Appetite 165 (2021) 105290

Contents lists available at ScienceDirect

Appetite

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

Female sweet-likers have enhanced cross-modal interoceptive abilities

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ARTICLE INFO

Keywords:
Sweet-liking
Homeostatic eating
Interoception
Hunger cues
Emotional eating
Mindfulness

ABSTRACT

There are well known phenotypic differences in sweet-liking across individuals, but it remains unknown whether these are related to broader underlying differences in interoceptive abilities (abilities to sense the internal state of the body). Here, healthy women ($N = 64$) classified as sweet likers (SLs) or sweet dislikers (SDs) completed a bimodal interoception protocol. A heartbeat tracking and a heartbeat discrimination task determined cardiac interoception; both were accompanied by confidence ratings. A water load task, where participants consumed water to satiation and then to maximum fullness was used to assess gastric interoceptive abilities. Motivational state, psychometric characteristics and eating behaviour were also assessed. SLs performed significantly better than SDs on both heartbeat tasks, independently of impulsivity, anxiety, depression, and alexithymia. No differences in metacognitive awareness and subjective interoceptive measures were found. With gastric interoception, SLs were more sensitive to stomach distention, and they ingested less water than SDs to reach satiety when accounting for stomach capacity. SLs also scored higher on mindful and intuitive eating scales and on emotional eating particularly in response to negative stimuli; emotional overeating was fully mediated via interoceptive performance. Overall, our data suggest the SL phenotype may reflect enhanced responsiveness to internal cues more broadly.

1. Introduction

Food choice and intake typically occur in response to need for energy and pleasure seeking (Berthoud, Münzberg, & Morrison, 2017). It should be noted that, while some have argued that the obesity epidemic has occurred among increased availability of highly palatable foods in Western and Westernising societies, suggesting an increasing role for hedonic drive in the control of food intake (Yeomans, Blundell, & Leshem, 2004), need-state still remains a critical aspect of human feeding behaviour (Berthoud et al., 2017). Moreover, the obesogenic environment puts pressure on the homoeostatic regulatory system: we misinterpret or confound internally generated nutritional and metabolic signals being unable to monitor food choice and intake in accordance to need state (Bilman, van Kleef, & van Trijp, 2017; Sample, Jones, Hargrave, Jarrard, & Davidson, 2016). However, some individuals appear to be less responsive to influences of the modern environment. Some

Abbreviations: BMI, Body Mass Index; BPQ, Body Perception Questionnaire; DEBQ, Dutch Eating Behaviour Questionnaire; EMAQ, Emotional Appetite Questionnaire; gLMS, generalized Labelled Magnitude Scale; IAcHDi, Interoception Accuracy from the Heartbeat Discrimination task; IAcHTr, Interoception Accuracy from the Heartbeat Tracking task; IAw, Interoceptive Awareness; IAwHDi, Interoceptive Awareness from the Heartbeat Discrimination task; IAwHTr, Interoceptive Awareness from the Heartbeat Tracking task; I S_HDi, Interoceptive Sensibility from the Heartbeat Discrimination task; IES, Intuitive Eating Scale; IS_HTr, Interoceptive Sensibility from the Heartbeat Tracking task; ITPE, Trait Prediction Error; MEQ, Mindful Eating Questionnaire; ROC, Receiver Operating Characteristic; SD, Sweet Disliker; SL, Sweet Liker; VAS, Visual Analogue Scale; WLT, Water Load Test.

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https://doi.org/10.1016/j.appet.2021.105290
Received 3 June 2020; Received in revised form 19 April 2021; Accepted 27 April 2021
Available online 6 May 2021
0195-6663/

researchers have focused on understanding individual differences in the susceptibility to the maladaptive effects of obesogenic environment on mechanisms involved in decision-making around food. Interpersonal variation in interoceptive ability, which is defined as one's ability to perceive their internal bodily state (Craig, 2002), may be especially relevant.

Historically, interoception has referred to sensing the state of various inner systems such as the viscera, skin, chemical/osmotic homeostatic systems, and emotions (Schleip & Jäger, 2012). Here, we focus more narrowly on the cardiac and gastric modes of interoception. Gastric interoception is believed to reflect aspects of the gut-brain communication (Stevenson, Mahmut, & Rooney, 2015), and, therefore, it may be involved in the decision-making around food: ingested food causes stomach distention which activates vagal afferent neurons that pass the information about the change in stomach volume to the brain (Ritter, 2004). Regarding cardiac interoception, while it is often considered as an indicator of 'general' interoceptive abilities (Tsakiris & Critchley, 2016), some evidence supports its link with experienced hunger (Herbert, Muth, Pollatos, & Herbert, 2012) and homeostatically-driven eating styles (Herbert, Blechert, Hautzinger, Matthias, & Herbert, 2013; Richard et al., 2019), as well.

Although putative relationships between reduced sensitivity to homeostatic signals and energy intake have been suggested for decades (Berthoud et al., 2017), only recently have researchers begun exploring whether variation in the ability to sense the state of the internal body – that is, interoception – might be associated with eating behaviour. To date, two eating patterns that encompass the principles of homeostatically-driven eating have been sufficiently documented: intuitive and mindful eating. The reports directly examining the relationship between cardioceptive accuracy and intuitive eating have shown positive correlations (Herbert et al., 2013; Richard et al., 2019); evidence of a relationship between objectively measured interoceptive accuracy and compliance to the principles of mindful eating is, however, lacking. Nonetheless, the mechanisms related to interoception have been proposed to explain the benefits of practising mindful eating vis-à-vis weight control (Warren, Smith, & Ashwell, 2017, pp. 272–283). A review by Quadt, Critchley, and Garfinkel (2018) proposing altered interoception in those with eating and feeding disorders further supports this rationale. Regarding the other element of interoception, that of its relation to emotions (Critchley & Garfinkel, 2017, pp. 7–14), some preliminary evidence has suggested that high interoceptive performers could be more prone to emotional eating (Koch & Pollatos, 2014; Young et al., 2017). The possible dissociable effect of positive versus negative emotions on gustatory decision making (Macht, 2008) has still to be elucidated.

Brain areas known to mediate interoceptive processes also receive afferents from the gustatory system (Avery et al., 2015; Kurth, Zilles, Fox, Laird, & Eickhoff, 2010), whilst homeostatic signals that serve the gut-brain communication also project to regions where interoception and gustation appear to be co-located (Simmons & DeVille, 2017). Can, then, individual differences in interoceptive abilities and variation in taste responses be linked as this shared neural representation of interoception and gustation suggests? Alliesthesia, a classical phenomenon whereby experienced pleasure for a given sensory stimulus changes depending on the internal state of the body (Cabanac, 1979), may provide some support for the hypothesized convergence of interoceptive and gustatory information. Taste is classically considered an exteroceptive sense, and taste hedonics are also key features in food choice and intake (Boesveldt & de Graaf, 2017; Hayes, 2020, pp. 1–25).

From a public health perspective, sweetness appears to be the taste modality of most interest. By signifying nutritious and safe food sources (Drewnowski, Mennella, Johnson, & Bellisle, 2012) and activating reward circuits in the brain (Wiss, Avena, & Rada, 2018), sweetness uniquely forms food preferences. Moreover, high-sugar consumption has been a common target of healthy eating campaigns (WHO, 2015) due to its contribution to obesity (Hu, 2013) and modern diseases (Stanhope, 2016). While studies reporting distinct hedonic responses to sweetness (sweet taste phenotypes) date back a half century, recent data have emphasized the importance of accounting for individual variation in sweet-liking (bIatridi, Hayes, & Yeomans, 2019b; Tan & Tucker, 2019). Despite some inconsistencies in methods used to identify distinct sweet taste phenotypes, when effects of these phenotypes on weight status were examined, some researchers (Grinker, 1977; Grinker & Hirsch, 1972; Johnson et al., 1979; Malcolm, O'Neil, Hirsch, Currey, & Moskowitz, 1980; Thai et al., 2011) have reported those liking ever-higher sweetness (i.e. sweet likers; SLs), were more often of normal weight compared to sweet dislikers (i.e. individuals expressing aversive responses to high sweetness; SDs). In a multi-country study, we recently found that SLs had either lower fat mass or greater fat free mass than SDs (Iatridi, Armitage, Yeomans, & Hayes, 2020). We concluded that, for SLs, hedonic response to sweetness matched their bodily needs, either in respect to energy stores or energy requirements. Conversely, SDs seemed to be less responsive to the internal state of their body, especially for the subgroup of SDs who were more exposed to an obesogenic environment. This aligns with a model arguing that the human body has drifted evolutionary in its responsiveness to positive feedback loops that relate to surplus in internal energy stores, i.e. it is less effective in resisting to weight increases (Speakman et al., 2011). Conversely, human body primarily defends undersupply in order to prevent or reverse body mass loss (Speakman et al., 2011). Further, SLs also exhibited behavioural characteristics analogous to those of high interoceptive performers, such as enhanced trait-hunger, intensity seeking, and reward sensitivity (Iatridi, Armitage, et al., 2020). Collectively then, interoception appears to be a good candidate to explain the observed effects of sweet taste phenotype on body composition and psychometric profiles.

