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GENETIC TASTE MARKERS AND FOOD PREFERENCES

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ABSTRACT:

Sensitivity to the bitter taste of 6-*n*-propylthiouracil (PROP) is an inherited trait. Although some people find PROP to be extremely bitter, others cannot distinguish PROP solutions from plain water. In a series of studies, greater PROP sensitivity was linked with lower acceptability of other bitter compounds and with lower reported liking for some bitter foods. Women, identified as "super-tasters" of PROP, had lower acceptance scores for grapefruit juice, green tea, Brussels sprouts, and some soy products. Many of these foods contain bitter phytochemicals with reputed cancer-protective activity. These include flavonoids in citrus fruit, polyphenols in green tea and red wine, glucosinolates in cruciferous vegetables, and isoflavones in soy products. Consumer acceptance of these plant-based foods may depend critically on inherited taste factors. This review examines the role of genetic taste markers in determining taste preferences and food choices.

The biology of bitter taste perception is poorly understood. Among bitter-tasting compounds are peptides and amino acids, sulfimides (saccharin), ureas, thioureas, terpenoids, phenols, and polyphenols. The fact that many structurally unrelated compounds give rise to a uniform bitter taste suggests the existence of multiple bitter taste receptors. McBurney (1978) proposed that at least three different bitter taste receptors exist, sensitive to quinine, to urea, and to phenylthiocarbamide (PTC[1]). However, recent studies of a novel family of bitter taste receptors suggest that the number of distinct receptors may be closer to 60 (Adler et al., 2000). The candidate taste receptors (T2Rs) are organized in the genome in clusters and are genetically linked to loci that influence bitter perception in humans and mice.

PTC and 6-*n*-propylthiouracil (PROP) are substances that taste bitter to some people but are tasteless to others (Fox, 1932). Sensitivity to PTC/PROP is an inherited trait, thought to be determined by a dominant gene (T) (Kalmus, 1971). Recent genetic linkage studies in humans have linked the ability to taste PROP with a locus at 5p15 (Reed et al., 1999). Early studies of these two substances used detection thresholds for PTC/PROP solutions to separate tasters from non-tasters (Fischer and Griffin, 1964; Fischer, 1967; Kalmus, 1971). More recent studies, based on both thresholds and the ratio of perceived PROP bitterness to the perceived saltiness of salt solutions, have identified three potential taster categories: non-tasters, medium-tasters, and super-tasters of PROP. Bartoshuk et al. (1994) have speculated that whereas non-tasters may have two recessive alleles (tt); medium-tasters are heterozygotes with one dominant allele (Tt); and super-tasters have two dominant alleles (TT). Consistent with this hypothesis, taster distribution among American women appears to be 25% non-tasters, 50% medium-tasters, and 25% super-tasters (Bartoshuk et al., 1994).

In early sensory studies, PTC/PROP tasters were likely to perceive caffeine and quinine, although not urea, as more bitter (Fischer, 1971; Hall et al., 1975). Bartoshuk (1979) observed that PROP tasters also rated saccharin solutions, at concentrations found in diet soft drinks, as more bitter than did non-tasters. One interpretation of those data was that PTC/PROP tasters might avoid both coffee and saccharin-sweetened beverages (Bartoshuk, 1993). Later reports that PROP tasting was associated with enhanced oral burn of capsaicin, the active ingredient of hot peppers, suggested that PROP tasters might avoid hot and spicy foods (Karrer and Bartoshuk, 1995). PROP tasters were also reported to be more sensitive to the trigeminal irritation by ethanol.

Additional studies suggested that PROP tasters were also more responsive to the sweet taste of sugar solutions (Gent and Bartoshuk, 1983) and tended to dislike intensely sweet foods. However, later studies found no major effect of PROP taster status on sensory response to sucrose solutions (Drewnowski et al., 1997c) or self-reported preferences for sweet foods (Drewnowski et al., 1999). Two studies reported that PROP super-tasters were more sensitive to the oral sensation of fat in unsweetened heavy cream (Duffy et al., 1996) or in a high-fat salad dressing (Tepper and Nurse, 1997). However, other studies found no effect of PROP taster status on the perception of sweetness or creaminess or on the overall acceptance of sweetened dairy products (Drewnowski et al., 1998).

