila, H., Keskitalo-Vuokko, K., Perola, M., Spector, T., \& Kaprio, J. (2017). Affective responses to sweet products and sweet solution in British and Finnish adults. Food Quality and Preference, 62, 128-136. https://doi.org/10.1016/j. foodqual.2017.06.021
Turner-Mcgrievy, G., Tate, D. F., Moore, D., \& Popkin, B. (2013). Taking the bitter with the sweet: Relationship of supertasting and sweet preference with metabolic syndrome and dietary intake. Journal of Food Science, 78(2), S336-S342. https://doi. org/10.1111/1750-3841.12008
Vink, J. M., Van Hooijdonk, K. J., Willemsen, G., Feskens, E. J., \& Boomsma, D. I. (2020). Causes of variation in food preference in the Netherlands. Twin Research and Human Genetics, 23(4), 195-203. https://doi.org/10.1017/thg.2020.66
Yang, Q., Kraft, M., Shen, Y., Macfie, H., \& Ford, R. (2019). Sweet Liking Status and PROP Taster Status impact emotional response to sweetened beverage. Food Quality and Preference, 75, 133-144. https://doi.org/10.1016/j.foodqual.2019.02.016
Yeomans, M. R. (2006). The role of learning in development of food preferences. CABI Books. [https://doi.org/10.1079/9780851990323.0093](https://doi.org/10.1079/9780851990323.0093).
Yeomans, M. R. (2012). Flavour-nutrient learning in humans: An elusive phenomenon? Physiology \& Behavior, 106(3), 345-355. https://doi.org/10.1016/j. physbeh.2012.03.013
Yeomans, M. R., Prescott, J., \& Gould, N. J. (2009). Acquired hedonic and sensory characteristics of odours: Influence of sweet liker and propylthiouracil taster status. Quarterly Journal of Experimental Psychology, 62(8), 1648-1664. https://doi.org/ 10.1080/17470210802557793

Yeomans, M. R., Vi, C., Mohammed, N., \& Armitage, R. M. (2022). Re-evaluating how sweet-liking and PROP-tasting are related. Physiology \& Behavior, 246, Article 113702. https://doi.org/10.1016/j.physbeh.2022.113702

Zandstra, E. H., \& de Graaf, C. (1998). Sensory perception and pleasantness of orange beverages from childhood to old age. Food Quality and Preference, 9(1), 5-12. https://doi.org/10.1016/S0950-3293(97)00015-3


[^0]:    Abbreviations: ESL, Extreme sweet likers; MSL, Moderate sweet likers; SD, Sweet dislikers.

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[^1]:    Note. Abbreviations: Body Mass Index [BMI]; Extreme Sweet Likers [ESL.]; Sweet Dislikers [SD]; Moderate Sweet Likers [MSL].
    ${ }^{\text {a }}$ BMI data is unavailable for seven participants in Experiment One (3\% of total participants).
    ${ }^{\mathrm{b}}$ One participant in Experiment One (1\%) classified as a moderate sweet liker has missing demographic information.

