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Re-evaluating how sweet-liking and PROP-tasting are related

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Abstract

Past research has identified distinct phenotypic differences in responses to sweet taste, although the origins of these differences remain unclear. One possibility is that these individual differences in sweet-liking are a manifestation of the more widely known differences in sensitivity to the bitter tastant 6-n-propylthiouracil (PROP), which has been related to wider differences in food liking and preference. However, previous studies exploring the relationship between sweet-liking and PROP-tasting have had mixed outcomes. This is possibly due to older studies using a more simplistic dichotic characterisation of sweet likers, whereas recent research suggests three sweet-liking phenotypes (extreme sweet likers, ESL; moderate sweet likers, MSL; and sweet dislikers, SD). To re-assess how sweet-liking and PROP tasting are inter-related, 236 volunteers evaluated their liking for 1.0M sucrose and the intensity of three concentrations of each NaCl and PROP. Using three different methods for classifying PROP taster status, our analysis confirmed that all three sweet-liking phenotypes were represented in all three PROP taster groups (super-tasters, ST; medium tasters, MT; and non-tasters, NT), but relatively few ESL were classified as ST, or SD as NT. Overall, these data suggest that while PROP tasting and sweet-liking are not causally related, the SD phenotype may partly be explained by a broader tendency for anhedonia.

Key words: sweet-liking, sweet-liking phenotypes, PROP tasting, taste sensitivity.
INTRODUCTION

Human liking for sweet taste has been widely researched and has long been considered an innate and universal preference. Positive responses to sweetness are evident from birth through the positive facial reactions of infants to the presence of sweet-tasting substances [e.g. 1, 2]. However, the idea of universal sweet liking was challenged by the classic work of Pangborn [3], whose analysis of the relationship between liking and sweetness intensity suggested three distinct hedonic profiles, where liking either increases or decreases with sweetness intensity, or peaks at moderate sweetness. This initial idea of distinct hedonic profiles in response to sweet taste is now widely accepted and defined using the sweet-liking phenotypes [3-5]. However, the majority of previous research has followed a two phenotype model of sweet likers and dislikers [5] until recently where the use of more advanced statistical techniques confirmed Pangborn’s original observation of three phenotypes: those whose liking increase as sweetness intensifies (extreme sweet likers, ESL); those who dislike higher levels of sweetness (sweet dislikers, SD); and an intermediate group who evidence optimal liking for moderate levels of sweetness (moderate sweet likers, MSL). This three-phenotype model has been confirmed in several recent studies using adult populations from multiple countries [6-10]. The existence of these different phenotypes is important since it challenges a prevailing view that universal sweet-liking drives overconsumption, yet why these different phenotypes exist remains unclear. The aim of this paper was to further investigate the possibility that these phenotypes are a manifestation of a different well-established genetic difference in taste sensitivity, based on the perceived bitterness intensity of the compounds phenylthiocarbamide (PTC) and 6-n-propylthiouracil (PROP) [11, 12].
It is now widely accepted that there are three phenotypic responses to the taste of PTC or PROP, based on the seminal work of Bartoshuk in particular [11, 13]: those perceiving minimal bitterness (non-tasters, NT); moderate bitterness (medium tasters, MT); or extreme bitterness (super-tasters, ST). These differences in perceived bitterness can be traced to differences in peripheral sensitivity and at least partly attributable to differences in the genes encoding for a specific bitter taste receptor (the TAS2R38 gene) [14-16]. These differences in PROP tasting have been associated with differences in liking for specific foods and sensory experiences [reviewed in: 17, 18, 19], including differences in liking for fruit and vegetables [e.g. 20, 21, 22] and fats [e.g. 23, 24]. In the present context, some [e.g. 25, 26], but not all [27], studies reported differences in sweet taste sensitivity between different PROP taster groups or found PROP-taster status or associated genes to predict preference for sweet taste [28]. A recent meta-analysis which summarised this literature found variations in the TAS2R38 bitter-taste gene, and not genes encoding the oral detection of sweetness, were significant predictors of sweet preference or intake [29], suggesting that individual differences in sweet-liking are related to bitter-taste sensitivity. However, most of those studies treated sweet-liking as a continuous variable rather than as discrete phenotypes.