On the other hand, there is agreement that PROP tasters are more responsive to some other bitter tastes and are more likely to dislike bitter foods (Bartoshuk, 1989). Whereas early studies focused on perceived bitterness of urea or potassium benzoate (Hall et al., 1975), more recent studies addressed the perceived bitterness of phytochemicals found in common plant foods (Drewnowski and Rock, 1995). Studies on cancer and disease prevention increasingly suggest that many of the dietary phytochemicals have a role in the prevention of cancer and coronary heart disease (Craig, 1997; Potter, 1997). Increas-

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[1] Abbreviations used are: PTC, phenylthiocarbamide; PROP, 6-*n*-propylthiouracil.

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ing consumption of vegetables and fruit is a major dietary strategy for disease prevention (Steinmetz and Potter, 1996). As a result, genetic taste factors that influence food preferences and food choices might alter dietary exposure to substances known to affect cancer risk. A study of genetic taste markers would thus have implications for chronic disease prevention and public health (Drewnowski and Rock, 1995).

Individual sensitivity to PROP solutions was determined using the detection threshold procedure (Drewnowski et al., 1997a). For this, we used a series of 15 PROP solutions, ranging in concentration from 1.0×10^{-6} mol/liter to 3.2×10^{-3} mol/liter PROP, and incremented in quarter log steps (Bartoshuk, 1979). The highest concentration, solution 15, contained 0.5446 g/liter PROP; the next concentration contained 0.3064 g/liter, and so on (Fischer, 1967; Kalmus, 1971). The four stock solutions (solutions 15, 14, 13, and 12) were prepared by dissolving PROP into deionized water. The less concentrated solutions (solutions 11–1) were prepared by diluting the stock solutions. Each subject was first presented with the least concentrated solution of PROP (solution 1), and then with increasingly higher solutions, until she reported detecting a taste distinct from that of water. Next, the subject was presented with two identical cups; one containing the detected concentration of PROP and the other containing deionized water. The water was at the same temperature and was stored in the same location as the PROP solution. The subject was asked to judge which of the two samples had the bitter taste (Fischer and Griffin, 1964; Bartoshuk et al., 1994; Drewnowski et al., 1997a,b). Subjects rinsed thoroughly with deionized water after tasting each PROP stimulus. Wrong answers led to the presentation of more concentrated PROP solutions, again paired with deionized water, whereas correct answers led to a second presentation of the same solution. Two consecutive correct answers at the same concentration led to the presentation of a less concentrated PROP solution. Reversal points were defined as the concentration at which a series of correct responses turned to an incorrect response or vice versa (Drewnowski et al., 1997a).

Subjects also tasted and rated five more concentrated solutions of PROP at concentrations of 0.032, 0.1, 0.32, 1.0, and 3.2 mmol/liter (solutions 7, 9, 11, 13, and 15). The five salt solutions contained 0.01, 0.032, 0.1, 0.32, and 1.0 mol/liter NaCl in deionized water. Subjects rated the bitterness of each stimulus using 9-point category scales, where 1 = "not at all bitter" and 9 = "extremely bitter". The acceptability of each stimulus was rated along the standard 9-point hedonic preference scale (Peryam and Pilgrim, 1957). This fully anchored 9-point category scale ranged from 1 = "dislike extremely" to 9 = "like extremely", with a neutral point at 5 ("neither like nor dislike"). Subjects tasted the solutions using whole mouth tasting and the standard sip-and-spit technique (Drewnowski et al., 1997a,b), rinsing with deionized water between samples. Successive tests were separated by a minimum of 45 s.

Consistent with previous studies (Kalmus, 1971), the distribution of PROP detection thresholds was bimodal. As shown in Fig. 1, tasters were defined as having thresholds of less than 1.0×10^{-4} mol/liter (equivalent to solution 9) and non-tasters as having thresholds in excess of 2.0×10^{-4} mol/liter (equivalent to solution 10).

Tasters were separated into medium-tasters and super-tasters on the basis of PROP detection thresholds and the ratio of PROP bitterness ratings to the perceived saltiness of NaCl solutions. Unlike Bartoshuk (1993), we established the bitterness to saltiness ratio using all five PROP and salt solutions. The mean ratio was $(p_1/n_1 + p_2/n_2 + p_3/n_3 + p_4/n_4 + p_5/n_5)/5$, where p_1 was PROP solution 1 and n_1 was NaCl solution 1, and so on. To qualify as super-tasters, subjects had to have PROP detection thresholds below 3.2×10^{-5} mol/liter (solution 7)

