



**UNIVERSITY
OF TURKU**

INDIVIDUAL DIFFERENCES IN TASTE PERCEPTION

Focus on food-related behavior

Sari Puputti



UNIVERSITY
OF TURKU

INDIVIDUAL DIFFERENCES IN TASTE PERCEPTION

Focus on food-related behavior

Sari Puputti

University of Turku

Faculty of Medicine
Paediatrics
Doctoral programme in Clinical Research
Functional Foods Forum

Supervised by

Professor Mari Sandell
Functional Foods Forum
Faculty of Medicine
University of Turku, Finland

Professor Harri Niinikoski
Institute of Biomedicine
Faculty of Medicine
University of Turku, Finland

Department of Food and Nutrition
Faculty of Agriculture and Forestry
University of Helsinki, Finland

Reviewed by

Associate Professor Caterina Dinnella
Department of DAGRI
University of Florence, Florence, Italy

Research Director Sophie Nicklaus
INRAE (French National Research
Institute for Agriculture, Food and
Environment)
Centre for Taste and Feeding Behavior,
Dijon, France

Opponent

Associate Professor John Hayes
Department of Food Science
The Pennsylvania State University
University Park, PA, USA

The originality of this publication has been checked in accordance with the University of Turku quality assurance system using the Turnitin OriginalityCheck service.

ISBN 978-951-29-7992-9 (PDF)
ISSN 0355-9483 (Print)
ISSN 2343-3213 (Online)
Painosalama Oy, Turku, Finland 2020

UNIVERSITY OF TURKU

Faculty of Medicine

Paediatrics

Functional Foods Forum

SARI PUPUTTI: Individual differences in taste perception – focus on food-related behavior

Doctoral Dissertation, 141 pp.

Doctoral Programme in Clinical Research

February 2020

ABSTRACT

The significance of taste perception in food-related behavior needs to be investigated to learn to more efficiently guide people toward a healthier diet. This study aimed to reveal the associations between food-related behavior and individual differences in taste perception regarding five taste modalities: sour, bitter, sweet, salty, and umami. Gender, age, education, body mass index, and smoking status were included as background factors.

Study subjects (N = 205) evaluated the intensity and identified the taste modality of five prototypical tastants at five concentration levels. Taste modality-specific sensitivity groups were determined as well as a taste sensitivity score describing overall taste sensitivity. Online questionnaires were used to gather data regarding background factors and food-related behavior, including consumption of vegetables, fruits, and berries; habits to mask or modify the taste of foods; and use-frequency and recalled pleasantness of foods and beverages.

The subjects varied the most in bitter and umami sensitivity. The most frequent taste confusions were between sourness and bitterness, and between umami and saltiness. Female gender and young age were related to higher taste sensitivity in general. None of the taste sensitivity measures was related to the pleasantness of foods. However, all of them were related to some aspects of food consumption, modality-specific sensitivity more broadly than the taste sensitivity score. The background factors were related to both food consumption and pleasantness.

This study highlights that actual behavior toward food should be investigated instead of hedonics concerning the associations with taste sensitivity. More detailed results can be achieved by focusing on sensitivity to taste modalities separately rather than using a general descriptor of taste sensitivity. Individual differences in taste perception should be acknowledged in all studies involving the sense of taste.

KEYWORDS: taste, perception, intensity, recognition, food, consumption, pleasantness

TURUN YLIOPISTO

Lääketieteellinen tiedekunta

Lastentautioppi

Funktionaalisten elintarvikkeiden kehittämiskeskus

SARI PUPUTTI: Yksilölliset erot maistamisessa – huomioiden erityisesti

ruokaan liittyvä käyttäytyminen

Väitöskirja, 141 s.

Turun kliininen tohtoriohjelma

Helmikuu 2020

TIIVISTELMÄ

Maistamisen merkitystä ruokakäyttäytymisessä täytyy tutkia, jotta ihmisiä osataan ohjata tehokkaammin kohti terveellistä ruokavaliota. Tämän tutkimuksen tavoitteena oli selvittää ruokakäyttäytymisen ja yksilöllisen maistamisen välisiä yhteyksiä huomioiden viisi makua: hapan, karvas, makea, suolainen ja umami. Taustamuuttujina olivat sukupuoli, ikä, koulutus, BMI ja tupakointi.

Tutkimukseen osallistujat (N = 205) arvioivat viiden makuyhdisteen maun voimakkuuden ja tunnistivat makuominaisuuden viidessä eri pitoisuudessa. Voimakkuusarvioiden perusteella muodostettiin makukohtaiset herkkyysryhmät ja laskettiin makuaistin kokonaisherkkyysmittari. Lisäksi kerättiin tietoja osallistujien taustoista sekä ruokakäyttäytymisestä, mukaan lukien vihannesten, hedelmien, ja marjojen kulutus; tavat peittää tai muokata elintarvikkeiden makuja; ja elintarvikkeiden käyttöuseus ja miellyttävyys.

Osallistujat erosivat toisistaan eniten karvaan ja umamin maun suhteen. Yleisimmät sekaannukset makujen tunnistamisessa olivat happaman maun sekoittaminen karvaaseen sekä umamin ja suolaisen sekoittaminen keskenään. Naispuolisuus ja alhainen ikä olivat yhteydessä herkempään makuaistiin. Mikään makuherkkyteen liittyvä muuttuja ei ollut yhteydessä elintarvikkeiden miellyttävyteen, mutta jokainen niistä oli yhteydessä johonkin elintarvikkeen kulutukseen; makukohtaiset herkkyudet useampaan kuin kokonaisherkkyysmittari. Taustamuuttajat olivat yhteydessä sekä kulutukseen että miellyttävyteen.

Tämä tutkimus korostaa, että olisi tärkeää tutkia varsinaista käyttäytymistä eikä niinkään ruuan miellyttävyttä, kun halutaan selvittää ruokakäyttäytymisen ja makuaistin herkkyuden yhteyttä. Keskittymällä makukohtaisten herkkyysien tutkimiseen saatetaan saavuttaa yksikohtaisempaa tietoa kuin yleisellä makuaistin mittarilla. Yksilölliset erot makuaistissa tulisi huomioida kaikissa maistamiseen liittyvissä tutkimuksissa.

AVAINSANAT: maku, aistiminen, voimakkuus, tunnistus, elintarvikkeet, kulutus, miellyttävyys

Table of Contents

Abbreviations	7
List of Original Publications	9
1 Introduction	10
2 Review of Literature	13
2.1 Taste perception	13
2.1.1 Taste receptors	15
2.1.2 Fungiform papillae density.....	16
2.1.3 Saliva	17
2.2 Taste sensitivity measurement	17
2.2.1 Detection and recognition thresholds.....	18
2.2.2 PROP tasting	18
2.2.3 Modality recognition	20
2.2.4 Intensity perception	21
2.2.5 Other measures.....	21
2.2.6 Challenges in methodology	22
2.2.6.1 Tastants.....	22
2.2.6.2 Tastant presentation	23
2.2.6.3 Intensity rating scales	23
2.3 Subjective factors related to taste sensitivity	24
2.3.1 Gender	27
2.3.2 Age.....	27
2.3.2.1 Health status and medication.....	28
2.3.3 Weight status	30
2.3.4 Smoking	31
2.4 The associations between taste sensitivity and food-related behavior	32
2.5 Summary.....	36
3 Aims	38
4 Materials and Methods	39
4.1 Participants and study design.....	39
4.2 Taste stimuli.....	40
4.3 Taste evaluation	41
4.4 Questionnaires	41
4.4.1 Subjects' background factors.....	42
4.4.2 Food-related behavior	42

4.4.2.1	Portions of vegetables, fruits, and berries per week.....	42
4.4.2.2	Masking and modifying the taste of food.....	43
4.4.2.3	Recalled pleasantness and use-frequency ...	43
4.5	Statistical analysis.....	44
5	Results.....	46
5.1	Subject characteristics	46
5.2	Modality-specific taste sensitivity clusters	47
5.3	Taste sensitivity score.....	51
5.4	Taste recognitions.....	52
5.5	Factors related to taste sensitivity	55
5.6	Portions of vegetables, fruits, and berries per week	57
5.7	Habits of masking or modifying taste.....	58
5.8	Factor analysis of recalled pleasantness.....	61
5.9	Factors related to recalled pleasantness	63
5.10	Factors related to use-frequency.....	65
6	Discussion.....	69
6.1	Individual taste perception.....	69
6.2	Factors related to taste perception	71
6.3	Factors associated with food-related behavior	72
6.3.1	Taste sensitivity and food-related behavior	73
6.3.2	Background factors and food-related behavior	75
6.4	Limitations.....	76
7	Conclusions and Future Prospects.....	78
	Acknowledgements.....	79
	References.....	81
	Appendix.....	93
	Original Publications.....	95

Abbreviations

ANOVA	Analysis of variance
AVI	Alanine, valine, isoleucine
BI	Bitter
BMI	Body mass index
CI	Confidence interval
DNA	Deoxyribonucleic acid
DT	Detection threshold
ENaC	Epithelial sodium channel
FCQ	Food Choice Questionnaire
FP	Fungiform papillae
gLMS	General labeled magnitude scale
HIV	Human immunodeficiency virus
IMP	Inosine monophosphate
ISO	International Organization for Standardization
IQR	Interquartile range
K ⁺	Potassium cation
KCl	Potassium chloride
Li ⁺	Lithium cation
LMS	Labeled magnitude scale
MANOVA	multivariate analysis of variance
MPG	Monopotassium glutamate
MSG	Monosodium glutamate
Na ⁺	Sodium cation
NaCl	Sodium chloride
ns	Not significant
OR	Odds ratio
OTOP1	Otopetrin-1
PAV	Proline, alanine, isoleucine
PC	Principal component
PROP	6- <i>n</i> -propylthiouracil
PTC	Propylthiocarbamide

QHCl	Quinine hydrochloride
RNA	Ribonucleic acid
RT	Recognition threshold
SA	Salty
<i>SCNN1x</i>	Non-voltage-gated sodium channel 1, subunit <i>x</i> gene
SNP	Single nucleotide polymorphism
SO	Sour
SW	Sweet
TxRx	Taste receptor protein type <i>x</i> , member <i>x</i>
<i>TASxRx</i>	Taste receptor type <i>x</i> , member <i>x</i> gene
TRPML3	Transient receptor potential mucolipin 3
TRPV1	Transient receptor potential cation channel subfamily V, member 1
TRS	Taste recognition score
TSS	Taste sensitivity score
UM	Umami
VAS	Visual analogue scale

List of Original Publications

This dissertation is based on the following original publications, which are referred to in the text by their Roman numerals:

- I Puputti, S., Aisala, H., Hoppu, U., & Sandell, M. Multidimensional measurement of individual differences in taste perception. *Food Quality and Preference*, 2018; 65: 10–17.
- II Puputti, S., Aisala, H., Hoppu, U., & Sandell, M. Factors explaining individual differences in taste sensitivity and taste modality recognition among Finnish adults. *Journal of Sensory Studies*, 2019; 34: 1–11.
- III Puputti, S., Hoppu, U., & Sandell, M. Taste sensitivity is associated with food consumption behavior but not with recalled pleasantness. *Foods*, 2019; 8: 444.

The original publications have been reproduced with the permission of the copyright holders.

1 Introduction

Taste perception likely has an evolutionary purpose: to become attracted by nutritious food and to feel aversion toward toxic food (Breslin, 2013). Presumably, humans taste the sweetness of carbohydrates to gain energy, the umami taste of amino acids and ribonucleotides from cooked or aged meat to gain protein, the salty taste of minerals to maintain osmotic balance of body fluids, and the sour taste of vitamin C to maintain health as well as to recognize fermented, spoiled or unripe foods. The bitter taste is assumed to be a warning of toxic foods. At present, as food has become plentiful in the Western world, the evolutionary importance of taste sensation has lost its purpose. In addition, our genome has not been able to adapt to the rapidly changing food consumption environment (Cordain et al., 2005). Compared to our very early ancestors, as well as more recent ones, we consume more sugar, salt, dairy products, refined cereals, refined vegetable oils, and fatty domestic meat, in general, more processed foods (Cordain et al., 2005). The present-day diet is, at least, partially to be blamed for chronic diseases and health problems that cause significant expenses to governments. Thus, motivating people to eat healthier would improve their wellbeing as well as the state of the economy.

Nutrition recommendations guide people to eat versatile and healthy foods. However, healthiness may not be an adequate motivator to guide food choices. The taste of food is thought to be a critical determinant of food choice, and thus, it is essential for the quality of life and health that food, particularly healthy food, would be tasty. If the taste of foods that are or should be consumed regularly is considered, better understanding of food-related behavior may be achieved.

For example, vegetables, fruits, and berries that are the foundation of a healthy diet are consumed less than recommended, and their consumption has been decreasing in Finland (Valsta et al., 2018). In 2017, the recommended amount of 500 g/day was consumed by only 10% of men and 20% of women (Valsta et al., 2018). This behavior may partly be explained by the taste of vegetables, fruits, and berries as their possible intense bitterness and sourness and mild sweetness can be challenging for some people. In contrast, excess consumption of calories, such as energy-rich foods and beverages that can be intensely sweet or salty, is increasing the prevalence of overweight and associated morbidities (World Health

Organization, 2018). Encouraging people to eat healthy food requires that the motives driving food-related behavior, such as consumption frequency and liking of foods, need to be understood. One challenge is that people perceive the tastes of foods differently.

People seem to differ most in bitter and umami tastes (Knaapila et al., 2012; Lugaz et al., 2002). Bitter taste sensitivity is the most studied since Fox (1932) first discovered that some people perceive phenylthiocarbamide (PTC) as extremely bitter, whereas others find it tasteless. This finding was followed by many studies exploring PTC and later 6-*n*-propylthiouracil (PROP) relative to other sensations and food-related behavior. Furthermore, many studies focused on gustatory genes since the connection between PTC/PROP and the taste receptor gene *TAS2R38* was revealed by Kim et al. (2003). Unfortunately, studies regarding sensitivity to other tastes or tastants are not as numerous.

The fundamental reasons for interindividual variation in taste perception can arise from the differences in the peripheral or central processing of taste sensation as well as from subjective and environmental factors (e.g. Bachmanov et al., 2014; Jayasinghe et al., 2017; Loper et al., 2015; Methven et al., 2012; Naik et al., 2010; Sartor et al., 2011). The factors that have been related to taste sensitivity, i.e. the sensitivity to recognize or detect taste modalities, are shown in **Figure 1**. However, some studies have shown no associations between these factors and taste sensitivity (e.g., Dinehart et al., 2006; Fischer et al., 2013; Low et al., 2016; Pepino et al., 2010). Contradictory results highlight the need for more studies that encompass all taste modalities regarding putative taste-related factors. Furthermore, other factors such as ethnicity (Holt et al., 2000; Williams et al., 2016), cognitive state (Liang et al., 2018), and personality traits (Fischer et al., 2013; Knaapila et al., 2014), affect taste perception at least indirectly, but more research is needed to interpret the overall picture.

Studies on the associations between food-related behavior and taste sensitivity have focused on PROP sensitivity (Catanzaro et al., 2013; Dinehart et al., 2006; Duffy et al., 2010; Kaminski et al., 2000; Tepper, 2008) and taste genetics (Duffy et al., 2010; Hayes et al., 2013; Sandell et al., 2015, 2014). Higher sensitivity has been thought to cause rejection of strong-tasting foods, whereas lower taste sensitivity leads to seeking more intense taste in food to reach optimal pleasantness. This theory was substantiated by Noel et al. (2017). They impaired sweet perception of subjects by providing them *Gymnema sylvestre*, a plant that can suppress sweet taste. They found that diminished sweet perception led to seeking for more intense sweetness in food. Moreover, higher sweet taste sensitivity has been associated with a lower liking of sweet beverages and lower intake of sweet foods (Jayasinghe et al., 2017). In contrast, some studies have found no association between sweet taste sensitivity and sweet-food related behavior (Cicerale et al., 2012; Keskitalo et al., 2007).