Other studies have directly explored the possible inter-relationship between sweet liking and PROP tasting phenotypes [9, 27, 30-34] with varied outcomes. In earlier research that used the simpler dichotomous classification of sweet liking, some studies reported disproportionately more PROP ST were sweet dislikers, and likewise, a higher proportion of PROP NT were sweet likers [27, 30, 31]. Although, other studies found no differences in proportions of PROP taster groups between sweet likers and dislikers [32, 33]. However,
what is clear across those studies is that sweet-liking and PROP tasting do not seem causally
related since no study found a perfect match between PROP-taster and sweet-liking status.
To our knowledge, only one study has since examined this association using the more
nuanced three-phenotype model of sweet liking [9] and found similar proportions of PROP
taster groups across the three sweet-liking phenotypes. Our earlier studies, using the
dichotic classification of sweet-liking, found a higher proportion of PROP ST expressing
sweet-disliking [27, 30, 31], but tested a younger population than did the more recent paper
by Yang et al. [9]. We therefore revisited this association here using the three sweet-liking
phenotype model in the same population we used previously to try and further clarify these
inter-relationships.

2.0 METHODS

2.1 Participants

Participants were 236 volunteers, aged 18-34, who were mainly staff or students at the
University of Sussex, UK. They were recruited for the hour lab-based study through
advertisements on a participant study website and flyers distributed around social spaces at
the university. Potential participants who had diabetes, a prior diagnosis of an eating
disorder, took prescription medications (excluding oral contraceptives) or smoked more
than five cigarettes a week were excluded. Smoking was included as this has been shown to
affect PROP tasting in particular [35]. 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/MARTIN/16), and the study and was conducted in
accordance with 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.

### 2.2 Rating scales and training

To increase the reliability of between-participant contrasts of the key intensity and liking ratings, participants were trained to correctly use the rating scales based on published protocols [36, 37]. Measures of the perceived intensity of sucrose (“How [sweet/bitter/sour/salty] is sample XXX?”) and PROP solutions (“How intense is sample XXX?”) were made using a 100pt vertical generalised Labelled Magnitude Scales (gLMS), with standard descriptors positioned at quasi-logarithmic intervals ranging from “No sensation” (0) to “The strongest sensation imaginable” (100), presented using Sussex Ingestion Pattern Monitor (SIPM version 2.0.13, University of Sussex, Falmer, UK). The nature of the scale was described verbally to participants, noting that the top of the scale represented the most intense sensation that they could ever imagine experiencing. To reduce the possible confound of participants using the labels as anchors [38], 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 then completed two practice ratings based on two non-taste examples recommended from previous studies [38, 39]. The two questions, both of which should have elicited responses close to the maximal “highest sensation imaginable” on the gLMS, were to rate the perceived intensity of “staring at the sun through binoculars” and “listening to a heavy metal song with headphones on maximum volume”.

Liking (“How much do you like Sample XXX?”) was assessed using a horizontal visual analogue scale (VAS) ranging from -50 to 50 and end-anchored with “Dislike extremely” and
“Like extremely”. 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’. After instruction on its use, participants rated four non-taste practice examples: “How much do you like walking in the rain?”, “How much do you like a warm fire on a cold day?”, “How much do you like the sound of a car alarm?” and “How much do you like watching your favourite movie?”.