To date, most research on interoceptive processes has focused on sensitivity to cardiac signals. Whether interoceptive abilities measured using cardiac or gastric interoception tasks can be considered to be equivalent entities has not been resolved thus far. Still, experimental data from objective interoceptive measures suggests some degree of overlap in perceiving these discrete visceral events. For example, Whitehead and Drescher showed accuracy in detecting stomach contractions and heartbeats were significantly correlated (Whitehead & Drescher, 1980). Using more modern techniques, other groups have confirmed this association, with cardiac accuracy predicting the amount of water volume required for fullness to be sensed (Garfinkel, Manassei, Engels, Gould, & Critchley, 2017; Herbert et al., 2012). However, Herbert and colleagues also noted there were no differences in subjective fullness ratings between high and low cardiac perceivers (Herbert et al., 2012). Discrepancies in interoceptive accuracy across senses have also been reported (Ferentzi et al., 2018) including a study where, unlike in previous investigations, a water load task accounting for individual differences in stomach capacity was used (van Dyck et al., 2016). To the best of our knowledge, no subsequent study has tested putative associations between the ability to sense gastric and cardiac signals while accounting for stomach capacity; we address this knowledge gap here. Given that the primary aim of the present study was to investigate the phenotype-specific differences in interoceptive abilities within an ingestive behaviour context, inclusion of a bimodal interoception task was deemed essential.

In summary, except for one study on multimodal interoception that found no correlation between bitterness liking and interoceptive accuracy operationalized via cardiac and gastric measures (Ferentzi et al., 2018), this is the first systematic attempt to link interoceptive abilities and distinct gustatory hedonic patterns for sweetness. To do so, we contrasted two extreme hedonic patterns for sweet taste: SL and SD phenotypes using a bimodal interoception protocol which incorporated state of the art cardiac (Garfinkel, Seth, Barrett, Suzuki, & Critchley, 2015) and gastric (van Dyck et al., 2016) interoception tasks. Based on previous work from our research group (Iatridi, Armitage, et al., 2020), we hypothesized SLs would exhibit better interoceptive performance than SDs. Likewise, the predictive utility of sweet taste phenotype for eating behaviours believed to relate to homeostatic or hedonic eating was also tested: we predicted that there would be a mediating effect of interoceptive performance in the phenotype-specific differences in intuitive, mindful, and emotional eating. To help address inconsistencies in the existing literature, we also adopted the following definitions to quantify distinct dimensions in interoception: *interoceptive accuracy* (i.e. interoceptive performance), which is an objective index of interoceptive ability and assessed using tests such as the heartbeat detection (Garfinkel et al., 2015; Garfinkel & Critchley, 2013) and voluntary water ingestion (i.e., water load: van Dyck et al., 2016) tasks; (2) *interoceptive sensibility*, which is a subjective measure of interoceptive ability as it represents the self-reported tendency to focus on signals of the inner body, assessed using confidence ratings or questionnaires for a range of sensations (Garfinkel et al., 2015; Garfinkel & Critchley, 2013); (3) *interoceptive awareness* that reflects the metacognitive awareness of interoceptive accuracy and calculated by combining the mathematical results of accuracy and sensibility (confidence ratings) measures (Garfinkel et al., 2015; Garfinkel & Critchley, 2013); and (4) *trait prediction error,* which quantifies the discrepancy between objective assessments of interoceptive accuracy and interoceptive sensibility (questionnaires) for a range of sensations (Garfinkel et al., 2016).

2. Methods

2.1. Participants

Sixty-four women aged 18–34 years old were recruited from students and staff at the University of Sussex. Sample size was determined from earlier studies in women where associations between interoceptive abilities and eating habits and behaviours such as intuitive eating (Richard et al., 2019) and emotional eating (Young et al., 2017), as well as the association between interoceptive performance across senses had been considered (Herbert et al., 2012). Given that men and women differ in both objective and subjective measures of interoception (Grabauskaitė, Baranauskas, & Griškova-Bulanova, 2017) and in many eating behaviours (Rolls, Fedoroff, & Guthrie, 1991), as well as sex influencing food-related activation of brain areas closely related to interoceptive processes (Chao et al., 2017, pp. 687–699), a decision was made to only recruit women for the study. As part of the recruitment process, potential participants were screened for their sweet taste phenotype: only those classified as SLs or SDs were invited back to complete the interoception tasks and behavioural questionnaires (see 2.2. for details). During screening, all but four participants (one SL and three SDs) attended a separate early morning session to obtain anthropometry; BMI and body composition were measured using bio-impedance (MC-780 MA P, TANITA, UK). Before anthropometry, participants were asked to abstain from food and water for 8 h, to not exercise for 12 h, and to avoid consuming alcohol for 24 h (Kyle et al., 2004); compliance was confirmed verbally upon arrival to the laboratory.

In addition to exclusion criteria related to the taste test (i.e., diabetes, prescription medication other than oral contraception, irregular menstrual cycle, smoking 5+ cigarettes per week, being on a weight loss regimen and/or on a special diet for medical reasons, current respiratory illness, history of a dental procedure within the past two weeks), potential participants were also screened for a current diagnosis of mental and psychiatric disorders, past or current diagnosis of gastro-oesophageal reflux disease and/or hiatal hernia, a current diagnosis of diabetes insipidus, and a current or past diagnosis of cardiac arrhythmias and/or any other cardiovascular and/or heart disease. All study procedures (Fig. 1) were carried out in accordance with the Declaration of Helsinki, and written informed consent was obtained at enrolment. The protocol was approved by the Science and Technology Cross-Schools Research Ethics Committee of the University of Sussex (ER/VI40/2).

2.2. Sweet taste test

Participants rated liking for a 1 M sucrose solution on a visual analogue scale (VAS) ranging from −50 to +50; liking scores above +15 and below −15 were used to define participants as SL or SD, respectively. These criteria were recently proposed by our lab (Iatridi, Hayes, & Yeomans, 2019a) and further validated in a multi-country study (Iatridi, Hayes, & Yeomans, 2020). During screening, potential participants rated two series of 0 M and 1 M sucrose solutions presented using a 'sip and spit' protocol with a rinsing step between the stimuli and a 2-min break between the two sets of stimuli. Participants were asked to refrain from consuming foods and flavored drinks, smoking, chewing gum, and tooth brushing for the 2 h prior screening; compliance was confirmed verbally upon arrival to the laboratory. Sucrose solutions were prepared weekly at room temperature (22 °C) by dissolving food-grade sugar in mineral water. All taste stimuli were stored at 4 °C and brought back to room temperature before tasting. Perceived liking ('How much did you like Sample X?') and intensity ('How sweet was Sample X?') were recorded on a visual analogue scale (VAS) anchored as 'Dislike Extremely' (−50) and 'Like Extremely' (+50) and a generalized labelled magnitude scale (gLMS) ranging from 'No Sensation' (0) to 'Strongest Sensation of any Kind' (100), respectively; training for scales was provided, presented using Sussex Ingestion Pattern Monitor (SIPM, University of Sussex, UK). Both 1 M replicates had to be rated higher than +15 or below −15 for the classification into the SL and SD phenotype, respectively (Mobini, Chambers, & Yeomans, 2007).

2.3. Interoception (objective measures) – interoceptive accuracy

2.3.1. Cardiac interoception

To determine interoceptive accuracy, two cardiac detection tasks were utilized: a heartbeat tracking (Schandry, 1981) and a heartbeat discrimination task (Whitehead, Drescher, Heiman, & Blackwell, 1977) using electrocardiography were employed; they were programmed in Psychtoolbox-3 for MATLAB (MathWorks Inc., Natick, MA) executed on a laptop computer running Microsoft Windows. The same researcher who was present during both tasks tested all participants. The researcher was blind to each trial's characteristics and accuracy of recorded responses (i.e. duration of each heartbeat tracking trial, synchronicity between played tones and heartbeats, and score earned per trial – see

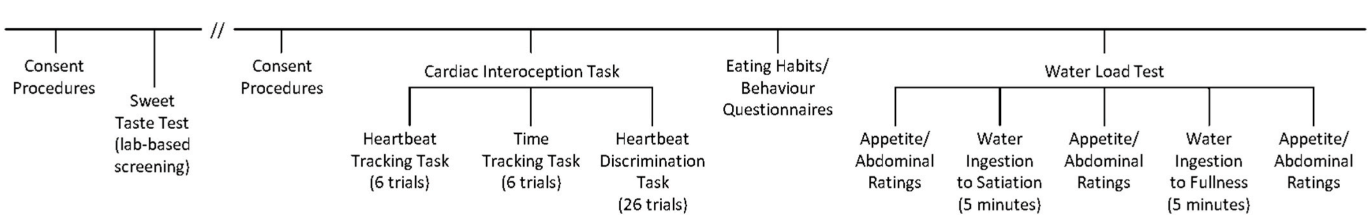

Fig. 1. The lab-based sweet taste test, as well as the analysis of participants' body composition (optional session; not shown) took place a few days before the interoception tasks.

2.3.1.1 and 2.3.1.2 for details). The researcher provided instructions, coordinated tasks, and made electronic records of participants' responses immediately after the end of each trial. A soft pulse oximeter (Xpod, Nonin, Medical Inc.) connected through a USB port to the laptop was attached to the participants' non-dominant index finger to record their actual heart rate. As opposed to hard-clip oximeters, soft pulse oximeters provide similar accuracy to an electrocardiogram (Murphy et al., 2019). During both cardiac tasks, participants remained seated, relatively still, and with their arm comfortably rested on a pillow placed on a flat surface in front of them. They were also instructed to breathe at a regular pace.

Upon completion of the heartbeat tasks, participants completed a series of mood questionnaires to assess known confounders of interoceptive performance. Specifically, anxiety (Domschke, Stevens, Pfleiderer, & Gerlach, 2010), depression (Paulus & Stein, 2010, pp. 451–463), alexithymia (Brewer, Cook, & Bird, 2016), and impulsivity (Chen et al., 2018) have all been associated with altered interoception, so the General Anxiety Disorder-7 (Spitzer, Kroenke, Williams, & Löwe, 2006), Patient Health Questionnaire-9 (Spitzer, Kroenke, & Williams, 1999), Toronto Alexithymia Scale (Bagby, Parker, & Taylor, 1994), and Barratt Impulsiveness Scale (Patton, Stanford, & Barratt, 1995) were administered. Participants' beliefs about heart rate ('Do you know what a heart rate is?', 'Do you know what your heart is?') were also obtained (Murphy, Millgate, et al., 2018).