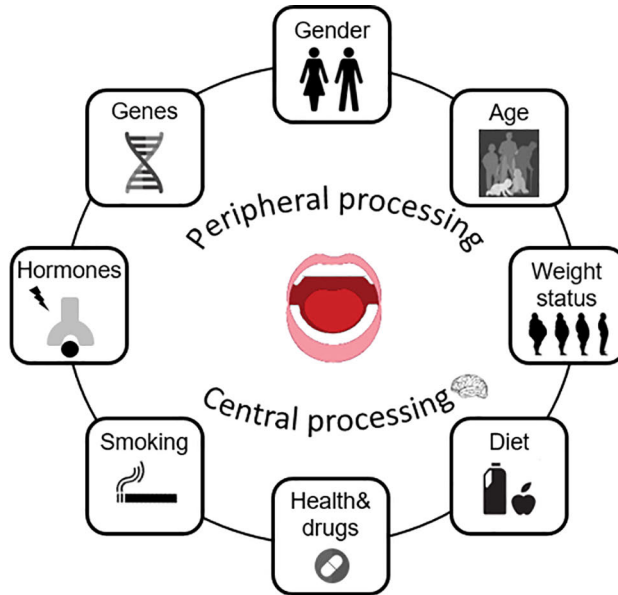


Figure 1. Putative taste-related factors that can affect human taste sensitivity independently or in interaction with the other factors. Gender differences; age-related changes; weight status; food consumption habits; health status, damage to nervous system, diseases, and medication; heavy smoking; sex hormones and hormones related to appetite regulation; genotype, e.g. taste receptor genes; peripheral and central processing of taste transduction including the effects of saliva, taste bud density, innervation, and brain function. Individual pictures reprinted from Pixabay under the Pixabay license.

This thesis focuses on individual taste perception in humans considering five traditionally accepted taste modalities and focusing on food-related behavior. In addition, subjective factors associated with the differences in taste perception are explored. Adults are the focus of interest in this thesis. Different factors may affect the food-related behavior in children in comparison to adults because children and adults are subjected differently to environmental and cultural effects that can modify food perception and food choice (Chamoun et al., 2016). In the experimental part, taste sensitivity was investigated relative to gender, age, body mass index (BMI), and smoking status among Finnish adults. Moreover, food-related behavior, including consumption frequency, habits to mask or modify the taste of food, and pleasantness, was studied concerning taste sensitivity and background factors of the subjects.

2 Review of Literature

2.1 Taste perception

According to current knowledge, humans can perceive at least five taste modalities, which are also referred to as “the basic tastes”: bitter, salty, sour, sweet, and umami. Umami, the meaty, brothy, or savory taste, is the most unfamiliar taste modality, although it is typical to Asian cuisine and can be found in familiar foods such as tomato, mushroom, cheese, and meat. Because of the unfamiliarity among general consumers, umami is frequently excluded from taste studies. The position of umami as a real taste was questioned recently and another term, “alimentary taste” was proposed (Hartley et al., 2019).

In addition to these five taste qualities, various other oral qualities have been suggested as taste. Fat or fatty acid taste has gained wide attention during recent years (Keast & Costanzo, 2015). Other taste candidates include metallic (Lawless et al., 2005), complex carbohydrates (Low et al., 2018), and calcium (Tordoff, 2001). Occasionally, kokumi has also been suggested to be a taste sensation, but it instead is a flavor attribute related to sensations of thickness, continuity, and mouthfulness (Bachmanov et al., 2014). Although these qualities, especially fat taste, may be relevant for nutrition and health, this thesis focuses on the traditionally accepted taste modalities.

The different aspects of taste perception are (i) modality recognition, (ii) intensity perception, (iii) temporal dynamics, (iv) spatial localization, and (v) hedonics (Breslin, 2013). For example, when one takes a sip of coffee, he/she could (i) recognize bitter and sour tastes, (ii) perceive the intensity of bitterness stronger than sourness, (iii) perceive a bitter aftertaste (iv) in the back of the mouth, and (v) like or dislike the taste. When human taste sensitivity in food context is considered, intensity perception is the most studied and relevant aspects of taste perception.

The peripheral structure for taste perception in the mouth is the gustatory epithelia: the papillae of the tongue (except for the underside of the tongue), soft palate, and pharynx (**Figure 2**) (Breslin, 2013). They are innervated by gustatory and trigeminal nerves (Breslin & Spector, 2008). Fungiform papillae (FP; **Figure 2**), located on the anterior tongue, are innervated by cranial nerve VII (the chorda tympani branch). Circumvallate papillae are located on the posterior tongue, and

foliate papillae are present on the sides of the posterior tongue (**Figure 2**). They are innervated by glossopharyngeal nerve IX. The soft palate is innervated by cranial nerve VII (the greater superficial petrosal branch), and the pharynx by the superior laryngeal branch of cranial nerve X (Vagus). The taste perception process begins when taste-eliciting non-volatile compounds bind to taste receptor proteins that are located in cell clusters called taste buds (Lawless & Heymann, 2010b). When a ligand binds to a receptor cell, a signal cascade stimulates the taste nerves, and signals are transmitted to the brain for central processing and interpreting (Lawless & Heymann, 2010b). Although the taste transduction pathway would function properly, people can distinctively perceive taste. In the peripheral processing of taste, at least three factors have been known to be associated with the differences in taste perception: diversity in taste receptors, FP density, and salivation.

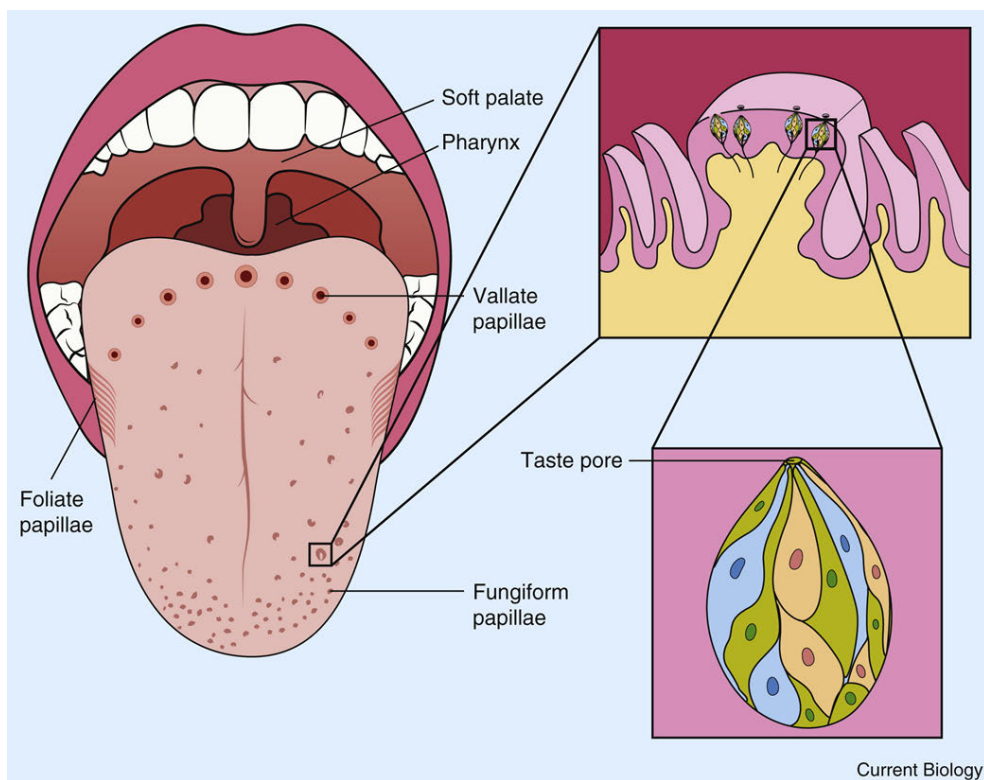


Figure 2. The gustatory epithelia in the mouth. Taste buds are located on all these epithelia. Fungiform papillae are housing 0–15 taste buds and are surrounded with filiform papillae that lack taste buds (the first inset). One taste bud (the second inset) contains 80–100 taste receptor cells that interact with taste stimuli via a taste pore. Reprinted from Current Biology, 2013, 23, Paul A. S. Breslin, An Evolutionary Perspective on Food and Human Taste, R409-R418, Copyright (2013) with permission from Elsevier (<http://www.sciencedirect.com/science/journal/current-biology>).

2.1.1 Taste receptors

Taste receptors are proteins that fulfill these criteria: they are expressed in taste receptor cells; they have known DNA, RNA, and protein sequence; they interact with taste-eliciting molecules; and their experimental alteration changes taste perception (Bachmanov et al., 2014). These requirements have been affirmed for bitter, sweet, umami, and salty taste receptors, but not for sour taste receptors. Candidates for sour taste receptors have been proposed, but more research is needed (Bachmanov et al., 2014). A recent study suggests that the sour taste receptor is Otopetrin-1 (OTOP1) (Zhang et al., 2019). Other receptor mechanisms than the assumed primary receptors listed below might exist (Bachmanov et al., 2014). Furthermore, many other molecules not mentioned here are involved in the taste transduction pathway.

The primary sweet and umami taste receptor proteins are encoded by *TAS1R1*, *TAS1R2*, and *TAS1R3* (taste receptor type 1 members 1, 2, and 3) genes (Bachmanov et al., 2014). These G protein-coupled receptors consist of heterodimers: T1R2 and 3 for sweet taste, and T1R1 and 3 for umami taste. Multiple single nucleotide polymorphism (SNP) sites exist in T1R genes (Chamoun et al., 2016). This polymorphism has been associated with sweet and umami taste sensitivity (Bachmanov et al., 2014; Chamoun et al., 2018; Shigemura et al., 2009) and consumption of sugars (Bachmanov et al., 2014).

Bitter taste is also transmitted by G protein-coupled receptor proteins (Bachmanov et al., 2014). In humans, multiple, at least 25 *TAS2R* (taste receptor type 2) genes encode T2R receptor proteins. The different T2R receptors interact with different bitter compounds with varying specificity (Meyerhof et al., 2010). Furthermore, bitter compounds can interact with one or several receptor types (Meyerhof et al., 2010).

The polymorphism in *TAS2R* genes has been linked to bitter taste sensitivity. The most studied case is the receptor TAS2R38 that responds differently to synthetic compounds PROP and PTC (Bufe et al., 2005), as well as other compounds with a thiourea (N-C=S) moiety, such as glucosinolates (Sandell & Breslin, 2006). Three SNPs in *TAS2R38* yield five different haplotypes that cause variation in the sensitivity to PROP and related compounds (Kim et al., 2003). In general, the least sensitive are AVI (A = alanine, V = valine, I = isoleucine) homozygote people and the most sensitive are PAV (P = proline) homozygotes. Heterozygotes of PAV and AVI or other, less common haplotypes AAV, PVI, and AAI, fall in between these homozygotes regarding sensitivity.

For salty taste perception, at least two transduction pathways (amiloride-sensitive and amiloride-insensitive) seem to exist (Bachmanov et al., 2014). One is mediated by the epithelial sodium channel (ENaC) and is cation-selective (Na⁺ and Li⁺). ENaC is a heterodimer that can consist of several subunits: α , β , γ , and δ . These proteins are coded by the genes *SCNNIA*, *SCNNIB*, *SCNNIG*, and *SCNNID* (non-

voltage-gated sodium channel 1), respectively. The other pathway is cation nonselective, but the mechanism has not been conclusively identified. Two potential receptor candidates are TRPV1 (transient receptor potential cation channel subfamily V, member 1) and TRPML3 (transient receptor potential mucolipin 3) (Bachmanov et al., 2014). SNPs in *SCNN1B* (Dias et al., 2013) and *TRPV1* (Chamoun et al., 2018; Dias et al., 2013) have been linked to phenotypic differences in saltiness perception.

2.1.2 Fungiform papillae density

FP density is considered as an indicator of taste nerve innervation. Logically, denser FP indicates more taste receptors, and hence more intense taste perception. Thus, FP density has been referred to as a visible marker of taste sensitivity.

FP density varies between individuals. In a large-scale study ($N = 2371$), the range was 0–212.2 papillae/cm², and the mean was 103.5 (standard deviation (sd) 32.8) papillae/cm² (Fischer et al., 2013). FP density is determined using a standard method (e.g., Hayes et al., 2010; Spinelli et al., 2018). The tongue is colored with blue food coloring to make the FP more readily visible and to distinguish them from filiform papillae, the epithelial structure not housing taste buds. The number of FP is counted from pictures of right and left sides of the tongue on 0.6 cm diameter circles.

PROP sensitivity and FP density have been reported to be correlated significantly with a modest correlation coefficient ($r = 0.33$ – 0.44) (Duffy et al., 2010; Hayes et al., 2010; Lanier et al., 2005). Hayes et al. (2008) found that the interaction between PROP tasting and FP density depended on the *TAS2R38* haplotype; FP density was not associated with PROP tasting among heterozygotes, but was strongly related among homozygotes. However, another study failed to find this relationship (Fischer et al., 2013). The correlations between FP density and other tastant sensitivities have been rather weak (with NaCl [sodium chloride] $r = 0.21$; with QHCl [quinine hydrochloride] $r = 0.27$) (Duffy et al., 2010; Hayes et al., 2010). Furthermore, higher FP density has been linked to higher sensitivity to caffeine and QHCl (Masi et al., 2015). However, several studies showed no significant correlations with the measures of sensitivity to PROP or to other tastants (Dinnella et al., 2018; Feeney & Hayes, 2014b; Fischer et al., 2013; Webb et al., 2015).

Piochi et al. (2019) divided subjects according to FP density and FP diameter distribution into four groups: high density + large FP, high density + small FP, low density + large FP, and low density + small FP. Individuals with high FP density tended to have broader variation in FP diameter than those with low density. They found that older age was related to lower FP density regardless of the diameter, and males and females were equally distributed in the four groups. Interestingly, the

perception of NaCl and umami, but not sucrose, caffeine, PROP, or citric acid, differed between the FP groups. The high density + large FP group was less sensitive to saltiness and umami and the high density + small FP group was less sensitive to umami than the low density + small FP group. These results indicate that FP diameter should also be considered in addition to FP density.

Taste receptors are also located in areas other than the FP (Breslin, 2013); thus, FP density alone does not represent the whole-mouth taste receptor density. Thus, not surprisingly, the whole-mouth intensity perception of taste does not correlate or correlates only weakly with FP density. FP is a physical feature that can be affected by other factors, such as pathologies (Feng et al., 2014; Piochi et al., 2018). Thus, FP density, as a physical feature, does not correspond to individual taste perception in reality (Feeney & Hayes, 2014b; Fischer et al., 2013).

2.1.3 Saliva

Saliva is needed to dissolve taste molecules and initiate interaction with taste receptors (Feron & Salles, 2018). Saliva can affect taste perception in at least three ways. By dilution effect, salivary flow rate can alter the concentration of taste molecules as well as other taste perception-related molecules such as hormones (Fábián et al., 2015). The effect of salivary flow rate may be tastant specific (Fábián et al., 2015; Heinzerling et al., 2011). Owing to the buffering capacity, saliva can affect the sourness perception, as sour taste-eliciting acids are strongly affected by the pH value (Fábián et al., 2015). Owing to molecule composition (e.g. ions, amino acids, and sugars), saliva stimulate taste receptors creating constant taste in the mouth that can change sensitivity to food tastants (Feron & Salles, 2018). Gustin (carbonic anhydrase VI) is a zinc-dependent salivary protein important for taste perception (Fábián et al., 2015). Thus, zinc deficiency can decrease gustin function as well as diminish taste perception. Lower zinc intake has been linked to lower sensitivity to salty and bitter tastes (McDaid et al., 2007).