2.3 Assessing sweet-liking phenotype

To determine sweet-liking phenotype status, participants evaluated two samples of 1.0M sucrose, alongside two water blanks, using the protocol recommended by Iatridi et al. [7]. Solutions were prepared at least 48h ahead of testing and were stored refrigerated at 4°C for up to seven days. Four 10ml samples were decanted into 60ml clear shot glasses and brought to room temperature at least 2h before the taste test. Two pairs of water and 1.0M sucrose solutions were sampled, water first, with a 30sec interval between the two sets of stimuli. Participants were instructed to swill the solution around their mouth while counting to ten and then expectorate the solution into an adjacent spittoon before immediately rating each sample and rinsing their mouth. Each solution was first rated for liking and then intensity (sweet, bitter, sour and salty). Instructions, timings and ratings were all presented using the SIPM.

2.4 PROP taste test

To classify PROP Taster Status, the three-solution test was used [40] to ensure comparability with our earlier study [27]. Six 10ml solutions were served in 60ml clear shot glasses: three concentrations of NaCl solutions (0.01M, 0.1M and 1.0M); and three
concentrations of PROP (0.032Mm, 0.32Mm and 3.2Mm). These solutions were prepared weekly (at least 48 hours before use), stored refrigerated at 4°C and served at room temperature. Using a swill and spit procedure, participants first evaluated the intensity of three NaCl and then the three PROP solutions: this reduced the possible negative effect carry-over effects from PROP. Timing and sampling were the same as the sweet-taste test and were presented using SIPM.

2.5 Procedure

All testing was conducted in small, windowless testing cubicles in the Sussex Ingestive Behaviour laboratory at the University of Sussex. Prior to testing, participants were required to abstain for at least two hours from consuming food and beverages (excluding water), smoking, chewing gum or brushing their teeth. This was confirmed on arrival. Participants who were suffering from any respiratory illness were asked to rebook when they had fully recovered. After these checks, participants completed informed consent.

Before the first taste test commenced, the experimenter explained to the participant that they would be completing two swill and spit taste tests but would first undergo training in the scales used (described in 2.2). As part of this, participants completed a disguised mood questionnaire to allow for controls for appetitive state. Using VAS, participants rated their hunger, fullness and thirst alongside three mood descriptors (happy, tired and anxious) presented in random order. After which, they completed the sweet-liking taste test followed by a 30-minute break where they completed a series of questionnaires (unrelated to the purpose of this report) before their height, weight and age were recorded. Finally, they finished the session with the PROP taste test, followed by debriefing and payment.
2.6 Data coding and analysis.

2.6.1 Classifying sweet-liking phenotype status

Sweet-liking status was determined by the ratings for the two 1.0M sucrose solutions. Initial checks confirmed whether participants had given consistent responses: where the rated liking for the two samples of 1.0M sucrose differed by >30pt on the VAS scale, and one rating indicated liking (>0) and the other dislike (<0), those participants (n=20) were classified as erratic and their data excluded from the analysis. Computer error meant data were missing for one further case. For the remaining 215 participants, both ratings above a score of +15 classified participants as ESL (n = 83), below a score of -15 classified as SD (n = 47), and between these scores as MSL (n=85).

