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Oral sensory phenotype identifies level of sugar and fat required for maximal liking

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ABSTRACT

A half-century ago, Fischer and colleagues found correlations between food preference and genetic markers of taste [6-*n*-propylthiouracil (PROP), quinine]. Recently, a number of studies report differences in sweet liking/disliking with taste phenotype or genotype. Here we modeled optimal liking for milk/sugar mixtures using the response surface method among 79 mostly normal weight adults (36 women) who reported low dietary restraint. Two non-overlapping phenotype analyses were performed: a) discordance in PROP versus quinine bitterness and b) number of fungiform papillae (FP, taste papillae on the tongue tip). Although all phenotype groups liked highly sweet and creamy sensations (in liking by sensation models), the fat and sugar levels for hedonic optima varied (in liking by concentration models). Males generally liked higher fat (20 to 40%) and sugar levels, with females disliking unsweetened cream. In quinine/PROP groups, liking peaked at 30% fat/15% sucrose for men and women who tasted 0.32 mM quinine more bitter than 3.2 mM PROP ($n=15$); a group previously shown to have highest sugar intakes (Duffy et al., 2003). Those tasting PROP more bitter than quinine ($n=14$) reported greater creamy/sweet sensations, with peak liking at lower fat and sweet levels (3.3% fat/10% sucrose). Generally, those in the high FP group perceived more creamy/sweet sensations with level of liking more influenced by sugar level, especially among high FP females. At high sugar/high fat levels low FP males and females retained this liking while liking fell off for those in the high FP group. In summary, although most liked sweet/creamy sensations, perceptual differences in these sensations varied with oral phenotype, explaining some of the differences in the amount of sugar and fat required to reach hedonic optima. A high affinity for high sugar/high fat mixtures among oral phenotype subgroups has relevance for energy consumption and could explain the link previously observed between oral sensation and body weight.

1. Introduction

How much a food is liked or disliked has long been deemed a major determinant of intake [1]. Elevated sweet preference associates with greater intake of added sugars and consumption of sweet foods [2,3] and vice versa [4]. Increased sweet affinity likely results from a genetic predisposition [2,5,6], variation in oral sensation associated with taste-related pathologies [2] and habitual level of intake [7,8]. Although many reports fail to link "a sweet tooth" with being overweight or obese, recent advances in assessing hedonic responses suggest sweet liking differs across normal and obese individuals [9]. More established is the fat liking-adiposity link. Heightened fat liking associates with increased intake [10] and adiposity in normal weight adults [11] and overweight/obese men [12]. Longitudinal data from an obesity prone population show greater weight gain among those with greater liking for sugar-fat mixtures [13]. Moreover, the relationships between sweetness, fat level and liking are influenced by taste phenotype [14,15], sex [14,16] and age [16].

The belief that differences in preference are influenced by phenotypic variation in oral sensation was reported by Fischer and colleagues in the 1960's [17]. The best-characterized phenotypic marker of genetic variation in oral sensation is the bitterness of 6-*n*-propylthiouracil (PROP). Those tasting PROP as less bitter typically report less tactile sensations from fat [18–21]: a weaker oral signal potentially explains why those tasting PROP as less bitter report greater preference for high fat foods [14,22,23] — a greater absolute amount is required to elicit the same hedonic response. PROP also associates with sweetness of sucrose in solution, sweet foods and qualitatively complex beverages (eg [2,24]). An individual minimally responsive to PROP perceives about half the sweetness from 20% sucrose as an individual for whom PROP is highly bitter [21]. When split into likers and dislikers (eg positive or negative slope with increasing concentration), disliking associates with PROP bitterness ratings [25] and thresholds [26], although differences in sweet intensity cannot completely explain liker/disliker classification [27].

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Assessed via questionnaire, liking of sweet foods negatively associates with PROP bitterness in women but not men, who show a flat relationship [14]; PROP may interact with number of fungiform papillae (FP), another marker of variation in taste [28], to influence sweet liking [25,27]. Although PROP bitterness and FP number are correlated, they capture separate but overlapping sources of variation in oral sensation [29].

Quinine response is a heritable phenotype [30] that is linked to ingestive behaviors like smoking [31] and eating [32]. Notably, food preference and liking are highly correlated for monozygotic but not dizygotic twins [33,34], a relationship that may be mediated via taste genetics. This early work also found lower quinine sensitivity was associated with increased preference for strongly flavored foods [33] while recent work supports various quinine measures as PROP independent predictors of vegetable liking [35], alcohol intake [36], sucrose intensity and liking of sampled sweet foods [2]. Although PROP and quinine bitterness are typically correlated in a population [37,38], some individuals are discordant in bitterness of these compounds and differ in liking of sweet foods, frequency of consuming sweet foods, and alcohol intake [39]. Why quinine relates to dietary behavior remains unclear — it may reflect overall taste responsiveness [37] as it covaries with the intensity of other tastants [40,41], even in the absence of cross-adaptation [40]. Alternatively, applied to specific regions of the tongue, it can serve as a marker of exposure to taste-related pathology [35,42]. While the receptor for quinine is unknown, hT2R7 was recently implicated as the receptor for two related antimalarials — quinacrine and chloroquine [43].