2.3.1.1. Heartbeat tracking task. For the heartbeat tracking task (Schandry, 1981), participants were asked to internally count their heartbeats across six trials varying in duration (25, 30, 35, 40, 40, 45 and 50 s in a randomized order). The start and end of each interval was signaled by an auditory cue ("start" and "stop") delivered via software. The instructions were: "Without manually taking your pulse, please count each heartbeat you feel from the time you hear "start" to when you hear "stop'' as it will be prompted by the computer."

Heartbeat tracking accuracy score (IAcHTr; Interoception Accuracy from the Heartbeat Tracking task) was calculated by averaging relevant accuracy scores across the six trials. The latter was computed from the following formula:

$1 - \frac{|n\text{beatsreal} - n\text{beatsreported}|}{(n\text{beatsreal} + n\text{beatsreported})/2}$ per trial (Hart, McGowan, Minati, & Critchley, 2013).

2.3.1.2. Heartbeat discrimination task. The heartbeat discrimination task comprised of 26 blocks of auditory tones played for 100 ms at 440 Hz; half of the blocks were synchronized with the participant's heartbeat and half were presented with a 300 ms delay in a randomized order (Garfinkel et al., 2015). Participants were asked to indicate synchronicity between the auditory stimuli and their own heartbeats. The specific instructions were: "The computer will play your heartbeat back to you in real time. Whenever the computer detects a heartbeat, it will play a tone. Without manually taking your pulse, you have to decide whether the tones you hear are synchronous or asynchronous with your heartbeat.".

A heartbeat discrimination accuracy score (IAcHDi; Interoception Accuracy from the Heartbeat Discrimination task) was calculated as the percentage of correct answers (i.e., affirmative responses under synchronous conditions or negative responses under asynchronous conditions) across the total number of trials.

2.3.1.3. Time tracking task. To control for guessing of the number of heartbeats and monitor participants' engagement, a time tracking task analogous to the 'heartbeat counting paradigm' was introduced between the two cardiac interoception tasks: participants were instructed to count number of seconds over six predetermined time-windows without using any help or receiving any feedback upon completion of each trial.

2.3.2. Gastric interoception

The gastric channel of interoception was tested by performing a modified water load test (WLT) protocol developed by van Dyck et al. (2016). To eliminate carry-over effects of a possible discomfort associated with ingestion of large amounts of water and to ensure a relatively empty stomach, the gastric interoception task was performed last and after approximately a 3-h abstinence from eating and drinking (water included). As the researcher was not allowed into the testing room other than to serve the water, written instructions guided participants through the steps, including advice to discontinue water ingestion if they felt unwell. Over two successive 5-min periods, participants drank from a hidden 5 L flask containing 1.5 L of commercial table water (ASDA, UK), served at room temperature, with an integrated tubing system which ended in a long (30 mm) wide (8 mm) flexible straw; the flask was weighed between the two periods and refilled. During the first period, ad libitum water ingestion was required until the point of perceived satiation, which was explained as 'the comfortable sensation you perceive when you have eaten a meal and you have eaten enough, but not too much'. Participants were then asked to continue ingesting water until fullness, i.e. 'sensation of stomach being entirely filled with water' was reached. Appetite ratings (hunger, satiety, fullness, thirst) and ratings about abdominal feelings (stomach tension, immobility, discomfort, guilt, sluggishness, nausea, arousal) were obtained before the first and after both the first and the second drinking tasks on computerized visual analogue scales (van Dyck et al., 2016). Participants remained seated in a half-supine position (i.e., leaning back at a 45° angle) during the entire test.

By weighing the flasks before and after each ingestion period, the water volume needed for satiation the additional volume required for fullness and the total stomach capacity (i.e., total volume ingested) were estimated. Gastric interoception was defined as the volume needed for satiation expressed as a percentage of total stomach capacity; lower values were interpreted as better gastric interoceptive ability (van Dyck et al., 2016).

2.4. Interoception (subjective measures) – interoceptive sensibility

2.4.1. Confidence ratings

Using a computerized VAS anchored as 'Total Guess/No heartbeat awareness' (0) and 'Complete Confidence/Full perception of heartbeat' (100), participants were asked to rate their confidence in the accuracy of their responses regarding the perceived number of heartbeats of the heartbeat tracking task (IS_HTr; Interoceptive Sensibility from the Heartbeat Tracking task) and perceived synchronicity with their heartbeats of the heartbeat discrimination task (IS_HDi; Interoceptive Sensibility from the Heartbeat Discrimination task) immediately after each trial.

2.4.2. Body perception questionnaire

The awareness subscale of the Porges Body Perception Questionnaire (BPQ: Porges, 1993) that measures one's beliefs about own sensitivity to a spectrum of bodily processes such as breathing, itching, sweating, swelling, digestion's noises, muscle tension, was administered after completion of the cardiac interoception tasks. The original subscale consists of 45 items rated on a five-point Likert scale ranging from 'Never' (1) to 'Always' (5). Here, we used the scoring protocol whereby full responses are summed to a total raw score (BPQ Manual, version 2); higher values represented higher levels of interoceptive sensibility.

2.5. Metacognitive interoceptive awareness

Metacognitive interoceptive awareness (IAw) was calculated separately for each heartbeat detection task based on the correspondence between accuracy and confidence (Garfinkel et al., 2015). As such, it illustrated how well one's confidence matched the correctness of their responses. For the heartbeat tracking task, we correlated accuracy (continuous responses) and confidence scores (Pearson r) on a within-subject trial-by-trial basis. To determine the heartbeat discrimination task-specific interoceptive awareness, the diagnostic value of the reported trial-by-trial confidence for accuracy (binary responses) was calculated from the area under the receiver operating characteristic (ROC) curve as described in Garfinkel et al. (2015). High metacognitive ability was yielded when correct trials (synchronicity or asynchrony judged correctly) were accompanied by high confidence or incorrect trials (synchronicity or asynchrony judged incorrectly) by low confidence (Garfinkel et al., 2015).

2.6. Trait prediction error (ITPE)

Interoceptive Trait Prediction Error (ITPE) quantifies the discrepancy between objectively assessed interoceptive performance measured during heartbeat detection tasks and interoceptive sensibility, i.e. one's beliefs about own sensitivity to interoceptive signals (Garfinkel et al., 2016). As described in Garfinkel et al. (2016), ITPE was computed separately for the heartbeat tracking and the heartbeat discrimination tasks as the difference between the awareness subscale of the BPQ and interoceptive accuracy. Prior to calculations, BPQ and accuracy scores were converted to standardised Z-values. Positive and negative values of ITPE indicate overestimation and underestimation of own interoceptive abilities, respectively.

2.7. Self-reported eating behaviours

Participants were asked to complete questionnaires on eating styles that encompass the principles of interoception, i.e. mindful eating and intuitive eating styles (Palascha, 2020). Mindful eating, which is conceptualized as being aware of physical versus emotional hunger and satiety cues and of associated effects of food choices on both the body and psychological state, was assessed through the Mindful Eating Questionnaire (MEQ: Framson et al., 2009). MEQ measures five distinct eating behaviour-related factors for a total of 28 items: (1) disinhibition (e.g. 'I stop eating when I'm full even when eating something I love'); (2) awareness (e.g.' I notice when there are subtle flavours in the foods I eat'); (3) external cues (e.g. 'I recognize when food advertisements make me want to eat'); (4) emotional response (e.g. 'When I'm sad I eat to feel better'); (5) distraction (e.g. 'My thoughts tend to wander while I am eating'). For intuitive eating which also concentrates on internally focused eating, the 23-item Intuitive Eating Scale (IES-2: Tylka, 2006) was administered. Items targeted four facets: (1) unconditional permission to eat (e.g. 'If I am craving a certain food, I allow myself to have it'); (2) eating for physical rather than emotional reasons (e.g. 'I stop eating when I feel full'); (3) reliance on internal hunger and satiety cues (e.g. 'I trust my body to tell me when to eat'); (4) body-food choice congruence (e.g. 'I mostly eat foods that give my body energy and stamina').

Whether the differential role played by external cues versus emotions in the control of food intake was reflected in the behavioural profile of SLs and SDs was also tested. Susceptibility to external food cues was quantified through the external eating subscale of the Dutch Eating Behaviour Questionnaire (DEBQ: Strien, Frijters, Bergers, & Defares, 1986). The DEBQ restraint eating subscale was also analysed. For emotional eating, the relevant subscale of DEBQ was analysed alongside the Emotional Appetite Questionnaire (EMAQ: Geliebter & Aversa, 2003) which explicitly separates effects of positive (e.g. confident, relaxed, falling in love) from effects of negative (e.g. sad, angry, when under pressure) emotions and emotional situations on eating behaviour, as well as considering the direction of disrupted food intake: that is whether a given emotion or emotional situation drives intake up or down. The effect of each emotion or emotional situation was rated on a 9-point Likert scale ('As compared to usual, do you eat … ') ranging from 'much less' to 'much more' including a middle point labelled 'the same', as well as a 'not applicable' and 'don't know' options. If any of the two latter options was selected, then this response was omitted from the analysis.