2.6.2 Classifying PROP taster status

Prior to analysis of the PROP data, we first checked that responses to the two non-taste training gLMS ratings confirmed that participants were using this scale as predicted, with the intention to then use one or both scales as an anchor against which to scale PROP ratings, as recommended to reduce the risk of apparent individual differences reflecting differences in scale use [41]. Since both questions were worded to imply these sensations should be perceived as strong sensations, we first looked for responses scoring less than 50 (Strong on the gLMS): as this was done blind to sweet-liker classification, this was based on the full sample of 236. For the question rating loud music, 37/236 had ratings less than 50, while 20/236 rated staring at the sun <50. Once these data were combined with sweet-liking classifications, five of those classified as erratic responders on the sweet-liking test rated both non-taste gLMS questions <50, and four further erratic responders rated either music or sun <50. As all erratic responders were excluded, this had no impact on outcomes.
However, that still left numerous cases where either music, sun or both were rated <50 for intensity. We noted that the average rated intensity for music (67.6) was only marginally higher than that for the strongest NaCl solution (62.3) and concluded that the item could not be used reliably to standardise gLMS scores for taste stimuli. In contrast, the average intensity for staring at the sun was 79.1, and although there remained 10 instances were this was <50, analysis confirmed to be statistical outliers. Notes from participant debriefing suggested the issue was the use of the word binoculars, which was included to try and maximise the intensity of the imagined experience. However, some participants reported being unfamiliar with that word and had interpreted it as a form of sunglasses. Therefore, we concluded that we should explore the inter-relationship between sweet-liking and PROP taster status based on raw gLMS data (to include the full sample) and with gLMS ratings adjusted using the rated intensity of the sun (excluding responses that were statistical outliers). For the rescaled analyses, all gLMS ratings were rescaled for each person using the formula: rescaled_value = (original_value/rated_sun_intensity)*100.

PROP Taster Status was first determined based on the gLMS ratings of PROP intensity using first the raw data and secondly rescaled data. In line with the broader recent literature [e.g. 42], and to be consistent with our 2009 paper [30], we only considered ratings for the strongest (3.2mM) PROP concentration. For the raw data, those with ratings greater than 70 were defined as ST, less than 30 as NT and in between those values as MT. For gLMS ratings adjusted by the non-taste “sun” standard, these boundaries were rescaled accordingly.

The second approach used the procedure introduced by Bartoshuk et al. [13] and recommended by Tepper et al. [40] to be consistent with our original 2007 paper examining sweet liking and PROP-taster status [27] and with other recent papers examining PROP
phenotypes [e.g. 43]. In brief, participants were classified based on visual inspection, participants whose intensity ratings for the three PROP solutions were consistently lower than those for the equivalent NaCl solution were defined as NT, where PROP and NaCl were rated as similar in intensity (typically <10pt difference) as MT and where PROP stimuli were rated as clearly more intense than NaCl as ST. Group assignment was completed blind to sweet-liking status and was conducted independently by three of the researchers (MY, NM and RA). Based on these rules, there was unanimous agreement on 195 cases (83%). The 41 cases of disagreement were either at the ST/MT (24 cases) or MT/NT (17 cases) boundary, and all cases were looked at closely. Where two assessors agreed, the majority view was accepted. Three cases could not be immediately classified (for example, one assessor classified as ST, one as MT and the third as borderline ST/MT). Of these, two were where both the PROP gLMS rating for the most concentrated solutions were near the top of the gLMS scale: based on Tepper et al., this could be interpreted as MT, but classifying an individual as MT when they rated all PROP concentrations as close to maximal on the gLMS intensity scale seemed problematic, and so these were classified as ST. The remaining participant was at the MT/NT border and tended to rate NaCl as more intense than PROP, but rated the highest PROP >50, which again seemed inappropriate to classify as NT: as there was no clear way of reaching an agreement, this participant was excluded from analysis (when the data for PROP and sweet-liking were then combined it transpired that this participant was also classified as an erratic sweet responder, and so may not have paid full attention to the rating tasks).

When we compared the classification across the two methods, in 212 cases, the outcome was the same. However, classification changed for 24, although only across one boundary (i.e., ST/MT or MT/NT). We, therefore, included both approaches in data analysis but
consider limitations due to the inherent subjectivity in classifying participants in the discussion.

2.6.3 Data analysis plan

To test whether PROP taster status varied with sweet-liking phenotype status, multinomial logistic regression was used to contrast whether the different sweet-liking phenotypes (as the dependent variable with three levels) was predicted by PROP taster status, including participant age, BMI, biological sex and rated hunger at the time of testing as covariates, with separate analyses for the two methods of classifying PROP taster status.