2.2 Taste sensitivity measurement

Several psychophysical measures of taste sensitivity can be applied to study human sensory psychology. The most common measures are detection and recognition thresholds, PROP/PTC tasting, and intensity rating. Other methods (not all purely psychophysical) include modality recognition, thermal tasting, electrogustometric thresholds, and tongue biopotential recordings. The choice of measurement level depends on the objective of the research as these measures differently describe taste sensitivity.

2.2.1 Detection and recognition thresholds

Taste threshold measures focus on the lowest concentration levels that can be detected (Lawless & Heymann, 2010a). Detection threshold (DT) is the lowest concentration at which a tastant can be perceived. Recognition threshold (RT) implies the lowest concentration when a taste modality can be recognized correctly. RT is higher than DT for the same tastant. The typical methods are 2- and 3-alternative forced-choice tests. Subjects receive sets of two or three samples containing one target taste sample and one or two blanks (water). The task is to identify which sample is different or contains a tastant. The evaluation starts with the lowest concentration level and proceeds to the stronger target sample. In the staircase method, the correct response leads to re-evaluation of the previous, more dilute sample, whereas incorrect response leads to evaluation of the next, more concentrated sample. The task continues until three correct answers are obtained. Alternatively, a subject evaluates the sets of samples once in the ascending order. In both methods, several sets at different target concentration levels are evaluated. Different versions of these methods are available, but typically, threshold determination is laborious with many samples to evaluate and demands to remember the previous samples in the set that can be a difficult task for a regular subject. As the thresholds are very low concentration levels, they might be irrelevant in explaining food-related behavior as food taste is perceived at suprathreshold levels (Duffy et al., 2004; Jayasinghe et al., 2017; Low et al., 2016). Furthermore, threshold and intensity measures for the same tastant are unrelated (Jayasinghe et al., 2017; Pepino et al., 2010), although opposite results have also been reported (Duffy, 2004; Hayes et al., 2008). Additionally, regarding PROP taster identification, intensity measure is superior to threshold measure in determining PROP taster groups (Hayes et al., 2008).

2.2.2 PROP tasting

The second aspect of taste sensitivity measure is PROP (or PTC) taster status. PROP is a single bitter tastant, but the term supertaster was efficiently popularized and PROP sensitivity has been used for representing general taste sensitivity, as PROP intensity perception has been found to be correlated with other tastant intensity perception (Bajec & Pickering, 2008; Dinnella et al., 2018; Hayes et al., 2008; Webb et al., 2015). PROP sensitivity is a phenotype related to bitter receptor genotypes, mainly *TAS2R38* (see 2.1.1). PROP sensitivity can be measured using both DT and suprathreshold intensity methods. DT can allow the discrimination of individuals who can perceive PROP from those who perceive it as tasteless. With intensity rating, subjects have been classified as supertasters, medium tasters, and non-tasters (Bartoshuk, 2000).

The underlying mechanism for increased overall taste responsiveness in PROP tasters needs further research but higher FP number and polymorphism in gustin gene are the suggested explanations. Gustin, the zinc-dependent protein in saliva, is suggested to be a trophic factor in taste bud development (Henkin et al., 1999), and an SNP has been related to its functionality (Padiglia et al., 2010). PROP tasters may carry more likely the active genotype (Calò et al., 2011; Melis et al., 2013) that has been linked to increased PROP sensitivity via FP morphology and activity, including increased FP density (Melis et al., 2013). In some studies, PROP tasters have shown to have more FP indicating that higher FP density equals to higher number of taste receptors and further, more intense taste perception (see section 2.1.2).

However, the view that PROP could serve as a general taste marker has been challenged, as the associations between PROP and other tastants have been weak (Coltell et al., 2019; Fischer et al., 2014; Lim et al., 2008; Webb et al., 2015). For example, statistically significant correlation coefficient (r) of 0.29–0.31 has been noted between PROP and NaCl (Duffy et al., 2004; Hayes et al., 2010), 0.089–0.39 between PROP and citric acid (Dinnella et al., 2018; Duffy et al., 2004), 0.122–0.17 between PROP and sucrose (Dinnella et al., 2018; Keskitalo et al., 2007), 0.116 between PROP and caffeine (Dinnella et al., 2018), and 0.128 between PROP and MSG (monosodium glutamate) (Dinnella et al., 2018). The correlation between PROP and QHCl, another bitter compound, has been mainly moderate ($r = 0.33$ – 0.46) (Dinehart et al., 2006; Duffy et al., 2003; Duffy et al., 2010; Lim et al., 2008; Sharafi et al., 2018).

Other tastants tend to be correlated stronger with each other than with PROP (Barragán et al., 2018; Coltell et al., 2019). In a sub-sample of the Italian Taste Project, a large-scale population study, PROP intensity correlated significantly with citric acid, caffeine, sucrose, and MSG intensity, but the correlation coefficients were very weak ($r = 0.089$ – 0.128), whereas the other tastant perception had higher correlation coefficients with each other than with PROP ($r = 0.283$ – 0.462) (Dinnella et al., 2018). When PROP sensitivity was categorized as supertasters, medium tasters and non-tasters, a positive association was found with caffeine bitterness (Ly & Drewnowski, 2001), QHCl bitterness, NaCl saltiness, sucrose sweetness, and tartaric acid sourness (Bajec & Pickering, 2008).

Lim et al. (2008) reported that, when subjects were categorized according to the PROP taster status, those who were the most sensitive to PROP perceived all the other tastants stronger than those less sensitive to PROP. However, when PROP intensity was analyzed as a continuous variable, it correlated statistically significantly only with QHCl ($r = 0.46$), whereas sucrose, NaCl, citric acid, and QHCl correlated modestly ($r = 0.33$ – 0.43) with each other. Moreover, Delwiche et al. (2001) found associations between PROP and other bitter compounds only when they categorized subjects to PROP taster groups; those insensitive to PROP

perceived the other compounds milder than did PROP-sensitive subjects. In all, they had 11 structurally diverse bitter compounds. PROP intensity did not correlate significantly with any of the compounds, whereas the other compounds correlated with at least one bitter compound.

A possible reason for the mixed results between continuous and categorized PROP sensitivity measures could be explained by the findings of a large-scale study (N = 1670) performed by Fischer et al. (2014). They reported that the correlation between PROP intensity and other tastant intensities varied according to *TAS2R38* genotype: PAV homozygotes had a stronger correlation than AVI homozygotes or heterozygotes. Thus, they suggested that PROP taster status should not be used as a general taste indicator because it can result in a high rate of imprecise estimation.

Moreover, PROP sensitivity measure relies only on one compound for defining taste function. PROP sensitivity is an extreme measure, as people tend to show less variation in sensitivity to many other tastants. Thus, whether studying human behavior with such an extreme sensitivity measure as an explanatory factor would be reasonable needs to be determined, if otherwise, taste perception does not vary considerably across individuals.

2.2.3 Modality recognition

Taste modality recognitions as a measure for taste sensitivity are not usually applied to understand human food-related behavior. Because modality recognition occurs at a higher concentration level than taste detection, and the result about individual sensitivity does not change with higher concentration, modality recognition is an approximate measure for taste sensitivity and is mainly applied in clinical use to study taste impairments.

The modality identification confusions are poorly understood. The recognition is affected by the testing procedure, and wide variation exists in tastants, concentration levels, and tastant presentation methods. Furthermore, umami is frequently excluded from studies (Doty et al., 2017; Hoogeveen et al., 2015; Landis et al., 2009; Nordin et al., 2007; Simchen et al., 2006; Vennemann et al., 2008; Welge-Lüssen et al., 2011). This decision is occasionally based on that people are unfamiliar with umami taste. Moreover, subjects may be assumed to have the ability to differentiate and identify bitter, sour, salty, and sweet taste. Usually, whether the subjects were familiarized with the taste modalities before the taste test is not mentioned (Doty et al., 2017; Hoogeveen et al., 2015; Landis et al., 2009; Nordin et al., 2007; Simchen et al., 2006; Vennemann et al., 2008; Welge-Lüssen et al., 2011). Introducing taste modalities before testing would provide a uniform perspective for the subjects as some subjects do not know, for example, what is meant by bitterness. Moreover, at least in the Finnish language, multiple words can be used to describe

bitter taste, such as “kitkerä,” “pistävä,” and “karvas,” but individuals may conceptualize these words differently. If the taste modalities were introduced, umami could be included in studies, even if it was an unfamiliar attribute.

Sweet taste seems to be the easiest to identify (Doty et al., 2017; Welge-Lüssen et al., 2011). Doty, Chen, & Overend (2017) found that among 1000 subjects sour–bitter confusion (identifying sour taste as bitter) was the most prevalent (19.3%), followed by bitter–sour (11.4%), salty–bitter (7.3%), salty–sour (7.0%), bitter–salty (3.5%), and sour–salty (2.4%) confusion. Repeated exposure can improve taste modality recognition (Bitnes et al., 2007; Han et al., 2018).

2.2.4 Intensity perception

In intensity measures, the subjects rate the intensity of sensation elicited by a tastant at a certain concentration level. Intensity is measured using intensity scales, such as general labeled magnitude scale (gLMS) or visual analogue scale (VAS; see 2.2.6.3 for more discussion about the scales). Sensitivity can be determined using one or several samples with varying concentrations. One sample generates one data point; in contrast, in threshold measures, typically three (or two) samples are required for one data point. Thus, intensity rating is less laborious for study subjects than threshold measures. Furthermore, intensity measures focus typically on concentrations above the threshold measures; hence, they are more relevant in studying food consumption and liking than the thresholds.

PROP sensitivity has been often determined using an intensity scale. Subjects' taste sensitivity has been more rarely determined using other tastant intensity while investigating food-related behavior.

2.2.5 Other measures

One more marker of taste sensitivity is thermal tasting. When a small area on the tongue is either heated or cooled with a thermal probe, thermal tasters perceive a phantom taste that is reported to be sweetness, saltiness, or sourness (Cruz & Green, 2000). Thermal tasters are known to perceive taste solutions as more intense than thermal non-tasters (Bajec & Pickering, 2008; Green & George, 2004). Thermal tasting has been linked to reduced liking of cooked fruits, cooked vegetables, and bitter foods/beverages (Bajec & Pickering, 2010).

Another measure of taste sensitivity can be achieved using electrogustometry. In this method, an electrode is placed on the tongue touching a small area, such as 50–100 mm² and the stimulus is current. Electrogustometry may be a useful tool for estimating taste function in clinical use, when appropriately used (Stillman et al.,

2003). It is thought to represent general taste sensitivity, but may not correlate well with suprathreshold tastant measures (Stillman et al., 2003).

Tongue biopotential recordings offer an objective way to measure taste sensitivity (Sollai et al., 2017). When a drop of a tastant solution is placed on the tongue, bioelectrical changes can be detected using two electrodes on the tongue. With this method, PROP taster groups can be identified according to variation in the waveform of signals. This new method seems practical in clinical use and more studies are needed to show its full potential.

2.2.6 Challenges in methodology

Variation in methods renders it difficult to compare the results between studies. Even within studies that measured taste sensitivity the same way, some aspects need to be considered. These include what prototypic compounds were used to represent taste modalities, how tastants were presented to the subjects, and what scale was used for intensity evaluation.

2.2.6.1 Tastants

Some prototypic tastants are widely used in taste studies, including sucrose for sweet; NaCl for salty; MSG for umami; citric acid for sour; and PROP, QHCl or caffeine for bitter taste. Of course, other compounds are also used depending on study objectives. Taste intensity and taste modality recognition depend on the compound and concentration level. Furthermore, some compounds have a side taste. MSG also tastes salty because of the sodium ion. KCl (potassium chloride) that is occasionally used as a prototypic salty tastant can taste intensely bitter (Van Der Klaauw & Smith, 1995). Some individuals perceive NaCl as mild sour (Van Der Klaauw & Smith, 1995) or sweet at a mild concentration (Galindo-Cuspinera et al., 2009; Wise & Breslin, 2013). Moreover, low concentrations of citric acid can have bitter or sweet taste (Kim et al., 2004; Wise & Breslin, 2013). Thus, the concentration also affects taste perception.

Mojet et al. (2003) used two prototypic tastants for each taste modality. They found no compound-specific differences in intensity judgments. For tastants other than PROP, correlations between tastant intensities and taste modalities have been mainly moderate or stronger (Barragán et al., 2018; Coltell et al., 2019; Dinnella et al., 2018; Duffy, 2004; Hwang et al., 2016; Lim et al., 2008; Webb et al., 2015).

2.2.6.2 Tastant presentation

Usually, tastants are applied regionally on the tongue, or they are presented as whole-mouth solutions. Whole-mouth testing represents better real-life taste perception. As taste sensitivity varies across tongue regions (Doty et al., 2016; Nordin et al., 2007; Williams et al., 2016), regional testing should be selected if it is necessary for study objectives. For example, regional testing is necessary for taste innervation studies.

Factors such as viral infections, oral infections, middle-ear surgeries, or head trauma can damage taste innervation. In general, they cause damage to only the chorda tympani branch of cranial nerve VII instead of affecting multiple cranial nerves. Thus, taste perception is affected only regionally, on the tongue tip where fungiform papillae are located. Damage on one cranial nerve might remain unnoticed because of whole-mouth taste functioning as other cranial nerves still function (Snyder & Bartoshuk, 2016). In these cases, evaluating taste perception as whole-mouth and tongue-tip measures and as their ratio would be useful.

When regional taste sensitivity is studied, filter paper strips are often used. These are small pieces of paper (2 cm²) impregnated with tastant solutions that are placed on the tongue placed outside the mouth (Landis et al., 2009). The subject must then imply the intensity of taste sensations and/or the taste modality. In whole-mouth studies, tastants are usually presented as liquid solutions that are sipped into the mouth. Occasionally, tastants are applied with cotton buds (e.g. Fischer et al., 2013), as a drop of solution on the tongue (e.g., Konstantinidis et al., 2010) and, more rarely, sprayed as a solution into the mouth (Welge-Lüssen et al., 2011).

Additionally, the matrix affects tastant perception. Taste sensitivity measurements are usually conducted using pure water solutions of tastant but real food is used sometimes. Food is more complex than water containing multi-modal stimuli that can affect the perception of the target tastant. The release of taste compounds during food oral processing also depends on food matrix composition (Feron & Salles, 2018). Thus, results may not be comparable when different matrixes are used.

2.2.6.3 Intensity rating scales

Intensity rating scales are applied to quantify sensory experiences. At present, a category scale is very rarely used in intensity rating. The main drawback of the category scale is the limited number of response options that cannot reveal subtle differences between samples. In contrast, line scales such as VAS or LMS have almost a limitless number of response options as a subject can mark the intensity of sensation at any point on the scale. Usually, the endpoints of VAS are marked with labels, such as not at all or extremely weak and extremely intense. Other points may also be marked.

LMS or gLMS has been widely used in taste intensity rating to achieve comparable values between groups. LMS is a quasi-logarithmic line scale (from 0 to 100) with

ratio properties and empirically determined verbal descriptors: 1.4 = barely detectable, 6.1 = weak, 17.2 = moderate, 35.4 = strong, 53.3 = very strong, and 100 = strongest imaginable (Green et al., 1993, 1996). In gLMS, the top anchor was changed from oral sensation to any kind of sensation (Bartoshuk et al., 2002). This top anchor is thought to represent about the same intensity for everyone, thereby providing valid comparisons between individuals across different taster groups such as PROP non-tasters and tasters. The top anchor and the wide space between the descriptors in the upper end of the scale help to avoid ceiling effect and to differentiate between intense samples (Schifferstein, 2012). However, with mild samples, LMS is not very sensitive as the anchors in the lower end of the scale are close to each other.

