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Explaining variability in sodium intake through oral sensory phenotype, salt sensation and liking

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Abstract

Our sodium-rich food supply compels investigation of how variation in salt sensation influences liking and intake of high-sodium foods. While supertasters (those with heightened propylthiouracil (PROP) bitterness or taste papillae number) report greater saltiness from concentrated salt solutions, the non-taster/supertaster effect on sodium intake is unclear. We assessed taster effects on salt sensation, liking and intake among 87 healthy adults (45 men). PROP bitterness showed stronger associations with perceived saltiness in foods than did papillae number. Supertasters reported: greater saltiness in chips/pretzels and broth at levels comparable to regular-sodium products; greater sensory and/or liking changes to growing sodium concentration in cheeses (where sodium ions mask bitterness) and broths; and less frequently salting foods. PROP effects were attenuated in women. Compared with men, women reported more saltiness from high-sodium foods and greater liking for broth at salt levels comparable to regular-sodium products. Across men and women, Structural Equation Models showed PROP and papillae number independently explained variability in consuming high-sodium foods by impacting salt sensation and/or liking. PROP supertasters reported greater changes in sensation when more salt was added to broth, which then associated with greater changes in broth liking, and finally with more frequent high-sodium food intake. Greater papillae number was associated with less frequent high-sodium food intake via reduced liking for high-fat/high-sodium foods. In summary, variation in sensations from salt was associated with differences in hedonic responses to high-sodium foods and thus sodium intake. Despite adding less salt, PROP supertasters consumed more sodium through food, as salt was more important to preference, both for its salty taste and masking of bitterness.

Keywords

Taste; genetics; sodium chloride; food preferences; hedonics; sex differences; dietary sodium; propylthiouracil; fungiform papillae; Structural Equation Modeling

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1. Introduction

Of the 71 million Americans with some form of cardiovascular disease, an estimated 65 million have hypertension [1]. Nearly one-third of deaths globally are attributed to cardiovascular diseases, and about 23% of these deaths for hypertensive and other heart conditions [2]. The link between dietary sodium and hypertension is well established [3] and dietary modification is a primary step in hypertension risk reduction. Yet, in spite of extensive public health education campaigns, sodium consumption exceeds recommendations. For example, according to the 2005–2006 Nutritional and Health Examination Survey Data, 20 to 29 year old men consume nearly double the recommended sodium intake (<2300 mg/d) while women consume 135%. [4]. Intake of sodium above recommended levels likely comes from consumption of processed foods and beverages [5,6] to which sodium salts have been added for flavor enhancement (eg, saltiness, blocking unpleasant sensations, increasing sweetness) [7,8] or functional reasons (eg, preservation, moisture control, texture). Since consumers report that taste is an important determinant of food selection [9], the present study examined whether normal variation in taste and oral sensation influenced salt sensation sufficiently to affect liking and consumption of high sodium foods.

The perceived intensity of sodium chloride varies such that a specific concentration required to elicit weak saltiness in one individual may be strongly salty to another. Critically, these differences are not merely the result of differences in response bias, but appear to result from underlying variation in taste sensation. The best-studied phenotypic marker of variation in taste and oral sensation is the perceived bitterness of propylthiouracil (PROP) [10]; some additional markers include the density of taste papilla on the tongue tip (fungiform papilla) and thermal tasting [11]. Differences in the perceived bitterness of PROP have repeatedly been shown to associate with the saltiness of simple salt solutions [11–13] and beef broth [14] when using methods that allow for valid across subject comparisons [15]. In beef broth, those who taste PROP as more bitter are able to detect smaller changes in salt concentration [14]. One prior study failed to find PROP effects on perceived saltiness of solid foods [16]; however, PROP phenotype was defined as the ratio of PROP bitterness to NaCl saltiness, which has limited validity for examining PROP effects on salt perception, as the phenotype was confounded with the outcome measure. In addition to behavioral measures, greater density of fungiform papillae explains heightened saltiness of salt solutions on the tongue tip [17,18], but may have less impact on whole mouth saltiness [12]. Thus, the question of whether commonly studied oral sensory phenotypes influence the perceived intensity of sodium chloride in foods remains unclear. Here, we address this knowledge gap by examining taste phenotype (perceived bitterness of PROP and number of fungiform papillae) and salt sensation/liking in aqueous solution, in chicken broths with increasing amounts of added sodium chloride, as well as sampled high-sodium foods.

The hedonic response to saltiness in humans results from a complex interplay of physiological, cultural, and environmental factors that influence avidity for and access to high sodium foods. Critically, humans are different from other animals in that there is little evidence for a general 'salt appetite' [19]. That is, humans consume salt for pleasure and not to meet physiological need. Thus, our goal here was to focus specifically on variation in salt sensation in healthy adults and the extent to which this variation may influence the liking for the sensation of salt in aqueous solution, broth and perceptually complex food products. As stated above, we also examined markers of variation in taste and oral sensation that are hypothesized to influence the development of food preferences (eg, [20,21] but also [22]).

In a liquid food such as a broth, the relationship between liking and sodium concentration forms an inverted U: liking is initially low before rising to a peak and subsequently falling, although the shape of the function varies across individuals [23,24]. Differences in perceived intensity

may affect the sodium chloride concentration required to achieve maximal liking. At higher concentrations, perceived intensity from salt would be comprised by both salty taste and irritation [25], although it is not clear whether individuals can reliably partition out the relative contributions of these qualities in the overall percept elicited by concentrated sodium chloride. In a previous study, those tasting PROP as more bitter (supertasters) showed greater hedonic response to changes in salt level in beef broth, preferring the addition of smaller amounts to the broths than did the nontasters [14]. Unfortunately, the study was confounded by sex differences in the taster groups, which could influence sodium chloride hedonics — only 8% of the supertasters were male versus 25% of the nontasters and 50% of the medium tasters. Here, in a cohort where the distribution of PROP bitterness did not differ between men and women, we tested a) whether oral sensory phenotype influenced perceived intensity enough to shift the concentration in broth where peak liking occurs and b) if the relationship between changing concentration and hedonic responsiveness varied by oral sensory phenotype.

Some reports suggest sex hormones may influence salt preference [26–28] although results in humans are inconsistent (see [19]). In rodents, estrogen present during development may moderate taste responses [26] with females being less averse to high concentrations of sodium chloride in solution [29]. In humans, changing hormone levels associate with changes in salt sensation and hedonics; a longitudinal study across pregnancy [30] shows that saltiness of aqueous sodium chloride falls with a concurrent reduction in the unpleasantness from 1st to 3rd trimesters. Likewise, preferred level of salt on popcorn varies with the phase of the menstrual cycle [27]; conversely, preference does not differ across prepubescent girls and boys [28]. However, apparent differences in salt preference associated with sex hormone fluctuations could be the result of cognitive control of eating (dietary restraint) as shown by Kanarek and colleagues [31]. The present study characterizes differences in salt sensation and hedonics across males and females who do not report an excessive level of dietary restraint on eating.

A substantial body of literature supports that food liking and preference are strong predictors of intake (eg [32,33]). Specific to salt, a small majority of studies report positive associations between salt hedonics and sodium intake [34]. Early work from the Pangborn laboratory found consistent trends between hedonics and intake in a small sample of college students. Individuals who habitually consumed more sodium added more salt to reach optimal saltiness in tomato juice [35] and in beef broth [24] and the concentration that elicited maximal liking also correlated with intake [24]. Shepherd and colleagues found that individuals who consume more sodium prefer greater salt concentrations in tomato soup [36], although they caution that preference may be more tightly linked to discretionary salt usage rather than total sodium intake [37] because many important sources of dietary sodium are not salty [38]. Recently, Kim and Lee reported associations between elevated salt thresholds, elevated liking for salt in broth, and elevated consumption of salty foods among Korean adolescents [39]. With a more distal outcome of sodium intake, Contreras [40], using data from Moskowitz and Abrahamson, showed the inverted U is shifted to the right for hypertensive individuals (ie, peak liking occurs at a higher concentration) as compared to normotensive individuals, while Mattes [41] did not find mean differences in salt preference across blood pressure groups.

