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A bio-cultural approach to the study of food choice: The contribution of taste genetics, population and culture

Davide S. Risso [a, b, *, 1], Cristina Giuliani [b, **, 1], Marco Antinucci [c], Gabriella Morini [d], Paolo Garagnani [e], Sergio Tofanelli [c, 2], Donata Luiselli [b, 2]

[a] Department of Genome Sciences, University of Washington School of Medicine, Seattle, WA 98195, USA
[b] Department of Biological, Geological and Environmental Sciences (BiGeA), Laboratory of Molecular Anthropology and Centre for Genome Biology, University of Bologna, Via Selmi 3, 40126 Bologna, Italy
[c] Department of Biology, University of Pisa, Via Ghini 13, 56126 Pisa, Italy
[d] University of Gastronomic Sciences, Piazza Vittorio Emanuele 9, Bra, Pollenzo 12042, CN, Italy
[e] Department of Experimental, Diagnostic and Specialty Medicine (DIMES), University of Bologna, Via San Giacomo 12, 40126 Bologna, Italy

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ABSTRACT

The study of food choice, one of the most complex human traits, requires an integrated approach that takes into account environmental, socio-cultural and biological diversity. We recruited 183 volunteers from four geo-linguistic groups and highly diversified in terms of both genetic background and food habits from whom we collected genotypes and phenotypes tightly linked to taste perception. We confirmed previous genetic associations, in particular with stevioside perception, and noted significant differences in food consumption: in particular, broccoli, mustard and beer consumption scores were significantly higher (Adjusted $P = 0.02$, Adjusted $P < 0.0001$ and Adjusted $P = 0.01$, respectively) in North Europeans, when compared to the other groups. Licorice and Parmesan cheese showed lower consumption and liking scores in the Sri Lankan group (Adjusted $P = 0.001$ and Adjusted $P < 0.001$, respectively). We also highlighted how *rs860170* (*TAS2R16*) strongly differentiated populations and was associated to salicin bitterness perception. Identifying genetic variants on chemosensory receptors that vary across populations and show associations with taste perception and food habits represents a step towards a better comprehension of this complex trait, aimed at improving the individual health status. This is the first study that concurrently explores the contribution of genetics, population diversity and cultural aspects in taste perception and food consumption.

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1. Introduction

Food choice is a highly complex human trait whose study requires an integrated multidisciplinary approach (Grimm & Steinle, 2011), which takes into account environmental, socio-cultural and biological factors (Armelagos, 2014; Pieroni, Pawera, & Shah, 2016; Rozin, 1982; Turner and Thompson, 2013). Food selection allows humans to fulfill the vital function of nutrition, constituting the deepest connection with the environment, and being a relevant factor to define human communities. During the course of human evolution the sense of taste, together with the other chemical senses smell and chemesthesis, has played a fundamental role in food choice, by ensuring an efficient discrimination between edible sources of nutrients and potentially toxic substances (Breslin, 2013; Glendinning, 1994). Plant secondary metabolites trigger environmental adaptation, providing defense mechanisms against pathogens and making plants unpalatable to predators. Phenols, flavonoids, terpenes, alkaloids and glucosinolates are in fact bitter or irritant plant compounds: for this reason, variants at genes encoding taste receptors have undergone adaptive changes in relation to eating habits (Campbell et al., 2012; Fischer, Gilad, Man, & Pääbo, 2005; Perry, Kistler, Kelaita, & Sams, 2015; Risso, Tofanelli, Morini, Luiselli, & Drayna, 2014). Most phytochemicals also exhibit a wide array of biological properties (Kabera, Semana, Mussa, & He,

* Corresponding author. Department of Genome Sciences, University of Washington School of Medicine, Seattle, WA 98195, USA.
** Corresponding author.
E-mail addresses: davide.risso2@unibo.it (D.S. Risso), cristina.giuliani2@unibo.it (C. Giuliani).
[1] These authors contributed equally.
[2] These authors contributed equally.

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2014; Wink, 2015) that humans have learnt to exploit for their therapeutic effects (Petrovska, 2012). This has added interest to the study of the genetic bases of taste preferences and health status in relation to the introduction of phytochemicals in the diet (Tepper, 1998; Dinehart, Hayes, Bartoshuk, Lanier, & Duffy, 2006; des Gachons, Beauchamp, & Breslin, 2009; Mennella, 2014; Mennella and Bobowski, 2015). *TAS2R* genes, which codify for bitter taster receptors, are also expressed in the gastrointestinal tract and in other extra-oral tissues such as gut, lungs and testis (Finger & Kinnamon, 2011), where they modulate systemic functions of tastants either endogenously produced or contained in food (Santa-Cruz Calvo & Egan, 2015; Clark et al., 2015; Shaik et al., 2016). The most studied taste-related gene is TAS2R38, which encodes the bitter taste receptor mediating the ability to be a "taster" (PAV haplotype) or a "non-taster" (AVI haplotype) for different bitter compounds, including the well-known phenylthiocarbamide (PTC) and 6-n-propylthiouracil (PROP) (Kim et al., 2003; Boxer & Garneau, 2015). Correlations have been identified between PROP/PTC taster status and dietary intake (Feeney, O'Brien, Scannell, Markey, & Gibney, 2011; Tepper, 2008; Turnbull & Matisoo-Smith, 2002). This, in addition to the particular worldwide distribution of TAS2R38 haplotypes, has suggested that natural selection may have been acted on this gene, since the earlier stages of human evolution (Campbell et al., 2012; Risso et al., 2016; Wooding et al., 2004).

