The impact of individual variations in taste sensitivity on coffee perceptions and preferences

Camilla Masi a,⁎, Caterina Dinnella a, Erminio Monteleone a, John Prescott b

a GESAAF, University of Florence, Via Donizetti, 6 50144 Firenze, Italy
b TasteMatters Research & Consulting, Sydney, Australia

HIGHLIGHTS
• Physiological measures underlying taste perception were investigated
• The impact of physiological indices on coffee liking and consumption was studied
• Fungiform papillae density affects both taste perception and coffee preference
• PROP taste status affects taste perception both in coffee and in standard solutions
• Sugar use depends both on fungiform papillae density and PROP taste status

ABSTRACT
Despite a few relationships between fungiform papillae (FP) density and 6-n-propylthiouracil (PROP) taster status have been reported for sensory qualities within foods, the impact on preferences remains relatively unclear. The present study investigated responses of FP number and PROP taster groups to different bitter compounds and how these affect coffee perception, consumption and liking. Subjects (Ss) with higher FP numbers (HFP) gave higher liking ratings to coffee samples than those with lower FP numbers (LFP), but only for sweetened coffee. Moreover, HFP Ss added more sugar to the samples than LFP Ss. Significant differences between FP groups were also found for the sourness of the coffee samples, but not for bitterness and astringency. However, HFP Ss rated bitter taste stimuli as stronger than did LFP Ss. While coffee liking was unrelated to PROP status, PROP non-tasters (NTs) added more sugar to the coffee samples than did super-tasters (STs). In addition, STs rated sourness, bitterness and astringency as stronger than NTs, both in coffee and standard solutions. These results confirm that FP density and PROP status play a significant role in taste sensitivity for bitter compounds in general and also demonstrate that sugar use is partly a function of fundamental individual differences in physiology.

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1. Introduction

Individual sensitivity to taste and other oral sensations shows considerable variability between individuals, and there is increasing evidence these variations are a significant influence on food preference and consumption [1–6]. Overall taste sensitivity is reflected in two commonly studied physiological measures. The first of these, the density of lingual fungiform papillae (FP) is positively associated with taste intensity [7] because the tongue’s taste buds are contained primarily within the FP. Thus, those who have higher numbers of FP are more sensitive to tastes [8–12].

The second measure, the intensity of the compounds phenylthiocarbamide (PTC) and 6-n-propylthiouracil (PROP), is a genetically mediated index of individual variation in oral sensations [13–16]. PROP responsiveness is typically expressed categorically as PROP taster status (PTS), which consists of three groups: PROP super tasters (STs), PROP medium tasters (MTs), and PROP non-tasters (NTs) [17]. PROP responsiveness has long been used as general orosensory responsiveness to a variety of stimuli (e.g., [13,18]). PROP tasters rate the intensity of other bitter compounds, including caffeine, quinine, and urea [19–22], as more intense than do NTs, sucrose as sweeter [23,24], sodium chloride as more salty [13], and citric acid as more sour [25]. PTS is also associated with responsiveness to other orosensory stimuli apart from tastes: STs perceive irritation from capsaicin [26,27], cinnamaldehyde [27], ethanol [27–29], and astringency [30–32] with greater intensity than NTs.

PROP intensity and the density of FP are often found to be positively correlated. The most plausible explanation for this is that, while the ability to taste PTC [33] or PROP [29,34] results from the presence of a functional bitterness receptor (TAS2R38), the intensity of all tastes results...
from the spatial summation of number of taste buds stimulated, itself a function of FP density.

Bitterness per se is instinctively rejected [35–37] and this is thought to have been crucial to survival via its impact on food choice, specifically the avoidance of bitter toxins [38].

However, sensitivity to bitterness in foods and beverages varies widely among individuals, and some foods are consumed despite the presence of potentially bitter compounds. Both FP density and PROP intensity appear to clearly reflect this variation [39]. A range of bitter foods, including Brussels sprouts, cabbage, broccoli and spinach [40–42], caffeinated coffee [40] and grapefruit juice [43,44], have been reported as more bitter and/or less preferred by PROP tasters than by NTs. Differences between PROP/PTC tasters and NTs have also been found with foods that are sour such as lemon juices, vinegar, and sauerkraut [43]. Some studies have reported relationships between FP density, PROP status and food consumption/preference: Ss who rated the least bitterness intensity of PROP or had lowest numbers of FP reported less burn and disliking of ethanol as well as more frequent consumption of sweeteners. The aim of this study was to investigate physiological measures underlying taste perception and how these influence perception, consumption of, and liking for coffee.

