Flavour

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A genetic variant near olfactory receptor genes influences cilantro preference

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Abstract

Background: The leaves of the *Coriandrum sativum* plant, known as cilantro or coriander, are widely used in many cuisines around the world. However, far from being a benign culinary herb, cilantro can be polarizing—many people love it while others claim that it tastes or smells foul, often like soap or dirt. This soapy or pungent aroma is largely attributed to several aldehydes present in cilantro. Cilantro preference is suspected to have a genetic component, yet to date nothing is known about specific mechanisms.

Results: Here, we present the results of a genome-wide association study among 14,604 participants of European ancestry who reported whether cilantro tasted soapy, with replication in a distinct set of 11,851 participants who declared whether they liked cilantro. We find a single-nucleotide polymorphism (SNP) significantly associated with soapy-taste detection that is confirmed in the cilantro preference group. This SNP, rs72921001 ($p = 6.4 \times 10^{-9}$, odds ratio 0.81 per A allele), lies within a cluster of olfactory receptor genes on chromosome 11. Among these olfactory receptor genes is *OR6A2*, which has a high binding specificity for several of the aldehydes that give cilantro its characteristic odor. We also estimate the heritability of cilantro soapy-taste detection in our cohort, showing that the heritability tagged by common SNPs is low, about 0.087.

Conclusions: These results confirm that there is a genetic component to cilantro taste perception and suggest that cilantro dislike may stem from genetic variants in olfactory receptors. We propose that one of a cluster of olfactory receptor genes, perhaps *OR6A2*, may be the olfactory receptor that contributes to the detection of a soapy smell from cilantro in European populations.

Keywords: Cilantro, Coriander, Olfactory receptor, Genetics of taste and smell

Background

The *Coriandrum sativum* plant has been cultivated since at least the second millennium BCE [1]. Its fruits (commonly called coriander seeds) and leaves (called cilantro or coriander) are important components of many cuisines. In particular, South Asian cuisines use both the leaves and the seeds prominently, and Latin American food often incorporates the leaves.

The desirability of cilantro has been debated for centuries. Pliny claimed that coriander had important medicinal properties: *'vis magna ad refrigerandos ardores viridi'* ('while green, it is possessed of very cooling and refreshing properties') [2]. The Romans used the leaves and seeds in many dishes, including moretum (a herb, cheese, and garlic spread similar to today's pesto) [3]; the Mandarin word for cilantro, 香菜 (*xiāngcài*), literally means 'fragrant greens.' However, the leaves in particular have long inspired passionate hatred as well, e.g., John Gerard called it a 'very stinking herbe' with leaves of 'venemous quality' [4,5].

It is not known why cilantro is so differentially perceived. The proportion of people who dislike cilantro varies widely by ancestry [6]; however, it is not clear to what extent this may be explained by differences in environmental factors, such as frequency of exposure. In a twin study, the heritability of cilantro dislike has been estimated as 0.38 (confidence interval (CI) 0.22–0.52) for odor and 0.52 (CI 0.38–0.63) for flavor [7].

The smell of cilantro is often described as pungent or soapy. It is suspected, although not proven, that cilantro dislike is largely driven by the odor rather than the taste.

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Table 1 Summary of the cohorts used in the analysis

	N	Proportion female	Age (SD)
Tastes soapy	1,994	0.566	49.0 (15.0)
Does not taste soapy	12,610	0.489	48.3 (15.2)
Total	14,604	0.500	48.4 (15.2)
Dislikes cilantro	3,181	0.487	47.1 (16.6)
Likes cilantro	8,906	0.420	43.8 (14.5)
Total	12,087	0.438	44.7 (15.1)

The key aroma components in cilantro consist of various aldehydes, in particular (E)-2-alkenals and *n*-aldehydes [8,9]. The unsaturated aldehydes (mostly decanal and dodecanal) in cilantro are described as fruity, green, and pungent; the (E)-2-alkenals (mostly (E)-2-decenal and (E)-2-dodecenal) as soapy, fatty, 'like cilantro,' or pungent [8,9].

