



Association of single nucleotide polymorphisms with taste and food preferences of the Hungarian general and Roma populations

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ABSTRACT

It is reasonable to suppose that poor diet underlies the unfavorable health status of the Roma population of Europe. Previously in the framework of a complex health survey, fruit and vegetable consumption, quantity of sugar added, salting frequency; bitter, salty, sweet and fat taste preferences were evaluated of Hungarian (HG, $n = 410$) and Roma (HR, $n = 387$) populations. In the present study the associations of taste and food preferences with TAS1R3, CD36, SCNN1B, TRPV1, TAS2R38, TAS2R19 and CA6 polymorphisms were tested in the same samples. Genotype frequencies did not differ significantly between the two populations. Although we initially observed associations between certain genetic polymorphisms and taste and food preferences in our study samples, none of the p values remained significant after the multiple test correction. However, some of our results could be considered promising ($0.05 < \text{corrected } p < 0.20$), which showed potential ethnicity-specific effects (CA6 rs2274333 with salty taste and raw kohlrabi preference, CD36 rs1527483 with fat taste preference, TAS2R19 rs10772420 with grapefruit preference, and TAS2R38 rs713598 with quantity of sugar added). Our results may suggest that genetics may mediate food preferences, and individuals with different ethnic background may require personalized interventions to modify diet. Further investigations with greater sample sizes are essential to explore the effect of these genetic variants on taste and food preferences.

1. Introduction

Suboptimal diet is a major risk factor for unfavorable health status, contributing to the development of metabolic abnormalities and consequent noncommunicable diseases (NCDs) of public health significance (type 2 diabetes, cardiovascular diseases and cancer) (Astrup, Dyerberg, Selleck, & Stender, 2008; World Cancer Research Fund, 2018). Globally, dietary risks were responsible for 11 million deaths in 2017, and found to be unevenly distributed within populations (GBD Collaborators, 2019). Moreover, dietary behaviors are different among and within ethnic minorities compared to majority populations (Leung & Stanner, 2011), suggesting that factors influencing eating habits may vary in ethnic minority groups (Satia-Abouta, Patterson, Neuhouser, & Elder, 2002).

Food preference is a complex trait influenced by the complex

interplay of genetic and environmental factors. Food intake is determined by individual food preferences, which are shaped during fetal development and childhood (Birch, 1999; Ventura & Worbey, 2013) and are highly influenced by taste perception and taste preference (Connors, Bisogni, Sobal, & Devine, 2001; Glanz, Basil, Maibach, Goldberg, & Snyder, 1998; Kearney, Kearney, Dunne, & Gibney, 2000; Kourouniotis et al., 2016). The genetic background of taste and related food preferences has been widely studied and found that individual taste preferences may also be explained by genetic variations (Diószegi, Llanaj, & Ádány, 2019). An estimate of genetic influence on perceived sensitivity, intensity and preference of standard prototypical tastants is expressed in terms of heritability (h^2), which describes the proportion of the variance in a trait that is due to additive genetic factors. Heritability estimates range from high to moderate for bitter tasting compounds [0.72, 0.71, 0.34, for 6-*n*-propylthiouracil (PROP) (Hansen, Reed, Wright, Martin, & Breslin, 2006), phenylthiocarbamide (PTC) (Knaapila

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Abbreviations

AVI	alanine-valine-isoleucine	NCD	noncommunicable disease
CA6	carbonic anhydrase VI (also called as gustin)	OR	odds ratio
CD36	cluster of differentiation 36 (also called as fatty acid translocase)	PAV	proline-alanine-valine
CI	confidence interval; DNA: deoxyribonucleic acid	PROP	6- <i>n</i> -propylthiouracil
EDTA	ethylenediaminetetraacetic acid	PTC	phenylthiocarbamide
ENaC	epithelial sodium channel	SCNN1A	sodium channel epithelial 1 subunit alpha
GP	General Practitioner	SCNN1B	sodium channel epithelial 1 subunit beta
GPMSSP	General Practitioners' Morbidity Sentinel Stations Programme	SCNN1D	sodium channel epithelial 1 subunit delta
GWAS	genome-wide association study	SCNN1G	sodium channel epithelial 1 subunit gamma
HWE	Hardy-Weinberg equilibrium	SNP	single nucleotide polymorphism
HG	Hungarian general population	TAS2R19	taste receptor type 2 member 19
HR	Hungarian Roma population	TAS1R2	taste receptor type 1 member 2
NaCl	sodium chloride;	TAS1R3	taste receptor type 1 member 3
		TAS2R38	taste 2 receptor member 38
		TRPV1	transient receptor potential cation channel subfamily V member 1
		vs	versus

et al., 2012) and quinine hydrochloride (Hansen et al., 2006), respectively] and moderate for sweet tasting substances (glucose: $h^2 = 0.31$, fructose: $h^2 = 0.34$) (Hwang, Breslin, Reed, Martin, & Wright, 2015). Accordingly, preferences for foods representing the basic taste qualities can also be characterized by similar heritability estimates [dessert foods (0.20), vegetables (0.37–0.54), fruits (0.49–0.53), protein foods (0.48–0.78) (Breen, Plomin, & Wardle, 2006; Fildes et al., 2014; Smith et al., 2016)] and the correlation for fat as a percentage of energy intake was found to be 0.61 for monozygotic twins in a study conducted in a population of French descent (Pérusse et al., 1988).

In the European Union, the Roma form the largest and most vulnerable ethnic minority population. This minority population suffers from disadvantages in multiple aspects of life, such as substandard living conditions, low educational level, high unemployment rates (Colombini, Rechel, & Mayhew, 2012) social exclusion, marginalization and discrimination (Cook, Wayne, Valentine, & Lessios, 2013) throughout Europe. All these factors give rise to unequal access to health care services (Colombini et al., 2012; Kósa et al., 2007; Kühlbrandt, Footman, Rechel, & McKee, 2014; McFadden et al., 2018), less favorable self-assessed health status (Cook, Wayne, Valentine, Lessios, & Ye, 2013) and presumably a higher risk of early mortality compared to non-minority populations of Europe (Cook et al., 2013). An estimated 10–12 million Roma people live in Europe (Committee on Civil Liberties, 2010), and Hungary is among the countries (together with Bulgaria, Romania, Slovakia, Serbia and North Macedonia) with the highest representation of Roma individuals in the total population. This largest Hungarian ethnic minority is the only ethnic group with a constantly increasing number and ratio in the total population of Hungary, comprising almost 9 percent (876 000 individuals) of the country's total population (Pásztor, Péntzes, Tátrai, & Pálóczi, 2016). Although many Roma people wish to assimilate into majority societies, most Roma communities have maintained their cultural identity and traditions (Cook et al., 2013), which strongly affect their lifestyles and health behaviors (Petek, Pavlic, Svab, & Lolic, 2006). Harmful health behaviors, such as unhealthy nutrition, may potentially underlie the unfavorable health status of this minority population.