Nonetheless, correlations between genetic variations and food preferences have been recognized hard to detect, since each food is constituted by several different chemical compounds that may be able to activate different receptors (Meyerhof et al., 2010; Roudnitzky et al., 2011, 2015). In addition, food choice is the result of the integration with other sensory inputs in the brain, and it is further complicated by different cultural backgrounds such as learning, memory and emotion (Bertino et al., 1983; Shepherd, 2012; Williams, Bartoshuk, Fillingim, & Dotson, 2016). For these reasons, food choice and habits have been recently explored under a different perspective, where the co-variation of taste phenotypes and genotypes is addressed within the context of population diversity in eating behaviors (Kumanyika, 2008; Pirastu et al., 2015; Robino et al., 2014). Under this approach, inter-populations variability is taken into account when performing genotype-phenotype association studies investigating the relationships between SNPs, structural variations, and taste perception (Campbell et al., 2012; Allen, McGeary, Knopik & Hayes, 2013a, 2013b; Roudnitzky et al., 2015, 2016).

In this explorative study we explored an integrated approach and recruited a total number of 183 volunteers belonging to four different geographical regions and highly diversified in terms of both genetic background and food habits: Italy, North Europe, Maghreb and Sri Lanka. After collecting bitter, sweet and umami taste-phenotypes using both natural and synthetic compounds, a food habits questionnaire on common bitter, sweet and umami-tasting foods was presented to the participants. A panel of 37 SNPs located in 14 genes involved in taste perception was also analyzed in order to explore potential associations between genetic variants, food habits, taste perception and population differences.

2. Materials and methods

2.1. Studied population

An overall number of 183 individuals were recruited and enrolled in the study. Subjects (81 females and 102 males with an average age of 42.71 ± 15.89) did not report any food allergies, were not following any prescribed diet or using drugs that might interfere with taste perception. Most of the participants (N = 111) were Italians, with the remaining subjects coming from the Maghreb region (N = 18), Sri Lanka (N = 26) and Northern Europe (N = 28) but recruited in Italy. Detailed information of samples included in the study is shown in Table 1. A written informed consent was obtained from all the volunteers and all the experimental protocols were in accordance with the ethical standards of the Ethics Committee of the University of Bologna and with the Helsinki Declaration of 1975, as revised in 2000.

2.2. DNA collection

Saliva samples were collected from participants using Oragene saliva collection kits (Genotek Inc. Kanata, Ontario, Canada). DNA was extracted according to the manufacturer's protocol and checked for quantity/quality by spectrophotometric analyses (GeneQuant™RNA/DNA Calculator, Amersham Biosciences, UK). We genotyped 37 SNPs selected from a panel of 14 taste-related genes (Table 2) using the SequenomMassARRAY technology (Sequenom, San Diego, CA, USA).

PCR fragments were analyzed by MALDI-TOF mass spectrometry (Gabriel, Ziaugra, & Tabbaa, 2009) and spectrograms were checked individually, in order to evaluate the presence of calling errors. As additional quality control, we checked that no significant deviations from Hardy-Weinberg equilibrium (p-value<0.001) were present in the analyzed SNPs and that their call rate was >0.95. Primer sequences are shown in Supplementary Table 1.

2.3. Food habits questionnaire

Participants completed a questionnaire on individual liking and consumption about 12 common foods: seven bitter-tasting ("Broccoli", "Radicchio", "Artichoke", "Arugula", "Licorice", "Mustard" and "Beer"), three sweet-tasting ("Date", "Honey" and "Torrone") and two umami-tasting foods ("Parmesan cheese" and "Bouillon cube"). Subjects were asked to rate each item on a 3-point liking scale: "Dislike" (score 1), "Sort of" (score 2) and "Like extremely" (score 3). In addition, these items were rated on a 3-points consumption scale: "Yearly" (score 1), "Monthly" (score 2) and "Weekly" (score 3). A "Never tasted" (score 0) option was also included. The liking and consumption scores were then pooled together to have a single 1-to-6 liking + consumption score. Supplementary Table 2 summarizes mean and standard deviation for each item score. Lastly, weight (in kg) and height (in m) were collected in order to calculate the body mass index (BMI).

2.4. Assessment of taste phenotypes

Taste perception phenotypes were collected for the three examined taste qualities (e.g. umami, sweet and bitter). Volunteers were asked to refrain from eating and drinking for at least 3 h before the beginning of the session and to rinse their mouth with room temperature deionized water before each tasting step. Subjects were informed that they may receive stimuli eliciting more than one taste quality. They were asked to hold the presented

Table 1
Characteristics of the study participants in the four analyzed populations. B.M.I. Body mass index.

Population	N (males/females)	Mean age (SD)	Mean B.M.I. (SD)
Italy	111 (55/56)	47.64 (16.06)	24.27 (3.52)
Maghreb	18 (18/0)	38.56 (13.80)	25.48 (3.31)
N. Europe	28 (6/22)	21.50 (6.35)	21.50 (2.93)
Sri Lanka	26 (23/3)	38.59 (13.12)	25.43 (2.34)
All	183 (102/81)	42.71 (15.89)	24.14 (3.47)