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Research report

Consumption of a high-fat soup preload leads to differences in short-term energy and fat intake between PROP non-taster and super-taster women ☆

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ABSTRACT

Taste blindness to the bitterness of PROP (6-n-propylthiouracil) has been used as a genetic marker for food selection and adiposity. We have shown that PROP non-taster (NT) women have higher BMIs and habitually consume more fat and energy than either medium-taster (MT) or super-taster (ST) women. These data imply that differences in dietary selection underlie the body weight differences among PROP taster groups. However, no studies investigated energy compensation in women classified by PROP status. We investigated if NTs would compensate less accurately for the calories and fat in a high-fat soup preload in a subsequent test meal compared to MTs and STs. Energy intake from a buffet meal was measured in 75 healthy non-diet-restrained, lean women 30 min after the ingestion of a high-fat soup preload (0.8 kcal/g; 55% calories from fat), calculated to represent 10% of resting energy expenditure for each subject, or the same volume of water. Subjects ($n = 20$–28/taster group) ate a standard breakfast followed 3 hr later by an ad-libitum buffet lunch, on two occasions. There were no differences in energy intake or macronutrient selection across taster groups after water. After soup, NTs consumed more energy than STs. Fat intake (as %-energy) was higher in NTs (46.4% ± 2.4) compared to either MTs (36.1 ± 1.9%) or STs (38.1% ± 2.3; $p < 0.05$). NTs overate by 11% ± 5 after the soup compared to MTs and STs who underrate by 16% ± 6 and 26% ± 10, respectively ($p < 0.01$). These data suggest that small discrepancies in short-term energy compensation and selection of fat after a mixed-nutrient, high-fat preload may play a role in positive energy balance and increased adiposity in women with the PROP non-taster phenotype.

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Introduction

Obesity remains a pervasive problem in developed countries and is an emerging threat to public health in many developing nations across the globe (Flegal et al., 2010; Wang et al., 2011). Obesity has many causes, but a primary contributor to this disease is chronic exposure to palatable, high-fat/energy-dense foods that promote excess energy intake and weight gain (Bray et al., 2004; Golay & Bobbioni, 1997). Some individuals may be more vulnerable than others to excess consumption of high-fat foods, and specific gene variants and phenotypes may play a role in this vulnerability (Brunkwall et al., 2013; Cecil et al., 2008; Keller et al., 2012; Pepino et al., 2012). A frequently-studied marker for individual differences in fat palatability and dietary selection is the 6-n-propylthiouracil (PROP) bitter-taste phenotype, which has been associated with variation in energy balance and body weight (Tepper, 2008; Tepper et al., 2008).

PROP tastes bitter to the majority of human beings worldwide, and is weak or tasteless to others (Guo & Reed, 2001). Based on phenotypic screening, individuals can be classified as non-tasters who perceive little or no bitterness from this compound, medium tasters who perceive moderate bitterness, and super-tasters who perceive intense bitterness from PROP (Bartoshuk, 2000; Bartoshuk et al., 2004; Tepper, 2008). Among Caucasians of Western European ancestry, the approximate population distribution of PROP taster groups (based on PROP bitterness intensity ratings) is: 30% non-tasters; 45% medium tasters; and 25% super-tasters (Bartoshuk et al., 1994; Tepper et al., 2009). However, the prevalence of non-tasters varies across the globe from a low of ~10% in East Asian populations to approaching 50% in some South Asian groups (Guo & Reed, 2001).

The ability to taste PROP is controlled by the bitter taste receptor gene *TAS2R38* (Kim et al., 2003). Three nucleotides in the sequence

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of this gene (P49A, A262V, and V296I) produce the two major alleles: AVI, the insensitive form; and PAV, the sensitive one. Those with two insensitive alleles (AVI/AVI) are phenotypic non-tasters, and those with one or two sensitive alleles (PAV/AVI or PAV/PAV) are considered phenotypic tasters (Bufe et al., 2005; Kim et al., 2003). Rare haplotypes (e.g., AAI and AAV) are also observed, and are more frequent in ancestral populations from sub-Saharan Africa (Wooding et al., 2004; Behrens, Gunn et al., 2013). Although sequence variation in *TAS2R38* defines the majority (65–85%) of the phenotype (Kim et al., 2003; Prodi et al., 2004; Tepper et al., 2008), a variety of other factors may also play a role (Hayes et al., 2008). One such factor is heterogeneity in PAV – allele mRNA expression in fungiform taste papillae, which controls the amount of receptor protein that individuals produce (Lipchock et al., 2012). Presumably, PAV/AVI carriers who express more of the protein encoded by the PAV allele would experience more intense bitterness from PROP than those with the same genotype who do not express more receptor protein. Other factors include differences in the secretion of salivary proteins Ps-1 and II-2 (from the basic-Proline-rich Protein (bPRP) family) (Cabras et al., 2012; Melis, Aragoni et al., 2013) and functional differences in gustin, a trophic factor for taste bud development and maintenance (Calo et al., 2011; Padiglia et al., 2010). Gustin is the product of the CA6 gene, and a recently identified polymorphism at this locus has been associated with differences in fungiform papillae densities and PROP bitterness perception across *TAS2R38* allelic groups (Melis, Atzori et al., 2013), although some studies do not support this finding (Feeney & Hayes, 2014).