The study conducted by Ciaian et al. analyzed diet quality of Roma with the aim of providing explanation for potential factors that may lead to different food consumption patterns of Roma living in Romania. In this study Roma had inferior diet diversity compared to the non-Roma with higher proportion of cereals and a lower proportion of dairy products and fruits and vegetables relative to other ethnic groups. Results suggested that only one-third of this diet diversity gap was explained by the differences in observed socioeconomic factors, the remaining part of the gap could be attributed to unobserved factors

(Ciaian, Cupák, Pokrivčák, & Rizov, 2018). In our previous study (Diószegi et al., 2020) Roma reported significantly less frequent consumption of fresh fruits and vegetables than Hungarian individuals. They also reported adding higher quantities of sugars to consumed foods and beverages, could be characterized by higher preferences for sweet foods, salted their food without tasting more often and had lower preferences for bitter tasting raw kohlrabi, black coffee, dark chocolate and grapefruit.

Since our findings related to taste and food preferences of the Hungarian Roma population may not solely be explained by socio-economic determinants, as suggested by Ciaian et al. (Ciaian et al., 2018), but may be attributed to genetic influences, in this study we aimed to evaluate the potential associations of genetic variants with taste and food preferences on samples of the Hungarian general adult population and Roma living in segregated colonies.

2. Materials and methods

In the framework of a complex comparative health survey (Ádány et al., 2020), representatives of the adult Hungarian general population and the Hungarian Roma population living in segregated settlements from Borsod-Abaúj-Zemplén and Szabolcs-Szatmár-Bereg counties (where Roma are concentrated) were randomly enrolled. The planned sample size was to involve 500 individuals in each study sample. According to the study protocol, if someone was not available to reach, it was possible to enroll another individual, but if someone refused to participate, another person was not allowed to include in the study population. Questionnaires were administered by practice nurses in the Hungarian general population and by Roma field workers in the Hungarian Roma population. Blood sample collection for genetic analysis was carried out in General Practitioners' (GPs) offices. Data collection was implemented between 17 May and August 29, 2018.

2.1. Samples

2.1.1. Sample representative of the Hungarian general population

The General Practitioners' Morbidity Sentinel Stations Programme (GPMSSP), a population-based disease registry established in 1998 to monitor NCDs of great public health importance provided the Hungarian reference sample. Detailed description of GPMSSP is presented elsewhere (Széles et al., 2005; Szigethy et al., 2012). The study population involved randomly selected individuals 20–64 years of age, who were registered by the participating GPs in Borsod-Abaúj-Zemplén and Szabolcs-Szatmár-Bereg counties (Northeast Hungary) and lived in private households. The planned sample size was 25 individuals from 20

randomly selected GP practices in these two counties. Two GPs refused to participate, so the final sample consisted of 450 people from the practices of 18 GPs.

2.1.2. Sample representative of Hungarian Roma living in segregated colonies

A stratified multistep sampling method was applied to enroll Roma participants from Hajdú-Bihar and Szabolcs-Számár-Bereg counties (Northeast Hungary), the region where the majority of Roma colonies are found. Segregated colonies exceeding 100 inhabitants were identified by Roma field workers during a previous environmental survey. Ethnicity was assessed by self-declaration (Kósa, Daragó, & Ádány, 2011). After the verification of this previously created database, twenty colonies were randomly selected. Subsequently, twenty-five households were randomly chosen from each colony. Then all individuals 20–64 years of age were identified in each household, and one person was selected by a random table.

The study was approved by the Ethical Committee of the Hungarian Scientific Council on Health (61327–2017/EKU). Written informed consent was obtained from all participants in each study population in accordance with the Declaration of Helsinki.

2.2. Food and taste preference assessment

In the questionnaire-based part of the complex health survey (Ádány et al., 2020), questions from the Hungarian version of the European Health Interview Survey (Hungarian Central Statistical Office, 2014) were included covering the following topics: fruit and vegetable consumption (categories: more than once a day, once a day, 4 to 6 times a week, 1 to 3 times a week, less than once a week, never); quantity of sugars added to consumed foods and beverages (on average, per day; categories: 0, 1–4, 5–10, >10 teaspoons), and frequency of salting without tasting food (categories: never, sometimes, often, always). Taste preference was evaluated by a food preference questionnaire using a five-point Likert scale proposed by Catanzaro (Catanzaro, Chesbro, & Velkey, 2013) and administered by an interviewer. Each enrolled individual was asked to rate sweet-, fatty-, salty- and bitter-tasting food items (ranging from 1 “dislike extremely”; 2 “dislike moderately”; 3 “indifferent”; 4 “like moderately”, to 5 “like extremely”; „have not tasted yet” was also given as an option). Foods were categorized into taste dimensions. Sweet, fatty and salty food preference was investigated by applying single questions with providing examples of each taste (sweet: cake, chocolate, ice-cream, cookies, wafer bars; fat: bacon, salami, sausage, gravy; salty: salty sticks, chips, crackers). Bitter taste was assessed with individual preference questions for six bitter-tasting food items (dark chocolate, black coffee, raw kohlrabi, raw white cabbage, raw cauliflower and grapefruit). The bitter-tasting thiourea moiety is present in cruciferous vegetables (Hanschen, Lamy, Schreiner, & Rohn, 2014), however other foods and beverages not containing this compound (grapefruit juice, coffee, alcohol, green tea and soy products) are also perceived as bitter for sensitive individuals (Dinehart, Hayes, Bartoshuk, Lanier, & Duffy, 2006; Gayathri Devi, Henderson, & Drewnowski, 1997; Lanier, Hayes, & Duffy, 2005; Sandell & Breslin, 2006) due to their phytonutrient content (Drewnowski & Gomez-Carneros, 2000). Research suggests that the individual differences in the perception of different bitter tasting food items and beverages may be linked to different genetic polymorphisms (Supplementary Table 1.), and no such differences were found related to other taste stimuli (Diószegi et al., 2019). Accordingly, the reason for including individual questions on six bitter-tasting food items was the genetic background of bitter taste perception and preference. The taste and food preference questionnaire included typically and frequently consumed foods in Hungary (Jilani et al., 2017), which are well-known and available for the Roma population as well (Abala, 2011). Factors influencing taste and food preferences and dietary habits were registered, such as smoking (Chérueil, Jarlier, & Sancho-Garnier, 2017; Hyun, Park, & Heon Kim, 2016; Pepino

& Mennella, 2007), heavy alcohol use (Silva et al., 2016) and special diet adherence.

2.3. Selection of SNPs investigated

Systematic literature search was conducted to identify the most relevant single nucleotide polymorphisms (SNPs) related to taste preferences (Diószegi et al., 2019), which may influence health status and the risk of chronic disease (Chamoun et al., 2018). Based on this search, altogether nine SNPs associated with salty, sweet, fat and bitter taste and related food preferences were identified. One of these (SCNN1B rs3785368) was dropped from the study as the assay method failed. The final SNP list included the following polymorphisms: TAS1R3 rs307355, CD36 rs1761667 and rs1527483, SCNN1B rs239345, TRPV1 rs8065080, TAS2R38 rs713598, TAS2R19 rs10772420 and CA6 rs2274333.

2.4. DNA preparation

DNA isolation was performed from 500- μ l aliquots of EDTA-anticoagulated blood samples. The MagNA Pure LC DNA Isolation Kit – Large Volume (Roche Diagnostics, Mannheim, Germany) was used following the manufacturer’s instructions. Extracted DNA samples were eluted in 200 μ l MagNA Pure LC DNA Isolation Kit-Large Volume Elution Buffer.