To test whether sweet-liking phenotypes also differed in their taste perception for NaCl and PROP, we analysed the intensity ratings for NaCl and PROP using a 4-way mixed ANOVA, with tastant (NaCl or PROP) and concentration (3 levels) as within-participant factors and sweet-liking phenotype and PROP taster status as between participants. Sphericity was checked and was found to be violated for the concentration x tastant interaction: therefore, the Greenhouse-Giesser adjustment was applied. As this initial analysis revealed significant 3-way interactions (reported in full in results), we then conducted separate ANOVAs for each tastant, with Bonferroni-protected contrasts of main effects: here, sphericity was violated for the main effect of concentration for PROP. All analyses were conducted using IBM SPSS version 25 run on Macintosh. Data are available at 10.25377/sussex.14822634.

3.0 RESULTS

3.1. Distribution of PROP tasters across the sweet-liking phenotypes

Based on classification using only 3.2mM PROP for the raw gLMS data, regression identified both PROP-taster status ($\chi^2 (4, N = 215) = 13.48, p = .009$) and participant sex ($\chi^2 (2, N = 215) = 12.66, p = .002$) as significant predictors of sweet-liking phenotype, but no
significant effects of age, BMI or rated hunger. To test whether the effect of PROP-taster status could have been caused indirectly by the effect of biological sex, separate follow-up regressions were conducted for men and women. In both cases, the effect of PROP-taster status remained significant (men, $\chi^2 (4, N = 44) = 10.48, p = .033$: women, $\chi^2 (4, N = 171) = 10.47, p = .033$). Repeating these analyses with the smaller sample using rescaled gLMS data, PROP-taster status ($\chi^2 (4, N = 205) = 12.89, p = .012$) and participant sex ($\chi^2 (2, N = 205) = 11.40, p = .003$) remained as significant predictors of sweet-liking phenotype, but again no significant effects were found for age, BMI or rated hunger, suggesting that the significant differences were not an artefact of differences in scale use between participants. Repeating these analyses based on PROP taster classification using the combination of PROP and NaCl ratings revealed similar, and slightly more significant, findings: PROP-taster status ($\chi^2 (4, N = 215) = 16.62, p = .002$) and participant sex ($\chi^2 (2, N = 215) = 14.18, p = .001$) were again significant predictors of sweet-liking phenotype, with no significant effects of age, BMI or rated hunger.

To identify how sweet-liking status differed depending on PROP taster status, the relative frequencies of each combination of sweet-liking and PROP tasting were contrasted (Table 2, left-hand panel). Setting ESL as the reference category in the regression, parameter estimates only found significant deviations from chance in the SD group, with significantly more ST and fewer NT than expected. The same pattern was seen when using the combination of PROP and NaCl to define taster status (Table 2, right-hand panel).

The effects of biological sex in all of these analyses were due to disproportionately more men classified as ESL (28/44 men cf 55/171 women), and relatively few men being classified as SD (4/44 men cf 43/171 women).
3.2. Analysis of PROP and NaCl intensity ratings.

Initial analysis of the rated intensity of the three concentrations of both NaCl and PROP using the Bartoshuk et al. [13] classification method found significant interactions between the tastant, concentration and sweet-liking phenotype \( [F(3.88, 412) = 4.29, \, p = .002, \, \eta^2 = 0.04] \) and between the tastant, concentration and PROP-taster status \( [F(3.88, 412) = 32.17, \, p < .001, \, \eta^2 = 0.24] \). Since classification of PROP taster status was determined by PROP intensity ratings, the interaction between PROP taster status and concentration was significant \( [F(4, 412) = 97.94, \, p < .001, \, \eta^2 = 0.49] \). However, while there were no significant interactions involving sweet-liking phenotypes, the main effect of sweet-liking was close to significant \( [F(2, 206) = 2.89, \, p = .058, \, \eta^2 = 0.03] \), with averaged PROP intensity ratings slightly, but significantly, higher for SD \( (34.7 \pm 1.5) \) than for ESL \( (30.4 \pm 1.1) \) or MSL \( (31.1 \pm 1.0) \).