The gLMS demands intensive training of study participants. Additionally, the use of gLMS relies on the assumption that people can match the intensity of different modalities of sensations. Frequently, weights or sounds have been used as standards to control scale-use bias (Delwiche et al., 2001). For example, the perception of heaviness of weight is assumed to be unrelated to taste perception, and, on average, weight is perceived equally intense between PROP tasters and non-tasters. Thus, tasters and non-tasters can be compared when their taste ratings are standardized relative to weight or sound ratings. Occasionally, PROP taster status is determined relative to NaCl intensity (Bartoshuk et al., 1994). This method is slightly vague as NaCl and PROP tasting may be related (Duffy, 2004; Hayes et al., 2010).

The gLMS is widely used, but its goodness depends on the subject training and guidance, like the goodness of any scale. Despite training, subjects may find it difficult to use gLMS, leading to the exclusion of participants (Spinelli et al., 2018). Fischer et al. (2013) reported that 15.1% of subjects had to be removed from their study because they did not understand how to use gLMS despite training. Most of them were elderly subjects. Furthermore, LMS scales also suffer from contrast and range effects (Lawless et al., 2000). Humans generally tend to compare items such as in intensity rating to compare a sample with that immediately preceding.

2.3 Subjective factors related to taste sensitivity

Another thing to consider in taste sensitivity research is the characteristics of study participants. Frequently, students or staff members are recruited as subjects. Recruiting subjects from near the testing facilities is convenient; however, this could cause a very homogenous sample population, for example, with narrow age range and healthy lifestyle. Many subjective factors are likely to affect taste sensitivity and need to be considered when the volunteer study participants are recruited.

Taste receptor genotype, FP density, and saliva are discussed in chapters 2.1.1–2.1.3. The other intrinsic factors that have been related to human taste sensitivity include gender, age, and hormonal status (also under the influence of environmental factors).

The studied extrinsic factors are more or less related to health: weight status, smoking, medication, and diseases. The interaction between all these factors complicates research. As stated earlier, intensity measures may be the most relevant concerning food habits. Thus, the following chapters focus on studies conducted using intensity measures concerning the putative taste-related factors. The studies related to the association between taste sensitivity and gender, age, BMI, and smoking are reviewed in **Table 1**. The focus was on studies from the current century that determined taste sensitivity with intensity measure by using any tastant other than PROP or PTC. Tepper et al. (2017) recently reviewed the topic concerning PROP. Moreover, only studies conducted with adults and water solutions of tastants were considered.

Table 1. Associations between the intensity perception of different tastants and gender, age, BMI, and smoking status.

Stimuli	Concentration	N (subjects)	Gender	Age	BMI	Smoking	Reference
Sweet							
Sucrose	200 mM	85		ns	ns		Cicerale et al. (2012)
	100–400 mM	60	ns		ns		Low et al. (2016)
	400 mM	381	ns		ns		Coltell et al. (2019)
	400 mM	1020	ns	-			Barragán et al. (2018)
	1800 mM	2374	f+	+		ns	Fischer et al. (2013)
	1.78–1000 mM	33			-		Sartor et al. (2011)
	0–1050 mM	57			ns	ns	Pepino et al. (2010)
	8.55–53.95 g/l	42	ns	-			Mojet et al. (2003)
Glucose monohydrate	240–960 mM	60	ns		ns	Low et al. (2016)	
Fructose	140–560 mM	60	ns		ns	Low et al. (2016)	
Sucralose	0.14–0.56 mM	60	ns		ns	Low et al. (2016)	
Erythritol	400–1600 mM	60	ns		ns	Low et al. (2016)	
Rebaudioside A	0.27–1.08 mM	60	ns		ns	Low et al. (2016)	
Aspartame	0.06–0.37 g/l	42	f+	ns		Mojet et al. (2003)	
Bitter							
QHCl	0.32 mM	59	ns				Duffy et al. (2010)
	1.0 mM	110	ns	ns	ns		Dinehart et al. (2006)

Stimuli	Concentration	N (subjects)	Gender	Age	BMI	Smoking	Reference
	1.0 mM	2374	f+	ns		+	Fischer et al. (2013)
	0.00–0.01 g/l	42	m+	-			Mojet et al. (2003)
Caffeine	0.16–1.00 g/l	42	ns	-			Mojet et al. (2003)
Sour							
Citric acid	34 mM	381	m+		-		Coltell et al. (2019)
	34 mM	1020	f+	-			Barragán et al. (2018)
	0.1 mM	2374	f+	ns		+	Fischer et al. (2013)
	1.26–7.92 g/l	42	ns	-			Mojet et al. (2003)
Acetic acid	0.63–4.00 g/l	42	ns	-			Mojet et al. (2003)
Salty							
NaCl	200 mM	381	f+		-		Coltell et al. (2019)
	200 mM	1020	f+	-			Barragán et al. (2018)
	1000 mM	2374	f+	ns		ns	Fischer et al. (2013)
	3.16–100 mM	33			-		Sartor et al. (2011)
	3.58–22.61 g/l	42	ns	-			Mojet et al. (2003)
KCl	5.68–35.83 g/l	42	ns	-			Mojet et al. (2003)
Umami							
MSG	0–180 mM	57			ns	ns	Pepino et al. (2010)
	1.99–12.58 g/l	42	ns	-			Mojet et al. (2003)
MPG (monopotassium glutamate)	200 mM	381	ns		-		Coltell et al. (2019)
	200 mM	1020	ns	-			Barragán et al. (2018)
IMP (inosine monophosphate)	1.26–7.94 g/l	42	ns	-			Mojet et al. (2003)
Total taste score							
		381	f+		-		Coltell et al. (2019)
		1020	f+	-			Barragán et al. (2018)

ns, no significant association; -, negative association; +, positive association, f+, females more sensitive; m+, males more sensitive.

2.3.1 Gender

No clear relationship exists between gender and taste intensity perception. Most of the studies that found a relationship suggested that females were more sensitive than males (**Table 1**). This finding is supported by two studies on taste modality recognition (Landis et al., 2009; Welge-Lüssen et al., 2011). However, many cases found no significant association, and umami taste sensitivity was not related to gender in any of the intensity studies. Concerning PROP, varying results have also been obtained, although females have been found to be more sensitive than males (Tepper et al., 2017).

If only those studies in which numerous subjects ($N > 100$) with a broad age and BMI range and whole-mouth taste test are considered, only one result is reported for each tastant. Females found to be more sensitive to PROP (Dinnella et al., 2018), citric acid, and NaCl (Barragán et al., 2018), whereas no difference was found for sucrose, monopotassium glutamate (MPG) (Barragán et al., 2018), and QHCl (Dinehart et al., 2006).

The reason for gender differences in taste perception is not completely understood. Differences in both peripheral and central processing of taste perception have been observed (Martin & Sollars, 2017). For example, FP density may be considered as one of the factors responsible for the difference, although mixed results have been reported. Some studies have found that females have more FP (Duffy et al., 2004; Feeney & Hayes, 2014b; Hayes et al., 2008), whereas some reported no difference between genders (Duffy et al., 2010; Lanier et al., 2005; Masi et al., 2015). The Italian Taste study and another large-scale study found that males had lower FP density (Dinnella et al. 2018; Fischer et al., 2013). In a smaller subsample of participants in the Italian Taste Project, Piochi et al. (2019) found no gender effect. They used automated counting of FP and claimed that this could be used to observe smaller FP than what could be counted manually. Logically, if the FP density is relative to tongue size, and tongue size is relative to body size, females would have higher FP density than males (Feeney & Hayes, 2014a).

Additionally, sex hormones have been related to taste sensitivity and can explain gender differences (Than et al., 1994).

2.3.2 Age

Most of the studies that found a relationship between age and taste sensitivity found a negative relationship: older subjects were less sensitive (**Table 1**). Interestingly, Fischer et al. (2013) found a positive association between sweet taste sensitivity and age (i.e., higher sensitivity was related to older age), whereas other taste sensitivities were not related to age in their large-scale study ($N = 2374$). The strength of their study is that they adjusted the statistical models with multiple putative taste-affecting

factors such as medication and health factors. This adjustment might be one reason why they did not find more associations between age and taste perception as medication use and health disorders become more likely in later life. Mojet et al. (2003) concluded that the age effect was general and not taste modality- or tastant-specific.

Only one large-scale study (N = 1020) was performed using whole-mouth testing. Barragán et al. (2018) found a negative association with age regarding all tastants they applied: sucrose, citric acid, NaCl, and MPG. Additionally, in the Italian Taste study, PROP intensity perception decreased with age (Dinnella et al., 2018).

Methven et al. (2012) reviewed the relationship between healthy aging and taste acuity. They concluded that, although the deterioration of the sense of taste is a continuous phenomenon, the age effect is more evident after 60 years of age. However, no clear consensus was found in studies that used suprathreshold intensities, except where sweet intensity perception did not seem to decline with age. However, DT and RT seemed to increase with age. Concerning DT, the extent of the decline was depended on tastant and taste modality.

Some studies showed no age effect on taste identification (Hoogeveen et al., 2015; Vennemann et al., 2008), whereas others reported an age-related decline in the ability to recognize taste modalities (Doty et al., 2017; Landis et al., 2009; Nordin et al., 2007). Additionally, the effect of age was more pronounced for the bitterness of QHCl and sourness of citric acid than for the saltiness of NaCl and sweetness of sucrose (Nordin et al., 2007). Bitnes et al. (2007) studied the effect of aging for the identification of taste samples among trained sensory panelists. In their study, older subjects could better recognize taste modalities among the healthy subjects.

Several factors can mediate age-related taste deterioration. These include reduced taste-bud density (Dinnella et al., 2018; Fischer et al., 2013), decreased regeneration of taste receptor cells (Doets & Kremer, 2015), reduced saliva secretion (Doets & Kremer, 2015; Sasano et al., 2015; Vandenberghe-Descamps et al., 2016), changed amino acid content of saliva (Doets & Kremer, 2015; Dsamou et al., 2012; Sasano et al., 2015), altered brain structure (Fjell et al., 2006), and changed central processing in the brain (de Boer et al., 2013; Doets & Kremer, 2015). The effect of these factors interacting with medication and diseases can alter taste function. The effect of medication and diseases can be age-independent, but as the prevalence of such conditions increases with age, they become increasingly relevant for the taste function as well as for food intake as people get older (Schiffman, 2018).

2.3.2.1 Health status and medication

Several diseases or conditions have been shown to affect peripheral or central processing of taste perception. Viral infections in the upper respiratory channel and

oral cavity have been reported as the most common causes of taste dysfunction (Feng et al., 2014; Henkin et al., 2013). Additionally, other viral infections such as HIV, autoimmune diseases, cancer, head injuries, cranial nerve damage (Feng et al., 2014; Henkin et al., 2013), and primary burning mouth syndrome (Kolkka-Palomaa et al., 2015) have been coupled with altered taste sensitivity. Furthermore, mild depression and anxiety have been related to stronger taste perception (Platte et al., 2013).

As already mentioned in chapter 2.2.6.2, damage to gustatory nerves can change taste perception. Otitis media and tonsillectomy are frequently associated with nerve damage to chorda tympani and glossopharyngeal nerves, which are also an essential part of taste transduction. Otitis media and tonsillectomy have been reported to be related to diminished taste function (Rawal et al., 2017). Bartoshuk et al. (2012) found that damage to only one nerve caused intensified whole-mouth taste sensations. The underlying theory is that damage to one nerve can release inhibition of other, non-damaged nerves. Extensive damage to both nerves led to diminished taste sensations.

Boesveldt et al. (2018) discussed the connections between poor health and taste perception in their review. Alzheimer's disease and Parkinson's disease are the most common degenerative disorders worldwide. Olfactory deficiency has been reported in both cases, and taste impairments can also evolve as an adverse effect. Typical for these diseases is reduced nutrition that can cause multiple behavioral, cognitive, and physical changes, possibly also change of taste perception.

It is also suggested that people with diabetes have lower sweet taste sensitivity (Wasalathanthri et al., 2014) as well as sour and salty taste sensitivity (Gondivkar et al., 2009) than non-diabetics. Notably, both studies had severe limitations. In a large-scale study (N = 2374), diabetes was not a significant predictor of any taste modality-specific sensitivity (Fischer et al., 2013). The cause-effect relationship between diabetes and gustatory sensitivity and whether it is mediated by medication are unclear.

Several drugs for different conditions have been related to taste disorders, either to altered taste sensitivity or perceptual distortions (Fischer et al., 2013; Naik et al., 2010; Schiffman, 2018). The most common disorder is dysgeusia, where the taste of food is misinterpreted because of persistent sweet, salty, bitter, or metallic taste sensation caused by medication (Naik et al., 2010). Other types of drug-induced abnormalities include ageusia, the absence of one or several taste sensation; parageusia, the perception of foul or abnormal taste in the mouth instead of normal food taste; hypogeusia, lowered taste sensitivity; and phantogeusia, taste sensation without oral stimulation (Naik et al., 2010; Schiffman, 2018). Additionally, drugs themselves often have unpleasant flavor, mainly bitter, sour, or metallic, when ingested or even later (Schiffman, 2018). A wide spectrum of medication seems to weaken sensitivity especially to sour and bitter tastes (Fischer et al., 2013). Lower

sensitivity has been detected even after the cessation of use for several months (Naik et al., 2010).

2.3.3 Weight status

The main reason for overweight is an excess intake of foods and beverages high in energy content. People with diminished taste sensitivity are proposed to seek more intense taste from foods than people with normal or elevated taste sensitivity. This phenomenon can lead to excess intake of high-calorie foods and further to overweight. Thus, overweight people would have diminished taste sensitivity. However, study findings have been inconsistent and have focused on sweet taste sensitivity.

When an association between BMI and taste sensitivity was found, it was negative (**Table 1**). Only one study used whole-mouth testing, had $N > 100$, and a wide BMI range. This study found no significant association between BMI and bitter taste sensitivity.

Cox et al. (2016) also reviewed links between taste perception and weight status, but they also included studies conducted with children or adolescents and those that measured taste perception in a food matrix. One of their findings was that further good-quality studies are needed. Many studies found no association between taste perception and weight status. Findings for sweet and salty perception were controversial. Very few studies were conducted with bitter (two studies) or umami (one study) stimuli, although they all stated a significant negative relationship. Regarding sour taste, one of the four studies found a relationship (negative). A more recent study with children found that normal-weight males perceived sucrose solutions more intensely than overweight/obese males, but no difference between weight status was observed with females or with salt and bitter perception (Feeney et al., 2017). Hardikar et al. (2017) found that obese subjects were more sensitive to sweet and salt by using threshold and intensity approaches as well as more sensitive to sour by using intensity measure compared to lean subjects. Regarding PROP, findings are also controversial, although several studies have shown that non-taster females have higher BMI than taster females (Tepper et al., 2017). In conclusion, it seems that if there is an association between taste sensitivity and BMI, it is a negative one.

Taste receptors may perform a dual role in weight status, as recent studies show an association between taste receptors and appetite regulation. Taste receptors are also expressed and function in the gastrointestinal tract where they may be involved in nutrient sensing, regulating neurotransmitters, and binding metabolic hormones, suggesting an association among taste, adiposity, and food intake (Depoortere, 2014). Many hormones have been found to bind receptors on taste cells, and thus

putatively modulate taste perception by affecting taste receptor cell activity. Loper et al. (2015) reviewed the role of hormonal modulation based on animal and human studies. Many of these hormones, such as leptin, insulin, and endocannabinoids, are related to the regulation of appetite. Thus, they might have dual input in ingestive behavior if they also modulate the intensity of taste perception. For example, diurnal leptin variation correlated strongly with diurnal variation of sweet thresholds (Nakamura et al., 2008). Current knowledge is still scarce, and more research is needed to reveal the connections between adiposity, hormones, and taste perception.