2.5. Genotype assessment

Genotyping of the selected genetic polymorphisms was performed by the Mutation Analysis Core Facility (MAF) of Clinical Research Center, Karolinska University Hospital (Stockholm, Sweden) on a Mass Array platform with iPLEX Gold Chemistry (Gabriel, Ziaugra, & Tabbaa, 2009). The validation, concordance analysis and quality control were conducted by MAF according to their protocol resulting in a successful genotyping rate of higher than 98 percent.

2.6. Statistical analyses

The data were analyzed using the STATA 10.0 Statistical software (StataCorp LP, College Station, TX, USA). The Shapiro-Wilk test was applied to test for normal distribution of age in both study populations. To compare the mean age and sex distribution of the two study groups the Mann-Whitney U and χ^2 tests were used. Hardy-Weinberg equilibrium (HWE) was estimated using STATA’s “hwsnp” function (Cleves, 2005). Allele frequencies were estimated by “genhw” program implemented in STATA (Cleves, 1999). To test the significant differences in the genotype frequencies between the two populations the χ^2 test was applied. In the association analysis all potential genotype-phenotype associations presented in the literature were analyzed (Supplementary Table 1.) by ordered logistic regression according to dominant and recessive models in our study samples separately and in the combined population of the Hungarian general and Roma populations as well. The covariates age, sex, smoking status and harmful alcohol consumption were controlled in all association analyses and individuals following special diets were excluded. A p value of $p < 0.001$ was applied for HWE, otherwise the threshold for significance was 0.05. In Tables 2–5, when multiple tests were performed nominal and Bonferroni-corrected p values are presented as well.

3. Results

Taste and food preference assessment was available for 410 individuals from the Hungarian general population (HG) and 387 subjects from the Hungarian Roma population (HR). A total of 405 HG and 364 HR DNA samples were obtained for genotyping. The mean age of the two study samples did not differ significantly (general Hungarian

Table 1
Genotype frequencies of selected polymorphisms in the Hungarian general and Roma populations.

Gene	SNP	Genotypes	HG genotype frequency (n)	HR genotype frequency (n)	p
TAS1R3	rs307355	CC	81.2 (329)	82.7 (301)	0.864
		TC	17.8 (72)	16.5 (60)	
		TT	1.0 (4)	0.8 (3)	
CD36	rs1761667	AA	23.4 (95)	18.2 (66)	0.178
		AG	48.9 (198)	50.7 (184)	
		GG	27.7 (112)	31.1 (113)	
CD36	rs1527483	AA	1.2 (5)	0.6 (2)	0.500
		AG	13.8 (55)	12.3 (44)	
		GG	85.0 (339)	87.1 (311)	
SCNN1B	rs239345	AA	3.5 (14)	5.5 (20)	0.380
		AT	31.6 (127)	31.8 (115)	
		TT	64.9 (261)	62.7 (227)	
TRPV1	rs8065080	CC	12.9 (52)	11.5 (42)	0.483
		CT	45.8 (185)	42.9 (156)	
		TT	41.3 (167)	45.6 (166)	
TAS2R38	rs713598	CC	34.1 (136)	37.1 (134)	0.203
		GC	43.6 (174)	45.7 (165)	
		GG	22.3 (89)	17.2 (62)	
TAS2R19	rs10772420	AA	19.3 (78)	16.4 (59)	0.215
		AG	49.6 (201)	46.8 (169)	
		GG	31.1 (126)	36.8 (133)	
CA6	rs2274333	AA	50.0 (199)	50.3 (182)	0.490
		AG	38.9 (155)	41.1 (149)	
		GG	11.1 (44)	8.6 (31)	

HG: Hungarian general population, HR: Hungarian Roma population, SNP: single nucleotide polymorphism. Genotype frequencies are presented as percentages. Numbers of genotypes are shown in parentheses. p value was calculated by χ^2 test.

Table 2
Associations of selected polymorphisms with salty taste preference.

Gene	SNP	Question item	Population	Model	OR (95% CI)	p	corrected p
TAS2R38	rs713598	Salting frequency	HR	GG vs GC + CC	1.91* (1.08–3.37)	0.026	0.312
TRPV1	rs8065080	Salting frequency	HR	TT vs CT + CC	1.66* (1.06–2.60)	0.031	0.372
TRPV1	rs8065080	Salty taste preference	HR	TT vs CT + CC	1.57** (1.01–2.43)	0.044	0.528
CA6	rs2274333	Salty taste preference	HR	GG + AG vs AA	1.59** (1.02–2.48)	0.041	0.492
CA6	rs2274333	Salty taste preference	HG + HR	GG + AG vs AA	1.52** (1.10–2.08)	0.010	0.120

HG: Hungarian general population, HR: Hungarian Roma population, SNP: single nucleotide polymorphism, OR= odds ratio, 95% CI: 95% confidence interval. Salting frequency presents the frequency of salting without tasting food (categories: never, sometimes, often, and always).

* OR for higher frequency categories.

Salty taste preference was measured on a five-point Likert scale (ranging from 1 “dislike extremely”; 2 “dislike moderately”; 3 “indifferent”; 4 “like moderately”, to 5 “like extremely”).

** OR for higher preference value was calculated by ordered logistic regression (covariates: sex, age, smoking, harmful alcohol consumption). corrected p: Bonferroni-corrected.

p value (number of tests: 12).

Only at least nominally significant associations are presented in the table. Italic indicates 0.05 < corrected p < 0.20.

Table 3
Associations of selected polymorphisms with fat taste preference.

Gene	SNP	Question item	Population	Model	OR (95% CI)	p	corrected p
CD36	rs1527483	Fat taste preference	HG	GG vs AG + AA	2.24 (1.18–4.25)	0.014	0.126
CD36	rs1527483	Fat taste preference	HG + HR	GG vs AG + AA	1.83 (1.19–2.82)	0.006	0.054
TAS2R38	rs713598	Fat taste preference	HG + HR	CC + GC vs GG	1.54 (1.04–2.27)	0.029	0.261

HG: Hungarian general population, HR: Hungarian Roma population, SNP: single nucleotide polymorphism, OR = odds ratio (for higher preference), 95% CI: 95% confidence interval.

Fat taste preference was measured on a five-point Likert scale (ranging from 1 “dislike extremely”; 2 “dislike moderately”; 3 “indifferent”; 4 “like moderately”, to 5 “like extremely”).

p value was calculated by ordered logistic regression (covariates: sex, age, smoking, harmful alcohol consumption). corrected p: Bonferroni-corrected p value (number of tests: 9).

Only at least nominally significant associations are presented in the table. Italic indicates 0.05 < corrected p < 0.20.

population: 44.3 ± 12.3 y, Roma population: 42.8 ± 12.1 y, p = 0.075). The proportion of male individuals was significantly lower in the Roma sample than that in the Hungarian sample (0.26 vs 0.44, p < 0.001) according to the χ^2 test.

3.1. Allele and genotype comparisons between the study groups

All SNPs were tested and none of the SNP deviated significantly from the Hardy-Weinberg equilibrium (p > 0.001) in either study population. The allele (not presented) and genotype frequencies (Table 1) did not differ significantly (p > 0.05) between the two study samples.