Several families of genes are important for taste and smell. The TAS1R and TAS2R families form sweet, umami, and bitter taste receptors [10,11]. The olfactory receptor family contains about 400 functional genes in the human genome. Each receptor binds to a set of chemicals, enabling one to recognize specific odorants or tastants. Genetic differences in many of these receptors are known to play a role in how we perceive tastes and smells [12-15].

Results and discussion

Here, we report on a genome-wide association study (GWAS) of cilantro soapy-taste detection. Briefly, the GWAS was conducted in 14,604 unrelated participants of primarily European ancestry who responded to an online questionnaire asking whether they thought cilantro tasted like soap (Table 1). Two single-nucleotide polymorphisms (SNPs) were genome-wide significant ($p < 5 \times 10^{-8}$) in this population. One SNP, in a cluster of olfactory receptors, replicated in a non-overlapping group of 11,851 participants (again, unrelated and of primarily European ancestry) who reported whether they liked or disliked cilantro (see the 'Methods' section for full details). Figure 1 shows *p* values across the whole genome; Figure 2 shows *p* values near the most significant associations. A quantile-quantile plot (Additional file 1) shows little ($\lambda = 1.007$) global inflation of *p* values. Index SNPs with *p* values under 10^{-6} are shown in Table 2 (along with replication *p* values); all SNPs with *p* values under 10^{-4} are shown in Additional file 2.

We found one significant association for cilantro soapy-taste that was confirmed in the cilantro preference population. The SNP rs72921001 ($p_{\text{discovery}} = 6.4 \times 10^{-9}$, odds ratio (OR) = 0.81, $p_{\text{repl}} = 0.0057$) lies on chromosome 11 within a cluster of eight olfactory receptor genes: *OR2AG2*, *OR2AG1*, *OR6A2*, *OR10A5*, *OR10A2*, *OR10A4*, *OR2D2*, and *OR2D3*. The C allele is associated with both detecting a soapy smell and disliking cilantro. Of the olfactory receptors encoded in this region, *OR6A2* appears to be the most promising candidate underlying the association with cilantro odor detection. It is one of the most studied olfactory receptors (often as the homologous olfactory receptor I7 in rats) [16-19]. A wide range of odorants have been found to activate this receptor, all of which are aldehydes [17]. Among the unsaturated aldehydes, octanal binds best to rat I7 [18]; however, compounds ranging from heptanal to undecanal also bind to this receptor [17]. Several singly unsaturated *n*-aldehydes also show high affinity, including (E)-2-decenal [17]. These aldehydes include several of those playing a key role in cilantro aroma, such as decanal and (E)-2-decenal. Thus, this gene is particularly interesting as a candidate for cilantro odor detection. The index SNP is also in high LD ($r^2 > 0.9$) with three non-synonymous SNPs in *OR10A2*, namely rs3930075, rs10839631, and rs7926083 (H43R, H207R, and K258T, respectively). Thus, *OR10A2* may also be a reasonable candidate gene in this region.

The second significant association, with rs78503206 ($p_{\text{discovery}} = 3.2 \times 10^{-8}$, OR = 0.68, $p_{\text{repl}} = 0.49$), lies in an intron of the gene *SNX9* (sorting nexin-9; see Figure 2). *SNX9* encodes a multifunctional protein involved in intracellular trafficking and membrane remodeling during endocytosis [20]. It has no known function in taste or smell and did not show association with liking cilantro in the replication population. This SNP is located about 80 kb upstream of *SYNJ2*, an inositol 5-phosphatase thought to be involved in membrane trafficking and signal