Food oral processing may also differ between obese and lean individuals (Feron & Salles, 2018). In obese subjects, the salivary flow rate can be lower and the composition can differ from lean individuals in addition to poorer oral health and different chewing behavior.

2.3.4 Smoking

The association between smoking and taste intensity perception has not been studied excessively. Instead, smoking is a common exclusion criterion in the recruitment of study participants, as it is thought to affect taste perception. In **Table 1**, two studies covered this subject. No significant association was noted between smoking and sweet, salty, and umami taste sensitivity. Bitter and sour tastes were perceived as more intense by smokers than non-smokers. These positive associations were found in the study by Fischer et al. (2013), who presented the tastants impregnated on filter paper discs. Thus, no large-scale studies ($N > 100$) with whole-mouth testing exist.

Vennemann et al. (2008) studied the relationship between smoking and taste impairment. They defined taste impairment as the incapacity to identify four taste samples of bitter, sour, sweet, and salty. They observed 19.8% of the subjects ($N = 1312$) with taste impairment. The status of former or current smoking was not related to taste impairment, but heavy smokers (20+ cigarettes per day) had more taste impairments than those who smoked fewer cigarettes per day.

The association between smoking and taste sensitivity has also been assessed using electrogustometric thresholds. Thresholds have been lower for non-smokers than for smokers, i.e., smokers were less sensitive (Chérueil et al., 2017; Pavlos et al., 2009). Moreover, as tobacco dependence increased (measured as the number of cigarettes/day and duration of smoking habit), the threshold increased (Chérueil et al., 2017). However, cessation of smoking improved electrogustometric sensitivity after two weeks (Chérueil et al., 2017).

Smoking can affect the shape and microcirculation of taste buds (Pavlos et al., 2009) as well as the number of FP (Fischer et al., 2013), thereby possibly shaping peripheral taste perception mechanism.

Moreover, some other taste-related factors have been found, but more research is needed. The cognitive state can affect taste perception suggesting that busy lifestyle and increased attention to mobile devices could reduce taste perception. Liang et al. (2018) showed how sweet and bitter threshold decreased while the difficulty of a memory load task increased. Ethnicity may also be related to taste sensitivity (Holt et al., 2000; Williams et al., 2016). However, further research is needed as cultural and other environmental factors may alter taste perception between ethnic groups. Furthermore, higher education predicted lower sensitivity to saltiness, sweetness, sourness, and bitterness (Fischer et al., 2013). This result was explained with stronger “adventurous” character among the highly educated, leading to broader experience in tasting different foods. The food consumed can also affect taste perception, or *vice versa*. The studies related to taste sensitivity and food-related behavior are reviewed in the next chapter.

2.4 The associations between taste sensitivity and food-related behavior

People sensitive to some taste modality have been thought to also perceive intense taste from foods. This sensitivity would lead to the rejection of strong-tasting foods. In contrast, those with low taste sensitivity would seek for strong-tasting foods to reach optimal pleasantness level. However, only few studies have covered this theory. The cross-sectional studies conducted with adults and concerning the relationship between food-related behavior and taste sensitivity determined with intensity perception are reviewed in **Table 2**. Studies conducted with PROP sensitivity are excluded. Food-related behavior comprises use-frequency, intake of foods, recalled or sampled food liking, and other consumption habits. Moreover, the focus was not on the intake of nutrients or energy. In the studies in **Table 2**, the subjects were considered healthy, and all taste sensitivities were determined using a gLMS or LMS scale.

Table 2. Studies concerning associations between taste sensitivity (intensity perception) and food-related behavior.

Reference and country of data collection	Subjects	Tastant for sensitivity	Target food	Food-related behavior data type	Results ¹
Duffy et al. (2003), USA	N = 82 46% females age 20–39 y (mean 26 y)	0.32 mM QHCl	sweet foods	- sweetness intensity of and preference for sampled foods (4 foods high in added sugar) - liking (11 items) - intake of foods high in added sugar (12 items)	• sampled foods: ns • liking questionnaire: + • intake: +
Jayasinghe et al. (2017), New Zealand	N = 44 all females age 20–40 y (mean 28 y)	125–1000 mM glucose	sweet foods	- sweet-food and beverage consumption frequency (8 categories) - sweet beverage liking (16 categories)	• frequency: - with baking/sweets intake, total sweet food intake; ns with other categories • liking: - with fruit juice and fruit drink; ns with other
Keskitalo et al. (2007), UK	N = 663 all females age 17.3–80.7 y (mean 55.6 y)	20% sucrose	sweet foods	liking and consumption frequency (6 categories)	ns
Cicerale et al. (2012), Australia	N = 85 89% females mean age 21 y	200 mM sucrose	mainly sweet foods	- dietary activities and food beliefs related to health (29 items) - food variety survey	• dietary activities: ns with the importance of not adding sugar to tea or coffee, and avoiding sugar-sweetened or fizzy drinks • food variety: ns with food variety score, with food variety measure for sugar and confectionary intake, or with selected fruit and vegetable consumption

Low et al. (2016), Australia	N = 60 53% females age 18–52 y (mean 26)	100–400 mM sucrose 240–960 mM glucose monohydrate 140–560 mM fructose 0.14–0.56 mM sucralose 400–1600 mM erythritol 0.27–1.08 rebaudioside A	sweet foods	- Food Frequency Questionnaire (80 items) - consumption frequency of foods or beverages sweetened with high-intensity sweeteners	ns
Low et al. (2018), Australia	N = 92 all females mean age 23.7 y	5.3–21.2% glucose	sweet and complex carbohydrate foods	- liking of sampled foods (16 items) - consumption frequency	ns
Spinelli et al. (2018), Italy	N = 1146 61% females age 18–60 y (mean 36.5 y)	4g/kg citric acid 3g/kg caffeine 200 g/kg sucrose 15 g/kg NaCl 10 g/kg MSG	pungent foods	consumption frequency of chili pepper and pungent foods	ns
Lipchock et al. (2017), USA	N = 20 60% females age 19–40 y (mean 31)	500 mM urea 8 mM caffeine 492 nM denatonium benzoate 119 µM QHCl	caffeine (coffee, tea, carbonated beverages) and quinine (tonic water) containing beverages	consumption frequency	• caffeine-containing beverages and caffeine sensitivity: + • other associations: ns
Duffy et al. (2004), USA	N = 83 48% females age 21–39 y (mean 26 y)	1 M NaCl 32 mM citric acid	alcohol	yearly intake (3 categories)	+ in multiple regression model adjusted with several variables: ns
Fischer et al. (2013), USA	N = 2374 53% females age 21–84 y (mean 48.8 y)	1 M NaCl 1.8 M sucrose 0.1 M citric acid 1 mM QHCl	alcohol	consumption during the past year	• with salt and sweet sensitivity: - • with other: ns

¹ns, no significant association with taste sensitivity; +, positive association with taste sensitivity; -, negative association with taste sensitivity

Six studies focused on sweet foods, two studies on alcohol beverages, one on pungent foods, one on ice creams, and one on caffeine- and quinine-containing beverages. Most of the studies found no associations. Of the significant associations, half were positive, and half were negative.

The associations between PROP sensitivity and food-related behavior have been reviewed before (Tepper, 2008). PROP sensitivity has been associated negatively with consumption and/or liking of bitter vegetables, bitter citrus fruits, alcohol beverages, caffeine-containing products, sweet foods, fatty foods, and pungent foods, but the results have been contradictory. Although PROP tasters and non-tasters differ in intensity perception or differentiation of some other properties, it may not cause differences in consumption habits or hedonics in adults.

Recent studies also present conflicting findings. Catanzaro et al. (2013) studied the recalled liking of 12 foods linked to PROP sensitivity among PROP taster groups. The items included in their questionnaire were several bitter-tasting and pungent vegetables, black coffee, dark chocolate, alcohol beverages as well as creamy salad dressing and mayonnaise. The only significant associations they reported were weak negative correlations with chili peppers and dark chocolate. Moreover, Masi et al. (2015) found no association between PROP sensitivity and sampled coffee liking. Interestingly, the least sensitive subjects added more sugar to coffee than the most sensitive ones did, although they perceived coffee samples to be milder in taste. Furthermore, PROP taster status (determined relative to NaCl perception) was not related to the liking of sampled ice cream varying in fat content (Shen et al., 2017). In a large-scale study (N = 1146), although PROP sensitivity was weakly positively correlated with capsaicin burn intensity, PROP tasting was not related to the liking or consumption of pungent foods (Spinelli et al., 2018). One study related higher PROP sensitivity to less consumption of vegetables (Duffy et al., 2010), whereas another study found no association between PROP taster status and vegetable liking and intake (Shen et al., 2016).

Some variations between results can be explained by the different methods used for data collection as well as subjects' characteristics as the results between PROP sensitivity and food-related behavior can depend on gender, age, FP density, and personality trait (Duffy et al., 2010; Spinelli et al., 2018; Tepper, 2008). The variations in methods to attain taste sensitivity are reviewed in chapter 2.2. The methods to gain data regarding food-related behavior also vary. Food consumption frequency can be measured using food diaries/records or questionnaires with lists of foods. Food hedonics can be measured using recalled liking or by tasting foods on the spot. The ratings of recalled and sampled liking have been reported to be correlated (Hayes et al., 2010; Ly & Drewnowski, 2001). Furthermore, surveyed liking and reported intake have been shown to be associated (Dinehart et al., 2006; Drewnowski & Hann, 1999; Ly & Drewnowski, 2001), indicating that liking could

be used as an alternative measure for intake. It is cognitively easier to recall liking than the frequency and amount of consumed food. Additionally, the liking of food is rather stable, whereas consumption can vary broadly between days. Moreover, food records have the limitation that they might encourage to consume differently from a typical day and to undereat on reporting days. If subjects report consumption in real-time without relying on memory, food records are a reliable tool to measure consumption on certain days. If the responses are based on memory, underreporting is more likely to appear than overreporting (Subar et al., 2015). Concerning any self-reported estimate, social desirability bias may occur, e.g., a desire to present oneself positively (Subar et al., 2015).

Finally, variation in the results can be explained with the complexity of food-related behavior. Multiple factors affect food choice independently or in interaction and taste sensitivity is only one putative factor.

2.5 Summary

The five traditionally accepted taste modalities are sour, bitter, sweet, salty, and umami. Taste eliciting chemical compounds bind to taste receptors located in the papillae on the tongue and in the oral cavity starting signal cascades. Nerves transmit the signals to the brain for the interpretation of perception including intensity, recognition, and liking. Taste perception can vary between individuals due to the variation in the peripheral or central processing of taste transduction. For example, individual variation in taste receptors, fungiform papillae morphology, saliva secretion, and nerve function can modulate taste perception. Additionally, many subjective and behavioral factors have been related to taste sensitivity, including gender, age, BMI, and smoking habit, but the results have been controversial.

One reason for the mixed results is the wide variety of methods. Regarding eating, the dominant tastes of food are readily perceivable and thus, intensity rating is the most relevant method to determine taste sensitivity when taste responsiveness is studied relative to food-related behavior. In general, few studies consider five taste modalities when taste intensity or recognition is measured. In the case of recognition, neglecting umami taste is a common practice.

Usually taste sensitivity is measured with PROP, the bitter-tasting synthetic compound. People can be categorized into PROP tasters, non-tasters and medium tasters. PROP taster status has been used as a marker for general taste sensitivity, although other tastant intensities seem to correlate more strongly with each other than with PROP. PROP sensitivity is an extreme example of taste sensitivity and people seem to vary less in responsiveness to other tastants. More studies using other tastants are needed to interpret the importance of taste sensitivity in food-related behavior.

When taste sensitivity is determined with other tastants than PROP, a quite low number of studies have been conducted to investigate the role of taste sensitivity in food consumption and liking. Especially, when the importance of food in everyday life and the relevance of the taste of food for food consumption are considered. Some results support the theory that heightened taste sensitivity leads to lower liking and consumption of intense tasting foods or the opposite in the case of lower taste sensitivity. The majority of the studies found insignificant results. Clearly, more studies are needed that are conducted with more subjects, more versatile food categories, and five taste modalities when the associations between taste sensitivity and food-related behavior are investigated.

3 Aims

The main objective of this study was to investigate the association between individual taste sensitivity and food-related behavior among adults. Taste sensitivity was analyzed separately with every taste modality as well as with a general taste sensitivity score. Food-related behavior comprised consumption of vegetables, fruits, and berries; use-frequency and recalled pleasantness of specific foods and beverages; and habits to mask or modify the taste of foods. Demographic and health-related background characteristics were also considered as explanatory factors for taste sensitivity and food-related behavior.

The specific aims were as follows:

- to categorize subjects to taste sensitivity groups regarding five taste modalities (I);
- to study subjects' ability to recognize taste modalities (II);
- to analyze whether gender, age, BMI, and smoking are related to taste perception (II);
- to explore whether taste sensitivity or subjects' background factors are associated with food-related behavior (III).

4 Materials and Methods

4.1 Participants and study design

The aim was to recruit as many volunteers as possible by advertisement around the University of Turku, on the University web pages, and at public events. The exclusion criteria were pregnancy or a lactating state. One subject was excluded later because of taste loss after an accident. Two hundred and five subjects (19–79 years old) were included in the analyses. Allergies or other eating restrictions were asked before the first visit and acknowledged in the testing situation. The participants were instructed not to wear intensely scented cosmetics during the test day and to avoid eating, drinking other than water, chewing gum, and smoking an hour before the sensory evaluation. After the study aims were explained, the subjects provided written informed consent. They were rewarded with food products after both study visits.

This study was a part of a larger research project concerning individual sensory perception and food-related behavior. The cross-sectional study design is described in **Figure 3**. The participants had two study visits in the sensory evaluation laboratory of Functional Foods Forum, University of Turku; additionally, they filled two online questionnaires at home. The data for this thesis were collected in the second taste test and from questionnaires I and II (**Figure 3**). As the subjects also completed other sensory tests, the procedure was carefully designed to prevent excessive fatigue and to keep up the interest. The study was approved by the Southwest Finland Hospital District’s Ethics Committee (145/1801/2014).

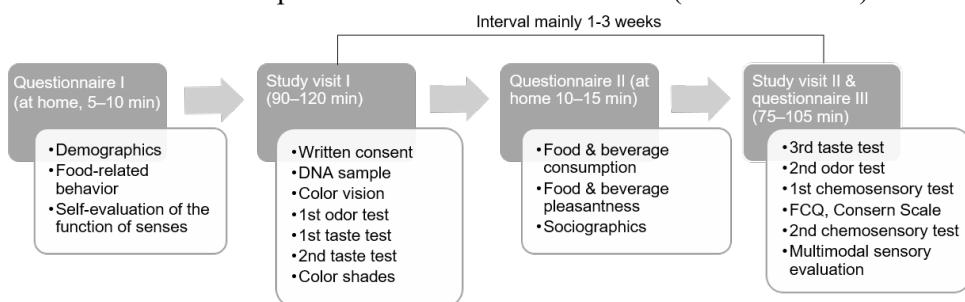


Figure 3. Overview of the project FoodTaste in Finland. FCQ, Food Choice Questionnaire.