2. Methods

2.1. Product selection

2.1.1. Subjects

As part of a pilot experiment to select suitable coffee samples for use in the main study, eight subjects (Ss), six females and two males, aged from 20 to 38 years, and regular coffee consumers, were recruited in the Florence area. The Ss had no history of disorders in oral perception. They were paid for their participation in the study. Written informed consent was obtained from each subject after the description of the experiment.

2.1.2. Samples

Seven espresso coffees varying in roasting degree (light, medium, dark) and caffeine content (<0.05–2%) were evaluated (Fig. 1). Coffee samples (25 g) were prepared with an espresso machine using coffee capsules.

2.1.3. Descriptive analysis (DA)

Ss participated in five sessions for training and term generation. Specifically, they were trained to recognize and rate the perceived intensity of the following qualities: sweetness, sourness, bitterness, and astringency using the following standard solutions - sucrose: 8.00, 12.00, 18.00 g/l; citric acid: 0.25, 0.38, 0.50 g/l; quinine monohydrochloride dihydrate 0.025, 0.037, 0.050 g/l; aluminium potassium sulphate: 0.3, 0.6, 0.9 g/l. During training sessions, Ss were asked to rate the intensity of the standard solutions on a 9-point category scale (1 = “extremely weak”; 9 = “extremely strong”).

An evaluation sheet consisting of 22 ratings was defined. In each of the five sessions, four or five samples were evaluated. Each sample was evaluated 3 times. Samples (25 g) were presented in a closed 80 cc plastic cup identified by a three digit code. Sample presentation was balanced across subjects within each session. For each sample, assessors were asked to rate the intensity of odor descriptors perceived by nose (aroma) first. Then they were asked to wait 3 minutes, take a sip of the sample and rate the intensity of odors perceived retro-nasally, taste and mouthfeel attributes. After each sample, subjects were asked to rate the intensity of the taste of saccharin (sweet liker status), in together with the intrinsic pleasantness of the taste of saccharin (sweetness) subjectively.

Correlation loading plot from Principal Component Analysis on panel averages of each significant attribute describing sample sensory properties. For each sample roasting degree of coffee beans and caffeine content (%) of coffee powder are reported in the table.

<table>
<thead>
<tr>
<th>Sample</th>
<th>Roasting degree</th>
<th>Caffeine (%)</th>
</tr>
</thead>
<tbody>
<tr>
<td>A</td>
<td>Light</td>
<td>0.8–0.9</td>
</tr>
<tr>
<td>B</td>
<td>Dark</td>
<td>0.8–0.9</td>
</tr>
<tr>
<td>C</td>
<td>Medium</td>
<td>1.50</td>
</tr>
<tr>
<td>D</td>
<td>Dark</td>
<td>1.50</td>
</tr>
<tr>
<td>E</td>
<td>Medium</td>
<td>&lt;0.05</td>
</tr>
<tr>
<td>F</td>
<td>Medium</td>
<td>0.8–0.9</td>
</tr>
<tr>
<td>G</td>
<td>Dark</td>
<td>about 2</td>
</tr>
</tbody>
</table>

Fig. 1. Correlation loading plot from Principal Component Analysis on panel averages of each significant attribute describing sample sensory properties. For each sample roasting degree of coffee beans and caffeine content (%) of coffee powder are reported in the table.
rinsed their mouths with distilled water for 50 sec, had some plain crackers for 50 sec and finally rinsed their mouths with water for a further 50 sec. Ss took a 15 min break every two samples. In the adopted experimental conditions aroma evaluation was performed at 65–67 °C and the in-mouth evaluation at 55–57 °C. Evaluations were performed in individual booths under red lights. Data were collected with the software Fizz (ver.2.47.B, Biosystemes, Couteron, France).

Intensity ratings from coffee samples were independently analyzed by a two-way ANOVA mixed model (sample as fixed and assessors as random factors), followed by a Fisher’s LSD post hoc test (significant for p ≤ 0.05). Principal Component Analysis (PCA) was computed on panel averages of each significant attribute arising from the ANOVA models. Samples were included as dummy variables (down-weighted in the data matrix) to improve the visual interpretation [52]. The full cross validation was computed to validate the interpretation of the first two components.