The bitter taste of PROP and its structural analogs (phenylthiocarbamide (PTC), sinigrin, goitrin, and others) is due to the presence of the thiourea group (N-C = S) within these compounds that binds the TAS2R38 receptor (Biarnes et al., 2010). Although TAS2R38 is capable of binding a few non-thiourea compounds (limonin, ethyl pyrazine), its repertoire is limited relative to other bitter receptors that are more broadly tuned (Meyerhof et al., 2010). It is frequently observed, however, that PROP super-tasters perceive greater intensity from non-thiourea bitter compounds (e.g., caffeine, naringin) as well as from other oral stimuli including sweet taste, salty taste (at higher concentrations), capsaicin heat and the mouthfeel of fats (Hayes & Duffy, 2007; Kirkmeyer & Tepper, 2003; Prescott et al., 2004; Tepper & Nurse, 1997; Yeomans et al., 2007). These effects presumably are indirect (i.e., unrelated to TAS2R38 receptor binding and activation) and reflect anatomical and functional differences in lingual tissues between phenotypic groups. Supertasters have a greater density of fungiform taste papillae on the anterior tongue (Essick et al., 2003; Melis, Atzori et al., 2013; Tepper & Nurse, 1997), which are heavily innervated by trigeminal (somatosensory) nerve fibers. These features may partially explain why PROP super-tasters are more responsive to oral stimuli and able to discern the texture of fats more readily than the other groups (Hayes & Duffy, 2007; Tepper & Nurse, 1997).

Our work has focused on PROP non-tasters since these individuals poorly discriminate fat content in salad dressings, spreads and fluid dairy products, and often prefer higher-fat over lower-fat versions of these foods (Hayes & Duffy, 2008; Tepper & Nurse, 1997, 1998). These foods are nutritionally important since they are a major source of added fats in the diet (U.S. Department of Agriculture and U.S. Department of Health and Human Services, 2010). We and others have proposed that the increased hedonic appeal of fats may be promoting the overconsumption of this nutrient, contributing to excess energy intake and greater adiposity in non-taster women, which has been observed in several studies (Feeney et al., 2011; Goldstein et al., 2005; Hayes & Duffy, 2008; Tepper et al., 2008; Tepper & Ullrich, 2002). PROP status may have a greater influence on body weight in females than in males (Feeney et al., 2011), and this difference may have its origins in early childhood as reported by Bouthoorn et al. (2014), who showed that non-taster girls were heavier than taster girls at 6 years of age. Why this gender imbalance exists is unknown, although the opposite finding (non-taster boys more heavy than taster boys) has also been reported (Keller et al., 2010).

Studies disagree on whether PROP status is involved in everyday eating patterns with some studies supporting this role (Goldstein et al., 2007; Keller & Tepper, 2004) and others failing to do so (Drewnowski et al., 2007; Yackinous & Guinard, 2002). Most diet studies depend on self-reported food intakes that are less reliable than direct dietary measures (Karelis et al., 2010). When we measured food intake in the laboratory during a buffet feeding regimen, lean, non-taster women consumed more energy than did super-taster women (Shafaie et al., 2013; Tepper et al., 2011). Further, when examined over multiple days of laboratory feeding, non-taster women consumed more servings of added fats and sweets such as cakes and pastries (Shafaie et al., 2013). These data are consistent with the hypothesis that access to high-fat/energy dense foods may be a risk factor for positive energy and weight gain in non-taster women.