Some studies fail to find associations between salt hedonics and sodium intake: the lack of consensus may be due to insensitivity in methods used to assess sodium intake [34]. Most prior studies estimate intake using un-validated questionnaires or single 24-hr urinary collection. Notably, the assumption that methods from analytical chemistry are superior for assessing intake should be tempered by two factors. First, large variation in intake across days makes any single point estimate suspect. More critically, excreted sodium may differ substantially from estimated intake, even when intake estimates are based on analysis of the foods actually consumed [42]; this is consistent with evidence that the rate of ion excretion is not stable even

when intake is constant [43]. The present study builds on prior work by associating salt sensation with multiple measures of sodium intake: quantitative food frequency, five non-consecutive 24-hr food records (see [44]), and liking for high-sodium foods, which may be an intermediate step between sensation and intake [45] and reflect habitual intake patterns [46, 47].

In summary, the present study examined variability in salt sensation and hedonics and the extent to which this variability was associated with consumption of high-sodium foods. Specifically, do phenotypic measures of variation in oral sensation explain differences in perceived saltiness and hedonic response across diverse stimuli including aqueous solutions and solid foods? This is conceptually consistent with our working hypothesis that variation in taste and oral sensations influence food liking and disliking, and ultimately dietary intake. We aimed to examine relationships between salt sensation, liking and intake in normally nourished adults and thus distinguish our work from the investigation of sodium appetite in response to dehydration and thirst (eg, [48]). Our general findings were that variation in perceived saltiness and liking across multiple foods were linked to sodium intake, and at least some of this variation in perception and hedonics was related to two commonly studied oral sensory phenotypes. PROP bitterness, was associated with differences in salt sensation in aqueous solution, broth, and foods for which saltiness is a predominant sensation (eg, pretzels and potato chips) or in cheese where salt serves to block bitterness. Those who tasted PROP as most bitter reported greater changes in perceived saltiness with changes in salt concentration. Salt sensation was linked to liking in these foods with predominant saltiness; oral sensory phenotype associated to the hedonic responses indirectly through salt sensation. Sex differences in saltiness or liking for high sodium foods attenuated the oral sensory phenotype effects. Women reported greater liking for moderate sodium chloride concentrations in either aqueous solutions or chicken broth. Evaluated via Structural Equation Models, oral sensory phenotypes were associated with variance in intake of high sodium foods indirectly—PROP effects on intake were mediated via salt sensation and liking while fungiform papilla number was related to sodium intake via liking of high-fat foods that are also high in sodium, rather than saltiness per se.

2. Methodology

2.1. Subjects and Procedure

Subjects came from an on-going observational study to examine relationships between oral sensation and dietary behaviors, similar to previous reports [49,50]. The sample included reportedly healthy males and females (n=87; 42 F), who ranged in age from 20–40 years. The majority (63 of 87) had a normal body mass index (BMI; weight (kg)/height (m²) from 19–24.9), while 23 were overweight (BMI 25 to 29.9) and 3 were obese (BMI>30). Men were more likely than women to fall in the overweight/obese category (17 of 45 men versus 6 of 42 women, $\chi^2=5.02$, $p<0.05$). The sample was composed of individuals without an excessive level of dietary restraint, who were not actively modifying their dietary intake, who did not have a significant history of taste-related pathologies (history of otitis media, head trauma), and who did not smoke cigarettes. There was no significant relationship between PROP bitterness and BMI. Participants were primarily of European ancestry. The University of Connecticut Institutional Review Board approved the protocol; subjects gave informed written consent and were paid for their time.

All of the data were collected in three laboratory sessions, usually one week apart. For sensory testing, the adults sampled stimuli presented in medicine cups and were instructed to expectorate and rinse with water after each sample. They were instructed on how to use a computer to rate the intensity and degree of liking/disliking on the general Labeled Magnitude Scale (gLMS) [51], which generalizes the Labeled Magnitude Scale [52] as reported previously [49]. The label at the top of the gLMS is 'strongest imaginable sensation of any kind' (100) for

intensity ratings and the ends of the scale labeled 'strongest imaginable liking/disliking of any kind' (+100/−100) for hedonic ratings. For the intensity gLMS, there are intermediate labels at 'barely detectable' (1.4), 'weak' (6), 'moderate' (17), 'strong' (35), and 'very strong' (53); the hedonic gLMS uses these same intermediate labels to quantify degree of liking/disliking. The generalized labels and instructions for scale usage are intended to have the subjects rate the stimulus in the context of all sensations and not those narrowly focused on oral sensations, which increases the validity of the gLMS as a tool for examining intensity [51] or hedonic [46] differences across individuals. Subjects also used the gLMS to report the intensity of a series of 1000 Hz-tones as a cross-modal standard. These tones were run multiple times throughout each testing session and used as a covariate in the statistical analyses (described below). Subjects were asked to report total intensity of taste in solution where saltiness was the predominant quality or the intensity of saltiness in broth. In solid foods, subjects were asked to rate the intensity of multiple taste and oral sensory qualities, although subjects were not asked to rate irritancy. For level of liking/disliking, subjects were asked to report the overall liking of the solution or food.

2.2 Measurement of Taste Phenotype

2.2.1 PROP Bitterness—The perceived intensity of PROP was assessed by direct scaling [49,50] at the end of the final session to minimize context effects, which might depress ratings for other stimuli in those who find PROP to be intensely bitter. PROP bitterness was measured in a protocol that included intensity ratings of NaCl and 1000 Hz-tones [53], presented in blocks of stimuli with the following order: tones, NaCl, tones, NaCl, tones, PROP, tones, PROP, tones. Within a block, stimulus presentation order was randomized. Taste stimuli were delivered in half-log steps: five NaCl (10mM to 1M) and five PROP (0.032 to 3.2mM) solutions. Tones were presented in 12 dB steps (50 to 98dB). For analyses, mean bitterness of the 3.2mM PROP replicates was treated as a continuous measure; it was also used to form PROP taster groups (see results below).

2.2.2 Fungiform Papilla Number—The number of fungiform papilla was assessed at the anterior tongue tip with a videomicroscopy method similar to that of Miller and Reedy [54]. The subject's anterior tongue was painted blue with food coloring and placed between two plastic slides connected with small screws. Subjects reclined on a table while the tongue was videotaped at 15× magnification — this magnification is sufficient to distinguish between fungiform and filiform papillae [54]. Videotaped images were later reviewed for counting papilla within 6mm circles on both the right and left tip. Mean number was used for analyses and to form papilla groups (see results below).

2.3 Sensory and hedonic responses to sodium chloride

2.3.1 Aqueous solution—In each testing session, subjects provided intensity and hedonic ratings for 0.32M NaCl in deionized (>15Ω) water. These data were treated as raw scores (eg, not standardized to tone ratings). Variability in intensity and hedonic ratings across testing sessions was quantified for each subject by calculating a change score: $(\Delta_{d1 \text{ to } d2}) + (\Delta_{d2 \text{ to } d3}) + (\Delta_{d3 \text{ to } d1})$.