For NaCl, there were significant interactions between concentration and sweet-liking phenotype \( [F(4,412) = 4.78, \, p = .001, \, \eta^2 = 0.04] \) and PROP taster status \( [F(4,412) = 2.80, \, p = 0.026, \, \eta^2 = 0.03] \). Rated intensity of NaCl appeared to increase similarly in all three PROP groups for those classified as ESL (see Figure 1 right-hand panels), but the intensity of NaCl increased more steeply with concentration for the PROP ST group than for the other PROP groups for those classified as MSL or SD. This impression was confirmed by analysis contrasting intensity of each concentration depending on sweet-liking and PROP taster groups. There was a significant effect of sweet-liking phenotype on intensity of 1.0M NaCl \( [F(2,206) = 3.91, \, p = .022, \, \eta^2 = 0.04] \), with the overall intensity significantly stronger for SD \( (67.1 \pm 3.0) \) than MSL \( (58.0 \pm 2.1, \, p = 0.046) \), with ESL intermediate \( (64.9 \pm 2.4) \). Intensity of 1.0M NaCl also varied significantly with PROP taster status \( [F(2,206) = 3.68, \, p = .027, \, \eta^2 = 0.03] \), and here it was the PROP ST who tended to rate this as the most intense \( (69.0 \pm 2.6) \).
compared with 61.2 ± 2.1 for MT and 59.8 ± 2.9 for NT, although these contrasts were not significant. No effects of sweet-liking phenotype or PROP taster status were seen with the two lower NaCl concentrations.

Repeating all the analyses of PROP and NaCl intensity using the gLMS PROP re-classification method produced a very similar pattern of results, although the tendency for SD to rate PROP as more intense was no longer evident: for brevity, we do not report those analyses here but include these as supplementary data.

4.0 DISCUSSION

Using the three-phenotype method, this study aimed to reconsider the relationship between individual differences in sweet liking and PROP tasting. Previously we reported examples of all three PROP taster groups in the dichotomous classification of sweet likers and dislikers, where we found more sweet likers tended to be PROP NT, and sweet dislikers to be ST [27, 30]. The present data broadly confirmed those earlier findings when using a more nuanced classification of sweet liking. Relatively few SD were also PROP NT (just 7 or 8 out of 46, depending on how we classified PROP tasting), and their modal PROP phenotype was ST. In contrast, relatively few ESL were NT, with 70% classified as MT or ST.

The present results contrast with those of Yang et al. [9], the only other study to assess these relationships using the 3-phenotype sweet-liking model, who found a tendency for more PROP NT in their low-sweet liking phenotype, although overall, they found no significant differences in the distribution of PROP tasters across their sweet liking groups. This may be due to differences in methodology. The Yang et al. study used slightly more sucrose solutions (five) that were consumed after sampling alongside water and crackers to cleanse their palate between each tasting. In contrast, we employed a swill-and-spit
methodology with just two sucrose samples and used only water between samples. Thus, it is possible that the effects of satiation due to ingestion of sucrose and crackers with possible fatigue from assessing multiple stimuli might have influenced the outcome. It is also noteworthy that the two studies differed in the way PROP sensitivity was tested: the earlier paper used a cotton-bud soaked in 0.32mM PROP rubbed on a small section of the tongue for three seconds, whereas in our study participants swilled 10ml of 3.2mM PROP for c. 10 seconds. It is therefore likely that our participants experienced much stronger bitterness, and this may have increased the accuracy of phenotype classification. However, it is also possible that the effects were down to chance, given that in all studies to date, examples of all PROP taster groups have been seen for all sweet-liking phenotypes. Thus, the conclusion remains that differences in sweet liking are not a direct consequence of differences in oral taste sensitivity as indexed by PROP tasting, which is not surprising given that the receptors for sweet and bitter taste detection are well defined and separate [44]. However, it is noteworthy that 4/7 studies that have looked at how PROP tasting and sweet liking are related have found disproportionately more PROP ST are also sweet dislikers, which does suggest that sweet disliking may be more likely for those who have greater oral taste sensitivity.