While a growing literature has examined spontaneous energy intakes in PROP-classified groups, little attention has been paid to understanding mechanisms of energy regulation in these same groups. Preloads are commonly employed to assess short-term energy compensation (Akhavan et al., 2010; Cecil et al., 2008; Rolls et al., 1994). In general, these studies show that subjects adjust short-term food intake reasonably well in response to variations in the energy content of a preload (Rolls & Hammer, 1995). However, this compensation may be incomplete and not uniform across macronutrients. In particular, some studies have demonstrated a relatively weak satiety response to fats (Rolls & Hammer, 1995; Rolls et al., 1994) and considerable individual variation in the ability to compensate for ingested calories, including fat calories (Caputo & Mattes, 1992; Rolls et al., 1997). Thus, by studying women classified by taster status and feeding them a high-fat diet challenge, we aimed to unmask individual differences in energy regulation and satiety response to fat presented in a mixed-nutrient high-fat soup preload.

The objective of this study was to determine the effects of a high-fat soup preload on short-term energy intake and macronutrient selection in lean women as a function of their PROP taster status. Subjects consumed a soup preload or no preload (water) followed by access to a buffet lunch. We hypothesized that non-taster women would: 1) compensate less well for the energy in the preload than super-taster women; 2) consume more fat from the buffet lunch than super-taster women; and 3) experience less fullness after the preloads than super-taster women. The study was limited to lean women to investigate dietary regulatory behaviors that predispose women to future weight gain in the absence of concurrent obesity.

Methods

Subject recruitment

Healthy, lean, women, 18–45 years of age were recruited from the Rutgers University campus and the local community. Potential subjects had to be weight stable (<2 kg change in weight) in the 3 months prior to the study. Women were excluded if they were restrained eaters, defined as a score of >11 on the restraint subscale of the Three Factor Eating Questionnaire (Stunkard & Messick, 1985) or if they showed evidence of disturbed eating behavior according to the Eating Attitudes Test (EAT26) (Garner et al., 1982). Additional exclusions included pregnancy or lactation; use of medications that affect taste, food intake, or appetite; the presence of major chronic diseases (e.g. diabetes, kidney disease, cancer or cancer treatment); major food allergies (e.g. wheat, dairy, nuts); and engagement in organized sports or physical activity for more than 3–5 h/wk. Health and demographic information were collected with a general screening questionnaire. To qualify for the study, women had to have a BMI = 18–25 kg/m². BMI was calculated based on body weight (measured to the nearest 0.2 kg) using an electronic scale and height was measured to the nearest 0.2 cm using a stadiometer. Measures were taken over lightweight clothing and without shoes in the laboratory. A food preference questionnaire was used to screen out women who disliked creamy soups or foods that they would be exposed to in the buffet meal.

The experimental protocol was approved by the Rutgers University Institutional Review Board. All subjects gave written informed consent to participate in the study and received financial compensation for their participation. Subjects were blind to the specific hypotheses of the study. They were told the experiment assessed the relationship between an appetizer (the preload) and food selection from a subsequent meal.

PROP screening and taster status

Women were screened for PROP status using a filter paper method developed by Zhao and colleagues (Zhao et al., 2003). Subjects first placed a filter paper disk impregnated with 1 M NaCl (VWR Scientific, Bridgeport, NJ) on the tip of their tongue, waited 30 seconds and then rated the intensity of the perceived taste by drawing a line across a 100 mm, semi-logarithmic Labeled Magnitude Scale (LMS) (Green et al., 1996). This 100 mm, semi-logarithmic scale is anchored at each end with descriptors "barely detectable" and "strongest imaginable". Subjects were instructed to rate the intensity relative to the strongest oral sensation they have ever experienced. Subjects rinsed thoroughly with water, and repeated the procedure with a second disk impregnated with 50 mM PROP (6-n-propylthiouracil, Sigma-Aldrich, St. Louis, MO). Subjects were classified as non-tasters (NTs), medium tasters (MTs) or super-tasters (STs) based on their intensity ratings for PROP. Classifications were based on empirically derived cutoff scores where non-tasters were defined by a score <13 on the LMS and super-tasters were defined by a score >67. Subjects who did not meet either of these criteria were classified as medium tasters. In rare cases in which a subject gave a borderline rating to PROP, the NaCl rating was used to resolve that individual's taster status (Tepper et al., 2001; Zhao et al., 2003). The validity and reliability of these procedures have been well established (Rankin et al., 2004; Zhao et al., 2003) and the method has been employed in numerous studies (Goldstein et al., 2005; Oftedal & Tepper, 2013; Tepper et al., 2008).