Finally, participants answered questions related to their dieting and body weight history. Behaviours akin to dietary restraint and overeating which are considered to underlie repetitive dieting and/or significant changes in body weight across the lifespan may also reflect attenuated interoceptive abilities (Bryant, Rehman, Pepper, & Walters, 2019; Speakman et al., 2011). Indeed, higher neural density in the insula for the obesity resistant phenotype as opposed to individuals prone to obesity has been reported (Smucny et al., 2012). Here, participants were prompted to make a series of choice from the following list of dichotomous responses, characteristic of an obesity resistant versus an obesity prone phenotype (Schmidt, Harmon, Sharp, Kealey, & Bessesen, 2012): (1) 'I am constitutionally thin, i.e. I believe it is difficult for me to gain weight and/or I expend little effort to maintain my weight' *vs.* 'I am chronically struggling with body weight control'; (2) 'I experience weight stability despite few to no attempts to lose weight' *vs.* 'I have a history of weight fluctuations despite putting effort into not gaining weight'; (3) 'I do not have any first degree relative (parents or siblings) who is obese' *vs.* 'I have at least one first degree relative (parents or siblings) who is obese'; (4) 'I have never been overweight or obese' *vs.* 'I have been at least one time or I am currently overweight or obese'. Responses for an obesity resistant phenotype were scored as 0 versus 1 for the alternatives, so the lower the total score, the more resistant they were to obesity.

2.8. Statistical analysis

First, basic descriptive statistics (i.e., percentages and means and standard errors of the means) were computed. Group differences (SLs versus SDs) in continuous and categorical variables were tested with independent t- and χ^2-tests, as appropriate. Regression analyses entering all confounders simultaneously were conducted to test the predictive utility of phenotype for each interoceptive accuracy score (heartbeat tracking, heartbeat discriminating, gastric) accounting for known confounders. To explore whether interoceptive accuracy in either heartbeat tasks related to gastric interoception independent of the sweet taste phenotype, additional regression models were employed. Pearson correlations of scores on emotional eating scales with interoceptive abilities and of cardiac with gastric interoception measures were also calculated.

The extent to which phenotypic differences in participants' characteristics were mediated by individual variation in interoception was tested using Hayes PROCESS macro v3.4 (Model 4: Hayes, 2013) with 5000 bootstrapped bias corrected resamples. Direct and indirect effects of sweet taste phenotype separately on each participants' characteristic of interest were estimated with interoceptive measures found to differ significantly by phenotype as the mediating variable; separate

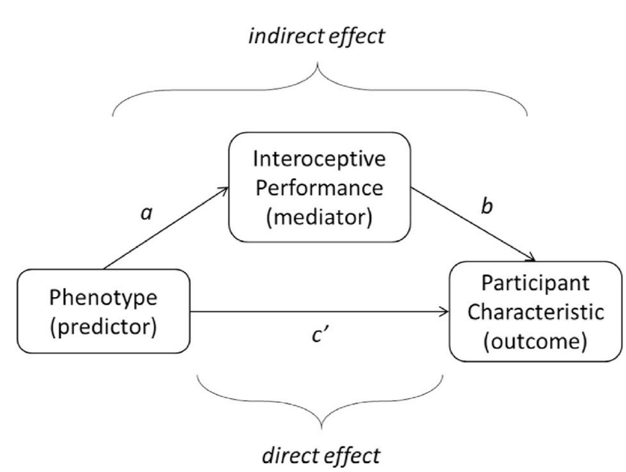

Fig. 2. The path model for mediation analysis (Hayes, 2013).

mediation analysis was carried out for each objective measure of interoception (i.e., interoceptive accuracy derived from the heartbeat tracking task, the heartbeat discrimination task, and water load test). As illustrated on Fig. 2, the direct effect, path c′, represents the effect of the predictor (i.e., sweet taste phenotype) on the outcome (i.e., participant characteristics) while accounting for the effect of the mediator (i.e., interoceptive performance). Path a shows the strength of the influence of predictor on the mediator and path b denotes the effect of mediator on the outcome when the predictor is statistically controlled. This type of mediation analysis determines whether the effect of the predictor on the outcome is fully explained by the mediator. For significant results 95% bias corrected confidence interval (CI) should not have included the zero value.

Cohen's d and f squared (f^2) were used as the effect size measures for pairwise comparisons and analyses of variance, respectively. Cohen's d was considered small when equal to 0.20, medium when equal to 0.50 and large when equal to 0.80. For f^2, 0.2, 0.15, and 0.35 were the thresholds for a small, medium and large effect size. (Cohen, 2013). The level of significance was set to $\alpha = 0.05$. Data were analysed using SPSS v25.0 and the MATLAB (R2019b) software package. All tested hypotheses and the main analysis plan were specified prior to data collection.

3. Results

The study sample comprised of 64 women, 31 SLs and 33 SDs with an age and BMI range of 18.8–33.8 years and 17.19–32.23 kg/m^2, respectively. 67.2% were self-identified as Caucasians and 21.9% were of Asian ancestry. As expected from similar datasets (e.g., in Armitage, Vi, Iatridi, & Yeomans, 2020; Garneau, Nuessle, Mendelsberg, Shepard, & Tucker, 2018), SDs were older than SLs (24.3 ± 0.08 SEM vs. 22.4 ± 0.05 SEM; $t(55.207) = -2.083$, $p = .042$); further, individuals of Asian ancestry were classified into the SD phenotype (92.9%) more often than participants of Caucasian ancestry (39.5%) or participants from other ethnicities (42.9%; $\chi^2(1,N = 64) = 12.262$, $p = .002$). Conversely, comparisons of sweet liker phenotypes by BMI (SLs: $M = 22.03$, $SEM = 0.42$; SDs: $M = 22.87$, $SEM = 0.60$), total body fat (SLs: $M = 25.2$, $SEM = 1.1$; SDs: $M = 26.1$, $SEM = 1.2$), and fat free mass (SLs: $M = 45.3$, $SEM = 0.7$; SDs: $M = 44.9$, $SEM = 1.4$) were not significant (all $ps > .05$).

Regarding interoception-specific measures, due to technical problems, cardiac and gastric interoception data were missing from two and one participant, respectively. Across participants, cardioceptive performance in the heartbeat tracking ($M = 0.600$, $SEM = 0.035$) and the heartbeat discriminating ($M = 0.576$, $SEM = 0.017$) tasks were comparable to recent work in non-clinical subgroups (Critchley et al., 2019). For the water load test, mean gastric interoceptive performance was .588 ($SEM = 0.018$), similar to values from van Dyck et al. (2016).

3.1. Interoceptive abilities by sweet taste phenotype

The different interoception constructs (i.e., accuracy, awareness, sensibility) across interoception modalities (i.e., cardiac, gastric) by sweet taste phenotype are shown in Fig. 3. SLs obtained higher accuracy scores than SDs in the heartbeat tracking ($t(61) = 2.538$, $p = .014$, $d = 0.64$) and the heartbeat discrimination ($t(60) = 2.785$, $p = .007$, $d = 0.71$) tasks (Fig. 3, panels a and b). Notably, the observed patterns persisted even after accounting for known confounders of interoceptive performance (Table 1) that is alexithymia, anxiety, depression, and impulsivity (IAcHTr: $\beta = -0.286$ *95%CI* $(-0.150, -0.006)$, $t = -2.157$, $p = .035$, $f^2 = 0.12$; IAcHDi: $\beta = -0.404$ *95%CI* $(-0.091, -0.019)$, $t = -3.086$, $p = .006$, $f^2 = 0.19$). Analysis of participants' performance in the time tracking task showed no differences between SLs ($M = 0.784$, $SEM = 0.026$) and SDs ($M = 0.769$, $SEM = 0.030$) in their overall engagement in the experimental procedures ($t(62) = 0.370$, $p = .713$; $d = 0.09$). SLs and SDs did also not differ in their knowledge of own heartbeats (41.9% SLs vs. 27.3% SDs reported knowledge of own heartbeat; $\chi^2(1,N = 64) = 1.523$, $p = .217$, $V = 0.02$).

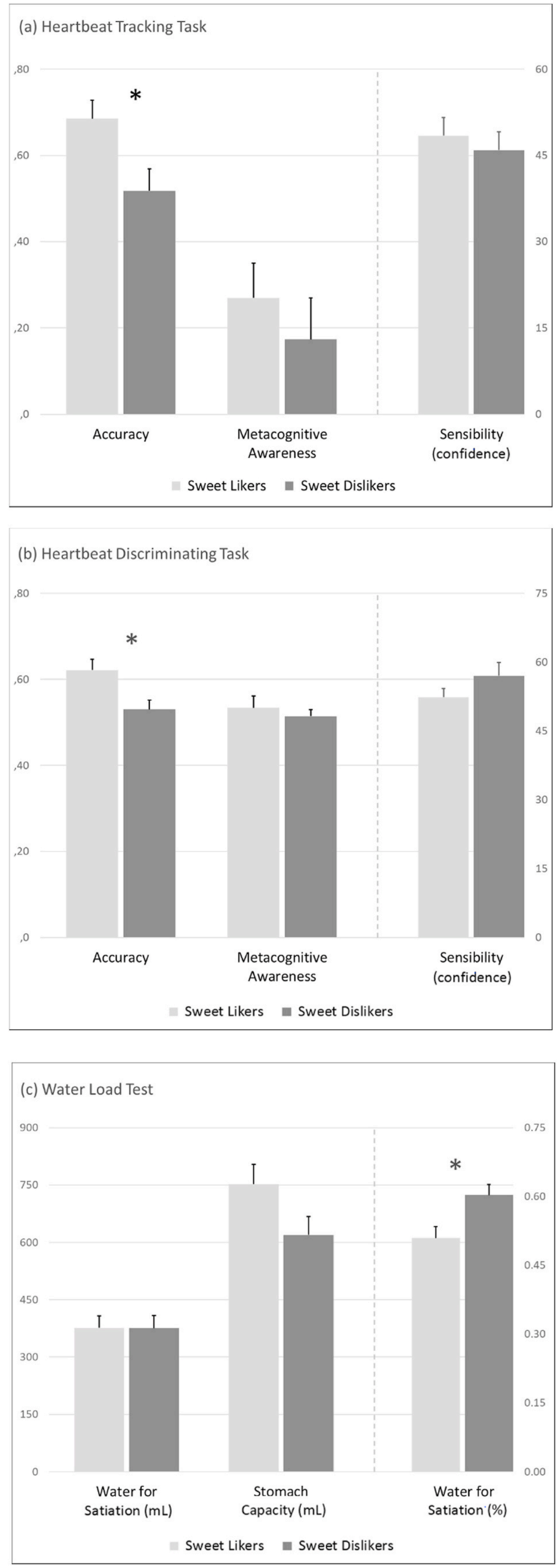

Fig. 3. a–c. Interoceptive dimensions by phenotype and task (a: heartbeat tracking task; b: heartbeat discrimination task; c: water load test).