Results of the PCA computed on descriptive data are summarized in the correlation loading plot reported in Fig. 1. The first two significant dimensions of the perceptual map accounted for 93% of the variation (PC1: 76% and PC2: 17%). PC1 was positively associated with flavor descriptors “coffee,” “overall intensity,” “roasted,” “bitter,” “brunt” and mouthfeel descriptor “body”, while a negative correlation was found for “metallic”, “barley coffee” and “sour” flavor descriptors. Samples were mainly discriminated along the first component according to roasting degree. PC2 contributed to separate product E from other coffees. Coffee sensory properties are affected by several factors: plant varieties, growing region/conditions, processing and brewing methods [53]. Roasting degree and time/temperature combinations determine the formations of compounds responsible for the coffee sensory profile [54,55].

The relative positions of samples on the perceptual map resulting from descriptive data were used for the selection of samples to be tested for consumer test. Samples A, B, C, D, E, G spanned the relevant variability of the sensory attributes within the whole sample set according to different caffeine content and roasting degree.

2.2. Study of coffee consumers

2.2.1. Subjects

One hundred and twenty Ss (51 males; 69 females; aged 20–60 years, regular coffee consumers), were recruited in the Florence area to participate in 3 evaluation sessions in 3 consecutive days. Data on mode of coffee consumption (black; with sugar; with milk; 1 “never”, 2 “occasionally”, 3 “regularly”) and frequency (1 “less than once a day”, 2 “once a day”, 3 “twice or three times a day”, 4 “four or five times a day”, 5 “more than five times a day”) were collected. The Ss had no history of disorders in oral perception. They were paid for their participation in the study. Written informed consent was obtained from each subject after the description of the experiment.

2.2.2. Coffee samples

Six espresso coffees (labeled A, B, C, D, E, G) were evaluated.

2.2.3. Taste stimuli

Psychophysical curves were constructed for caffeine and quinine-HCl over 6 concentrations (caffeine: 0, 3, 6, 12, 24, 48 mM; quinine-HCl: 0, 0.05, 0.10, 0.15, 0.20, 0.25 mM). A single solution of PROP (3.2 mM) was rated using the general Labeled Magnitude Scale (gLMS) [56] to determine PROP taster classification [57,58]. All solutions were prepared with deionized water and were stored in glass bottles and were brought to room temperature prior to testing.

2.2.4. Procedure

2.2.4.1. First session: liking for coffee samples.

Ss were presented with each sample (25 g) in a closed 80 cc plastic cup along with 10 g of sugar (about three coffee spoons) in a plastic cup both identified with the same random three digit code. Samples were presented one by one and the presentation order was balanced across Ss. For each sample, Ss were asked to smell and rate their liking for the aroma first. Then they were asked to take a sip and rate their liking for the flavor (flavor1). Finally they were asked to freely add sugar, if they thought it was necessary independently of their habit, take a sip and rate again their liking for the flavor (flavor2). Hedonic ratings were collected using a 9-point hedonic scale [59], from 1 (“dislike extremely”) to 9 (“like extremely”) with a neutral point at 5 (“neither like nor dislike”). The amount of sugar used for each sample by each S was measured by weighting the sugar cup after each evaluated sample.

After each sample, Ss rinsed their mouths with distilled water for 50 s, had some plain crackers for 50 s, and finally rinsed their mouths with water for a further 50 s. Ss took a 10 min break after every 2 samples. In the adopted experimental conditions, coffee temperature was 65 to 67 °C for aroma evaluation and 55 to 57 °C for in-mouth evaluation. Evaluations were performed in individual booths under white lights. Data were collected with the software Fizz (ver.2.47.B, Biosystemes, Couteron, France).