The present study defined orosensory phenotype in two ways – by PROP/quinine discordance as well as by FP number in men and women – and used the Response Surface Method (RSM) to examine differences in amount of sugar and fat required for optimal liking (physicohedonic functions) and to study sweet/fat sensation related to optimal liking (psychohedonic functions). The relationship between pleasantness and intensity was noted as a single peaked inverted U shape by Joseph Priestley in 1775 and Wilhelm Wundt in 1874 [44], empirically tested by Saidullah and Engel in the 1920s [45], and later by Pfaffmann [46] and Moskowitz [47]. In a uni-dimensional system, the liking function can be modeled with a quadratic best fit line (a univariate second order polynomial). In a two-dimensional system, a parabolic surface (a bivariate second order polynomial) can describe how changes in either dimension influence liking and provides the basis of RSM [48]. The RSM contour plots allow easy visualization of synergy (ie, the sum is greater than would be predicted from the individual parts) and deviation from additivity. The study of individual differences in oral sensation has shown that concentration is not synonymous with sensation. Yet, the need for discrete factors in techniques like ANOVA precludes asking about the psychohedonic function; in contrast, RSM provides information about liking as a function of concentration or sensation.

RSM models have been used to study liking of sugar–fat mixtures in normal [49], and overweight [50] adults, individuals with eating disorders [51], and the elderly [52]. Although, the link between oral phenotype and liking in these mixtures has been tested previously [53], RSM models have never been used to study groups who differ in oral phenotype. We address this knowledge gap by providing response surfaces that describe the hedonic optima of liquid sugar–fat mixtures in a sample of primarily normal weight adults.

2. Methods

Intensity and hedonic testing were conducted in a laboratory setting in three sessions, typically one week apart. Participants were characterized phenotypically for the discordance between PROP and quinine bitterness and for fungiform papillae number via videomicroscopy [28] as described previously [54].

2.1. Subjects

The 79 subjects, described previously [2,21], participated in an Institutional Review Board-approved procedure, provided written consent, and were paid for their time. Using body mass index (BMI; kg/m^2) calculated from weights and heights measured in the laboratory, 57 were normal weight ($18.5 \le BMI < 25$) with one underweight ($BMI < 18.5$), 18 overweight ($25 \le BMI < 30$), and 3 obese ($BMI \ge 30$) subjects. The men were more likely ($\chi^2(1) = 8.1$, $p < 0.01$) to be overweight or obese. All had low levels of dietary restraint, a common construct [55] measured here with two instruments; potential participants were screened with the concern for dieting subscale of the Restraint Scale [56,57] and then administered the Three Factor Eating Questionnaire (TFEQ) [58] during the first laboratory visit. Individuals with low 'cognitive restraint of eating' – defined as a TFEQ-R score of 13 or below – were included in the study. Men and women had restraint scores of 5.1 ± 3.28 and 6.41 ± 3.37, which are below collegiate norms of 6.1 and 10.2 [59].

2.2. Stimuli

Participants tasted 15 mixtures — heavy cream (36% fat), whole milk (3.5%), skim milk (<0.5%) and water (0% fat) that varied in added sucrose (0, 5, 10, 20% w/v); data from the sucrose–water mixtures were excluded from analysis to avoid any odor effects when shifting from water to milk [21]. Samples were served cold (5 °C) in duplicate; participants rated degree of liking, sweetness and creaminess within a trial. They rinsed between each sample with room temperature deionized (>15 MΩ) water.

The participants rated the bitterness of 0.32 mM quinine monohydrochloride (Pfaltz & Bauer, Waterbury, CT) within a battery of prototypical tastants during the first day. In a protocol described previously [2,35,60], PROP solutions – 3.2, 1, 0.32, 0.1, 0.032 mM 6-*n*-propthiouracil (Sigma, St. Louis, MO) – were presented randomly in blocks along with 1 kHz tones (50–98 dB in 12-dB steps) and NaCl solutions (.01, .032, .1, .32, 1 M). This was done at the end of the third testing session to minimize contrast and range effects [61,62] that may vary non-randomly with PROP response. Raw PROP data were used; tone normalized and raw data produce comparable PROP functions and relationships with sensory and diet variables [54].

2.3. Data collection

2.3.1. Measuring intensity and liking

Adults were instructed to use the general Labeled Magnitude Scale (gLMS) [63,64] to report the intensity and degree of liking/disliking of the samples. For intensity, the gLMS ranges from 'no sensation' at the bottom (0) to 'the strongest imaginable sensation of any kind' at the top (100) with intermediate labels at 'barely detectable' (1.4), 'weak' (6), 'moderate' (17), 'strong' (35), and 'very strong' (53). This scale generalizes the Labeled Magnitude Scale [65,66] by broadening the context from oral sensations to all sensations of any kind. Changing the top anchor is critical because individuals do not use adjective labels to denote the same perceived intensities [63]. The flawed assumption that subjects use adjective labels in a similar manner can attenuate, obfuscate or even reverse intensity effects [67]. For hedonic ratings of milk samples, subjects were instructed to anchor the top of the scale to either 'strongest imaginable liking' (+100) or the 'strongest imaginable disliking' (−100) with neutral being zero, as reported previously [35,68].

2.3.2. Fungiform papillae number

Mean FP number in a 6 mm circular area averaged across the right and left tongue tip was ascertained by staining the tongue blue and viewing the recorded image collected via videomicroscope, as described elsewhere [54,60]. Using the overall median (23.5 FP), we