Table 1
Trait mood and behaviour characteristics by sweet taste phenotype.

	Sweet Likers (n = 31)	Sweet Dislikers (n = 33)
	Mean (SEM)	
GAD-7 (anxiety)	8.4 (0.9)	8.8 (1.0)
PHQ-9 (depression)	7.2 (0.8)	9.0 (1.1)
TAS-20 (alexithymia)	46.6 (2.1)	50.2 (2.1)
BIS (impulsivity)	57.9 (1.8)	62.1 (1.6)

BIS, Barratt Impulsiveness Scale; GAD-7, General Anxiety Disorder-7; PHQ-9, Patient Health Questionnaire-9; TAS, SEM, Standard Error of the Mean; Toronto Alexithymia Scale.
All group comparisons were non-significant ($p > .05$).

SLs also exhibited enhanced gastric interoceptive abilities, as they ingested less water to sense satiety in relation to their stomach capacity when compared to SDs ($t(61) = -2.722$, $p = .008$, $d = 0.69$: Fig. 3c); notably, this was independent of their pre-test levels of satiety and thirst ($\beta = 0.333$ *95%CI* (0.013, 0.082), $t = 2.758$, $p = .008$, $f^2 = 0.16$). The low pre-test levels of satiety (SLs: $M = 31.2$, $SEM = 3.8$; SDs: $M = 33.4$, $SEM = 4.0$; $t(61) = -0.395$, $p = .694$) and relatively high levels of thirst (SLs: $M = 66.3$, $SEM = 4.1$; SDs: $M = 67.0$, $SEM = 4.3$; $t(61) = -0.107$, $p = .916$) seen here were unsurprising given the 3-h food and water abstinence protocol. The full list of appetite ratings and abdominal sensations recorded at the different time points during the WLT can be found in the Supplementary Material (Table S1). The importance of accounting for stomach capacity in assessing gastric interoception also deserves note: if absolute ingested water volume had been used as a measure of gastric interoception, no phenotype-specific difference in gastric interoception would have been observed ($t(61) = 0.003$, $p = .998$: Fig. 3c). Likewise, adding total stomach capacity to the multivariate regression model that tested the effect of phenotype on gastric interoception improved the model's predictive ability at a larger degree ($R^2 = 0.141$), compared to using the absolute ingested water volume ($R^2 = 0.029$).

Here, an effect of phenotype on objectively measured sensitivity to internal signals was not confirmed for constructs entailing subjective assessment of interoceptive abilities. Mean confidence from the heartbeat tracking task ($t(61) = 0.558$, $p = .579$; $d = 0.14$) and the heartbeat discrimination task ($t(60) = -1.335$, $p = .187$; $d = 0.34$) each failed in distinguishing SLs from SDs (Fig. 3a–b); this failure was also seen for interoceptive awareness (IAwHTr: $t(61) = 0.763$, $p = .448$; $d = 0.19$; IAwHDi: $t(60) = 0.625$, $p = .534$; $d = 0.16$: Fig. 3a–b). Although the mean scores for the SLs on the BPQ were slightly higher than for the SDs, this apparent difference was not significant (SLs: $M = 75.4$, $SEM = 3.3$; SDs: $M = 68.7$, $SEM = 2.9$; $t(62) = 1.547$, $p = .127$; $d = 0.39$). Finally, while there were no phenotype-specific differences in interoceptive trait prediction error as assessed using either the heartbeat tracking task (SLs: $M = -0.114$, $SEM = 0.263$; SDs: $M = 0.144$, $SEM = 0.291$; $t(61) = -0.657$, $p = .514$; $d = 0.17$) or the heartbeat discrimination task (SLs: $M = -0.138$, $SEM = 0.267$; SDs: $M = 0.143$, $SEM = 0.225$; $t(60) = -0.807$, $p = .323$; $d = 0.21$), SLs were prone towards underestimating their interoceptive abilities as opposed to SDs who tended to overestimate their abilities to sense the internal state of their body accurately.

An asterisk (*) denotes statistically significant differences ($p < .05$) between the sweet taste phenotypes for each interoceptive measure. Error bars indicate standard errors of the mean. Notably, scores for the satiation measure are reversed relative to the cardioceptive accuracy scores; that is, higher values indicate lower gastric interoceptive abilities.

3.2. Eating habits and behaviours by sweet liker phenotype

In relation to our main hypothesis – those classified into the SL phenotype would have enhanced interoceptive abilities – eating habits and behaviours associated with responsiveness to internal signals and bodily needs were analysed by phenotype (Table 2). Overall, SLs scored higher than SDs in mindful eating ($t(62) = 3.060$, $p = .003$, $d = 0.76$) and intuitive eating ($t(62) = 4.321$, $p < .001$, $d = 1.09$). From the different subscales under investigation, phenotype-specific differences were significant for awareness of feeding-specific internal states of the body ($t(62) = 2.620$, $p = .011$, $d = 0.65$) and of external feeding cues ($t(62) = 2.682$, $p = .009$, $d = 0.67$) of the mindful eating questionnaire, as well as eating to meet physical rather than externally-generated needs ($t(62) = 2.795$, $p = .007$, $d = 0.70$), favoring food choices that benefit the body ($t(62) = 4.286$, $p < .001$, $d = 1.08$), or tending to refrain from placing external restrictions on eating ($t(62) = 1.872$, $p = .066$, $d = 0.47$) as derived from the intuitive eating questionnaire. SLs were also more likely than SDs to have an obesity resistant profile ($t(62) = 2.151$, $p = .035$, $d = 0.54$).

Table 2
Eating habits and behaviours by sweet taste phenotype.

	Sweet Likers (n = 31)	Sweet Dislikers (n = 33)
	Mean (SEM)	
Intuitive Eating Scale		
Total score	3.506 (.040)*	3.204 (.056)
Unconditional eating	3.371 (.081)	3.172 (.069)
Physical eating	3.323 (.060)*	3.030 (.084)
Hunger-driven eating	3.586 (.119)	3.424 (.118)
Body-food convergence	4.108 (.110)*	3.293 (.153)
Mindful Eating Scale		
Total score	2.489 (.048)*	2.291 (.044)
Awareness	2.805 (.082)*	2.516 (.075)
External cues	2.955 (.093)*	2.616 (.086)
Emotional response	1.989 (.097)	1.861 (.108)
Distraction	2.258 (.117)	2.132 (.082)
Dutch Eating Behavioural Questionnaire		
Restrained eating	22.9 (1.3)	24.2 (1.7)
Emotional eating	36.8 (2.1)*	30.6 (1.9)
External eating	31.6 (.9)	32.1 (1.2)
Emotional Appetite Questionnaire		
Positive	5.0 (.1)*	5.4 (.1)
Negative	4.9 (.2)	4.5 (.2)
Resistant obesity (%)	52.4 (2.9)*	43.2 (3.1)

SEM, Standard Error of the Mean.
An asterisk (*) denotes statistically significant differences between phenotypes.

SLs also scored higher on the DEBQ emotional eating scale ($t(62) = 2.153$, $p = .035$, $d = 0.54$). Examining the positive and negative scales of the Emotional Appetite Questionnaire (EMAQ), SLs reported to increase their food intake at a significantly lower degree than SDs for positive emotions ($t(62) = -2.245$, $p = .028$, $d = 0.56$) but more in response to negative emotional stimuli ($t(62) = 1.651$, $p = .104$, $d = 0.41$). To note, in the total sample, positive emotional stimuli triggered significantly greater increases in food intake than negative emotions or emotional situations ($t(63) = 2.968$, $p = .009$, $d = 0.52$). In fact, only a third of our study sample (39.1%) reported eating more than usual (i.e. mean score >5) when experiencing negative emotions compared to 51.6% who increased their food intake in response to positive emotions or emotional situations. Emotional eating in response to positive stimuli was also negatively associated with heartbeat accuracy scores across tasks (HTr: $r(63) = -0.294$, $p = .019$; HDi: $r(62) = -0.302$, $p = .017$), while the higher the increase in food intake in response to negative emotions, the better the measured cardioceptive performance (HTr: $r(63) = -0.290$, $p = .021$; HDi: $r(62) = -0.262$, $p = .040$). When the link between interoceptive abilities and emotional eating captured by the more generic subscale of the DEBQ was tested, weaker correlations emerged (IAcHTr: $r(63) = 0.242$, $p = .056$; IAcHDi: $r(62) = 0.245$, $p = .055$). No differences between phenotypes were observed for DEBQ-external eating or frequency of dieting (all $ps > .05$).

3.3. Mediation effect of interoception on phenotype-specific differences in eating habits and behaviour

To test whether the observed phenotypic differences in

Table 3
Results of mediation analysis for the role of interoceptive performance on the effect of sweet taste phenotype on eating habits and behaviours.