3.2. Association of SNPs with food and taste preferences

The number of individuals not following special diets was 264 in the Hungarian general population and 320 in the population of Hungarian Roma living in segregated colonies, who were included in the association analyses. In our present study we did not find any statistical evidence of association in the study samples between TAS1R3 rs307355, CD36 rs1761667 and SCNN1B rs239345 polymorphisms with either phenotypes of our interest.

Nominally significant associations between the selected polymorphic variants and taste and food preferences in HG, HR and in the combined population of the Hungarian general and Roma populations (HG + HR) were observed in the following cases: In HG CD36 rs1527483 was associated with fat taste preference; CA6 rs2274333 with dark chocolate preference; TAS2R19 rs10772420 with raw white cabbage preference; and TAS2R38 rs713598 with vegetable consumption frequency. In HR TAS2R38 rs713598 and TRPV1 rs8065080 showed significant associations with salting frequency; TRPV1 rs8065080 and CA6 rs2274333 with salty taste preference; CA6 rs2274333 with raw kohlrabi preference; TAS2R19 rs10772420 with grapefruit preference; and TAS2R38 rs713598 with quantity of sugar added. In the combined HG + HR

Table 4
Associations of selected polymorphisms with bitter taste preference.

Gene	SNP	Question item	Population	Model	OR (95% CI)	P	corrected p
CA6	rs2274333	Dark chocolate preference	HG	GG vs AG + AA	1.99 (1.01–3.91)	0.047	0.423
TAS2R19	rs10772420	Raw white cabbage preference	HG	GG + AG vs AA	1.86 (1.03–3.38)	0.041	0.369
CA6	rs2274333	Raw kohlrabi preference	HR	GG vs AG + AA	<i>0.36 (0.15–0.84)</i>	<i>0.018</i>	<i>0.162</i>
TAS2R19	rs10772420	Grapefruit preference	HR	AA + AG vs GG	<i>0.59 (0.38–0.91)</i>	<i>0.018</i>	<i>0.162</i>

HG: Hungarian general population, HR: Hungarian Roma population, SNP: single nucleotide polymorphism, OR = odds ratio (for higher preference), 95% CI: 95% confidence interval.

Bitter tasting food preferences were measured on a five-point Likert scale (ranging from 1 “dislike extremely”; 2 “dislike moderately”; 3 “indifferent”; 4 “like moderately”; to 5 “like extremely”).

p value was calculated by ordered logistic regression (covariates: sex, age, smoking, harmful alcohol consumption). corrected p: Bonferroni-corrected p value (number of tests: 9).

Only at least nominally significant associations are presented in the table. Italic indicates $0.05 < \text{corrected } p < 0.20$.

Table 5
Associations of selected polymorphisms with taste and food preferences.

Gene	SNP	Question item	Population	Model	OR (95% CI)	P	corrected p
TAS2R38	rs713598	Quantity of sugar added	HR	CC + GC vs GG	2.76* (1.22–6.22)	0.014	0.084 ^a
TAS2R38	rs713598	Vegetable consumption frequency	HG	CC vs GC + GG	1.70** (1.05–2.75)	0.032	0.288 ^b

HG: Hungarian general population, HR: Hungarian Roma population, SNP: single nucleotide polymorphism, OR= odds ratio, 95% CI: 95% confidence interval.

Quantity of sugar added represents the quantity of sugars added to consumed foods and beverages on average, per day (categories: 0, 1–4, 5–10, >10 teaspoons).

* OR for higher quantities.

Vegetable consumption frequency represents vegetable consumption during a week (categories: never, less than once a week, 1 to 3 times a week, 4 to 6 times a week, once a day, more than once a day).

** OR for higher consumption frequency.

p value was calculated by ordered logistic regression (covariates: sex, age, smoking, harmful alcohol consumption).corrected p: Bonferroni-corrected p value.

Only at least nominally significant associations are presented in the table. Italic indicates $0.05 < \text{corrected } p < 0.20$.

^a (number of tests for “Quantity of sugar added”, i.e. sweet taste: 6).

^b (number of tests for “Vegetable consumption frequency”, i.e. bitter taste: 9).

population significant associations were found between CA6 rs2274333 and salty taste preference; CD36rs 1527483 and TAS2R38 rs713598 and fat taste preference (Tables 2–5). Only nominally significant associations are presented in these tables, where the odds ratios (ORs) indicated show the direction of the effect comparable with our previous findings of Roma taste and food preferences (Diószegi et al., 2020).

3.2.1. Sample representative of the Hungarian general population

Ordered logistic regression analysis of the association of CD36 rs1527483 with fat taste preference resulted in an odds ratio of 2.24 (GG vs AG + AA; 95% CI: 1.18–4.25, $p = 0.014$) in the Hungarian sample. There was a significant association between the CA6 rs2274333 polymorphism and dark chocolate preference (GG vs AG + AA; OR = 1.99, 95% CI: 1.01–3.91, $p = 0.047$) among Hungarian individuals. The TAS2R19 rs10772420 polymorphisms was associated with raw white cabbage preference, GG homozygotes and AG heterozygotes having higher preference (OR = 1.86, 95% CI: 1.03–3.38, $p = 0.041$). The presence of two C alleles of TAS2R38 rs713598 was associated significantly with higher vegetable consumption frequency (OR = 1.70, 95% CI: 1.05–2.75, $p = 0.032$) in the HG sample. However, none of the p values remained significant after the multiple test correction (Tables 3–5).

3.2.2. Sample representative of Hungarian Roma living in segregated colonies

The analysis revealed that homozygosity of TAS2R38 rs713598 (GG vs GC + CC) and TRPV1 rs8065080 (TT vs CT + CC) was significantly associated with higher frequency of salting without tasting food (OR = 1.91; 95% CI: 1.08–3.37 $p = 0.026$ and OR = 1.66, 95% CI: 1.06–2.60, $p = 0.031$, respectively) among Roma. The same genotype of TRPV1 rs8065080 (TT vs CT + CC) was also associated with salty taste preference (OR = 1.57, 95% CI: 1.01–2.43, $p = 0.044$) and individuals with carrying at least one G allele of CA6 rs2274333 showed an odds ratio of 1.59 (95% CI: 1.02–2.48, $p = 0.041$) for higher salty taste preference in

the same study sample. The odds for higher degree of liking raw kohlrabi of CA6 rs2274333 GG homozygotes was 0.36 (95% CI: 0.15–0.84, $p = 0.018$) and for Roma hetero- or homozygous for the A allele of TAS2R19 rs10772420, the OR for higher grapefruit preference was found to be 0.59 (95% CI: 0.38–0.91, $p = 0.018$). For TAS2R38rs713598 the odds for higher quantities of sugar added to consumed foods and beverages on average, per day was 2.76 (CC + GC vs GG; 95% CI: 1.22–6.22, $p = 0.014$) in HR. These associations significant at the nominal significance level did not persist after the Bonferroni correction (Tables 2, 4 and 5).