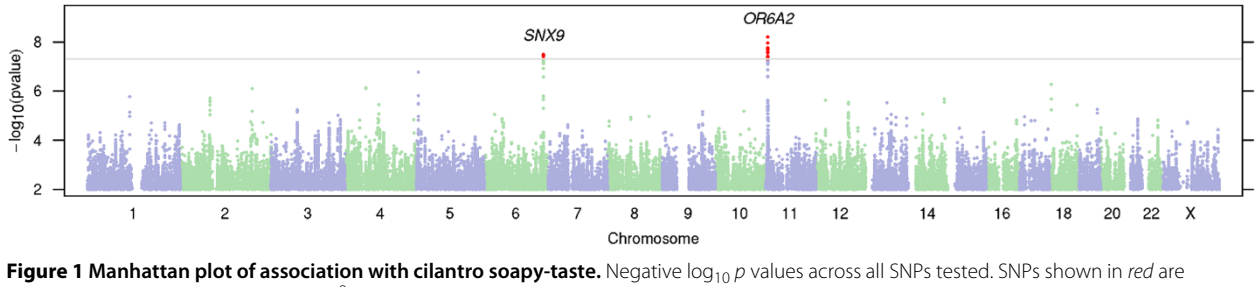

Figure 1 Manhattan plot of association with cilantro soapy-taste. Negative $\log_{10}$ *p* values across all SNPs tested. SNPs shown in *red* are genome-wide significant ($p < 5 \times 10^{-8}$). Regions are named with the postulated candidate gene.