	Mediation by Heartbeat Tracking Accuracy				Mediation by Heartbeat Discriminating Accuracy				Mediation by %Water for Satiation			
	Direct effect *b* (*SEM*)	Unstandardised coefficient *b* (*SEM*)		Indirect effect (95% *BSCI*)	Direct effect *b* (*SEM*)	Unstandardised coefficient *b* (*SEM*)		Indirect effect (95% *BSCI*)	Direct effect *b* (*SEM*)	Unstandardised coefficient *b* (*SEM*)		Indirect effect (95% *BSCI*)
	c'	a	b	a x b	c'	a	b	a x b	c'	a	b	a x b
DEBQ-emotional scale	−2.410 1.518 $p = .118$	**-.084 (.033) $p = .014$**	7.738 (5.584) $p = .171$	-.650 (−1.91, .429)	−2.263 (1.557) $p = .151$	**-.046 (.016) $p = .007$**	15.730 (11.492) $p = .176$	-.721 (−2.224, .420)	**−3.555 (1.497) $p = .021$**	**.047 (.017) $p = .008$**	1.568 (10.545) $p = .882$	.073 (−1.041, 1.228)
EMAQ-positive	.153 (.094) $p = .109$	**-.084 (.033) $p = .014$**	-.630 (.347) $p = .074$	**.053 (.001, .135)**	.161 (.096) $p = .098$	**-.046 (.016) $p = .007$**	−1.258 (.709) $p = .081$	.058 (−.005, .142)	.153 (.096) $p = .116$	**.047 (.017) $p = .008$**	1.101 (.674) $p = .107$	.051 (−.008, .157)
EMAQ-negative	-.121 (.137) $P = .381$	**-.084 (.033) $p = .014$**	.992 (.503) $p = .053$	**-.083 (-.206, -.002)**	-.128 (.142) $p = .369$	**-.046 (.016) $p = .007$**	1.742 (1.045) $p = .108$	-.080 (−.219, .021)	-.174 (.142) $p = .225$	**.047 (.017) $p = .008$**	-.953 (1.000) $p = .344$	-.044 (−.182, .056)
Intuitive eating (total score)	**-.132 (.036) $p = .001$**	**-.084 (.033) $p = .014$**	.257 (.134) $p = .060$	-.022 (−.070, .005)	**-.148 (.038) $p < .001$**	**-.046 (.016) $p = .007$**	.237 (.279) $p = .398$	-.011 (−.040, .012)	**-.137 (.037) $p < .001$**	**.047 (.017) $p = .008$**	-.410 (.259) $p = .119$	-.019 (−.061, .013)
Intuitive eating (physical cues)	-.098 (.053) $p = .068$	**-.084 (.033) $p = .014$**	**.567 (.194) $p = .005$**	-.048 (−.135, .001)	**-.132 (.0576) $p = .026$**	**-.046 (.016) $p = .007$**	.2913 (.425) $p = .496$	-.013 (−.049, .017)	**-.127 (.056) $p = .026$**	**.047 (.017) $p = .008$**	-.513 (.392) $p = .196$	-.024 (−.094, .018)
Intuitive eating (body-food convergence)	**-.352 (.097) $p = .001$**	**-.084 (.033) $p = .014$**	.671 (.366) $p = .072$	-.056 (−.155, .012)	**-.399 (.104) $p < .001$**	**-.046 (.016) $p = .007$**	.446 (.768) $p = .564$	-.020 (−.107, .053)	**-.357 (.101) $p = .001$**	**.047 (.017) $p = .008$**	−1.105 (.712) $p = .126$	-.052 (−.148, .017)
Mindful eating (total score)	**-.087 (.034) $p = .014$**	**-.084 (.033) $p = .014$**	.088 (.126) $p = .486$	-.007 (−.037, .009)	**-.091 (.035) $p = .013$**	**-.046 (.016) $p = .007$**	.062 (.261) $p = .814$	-.003 (−.031, .024)	**-.094 (.035) $p = .009$**	**.047 (.017) $p = .008$**	-.182 (.245) $p = .459$	-.008 (−.040, .016)
Mindful eating (awareness)	-.108 (.057) $p = .065$	**-.084 (.033) $p = .014$**	.339 (.212) $p = .115$	-.028 (−.089, .007)	**-.117 (.058) $p = .050$**	**-.046 (.016) $p = .007$**	.652 (.438) $p = .135$	-.030 (−.086, .014)	**-.158 (.060) $p = .010$**	**.047 (.017) $p = .008$**	.202 (.421) $p = .632$	.009 (−.033, .056)
Mindful eating (external cues)	**-.196 (.066) $p = .004$**	**-.084 (.033) $p = .014$**	-.3761 (.245) $p = .130$	.032 (−.014, .072)	**-.182 (.069) $p = .011$**	**-.046 (.016) $p = .007$**	-.367 (.512) $p = .477$	.017 (−.024, .070)	**-.161 (.067) $p = .019$**	**.047 (.017) $p = .008$**	-.464 (.469) $p = .327$	-.022 (−.070, .025)
Resistant obesity	-.163 (.092) $p = .080$	**-.084 (.033) $p = .014$**	.304 (.338) $p = .371$	-.026 (−.052, .118)	-.147 (.093) $p = .119$	**-.046 (.016) $p = .007$**	1.010 (.687) $p = .147$	-.046 (−.009, .130)	-.181 (.091) $p = .051$	**.047 (.017) $p = .008$**	-.466 (.640) $p = .469$	-.022 (−.037, .103)

BSCI, Bootstrapped Confidence Interval; DEBQ, Dutch Eating Behavioural Questionnaire; EMAQ, Emotional Appetite Questionnaire; SEM, Standard Error of the Mean Statistically significant results (p > .05) are bolded.

characteristics related to eating habits and behaviour might be explained by individual differences in interoceptive abilities, mediation analyses were used. Specifically, we treated sweet taste phenotype as the categorical predictor, different eating habits and behaviours as outcomes and objective measures of interoception separately as mediators (Fig. 2). Table 3 shows the statistics of the simple (i.e., mediator predicted from the predictor), direct (i.e. outcome predicted from the predictor accounting for mediator and from the mediator accounting for the predictor) and indirect (moderator mediating the relationship between the predictor and the outcome) effects.

Mediation (Table 3) was present only for the positive and negative scales of the Emotional Appetite Questionnaire (EMAQ): the effect of phenotype on eating in response to positive or negative emotions and emotional situations was due to the relationship of the predictor (i.e., sweet taste phenotype), and the outcome (i.e., EMAQ-scales), with the mediator (i.e., interoceptive performance –accuracy- in the heartbeat tracking task). Besides this indirect effect, interoceptive performance (accuracy) across all three tasks (heartbeat tracking and discrimination tasks and water load task) failed to independently predict all eating habits and behaviours; only the physical eating-scale of the intuitive eating questionnaire was independently and significantly predicted by interoceptive performance (accuracy) measured during the heartbeat tracking task (Table 3). Finally, phenotype significantly predicted intuitive and mindful eating (total scores) independent of interoceptive performance (accuracy) across both heartbeat tasks and the water load task, further supporting our earlier finding about enhanced intuitive and mindful eating in SLs (Table 3). This independent relationship was also evident across all three tasks for the body-food convergence- and external cues-scales of the intuitive eating and mindful eating questionnaires, respectively (Table 3). Finally, as expected from the results of the independent t-tests for the differences between SLs and SDs (Fig. 3a–c), a significant influence of sweet-liking phenotype on interoceptive accuracy was calculated across all three interoceptive tasks (Table 3).

3.4. *Effect of sweet liker phenotype on the relationship between cardiac and gastric axes of interoception*

Across participants, we observed a significant inverse relationship between accuracy scores from both the heartbeat tracking and discrimination tasks, and the percentage amount of ingested water volume from the water load test (HTr: $r(61) = -0.298$, $p = .019$; HDi: $r(60) = -0.244$, $p = .058$), suggesting that ability to sense one's own heartbeats was linked to sensitivity for gastric functions (Fig. 4). Cardiac interoceptive performance from both heartbeat tasks was also correlated with total stomach capacity (HTr: $r(62) = 0.410$, $p = .001$; HDi: $r(61) = 0.283$, $p = .027$), but not absolute ingested water volume for satiation (HTr: $r(62) = -0.196$, $p = .126$; HDi: $r(61) = 0.110$, $p = .398$). Regression analysis accounting for pre-test level of satiety and thirst provide similar results (all *ps* < .05 for stomach capacity and >.05 for absolute ingested water volume).

Cardioceptive performance as gauged from the heartbeat tracking task was negatively associated with the percentage ingested water volume that produces satiation suggesting that the higher the sensitivity to cardiac signals the better the ability for gastric distention to be perceived effectively. Interoceptive accuracy scores specific to the heartbeat discriminating task also tended to correlate with gastric interoception.

Adding sweet taste phenotype as a factor to the regression model testing the relationship between heartbeat tracking performance and gastric interoception significantly improved the variance explained by the model ($\Delta R^2 = 0.063$, $p_{\Delta F} = .041$). The contribution of sweet taste phenotype to the model remained significant even after controlling for known confounders of cardiac and gastric interoception, i.e. alexithymia, anxiety, depression, impulsivity and pretest levels of satiety and thirst ($\beta = 0.284$ *95%CI* (0.004, 0.078), $t = 2.197$, $p = .032$); heartbeat tracking performance did not significantly predict gastric