2.3.2 Chicken Broth—Subjects reported the saltiness and overall liking across seven concentrations of sodium in sampled chicken broth, ranging from levels found in low sodium and regular sodium products to levels well beyond typical concentrations found in commercial products, where salt is an irritant. The samples were made from Campbell's® Low Sodium Chicken Broth (0.02 M sodium, Campbell Soup Co, Camden, NJ) with added Kosher salt (Cargill, Inc, Minneapolis, MN) to make seven sodium chloride concentrations in quarter log steps: 35mM, 63mM, 112mM, 0.2 M, 0.355 M, 0.63 M, and 1.12 M. These concentrations ranged from low-sodium soups, regular sodium soups (~.16M to 0.28M), to levels above which

NaCl is an oral irritant ($>0.4\text{M}$) [55]. Broths were prepared in batches, stored frozen in 50 ml aliquots, and warmed to 40°C using a water bath before serving 15 ml samples in medicine cups. In the procedure, subjects rated the intensity of blocks of stimuli including five 1000 Hz tones (12 dB steps, 50 dB to 98 dB) and 7 broths, in random order within each type of stimulus (eg, each stimulus block). This was repeated and followed by a final set of tones. Subjects were asked to rate the degree of liking/disliking and then perceived saltiness for each broth. The intensity and hedonic ratings for each concentration replicate were averaged.

Mean broth intensity and hedonic ratings were examined for phenotype and sex differences at each concentration (via ANCOVA) and for concentration differences at maximal liking (ie, peak preference concentration). Additionally, to examine phenotype and sex differences in changes in intensity and hedonic ratings, the repeated measures from the different broth concentrations were reduced to a single parameter for analyses by calculating the area under the curve (AUC) using the trapezoid rule [56]—the sum of a series of isosceles trapezoids, each with an area equal to $[(\text{height}_1 + \text{height}_2) * \text{width}] / 2$. AUC measures may be extracted from time- or concentration-series data to simplify analyses and increase power without sacrificing information contained in repeated measures [57]. Within sensory science, AUC has classically been applied to time-intensity data [58,59], where it provides similar results to more complex PCA based parameterization methods [60]. Here we applied an AUC approach to the concentration-intensity (psychophysical) and concentration-liking (physicohedonic) functions, resulting in two summary values for each subject, one for intensity and one for liking. Since broth concentrations were spaced at regular quarter-log intervals (ie, the width of the trapezoid was constant), we dropped the widths from our calculations, so our AUCs are more precisely termed index of change values. As they are direct linear transformations of the true area, we refer to them as AUC for simplicity. The intensity and hedonic AUCs were used in linear regression and the Structural Equation Model to test the hypothesis that oral sensory phenotype influences the degree of change in intensity and liking experienced by an individual.

2.4 Liking and Sensory Ratings for Salty Foods and Condiments

2.4.1 Sampled foods and condiments—Subjects tasted foods that are predominantly salty as well as lower sodium variants (LaChoy® soy sauce, 7733 mg/100 ml; Bachman® regular pretzel sticks, 1,837 mg/100 g; Lays® Classic regular potato chips, 643 mg/100 g; Lays® salt & vinegar potato chips, 1,640 mg/100 g; Stop & Shop® no salt added potato chips, 10 mg/100 g; Cracker Barrel® Extra Sharp white cheddar cheese, 643 mg/100 g; Stop & Shop® very low sodium white cheddar, 7 mg/100 g). Foods were served in a medicine cup and included 1 chip/pretzel, 1-inch cube of cheese, and 5 mL of soy sauce. To minimize variability in testing, food samples were allowed to come to room temperature before serving. Individuals were instructed to use the gLMS to rate the intensity of their hunger prior to sampling the foods and then to rate level of liking/disliking and perceived sweetness, sourness, saltiness and bitterness based on present experiences, not previous beliefs or values (eg, I have always loved this food, this food tastes good but I dislike it because it is bad for me) similar to procedures described previously [46,49]. Subjects were free to swallow or expectorate the samples after ratings, rinsing their mouths with deionized ($>15\text{M}\Omega$) water between each sample.

2.4.2 Surveyed Foods—In the second session, subjects rated their liking for a list of 38 foods that vary in taste and somatosensory quality. Subjects were instructed not to take into account how frequently a food was consumed, but simply rate how much the food was liked or disliked. For the analyses, a conceptual grouping of foods that had a salty taste and were a significant source of sodium (according to the USDA National Nutrient Database [61]) was formed; the group was statistically reliable (Cronbach's $\alpha=0.60$) and specific foods included breakfast sausage (827 mg/100 gm), bacon (2428 mg/100 gm), cheddar cheese (643 mg/100 g), dinner ham (846 mg/100 gm), and American cheese (1596 mg/100 gm).

2.5 Intake of Sodium

2.5.1 Sodium intake from consumption of high-sodium foods—A registered dietitian (RD) interviewed each subject using a validated food frequency survey (Block ver. 98.1), asking subjects to assess their usual frequency of consuming foods over the previous year. Responses were converted to frequency over 1 year (eg, 1/day=365) and a total frequency of consuming 38 foods that are significant sources of sodium [62] was calculated. The high-sodium intake group contained foods generally thought of as having a salty taste and also those containing high levels of sodium that may not be perceived as being salty (ie, hidden sources of sodium). Standardizing the high-sodium intake group per kg of measured body weight minimized intake differences across males and females ($t=1.45$, $p=0.15$).

2.5.2 Sodium intake from food records—Subjects completed five, non-consecutive food records across the three laboratory sessions, including weekend and non-weekend days. An RD provided brief instruction on keeping the food records over the telephone while scheduling the first session. During session one, the RD reviewed the food record with the subject, clarifying the foods consumed and portion sizes, and probing for missed items and condiments. Subjects kept two records in between the next two sessions. The RD reviewed the records during each session and completed the dietary analyses using the Food Processor software (ESHA ver. 8.2) for intake of total sodium. Sodium intake was averaged across the 5 days and standardized as mg/kg body weight [63] to minimize differences across males and females ($t=1.02$, $p=0.31$). Sodium intake in mg/kg body weight was used for analyses. When surveying discretionary salt use, the participants reported how often salt was added to foods, answering 'usually,' 'sometimes,' or 'hardly ever.'

2.6 Statistical Analyses

Data were analyzed using Statistica version 4.2 (StatSoft, Tulsa, OK), SPSS 11.0.2 for OSX (SPSS, Chicago, IL) and AMOS 6.0 (Smallwaters, Chicago, IL). Significance criterion was $p \leq 0.05$ and mean $\pm$ std. error are presented. For the 0.32 M NaCl in solution, sex differences were tested by comparing the variance of the change score across the testing sessions with the F distribution and a two-tailed K-S (Kolmogorov-Smirnov) statistic for central tendency, dispersion and skew. Multiple regression analyses were used to test for influence of both oral sensory phenotypes on intensity, hedonic and intake variables as well as responsiveness to changes in broth sodium levels (eg, the AUC values). For these analyses, variables were transformed for normality and outliers were removed by the standardized residual and Mahalanobis distance criteria (critical chi-square at $p < 0.001$ with $df =$ independent variables [64]). Repeated measures ANCOVA were used to test for mean differences in the intensity or hedonic ratings of chicken broth by concentration, sex and taste phenotype. Differences in peak preference concentration (ie the bliss point) across sex were tested via t-test, and interactions between sex and phenotypes were assessed via ANOVA. For the sampled salty foods, multiple regression analyses were used to predict preference from oral sensory phenotypes as well as the endogenous sensory qualities of the foods (eg, saltiness, bitterness, etc). Because the intensity of the other stimuli (sound, touch) should not correlate with taste sensations [65], a mean intensity rating of an 86 dB tone rating was used as a covariate in ANCOVA and regression models to adjust for variability from individual scale usage differences in these analyses. BMI and hunger ratings (for the food sampling) were also included as covariates. Structural Equation Modeling (SEM) was used to test the theoretical model that oral sensory phenotypes (PROP, fungiform papillae number) influence sensation from or liking for salty foods, which in turn influences intake of sodium. Because tones did not substantially alter the regression findings above, they were not included in the SEM model. Measures of fit (chi-square, TLI and RMSEA) were selected *a priori*, consistent with prior work [66,67]. SEM was used here as an extension of multiple regression analysis to test a complex web of nested relationships simultaneously between the variables of interest, so it should be noted that the

path directions simply indicate the underlying linear equations within model. That is, the model cannot address whether the causal relationship may be reversed for some variables.