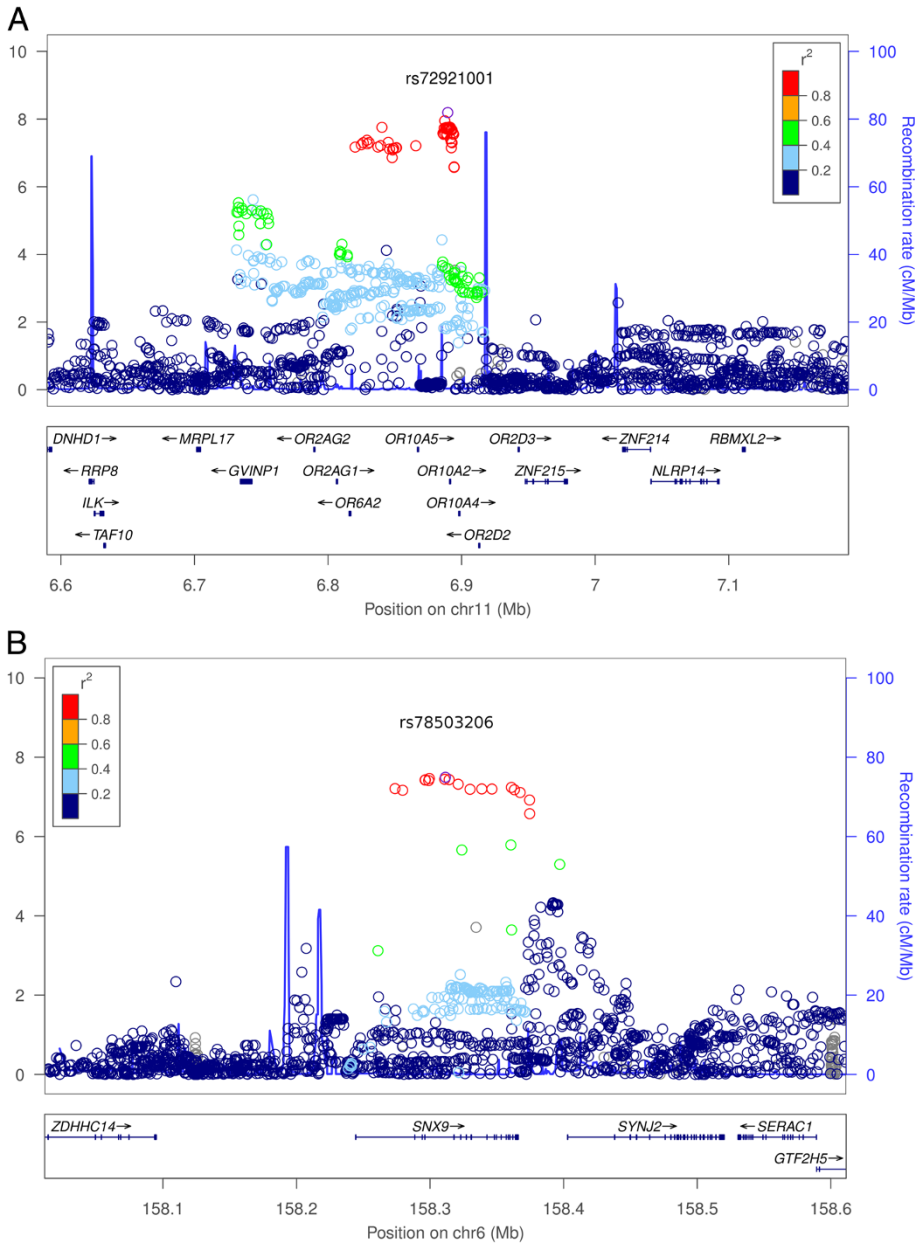

Figure 2 Associations with cilantro soapy-taste near rs72921001 (A) and rs78503206 (B). Negative $\log_{10}$ *p* values for association (*left axis*) with recombination rate (*right axis*). *Colors* depict the squared correlation (r^2) of each SNP with the most associated SNP ((A) rs72921001 and (B) rs78503206, shown in *purple*). *Gray* indicates SNPs for which r^2 information was missing.

transduction pathways. In candidate gene studies, *SYNJ2* SNPs were found to be associated with agreeableness and symptoms of depression in the elderly [21] and with cognitive abilities [22]. In mice, a *Synj2* mutation causes recessive non-syndromic hearing loss [23]. Given recent evidence that the perception of flavor may be influenced by multiple sensory inputs (*cf.* [24,25]), we cannot exclude the *SYNJ2*-linked SNP as conveying a biologically meaningful association. While this SNP may be a false positive, it could also be the case that this SNP is associated only with detecting a soapy smell in cilantro (and not in liking cilantro). In addition, we were unable to replicate the SNPs that were found to be nominally significant for cilantro dislike in [26] (we saw *p* values in the GWAS of 0.53, 0.41, and 0.53 for rs11988795, rs1524600, and rs10772397, respectively).

We have used two slightly different phenotypes in our discovery and replication, soapy-taste detection and

Table 2 Index SNPs for regions with $p < 10^{-6}$ for cilantro soapy-taste

SNP	Chromosome	Position	Gene	Allele	MAF	r^2	$p_{discovery}$	p_{repl}	OR (CI)
rs72921001	11	6,889,648	*OR6A2*	C/A	0.364	0.969	6.4×10^{-9}	0.0057	0.809 (0.753–0.870)
rs78503206	6	158,311,499	*SNX9*	C/T	0.077	0.980	3.2×10^{-8}	0.49	0.679 (0.588–0.784)
chr5:4883483	5	4,883,483	*ADAMTS16*	C/T	0.032	0.885	1.7×10^{-7}	0.51	0.526 (0.405–0.683)
rs7227945	18	4,251,279	*DLGAP1/LOC642597*	T/G	0.055	0.920	5.3×10^{-7}	0.96	1.447 (1.258–1.663)
rs6554267	4	56,158,891	*KDR/SRD5A3*	T/G	0.019	0.651	7.4×10^{-7}	0.85	1.975 (1.529–2.549)
rs13412810	2	192,420,461	*MYO1B/OBFC2A*	G/A	0.141	0.942	7.9×10^{-7}	0.78	0.770 (0.693–0.857)

The index SNP is defined as the SNP with the smallest *p* value within a region. The listed gene is our postulated candidate gene near the SNP. Alleles are listed as major/minor (in Europeans). MAF is the frequency of the minor allele in Europeans, and r^2 is the estimated imputation accuracy. $p_{discovery}$ and p_{repl} are the discovery and replication *p* values, respectively. The OR is the discovery odds ratio per copy of the minor allele (e.g., the A allele of rs72921001 is the allele associated with a lower risk of detecting a soapy taste).

cilantro preference, which are correlated ($r^2 \approx 0.33$). Detection of a soapy taste is reportedly one of the major reasons people seem to dislike cilantro. Despite having over 10,000 more people reporting cilantro preference, we have used soapy-taste detection as our primary phenotype because it is probably influenced by fewer environmental factors. Indeed, we see a stronger effect of rs72921001 on soapy-taste detection than on cilantro preference (OR of 0.81 versus 0.92). A GWAS on the replication set gave no genome-wide significant associations. SNPs with *p* values under 10^{-6} for this analysis are shown in Additional file 3.

