Abstract
The genetically determined ability to taste 6-n-propylthiouracil (PROP) has been linked with lowered acceptance of some bitter foods. Fifty-four women, aged 18–30 years, tasted and rated PROP-impregnated filter paper and seven solutions of PROP. Summed bitterness intensity ratings for PROP solutions determined PROP taster status. Respondents also tasted five sucrose and seven caffeine solutions, as well as seven solutions each of caffeine and PROP that had been sweetened with 0.3 mmol/l neohesperidin dihydrochalcone (NHDC). Respondents also rated three kinds of chocolate using 9-point category scales. PROP tasters rated caffeine solutions as more bitter than did non-tasters and liked them less. PROP tasters did not rate either sucrose or NHDC as more sweet. The addition of NHDC to PROP and caffeine solutions suppressed bitterness intensity more effectively for tasters than for non-tasters and improved hedonic ratings among both groups. PROP tasters and non-tasters showed the same hedonic response to sweetened caffeine solutions and did not differ in their sensory responses to chocolate. Genetic taste markers may have only a minor impact on the consumption of such foods as sweetened coffee or chocolate.

Introduction
The ability to taste some bitter compounds is genetically determined (Snyder, 1931). Two compounds, phenylthiocarbamide (PTC) and 6-n-propylthiouracil (PROP), taste bitter to some people and are tasteless to others (Blakeslee and Fox, 1932; Fox, 1932; Fischer, 1964). In past studies assignment of PROP taster status was based on the bimodal distribution of taste detection thresholds obtained using PROP solutions (Drewnowski and Rock, 1995; Drewnowski et al., 1997a). Other studies simply relied on the distribution of taste responses to PROP-impregnated filter paper (Snyder, 1931; Blakeslee and Fox, 1932).

The genetic ability to taste PTC/PROP has been linked to greater perceived bitterness of some bitter compounds (Hall et al., 1975; Bartoshuk, 1979). However, the data have not always been consistent. Using threshold detection methods some studies have failed to find a link between PTC/PROP sensitivity and the sensitivity to caffeine, quinine HCl and urea (Leach and Noble, 1986; Mela, 1989; Schifferstein and Frijters, 1991; Smagghe and Louis-Sylvestre, 1998). Others (Hall et al., 1975) found that PTC tasters rated low caffeine concentrations (0.0056–0.03 mol/l) as more intensely bitter than did non-tasters. In a time–intensity study (Neely and Borg, 1999), tasters gave higher aftertaste intensity ratings to a low concentration of caffeine (0.018 mol/l) than did non-tasters.

Whether PROP tasters and non-tasters differ in their perception of sweetness intensity is another unresolved issue. In some studies sucrose and neohesperidin dihydrochalcone (NHDC), an intense sweetener, tasted sweeter to tasters than to non-tasters (Bartoshuk, 1979; Gent and Bartoshuk, 1983). In contrast, other studies found no relationship between PROP tasting and the perceived sweetness of sucrose solutions (Drewnowski et al., 1997a,b). Other studies compared taste responses of PROP tasters and non-tasters to compounds that simultaneously exhibit both sweet and bitter qualities (Bartoshuk, 1979). PROP tasters perceived low concentrations of saccharin as both sweeter and more bitter than did non-tasters.

One question is whether genetic ability to taste PROP influences sensory response to bitter phytonutrients. Plant-derived phenolic compounds, including flavonoids in grapefruit, isoflavones in soy products and catechins in tea, are almost always bitter. In past studies PROP tasters rated naringin solutions and infusions of Japanese green tea as more bitter than did non-tasters and liked them less (Akella et al., 1997; Drewnowski et al., 1997c). PROP tasters rated soybean tofu as less acceptable than did non-tasters and reportedly lower preference for grapefruit juice (Akella et al., 1997; Drewnowski et al., 1997c). Chocolate contains caffeine and has four times the amount of a bitter polyphenol catechin than tea (Arts et al., 1999). However, bitter beverages and chocolate are almost always sweetened.
The bitterness of foods can be masked by the addition of sweeteners. The mutual suppression of bitter and sweet tastes may be due to neural interactions as opposed to competition at the receptor level (Lawless, 1979). In one study of bittersweet mixtures of PTC and sucrose, tasters of PTC showed a stronger suppression of sweetness than did non-tasters (Lawless, 1979). There is little additional information on the impact of genetic taste factors on taste mixtures and mixture interactions. We therefore examined whether the addition of an intense sweetener, NHDC, would differentially affect taste responses to PROP and caffeine solutions by PROP taster status. We also examined whether PROP tasters and non-tasters differed in their sensory responses to white, milk and bittersweet chocolate. Respondents were also asked about their food choices and the consumption of chocolate and coffee beverages.