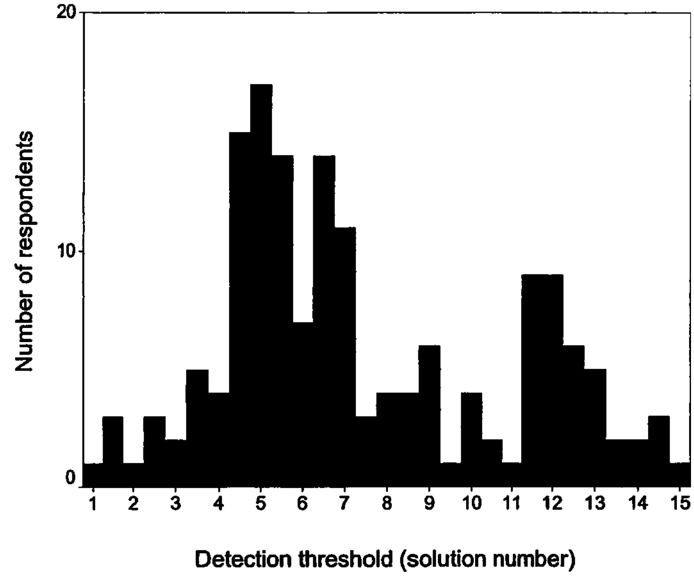

FIG. 1. *Distribution of taste thresholds for tasters and non-tasters of PROP.*

and mean PROP/NaCl ratios greater than 1.6. The final sample included 39 non-tasters, 49 medium-tasters, and 35 super-tasters of PROP (Drewnowski et al., 1997b).

As shown in Fig. 2, mean bitterness intensity and mean hedonic ratings, averaged over the five PROP solutions, were strongly and inversely linked ($r = -0.83$; $P < 0.01$). Tasters and super-tasters disliked the bitter taste of PROP more than did non-tasters (Drewnowski et al., 1997a,b). The slope of the inverse relationship between perceived bitterness and hedonic ratings was the same for non-tasters, medium-tasters, and super-tasters of PROP, suggesting that perceived bitterness was the key determinant of dislike. Bitterness intensity profiles for PROP, plotted separately for non-tasters, medium-tasters, and super-tasters, showed that intensity and hedonic ratings were mirror images of each other. Increased perceived bitterness was invariably associated with greater dislike of bitter PROP solutions. In contrast, the three PROP taster groups did not differ in their responses to salt solutions. Only the main effect of NaCl concentration was significant ($P < 0.01$), and no effects of PROP taster status were observed.

PROP Tasting and Naringin

We then examined the impact of PROP taster status on the perception and preferences for naringin, a bioactive flavonoid that is the principal bitter component of grapefruit juice (Drewnowski et al., 1997b). Naringin does not occur in orange juice. Although tasters and super-tasters of PROP rated five naringin solutions in 4% sucrose as more bitter than did non-tasters, this effect failed to reach significance. An analysis of hedonic ratings for naringin solutions showed a significant interaction between taster status and naringin concentration. PROP super-tasters gave significantly lower hedonic ratings to naringin solutions than did the pooled group of regular tasters and non-tasters. Increased bitterness of naringin solutions was associated with lower acceptability ratings. As expected, increased perceived bitterness was associated with an increased dislike of naringin solutions ($r = -0.49$; $P < 0.01$).

In parallel with taste data, self-reported preferences for grapefruit and grapefruit juice also showed a bimodal distribution. Some respondents liked grapefruit juice whereas others clearly did not. A cross-tab analysis of mean preferences by taster/non-taster status revealed that 19 of 84 PROP tasters had acceptance scores below 3 on a 9-point

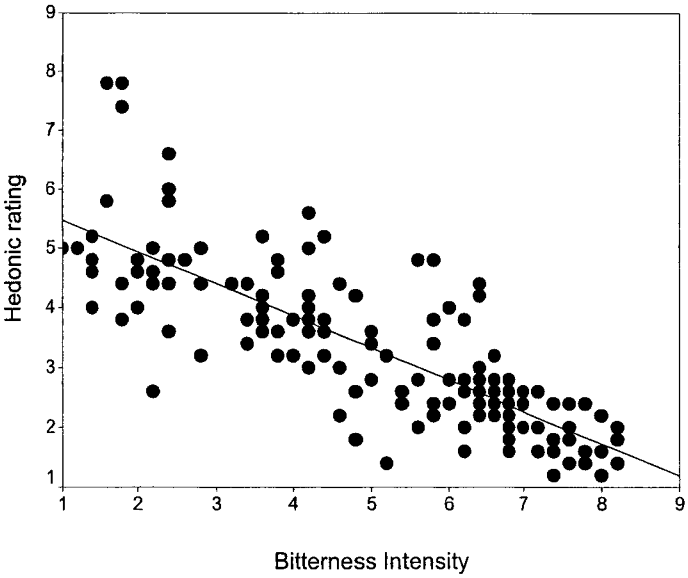

FIG. 2. *Inverse relationship between perceived bitterness and rated acceptability of PROP solutions.*

Both intensity and hedonic ratings have been averaged over five solutions of PROP.