4.2 Taste stimuli

Five taste modalities were studied with one prototypic compound for each: citric acid for sour, caffeine for bitter, sucrose for sweet, NaCl for salty, and MSG for umami taste. Five dilutions of every tastant were prepared in active-carbon filtered water and refrigerated (**Table 3**). The concentrations were selected according to ASTM (1981) standard for measuring taste intensity, as well as previous experience at the sensory evaluation laboratory of Functional Foods Forum. The concentration ranges were selected across threshold and suprathreshold levels rather than choosing only one suprathreshold concentration. The samples were diluted by the quarter-logarithmic dilution factor for each step. The strongest concentration of each taste modality was expected to be readily perceivable for people with a normal taste function. No stronger concentration levels were selected to avoid a severe ceiling effect in intensity judgments obtained using VAS. The samples were stored maximum for four days except umami samples, which were stored maximum of two days. The samples were allowed to settle at room temperature before evaluation.

The samples (5 ml) were served in glass beakers marked with random three-digit numbers. The samples were presented in two blocks of 14 samples in one session (total of 28 samples; **Table 3**). Within the blocks, the sample order was randomized. The first block included the mildest samples: E and D samples of every modality, C samples of NaCl and citric acid, and two blanks (active-carbon filtered water). The second block included the remaining samples and one blank. C dilutions of NaCl and citric acid were included in the first block to balance the number of samples in the blocks, and the taste of these modalities is easier to rinse off than that of caffeine or MSG samples. The intention was to avoid interfering the evaluation of very mild samples with the lingering aftertaste of strong-tasting samples. Overall, this sample presentation design was expected to prevent the effect of positional bias and excessive fatigue. All samples were evaluated once.

Table 3. Samples and their presenting order. All samples were evaluated in a single session.

Taste	Prototypic tastant	Sample A (mM) ^d	Sample B (mM) ^d	Sample C (mM)	Sample D (mM) ^c	Sample E (mM) ^c
Sour	Citric acid ^a	3.33	1.87	1.05 ^c	0.57	0.33
Bitter	Caffeine ^a	3.60	2.03	1.14 ^d	0.62	0.36
Sweet	Sucrose ^b	58.4	32.9	18.5 ^d	10.5	5.84
Salty	NaCl ^a	34.2	19.2	10.8 ^c	5.99	3.42
Umami	MSG ^a	10.7	6.01	3.38 ^d	1.87	1.07

^a produced by Sigma-Aldrich, St. Louis, USA, ^b produced by Alfa Aesar GmbH&Co KG, Karlsruhe, Germany, ^cserved in the first block of samples for evaluation, ^dserved in the second block of samples for evaluation. Modified from publication I.

4.3 Taste evaluation

The subjects were familiarized with the taste modalities and intensity evaluation during the first taste test (**Figure 3**). They evaluated the intensity and modality of the strongest concentration level of each taste dilution. If a subject recognized incorrectly any taste modality, he/she tasted that taste modality again. Thus, every subject had knowledge to recognize all taste modalities in the actual taste test.

The subjects were instructed to sip the entire sample, spin it around the mouth for five seconds, and spit it out into an adjacent basin. Active-carbon filtered water and cream crackers were provided for mouth neutralization. Intensity and modality recognition were evaluated from the same sip.

The subjects were informed that each sample contained one of the five taste modalities or water. First, the subjects rated the intensity of the taste on a VAS (0–10) labeled both numerically and verbally: 0 = no sensation, 2 = very mild, 4 = quite mild, 6 = quite strong, 8 = very strong, and 10 = extremely strong. The subjects were also instructed that a sample with a rating of zero would have a taste similar to water; thus, if they perceived any taste they should rate the intensity of taste above zero. Additionally, five on the scale was explained to be a clearly detectable taste sensation. The subjects were instructed to make a mark on the line scale at any point they felt appropriate. The intensity judgments of samples A–D were used to determine modality-specific sensitivities as well as the descriptor of overall taste sensitivity, the taste sensitivity score (TSS).

Second, the subjects indicated the taste modality they perceived. The response options of the forced-choice question were “sweet,” “salty,” “sour,” “bitter,” “umami,” “water,” and “something else.” The maximum number of correct recognitions (e.g., sucrose solution recognized as sweet) for one taste modality was five as there were five concentration levels. A taste recognition score (TRS) was computed to describe the overall capability to recognize taste modalities. The score was the mean number of correct recognitions over all taste modalities. The theoretical score range was from 0.0 (all samples incorrectly identified) to 5.0 (all samples correctly identified).

Taste evaluation was performed under standardized test conditions at the sensory evaluation laboratory (ISO 8589; Functional Foods Forum, University of Turku). The data were collected using Compusense *five* plus software (Compusense, Guelph, Canada).

4.4 Questionnaires

The questionnaire data were collected using the Webropol online questionnaires (Webropol Inc., Helsinki, Finland), before the first and second study visit.

4.4.1 Subjects' background factors

Gender was changed to a dummy variable: 0 = male, 1 = female. As age was not normally distributed, it was divided into three categories: the youngest subjects, 19–34 years old [M (sd) = 27.8 (4.1) years]; the middle-aged subjects, 35–49 years old [M (sd) = 42.5 (4.3) years]; and the oldest subjects, 50–79 years old [M (sd) = 61.8 (8.5) years]. In the oldest age group, the majority were 50–59 years old (N = 25, 43.1%), 34.5% (N = 20) were 60–69 years old, and the minority were 70–79 years old (N = 13, 22.4%). BMI was calculated from the self-reported height and weight, according to the formula $\text{kg}/(\text{m})^2$. BMI was also non-normally distributed, and thus divided into three categories: lean subjects with BMI < 25.0 [M (sd) = 21.8 (2.0)], including three underweight persons (BMI < 18.5); overweight subjects with BMI 25.0–29.9 [M (sd) = 27.2 (1.4)]; and obese subjects with BMI \geq 30.0 [M (sd) = 34.9 (4.3)]. Education was divided into two categories: lower education, including comprehensive school, high school, and lower vocational degree; and higher education, including a polytechnic degree or any university degree. Education was not expected to be an explanatory factor for taste perception; thus, it was not included in study II. Smoking habit was asked with the response options “yes, daily,” yes, occasionally,” “not currently but used to,” and, “no.” The first three categories were combined for the statistical analysis because only six subjects (all females) smoked daily, and 11 subjects smoked occasionally (seven females and four males). Smoking was applied as a potential explanatory variable for taste sensitivity and recognition (II), but not for food consumption behavior and liking (III). In the latter case, daily smokers were removed from the data set because smoking and food-related behavior might be associated but studying that with only six daily smokers would be futile.

4.4.2 Food-related behavior

4.4.2.1 Portions of vegetables, fruits, and berries per week

The typical number of portions of vegetables, fruits, and berries per day was separately obtained for each food category by using a category scale from 0 to 6 portions and with an option “I cannot say.” The instructions guided that, for example, one carrot, tomato, or apple, or 100 ml of berries or grated vegetables represents one portion. The consumption frequency of vegetables, fruits, and berries was also asked separately for each food category with the response options “every day,” “5–6 days per week,” “3–4 days per week,” “1–2 days per week,” and “more seldom than once per week.” These two responses were combined to generate a new variable separately for vegetables, foods, and berries called portions per week (range 0–42). This variable was computed as portions per day multiplied by use-frequency.

4.4.2.2 Masking and modifying the taste of food

The frequencies of certain consumption habits were assumed to describe the tendency to mask or modify the taste of foods and beverages. The questions are shown in **Table 4**. The response options were “always,” “often,” “sometimes,” “rarely,” “never,” and, when appropriate, “I don’t drink coffee/drink tea/prepare food.” The last response was removed (marked as missing) before statistical analysis, and two new dichotomous variables were generated: the habit of drinking coffee vs. not drinking coffee, and habit of drinking tea vs. not drinking tea.

Table 4. Questions asked to study consumption habits related to masking or modifying the taste of foods and beverages.

Assumed goal of consumption habit	“How frequently do you add...?”
Masking bitterness	milk to coffee
	cream to coffee
	sugar to coffee
	sweetener to coffee
	sugar or honey to tea
	sweetener to tea
	milk to tea
Modifying taste with salt or condiments	salt to water when cooking vegetables
	salt to a meal
	aromatic salt ^a to a meal
	ketchup to a meal
	soy sauce to a meal
Masking bitterness, sourness, or astringency	sugar, honey, or something else sweet to berries

^a mixture of salt and seasoning

4.4.2.3 Recalled pleasantness and use-frequency

Recalled pleasantness and use-frequency of foods and beverages (N = 58, appendix 1) belonging to Finnish food culture were studied. The items were thought to elicit diverse sensory experiences, and to divide people’s opinions. Recalled pleasantness was evaluated using a 9-point hedonic scale (from 1 = extremely unpleasant to 9 = extremely pleasant). Additionally, the subjects were provided with an option “I cannot say” in the case of unfamiliar food or beverage. These responses were removed (marked as missing) before statistical analysis. Use-frequency of the same

foods and beverages were inquired about with the response options “daily,” “a few times per week,” “once per week,” “once or twice per month,” “a few times per year,” and “more seldom or never.”

4.5 Statistical analysis

Associations between categorical variables were analyzed using chi-squared or Fisher’s exact test. The *t*-test or one-way analysis of variance (ANOVA; Tukey as a *post hoc* test when variances were equal, otherwise Tamhane’s test) was applied to compare the means between groups. If a parametric method was not applicable, Kruskal–Wallis and/or Mann–Whitney U test was applied. Bonferroni correction was applied for multiple comparisons, when appropriate. Correlations between normally distributed variables were analyzed using Pearson correlation. In the case of non-normally distributed variable(s), Spearman rank correlation was applied.

Taste sensitivity groups were determined using hierarchical clustering to achieve data-driven segmentation of the subjects. The clustering was performed with the squared Euclidean distance measure and Ward’s Method by using standardized intensity ratings (rescaled to population mean zero and sd one). For each taste modality, a three-cluster solution was retained. The least sensitive cluster was labeled with 1; semi-sensitive cluster 2; and most sensitive cluster 3. A taste sensitivity score for describing the overall taste sensitivity was computed as the mean of all taste modality-specific cluster memberships (theoretical range, 1.0–3.0). Thus, the closer the score was to 1.0, the less sensitive was the subject. The cluster differences in intensity ratings were analyzed using multivariate analysis of variance (MANOVA) with Tukey’s or Tamhane’s test (the latter when variances were not equal) as a *post hoc* test. Associations between the taste sensitivity clusters were analyzed with multinomial logistic regression so that one model for each taste modality was generated with other taste modalities as predictors.

The taste modality-specific sensitivities were predicted using multinomial logistic regression by using gender, age, BMI, smoking habit, and correct taste modality recognition as explanatory factors. These same factors were applied in two-way ANOVA to study the taste sensitivity and recognition scores. None of the two-way interactions was significant, and thus, they were removed from the models leaving only the main effects.

Factor analysis was applied to the recalled pleasantness ratings for food and beverage categories. The categories comprised vegetables (bitter, pungent, mild), vegetable dishes, and pungent condiments (N = 20); fruits and berries (N = 13); sweet, salty, and fatty foods (N = 13); and alcoholic and non-alcoholic beverages (N = 12). The purpose of the categorization was to meet the assumption for sample size in factor analysis and it was done based on subjective logical insight. The analyses

were conducted using the principal component method for component extraction and varimax rotation for gaining more interpretable results. The number of factors was decided based on three principals: Eigenvalue greater than one, scree plot inspection, and meaningful component content. The models were improved by removing variables possessing communality (estimate of variance in a variable accounted for by the extracted components) under 0.300. Component scores for further analyses were obtained using the regression method.

The new pleasantness components were analyzed using the hierarchical multivariate linear regression with taste sensitivity and background factors as explanatory variables. In the first step, gender and age were entered into the model. In the second step, BMI and/or education were entered, if they had a significant contribution to the model after controlling for gender and age. In the third step, taste modality-specific sensitivities were entered in one model and the taste sensitivity score in another model, if they had a significant contribution to the final model after controlling for the previously entered predictors. The forward method was applied for the second and third steps to attain the simplest model. The inclusion criterion for a variable was the significance of the regression coefficient at the level $p \leq 0.1$. This hierarchical approach enabled to determine whether BMI and education in the second step enhanced the prediction model and whether taste sensitivities in the third step enhanced the previous model.

Following the categories of the pleasantness components, new use-frequency variables were computed as the mean of use-frequency. Thus, the new use-frequency variables and pleasantness components were composed of the same food and beverage items. The correlation between pleasantness and use-frequency was analyzed using Pearson correlation. The hierarchical multivariate linear regression was also applied to determine the factors that explained use-frequency. The steps were similar to the pleasantness component analysis except that in the third step, the equivalent pleasantness component was entered into the model if it had a significant contribution because it was expected to be a major explanatory factor. Finally, taste sensitivities were added in the fourth step. The forward method was applied for steps 2–4.

The criterion for significance was set to be $p < 0.05$. All statistical analyses were computed using IBM SPSS Statistics 23.0 or a later version (IBM Corporation, Armonk, NY, USA).

Some of the participants were not able to complete all sections of the study because of time constraints, technical issues, or self-reported hypersensitivity to caffeine. This missing data were dealt with in each analysis rather than entirely excluding the participants with missing responses. Only the subjects who had evaluated all variables in question were included in the analysis. The number of subjects included in the analyses is provided in the text, tables, and figures.

5 Results

5.1 Subject characteristics

The subject characteristics are reported in **Table 5**. The same subjects were included in all studies except that daily smokers were excluded in study III. The majority were women, highly educated, and non-smokers. Gender and smoking were related ($X^2 [1] = 8.1, p = 0.004$) as females (78.6% of females) were more likely to be non-smokers than males (56.4% of males), although all daily smokers ($N = 6$) were females. Additionally, BMI was related to smoking ($X^2 [2] = 13.9, p = 0.001$), when the lean and overweight subjects were predominantly non-smokers (81.1% and 76.5%, respectively), whereas half of the obese subjects had a history of smoking. Age and BMI were also associated (I and II: $X^2 [4] = 24.2, p < 0.001$, III: $X^2 [4] = 25.3, p < 0.001$) as the youngest subjects were more likely to be lean than the middle-aged or oldest subjects who were more likely overweight. Otherwise, gender, age, BMI, education, or smoking were not associated.

Table 5. Subjects' characteristics.

Variable	Study I and II			Study III		
	N	%	Missing (N)	N	%	Missing (N)
Gender	205		0	199		0
Female	164	80.0		158	79.4	
Male	41	20.0		41	20.6	
Age	205		0	199		0
19–34 years	88	42.9		86	43.2	
35–49 years	59	28.8		56	28.1	
50–79 years	58	28.3		57	28.6	
BMI	198		7	192		7
< 25.0	111	56.1		110	57.3	
25.0–29.9	51	24.9		49	24.6	
≥ 30.0	36	17.6		33	17.2	
Education	202		3	193		3
Lower	73	36.1		73	37.2	
Higher	129	63.9		123	62.8	
Smoking	198		7	192		7
Currently/formerly	51	25.8		45 ¹	23.4	
Non-smoker	147	74.2		147	76.6	

¹ Only former smokers included

5.2 Modality-specific taste sensitivity clusters

Hierarchical clustering was applied to reveal distinctive clusters based on the intensity judgments. For every taste modality, the clusters differed significantly in intensity perception (**Table 6; Figure 4**).

Clearly, a group of the least, semi- and most sensitive subjects was present for every taste modality except for salty taste. The number of subjects in clusters varied between taste modalities. Except for sweet taste, the least sensitive cluster evaluated the strongest sample equally or less intensely as the most sensitive cluster evaluated the mildest sample.