3.2.3. Combined population of the Hungarian general and Roma populations

When analyzing the set of both HG and HR populations merged, CA6 rs2274333 was significantly associated with salty taste preference (GG + AG vs AA; OR = 1.52, 95% CI: 1.10–2.08, $p = 0.010$); CD36 rs1527483 with fat taste preference (GG vs AG + AA; OR = 1.83, 95% CI: 1.19–2.82, $p = 0.006$); and TAS2R38 rs713598 also with fat taste preference (CC + GC vs GG; OR = 1.54, 95% CI: 1.04–2.27, $p = 0.029$). After the Bonferroni correction these associations could not be confirmed (Tables 2 and 3).

4. Discussion

Understanding the nature of ethnic-specific differences in taste responses and perception is important, because taste perception may contribute to the development of unhealthy dietary practices. Individuals with different ethnic background may require personalized interventions to modify diet, taking into account the different sensory experiences when consuming foods. These differences can be a cause and/or consequence of cultural diversity in dietary habits or genetic-driven phenomena. Policies targeting only economic determinants of food choices to the equalization of the food diet between Roma and non-Roma are very simplified approaches. Early experiences with tastes during infancy and childhood plays an important role in the

development of dietary practices, since it is suggested that individuals with prior experience and higher consumption frequency with a food item generally express a greater liking compared to those with no prior exposure (Jamel, Sheiham, Cowell, & Watt, 1996; Mahar & Duizer, 2007; Tuorila, 1996.). Dietary taste experiences in different cultural/ethnic settings in later life stages may also alter preferences for simple taste stimuli (Beckerman, Alike, Lovin, Tamez, & Mattei, 2017; Moskowitz, Kumaraiah, Sharma, Jacobs, & Sharma, 1975) and lead to the development of ethnic based difference in suprathreshold sensitivity (Bertino, Beauchamp, & Jen, 1983). For instance sugary beverage consumption is more common among racial and ethnic minority groups and those of low socioeconomic status (Demmer, Cifelli, Houchins, & Fulgoni, 2018; Fundación Secretariado Gitano, 2007; Hamner, Perrine, Gupta, Herrick, & Cogswell, 2017; Larson, Ward, Neelon, & Story, 2011; Mennella, Ziegler, Briefel, & Novak, 2016; Parraga, Weber, Engel, Reeb, & Lerner, 1988; Rehm, Penalvo, Afshin, & Mozaffarian, 2016; Taveras, Gillman, Kleinman, Rich-Edwards, & Rifas-Shiman, 2013; Tovar, Vadi-veloo, Østbye, & Benjamin-Neelon, 2019), and more prevalent among Roma than majority populations in Europe as well (Bartosovic et al., 2014; Hijová, Gecková, Babinská, & HepaMeta Team, 2014; Olišarová et al., 2018; Rambousková et al., 2009; Sárváry et al., 2019; Velcheva & Baev, 2016). However, beyond socioeconomic status, other factors also play an important role in shaping the dietary habits of Roma, as proved by Ciaian et al. (Ciaian et al., 2018). Since results of studies suggest that perceived taste of foods may differ in terms of ethnic background [sweet (Baharuddin & Sharifudin, 2015; Bertino et al., 1983; Desor, Greene, & Maller, 1975; Druz & Baldwin, 1982; Mennella, Lukasewycz, Griffith, & Beauchamp, 2011; Salbe, DelParigi, Pratley, Drewnoski, & Tataranni, 2004; Shu-Fen, Forde, Tey, & Henry, 2018; Williams, Bartoshuk, Fillingim, & Dotson, 2016), bitter (Moskowitz et al., 1975; Shu-Fen, Forde, Tey, & Henry, 2018; Williams et al., 2016), salty (Bertino & Chan, 1986; Bertino et al., 1983; Desor et al., 1975; Shu-Fen, Forde, Tey, & Henry, 2018; Williams et al., 2016), fatty (Salbe et al., 2004) and sour (Baharuddin & Sharifudin, 2015; Moskowitz et al., 1975; Shu-Fen, Forde, Tey, & Henry, 2018; Williams et al., 2016; Yang, Williamson, Hasted, & Hort, 2020) food and taste preferences], it is reasonable to suppose the effect of genetic variations behind these phenomena.

4.1. Salty taste

In this current study, most of the nominally significant associations were found related to salty taste in the sample of Hungarian Roma, while no associations were revealed among representatives of the Hungarian general population. The molecular mechanism of salty taste detection is not clearly elucidated. However, the involvement of epithelial sodium channels (ENaCs), which are located in taste cell membranes in fungiform papillae and amiloride-sensitive vanilloid receptors (Trpv1), have been hypothesized in salt perception (Heck, Mierson, & De Simone, 1984; Lin, Finger, Rossier, & Kinnamon, 1999; Lyall et al., 2004). The ENaC channel is a heteromer consisting of four subunits ($\alpha\beta\gamma\delta$), which are coded by SCNN1A, SCNN1B, SCNN1G and SCNN1D genes in humans, respectively. The present study did not find any statistical evidence of association between the SCNN1B variant with either question item related to salty taste in the study populations. Findings related to this variant are inconclusive. In a study with 95 participants, rs239345 AA homozygotes perceived salt solutions as significantly weaker than heterozygotes or other allele homozygotes (Dias et al., 2013), and in another study with a sample size of 1020 Caucasian subjects, salty taste (NaCl, 200 mM) intensity ratings were significantly associated with this variant (AA genotype with highest means) (Barragán et al., 2018). However, this polymorphism was not significantly associated with salt sensitivity or salt taste thresholds in a sample of 20 predominantly young Caucasian subjects (Pilić & Mavrommatis, 2018).

In our study the TT genotype of TRPV1 rs8065080 was nominally associated with more frequent salting and also with higher salty taste preference among Roma. This polymorphism is a missense mutation

causing an amino acid change from isoleucine to valine, being potentially a functional variant in humans, the C allele resulting in a loss of function variant (Cantero-Recasens et al., 2010). In the Toronto Nutrigenomics and Health Study carriers of the T allele were significantly more sensitive to salt solutions at suprathreshold levels (potentially aversive, concentrations) than individuals with the CC genotype (i.e. reduced response), however liking/consumption was not assessed (Dias et al., 2013). A study conducted among twenty Caucasian subjects found that although the T allele was associated with higher sensitivity, T allele carriers consumed higher amounts of sodium than C allele carriers (Pilić & Mavrommatis, 2018). Although this latter finding is in line with our results in HR but only at the nominal significance level and could not be confirmed after the multiple test correction.

Only a limited number of studies are available related to the effect of TAS2R38 rs713598 and CA6 rs2274333 on salty taste preference but to make a comprehensive analysis, these genetic polymorphisms were also included in the association analyses. A study including 198 reportedly healthy, nonsmoker university students confirmed no association with rs713598 when rating the intensity of 1 M sodium chloride (Hayes, Bartoshuk, Kidd, & Duffy, 2008). However, PAV/PAV individuals were characterized by higher ratings for saltiness (NaCl) intensity in a population consisting of 393 individuals (Deshaware & Singhal, 2017). In our analysis, rs713598 GG homozygotes were more likely to salt without tasting food at higher frequencies than other genotypes among Hungarian Roma individuals, however this finding did not persist after the Bonferroni correction.