Materials and methods

Respondents

Respondents were 54 young women between the ages of 18 and 30 years, recruited through advertisements and flyers posted in the University of Washington. The sample was 75.9% Caucasian, 18.5% Asian/Pacific Islander, 1.9% African-American, 1.9% Native American and 1.9% listed as ‘other’. Women reporting use of tobacco or medication that would alter taste or smell were excluded from the study. All respondents were weighed and measured and body mass indices (BMI, kg/m²) were calculated. Compensation was provided for completing each taste session. All research protocols were approved by the Human Subjects Review Board of the University of Washington.

Taste stimuli

PROP-saturated filter paper

PROP filter papers were prepared by dipping Whatman no. 1 filter paper into a concentrated solution of PROP heated close to boiling point, as described in previous studies (Drewnowski et al., 1997a; Kaminski et al., 2000). Filter papers were dried and cut into 1 inch squares that were then stored in glassine envelopes.

PROP solutions

Seven solutions of PROP (Pfalz & Bauer, Waterbury, CT) were prepared in distilled water using progressive serial dilutions of the most concentrated solution. The concentrations of PROP increased in half-log steps and were determined as described in previous studies (Drewnowski et al., 1997a). The PROP concentrations were $3.2 \times 10^{-6}$, $10.0 \times 10^{-5}$, $3.2 \times 10^{-5}$, $10.0 \times 10^{-4}$, $3.2 \times 10^{-4}$, $10.0 \times 10^{-3}$ and $3.2 \times 10^{-3}$ mol/l. These correspond to solutions 3, 5, 7, 9, 11, 13 and 15 in the regular PROP series (Drewnowski et al., 1997a). The solutions were prepared at least 1 day before testing and were stored at 4°C.

Sucrose solutions

The concentrations of five sucrose solutions in distilled water were 2, 4, 8, 16 and 32% (w/v) (Drewnowski et al., 1997a,b).

Caffeine solutions

Seven solutions of caffeine (Sigma Chemical Co.) were prepared using distilled water. Caffeine concentrations, increasing in quarter-log steps, were $1.8 \times 10^{-3}$, $3.2 \times 10^{-3}$, $5.6 \times 10^{-3}$, $10.0 \times 10^{-2}$, $1.8 \times 10^{-2}$, $3.2 \times 10^{-2}$ and $5.6 \times 10^{-2}$ mol/l.

NHDC solution

The solution of NHDC (Zoster SA, Barcelona, Spain) in distilled water had a concentration of $3 \times 10^{-4}$ mol/l. Sweetness intensity of this concentration of NHDC was equivalent to that of an 11% sucrose solution (Borrego et al., 1991). All solutions were prepared at least 1 day prior to tasting and were stored at 4°C.

Food stimuli

White chocolate (Guittard, Burlingame, CA), milk chocolate (Felchlin, Schwyz, Switzerland) and bittersweet chocolate (Felchlin, Schwyz, Switzerland) were purchased and stored at room temperature for 2 weeks before testing. The percentages of fat (cocoa butter) for the white, milk and dark chocolate were 36, 35.1 and 43.6%, respectively.

Scaling procedures

Respondents placed a PROP filter paper on their tongue, allowed it to moisten and then rated bitterness intensity using a 9-point category scale, anchored at each end, where 1 is not at all bitter and 9 is extremely bitter. Sensory response to PROP solutions was assessed using whole mouth tasting and the standard sip-and-spit technique (Drewnowski et al., 1997a,b,c; Kaminski et al., 2000). Respondents were asked to take a sip of each solution, hold it in the mouth for ~3 s and then expectorate into the cup provided. The solutions, mean volume 10 ml, were presented in 30 ml medicine cups. Respondents were required to rinse with water between tasting each sample and each successive tasting was separated by a minimum 60 s interval. Taste intensity was assessed using a 9-point category scale where 1 was not at all sweet (or bitter) and 9 was extremely sweet (or bitter). Hedonic preferences were also assessed using a 9-point category scale that ranged from 1 (dislike extremely) to 9 (like extremely) (Drewnowski et al., 1997a,b). Bitterness intensity, sweetness intensity and preference for the three types of chocolate were also assessed using 9-point category scales.