We find significant differences by sex and ancestral population in soapy-taste detection (Tables 1 and 3). Women are more likely to detect a soapy taste (and to dislike cilantro) (OR for soapy-taste detection 1.36, $p = 2.5 \times 10^{-10}$; Table 1). African-Americans, Latinos, East Asians, and South Asians are all significantly less likely to detect a soapy taste compared to Europeans (ORs of 0.676, 0.637, 0.615, and 0.270, respectively, $p < 0.003$; see Table 3). Ashkenazi Jews and South Europeans did not show significant differences from Northern Europeans ($p = 0.84$ and 0.65, respectively). We tested the association between rs72921001 and soapy-taste detection within each population. Aside from the European populations, there was only a significant association in the small South Asian group ($p = 0.0078$, OR = 0.18, 95% CI 0.053–0.64). This association is in the same direction as the association in Europeans. Note that the GWAS population in Table 1 is a subset of the 'Europe all' population in Table 3, filtered to remove relatives (see the 'Methods' section). While the differences in allele frequency across populations do not explain the differences in soapy-taste detection, our analysis does suggest that this SNP may affect soapy-taste detection in non-European populations as well.

We calculated the heritability for cilantro soapy-taste detection using the GCTA software [27]. We found a low heritability of 0.087 ($p = 0.08$, 95% CI −0.037 to 0.211). This estimate is a lower bound for the true heritability, as our estimate only takes into account heritability due to SNPs genotyped in this study. While this calculation does not exclude a heritability of zero, the existence of the association with rs72921001 does give a non-zero lower bound on the heritability. Despite the strength of the association of the SNP near *OR6A2*, it explains only about 0.5% of the variance in perceiving that cilantro tastes soapy. Our heritability estimate is lower than those given in a recent twin

Table 3 Cilantro soapy-taste by ancestry

Population	Not soapy (%)	Soapy (%)	Total	MAF	*p* value
Ashkenazi	634 (85.9%)	104 (14.1%)	738	0.355	0.56
South Europe	458 (86.6%)	71 (13.4%)	529	0.335	0.25
Europe all	13,213 (87.0%)	1,973 (13.0%)	15,186	0.373	1.23×10^{-8}
North Europe	11,794 (87.2%)	1,736 (12.8%)	13,530	0.376	1.17×10^{-8}
All	16,196 (87.6%)	2,299 (12.4%)	18,495	0.356	3.94×10^{-8}
African-American	545 (90.8%)	55 (9.2%)	600	0.224	0.87
Latino	820 (91.3%)	78 (8.7%)	898	0.350	0.29
East Asia	424 (91.6%)	39 (8.4%)	463	0.283	0.22
South Asia	322 (96.1%)	13 (3.9%)	335	0.371	0.0078

Number of people detecting a soapy taste by ancestry group, sorted from most to least soapy-taste detection. For reference, we have added the minor allele frequency of rs7107418 in each group. This SNP is a proxy for rs72921001 ($r^2 > 0.98$), with the minor G allele of rs7107418 corresponding to the minor A allele of rs72921001 (which is associated with less soapy tasting). The *p* value is the *p* value of association between soapy-taste and rs7107418 in each group.

study (0.38 for odor and 0.52 for flavor) [7]. This could be due to the differences in phenotypes measured between the two studies, or it could be possible that other genetic factors not detected here could influence cilantro preference. For example, there could be rare variants not typed in this study (possibly in partial linkage disequilibrium with rs72921001) that have a larger effect on cilantro preference. Such rare variants could cause the true heritability of this phenotype to be larger than we have calculated. For example, the heritability of height is estimated to be about 0.8; however, the heritability tagged by common SNPs is calculated at about 0.45 [26]. We note that there can be epigenetic modifiers of taste as well, for example, food preferences can even be transmitted to the fetus *in utero* through the mother's diet [24].