The key question is then, why would sweet-liking and PROP tasting be related? Since PROP and sucrose are detected orally by different receptor systems, an explanation in terms of taste perception per se is unlikely, especially since it has been well established that individual differences in sweet-liking are not themselves due to differences in perception of the intensity of sweetness [7, 8, 27]. We suggest two possible explanations why more PROP ST may be SD, both underpinned by anhedonia. The first is based on the suggestion of an association between PROP sensitivity and more general anhedonia. Early work suggested
specific personality traits were associated with tasting phenylthiocarbamide [PTC: 45]; the compound used initially to screen for bitterness sensitivity before PROP. These traits included greater tenseness or apprehension in those most sensitive to PTC. Subsequent research found that PTC sensitivity was correlated with a questionnaire measure of anhedonia [46] and that PROP ST were more reactive on behavioural measures of approach/avoidance [47]. This suggestion of wariness and reduced reward activity is also seen in studies contrasting sweet-liking phenotypes. In particular, SD had lower reward sensitivity and reduced sensation-seeking than the other phenotypes [48]. Thus we hypothesise that the tendency for SD to be PROP ST reflects this shared wariness and reduced sensitivity to reward.

The second draws on wider research with PROP, suggesting that PROP ST exhibit reduced preferences for a wide range of foods [49]. As noted in the introduction, sweet preference and intake have been reliably shown to be predicted by TAS2R38 polymorphisms [29], which are established predictors of PROP taster status [14]. PROP ST also show heightened sensitivity to artificial sweeteners, partly driven by increased sensitivity to the bitter-taste component seen in some sweeteners [50, 51], but also reduced focus on sweetness [50]. It is also plausible that the particular sensitivity of SD to different components of taste in determining food preferences could itself be a specific food-related manifestation of a wider tendency towards anhedonia. Further studies into broader hedonic responses of SD are thus needed.

When designing the present study, it became clear that there are many different approaches to classifying PROP taster groups. Since there is no one recommended approach, we tested the association with sweet-liking using two different approaches, with and without controlling for individual differences in using gLMS. All analyses had the same
outcome suggesting that individual differences in sensitivity to PROP are robust enough not
to vary with slight differences in methodology. Nevertheless, the data also suggest that the
older method of contrasting the intensity of PROP with NaCl is less effective. Firstly, that
approach relies on a degree of subjectivity in what constitutes clear differences in intensity:
there is no defined standard, and although for the vast majority of participants, clear
differences are evident (demonstrated here by the consistency in classification for the
majority of participants), there are inevitably ambiguous cases which are prone to bias
judgements. Secondly, that method assumes that PROP taster groups respond similarly to
the taste of NaCl, but the present data and many others [12, 52, 53] have reported that
PROP ST rate NaCl as more intense, in line with evidence of broader hyper-sensitivity to
taste [12]. Indeed, recent studies found that sensitivity to PROP was predicted by sensitivity
to salthy taste [54]. For these reasons, the present study provides support for the use of
standardised gLMS scales as the preferred method to classify taster groups, but notes the
need for generally accepted evidence-based cut-off values to ensure more reliable
comparisons across studies.