2.2.4.2. Second session: sourness, bitterness and astringency in coffee samples.

Ss were trained to recognize the following qualities and the respective intensities: sourness, bitterness, and astringency using the following standard solutions - citric acid: 0.25, 0.38, 0.50 g/l; quinine monohydrochloride dihydrate 0.025, 0.037, 0.050 g/l; aluminium potassium sulphate: 0.3, 0.6, 0.5 g/l. In particular, Ss were presented with 9 samples identified with the name of the taste/sensation (sourness, bitterness, astringency) and the respective intensity (weak, moderate, strong). Ss were instructed to hold the sample in their mouth for 10 s, then expectorate, wait 20 s and memorize the perceived taste/sensation and also its intensity. Ss tasted first sour solutions, then bitter solutions and last astringency solutions in increasing intensity order. After each sample, Ss rinsed their mouths with distilled water for 90 s. Ss took a 10 min break after every taste/sensation.

30 min after training, Ss were presented with the six unsweetened coffee samples (8 ml) in a closed 80cc plastic cup identified with a random three digit code. Samples were presented one by one and the presentation order was balanced across subjects.

Ss were instructed to hold the sample in their mouth for 10 s, then expectorate, wait 20 s and evaluate the intensity of sourness, bitterness and astringency using the Labeled Magnitude Scale (LMS) [60]. The evaluation order of attributes was balanced across Ss. After each sample, Ss rinsed their mouths with distilled water for 50 s and some plain crackers for 50 s and finally rinsed their mouths with water for a further 50 s. They took a 10 min break after every 2 samples. The evaluation was performed at 55 to 57 °C. Evaluations were performed in individual booths under white lights. Data were collected with the software Fizz (ver.2.47.B, Biosystemes, Couteron, France).

2.2.4.3. Third session: bitterness of caffeine, quinine and PROP solutions and measure of fungiform papillae number.

Caffeine, quinine-HCl and PROP solutions were presented in 3 different blocks and the evaluation order of the blocks was balanced across Ss. Ss took a 30 min break after each block. Ss were presented with each sample (10 ml) in a 80cc plastic cup identified with a random three digit code. The presentation order of the samples in each block was balanced across Ss. Ss were instructed to hold the sample in their mouth for 10 s, then expectorate, wait 20 s and evaluate the intensity of bitterness, using the gLMS.

After each sample, Ss rinsed their mouths with distilled water for 90 s. Ss took a 10 min break after every 2 samples. Evaluations of caffeine and quinine-HCl were performed once, of PROP twice. Evaluations were performed in individual booths under white lights. Data were
collected with the software Fizz (ver.2.47.B, Biosystemes, Couteron, France).

The anterior portion of the dorsal surface of the tongue was swabbed with household blue food coloring (F.lli Rebecchi), using a cotton-tipped applicator. This made the FP easily visible as red structures against the blue background of the stained tongue [7]. Images of the tongue were recorded using a digital microscope (MicroCapture, version 2.0 for 20x-400x). For each participant, the clearest image was selected, and the number of FP was counted in two 0.6 cm diameter circles, one on right side and one on left side of tongue, 0.5 cm from the tip and 0.5 cm from the tongue midline. The number of FP was counted by two researchers independently, blind to the performance of participants in the sensory evaluation tests. The average of these values was used for each S.

2.3. Data analysis

Liking ratings expressed for aroma, flavor1 and flavor2 were independently submitted to a two-way ANOVA model (assessors and sample as factors) with Fisher's LSD post hoc test (significant for $p \leq 0.05$).

Liking ratings expressed for flavor1 and flavor2 were analyzed by a two-way ANOVA model (sample — 6 levels — and condition — 2 levels: with or without sugar added— as factors), with Fisher LSD post hoc test (significant for $p \leq 0.05$).

Ss were divided into groups based on median value of FP distribution (12.12; range 4 - 22): Low FP (LFP) and High FP (HFP). PROP taster status was based on the average rating of the two replicates, and groupings were based on percentile distribution: PROP nontasters (NTs: 30 Ss) $\leq$21.75; PROP medium tasters (MTs: 60 Ss), 22–65; and PROP super-tasters (STs: 30 Ss) $\geq$65.125. The relationship between FP number and PROP status was estimated by Pearson's correlation coefficient.

A two-way ANOVA (group and sample as factors), with Fisher's LSD test ($p \leq 0.05$) were used to independently test both the effect of FP number and PROP status on liking and intensity ratings in both coffee samples and standard solutions. The associations of clusters with gender, coffee consumption frequency and consumption of sweetened/unsweetened coffee (categorical variables) were estimated by a homogeneity chi-square test.