The associations between the taste clusters were investigated using logistic regression, and the results are shown in **Table 7**. One taste modality-specific sensitivity at a time was predicted with other taste sensitivities. The models fitted well to the data according to the Goodness-of-Fit test statistics ($p > 0.05$) and explained well the dependent factor in each case. An odds ratio (OR) implies a relative risk ratio between the comparison and reference groups of the predictor variable to fall in the comparison group rather than in the reference group of the dependent variable. For example, a subject in SO3 had 5.05 times greater risk than a subject in SO2 to be in SW3 rather in SW1, i.e. the most sensitive subjects to sour taste had 5-times greater probability than the semi-sensitive subjects to be also among the most sensitive subjects to sweet taste rather than among the least sensitive subjects. The associated taste sensitivity clusters were sour and bitter, sour and sweet, bitter and umami, sweet and salty, and sweet and umami. The association were positive in all cases.

Correlation analysis that was computed using the mean ratings of each tastant showed low to moderate correlation between all taste modalities (**Table 8**).

Table 6. Cluster and the whole population mean intensities \pm sd (95 % CI) for every sample (A–D, see Table 3) and the distribution of subjects between the clusters (N).

Taste	Test statistics ¹	Sample	Cluster 1	Cluster 2	Cluster 3	All
Sour	$p < 0.001$, F (8,392) = 75.1, Wilk's $\Lambda = 0.156$, partial $\eta^2 = 0.605$	A	5.29 \pm 1.06 (4.99–5.58) c	7.21 \pm 1.22 (6.97–7.45) b	8.52 \pm 0.91 (8.26–8.78) a	7.04 \pm 1.60 (6.81–7.26)
		B	4.02 \pm 1.48 (3.60–4.43) c	6.35 \pm 1.41 (6.08–6.63) b	7.81 \pm 1.23 (7.46–8.16) a	6.12 \pm 1.94 (5.85–6.39)
		C	2.15 \pm 0.78 (1.93–2.37) c	4.41 \pm 1.35 (4.15–4.68) b	6.07 \pm 1.23 (5.72–6.42) a	4.24 \pm 1.83 (3.99–4.50)
		D	1.14 \pm 1.07 (0.84–1.44) c	2.14 \pm 1.29 (1.89–2.39) b	4.56 \pm 1.16 (4.22–4.89) a	2.47 \pm 1.73 (2.23–2.71)
		N (%)	51 (25.2)	102 (50.5)	49 (24.3)	202 (100)
Bitter	$p < 0.001$, F (8,390) = 87.1, Wilk's $\Lambda = 0.129$, partial $\eta^2 = 0.641$	A	2.38 \pm 1.69 (1.80–2.96) c	6.90 \pm 1.52 (6.58–7.23) b	8.14 \pm 1.52 (7.80–8.49) a	6.60 \pm 2.55 (6.25–6.96)
		B	1.20 \pm 1.45 (0.70–1.70) c	5.07 \pm 1.90 (4.67–5.48) b	7.12 \pm 2.02 (6.67–7.57) a	5.20 \pm 2.79 (4.82–5.59)
		C	0.65 \pm 1.22 (0.23–1.07) c	2.19 \pm 1.80 (1.81–2.58) b	5.71 \pm 2.05 (5.26–6.18) a	3.31 \pm 2.71 (2.93–3.69)
		D	0.59 \pm 0.75 (0.33–0.85) b	0.71 \pm 0.79 (0.54–0.88) b	3.50 \pm 2.08 (3.03–3.97) a	1.78 \pm 1.99 (1.51–2.06)
		N (%)	35 (17.4)	87 (43.3)	79 (39.3)	201 (100)
Sweet	$p < 0.001$, F (8,396) = 60.5, Wilk's $\Lambda = 0.203$, partial $\eta^2 = 0.550$	A	4.74 \pm 1.27 (4.46–5.02) c	6.81 \pm 1.21 (6.54–7.08) b	7.99 \pm 1.18 (7.62–8.36) a	6.20 \pm 1.78 (5.96–6.45)
		B	2.93 \pm 1.21 (2.66–3.19) c	5.14 \pm 1.29 (4.85–5.43) b	6.39 \pm 1.53 (5.91–6.87) a	4.49 \pm 1.90 (4.23–4.75)
		C	1.68 \pm 0.96 (1.47–1.89) c	2.49 \pm 1.36 (2.19–2.79) b	5.02 \pm 1.14 (4.66–5.38) a	2.67 \pm 1.69 (2.45–2.90)
		D	0.79 \pm 0.83 (0.61–0.97) b	1.10 \pm 1.01 (0.88–1.32) b	2.45 \pm 1.81 (1.88–3.02) a	1.25 \pm 1.30 (1.06–1.43)
		N (%)	83 (40.7)	80 (39.2)	41 (20.1)	204 (100)
Salty	$p < 0.001$, F (8,394) = 68.5, Wilk's $\Lambda = 0.175$, partial $\eta^2 = 0.582$	A	4.73 \pm 1.65 (4.43–5.03) b	7.56 \pm 1.30 (7.20–7.93) a	7.47 \pm 1.63 (6.92–8.03) a	5.93 \pm 2.09 (5.64–6.22)
		B	2.63 \pm 1.45 (2.36–2.89) b	5.86 \pm 1.58 (5.41–6.30) a	5.23 \pm 2.28 (4.46–6.00) a	3.90 \pm 2.22 (3.59–4.21)
		C	1.65 \pm 1.26 (1.42–1.88) c	3.08 \pm 2.06 (2.49–3.65) b	5.01 \pm 1.26 (4.59–5.44) a	2.60 \pm 1.96 (2.33–2.87)
		D	1.44 \pm 1.12 (1.23–1.65) b	1.05 \pm 0.87 (0.81–1.30) b	4.21 \pm 1.15 (3.82–4.60) a	1.83 \pm 1.54 (1.62–2.05)
		N (%)	116 (57.1)	36 (17.7)	51 (25.1)	203 (100)
Umami	$p < 0.001$, F (8,394) = 54.4, Wilk's $\Lambda = 0.226$, partial $\eta^2 = 0.525$	A	2.01 \pm 1.11 (1.60–2.42) c	5.53 \pm 1.34 (5.30–5.75) b	8.01 \pm 1.11 (7.64–8.37) a	5.47 \pm 2.14 (5.18–5.77)
		B	2.33 \pm 1.37 (1.82–2.85) c	4.22 \pm 1.85 (3.91–4.54) b	7.06 \pm 1.67 (6.51–7.61) a	4.48 \pm 2.24 (4.17–4.79)
		C	1.14 \pm 1.09 (0.73–1.55) c	3.26 \pm 1.67 (2.97–3.54) b	6.34 \pm 1.48 (5.85–6.82) a	3.52 \pm 2.19 (3.22–3.82)
		D	0.85 \pm 0.70 (0.58–1.11) c	2.51 \pm 1.75 (2.21–2.80) b	3.89 \pm 2.39 (3.10–4.67) a	2.52 \pm 1.98 (2.25–2.79)
		N (%)	30 (14.8)	135 (66.5)	38 (18.7)	203 (100)

Different lower cases indicate statistically significant ($p < 0.05$) differences between the clusters in a sample. ¹one-way MANOVA for the differences in cluster intensities. Modified from original publication I.

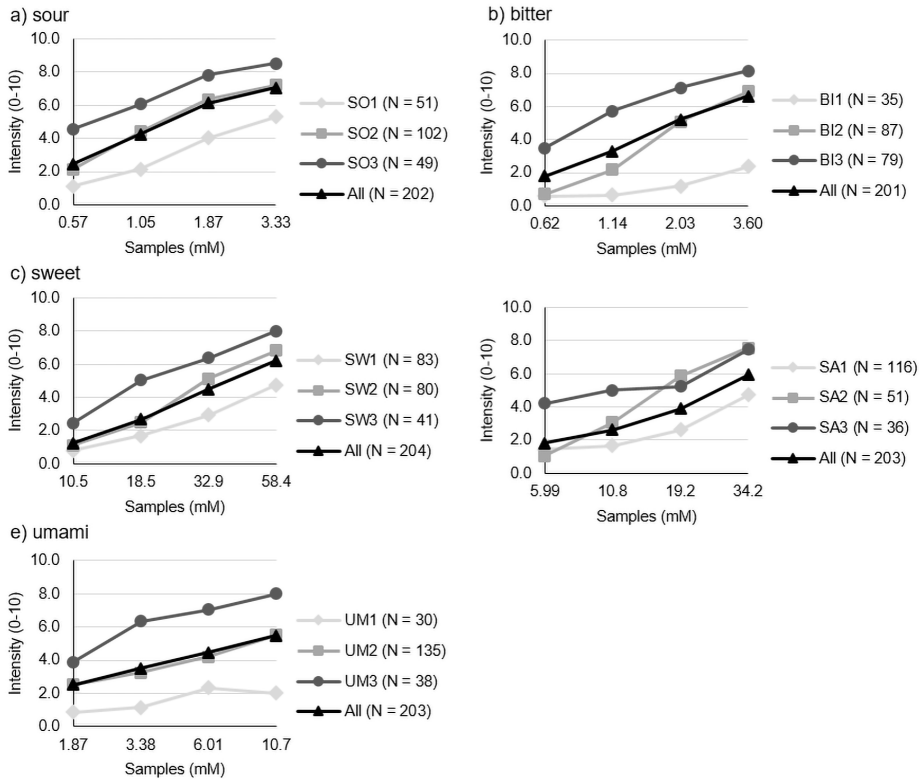


Figure 4. Taste intensity perception (means) in taste sensitivity clusters and in the entire study population for all concentration levels. a) sourness of citric acid, b) bitterness of caffeine, c) sweetness of sucrose, d) saltiness of NaCl, e) umami of MSG. SO, sour; BI, bitter; SW, sweet; SA, salty; UM, umami. 1, the least sensitive cluster; 2, the semi-sensitive cluster; 3, the most sensitive cluster. Modified from original publication 1.

Table 7. Associations between taste modalities using multinomial logistic regression.

Predictor variable	Dependent variable, OR (95% CI)									
	SO1	SO3	BI1	BI3	SW2	SW3	SA2	SA3	UM1	UM3
SO1			0.88 (0.32–2.40)	0.19** (0.06–0.63)	0.47 (0.18–1.24)	0.90 (0.22–3.60)	0.42 (0.13–1.31)	0.45 (0.08–2.38)	3.26* (1.02–10.45)	0.34 (0.07–1.67)
SO3			0.39 (0.07–2.06)	1.24 (0.56–2.74)	2.46 (0.83–7.28)	4.81* (1.42–16.36)	1.44 (0.58–3.56)	2.79* (1.05–7.40)	2.26 (0.33–15.22)	1.12 (0.48–2.63)
BI1	0.87 (0.32–2.36)	0.36 (0.06–1.98)			0.61 (0.21–1.80)	0.24 (0.02–2.34)	1.09 (0.32–3.77)	1.06 (0.17–6.63)	2.65 (0.90–7.84)	0.57 (0.11–2.93)
BI3	0.19** (0.06–0.63)	1.22 (0.55–2.71)			1.16 (0.50–2.70)	1.76 (0.62–4.95)	0.94 (0.42–2.11)	2.29 (0.86–6.14)	-	0.90 (0.39–2.08)
SW2	0.44 (0.17–1.17)	2.57 (0.85–7.78)	0.61 (0.21–1.79)	1.10 (0.47–2.55)			2.32 (0.93–5.77)	3.36 (0.95–11.87)	0.20* (0.05–0.80)	3.27* (1.01–10.64)
SW3	1.00 (0.25–4.02)	5.05* (1.46–17.42)	0.22 (0.02–2.05)	1.72 (0.62–4.81)			5.80** (1.88–17.89)	7.80** (1.83–33.31)	-	4.19* (1.13–15.47)
SA2	0.40 (0.13–1.26)	1.43 (0.58–3.51)	1.14 (0.33–3.94)	1.00 (0.45–2.22)	2.25 (0.91–5.56)	5.56** (1.82–16.94)			0.25 (0.03–2.26)	1.48 (0.60–3.66)
SA3	0.44 (0.08–2.36)	2.79* (1.05–7.37)	1.08 (0.18–6.53)	2.48 (0.93–6.62)	3.51 (0.99–12.36)	7.87** (1.85–33.58)			0.87 (0.80–9.38)	1.56 (0.55–4.38)
UM1	3.55* (1.18–10.70)	2.91 (0.43–19.82)	2.98* (1.05–8.46)	-	0.21* (0.05–0.84)	-	0.19 (0.02–1.63)	0.61 (0.05–6.89)		
UM3	0.39 (0.81–1.91)	1.13 (0.48–2.64)	0.61 (0.12–3.16)	0.96 (0.42–2.18)	3.12 (0.95–10.23)	4.03* (1.08–14.99)	1.47 (0.59–3.66)	1.47 (0.52–4.20)		
correctly predicted, %	63.8		53.8		59.3		63.3		68.8	
Model fit (-2-log-likelihood) ¹	140.4, X ² (16) = 85.6, p < 0.001		143.5, X ² (16) = 75.8, p < 0.001		143.8, X ² (16) = 94.4, p < 0.001		148.1, X ² (16) = 67.3, p < 0.001		115.8, X ² (16) = 90.1, p < 0.001	

¹The test statistics of logistic regression model fitting SO, sour; BI, bitter; SW, sweet; SA, salty; UM, umami. 1, the least sensitive cluster; 2, the semi-sensitive cluster; 3, the most sensitive cluster. The reference categories were SO2, BI2, SW1, SA1, UM2. “-” indicates too wide confidence intervals for appropriate comparisons. Bolded OR indicates a statistically significant main effect of the taste modality in the model. *post hoc* comparisons **p* < 0.05 ***p* < 0.01. Modified from original publication I.

Table 8. Correlation coefficients between mean intensities. All correlations were statistically significant at level $p < 0.001$.

	Sour taste (N = 204)	Bitter taste (N = 201)	Sweet taste (N = 204)	Salty taste (N = 204)	Umami taste (N = 203)
Sour taste (N = 204)	1	0.484	0.530	0.516	0.425
Bitter taste (N = 201)		1	0.422	0.309	0.498
Sweet taste (N = 204)			1	0.504	0.452
Salty taste (N = 204)				1	0.362
Umami taste (N = 203)					1

5.3 Taste sensitivity score

TSS describes the overall taste sensitivity of a subject as it was computed from the modality-specific cluster membership. The mean score was 1.94 (sd 0.50). The distribution of TSS is shown in **Figure 5**. The higher the TSS, the more sensitive was the subject. A score of 2.6–3.0 meant that a subject belonged to the most sensitive cluster in the majority of taste modalities and to the semi-sensitive cluster in the remaining modalities. Thus, these subjects could be called as hypersensitive tasters (13.6% of all subjects). The hyposensitive tasters scored 1.0–1.4 as they belonged to the least sensitive cluster in the majority of taste modalities and to the semi-sensitive cluster in the remaining taste modalities (22.1% of all subjects). The remaining (64.3%), with a score of 1.6–2.4, were called semi-sensitive tasters.

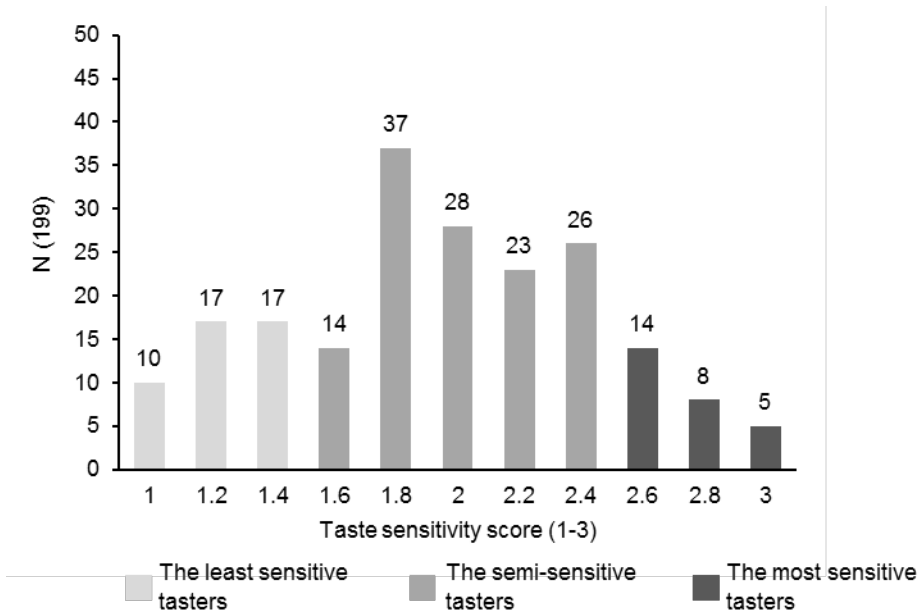


Figure 5. The distribution of taste sensitive score. Modified from original publication I.