Preloads

The preload was a high-fat commercial soup (Progresso Potato, Broccoli and Cheese Chowder, General Mills, Minneapolis, MN) composed of 55% energy as fat, 37% energy as carbohydrate and 8% energy as protein. The soup was pureed in a household blender for 15 seconds on high speed. The amount of soup (g) served to each subject was calculated to deliver 10% of each woman's resting energy expenditure according to Mifflin et al. (1990). The typical serving size was 148 g (range 143–156 g) that delivered 109 kcal (range = 105–115 kcal) at 0.734 kcal/g. Since stomach volume affects food intake (Geliebter, 1988), plain water was used as a control to match the gastric distention of the soup.

Breakfast

On each day of the study, subjects consumed a standard 300 kcal breakfast in the laboratory between 8:00 and 9:00 AM. Breakfast consisted of orange juice (118 ml; Tropicana Pure Premium, Bradenton, FL), low-fat, blended fruit yogurt (170 g; La Yogurt, Johanna Foods, Flemington, NJ), bread (22 g; Arnold White or 100% Whole Wheat, Bimbo Bakeries USA, Horsham, PA); margarine (5 g; Shoprite Brand, Wakefern Foods, Elizabeth, NJ), instant coffee or brewed tea (237 ml) with (optional) non-nutritive sweetener (Splenda packets, McNeil Nutritionals, Fort Washington, PA) and/or non-fat, non-dairy creamer (2 g; Coffee Mate, Nestle, USA). The meal contained 6 g fat, 7 g protein, and 55 g carbohydrate.

Buffet lunch

A buffet lunch was offered consisting of an assortment of: lunch meats; cheeses, breads and rolls; condiments; cookies and pastries; fresh fruit; chips; and beverages. Subjects also had access to a salad bar with a variety of salad dressings. A list of the foods offered including their energy and macronutrient compositions appears in Supplementary Table S1. All items were either pre-weighed prior to serving and offered in standard USDA portion sizes (U.S. Department of Agriculture, Agricultural Research Service, 2002) or were commercially packaged and served in their original containers (e.g., chips, beverages). Labels indicating the name of the foods were displayed with every food item. Subjects could return to the buffet for more food as many times as they wished.

Hunger, fullness and motivation to eat

Subjects rated their level of hunger, fullness, desire to eat a meal and desire to eat a snack using 15 cm visual analog scales (VAS). The scales were anchored with the phrases "not at all" on the left side and "extremely" on the right side.

Procedure

Each subject participated in two test sessions scheduled over a 2-week period. There were 6 washout days between the two sessions. Subjects were randomly assigned to receive the soup preload first or the water control first. During study days, subjects came to the laboratory between 8:00 and 9:00 AM to consume the standardized breakfast. They were required to consume the entire meal. Subjects were then free to leave the lab to engage in their normal routine, and returned 3 hr later for lunch. During free time, they were prohibited from eating or drinking anything (except plain water) and from exercising, with the exception of walking. When they returned to the laboratory, subjects first consumed the preload (soup or water). They had to consume the entire portion within 5 min. They then waited 30 min, consumed the buffet lunch, and then waited an additional 30 min. They rated their hunger, fullness, and motivation to eat using visual-analog scales, as previously described. VAS ratings were completed at 5 time points: when subjects arrived at the laboratory at lunchtime (baseline); immediately after the preload (post-preload); after the 1st 30 min wait (prior to lunch); immediately post-lunch; and after the 2nd 30 min wait (at the end of the session). The entire session took approximately 90 min to complete.

Subjects were seated in individual testing booths during the sessions. The booths were equipped with the FIZZ (Biosystemes, Counternon, France) direct-data entry software. The VAS scales appeared at timed intervals on the computer monitor in the booths, and subjects responded by pointing and clicking with a mouse on the screen. During the waiting periods, subjects were free to read or listen to music; however, they were prohibited from interacting with each other. During buffet lunches, foods were presented on a table adjacent to the booth area. Subjects placed their selections on their food trays and carried their meals to their individual testing booths. At the end of each meal, empty packages were counted and plate waste was collected and weighed (to the nearest 0.2 g). Food intake was measured by subtracting uneaten food from the starting weight of each package.

At the end of each session, subjects completed a brief exit questionnaire to express their opinions about the soup preload, the buffet foods and their general satisfaction with the study.

Data compilation and statistical analyses

Food intake data were compiled using Nutrition Data System for Research software (NDS-R version 2010) from the Nutrition Coordinating Center, University of Minnesota, Minneapolis, MN. Outputs included: energy intake (kcal); fat, carbohydrate, and protein (as %-en). Intake was also calculated from USDA food groups (fruits, vegetables, etc.; in servings) and food subgroups of interest (sweets, sweetened beverages, etc.).