3. Results

3.2.1. General overview

A significant sample effect on liking for aroma was found ($F_{5,719} = 11.22, p \leq 0.0001$). Mean liking scores for flavor resulted significantly affected by the conditions adopted for data acquisition (w/o or with sugar) ($F_{1,1439} = 64.30, p \leq 0.0001$). In particular, mean liking score for flavor1 resulted significantly lower than those for flavor2 (4.68 and 5.49, respectively). A significant sample effect on liking was found ($F_{1,1439} = 37.74, p \leq 0.0001$). No significant effect sample*condition interaction was found.

A significant sample effect was found on liking for both flavor1 ($F_{5,719} = 22.36, p \leq 0.0001$) and flavor2 ($F_{5,719} = 33.18, p \leq 0.0001$). However, when sugar was added to the samples (flavor2), different samples were rated as more different than when coffees were evaluated without sugar (flavor1), and in particular a higher difference between the liking rates of the most preferred coffee and of the least one was found. So, flavor2 better discriminated between samples ($F_{719,113} = 1.15, p = 0.035$).

Significant differences between samples were found for perceived intensity of sourness, bitterness and astringency ($F_{5,719} = 10.13, p \leq 0.0001$; $F_{5,719} = 11.75, p \leq 0.0001$; $F_{5,719} = 2.40, p = 0.036$; respectively). Samples A and C were the most intense for sourness; bitterness significantly differed among samples based on roasting degree; samples C and B were the most and the least astringent respectively.

Psychophysical curves for caffeine and quinine-HCl are shown in Fig. 2. Bitterness significantly increased with concentration ($F_{5,719} = 348.07, p \leq 0.0001$; $F_{5,719} = 279.31, p \leq 0.0001$, respectively). No significant differences in ratings of bitterness between caffeine and quinine-HCl were found, excepted for the most concentrated solutions ($F_{1,1439} = 242.50, p \leq 0.0001$).

3.2.2. Fungiform papillae number

The distribution of FP papillae is shown in Fig. 3. No significant differences were found for FP counts conducted by the two different researchers ($z_{138.1.97} = 1.41, p = 0.160$), or on the two tongue sides ($z_{238.1.97} = 0.14, p = 0.888$). No significant difference was found between males and females for FP number ($t_{118;1.98} = -0.86, p = 0.391$). No significant difference between the FP groups in terms of either gender ($x^2 = 0.85$, df = 1, $p = 0.356$) or age ($t_{118;1.98} = 0.27, p = 0.784$) was found. No significant difference between the FP groups in terms of coffee consumption frequency was found ($x^2 = 0.04$, df = 1, $p = 0.838$).

3.2.2.1. Effect of FP number on liking. The effect of FP number on coffee preferences is shown in Fig. 4. No significant effect of FP group on liking for aroma and flavor1 were found. HFP Ss gave higher liking ratings than LFP Ss overall when asked to add sugar to taste ($F_{1,708} = 6.79, p = 0.009$). Moreover, HFP Ss added more sugar to the samples than LFP Ss (2.04 g vs 1.56 g, $F_{1,708} = 9.26, p = 0.002$). Consistent with this, greater sugar use by HFP Ss was also evident in the
consumption data (52% of HFP Ss vs 33% of LFP Ss who consume regularly coffee with sugar; $\chi^2 = 4.13, \text{df} = 1, p = 0.042$). No significant group*sample interaction was found.

3.2.2. Effect of FP number on taste perception. HFP Ss rated the bitterness of both caffeine and quinine solutions as stronger than did LFP Ss ($F_{1,708} = 4.21, p = 0.041; F_{1,708} = 10.42, p = 0.001$, respectively) (Fig. 5a and b). No significant effect of group*sample interaction was found. The effect of FP number on taste perception in coffee is shown in Fig. 6. HFP Ss rated coffee sourness as stronger than LFP Ss ($F_{1,708} = 3.83, p = 0.050$). No significant differences between FP groups were found for coffee bitterness or astringency. No significant group*sample interaction was found.