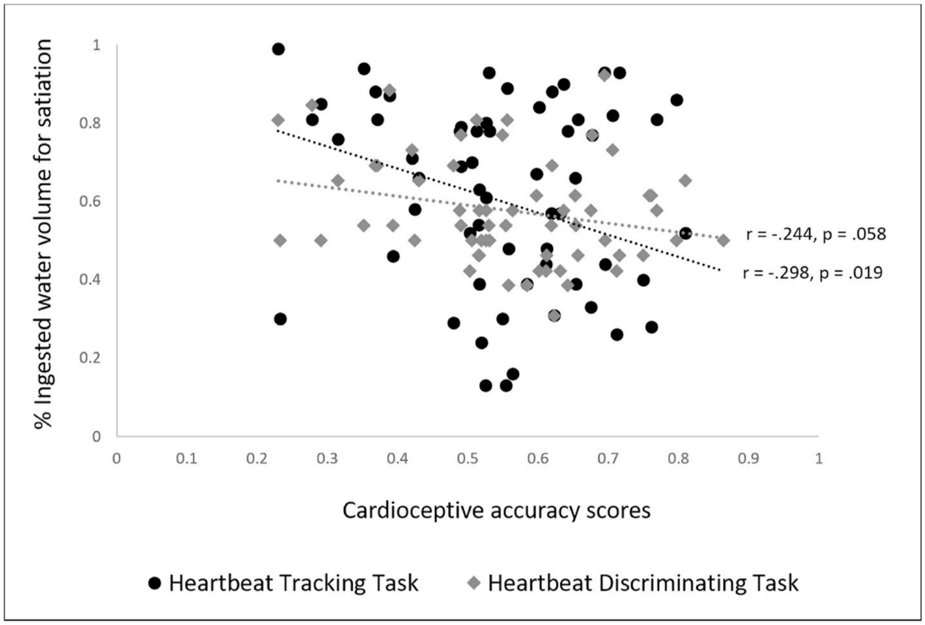

Fig. 4. Scatterplots depicting correlations of cross-modal interoceptive performance.

performance in the fully adjusted model ($\beta = -0.182$ *95%CI* (-0.229, 0.037), $t = -1.451$, $p = .153$). Additional regression analysis demonstrated similar results regarding the effect of sweet liker phenotype on the relationship between interoceptive accuracy scores obtained during the heartbeat discrimination task and percentage amount of ingested water volume from the water load test (phenotype: $\beta = .316$ *95%CI* (0.006, 0.085), $t = 2.292$, $p = .026$; $f^2 = 0.36$; IAcHDi: $\beta = -0.111$ *95% CI* (-0.393, 0.159), $t = -0.851$, $p = .399$; $f^2 = 0.35$).

4. Discussion

This is the first study to report a clear link between objectively assessed accuracy in detecting internal bodily sensations and hedonic responses to concentrated sweet stimuli. By employing two distinct heartbeat detection tasks (tracking and discrimination) alongside a gastric interoception task in the same sample of healthy adults, we also avoid limitations that arise from focusing too narrowly on individual measures of interoception. Statistically significant differences in interoceptive abilities between the two sweet taste phenotypes were observed for all accuracy-based tasks. Specifically, participants who expressed heightened liking for strong sweetness (that is, SLs), performed better than SDs in detecting their heartbeats accurately despite being similarly confident about their responses. For the gastric mode of interoception, SLs reported to feel satiated after they ingested a lower amount of water in relation to their total stomach capacity compared to SDs. The calculated medium to large effect sizes of these differences and the fact that phenotypic variation in interoceptive performance was confirmed in two distinct body systems (i.e., heart and stomach), may further strengthen the robustness of the proposed enhanced interoceptive ability in sweet likers.

To our knowledge, only one research group has examined potential links between interoception and taste hedonics. In those studies, participants were asked to taste and rate a single concentration of a bitter herbal extract; neither pleasantness nor intensity ratings were correlated with accuracy scores from the heartbeat tracking task (Ferentzi et al., 2017). Subsequently, Ferentzi and colleagues extended their finding by proposing a dissociation between bitterness pleasantness and gastric interoception, as measured by a water load test (Ferentzi et al., 2018). Interestingly, an inverse relationship between bitterness pleasantness and sensitivity to the internal sensation of pain was reported in the first study (Ferentzi et al., 2017), which might be of relevance to the current dataset as sweetness has also been proposed to have implications in mechanisms of pain (Fantino, Hosotte, & Apfelbaum, 1986; Yeomans & Wright, 1991). On the other hand, given that, unlike most bitter taste stimuli, the oft-used sweet tastants contain some energy, closer links between hedonic responses to sweetness than bitterness and the homeostatic system, which is centre to feeding-related interoceptive abilities, could be expected. Indeed, additional to the role of sweetness in signposting safe sources of energy (Steiner, Glaser, Hawilo, & Berridge, 2001), animal research recently identified taste receptors in the hypothalamus, a brain structure directly associated with body's homeostatic control (Kohno et al., 2016).

Consistent with the common neural site that monitors interoception and taste perception, Frank and colleagues, who served 1 M sucrose solution while participants were undergoing functional magnetic resonance imaging, reported a positive correlation between accuracy in identifying sweetness and activation of the insular cortex in their healthy subgroup, as well as a tendency towards a relationship between accuracy in identifying sweetness and interoceptive deficits assessed by an eating-disorder questionnaire (Frank, Shott, Keffler, & Cornier, 2016). Our finding of a novel link between hedonic responses to sweetness and interoception may, then, have support in insula's connectivity with higher order brain structures including the orbitofrontal cortex, which is known to respond to taste affective valence (Small, 2010). Notably, insular activation has been related both to cardiac (Schulz, 2016) and gastric cues (e.g., stomach distention, subjective satiety/fullness; see: Wang et al., 2008). Therefore, it seems reasonable to speculate that if a broader relationship between affective valence of external stimuli and ability to sense the internal state of the body was suggested, this may have implications in the level of pleasure one seeks from a given stimulus to match their homeostatic or emotional internal needs. Considering the vulnerable interoceptive sensitivity to insults from the obesogenic environment (Bilman et al., 2017; Sample et al., 2016), such a relationship could point to additional mechanisms underlying obesity epidemic and illustrate how attenuated interoceptive abilities may confer elevated risk of obesity susceptibility.

In contrast to our observation that SLs outperformed SDs in objective interoceptive measures, when participants self-reported their beliefs about their capacity in detecting and self-focusing on internal bodily sensations, there were no phenotypic differences across either measure of interoceptive sensibility. Regarding confidence scores, they were averaged around the middle point (i.e., neither guess nor complete confidence), while relatively small variances were calculated indicating that, overall, participants did not provide guess responses neither were they familiarized with the tasks. The results from the BPQ (which provides a measure of interoceptive sensibility across a range of internal bodily sensations) further confirmed the divergence between interoceptive performance and sensibility (i.e., true ability versus confidence in one's ability). We also examined the phenotypic differences in metacognitive interoceptive awareness derived from each of the heartbeat detection tasks, and found that SLs and SDs did not differ in their metacognitive insight into own interoceptive abilities. That is, their ability to know when their responses did or did not correspond to their actual heartbeat data.

The distinct effect of phenotype on interoceptive performance versus sensibility, metacognitive awareness, or trait prediction error is not entirely surprising given the clear dissociation between the different constructs of interoception in the framework proposed by Garfinkel and Critchley (2013). As detailed by Garfinkel et al. (2015), an individual's belief in their own interoceptive aptitudes should not necessarily be taken as an accurate predictor of the their ability in detecting interoceptive signals; this idea is further supported by the notion that top down and bottom up processes are rather distinguishable. It has also been argued by others that – unlike with one's broader psychological state – experiencing significant changes in emotions and perceptions requires one to be consciously aware of their internal signals (Gibson, 2019). Considering the metacognitive aspects of self-regulation (Whitebread & Pino-Pasternak, 2010, pp. 673–711) and the consequences of self-dysregulation (Vainik, Dagher, Dubé, & Fellows, 2013) and particularly impaired emotional regulation (Fernandes, Ferreira-Santos, Miller, & Torres, 2018) in eating behaviour, attenuated ability to mentally represent internal body state may leave one more vulnerable to influences of the modern affluent food environment. Recently, Willem and colleagues demonstrated a link between obesity and both interoceptive sensibility deficits and self-dysregulation (Willem et al., 2019). In similar work, enhanced awareness of internal state of the body has been theoretically (Calì, Ambrosini, Picconi, Mehling, & Committeri, 2015) and empirically (Willem et al., 2020) suggested to compensate for the positive association between different interoceptive facets and emotional eating. Our data showing that SLs were more prone to emotional eating than SDs supports this premise. Notably, although acute changes in interoceptive performance have been achieved at experimental settings (Ainley et al, 2012, Ainley et al., 2013; Filippetti & Tsakiris, 2017), interoceptive performance is regarded as a relatively stable trait (e.g. Bornemann, Herbert, Mehling, & Singer, 2014; Melloni et al., 2013). Conversely, interoceptive sensibility and awareness have been reported to improve subsequent to interventions targeting the brain-to-body axis such as meditation or contemplative practice (e.g. Garfinkel, Mclanachan, & Critchley, 2017; Khalsa et al., 2008; Parkin et al., 2014).

In line with their enhanced abilities to detect internal body sensations more accurately, SLs in our study were both more mindful and intuitive eaters than SDs. Our data align with previous research showing positive correlations between interoceptive accuracy scores derived from heartbeat tracking tasks and intuitive eating (Herbert et al., 2013; Richard et al., 2019). In support to the genetic basis of obesity development and either the setting or settling point theories (reviewed in Speakman et al., 2011), SLs also appeared to be better at 'resisting to obesity'. Resistant obesity profile is assumed to reflect a weaker inherent predisposition to obesity development along with a better ability to maintain a healthy body weight more effortlessly. Smucny et al. (2012) have linked increased grey matter volume in the insula, which is known to be important in interoceptive processes in the brain, with this 'obesity resistant' profile.

Regarding our mediation analyses, only the relationship between sweet liker phenotype and emotional eating in response to positive and negative stimuli was fully explained by interoceptive performance. This supports the increasingly recognized relationship between sensing the internal body and emotional experiences (Critchley & Garfinkel, 2017, pp. 7–14). Further, it highlights a closer relevance of sweet-liking to the homeostatic aspect of interoception. By illustrating such independence from interoceptive performance of the relationship between sweet liker phenotype and eating habits and behaviours that rely on internal cues to monitor feeding behaviour, it also seems reasonable to conclude that being a SL may reflect a better attuned sense of bodily state. Following this reasoning, the present data suggests the sweet liker phenotype classification we recently put forward (Iatridi et al., 2019a) could be conceived as a means to operationally characterize a profile that links exteroceptive and interoceptive information. For instance, considering the argument that ingestion of sugars may facilitate synthesis of neurotransmitters that elicit positive emotional cues (Gibson, 2012, pp. 442–460), our preliminary evidence that SLs recruited more coping mechanisms such as increases in food intake in response to negative compared to positive emotions, may further support SLs' enhanced sensitivity to interoceptive signals.