Survey responses, while very efficient for collecting large amounts of data, can only approximately measure the detection and/or perception of the chemicals in cilantro. This has implications for the interpretation of our results. For example, it is possible that the SNP rs72921001 could have a large effect on detection of a specific chemical in cilantro, but that the resulting effect on liking cilantro is much weaker, being modulated by environmental factors. For example, many people might initially dislike cilantro yet later come to appreciate it. This environmental component could also be the reason that our heritability estimates are low. It would thus be interesting to study the genetics of cilantro taste/odor perception in a group without prior exposure to cilantro to reduce the environmental effect, using more direct measures of cilantro perception (i.e., having the subjects actually taste and smell cilantro).

Conclusions

Through a GWAS, we have shown that a SNP, rs72921001, near a cluster of olfactory receptors is significantly associated with detecting a soapy taste to cilantro. One of the genes near this SNP encodes an olfactory receptor, OR6A2, that detects the aldehydes that may make cilantro smell soapy and thus is a compelling candidate gene for the detection of the cilantro odors that give cilantro its divisive flavor.

Availability of supporting data

We have shared full summary statistics for all SNPs with p values under 10^{-4} in Additional file 2. Due to privacy concerns, under our IRB protocol, we are unable to openly share statistics for all SNPs analyzed in the study.

Methods

Subjects

Participants were drawn from the customer base of 23andMe, Inc., a consumer genetics company. This cohort has been described in detail previously [15,28]. Participants provided informed consent and participated in the research online, under a protocol approved by an external AAHRPP-accredited IRB, Ethical and Independent Review Services (E&I Review).

Phenotype data collection

On the 23andMe website, participants contribute information through a combination of research surveys (longer, more formal questionnaires) and research 'snippets' (multiple-choice questions appearing as part of various 23andMe webpages). In this study, participants were asked two questions about cilantro via research snippets:

- 'Does fresh cilantro taste like soap to you?' (Yes/No/I'm not sure)
- 'Do you like the taste of fresh (not dried) cilantro?' (Yes/No/I'm not sure)

Among all 23andMe customers, 18,495 answered the first question (as either yes or no), 29,704 the second, and 15,751 both. Participants also reported their age. Sex and ancestry were determined on the basis of their genetic data. In both the GWAS set and the replication set, all participants were of European ancestry. In either group, no two shared more than 700 cM of DNA identical by descent (IBD, approximately the lower end of sharing between a pair of first cousins). In total, we were left with a set of 14,604 participants who answered the 'soapy' question for GWAS and 11,851 who answered only the taste preference question for a replication set. IBD was calculated using the methods described in [29]; the principal component analysis was performed as in [15]. To determine European and African-American ancestry, we used local-ancestry methods (as in [30]). Europeans had over 97% of their genome painted European, and African-Americans had at least 10% African and at most 10% Asian ancestry. Other groups were built using ancestry-informative markers trained on a subset of 23andMe customers who reported having four grandparents of a given ancestry.

Genotyping

Subjects were genotyped on one or more of three chips, two based on the Illumina HumanHap550+ BeadChip and the third based on the Illumina OmniExpress+ BeadChip (San Diego, CA, USA). The platforms contained 586,916, 584,942, and 1,008,948 SNPs. Totals of 291, 5,394, and 10,184 participants (for the GWAS population) were genotyped on the platforms, respectively. A total of 1,265 individuals were genotyped on multiple chips. For all participants, we imputed genotypes in batches of 8,000–10,000 using Beagle and Minimac [31-33] against the August 2010 release of the 1000 Genomes reference haplotypes [34], as described in [35].