3. Results

3.1 Taste Phenotype

The sample showed diversity in taste phenotype. When categorized by perceived bitterness of 3.2 mM PROP, there were 21 nontasters ($gLMS \leq$ moderate), 37 medium tasters ($>$ moderate and $<$ very strong) and 29 supertasters ($\geq$ very strong). Females and males did not differ significantly in the mean or distribution of PROP ratings. Fungiform papillae per 6mm area (range 11 to 42) correlated significantly with 3.2 mM PROP bitterness ($r=0.37$, $p<0.001$). For categorical analyses, average papillae number was split at the median (23.5) to form low and high groups. There tended to be more women than men in the high (25 versus 17) than in the low (17 versus 28) papillae groups ($\chi^2=3.289$, $p=0.07$).

3.2 Saltiness and hedonics of aqueous sodium chloride solutions

The single aqueous solution (0.32 M NaCl in deionized water) tested at each of the three testing session was averaged and had a mean intensity near moderate ($+23.6 \pm 1.0$) and liking close to neutral (-1.0 ± 1.6 SE). Greater saltiness was reported by those who tasted PROP as more bitter ($r=0.29$, $p<0.01$) and had more papillae ($r=0.21$, $p=0.05$) as shown in Figure S1. Those who tasted greater saltiness liked the solution less ($r=-.44$, $p<0.01$) and there was no direct relationship between sensory phenotypes and solution liking ($p's>0.25$). Although men and women failed to differ significantly on mean intensity ($t=0.76$, $p=0.45$) or hedonic ($t=1.14$, $p=0.26$) ratings, the distribution of hedonic ratings tended to vary. The point of maximal separation of scores occurred near neutral: 56% of men disliked the 0.32 M solution compared to only 31% of the women (K-S statistic: $D=0.270$, $p=0.07$).

Across the three sessions, the hedonic variance scores also showed a sex difference— females had a greater variance [$F(42,45)=1.731$, $p<0.05$] compared to males. Conversely, a sex difference was not observed either for the distribution of intensity ratings ($D=0.086$, $p=1.00$) or variance in intensity change scores [$F(42,45)=1.731$, $p<0.15$] across the testing sessions.

These results from simple solution suggested that sensory phenotypes influenced the intensity of saltiness, which in turn, indirectly influenced the liking of the sensation. Women have more variability in hedonics (but not intensity) and tended to report greater liking/less disliking for this moderately salty sensation.

3.3 Saltiness and hedonics of Chicken Broth

Figures 1 and 2 show the average intensity and hedonic ratings of saltiness in chicken broth separately for women and men. As described in the methods, change in intensity and hedonic ratings in response to increasing sodium concentration in broth was examined through a single parameter—an area under the curve (AUC) value across the concentration series. Specifically, we tested whether oral sensory phenotypes and sex explained variance in these AUC values.

Individuals who tasted PROP as more bitter had significantly greater intensity AUC values ($sr=0.28$, $p<0.01$), independent of sex and other covariates (all $p's>0.05$), meaning they were more responsive to changes in salt concentration. In contrast, papillae number did not explain variation in the intensity AUC values ($sr=0.06$, $p=0.6$). When comparing intensity AUC values across men and women, there was no apparent distributional difference (K-S statistic: $D=0.24$, $p=0.14$).

Although the hedonic AUC showed a significant correlation with the intensity AUC ($r=0.59$, $p<0.01$), neither PROP bitterness nor number of papillae were independent contributors in the regression models ($p's>0.25$). This suggests that PROP bitterness predicts increasing intensity when concentration changes, which may indirectly influence the liking response to concentration changes (as tested below with the Structural Equation Model). Women had higher hedonic AUC values ($p\leq 0.05$) independent of covariates. The distribution of hedonic AUC values differed by sex – the women were skewed toward higher hedonic AUC values (K-S statistic: $D=0.32$, $p=0.02$), suggesting changes in salt concentration have a larger impact on hedonics for women.

Based on these results, we undertook two additional analyses to characterize how oral sensory phenotype and sex influence the relationships between concentration, sensation and liking. First, we determined the level of added salt that elicited the maximal liking rating (peak preference concentration). The peak preference concentration of salt in broth was greater in women compared to men (0.33 ± 0.04 M versus 0.23 ± 0.04 ; $t=1.97$, $p=0.05$) and tended to show an interaction between sex and PROP group ($F=2.66$, $p=0.077$), with male supertasters reporting significantly lower concentration of peak preference than did male nontasters (0.35 vs. 0.16 M, $p<0.05$). Visually, the peak preference for women fell in the region of salt concentration in commercially available soups. Men tended to have a lower concentration for peak preference, except for the male medium tasters, who showed a relatively flat and ambivalent liking response across a 3-fold difference in concentration.

Second, we analyzed the mean intensity and hedonic ratings for the 7 replicated chicken broth samples, testing the effect of the oral sensory phenotype groups, sex and concentration in separate 3-way repeated measures ANCOVAs. Results are summarized in Table 1 and the presentation of results is focused on PROP groups as the parallel analyses for fungiform papillae group revealed no significant interactions or main effects.

For intensity, the 3-way Sex by PROP Group by Concentration interaction was significant (Table 1; left side). In plotting the concentration by PROP effects conditional on sex (not shown), it was clear that PROP effects were seen primarily in the men. Male nontasters and medium tasters reported significantly lower intensities for the top 4 concentrations (range of commercially available broth and above) than did male supertasters (all $p's<0.05$). The same pattern, somewhat attenuated, was seen when collapsing across sex (Figure S2). Since salt concentrations above 0.4M have an increasing trigeminal component [55], the greater intensity ratings by the supertasters at the highest concentrations may reflect increased irritation as well as greater salt taste.

When collapsed across PROP group, women reported greater intensities for the top two sodium concentrations in chicken broth (0.63 and 1.12 M; $p's<0.01$) and, consistent with the 0.32 M NaCl aqueous solution, did not differ significantly in broth saltiness at or below 0.355 M NaCl. However, when concentration by sex effects were plotted conditionally by PROP group (shown in Figure 1), the effect was driven almost entirely by sex differences among the nontasters. Among nontasters, women gave higher intensity ratings for concentrations above those typically found in commercial soups (gray box). Among supertasters, women appeared to have a more quickly accelerating psychophysical function, and lower intensity ratings at concentrations typically found in commercial soups (gray box). No sex effects were found in medium tasters.

As expected, the hedonic function for salt in chicken broth had an inverted U-shape for men and women. Visual inspection of Figures 2 and S3 suggests the women are peakier in their response, irrespective of PROP group, which is consistent with the hedonic AUC data reported above. As would be expected with a mediated path, the direct effect of PROP on hedonics was

less robust than the direct effect of PROP on intensity, consistent with the hedonic AUC data above. The 3-way Sex by PROP Group by Concentration interaction was not significant (Table 1; right side), although the two-way Concentration by Sex and Concentration by PROP group interactions were both significant. For the Sex by Concentration interaction (collapsing across PROP group), women provided higher hedonic ratings for 0.2 and 0.355 M sodium ($p < 0.05$) compared to men (Figure S3), which is similar to findings for the aqueous solution above. Also, inspection of the hedonic functions in Figures 2 and S3 (and analyses of the peak preference described above), all suggest the liking function was shifted toward a lower concentration for men.