Feeney et al. suggested that the CA6 Ser90Gly rs2274333 could be related to difference in salt perception (Feeney & Hayes, 2014), but till now no other studies are available to strengthen this assumption. Our results indicated that Roma individuals carrying one or two G alleles (rs2274333) were characterized by higher salty taste preference, which effect was not changed when analyzing subjects of the Hungarian general population together with Hungarian Roma. However, the p values did not remain significant after the multiple test correction.

In brief, although nominally significant associations were observed between TRPV1, TAS2R38 and CA6 variants and salty taste phenotypes among Hungarian Roma, none of these remained significant after correction for multiple testing. Our most promising finding was observed in the combined population of Hungarian Roma and general populations between rs2274333 and salty taste preference ($0.05 < \text{corrected } p < 0.20$). Future studies with sufficient sample sizes are essential to analyze the effect of this polymorphism in Roma and also in other populations and should assess preference to elucidate the nutritional implications of this polymorphism in majority and minority populations.

4.2. Fat taste

The fatty acid translocase, coded by the CD36 gene is suggested to be involved in oral detection of fatty acids. It serves as a scavenger receptor and is responsible for the uptake of long-chain fatty acids across cell membranes, which is first step in fat metabolism (Hajri & Abumrad, 2002). CD36 is expressed on taste bud cells of rodents, pigs and humans (Fukuwatar et al., 1997; Laugerette et al., 2005; Pepino, Kuda, Samovski, & Abumrad, 2014) and has been detected in human foliate and circumvallatae papillae (Simons, Kummer, Luiken, & Boon, 2011). Two variants of this gene have been subject to research lately. Although according to previous results, the AA genotype of rs1761667 was associated with higher thresholds for lipid taste perception (decrease in sensitivity and consequent higher acceptance of fatty acids) compared to those with GG genotypes in several studies (Keller et al., 2012; Melis, Sollai, Muroi, Crnjar, & Barbarossa, 2015; Mrizak et al., 2015; Ong, Tan, & Say, 2017; Pepino, Love-Gregory, Klein, & Abumrad, 2012; Sayed et al., 2015), but this was not replicated in our study. Our finding may be related to the ethnic-specific association of this variant with fat taste perception (Burgess et al., 2018).

In our present study, the GG genotype of rs1527483 was nominally associated with higher fat taste preference (presumably lower sensitivity) in HG and also when increasing the sample size with adding HR to the study sample. It is important to mention that these nominally significant associations did not persist after the multiple test correction, although could be considered as promising ($0.05 < \text{corrected } p < 0.20$). These results significant at the nominal significance level are supported by previous findings as well. In case of this intronic polymorphism C/T or T/T subjects perceived greater fat content of salad dressings and cream crackers, independent of fat concentration in previous studies (Keller et al., 2012), (Ong et al., 2017). However, in one study no association was revealed with threshold for oleic acid (Melis et al., 2015). The ethnic-specific effect of a CD36 variant on fat taste perception was demonstrated in case of the rs1761667. The polymorphism was associated with differences in the perception of fattiness and creaminess among East Asians, but not Caucasians (Burgess et al., 2018). The rs1527483 could be a focus of future studies to confirm or results and explore its role in fat taste preference.

Preceding findings related to TAS2R38 variants and fat taste preference are inconclusive. No association of rs713598 was found with fat intake during a test meal among children and among adults (rs713598, rs10246939) (Inoue et al., 2013; Keller et al., 2014). In contrast, AVI/-AVI subjects exhibited a 5-fold higher oleic acid threshold than PAV/-PAV subjects in a study conducted among 64 non-smoking Caucasian subjects from Sardinia, Italy (Melis et al., 2015). Still, we chose to include rs713598 in our analysis to provide a comprehensive view about fat taste preference in our study populations. Participants carrying the C allele showed an odds ratio of 1.54 for higher preferences, but only in the combined HG + HR population and only at the nominal significance level and not after the multiple test correction. Further investigations with greater sample sizes are essential to elucidate the effect of this genetic variant on fat taste preference.

4.3. Bitter taste

The genetically determined bitter PROP taster phenotype has been the most extensively studied with the majority of genetic association studies focusing on sequence variations in the TAS2R38 gene. The three PROP taster categories, supertaster-taster-non-taster (Bartoshuk, Duffy, & Miller, 1994; Harris & Kalmus, 1949) are linked to combinations of three functional TAS2R38 SNPs (rs713598, rs1726866, rs10246939). The homozygous PAV (proline-alanine-valine) haplotype specifies the taster phenotype, the homozygous AVI (alanine-valine-isoleucine) haplotype defines the non-taster category and heterozygotes possess intermediate sensitivity to PROP and PTC (Kim & Drayna, 2005; Kim et al., 2003), accounting for 85% in PTC perception variance (Bufe et al., 2005; Wooding et al., 2004). Based on the results of in vitro assays, rs713598 has the greatest effect, rs1726866 possesses weaker effects, and rs10246939 has no detectable effect at all on bitter taste signal transduction (Bufe et al., 2005). In addition to the bitter compounds PROP and PTC, the association of these variants was widely tested and found to be associated with the preference of bitter tasting food items and sweeteners, i.e. bitter tasting vegetables, berries, wine/alcohol, thioamide and salicin (Behrens, Gunn, Ramos, Meyerhof, & Wooding, 2013; Bering, Pickering, & Liang, 2014; Carrai et al., 2017; Colares-Bento et al., 2012; Keller et al., 2014; Kim et al., 2003; Ledda et al., 2014; Lucock et al., 2011; Melis et al., 2013; Mennella, Pepino, Duke, & Reed, 2011; Mennella, Reed, Roberts, Mathew, & Mansfield, 2014; Ooi, Lee, Law, & Say, 2010; Risso et al., 2017; Robino et al., 2016; Wooding et al., 2010). The results regarding cruciferous/Brassica vegetable intake are inconclusive showing associations (Feeney, O'Brien, Scannell, Markey, & Gibney, 2011; Sacerdote et al., 2007), but no associations were sporadically reported as well (Inoue et al., 2013; Negri et al., 2012).

The present study revealed no association of the TAS2R38 variant with the preference of either bitter tasting food items (vegetables: raw

kohlrabi, raw white cabbage, raw cauliflower; grapefruit, dark chocolate, black coffee). As described above, the majority of the studies proved associations with bitter-tasting vegetable preference. In one study, conducted on 7–13 year old Irish children, TAS2R38 genotype had no significant impact on bitter vegetable liking (Feeney, O'Brien, Scannell, Markey, & Gibney, 2014). It is also possible that the preference of these bitter vegetables is linked to other genes not investigated in our present study, since the preference of broccoli, belonging also to the Brassica genus, was found to be related to rs2530184 and rs9832668 using a food preference questionnaire in a genome-wide association study (GWAS) and other polymorphisms, LINC02346 rs8034691, LOC105377448 rs28849980 were found associated with artichokes liking (Pirastu, Kooyman, Traglia, et al., 2016). Furthermore, another reason for non-replication could be, that liking of these vegetables was analyzed separately in our study, which approach was not applied before in genetic association studies.