Food intake data are presented as means ± SEM. Repeated measures analysis of variance (ANOVA) was used to examine taster group differences in the dietary variables across preload conditions (soup or water). When the taster group × condition interaction was significant, separate analyses were carried out for soup and water, and these calculations are reported in the text. Body weight was used as a covariate to adjust for differences in weight status. Repeated measures ANOVA was also used to track changes in VAS ratings over time. Post-hoc comparisons were done using Duncan's New Multiple Range Test, where appropriate.

Caloric adjustment during lunch (as % compensation) for the soup preload was calculated according to Rolls, Bell, and Thorwart (1999) using the following equation:

$$\%\ \text{compensation} = [\text{energy intake (kcal) after water} / \text{energy (kcal) content of soup} + \text{energy intake (kcal) after soup}] \times 100.$$

Values of 100% indicate perfect compensation; values >100% indicate over-compensation (i.e., under-eating) and values <100% indicate under-compensation (i.e., overeating) (Rolls, Bell et al., 1999). Group differences in % compensation were assessed using 1-way ANOVA. All data were analyzed using SAS for Windows (Version 9.2, SAS Institute, Carey, NC) with $\alpha = 0.05$ for all tests.

Results

Subject characteristics

A total of 80 women qualified for the study following screening for body weight, restrained eating score, and PROP taster status. Five women were admitted into the study but did not participate due to various reasons (lack of interest, scheduling conflicts, etc.). The final study cohort consisted of 20 non-tasters, 32 medium-tasters, and 23 super-tasters. Since published data do not exist on preload responses in PROP-classified individuals, a power calculation was not computed. Cell size was based on previously published studies that typically utilized 12–28 subjects/group (Potier et al., 2010; Rolls et al., 1994; Shide & Rolls, 1995). Our smallest group (n = 20 for non-tasters) was well within this range.

The study cohort had a mean age of 24.3 ± 1.1 years and mean BMI of 21.9 ± 0.5 kg/m². The majority (59%) of subjects were Caucasians, 24% were Asians, and 17% came from other ethnic groups (combined). Subject characteristics are shown in Table 1. There were no significant differences or trends for any of the individual variables as a function of taster status.

Buffet lunch energy and macronutrient intakes

As shown in Table 2, energy and macronutrient intakes from the buffet lunch did not differ by taster group in the water condition, although there was a directional trend for non-taster women to consume more fat and less carbohydrate than the other groups. Following the soup preload, non-taster women consumed more energy from lunch than did super-taster women ($p < 0.05$ by Duncan's test subsequent to ANOVA for taster effect, $F(2,72) = 2.67$; $p < 0.05$). Mean energy intake of the medium taster women did not differ from the other groups. Also in the soup condition, percent fat intake was higher in non-taster women compared with both the medium and super-taster women ($p < 0.05$ by Duncan's test subsequent to ANOVA for taster effect, $F(2,72) = 6.98$; $p < 0.01$).

Table 1
Subject characteristics.[a]

	Non-taster (n = 20)	Medium-taster (n = 32)	Super-taster (n = 23)	All subjects (n = 75)
Ethnicity (n)				
Caucasian	13	16	15	44
Asian	2	10	6	18
Hispanic	2	3	1	6
African-American	1	0	0	1
Other	2	3	1	6
Age (year)	23.8 ± 1.1	24 ± 0.7	25.1 ± 1.5	24.3 ± 1.1
Weight (kg)	60 ± 1.8	57.1 ± 1.6	55.1 ± 1.7	57.4 ± 1.7
Height (m)	1.6 ± 0.1	1.6 ± 0.0	1.6 ± 0.0	1.6 ± 0.01
BMI (kg/m²)	22.3 ± 0.5	22.4 ± 0.6	21.1 ± 0.5	21.9 ± 0.5
Restraint score	6.0 ± 0.7	7.2 ± 0.5	6.9 ± 0.6	6.7 ± 0.6
Disinhibition score	6.1 ± 0.6	5.5 ± 0.6	5.4 ± 0.7	5.7 ± 0.6
Hunger score	4.8 ± 0.5	5.0 ± 0.4	4.9 ± 0.6	4.9 ± 0.5

[a] Except for ethnicity, values are means ± SEM; there were no significant differences in mean values for any individual characteristics across taster groups.