As is apparent from Figures 2 and S4, the PROP by Concentration interaction was driven by differences at the top 2 concentrations: supertasters reported significantly greater disliking of the 0.63 M, and 1.12 M broths than did PROP medium or nontasters (all p 's ≤ 0.05) regardless of sex.

In summary, the results from the broth extend the findings from a single aqueous solution, by testing for effects of oral sensory phenotypes across a range of sodium concentrations (covering those found in low and regular sodium products, as well as those well above levels typically found in commercial products), as well as on differential response to changes in sodium concentration. Those who tasted PROP as more bitter had bigger changes in intensity with changes in salt concentration and reported greater intensity from highly concentrated sodium chloride in broth (beyond levels in commercial soups, where salt is an irritant). Number of fungiform papillae did not explain intensity differences in salt sensations in the broth, in contrast to the aqueous solution in section 3.2. PROP phenotype had minimal direct impact on the hedonic response to salt in broth as it only directly predicted liking at the highest concentrations, well beyond those found in commercial soups; nonetheless, PROP phenotype appeared to impact hedonic response indirectly by influencing perceived saltiness in the broth (ie, PROP effects on liking were wholly mediated through intensity). The path of association between PROP bitterness, perceived saltiness and hedonics in broth is formally tested below in the Structural Equation Model. Sex differences in hedonic response to the salt in broth also appeared to attenuate the PROP effects, particularly in women who reported greater liking for broth at sodium levels typically found in commercially available soups.

3.4 Saltiness and hedonic ratings of salty foods

3.4.1. Saltiness of sampled foods—Perceived saltiness of the sampled foods ranged from between “strong” and “very strong” for soy sauce to just below “strong” for the salty snacks (pretzels, regular and salt/vinegar chips), “moderate” for extra sharp cheddar cheese, to near “weak” for the low-sodium chips and cheese (Table 2). The bitterness of PROP explained variance in the saltiness only for the salty snacks, and the effects were most pronounced in men as seen in a regression interaction model (cross product coefficient $p = 0.045$). Overall, women reported greater intensities than did men, and the women did not show differential intensities by PROP bitterness. In contrast, salt intensity increased with PROP bitterness for men, meaning that male supertasters were more similar to the women (not shown). In a similar analysis replacing fungiform papillae number for PROP, neither sex nor interaction were significant (p 's > 0.45), yet, unexpectedly, higher papillae number was associated with less perceived saltiness in salty snacks ($p < 0.05$).

In summary and similar to the chicken broth findings above, PROP bitterness predicted the saltiness of salty snacks, but the impact of PROP phenotype was attenuated in women.

3.4.2. Liking of sampled foods—The snack foods and regular sodium cheddar cheese were most liked (Table 2). Greater saltiness in the snack foods was associated with more liking; conversely the saltiness of cheddar cheese was not a predictor of cheddar cheese liking.

Notably, regularly salted snack foods and cheddar cheese have similar levels of sodium (~630 mg/100g) yet the perceived saltiness of potato chips was nearly double that for regular cheddar cheese. Neither PROP bitterness nor papillae number were direct predictors of snack food liking.

Because the sampled foods are more perceptually complex than broth and have multiple sensory qualities that may impact liking, Table 2 summarizes the regression analyses predicting liking for each food, including the predominant oral sensory characteristics. The mean hedonic rating for low-sodium cheese was just below neutral with half of the subjects reporting it as disliked, although the range was quite large (−90 to +88). Compared to regular cheese, low-sodium cheese was less liked (-1.8 ± 3.4 vs. 29.3 ± 2.8 , $t = -9.9$, $p < 0.001$) and concomitantly rated as less salty (8.0 ± 1.0 vs. 15.8 ± 1.3 , $t = -6.9$, $p < 0.001$) and more bitter (16.8 ± 1.5 vs. 8.0 ± 1.3 , $t = 5.7$, $p < 0.001$), consistent with findings that sodium salts block bitterness in model systems [68,69]. Because low-sodium cheese was more bitter and less salty, we assessed whether high PROP bitterness/fungiform papillae individuals were more sensitive to changes in cheese sodium level to impact liking. Accordingly, we correlated taste phenotype with two scores – one for perceived bitterness and another for saltiness – for differences between low and regular sodium cheese. As expected, those with greater papillae numbers reported a greater difference in saltiness between the two cheeses ($r = 0.35$, $p < 0.005$). Similarly, the difference score for cheese bitterness was correlated with PROP bitterness ($r = 0.30$; $p < 0.01$): those who tasted PROP as more bitter had higher scores, meaning they were more responsive to changes in sodium levels. PROP was not related to the saltiness difference score and fungiform papillae number was not related to the bitterness difference score, supporting that these two oral phenotypes influence food liking through different pathways.

In summary, taste intensity (saltiness, bitterness) was associated with the degree of liking for snack foods (chips, pretzels) and cheeses, respectively. Taste intensity increased with PROP bitterness, similar to the chicken broth analyses for saltiness. Thus, PROP bitterness was only related to liking for snack food through greater perceived saltiness, consistent with prior findings (eg, [66]) showing that PROP effects are mediated through intensity differences in endogenous taste qualities of the food.

3.4.3. Liking for salty foods assessed via survey—Surveyed liking appears to have strong face validity as correlations between liking ratings of sampled foods and the same food assessed via survey ranged from 0.43 to 0.64 (all p 's < 0.001). Group means for the survey salty foods (bacon, dinner ham, breakfast sausage, cheddar and American cheese) averaged above moderately like, ranging from weakly dislike to above strongly like. In separate multiple regression analyses controlling for sex and BMI, only fungiform papilla number ($sr = -0.22$, $p < 0.05$) and not PROP bitterness ($sr = 0.08$, $p = 0.47$) directly predicted liking of these foods; those with greater papillae number reported less liking for the high-fat salty foods. These results suggest that papillae number captured variance in liking of these foods that was not explained by PROP, possibly fat-related sensations.

3.5 Sodium intake from food frequency & food records, and discretionary salt use

Consumption of the high-sodium food group from the food frequency questionnaire averaged between five to six times per week. Of the 38 foods in this food group, those that were higher in fat (eg bacon, sausage, cheese, snack foods) were consumed more frequently than those lower in fat (eg vegetable soup, pasta dishes with tomato sauce). According to the food records, mean sodium intake was 3187 mg/day, which is similar to but slightly lower values seen (3,329 mg/day) in national surveillance data closest to the time of data collection [70] which may be due demographic differences between our cohort and National Nutritional and Health Examination Surveys, which oversamples low income individuals and ethnic minorities and

adjusts the intake values for salt added in cooking. In our cohort, mean sodium intake was significantly higher in men (3669 ± 190 mg) than in women (2697 ± 150 mg) ($t=3.97$, $p<0.01$). Standardized to body weight, mean sodium intakes were 46.4 ± 17.5 mg/kg BW and were not significantly different across men and women ($t=0.56$, $p=0.58$). There was a weak but significant association between the high-sodium food intake group (food frequency questionnaire) and mg sodium intake/kg BW (food records). In multiple regression analyses, 19% of the variance in mg sodium intake/kg BW was explained through the high-salt food intake group ($sr=0.25$, $p<0.05$), age ($sr=-0.31$, $p<0.005$) and sex ($sr=0.27$, $p<0.05$, men>women).

3.5.1 Intensity, Liking and Sodium Intake—The salt-related liking variables showed stronger association with the measures of sodium intake than did the intensity variables. Consistent with Pangborn's earlier findings [35], sodium concentration of peak liking in chicken broth showed a positive association with consuming high-sodium foods (frequency survey) and intake of sodium (food record), but only in men. Men with higher peak liking tended to report more frequent consumption of high-sodium foods ($r=0.28$, $p=0.07$) and more sodium intake via food records ($r=0.31$, $p<0.05$). In contrast, the hedonic AUC value did not show sex differences in association with sodium intake variables: it was a significant predictor of frequency of consuming high-sodium foods ($sr=0.30$, $p=0.005$) in a regression model that controlled for sex ($p=0.5$). Salt liking assessed via survey also explained variance in sodium intake. Independent of age and sex effects, liking for the surveyed group explained 12.2% of the variance in the consumption of the high-sodium food group ($p=0.001$); in a parallel model, survey liking also explained variance in mg sodium intake/kg BW ($sr=0.25$, $p<0.05$).