Food preference questionnaire

Respondents rated preferences for three types of chocolate (white, milk and dark) and for coffee beverages. They were asked how often they consumed these foods [several times a week, once per week, several times per month, rarely (less
than once per month) or never] and what type of coffee beverages they usually consumed (drip or espresso beverages). Those who drank drip coffee were asked if they consumed it black, with milk/cream or with sweetener only, or with milk/cream and sweetener. Those who drank espresso beverages were asked what type they usually selected (espresso shots, Americanos or lattes) and if they drank it sweetened or not.

**Study design and procedures**

Respondents rated the bitterness intensity of PROP filter papers during the screening session. Those who rated the papers 1 or 2 on a 9-point scale were classified as potential non-tasters, whereas those who gave ratings between 3 and 9 were classified as potential tasters.

During the first tasting session respondents tasted and rated five sucrose solutions, followed by one solution of NHDC, seven solutions of caffeine and seven solutions of PROP. All solutions were presented in a random order of concentrations. PROP solutions were always presented last. All respondents but one returned no more than 1 week later for the second tasting session, during which they tasted and rated seven caffeine and seven PROP solutions sweetened with NHDC and tasted and rated three types of chocolate. Sweetness, bitterness and the hedonic response were the only qualities rated. Respondents also completed food preference questionnaires. Respondents tasted three PROP filter papers on three separate occasions to assess the reliability of PROP filter paper rating.

**Statistical analyses**

Statistical tests were conducted using SPSS for Windows 9.0 (SPSS Inc., Chicago, IL). Taste data were analyzed using repeated measures ANOVA where taster status was the between subject variable and stimulus concentration or stimulus type (PROP or caffeine solutions with and without NHDC) was the within subject variable. Questionnaire data were analyzed using cross-tab analyses followed by \( \chi^2 \) statistics. Significance of correlations among variables was tested using Pearson correlation coefficients.

**Results**

**PROP tasters and non-tasters**

Summed bitterness intensity ratings for the three PROP filter papers were initially used to assess the perception of PROP (Drewnowski et al., 1997a; Kaminski et al., 2000). Reliability tests showed high correlations between successive bitterness scores (\( r = 0.84 \) for filter papers 1 and 2; \( r = 0.89 \) for filter papers 1 and 3; \( r = 0.89 \) for filter papers 2 and 3). The sum of bitterness intensity ratings for the three PROP filter papers showed a bimodal distribution.

As shown in Figure 1, the sum of bitter intensity ratings for seven PROP solutions also showed the expected bimodal distribution. There was a high degree of correlation (\( r = 0.79, P < 0.01 \)) between bitterness intensity ratings for the seven solutions and the three filter papers, as shown in Figure 2 (Drewnowski et al., 1997a,b,c; Kaminski et al., 2000). Since the use of solutions appeared to be less subject to ceiling effects, the sum of bitter ratings for the seven PROP solutions served as the main method for assigning PROP taster status (Lawless, 1980). Respondents whose summed responses were 21 or less were classified as non-tasters, whereas those with summed ratings in excess of 21 were classified as tasters. The subject sample was thus divided into 33 tasters and 21 non-tasters of PROP. As shown in Table 1, PROP tasters and non-tasters did not differ from each other in their age, height, weight or BMI.

**Taste responses to PROP and caffeine**

Taste response profiles for PROP solutions supported the taster–non-taster distinction (see Figure 3, top). As expected, non-tasters gave very low bitterness ratings to all PROP solutions, except for solution 15. In contrast, tasters rated all solutions as more bitter and had lower hedonic ratings than did non-tasters. As in past studies, PROP
tasters disliked PROP solutions more than did non-tasters. The correlation between bitterness and hedonic ratings was significant ($r = -0.77$, $P < 0.01$).

Tasters found caffeine solutions to be more bitter than did non-tasters [$F(1,52) = 4.9$, $P < 0.05$] and disliked them more than did non-tasters [$F(1,52) = 5.2$, $P < 0.05$]. These data are shown in the bottom panels of Figure 3. As was the case with the PROP solutions, respondents who found caffeine solutions to be more bitter also liked them less ($r = -0.71$, $P < 0.01$).

The relationship between summed bitterness intensity ratings for PROP and those for caffeine is shown in Figure 4. Whereas some PROP non-tasters gave high bitterness ratings to caffeine solutions, others did not. In contrast, PROP tasters also tended to give higher ratings to caffeine. These data are consistent with the notion that PROP tasting may involve both a specific sensitivity to PROP and a more general bitter taste responsiveness (Olson et al., 1989).