From an evolutionary standpoint, it is believed that taste systems were initially evolved to inform us about the nutritional value or toxicity of food stimuli and therefore, we developed mechanisms that facilitated the intake of calorically dense foods to cope with food scarcity (Drewnowski et al., 2012). A classic demonstration of this phenomenon is featured by sensory experiments in human and non-human neonates whereby sweetness, as opposed to bitter and sour tastes, elicited positive facial expressions and matching sucking responses (Desor, Maller, & Turner, 1973; Maone, Mattes, Bernbaum, & Beauchamp, 1990; Rosenstein & Oster, 1988; Steiner et al., 2001); both behaviors may resonate an inherent drive towards foods providing a safe and useful source of energy and rejection of those being potentially poisonous. Such typical sensory reactions have also been linked to biological indices of growth in children and adolescents (Coldwell, Oswald, & Reed, 2009; Mennella, Finkbeiner, Lipchock, Hwang, & Reed, 2014). The above considered, liking for potent sweetness may constitute a physiological mechanism that contributes to the feedback loops generated as a response to the internal state of the body; such conclusion seems to be supported by the enhanced interoceptive abilities observed in SLs in the present dataset, as well.

In addition to our novel finding that sweet-liking associates with interoceptive performance, we also provided evidence about a potential general body control system that monitors one's ability to sense cardiac and gastric signals. To interpret these data, two issues require consideration. First, the observed correlations of interoceptive performance during heartbeat and gastric tasks reached significance only when the accuracy scores from the heartbeat tracking task were analysed. Taking into consideration that the pattern of correlation was the same across heartbeat tasks, that is, independent of the heartbeat task, cardioceptive accuracy was negatively associated to percentage ingested volume of water required to produce satiation, the difference in statistical significance may be attributed to characteristics inherent to the distinct heartbeat detection tasks (Garfinkel et al., 2015). Presently, there is very little information regarding correlations of heartbeat discriminating ability with gastric interoception. An early report by Whitehead and Drescher (1980) is the only one we can find that tested the relationship between interoceptive performance in a heartbeat discrimination task and gastric sensitivity. In that study, participants were instructed to indicate possible synchronicity between a visual stimulus (i.e. flashing light) and their gastric contractions evoked through an inflating balloon within participants' stomach, as well as their heartbeats (Whitehead & Drescher, 1980).

The second issue of note concerns the gastric interoception protocol. Although the water load tests introduced in the field eliminated methodological constraints attached to measuring gastric sensitivity by producing mechanical distention through barostats (e.g. gastric balloons filled with water: Geliebter & Hashim, 2001), a serious confounding variable remains underconsidered: individual differences in stomach capacity. As shown here, if absolute ingested water volume had been the gastric sensitivity measure of choice, we would have failed to observe phenotypic differences in interoceptive performance. Our findings agree with those of Herbert et al. (2012) where, besides controlling for substantial variations in stomach capacity by recruiting only normal weight women, they measured changes in gastric movements via electrical sensors, which further reduced potential noise from subjectivity in participants' responses regarding sensed satiety. Following a different approach where participants ingested a predetermined water volume adjusted for their body size, Ferentzi et al. (2018) proposed a divergence of gastric and cardiac interoceptive axes. Critically, van Dyck and colleagues who put forward the water load protocol used here, reported a non-significant ($p = .107$) correlation between cardiac and gastric interoceptive abilities; the extent to which an interoception task that exclusively relies on eating-related stimuli/memory could match interoceptive performance across discrete visceral events was questioned (van Dyck et al., 2016). Further research to disentangle these issues is needed. Notably, the overlap between the two modes of interoception measured here was partially dependent on the sweet liker phenotype, with SLs (who showed enhanced interoceptive abilities) showing a stronger cross-modal relationship. Indeed, in prior reports where the two interoceptive axes were not associated, checks for interactions of groups differing in interoceptive performance on correlations under investigation were not reported (Ferentzi et al., 2018; Keenan, 2015; van Dyck et al., 2016). Further, sex-mixed cohorts (Keenan, 2015) are expected to suffer more from limitations such as not accounting for differences in stomach capacity unless a measure of body size is considered (discussed in Monrroy et al., 2019).

Our study has several strengths and weaknesses that should be noted. Strengths include the examination of interoceptive processes across constructs and senses, as well as consistent testing conditions across participants using specific wording in instructions (Desmedt, Luminet, & Corneille, 2018; van Dyck et al., 2016) and the same equipment throughout (Murphy et al., 2019), as well as not providing feedback on the participants' performance (Ring, Brener, Knapp, & Mailloux, 2015).

In addition, comparison of the present dataset with similar reports in literature suggests that the magnitude of phenotypic differences in interoceptive accuracy across all three objective interoceptive tasks (heartbeat tracking: $\Delta Mean = .168$; heartbeat discrimination: $\Delta Mean = .092$; WLT: $\Delta Mean = .093$) is of both statistical and clinical significance. For example, in a 2016 study, anorexic patients were presented with significantly lower heartbeat tracking-specific interoceptive accuracy than their matched healthy controls ($\Delta Mean = .017$: Fischer et al., 2016). Likewise, Critchley and colleagues reported nearly half, yet significant ($p = .03$), difference in interoceptive accuracy derived from the heartbeat discrimination task between psychiatric outpatients and healthy controls (Critchley et al., 2019). For the WLT, in van Dyck et al. (2020) where the same experimental protocol was used, water needed for satiation as a percentage of total stomach capacity was calculated at 0.620 and 0.565 in patients with eating disorders and their healthy counterparts, respectively (higher values indicate lower gastric interoceptive abilities).

Some limitations, however, call for caution. First, due to time constraints, our measurements of anxiety and depression were based on widely used but brief assessment tools (i.e., the General Anxiety Disorder-7 and Patient Health Questionnaire-9) rather than more exhaustive psychometric tests such as the State-Trait Anxiety Inventory and the Beck Depression Inventory. However, this limitation is tempered somewhat in that we recruited participants from a non-clinical population, and also excluded participants with known mental disorders from participation, so we believe use of a brief assessment tool is justified. We should also note that the participants were young, educated women of mostly normal weight, so these data may not generalize to men, older individuals, or individuals with obesity, especially since sex (Grabauskaitė et al., 2017), age (Murphy, Geary, Millgate, Catmur, & Bird, 2018), and BMI (Herbert & Pollatos, 2014) have also shown to influence interoception measures.

5. Conclusion

Consistent with the literature on newborns (e.g., Steiner et al., 2001) and children in acute developmental stages (Coldwell et al., 2009; Mennella et al., 2014) where signals for strong liking for high sweetness are generated internally, our data suggest a connection between sweet-liking and interoceptive abilities in adults: individuals with strong liking for high sweetness had enhanced interoceptive performance and were more mindful and intuitive eaters than those who exhibited aversive responses to high sweetness. We also noted interesting parallels between cardiac and gastric interoception, suggesting a possible generalized precision in sensing visceral events.

Overall, we propose that measurement of individual variation in sweet-liking may prove useful to identify those predisposed to poorer interoceptive abilities and, hence, to food choices beyond internal needs and ultimately unhealthy body weights. In fact, being overweight or obese has been associated with attenuated interoceptive abilities (Herbert & Pollatos, 2014; Koch & Pollatos, 2014), while a negative correlation between BMI and adiposity and insular cortex's grey matter volume, i.e. the primary cortical substrate involved in interoception, has also been observed (Rasmussen et al., 2017; Smucny et al., 2012). Similarly, individuals who like ever higher sweetness and, therefore, are also likely to be highly interoceptive, might be benefitted by healthy eating advice and obesity interventions that address specifically their elevated sensitivity to emotional eating. Whether these will be confirmed by clinical trials, it remains to be seen.

Authors' contribution

VI conceptualized this study, developed study's protocol, collected and analysed the data, interpreted the results, and drafted the manuscript. LQ contributed to development of study's protocol and data analysis, and critically reviewed the manuscript. JEH and SNG critically reviewed the manuscript. MRY contributed to development of study's protocol and interpretation of the results, and critically reviewed the manuscript. All authors approved the final version of the manuscript.

Funding

This work was supported by the by the Doctoral School of the University of Sussex and the World Sugar Research Organization (WSRO). JEH is an Associate Professor in the Penn State College of Agricultural Sciences where he receives partial salary support from the United States Department of Agriculture (UDSA) via federal Hatch Act appropriations (Project #PEN04708 and Accession #1019852). The findings and conclusions in this publication are solely those of the author(s) and should not be construed to represent any official US Government determination or policy. MRY has received direct research funding from numerous sources including national and international companies, as well as speaker fees, travel reimbursements, and consultancy fees from various companies. None of these organisations or companies has had any role in study conception, design or interpretation, or the decision to publish these data.

Data and code availability

The data reported here are available through Figshare at https://figshare.com/s/1a05ffceac2ff64928a7 and the lead author has full access to them.

Declaration of competing interest

The authors have no declarations of interest.

Acknowledgements

We thank Marta Silva for assisting in setting up the testing equipment and Rhiannon Armitage for her help with participants' recruitment and screening.

Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.appet.2021.105290.

Ethical statement

All study procedures were carried out in accordance with the Declaration of Helsinki, and written informed consent was obtained at enrolment. The protocol was approved by the Science and Technology Cross-Schools Research Ethics Committee of the University of Sussex (ER/VI40/2).

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