3.2.3. PROP status

The distribution of PROP intensity ratings is shown in Fig. 7 and is similar to those in other published studies of PROP sensitivity. No significant difference between the two replicates was found ($t_{119} = 0.07, p = 0.942$). No significant difference was found between males and females for PROP status ($t_{118} = -0.50, p = 0.613$). No significant difference between the PROP groups in terms of either gender ($\chi^2 = 0.85, \text{df} = 2, p = 0.653$) or age ($F_{2,117} = 0.23, p = 0.796$) was found. No significant difference between the PROP groups in terms of coffee consumption frequency was found ($\chi^2 = 1.38, \text{df} = 2, p = 0.502$).

3.2.3.1. Effect of PROP status on liking. No significant effect of PROP status on coffee liking was found (Fig. 8). While coffee liking was unrelated to PROP status, NTs added more sugar to the coffee than did MTs and STs ($F_{2,702} = 8.34, p \leq 0.0001$). However, no significantly different habits of sugar use were reported in the consumption data ($\chi^2 = 0.58, \text{df} = 2, p = 0.748$). No significant effect of group*sample interaction was found.

3.2.3.2. Effect of PROP status on taste perception. STs rated the bitterness of both caffeine and quinine solutions as stronger than did PROP NTs and MTs ($F_{2,702} = 16.33, p \leq 0.0001; F_{2,702} = 15.83, p \leq 0.0001$, respectively) (Fig. 9a and b). No significant differences between NTs and MTs were found. No significant group*sample interaction was found.

The effect of PROP status on taste perception in coffee is shown in Fig. 10. PROP STs rated coffee sourness ($F_{2,702} = 6.73$), bitterness ($F_{2,702} = 16.68, p \leq 0.0001$) and astringency ($F_{2,702} = 15.09, p \leq 0.0001$) as stronger than NTs and MTs. Significant difference between NTs and MTs was found only on astringency perceived intensity. No significant effect of group*sample interaction was found.

3.2.4. Relationship between FP number and PROP status

No significant relationship was found between FP number and PROP intensity ($r = 0.05, p = 0.592$). No significant effect of FP group

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**Fig. 4.** Effect of FP cluster (LFP and HFP) on liking for aroma, flavor1 and flavor2: mean ratings and standard error values. * indicates a significant difference ($p \leq 0.05$).

**Fig. 5.** Mean bitterness ratings for each FP group (LFP and HFP) as a function of variations in caffeine (A) and quinine-HCl (B) concentration.

**Fig. 6.** Effect of FP cluster (LFP and HFP) on sourness, bitterness and astringency perception in coffee: mean ratings and standard error values. * indicates a significant difference ($p \leq 0.05$).
on the bitterness rating of PROP solution was found ($t_{118} = 0.88$, $p = 0.382$) and no significant differences in PROP groups for FP number were found ($F_{2,117} = 0.53$, $p = 0.382$) and no significant differences in PROP groups for FP number were found ($F_{2,117} = 0.53$, $p = 0.590$).

### 4. Discussion

A number of recent studies have examined the influence of underlying physiology or genetics on food acceptability, preferences or intake [36,41,42,45,57,61]. However, the question of how these underlying influences might shape food behaviors has received little attention. Given that culture is probably the most pervasive influence on food choices, the impact of variations in underlying physiology/genetics will take place within a cultural context. For example, while there are large variations in the perception of hot (spicy) food ingredients [26], in countries such as Mexico or Korea, the consumption of chili is universal and frequent. However, it might be expected that individuals tailor the degree of spiciness in their foods to a comfortable level. The bite of alcohol is similarly influenced by variations in physiology [45] and it is commonplace in some cultures for alcohol to be diluted when it is first consumed.

The present data on coffee appear to show a similar pattern. The consumption of espresso coffee is near ubiquitous in Italy and it represents a part of the common food culture for Italians. Against this background, and in common with other coffee users worldwide, some Italians modify the sensory characteristics of their coffee using sweeteners or sometimes milk. In this study, 68.33% of consumers declared that they usually sweeten coffee and 82.50% of subjects added sugar after the first tasting. The general disliking for unsweetened samples resulted in a minor significant sample effect. Thus, tasting without sugar added does not seem appropriate for evaluation of liking of coffee samples.