Prop tasting and response to sweet taste

PROP tasting had no effect on intensity or on hedonic ratings for sucrose solutions. Only a main effect of sucrose concentration, but no effect of taster status and no interactions, was observed. These data are consistent with previous studies, based on a larger sample of young women (Drewnowski et al., 1997a). Tasters and non-tasters did not differ in their sensory responses to a single NHDC solution. Mean sweetness intensity ratings for NHDC were $7.12 \pm 1.8$ for tasters and $6.81 \pm 2.38$ for non-tasters.

Response to sweetened PROP and caffeine solutions

Adding NHDC to PROP solutions reduced bitterness intensity and increased hedonic ratings. As shown in Figure 5, the suppression of bitterness was stronger for PROP tasters than for non-tasters, whose ratings were already at baseline. Analysis of variance of bitterness ratings showed a significant stimulus type by taster status interaction [$F(1,51) = 8.6$, $P < 0.01$] and no main effect of stimulus. Analysis of variance of hedonic ratings showed a significant main effect of stimulus type [$F(1,51) = 17.1$, $P < 0.001$].

The addition of NHDC to caffeine solutions reduced perceived bitterness and increased hedonic ratings, as shown in Figure 6. PROP tasters still perceived sweetened caffeine solutions as more bitter than did non-tasters [$F(1,50) = 5.5$,

Table 1  Respondent characteristics (means ± SEM)

<table>
<thead>
<tr>
<th></th>
<th>Non-tasters</th>
<th>Tasters</th>
<th>All subjects</th>
</tr>
</thead>
<tbody>
<tr>
<td>Age (years)</td>
<td>23.4 ± 0.7</td>
<td>24.1 ± 0.7</td>
<td>23.8 ± 0.5</td>
</tr>
<tr>
<td>Height (cm)</td>
<td>165.8 ± 0.6</td>
<td>165.5 ± 0.4</td>
<td>165.2 ± 0.4</td>
</tr>
<tr>
<td>Weight (kg)</td>
<td>58.4 ± 1.8</td>
<td>61.7 ± 1.6</td>
<td>60.4 ± 1.2</td>
</tr>
<tr>
<td>BMI (kg/m²)</td>
<td>21.4 ± 0.5</td>
<td>22.5 ± 0.5</td>
<td>22.1 ± 0.4</td>
</tr>
</tbody>
</table>

Figure 3  (Top) Mean bitterness intensity and hedonic ratings for PROP solutions by PROP taster status. (Bottom) Mean bitterness intensity and hedonic ratings for caffeine solutions, by PROP taster status.
However, tasters and non-tasters no longer differed in their hedonic response to sweetened caffeine. Only the main effect of caffeine concentration was significant \[ F(6,46) = 53.8, P < 0.001 \].

**PROP tasting and coffee and chocolate consumption**

With this small sample size there were no significant differences by PROP taster status in the reported consumption of chocolate or coffee beverages. However, out of respondents who consumed drip coffee \( (n = 22) \), tasters were more likely \( (77\%) \) to drink coffee with milk/cream and sweetener than were non-tasters \( (44\%) \). Conversely, a greater percentage of non-tasters \( (22\%) \) preferred their coffee black as opposed to tasters \( (7\%) \), although these results also were not significant. There were no differences between taster groups in their sensory evaluation of white and dark chocolate and in their bitter intensity ratings for milk chocolate.

**Taste factors, food preferences and food consumption**

Taste and food preferences and self-reported frequencies of food consumption are associated variables. The correlations between taste preferences, food preferences and reported frequencies of consumption for coffee and chocolate are shown in Table 2. All correlations were significant, suggesting that hedonic ratings obtained in the laboratory are linked with self-reported food preferences and with self-reported frequencies of food use. Since food frequency question-

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**Figure 4** Summed bitterness ratings for PROP solutions plotted against summed bitterness ratings for caffeine, by PROP taster status.

**Figure 5** Intensity (left) and hedonic ratings (right) for PROP solutions before and after the addition of NHDC, by PROP taster status.

**Figure 6** Intensity (left) and hedonic ratings (right) for caffeine solutions after the addition of NHDC, by PROP taster status.
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naires are the mainstay of nutritional epidemiology, showing that food preferences and food frequencies are in fact linked suggests that chemical senses are an important predictor of dietary behavior (Kaminski et al., 2000).