Consistent with the findings predicting liking of high sodium foods, neither PROP bitterness nor fungiform papillae number directly predicted intake of sodium, either by surveyed frequency or food records. Nonetheless, reported addition of salt to foods varied across PROP nontaster and supertaster groups: supertasters were less likely to report 'always' adding salt to food while nontasters were evenly split between 'always' or 'never'/'sometimes' adding salt to foods ($\chi^2=5.337$, $p<0.05$).

In summary, estimated intakes were roughly consistent with values from national surveillance data. Again, as with snack food liking, neither PROP bitterness nor fungiform papillae number were direct predictors of estimated sodium intake. Liking and intake were linked in several ways: men who preferred saltier soups had greater sodium intake, greater reported liking for surveyed foods predicted greater reported intake, and higher hedonic AUC scores (ie, individuals showing a larger change in ratings of liking with changing concentration) were predictive of greater intake, regardless of sex.

3.6 Overall model relating taste phenotypes to consumption of high sodium foods

Because the findings presented above and those from other foods (eg [66]) suggest that the relationship between the phenotypes and intake are mediated through sensation and liking, Structural Equation Modeling was used to test a global model that connects oral sensory phenotypes, salt sensation, hedonics and sodium intake (Figure 3). The initial model was guided by preceding analyses: the path with PROP bitterness included the chicken broth AUC values for intensity and hedonics while the path with fungiform papillae number included liking for surveyed high-fat salty foods. The global model (Figure 3) was provisionally accepted as all paths were significant, and global fit was excellent; with 7 parameters, this model exceeds ratio of cases to parameters (10:1) recommended by Kline [71]. Sex was tested in an alternative model but it was not retained, as it did not make any significant contributions. While some of the observed variables did have sex differences above (eg, survey liking for salty foods, hedonic AUC), sex did not contribute significantly to predicting the final intake variable, which was

standardized to body weight (see methods). The final model indicated the oral sensory phenotypes only influenced intake indirectly via liking. Notably, those who tasted PROP as more bitter showed greater intensity responses to changes in salt concentration, which predicted greater changes in liking with changing concentration, and this increased salience predicted greater liking and consumption of high-sodium foods. Conversely, greater numbers of fungiform papillae associated with reduced liking for the high fat, high-sodium foods in the surveyed liking group, and thus lower intake; papillae number did not predict chicken broth liking.

4. Discussion

4.1 General Findings

Multiple physiological, socio-cultural, economic and environmental factors influence the ingestion of sodium and the study of these factors are of great interest for health and wellness. The present study focused specifically on individual differences in salt sensation and the relationship with salt sensation, liking for high salt foods, and sodium consumption in a sample of reportedly healthy adult men and women who were mostly of normal weight and who did not report excessive levels of dietary restraint. Additionally, the study examined the extent to which two commonly studied markers of oral sensory phenotype—the bitterness of propylthiouracil and fungiform papilla number, might explain variation in salt sensation as it relates to sodium liking and intake. Both oral sensory phenotypes were associated with variation in sodium intake through salt intensity and liking of salty foods, albeit in different ways. Those who tasted PROP as most bitter reported greater changes in saltiness as the salt level in broth increased, which in turn, explained greater differences in hedonic ratings across the salt levels in broth. Additionally, bitterness of PROP explained differences in perceived saltiness within broth and snacks (chips, pretzels) where saltiness was the dominant sensation. For broth, those who tasted PROP as most bitter reported greater perceived intensity, especially at levels where sodium chloride elicits both gustatory and chemesthetic sensations (eg, saltiness and burn). The PROP effects on salt sensation and liking were more apparent in the men; the distribution for women was shifted toward greater intensities at high salt concentrations. Nonetheless in the structural equation model, PROP bitterness was indirectly associated with consumption of high-sodium foods through these intensity and hedonic responses to changes in sodium concentration in broth, which is consistent with prior work on other taste qualities [66,72]. Number of fungiform papilla also explained difference in consumption of high-sodium foods indirectly; individuals with higher numbers of papillae gave lower liking ratings for foods that were high in both fat and sodium.

Saltiness may have greater salience for PROP supertasters as they appear to be more attuned to changes in sodium concentration; additionally, supertasters may be more susceptible to functional properties unrelated to saltiness (eg, bitter masking in perceptually complex foods). Together, these factors would appear to encourage frequent consumption of high sodium foods by PROP supertasters. In regards to salt as a condiment, the PROP supertasters were least likely to endorse the addition of salt to foods, suggesting the sodium levels in our contemporary food supply are sufficiently high to facilitate intake without further modification. However, this finding may have little real impact on health, as only 10–15% of intake is discretionary. Individuals who have high numbers of fungiform might consume less sodium through reduced liking for high fat foods that are also sodium rich. This finding is consistent with our previous report in the same cohort of individuals, that higher numbers of fungiform papillae was associated with greater awareness of fat in the fat/sweet milks and less liking for high fat/sweet mixtures [73].

4.2 Salt sensations, propylthiouracil bitterness, and number of fungiform papillae

The present study recapitulates prior evidence that the intensity of salt in water is not independent of PROP bitterness [11,74,75]. Present data and other recent work [14] indicate this relationship also extends to more complex liquids. However in contrast, fungiform papillae number predicted the perceived intensity of aqueous sodium chloride but not more perceptually complex liquid foods, as seen previously with this cohort [76]. The failure of papillae number to predict intensity in foods is striking, as contemporary theory stipulates that greater receptor density should result in a greater signal being projected centrally. Yet, in foods, PROP bitterness was a better predictor of oral sensory differences, both here and elsewhere [76]. Logically, receptor polymorphisms that drive functional differences in bitter taste response should not predict heightened oral sensory response across diverse taste qualities. Indeed, we recently showed that *TAS2R38* gene SNPs do not explain supertasting [12]. Paradoxically however, we also showed that after partitioning out the effects of genotype, PROP bitterness (the phenotype) still predicts elevated oral sensation. Why PROP associates with the intensity of oral sensations beyond the density of taste receptors or nerve innervation is not fully understood. PROP may be a better marker of difference in oral sensation because it shows the greatest variance across a sample, ranging from no taste to above very strong. Since the bitterness of PROP and the saltiness of sodium chloride are correlated, the findings from this paper and others continue to suggest that using sodium chloride as a standard in studies of PROP phenotype could result in subject misclassification, which would attenuate effect sizes. Thus, studies of sodium intake that use salt based classification methods [16] are uninterpretable because the phenotype is defined in part by (and thus confounded by) the outcome variable.

Fungiform papilla number was associated with level of saltiness only in aqueous solution. Individuals with higher numbers of these papilla report heightened taste and nontaste oral sensations [77,78] and tactile acuity [79]; papillae number likely serves as a proxy for chorda tympani and trigeminal innervation density. In the present study, fungiform papilla number was less predictive than PROP of saltiness in broth or sampled solid foods; this is consistent with previous findings in the same cohort with sugar-fat mixtures in fluid milk [76], where PROP bitterness showed stronger association with level of sweetness in these complex liquids than did fungiform papillae number. In both cases, replication in another cohort is needed, but it may be that papillae density on the anterior tongue is less important in the context of whole mouth sensations from foods than previously thought.