The most significant finding of the current study is the fact that a food-related behavior – sugar use – is influenced by both sensitivity to the bitter compound PROP as well as the density of FP. Subjects with higher FP numbers routinely added more sugar to their coffee, added more sugar when asked to do so for the study samples, and gave higher liking ratings to the coffees than low FP Ss for the sweetened coffee samples. In the context of the finding that HFP Ss rated coffee sourness as stronger than did LFP Ss, this suggests that their addition of sweetness was an attempt to modify an undesirable sensory characteristic that they perceived in the coffees. It is quite plausible that this difference in sugar use underlies the fact that the HFP shows higher liking for the coffees. Sweetness is innately liked, and the addition of sweetness to a wide variety of foods and drinks increases their immediate acceptability [62].

In an apparently paradoxical finding, PROP NTs, who rated coffee sourness, bitterness and astringency as less intense than PROP STs, added more sugar to the coffee than did either MTS and STs. Tentatively, it could be suggested that NTs might be attempting to modify the sensory properties of the coffee, enhancing its overall flavor by adding sweetness. One other factor that might be influential is the fact that PROP NTs are reportedly more likely to be sweet-likers as determined by their responses to sweet tastes in solution [50,63,64].

Unexpectedly, PROP ratings and FP counts were not positively correlated as they have been in some previous studies [11,58,65–73]. This may be explained by sampling effects. Indeed, the distribution of PROP taster was similar to that found in many other studies, with approximately 25% of the sample NTs and another 25%, STs. The range of FP was, however, lower than has been reported: 4–22, as compared to 11.75–40.25 [58] and 12–51 [73] (see [72] for a review). This raises the prospect that our sampling excluded high FP individuals who either do not regularly consume coffee perhaps because of its high sourness and bitterness, or were less inclined to volunteer for research on this topic, possibly for the same reasons. It is also possible that papillae number measurements were an issue. Papillae counts depend on several factors, such as considered area, resolution of images, as well as the criteria used to decide on the presence of individual papillae. Some papillae are flat and short with little elevation, others are double papillae, thus making consistent identification an issue.

Even without high FP individuals, strong relationships between FP density and the bitterness of quinine and caffeine in solution, sourness in coffee samples, and, importantly, the propensity to add sweetener were found. Together, these effects reinforce the idea of FP density as a general index of taste intensity. It is somewhat puzzling that bitterness in coffee was not indexed by FP density, but to date there are no data on FP density and taste discrimination, as there are for PROP (e.g. [18,30,57]), and it may be that the bitterness of the coffee samples was sufficiently alike not to be discriminated as a function of FP density in this study. Moreover, coffee flavor is very complex. Indeed, coffee solids contain tannins that are sour (such as 4-vinylcatechol oligomers and quinic acid lactones) generated during roasting of the beans, as well as many bitter compounds other than caffeine [74,75]. Hence, the taste of a low concentration of caffeine is liable to be masked by both the bitter taste of the roasted coffee and the sour taste that may be confused with it [76]. Moreover, in coffee, a certain degree of bitterness is expected and liked [77]. On the contrary, sourness is not associated with coffee for consumers and subjects frequently confuse sour and bitter taste qualities [78,79]. The lack of a significant FP group effect on astringency is expected, because astringency is a mouthfeel sensation and its perception is not directly related to FP number [32,80,81].
The effect of PROP taste status on sourness and bitterness evaluation in coffee samples also confirms that PROP status is related to general orosensory responsiveness to a variety of stimuli in both standard solutions and foods [18,57]. The results concerning astringency perception are less clear, in particular why MTs rated astringency as weaker than NTs [30]; on the other hand also NTs rate the overall astringency higher than STs [31]. Furthermore, individual differences in astringency perceptions have been shown [81].

Bitterness intensity ratings in standard solutions seem to confirm that bitterness perception is very complex, even though there is large variation in bitter taste perception, there is some commonality to bitter taste elicited by different compounds [82–86]. Furthermore, these results are consistent with previous studies that showed strong relationships between FP density and the intensity of taste compounds [7–9, 11,87] and also that PROP status is linked with heightened sensitivity to bitter compounds as caffeine and quinine hydrochloride [77].

These results not only confirm that FP density and PROP status play a significant role in taste sensitivity for bitter compounds in general but also that sugar use is partly a function of fundamental individual differences in physiology. Thus, it appears that those more sensitive to tastes that might be unpalatable in coffee compensate by altering its overall flavor. Clearly, measures of food/beverage intake are likely to be only partly related to physiological measures such as FP density or PROP status unless such food behaviors are taken into account.

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