The present finding of greater taste intensity for NaCl and PROP by SD might suggest that
this group’s dislike for sweetness could be because they also perceived sweetness as more
intense and that their apparent dislike for sweetness based on sucrose concentration was
due to that enhanced sweetness. However, previous studies have shown this not to be the
case: phenotypic differences in sweet liking were equally evident when liking was analysed
both as a function of sucrose concentration or as perceived sweetness both using the older
dichotic classification into sweet likers and dislikers [27] and the more recent 3-phenotype
model [7]. Thus, any increased taste sensitivity by SD seems to be a characteristic of that
phenotypic group.
A cautionary note in interpreting the group differences in sensory ratings is the validity of comparing intensity ratings across individuals. This issue has been widely debated, with concerns that individual differences in rating scale use could generate apparent differences which were down to scale interpretation [55]. The gLMS was developed to counter these concerns, and we adopted the accepted practice of specific training on the use of the gLMS, using defined extremes to reduce any confounding effects of scale use [36, 37]. We also used the same gLMS approach here as in our earlier work to ensure we could compare the outcomes of this study with earlier papers. A limitation of the present study, however, was our choice of non-taste control stimuli used in gLMS scale training. We selected two items that have been widely used [e.g. 38, 55, 56] which we believed would be relevant to the young-adult population we were testing. However, it was clear that the wording of both questions caused some confusion for a significant minority of participants. For the music question, the surprisingly high number of unexpectedly low scores we believe reflected conflation of intensity and liking, with people who like that genre of music rating the intensity as low. While the addition of the word binoculars to the question on looking at the sun confused a small number of participants. There is, however, no published set of questions that are universally accepted to standardise gLMS training and use, and the current study suggests that would be a useful advance.

In summary, the present data further clarify the relationship between sweet-liking and PROP tasting, confirming that these are not causally related but suggesting that both extreme sensitivity to bitterness and disliking for sweetness may both be in part founded by differences in orosensory sensitivity.
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Table 1. Age, BMI and rated hunger of the final analysed sample, broken down by participant sex. Data are mean ± SEM and range.

<table>
<thead>
<tr>
<th></th>
<th>Women (n = 171)</th>
<th>Men (n = 44)</th>
<th>All (n = 215)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Age (years)</td>
<td>20.4 ± 0.1 (18 - 28)</td>
<td>20.7 ± 0.3 (18 – 30)</td>
<td>20.5 ± 0.1 (18 – 30)</td>
</tr>
<tr>
<td>BMI (kg/m(^2))</td>
<td>22.5 ± 0.3 (14.4 – 48.6)</td>
<td>23.2 ± 0.8 (16.9 – 50.2)</td>
<td>22.7 ± 0.3 (14.4 – 50.2)</td>
</tr>
<tr>
<td>Rated hunger (100pt VAS)</td>
<td>48.1 ± 2.1 (0 – 96)</td>
<td>52.9 ± 3.7 (0 – 91)</td>
<td>49.0 ± 1.8 (0 – 96)</td>
</tr>
</tbody>
</table>
Table 2. Numbers of participants classified into the three sweet-liking phenotypes and the three PROP taster groups.

<table>
<thead>
<tr>
<th>Sweet liking phenotype</th>
<th>Classified by 3.2mM PROP only</th>
<th>Classified by PROP and NaCl ratings</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Extreme likers</td>
<td>Moderate likers</td>
</tr>
<tr>
<td>PROP taster group</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Supertasters</td>
<td>18 (22%)</td>
<td>32 (38%)</td>
</tr>
<tr>
<td>Medium tasters</td>
<td>41 (49%)</td>
<td>31 (36%)</td>
</tr>
<tr>
<td>Non tasters</td>
<td>24 (29%)</td>
<td>22 (26%)</td>
</tr>
</tbody>
</table>

1. Percentage figures show the distribution of PROP tasters within each sweet-liking phenotype.
Figure legends

Figure 1. gLMS ratings of the intensity of the PROP (left hand panels) and NaCl (right hand panels) solutions by each of the three sweet-liking phenotypes (ESL, extreme sweet likers: MSL, moderate sweet likers: SD, sweet dislikers), depending on their PROP taster status: super-tasters (ST●●●), medium tasters (MT▲▲▲) or nontasters (NT●●●). All data are mean ± SE. Ratings were scaled from “No sensation” (0) to “The strongest sensation imaginable” (100).