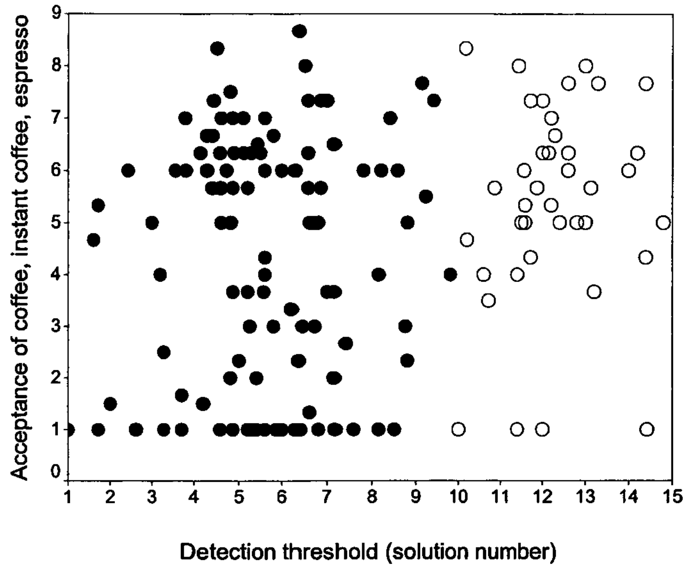

FIG. 3. *Relationship between PROP detection thresholds and mean acceptance ratings for coffee, instant coffee, and espresso.*

●, tasters; ○, non-tasters.

scale. In contrast, only a few PROP non-tasters (3/37) disliked grapefruit or grapefruit juice to that degree ($\chi^2 < 0.05$). The distribution of preferences for oranges, orange juice, and apples was unimodal, and no effect of PROP taster status was observed.

In another study (Akella et al., 1998), genetic sensitivity to PROP was linked to lower acceptance scores for increasing concentrations of bitter Japanese green tea. These data suggest that PROP-sensitive individuals may also be sensitive to bitter polyphenols, catechin and epicatechin. In addition, PROP tasters gave lower self-reported acceptability ratings to soy foods, including miso and tofu (Akella et al., 1998). Soy products, especially fermented ones, contain bitter isoflavones, genistein, and dadzein (Rousseff, 1990).

Most recently we have found (Drewnowski et al., 1999) that PROP tasting was associated with a lower acceptability rating for coffee beverages, namely coffee, instant coffee, and espresso. As shown in Fig. 3, female tasters were more likely to give lower hedonic ratings to coffee beverages than were non-tasters ($P < 0.01$). Furthermore, respondents who expressed a decided dislike for coffee (ratings <3 on a 9-point scale) were, with only a few exceptions, tasters of PROP. Although many factors, including taste, may be responsible for food preferences, taste is often the key reason for food rejection (Drewnowski et al., 1999).

Bitter Taste and Chemoprevention

Many phytochemicals, including phenols, flavonoids, isoflavones, and glucosinolates, have been shown to have antioxidant and anticarcinogenic effects and a wide spectrum of tumor-blocking properties (Craig, 1997; Potter, 1997). Most of these phytochemicals taste bitter. In fact, phenolic compounds are directly responsible for the bitterness and astringency of many foods and beverages, from vegetables, fruits, and legumes to tea, cocoa, coffee, and wine (Rousseff, 1990). Humans, conditioned through evolution to be wary of bitter plant-derived alkaloids and other toxins, find excessive bitterness objectionable. Bitterness is the most commonly cited reason for disliking a particular food (Rousseff, 1990), and has been shown to lead to food rejection (Rozin and Vollmecke, 1986; Drewnowski et al.,1997a,b).