Caloric compensation

Figure 1 shows combined energy intakes (lunch plus preload) and percent compensation for the soup preload across taster groups. In the water condition, there were no differences in energy intake across the taster groups. In the soup condition, total energy intake (lunch plus preload) was higher in non-taster women compared to super-taster women ($p < 0.05$ by Duncan's test subsequent to ANOVA for taster effect, $F(2,71) = 5.8$; $p < 0.01$). Total energy intake of medium taster women did not differ from the other groups.

Energy intakes from lunch in the water condition were compared to energy intakes in the preload condition for the entire cohort. As expected, the women consumed more energy during the water condition than they did during the soup condition (754 ± 41 vs. 612 ± 42 kcal, respectively; $p < 0.01$ by t-test).

Non-taster women undercompensated (i.e., over ate) for the energy in the soup compared to both medium taster and super-taster women who overcompensated (i.e., under-ate) relative to the

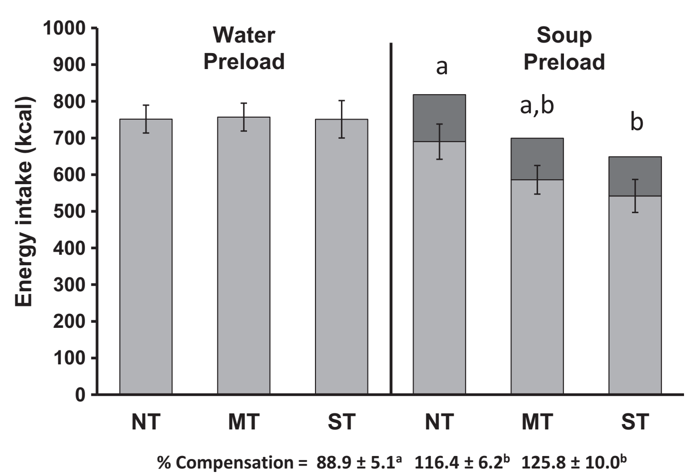

Fig. 1. Energy intakes of PROP non-taster (NT; n = 20), medium taster (MT; n = 32) and super-taster (ST; n = 23) women from a buffet lunch after a water preload (left) or after a high-fat soup preload (right). The shaded areas represent the contribution of the soup to energy intake. Bars with different superscript letters are significantly different at $p < 0.05$. In the soup preload condition, NT women consumed more energy (preload + lunch) than did MT or ST women. There were no differences in energy intake across the taster groups in the water condition.

Table 2
Energy and macronutrient intakes from a buffet meal following water or soup preloads.*

	Water preload			Soup preload		
	NT	MT	ST	NT	MT	ST
Energy intake (kcal)	752 ± 38	757 ± 37	750 ± 54	690 ± 48[a]	586 ± 39[a,b]	542 ± 45[b]
Energy density	1.1 ± 0.1	1.2 ± 0.1	1.3 ± 0.1	1.1 ± 0.1	1.1 ± 0.1	1.0 ± 0.1
% Fat	42.6 ± 2.2	38.1 ± 1.9	37.1 ± 2.9	46.4 ± 2.4[a]	36.1 ± 1.9[b]	38.1 ± 2.3[b]
% Carbohydrate	41.2 ± 1.9	45.7 ± 2.1	44.8 ± 2.9	42.2 ± 2.1	49.1 ± 1.7	46.6 ± 2.6
% Protein	17.4 ± 0.7	17.1 ± 0.8	16.9 ± 0.9	16.1 ± 0.7	17.2 ± 0.6	17.3 ± 1.1

* Values are means ± SEM. Values within preload type with different superscript letters (a, b, etc.) are different at $p < 0.05$ based on Duncan's Multiple Range Test.

water condition ($F(2,71) = 6.31$; $p < 0.01$). Non-taster women overate by 11%, whereas medium and super-taster women under ate by 16% and 26%, respectively (see Fig. 1).

Percent compensation for the energy in the soup was also calculated for the entire cohort. As a group, the women under ate by 9.6 ± 1.3%.

Hunger, fullness and motivations to eat

Baseline ratings of hunger, fullness, and desire to eat a meal or snack did not differ by PROP taster group, and PROP status did not influence changes in VAS ratings over time. For this reason, VAS ratings were collapsed across taster groups, as shown in Fig. 2.

VAS ratings changed in a predictable pattern across time ($F(2,228) = 20.2–50.7$; $p < 0.001$ for all). Following the preloads, hunger fell and then recovered 30 min later; fullness showed the opposite pattern, increasing immediately after the preloads and diminishing thereafter. Motivations to eat were initially suppressed by the preloads, and recovered 30 min later. As expected, soup suppressed hunger and motivations to eat, and increased fullness more than water ($F(2,228) = 3.56–23.5$; $p < 0.03–0.001$).