In accordance with our results, the relationship between TAS2R38 and dark chocolate and coffee liking was examined and no associations were revealed by others (Pirastu et al., 2012). However, other genetic variations were found to associate with these phenotypes. TAS2R3, -R4, and -R5 haplotype allelic variation explained variability in coffee bitterness (Hayes et al., 2011); rs14567120 associated with coffee liking in a GWAS (Pirastu, Kooyman, Traglia, et al., 2016); PRH1-TAS2R14 rs8181 associated with caffeine detection threshold and rs2708377 associated with the perceived bitterness and detection threshold of caffeine (GWAS) (Ledda et al., 2014). The association of TAS2R43 variants (rs35720106, rs68157013, rs71443637) was demonstrated with coffee liking (Pirastu et al., 2014) and PDSS2 polymorphisms (rs2216084, rs6568479, rs6942255, rs7745311, rs7754744, rs9386630) with coffee consumption (GWAS) (Pirastu, Kooyman, Traglia, et al., 2016). Furthermore, DFNA5 rs73082019 showed a significant association with preference of dark chocolate (GWAS) (Pirastu, Kooyman, Traglia, et al., 2016). These polymorphisms should also be tested in future studies with preference of the bitter-tasting dark chocolate and black coffee.

In addition, the bitter taste PROP phenotype may also be influenced by the salivary carbonic anhydrase VI (CA6) or gustin protein, which is secreted by the parotid, submandibular and von Ebner glands (Henkin, Lippoldt, Bilstad, & Edelhoch, 1975; Piras, Tandler, Tomassini Barbarossa, & Piludu, 2012). Our analysis revealed a nominally significant association of rs2274333 with dark chocolate preference (GG vs AG + AA, OR = 1.99) in the reference sample and with raw kohlrabi preference (GG vs AG + AA, OR = 0.36) among Roma, but none of the p values remained significant after the multiple test correction. The CA6 rs2274333 SNP causes the amino acid substitution at position Ser90Gly in the protein sequence (Henkin et al., 1975) and was found to be associated with formation and function of fungiform papillae (Barbarossa et al., 2015), but findings related to the association between this variant and bitter taste sensitivity and preference are inconclusive (Bering, Pickering, & Liang, 2014; Cabras et al., 2012; Calo et al., 2011; Feeney et al., 2014; Melis et al., 2013; Padiglia et al., 2010; Risso et al., 2017). Studies with positive associations found that the AA genotype and A allele were more frequent in PROP supertasters, whereas genotype GG and allele G were more frequent in non-tasters (Cabras et al., 2012; Calo et al., 2011; Melis et al., 2013; Padiglia et al., 2010), but other studies found no association with PROP taster status (Bering, Pickering, & Liang, 2014; Feeney & Hayes, 2014; Risso et al., 2017). Our result shows a similar inconclusive pattern at the nominal significance level and even the direction of the effect of this variant is different in the two populations. Although certainly it is important to highlight that no studies investigated the effect of this polymorphism on these phenotypes before.

The variant TAS2R19 rs10772420, coding for an arginine-to-cysteine substitution at amino acid 299 (Allen, McGeary, Knopik, & Hayes, 2013) showed associations with quinine and grosheimin intensity ratings, grosheimin detection threshold and bitterness perception of grapefruit

juice (Hayes et al., 2011; Hayes, Feeney, Nolden, & McGeary, 2015; Knaapila et al., 2012; Reed et al., 2010; Roudnitzky et al., 2015) and no association with PROP phenotype (Bering, Pickering, & Liang, 2014) in former studies. Although, these confirmed associations may be due to strong linkage disequilibrium (LD) between the Arg299Cys (rs10772420) polymorphism, and other SNPs located in nearby TAS2R genes (Allen et al., 2013; Hayes et al., 2015), since quinine did not activate TAS2R19 *in vitro* (Meyerhof et al., 2009; Thalmann, Behrens, & Meyerhof, 2013). In line with previous studies, we demonstrated that the A allele carriers reported lower grapefruit preference in the Roma study sample compared to GG homozygotes. We discovered a new association between this variant and raw white cabbage preference in HG, where individuals with the G allele showed higher preference. This latter finding was not investigated before. None of our results related to TAS2R19 persisted after the multiple test correction.

Among all the nominal significant *p* values presented herein for bitter taste preferences, the associations between CA6 rs2274333 and raw kohlrabi preference and TAS2R19 rs10772420 and grapefruit preference are noteworthy ($0.05 < \text{corrected } p < 0.20$) in the Roma sample. Independent replication of these associations would be an important aspect for the interpretation of our results.

4.4. Vegetable consumption

Although the literature about the association between bitter tasting vegetable preference and TAS2R38 polymorphisms is abundant, but the number of studies focusing on the consumption of bitter tasting vegetables is low and the results are inconclusive. Similarly, the number of studies investigating vegetable consumption in general, without grouping them based on taste attributes, is limited and ambiguous. No association of rs713598 genotype was found with vegetables in a cross-sectional study in Italy and no aversion to vegetables was revealed among Malaysian subjects either (Ooi et al., 2010; Perna et al., 2018). Some studies investigated not only the rs713598, but haplotypes, but the results were still conflicting. PAV homozygotic Finnish women consumed fewer vegetables than did the AVI homozygotic women and participants with PAV homozygous or heterozygous haplotype had lower odds of being in the higher vegetable intake group compared to TAS2R38 AVI homozygotes (Sandell et al., 2014; Smith et al., 2020). Moreover, AVI homozygotes reported consuming significantly more servings of vegetables than did individuals carrying at least one copy of the PAV allele in a sample of college-aged 59 reportedly healthy individuals (Duffy et al., 2010). These findings may be attributed to the different diet composition of populations, i.e. the proportion of bitter-tasting vegetables among the total vegetables consumed may vary in different study populations. In our present research, we did not obtain information on the type or taste of the vegetables (bitter/sweet) (Ooi et al., 2010), only on the frequency of consumption, therefore our result should be interpreted with caution and prospectively replicated.

In our study we observed that CC homozygotes of TAS2R38 rs713598 in the Hungarian general population were more likely to consume vegetables more frequent. Although this finding could not be confirmed after the multiple test correction. There is no information available about the types of vegetables consumed in our study groups, but it is reasonable to suppose that the diversity of vegetables consumed by Roma is inferior compared to HG and according to our previous research Hungarian Roma are less likely to prefer and presumably consume bitter-tasting vegetables compared to Hungarian individuals (Diószegi et al., 2020). Based on our current result, we cannot draw a clear conclusion considering the effect of this genetic polymorphism on vegetable consumption.

4.5. Sweet taste

The two G protein-coupled receptors, taste receptor type 1 member 2 and taste receptor type 1 member 3 (Li et al., 2002; Nelson et al., 2001;

Zhao, 2003), which are encoded by genes TAS1R2 and TAS1R3, are two transmembrane proteins, which form a heterodimer and respond to sweet substances. The number of studies investigating TAS1R2 and TAS1R3 polymorphisms in connection with sweet taste preference and sensitivity is limited and findings are ambiguous (Diószegi et al., 2019). It was demonstrated that the T allele of the TAS1R3 rs307355, which resides upstream of the TAS1R3 coding sequence, results in reduced promoter activity in comparison to the C alleles, which is in line with human data, where the T allele was found to be associated with reduced sweet taste sensitivity (Fushan, Simons, Slack, Manichaikul, & Drayna, 2009) and was also found to be an independent risk factor for dental caries among school-aged children (Haznedaroğlu et al., 2015). Still, in the study of 32 adult students and staff of the University of Queensland no correlation with sweet taste sensitivity was demonstrated (Han, Keast, & Roura, 2017). Similarly, in our study this polymorphism was not associated either with sweet taste preference or quantity of sugar added to consumed foods or beverages.