4.3 Sex effects on salt intensity and hedonics

Male/female differences in salt intensity in solution and foods are consistent with the literature on potential roles of sex hormones on salt perception. Prior studies have demonstrated salt intensity and hedonic changes in women across pregnancy (eg [30]) as well as salt threshold differences across males and females—men have higher salt thresholds (lower sensitivity) than do women [80]. The women in our study had greater variability of liking ratings across the testing sessions. Variation in sex hormone level and salt preference has been seen in rodent [26,29] and human [27] studies and could provide one explanation of why PROP effects on salt sensation and liking in the present study were attenuated in women.

Although the hedonic function for salt in chicken broth had an inverted U-shape (Figure 2), consistent with prior reports [23,81,82], women generally gave higher hedonic ratings and reported peak liking at a concentration that was significantly higher than in men. In addition, the women had a larger hedonic shift with changing salt concentration – visual inspection shows that women were peakier across all three taster groups, and this was confirmed statistically via the greater hedonic AUC values. Because of the role sodium plays in

maintaining fluid balance during pregnancy, there may be a biological rationale for women being more responsive to changes in sodium concentration [30,83].

Limited data are available in the published literature on how sex differences influence salt hedonics or sodium intake. Many studies fail to show or discuss potential sex effects with regard to salt intensity and food habits [34–36,84–86]. In our cohort of 20 to 40 year old adults, men preferred a lower salt concentration in water or broth than did women. Our findings conflict with data from Israeli students showing that men prefer more heavily salted soups [19]. The source of this discrepancy is unclear and could result from differences in culture of the study samples, ambient temperatures, psychophysical methodologies and test stimuli (pea soup vs. chicken broth). Additionally, our findings suggest commercial soups in the United States typically offer a higher sodium concentration (155mM to 178mM; see [87] and [88]) than the hedonic peak in broth for men. This may reflect a known issue with consumer product testing and development. Although foods are usually consumed as full portions, testing conditions often involve receiving pairs of small samples and selecting the most preferred. The more intense sample usually wins under these conditions, even if consuming a full portion of the more intense food would be cloying or noxious. Here, we used replicated direct scaling of a full range of samples, including some well beyond the level a product developer might typically present. This simultaneously avoided the 'stronger is better' bias and provided participants with a sizable portion, as the 14 replicate samples should offset the small sample size (15ml). Our finding that men preferred lower concentrations than typical commercial products also may have arisen from an implicit or intentional selection of females for consumer product testing (eg, selecting panelists based on purchase habits, which may be gender biased).

4.4 Saltiness-liking relationships are food specific

Shepherd and colleagues [37] speculated that preference for high levels of salt are food specific rather than a global trait. Here, we provided empirical evidence that the impact of saltiness on liking varied across the type of food, consistent with the findings of Leshem [19]. For salty snacks, saltier was better while the reverse was true for soy sauce. Food specific salty-liking relationships presumably reflects real world consumption patterns: pretzels and chips are chosen as foods largely because they are salty whereas soy sauce is added to increase the salty and savory (umami) aspects of the underlying food. When sampled neat from a plastic cup, heightened overall oral sensation from soy sauce only served to increase its irritancy and aversiveness.

The liking patterns of regular and low-sodium cheese emphasize that salt is added to foods for functional reasons unrelated to perceived saltiness. Specifically, within a cheese, liking and the degree of perceived saltiness were unrelated. However, when comparing the regular versus low-sodium cheese, liking was still influenced by sodium level, as the low sodium cheese was substantially more bitter and less liked, especially by the PROP supertasters. Sodium ions mask or inhibit bitterness as shown previously in model systems [68,69]. The PROP supertasters would have elevated sodium intakes because they require sodium to mask the bitterness, avoiding the strong bitterness that makes the low sodium product aversive. Thus, it appears oral sensory phenotype may drive sodium intake even in the absence of direct effects on perceived saltiness.

4.5 PROP bitterness influences liking through salt sensation

For the chicken broths with seven different concentrations of added salt, the adults who tasted PROP as more bitter showed greater change in intensity to changes in sodium concentration (as expected [11,12,14]), which in turn was related to greater changes in liking ratings for these broths. Although the PROP effects on salt sensation were attenuated in females, the PROP supertasters reported the greatest intensity for the highest concentrations of salt in broth at

levels in commercially available soups (men only) and above, where salt takes on irritation as well as taste qualities (men and women). Not surprising, PROP bitterness was directly associated with dislike of broths with the highest sodium concentration. In the structural equation model, change in hedonic ratings as a function of change in concentration contributed significantly to explaining variance in intake of high sodium foods.

In addition, PROP bitterness was related to greater saltiness for salted snacks (chips, pretzels), which was in turn predictive of greater liking for these foods. The snack foods have saltiness as a primary taste quality. However, within cheese, where saltiness competes with bitterness, those experiencing greater PROP bitterness or those with higher numbers of fungiform papilla were more responsive to changes in sodium level, which appeared to impact low-sodium cheese liking by masking bitterness rather than by directly effecting saltiness.

Regarding discretionary salt usage, we initially interpreted the decreased likelihood of supertasters adding salt to food as evidence they find foods too salty. However, in light of other data, this may instead be suggestive of an acceptability step-function coupled with reward seeking behavior. Namely, if saltiness is generally preferable in many foods, supertasters may – in our contemporary salt-rich food supply – find foods to be sufficiently salty, whereas nontasters seek to increase the stimulus levels to achieve desired levels of saltiness. Notably, at least for sweetened beverages, the form of the inverted U function for liking and consumption differs somewhat: maximal liking exhibits a sharp narrow peak whereas intake has a much flatter shape [89]. This suggests the existence of a singular bliss point for maximal liking versus a larger acceptability plateau for intake. Nontasters too have been described to live in a “pastel” food world, experiencing less intensity from taste, somatosensory and retronasal sensations [90]. The nontasters could add salt to food as a way of enhancing the overall flavor of food, an action not needed by the supertaster who perceives heightened overall oral sensation. Since much of saltshaker use is habitual, the nontasters may have acquired a predilection to reach for the shaker over time, whereas supertasters have not.

4.6 A Model Predicting Sodium Intake from Observed Variables

To integrate all the markers discussed above, Structural Equation Modeling was used to link oral sensory phenotypes and oral sensation to intake through hedonics. SEM can be thought of as an extension of multiple regression that allows for simultaneous analysis of a complex web of relationships between variables. Previously, we used SEM to identify spurious correlations between oral sensory phenotype and intake by demonstrating that these associations were entirely mediated via taste intensity and liking [55]. Here, we aimed to assess the relationships between two oral sensory phenotypes (PROP and fungiform papilla), salt sensation, liking and intake, consistent with our working hypothesis linking multiple oral sensory phenotypes to intake. In the provisional model, we found that variance in intake of salty foods was explained by PROP bitterness through change in saltiness sensation and liking in broth with increasing salt concentration and fungiform papillae through liking high fat, high sodium foods. Because salt is both perceptually prominent in foods (salty snacks) and hidden (breads, tomato products, breakfast cereals, baked goods, other processed foods), it is not surprising that multiple markers of oral sensation that capture simple and complex oral sensations from high-sodium foods can predict intake of sodium. As a caveat however, this interpretation makes certain assumptions about the causal relationships between variables: it may be that some of the causal relationships could be reversed (eg, habitual intake might influence salt liking and perceived salt intensity).