Discussion

The finding that PROP tasters found caffeine to be more bitter than did non-tasters confirms some previous studies (Hall et al., 1975; Neely and Borg, 1999). PROP tasters also disliked caffeine solutions more than did non-tasters. The difference between PROP tasters and non-tasters was observed across a wide range of caffeine concentrations, including those found in coffee and in soft drinks (0.003–0.004 mol/l) (Hall et al., 1975). Bartoshuk suggested at one point that PROP tasters’ sensitivity to caffeine or saccharin might lead them to avoid coffee or diet soft drinks (Bartoshuk, 1979). However, it now appears that moderate sweetening of caffeine solutions minimizes the impact of genetic taste differences. Whereas the sweetening of PROP solutions with NHDC reduced, but did not eliminate, differences in taste response between tasters and non-tasters, sweetening of caffeine solutions eliminated differences in hedonic response altogether.

These findings may explain why past studies have found only a weak effect of PROP taster status on reported preferences for bitter foods (Drewnowski and Rock, 1995; Drewnowski et al., 1997c, 1998; Kaminski et al., 2000). Consumers often mask the taste of bitter foods through the addition of fat, sugar or salt. Rather than avoid bitter foods, PROP tasters may choose to suppress bitterness through the addition of fat, sugar or salt. Debittering of plant foods, in particular, is a major concern of the food industry.

NHDC has proved to be an effective debittering agent. Currently, the most common commercial method for masking bitter taste is the addition of a sweetening agent (Roy, 1990; Schiffman et al., 1994a,b). Schiffman and co-workers found that the addition of sucrose and sorbitol to caffeine solutions significantly decreased the perception of bitterness (Schiffman et al., 1994a,b). Commercially, it is the citrus juice industry that relies the most on debittering to mask or remove the bitterness of citrus juices (Roy, 1990). While neohesperidin, a flavonoid extracted from bitter oranges, is intensely bitter, NHDC is intensely sweet. NHDC has been used as a debittering agent when added to bitter foods, antibiotics, vitamins or bitter pharmaceuticals (Borego et al., 1991). PROP tasters, who often reject bitter tasting foods (Drewnowski 1990; Drewnowski and Rock, 1995; Drewnowski et al., 1998), may be more likely to use caloric and non-caloric sweeteners than PROP non-tasters.

The relationship between PROP tasting and bitterness ratings for caffeine was of particular interest. Among PROP non-tasters were some who rated caffeine as very bitter and some who did not. In contrast, PROP tasting was associated with higher bitterness ratings for caffeine. This may explain why attempts to link PROP taster status with enhanced perception of other bitter compounds have produced inconsistent results (Leach and Noble, 1986; Mela, 1989; Smagghe and Louis-Sylvestre, 1998). Subject selection procedures or methodological differences in assigning PROP taster status may also have played a part. These observations are also consistent with past suggestions that PROP tasting may carry with it a more general ability to taste bitter compounds (Olson et al., 1989).

As in some past studies conducted with college age

Table 2 Pearson correlations among taste preferences, food preferences and frequency of food consumption (n = 53)

<table>
<thead>
<tr>
<th>Food item</th>
<th>Taste preference × food preference</th>
<th>Food preference × food frequency</th>
<th>Taste preference × food frequency</th>
</tr>
</thead>
<tbody>
<tr>
<td>White chocolate</td>
<td>0.87 a</td>
<td>0.50 a</td>
<td>0.47 a</td>
</tr>
<tr>
<td>Milk chocolate</td>
<td>0.53 a</td>
<td>0.50 a</td>
<td>0.22</td>
</tr>
<tr>
<td>Bittersweet chocolate</td>
<td>0.67 a</td>
<td>0.75 a</td>
<td>0.56 a</td>
</tr>
<tr>
<td>Coffee/coffee beverages</td>
<td>0.66 a</td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

*The correlation is significant at the 0.01 level (two-tailed test).*
females, there was no relationship between PROP sensitivity and taste responsiveness to sucrose solutions (Drewnowski et al., 1997a,b). There was no difference between PROP tasters and non-tasters in their sensory responses to NHDC at a concentration of 0.3 mmol/l. Gent and Bartoshuk observed no differences in the sweetness intensity ratings of NHDC at a concentration of 0.32 mmol/l although differences by PROP taster status were observed at lower concentrations (Gent and Bartoshuk, 1983).

Finally, greater perceived bitterness was associated with lower preference ratings. This inverse relationship held when PROP and caffeine solutions were sweetened with NHDC. Given that bitterness and hedonic functions are mirror images of each other, hedonic ratings may provide an alternative measure of the genetic ability to taste PROP (Akella et al., 1997; Drewnowski et al., 1997a,c; Kaminski et al., 2000).

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References


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