How PTC/PROP status determines food acceptance and rejection is unclear. In early studies, based on food preference checklists, PTC/PROP tasters tended to dislike cruciferous and green vegetables, rhubarb, sauerkraut, beer, coffee, and various sharp cheeses (Boyd, 1950; Fischer et al.,1961; Fischer and Griffin, 1964; Glanville and Kaplan, 1965; Forrai and Bankovi, 1984). However, other studies have failed to link PTC or PROP sensitivity with a consistent pattern of food dislikes (Mattes and Labov, 1989). In particular, studies on the consumption of cruciferous vegetables by elderly women showed only modest effects of PROP sensitivity on food choices (Niewind et al., 1988; Jerzsa-Latta et al., 1990). Although women tasters appeared more sensitive to the bitter taste of raw cruciferous vegetables, there was no evidence for a pattern of food rejection. Vegetable consumption was low, in tasters and non-tasters alike (Niewind et al., 1988).

Our studies (Drewnowski et al., 1999) confirmed earlier reports that genetically mediated sensitivity to the bitter taste of PROP was associated with lowered acceptability of Brussels sprouts, cabbage, spinach, and coffee. In turn, self-reported food preferences were associated with dietary outcome variables. Reduced acceptability of vegetables and fruit was associated with lower intakes of carbohydrate, fiber and β-carotene, as estimated from 3-day food records. Taste factors and food preferences influence eating habits and may have an impact on the selection of healthful diets.

Increasing fruit and vegetable consumption is the key dietary strategy for cancer prevention (Steinmetz and Potter, 1996; Potter, 1997). Diets high in plant foods, notably cruciferous and green vegetables, allium vegetables, soy products, tomatoes, and citrus fruit, appear to confer a degree of protection against cancer (Steinmetz and Potter, 1996). Given that such diets are the cornerstone of current public health strategies for cancer prevention (Havas et al., 1994; Potter, 1997), the role of genetic taste markers in food acceptance or rejection needs to be better understood. If PROP taster status does predict the consumption of bitter vegetables, then inherited taste factors might pose a barrier to the adoption of a plant-based diet. We therefore examined self-reported food preferences as a function of PROP taster status in a clinical sample of 326 female breast cancer patients and cancer-free controls. All patients were tested before (or shortly after) diagnosis and before any surgical, chemotherapy, or nutritional intervention (Drewnowski et al., 2000).

All respondents completed a 171-item food preference checklist, also based on a 9-point category scale (Peryam and Pilgrim, 1957). The list included grapefruit, grapefruit juice, lemons, oranges, and orange juice, as well as a variety of other vegetables and fruits. Respondents were asked to indicate how much they liked or disliked each food using the 9-point hedonic preference scale, following procedures used in food preference studies conducted with U.S. Army personnel (Meiselman et al., 1974). There were no differences in taste responsiveness between breast cancer patients and controls. On the other hand, super-tasters and medium-tasters showed lower mean acceptance scores for cruciferous vegetables than did non-tasters. Reported preferences for sweet fruit were not affected by PROP taster status (Drewnowski et al., 2000).

These data suggest that genetic responsiveness to PROP may alter food choices and affect eating habits. Women who are tasters of PROP may be less likely to comply with dietary strategies that emphasize increased consumption of bitter-tasting cruciferous vegetables and salad greens. Alternatively, PROP-sensitive women may seek to mask bitter taste by the addition of fat, sugar, or salt (Drewnowski et al., 2000).

Summary

PROP tasting, a heritable trait, was associated with lower acceptance of cruciferous and some raw vegetables. In addition, PROP tasting was linked to lower acceptance ratings for naringin solutions, Japanese green tea, and soybean tofu. Women who expressed a dislike for these foods were more likely to be medium- or super-tasters as opposed to non-tasters of PROP. These data support earlier reports that PTC/PROP tasters tended to dislike bitter- and sharp-tasting foods.

Many of the biologically active phytochemicals found in vegetables and fruits have bitter tastes (Rousseff, 1990; Drewnowski and Rock, 1995). Isothiocyanates, indoles, flavonoids, carotenoids, and phenolic acids are among the bitter phytochemicals that have been linked with cancer prevention in both animal and clinical studies. Naringin, a bitter flavonoid found in grapefruit juice, acts as an antioxidant and inhibits tumor growth (Drewnowski et al., 1997b). Bitter isoflavones in soybeans inhibit the growth of hormone-dependent and hormone-independent cancer cells, in vitro (Akella et al., 1998). Many researchers believe that diets high in vegetables and fruits confer a degree of protection against cancer, including breast cancer (Craig, 1997). However, bitter-tasting foods are frequently disliked, and bitter taste is one reason for low acceptance of cruciferous and leafy green vegetables (Drewnowski et al., 1999). Genetic taste markers may therefore affect taste preferences and the selection of healthful diets.

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