4.7 Strengths, Limitations and Conclusions

The strengths of this study include the broad approach, the psychophysical methods, the study sample, and the separate but complementary means of assessing sodium intake. We used

contemporary scaling methods that maximize the validity of making comparisons across individuals (see [15]) and included two related but distinct oral sensory phenotypes in our analyses. We had an ethnically homogeneous, gender-balanced sample of adults who did not report excessive dietary restraint, which should maximize the ability to associate oral sensory phenotypes with dietary behaviors. To estimate sodium intake, we used independent but complementary measures over multiple days that were collected by Registered Dietitians, in direct contrast to many earlier reports based upon un-validated questionnaires or single point estimates. Surveyed liking for high-sodium foods was a good proxy of sodium intake and the intermediate step between taste phenotype and sodium intake, supporting the utility of food liking surveys as a potential basis for individualizing dietary recommendations to modify sodium intake. Finally, we took a holistic approach by examining simple solution, broth, and solid foods in one cohort – although this increases the volume of results and number of comparisons, it also enhances the quality of the findings by highlighting commonalities and differences across the various stimuli.

Limitations to the study include validity of sodium intake measures. Food frequency intakes are inaccurate due to memory recall, interviewer and subject bias, and responder fatigue [91], all of which contribute to underestimating sodium intake by as much as 30–50% on food frequency intake measures [92]. Here, however, the inclusion of subjects without excessive cognitive restraint on eating has shown to reduce the level of under-reporting that typically plagues food intake assessments [93]. Also, our use of a preference or liking measure may have improved our assessment of habitual intake [46,94,95]. Although the women were more responsive to changes in salt concentration, the sex grouping variable did not add to the Structural Equation Model, as any variability across men and women in the current cohort was captured in the hedonic AUC scores, and because estimated sodium intake standardized to body weight removed the differences across men and women. A larger study sample could verify the oral sensory-liking-intake relationship in both men and women by using multi-group structural equation modeling (eg, formally test whether the path coefficient weights vary by sex). Also, propylthiouracil and fungiform papillae density are only two sensory phenotypes out of many (albeit the two most studied); other sensory phenotypes may also have utility in predicting sodium intake in future work. Finally, because the present study included a relatively homogenous sample of adults, the findings may not apply to individuals of diverse ethnicities/race, those who have conditions requiring sodium restrictions, or who are overweight or obese. Present data supported that adults vary in salt sensation and this variability explains differences in level of salt liking sufficiently to influence consumption of sodium. These data, as collected in a laboratory setting, also show that the bitterness of PROP explained some variability in oral sensations from high sodium foods, indirectly explaining sodium liking and intake, as well as use of salt at the table. The utility of PROP as a marker for differences in sodium liking and intake and salt use at the table needs verification in additional studies, including population-based studies.

In summary, sodium salts play a complex role in foods and are heavily added to the processed food supply for sensory or functional reasons. Health professionals have expressed strong concern that the level of sodium in the food supply increases the chronic disease risk. The present research demonstrated that some of the variation in saltiness of sodium chloride in aqueous solutions, broths, and solid foods can be explained by the bitterness of propylthiouracil, a marker of taste phenotype. Bitterness of PROP and another marker of oral sensory phenotype, number of taste papillae, indirectly explained variability in sodium intake either through saltiness and liking or through liking for high-sodium/high-fat foods. Those with elevated papillae number may consume less sodium due to lower liking for high-sodium/high-fat foods. Because most of sodium consumption in the Western diet comes from the ingestion of processed foods, PROP supertasters who select primarily unprocessed foods could be somewhat protected from elevated sodium intakes by less discretionary salt use at the table.

On the balance however, many PROP supertasters likely have higher intakes of sodium as saltiness is a salient and desirable sensation in many foods and because sodium salts masks unpleasant bitterness in products such as cheese and presumably other foods like vegetables.

Supplementary Material

Refer to Web version on PubMed Central for supplementary material.

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Figure 1.

The saltiness of a sodium concentration series in chicken broth, measured on the gLMS with subjects classified by 3.2 mM PROP bitterness into nontasters (greater than moderate on the gLMS), medium tasters (between moderate and very strong) and supertasters (greater than very strong). The shaded box indicates sodium levels typically found in regular versions of commercial soups. Increasing sodium concentration were achieved via the addition of kosher salt.

Figure 2.

Same as Figure 1, but for liking/disliking, as measured on the hedonic version of the gLMS. Examples of sodium levels found in regular sodium commercial soups are indicated by dots labeled a through i. The soups are: a) Swanson's Chicken Broth; b) College Inn Chicken Broth; c) Progresso Traditional Chicken; d) Publix Chicken Soup; e) Campbell's Chicken Broth; f) Kroger Chicken & Rice; g) Campbell's Chicken Noodle; h) Kroger Chicken Noodle; and i) Campbell's Chicken & Dumplings.

Figure 3.

Structural Equation Model testing relationships between oral sensory phenotypes, chicken broth intensity and hedonic Area Under the Curve values (AUCs; see methods and [56,57] for details), liking/disliking of sampled salty foods and those from a survey, and intake of salty foods reported on a frequency survey. Numerical values next to arrowed lines represent path coefficients, which may be interpreted like standardized regression weights. Percentages adjacent to boxed variables represent the variance explained for that variable.

Table 1

Summary results from two repeated measures ANCOVA models testing effects of sex, PROP group, and sodium concentration on mean intensity (left) and hedonic (right) ratings for chicken broth

Effect	INTENSITY				HEDONICS			
	Num DF	Den DF	F Value	Pr > F	Num DF	Den DF	F Value	Pr > F
Sex by PROP Group by Concentration	12	456	2.29	0.008	12	456	0.63	0.82
PROP Group by Concentration	12	456	5.31	<0.0001	12	456	1.91	0.03
Sex by Concentration	6	456	4.60	0.0002	6	456	3.59	0.002
Sex by PROP Group	2	76	0.87	0.42	2	76	1.14	0.33
Sex	1	76	0.75	0.39	1	76	0.58	0.44
PROP Group	2	76	3.15	0.05	2	76	1.10	0.34
Concentration	6	456	487.47	<0.0001	6	456	32.15	<0.0001

Table 2
Variance explained from sampled foods from oral sensory ratings in men and women using multiple regression analyses.

Sampled Food (DV)	Hedonic Variance Explained	Mean Hedonic Rating±SEM	Explanatory variables	Mean±SEM	Semipartial correlation	p value
Extra Sharp Cheddar Cheese	18%	29.4±2.8	Sex (1=F;2=M)		0.03	0.77
			Bitterness	7.7±1.3	-0.22	0.05
			Fattness	21.5±1.4	0.26	0.02
Low Sodium Cheddar Cheese	20%	-1.5±3.4	Fungiform Papilla	24.7±0.8	-0.25	0.03
			Sex (1=F;2=M)		0.24	0.02
			Bitterness	16.8±1.6	-0.26	0.02
Potato Chips	33%	34.0±1.8	Fattness	20.4±1.4	0.03	0.81
			PROP	38.9±2.3	-0.25	0.02
			Sex (1=F;2=M)		0.25	<0.01
Pretzels	20%	30.6±2.2	Saltiness	26.9±1.4	0.51	<0.01
			Fattness	18.9±1.3	-0.02	0.87
			Sex (1=F;2=M)		-0.09	0.39
Low Salt Potato Chips	17%	21.1±1.8	Saltiness	32.2±1.5	0.42	<0.01
			Sex (1=F;2=M)		0.06	0.56
			Saltiness	9.1±1.1	0.48	<0.01
Salt/Vinegar Chips	24%	19.1±2.9	Fattness	15.4±1.2	0.1	0.32
			Sex (1=F;2=M)		0.01	0.92
			Sour	22.5±1.8	-0.07	0.45
Soy Sauce	15%	-13.3±3.4	Salty	31.3±1.8	0.32	<0.01
			Fattness	18.3±1.4	0.01	0.96
			Hunger	16.6±1.7	0.32	<0.01
Soy Sauce	15%	-13.3±3.4	Sex (1=F;2=M)		0.02	0.98
			Saltiness	48.2±2.0	-0.21	0.04
			Bitterness	15.2±2.0	-0.34	<0.01