The current association analysis of TAS2R38 rs713598 revealed a nominally significant association with higher quantities of sugar added to consumed food items (CC + GC vs GG) in the Roma study sample, which population was found to add more sugars compared to the Hungarian reference sample previously (Diószegi et al., 2020). Although this effect of the polymorphism on sweet preference is supported by the literature, after the Bonferroni correction the associations could not be confirmed. Higher preference of PP children compared to AA children (AP intermediate preference) was demonstrated for sucrose and beverages with higher sugar content, and GG subjects did not prefer dessert and chocolate. Furthermore, the P allele was found to be more common in children with lower sucrose thresholds (Joseph, Reed, & Mennella, 2016; Lipchok, Reed, & Mennella, 2012; Perna et al., 2018). The PP/PA genotype was associated with a higher intake of sweet tasting foods in children, and children with AP or PP consumed more chocolate chip cookies at the test-meal, than children with the AA genotype (Keller et al., 2014; Pawellek et al., 2016). The majority of PAV/PAV and PAV/AVI children liked the bilberries with high sugar content and PAV homozygotes consumed more sweet foods than AVI homozygotes (Sandell et al., 2014; Suomela et al., 2012). Considering these results reported in the literature and the Bonferroni-corrected *p* values ($0.05 < \text{corrected } p < 0.20$) in our analysis, TAS2R38 rs713598 could be considered as a promising result of our study.

5. Interpretation

In summary, none of the genetic variants investigated in our current study passed the Bonferroni-corrected probability criterion. Meanwhile, our most promising results (CA6 rs2274333 with salty taste and raw kohlrabi preference, CD36 rs1527483 with fat taste preference, TAS2R19 rs10772420 with grapefruit preference, and TAS2R38 rs713598 with quantity of sugar added) showed potential ethnicity-specific effects. This ethnicity-dependent phenomenon is supported by results of other genetic association studies. Significant results identified in one ethnic group were not found to be always reproducible on other ethnicities even in well-powered studies according to several reviews, meta-analyses and studies of case-control design (Castaño-Rodríguez, Kaakoush, Goh, Fock, & Mitchell, 2013; Chen et al., 2012; Fang, Xiao, Fang, Li, & Fei, 2020; Garte, 1998; Goldenberg et al., 2006; C.; Han, Han, Liu, & Huang, 2017; Harishankar, Selvaraj, & Bethunaickan, 2018; Jia, Xie, Shi, & Li, 2017; Jing, Su, & Ring, 2014; Radha et al., 2006; Swinney et al., 2011). Similar findings were published related to the single nucleotide polymorphism rs1761667 of CD36, which has been shown to differentially impact the perception of fatty acids in the samples of Caucasian and East Asian young adults (Burgess et al., 2018). The possible reasons for different associations of certain genetic markers among ethnic groups could be due to the existence of ethnic differences in genetic linkage disequilibrium (LD) (Garte, 1998; Jia et al., 2017). The effect alleles investigated may be linked to other real causative

allele(s) with differing strengths between the ethnic groups (Jing et al., 2014). Consequently, the impact of polymorphisms of interest might be diluted or masked by other as-yet unidentified causal genes involved in the development of phenotypes (Han, Han, et al., 2017). Future studies should therefore investigate adjacent polymorphisms to confirm whether the association is causal or is related to different ethnic-specific extent of LD, due to regional variability, genetic drift, and mating patterns (Salanti, Sanderson, & Higgins, 2005). Other possible explanations include that certain alleles act in a different manner in different populations (Garte, 1998; Jing et al., 2014). Using self-reported ethnicity may alter results of association studies as well (Cardon & Palmer, 2003; Jing et al., 2014). It is also important to mention, that convincing findings of genetic association studies available in the literature only exist for bitter taste. Many of the results of genetic association studies on different taste modalities have not been or couldn't have been replicated, which could be explained by different factors. Some studies had relatively small sample sizes and used various phenotype assessment methods. Results suggest that culture and experience may override effects of genotype on food preferences during adulthood (Chamoun et al., 2018; Mennella, Pepino, & Reed, 2005). The effect of other modifying factors not included in our study should also be considered, which could be even ethnicity specific or independent of it. The effects of environmental factors on food preferences in the Roma population are certainly not negligible.

6. Limitations

Several limitations must be considered when interpreting the findings of our study. The Roma study population was not representative of the overall Hungarian Roma population. The sample contained randomly drawn subjects from Roma living in segregated colonies in Northeast Hungary. Roma individuals who were, to various degrees, assimilated with the Hungarian general population were not included in the analysis. Many people are reluctant to self-define themselves as Roma; therefore, the reference sample of the Hungarian general population included some Roma people as well. Furthermore, sweet, fat and salt preference was assessed by only single questions, while bitter preference was assessed with questions for six bitter-tasting food items and beverages individually. We have adapted these type of questions from a two-center, cross-sectional Italian study, which tested some preferences with single questions (Perna et al., 2018). It was important to include several questions for bitter preference, due to several receptors and associations identified for bitter taste (not the case for sweet taste) (Diószegi et al., 2019). It is also important to note that we did not have information of medication used, which may have potentially affected taste perception and preference.

Although we initially observed associations between certain genetic polymorphisms and taste and food preferences, the p values did not remain significant after the Bonferroni correction. Since the sufficient number of genetic association studies, with the exception of TAS2R38 on bitter taste is lacking in the literature and genetic association studies related to taste and food preferences have not been conducted in the Hungarian general and Roma populations, our results raise the possibility that genetic polymorphisms may influence taste and food preferences in our study samples.

7. Conclusion

This paper is the first report on potential associations between genetic polymorphism and taste and food preferences on a Roma population sample. Our results should be interpreted with caution, but findings may suggest that genetics may mediate food preferences in populations with different ethnic background which may require personalized interventions to modify diet. Since no other studies are available in Roma ethnic groups to determine whether ethnicity is a factor that modulates the effects of polymorphism investigated in our study in predicting taste

and food preferences, it is still important to emphasize that further genetic research is needed to elucidate the effect of genetic variants on food preference and nutritional behavior. Future work in this area is needed to better identify factors and their effects on diet diversity differentials between Roma and non-Roma.

Author contributions

JD was involved in the development of the questionnaire regarding taste and food preferences, selection of genetic variants investigated, data analysis and manuscript writing. AAMK participated in the manuscript preparation and data analysis. PP took part in the creation of the database, and in the coding and sorting process and analysis of data. ZK and JS were involved in the design of the complex comparative health survey and data collection. RÁ took part in all steps of the development of the complex comparative health survey, guided the writing of the manuscript and was involved in finalizing it.

Ethical statement

The study was approved by the Ethical Committee of the Hungarian Scientific Council on Health (61327–2017/EKU). Written informed consent was obtained from all participants in each study population in accordance with the Declaration of Helsinki.

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Declaration of competing interest

None.

Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.appet.2021.105270>.

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