Supplementary Figs. S1 and S2 show the VAS ratings for hunger, fullness and motivations to eat as a function of preload type in non-taster, medium taster and super-taster subgroups.

Discussion

The primary objectives of the present study were to examine short-term energy regulation and selection of fat in women classified by PROP taster status. Results showed that lean, non-taster women consumed more fat and energy from a buffet lunch following a high-fat soup challenge than did super-taster women. Non-taster women overate by 11% following the high-fat soup (compared to water control) whereas medium and super-taster women under-ate by 16% and 26%, respectively. These data demonstrate for the first time that short-term compensation for excess energy consumed as a high-fat soup may be compromised in non-taster women, although the size of the energy discrepancy was modest.

Why medium and super-taster women overcompensated (i.e., underate) in response to the soup preload is unclear. All women were screened for restrained eating, and all subject groups had comparably low scores on all three subscales of the Three Factor Eating Questionnaire. It is possible that small differences in eating attitudes existed among the groups that we were unable to detect using standardized questionnaires. On the other hand, subjects in preload studies have been known to cognitively control their subsequent food based on the belief that the test food was high in fat (Shide & Rolls, 1995). The soup was homogenized prior to serving to eliminate chunks of vegetables that might alter its digestion. However, we made no effort to visually disguise the soup (e.g., with red lights) or to alter its textural properties. Previous

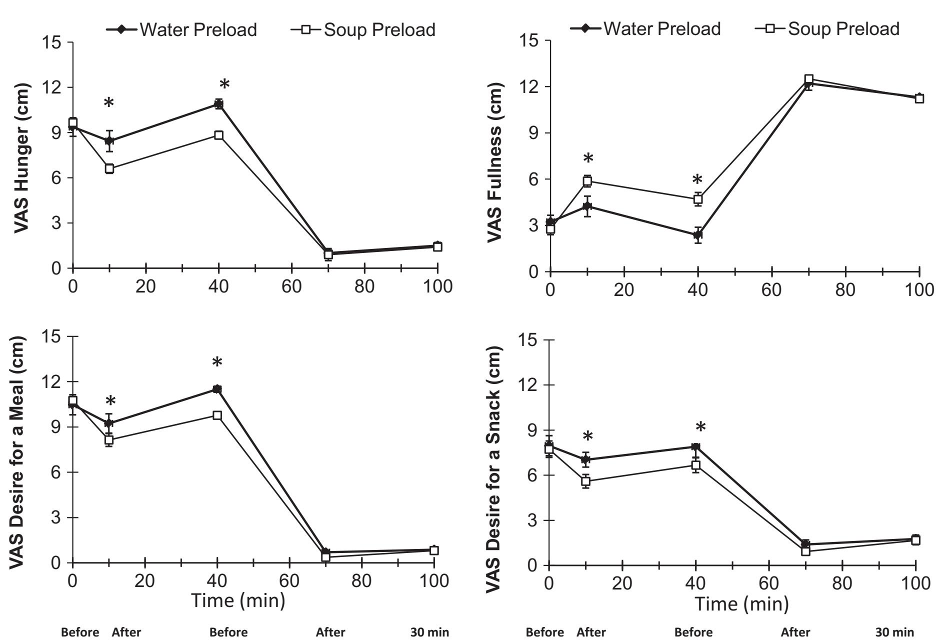

Fig. 2. VAS ratings for hunger, fullness and motivations to eat a meal or snack during test sessions with a water preload (control) or high-fat soup preload. Data were collapsed across taster groups for presentation. *Significant difference between soup and water at individual time points ($p < 0.05$).

studies have shown that non-tasters are less discriminating of the fat content of foods, especially creamy foods such as dairy products and salad dressings (Hayes & Duffy, 2007; Kirkmeyer & Tepper, 2003; Tepper & Nurse, 1997). It is reasonable to assume that these findings would extend to cream-based soups, as well. Thus, we can speculate that non-taster women may have been less sensitive to the perceived fat cues from the soup, and hence less likely to reduce their subsequent intake based on these signals.