A total of 11,914,767 SNPs were imputed. Of these, 7,356,559 met our thresholds of 0.001 minor allele frequency, average r^2 across batches of at least 0.5, and minimum r^2 across batches of at least 0.3. The minimum r^2 requirement was added to filter out SNPs that imputed less well in the batches consisting of the less dense platform. Positions and alleles are given relative to the positive strand of build 37 of the human genome.

Statistical analysis

For the GWAS, p values were calculated using a likelihood ratio test for the genotype term in the logistic regression model:

$$Y \sim G + \text{age} + \text{sex} + \text{pc}_1 + \text{pc}_2 + \text{pc}_3 + \text{pc}_4 + \text{pc}_5,$$

where Y is the vector of phenotypes (coded as 1 = thinks cilantro tastes soapy or 0 = does not), G is the vector of genotypes (coded as a dosage 0–2 for the estimated number of minor alleles present), and $\text{pc}_1, \ldots, \text{pc}_5$ are the projections onto the principal components. The same model was used for the replication, with the phenotype coded as 1 = dislikes cilantro or 0 = likes. We used the standard cutoff for genome-wide significance of 5×10^{-8} to correct for the multiple tests in the GWAS. ORs and p values for the differences in soapy-taste detection between sexes and population were calculated directly, without any covariates. Table 3 uses a proxy SNP for rs72921001, as our imputation was done only in Europeans, so we did not have data for rs72921001 in other populations.

For the heritability calculations, we used the GCTA software [27]. The calculations were done on genotyped SNPs only within a group of 13,628 unrelated Europeans. Unrelated filtering here was done using GCTA to remove individuals with estimated relatedness larger than 0.025. Thus, this group is slightly different from the GWAS set, as the GWAS set's relatedness filtering was done using IBD. We assumed a prevalence for soapy-taste detection of 0.13 for the transformation of heritability from the 0–1 scale to the liability scale. Otherwise, default options were used. We calculated heritability for autosomal and X chromosome SNPs separately; the estimates were 0.0869 (standard error 0.0634, p value 0.0805) for autosomal SNPs and 2×10^{-6} (standard error 0.010753, p value 0.5) for the X chromosome.

Additional files

Additional file 1: Quantile-quantile plot of association with cilantro soapy-taste. Observed p values versus theoretical p values under the null hypothesis of no association. The genomic control inflation factor for the study was 1.007 and is indicated by the red line; approximate 95% confidence intervals are given by the blue curves.

Additional file 2: All SNPs with $p < 10^{-4}$ for cilantro soapy-taste. Alleles are listed as major/minor. MAF is the frequency of the minor allele in Europeans, and r^2 is the estimated imputation accuracy. Positions and alleles are given relative to the positive strand of build 37 of the human genome. The gene column shows the position of the SNP in context of the nearest genes. The SNP position is within brackets, and the number of dashes gives approximate $\log_{10}$ distances.

Additional file 3: Index SNPs with $p < 10^{-6}$ for cilantro preference in the replication set. Results of a GWAS on cilantro preference in the replication set. Columns are as in Table 2.

Abbreviations

AAHRPP: Association for the Accreditation of Human Research Protection Programs; BCE: before common era; CI: confidence interval; GWAS: genome-wide association study; IRB: institutional review board; OR: odds ratio; *OR2AG2*, *OR2AG1*, *OR6A2*, *OR10A5*, *OR10A2*, *OR10A4*, *OR2D2*, *OR2D3*, members of olfactory receptor gene families 2, 6, and 10; SNP: single-nucleotide polymorphism; TAS1R/TAS2R: taste receptor gene families 1 and 2.

Competing interests

The authors of this paper are 23andMe employees and own stock options in the company.

Authors' contributions

NE, SW, CBD, AKK, JLM, DAH, UF, and JYT conceived and designed the experiments. NE analyzed the data and drafted the manuscript with contributions from all other authors. All authors read and approved the final manuscript.

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