Previous studies have shown that short-term energy regulation is influenced by a number of personal factors such as physical activity, age, gender, BMI and restrained eating (Appleton et al., 2011; Long et al., 2002; Rolls et al., 1994, 1995). Typically, compensation is more precise in males and unrestrained eaters, and less precise in overweight and restrained eaters (Rolls & Hammer, 1995; Rolls et al., 1994). Nevertheless, even among young, normal weight young adults, there is considerable individual variation in the ability to compensate for covert excess energy from a test meal, especially from those high in fat (Caputo & Mattes, 1992). Fats are considered less satiating than the other macronutrients (Potier et al., 2010; Rolls & Hammer, 1995; Rolls et al., 1994) but previous studies do not support macronutrient specific compensation for excess energy intake (Rolls et al., 1991, 1994). For example, Rolls and coworkers (Rolls et al., 1997) reported that subjects compensated for only 79% of the energy in a high-fat soup preload that was similar in composition to the soup used here. However, no specific adjustment in fat intake was observed. Importantly, the cohort studied by Rolls and colleagues (Rolls et al., 1997) included obese and diet-restrained individuals. The women we studied were young, lean and not diet-restrained. Thus none of the factors previously described explain our findings of higher fat and energy intakes in non-taster women. By classifying women by their PROP bitter taste phenotype, we were able to unmask individual differences in short-term compensation for fat and energy from a mixed-nutrient high-fat soup that had gone unnoticed in previous experiments that did not phenotype women for PROP status.

The soup provided a modest caloric load of 10% of a woman's resting energy expenditure (~109 kcal). Although subjects were less hungry and more full after soup compared to water, we did not detect differences in VAS ratings between non-taster women and the other groups. Perhaps a more generous caloric challenge is necessary to reveal these differences. The absence of post-load differences in appetite ratings across groups provides little insight into the mechanisms underlying the eating behaviors of non-taster women in this experiment. Nor does the literature provide guidance on this issue, as previous studies have not examined PROP-related differences in gut peptides or other mediators (central or peripheral) involved in feeding. Our findings suggest the need for more comprehensive studies of these issues in individuals classified by PROP phenotype.

Our study had several limitations that need to be addressed in future studies. First, the present study focused on compensatory responses to a high-fat preload; we did not test a low-fat preload or preloads varying in carbohydrate and protein. Thus we do not know if compensation for other variations in nutrient composition is also compromised in non-taster women. We also excluded overweight and obese women who might have responded differently to a preload challenge than lean women. Additionally, this study was designed to examine the acute effects of a diet challenge on subsequent meal intake. Studies are needed to assess daily and longer-term adjustments in energy regulation in non-taster women. Several procedural limitations should also be mentioned. Sensory testing of the soup preload was not done in this study. Nevertheless, several criteria were used to insure that the foods used in the study were palatable to subjects. Specifically, subjects were pre-screened for liking of creamy soups (by questionnaire) and they were told in advance the type of soup they would be asked to consume. Exit questionnaires at the end of each session failed to detect dissatisfaction with the preload or the buffet foods. Creamy soup consumption data were not collected, thus the extent to which the satiety responses we observed may have been influenced by learning is unknown. Finally, we allowed subjects to leave the laboratory between breakfast and lunch. Although subjects were instructed not to eat or drink anything but plain water during this time period, and they were questioned about their activities, we do not know with certainty if they complied with this requirement.

In summary, this study revealed that short-term regulation of fat and energy intake was modestly compromised in women with the PROP non-taster phenotype. These results complement previous data showing that under free-feeding conditions, non-taster women consume more energy and added fats when exposed to high-fat/energy dense foods (Shafaie et al., 2013; Tepper et al., 2011). Taken together, our findings suggest that enhanced palatability for fat may be driving higher dietary selection of fat, and when combined with small discrepancies in fat regulation may contribute to positive energy balance and increased BMI in non-taster women (Goldstein et al., 2005; Tepper et al., 2008; Tepper & Ullrich, 2002).

Finally, the notion that chronic exposure to dietary fat may blunt satiety signals and lead to excess weight gain and adiposity has been steadily gaining ground (Erlanson-Albertsson, 2010; Stewart & Keast, 2012; Stewart et al., 2011). Our findings suggest that genetic predispositions which enhance the hedonic appeal of fats, may exacerbate the risks of dietary fat exposure to affected individuals, setting the stage for weight gain and metabolic dysregulation. A greater understanding of risk phenotypes such as PROP status and other phenotypes involved in the sensory processing of fat-related food cues (Keller et al., 2012) will provide important insights into the etiology of obesity and may give rise to new weight control alternatives.

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Appendix: Supplementary material

Supplementary data to this article can be found online at doi:10.1016/j.appet.2015.02.009.