5.4 Taste recognitions

The distributions for taste modality-specific recognitions are presented in **Figure 6**. Depending on the taste, three or four strongest dilutions were recognized correctly by the majority. In the most dilute samples, the sourness of citric acid was confused with bitterness, the saltiness of NaCl was confused with umami, and the umami taste of MSG was confused with saltiness and bitterness. Additionally, some perceived the mildest MSG as water. Furthermore, the mild caffeine and sucrose samples were perceived as water, if they were incorrectly identified.

The associations between subject characteristics and the mean number of correct taste recognitions are shown in **Table 9**. Females recognized correctly 0.4 sour samples more than males ($t [200] = -2.2, p = 0.032$). Age and recognition were associated in every taste modality (sour: $F [2,199] = 6.1, p = 0.003$; bitter: $F [2,199] = 9.7, p < 0.001$; sweet: $F [2, 200] = 3.6, p = 0.030$; salty: $F [2, 200] = 4.0, p = 0.020$; umami: $F [2,199] = 8.5, p < 0.001$). Mainly, younger age predicted more correct recognitions. Exception was sweet taste as the middle-aged subjects made more correct recognitions than the youngest subjects. Umami recognition was also related to BMI ($F [2,192] = 3.8, p = 0.025$) as the lean subjects made more correct recognitions than the overweight subjects.

Expressed as the total number of correct recognitions among 25 samples, the mean was 15 correct recognitions, the minimum was 6, and the maximum was 24.

TRS was the mean of samples correctly recognized in every taste modality. The distribution is illustrated in **Figure 7**. The mean TRS was 3.09 (sd 0.70).

TRS depended on age ($F [2,185] = 13.2, p < 0.001$): both the youngest and middle-aged subjects had higher scores ($M [sd] = 3.25 [0.66]$ and $3.22 [0.65]$, respectively) than the oldest subjects ($M [sd] = 2.67 [0.64]$). Gender, BMI, or smoking were not related to TRS.

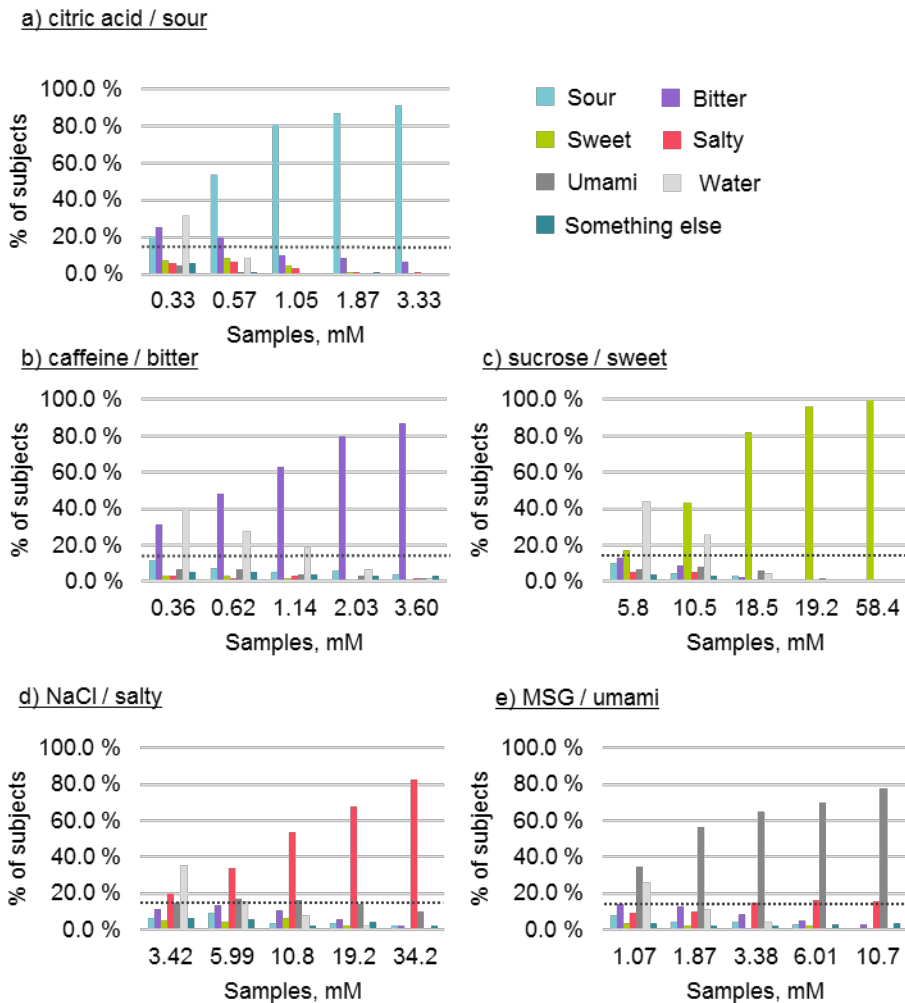


Figure 6. The distributions of taste recognitions for all samples: a) sour citric acid ($N = 203-204$), b) bitter caffeine ($N = 202$), c) sweet sucrose ($N = 203-204$), d) salty NaCl ($N = 203-204$), and e) umami MSG ($N = 202-204$). The dotted line is the chance level (14.3%) for guessing correctly. Modified from original publication II.

Table 9. Associations between correct taste recognition and subject characteristics. Bolded mean values indicate statistically significant different means between variable groups ($p < 0.05$).

	Sour		Bitter		Sweet		Salty		Umami	
	Mean (sd)	N (%)	Mean (sd)	N (%)	Mean (sd)	N (%)	Mean (sd)	N (%)	Mean (sd)	N (%)
Gender										
Female	3.40 (1.02)	162 (80.2)	3.08 (1.37)	162 (80.2)	3.33 (0.90)	162 (79.8)	2.64 (1.19)	162 (79.8)	3.09 (1.39)	161 (79.7)
Male	3.00 (1.18)	40 (19.8)	3.15 (1.39)	40 (19.8)	3.59 (0.89)	41 (20.2)	2.39 (1.07)	41 (20.2)	2.85 (1.37)	41 (20.3)
Missing (N)		3		3		2		2		3
Age										
19–34 years	3.47 a (0.91)	88 (43.6)	3.44 a (1.34)	88 (43.6)	3.23 b (0.88)	88 (43.3)	2.78 a (1.09)	88 (43.3)	3.34 a (1.27)	88 (43.3)
35–49 years	3.50 a (1.00)	58 (28.7)	3.17 a (1.18)	59 (29.2)	3.63 a (0.91)	59 (29.1)	2.63 ab (1.14)	59 (29.1)	3.19 a (1.36)	59 (29.1)
50–79 years	2.91 b (1.24)	56 (27.7)	2.45 b (1.41)	55 (27.2)	3.38 ab (0.89)	56 (27.6)	2.23 b (1.25)	56 (27.6)	2.42 b (1.42)	56 (27.6)
Missing (N)		3		3		2		2		2
BMI										
< 25.0	3.39 (0.94)	109 (55.9)	3.26 (1.35)	108 (55.4)	3.40 (0.87)	109 (55.6)	2.63 (1.21)	109 (55.6)	3.31 a (1.35)	108 (55.4)
25.0–29.9	3.08 (1.21)	51 (26.2)	2.92 (1.52)	51 (26.2)	3.35 (0.77)	51 (26.0)	2.61 (1.15)	51 (26.0)	2.71 b (1.38)	51 (26.2)
≥ 30.0	3.49 (1.12)	35 (17.9)	2.94 (1.26)	36 (18.5)	3.39 (1.15)	36 (18.4)	2.50 (1.13)	36 (18.4)	2.86 ab (1.46)	36 (18.5)
Missing (N)		10		10		9		9		10
Smoking										
Non-smoker	3.35 (1.05)	146 (74.9)	3.05 (1.40)	145 (74.4)	3.34 (0.80)	146 (74.5)	2.63 (1.19)	146 (74.5)	3.04 (1.39)	145 (74.4)
Currently/formerly	3.27 (1.09)	49 (25.1)	3.30 (1.33)	50 (25.6)	3.54 (1.15)	50 (25.5)	2.52 (1.16)	50 (25.5)	3.14 (1.41)	50 (25.6)
Missing (N)		10		10		9		9		10
All subjects	3.32 (1.06)	203	3.09 (1.37)	202	3.38 (0.90)	203	2.59 (1.17)	203	3.04 (1.39)	202

Modified from original publication II.

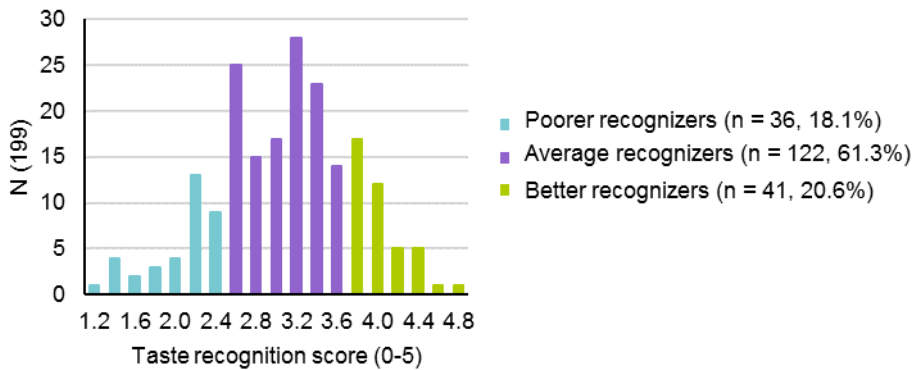


Figure 7. Taste recognition score distribution. Modified from original publication II.

5.5 Factors related to taste sensitivity

Taste modality-specific sensitivity was predicted using logistic regression, with gender, age, BMI, smoking, and correct recognition as explanatory factors. Goodness-of-Fit test statistics were above the significance level for all taste modalities indicating that the logistic regression models could be applied to predict taste sensitivities. The models significantly predicted taste sensitivities except for sweet and salty taste ($-2\text{-log-likelihood} = 220.9$, $X^2 [14] = 22.5$, $p = 0.069$, and $-2\text{-log-likelihood} = 220.8$, $X^2 [14] = 21.7$, $p = 0.085$, respectively). The results are shown in **Tables 10–12**. An OR implies a relative risk ratio between the comparison category and reference category of an explanatory variable to fall in the comparison category rather than in the reference category of the dependent variable when adjusted with the other factors in the model.

Gender was the only significant predictor of sour taste sensitivity. The main effect of age was insignificant, although a trend existed that the oldest subjects rather than the youngest ones were more likely in the least sensitive cluster than in any other sensitivity cluster.

Age and correct bitter taste recognition were significant predictors of bitter taste sensitivity. Further analysis revealed that the only significant difference between age groups was that the younger subjects were 3.45 times (1/OR in Table 11.) more likely than the oldest subjects to be hypersensitive rather than semi-sensitive. Better recognition ability predicted higher sensitivity.

The significant predictors of umami taste sensitivity were age, BMI, and correct umami recognition. Lower age, lower BMI, and higher recognition rate predicted higher sensitivity.

Table 10. The results of multinomial logistic regression predicting sour taste sensitivity with subject characteristics and sour taste recognition. Odds ratios (95 % confidence intervals) for all pairs of sensitivity groups and model fit statistics are displayed. Variables having a significant main effect in the model are bolded.

Sour (N = 195)	SO1, ref. SO3 OR (95 % CI)	SO2, ref. SO3 OR (95 % CI)	SO1, ref. SO2 OR (95 % CI)
Male¹	6.09* (1.52–24.44)	4.28* (1.16–15.84)	1.42 (0.61–3.31)
Age²			
18–34	0.29* (0.09–0.92)	0.83 (0.30–2.26)	0.35* (0.14–0.88)
35–49	0.37 (0.12–1.18)	0.55 (0.19–1.60)	0.68 (0.28–1.67)
BMI³			
< 25.0	0.42 (0.12–1.53)	0.42 (0.14–1.26)	1.01 (0.37–2.77)
25.0–29.9	0.84 (0.21–3.40)	0.61 (0.17–2.15)	1.38 (0.48–3.93)
Non-smoker ⁴	1.41 (0.49–4.07)	1.24 (0.50–3.03)	1.14 (0.48–2.69)
Sour taste recognition	0.87 (0.56–1.34)	0.86 (0.59–1.27)	1.01 (0.72–1.41)

Model fit statistics -2-log-likelihood 241.5, $\chi^2(14) = 24.6$, $p = 0.039$

SO1 was the least sensitive, SO2 the semi-sensitive, and SO3 the most sensitive cluster. * $p < 0.05$.
¹ Reference category female. ² Reference category 50–79 years old. ³ Reference category ≥ 30.0 . ⁴ Reference category current or former smoker. Modified from original publication II.

Table 11. The results of multinomial logistic regression predicting bitter taste sensitivity with subject characteristics. Odds ratios (95 % confidence intervals) for all pairs of sensitivity groups and model fit statistics are displayed. Variables having a significant main effect in the model are bolded.

Bitter (N = 194)	BI1, ref. BI3 OR (95 % CI)	BI2, ref. BI3 OR (95 % CI)	BI1, ref. BI2 OR (95 % CI)
Male¹	2.83 (0.78–10.31)	1.01 (0.40–2.52)	2.80 (0.87–9.07)
Age²			
18–34	0.30 (0.08–1.13)	0.29** (0.11–0.72)	1.07 (0.32–3.53)
35–49	0.58 (0.15–2.30)	0.94 (0.37–2.43)	0.62 (0.19–2.06)
BMI³			
< 25.0	0.43 (0.10–1.85)	0.68 (0.26–1.80)	0.64 (0.17–2.36)
25.0–29.9	0.66 (0.14–3.16)	0.62 (0.21–1.87)	1.06 (0.27–4.20)
Non-smoker ⁴	1.99 (0.50–7.85)	0.91 (0.40–2.05)	2.19 (0.61–7.81)
Bitter taste recognition	0.24*** (0.15–0.39)	0.69* (0.51–0.93)	0.35*** (0.23–0.54)

Model fit statistics -2-log-likelihood 198.8, $\chi^2(14) = 85.5$, $p < 0.001$

BI1 was the least sensitive, BI2 the semi-sensitive, and BI3 the most sensitive cluster. * $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$. ¹ Reference category female. ² Reference category 50–79 years old. ³ Reference category ≥ 30.0 . ⁴ Reference category current or former smoker. Modified from original publication II.

Table 12. The results of multinomial logistic regression predicting umami taste sensitivity with subject characteristics. Odds ratios (95 % confidence intervals) for all pairs of sensitivity groups and model fit statistics are displayed. Variables having a significant main effect in the model are bolded.

Umami (N = 194)	UM1, ref. UM3 OR (95 % CI)	UM2, ref. UM3 OR (95 % CI)	UM1, ref. UM2 OR (95 % CI)
Male ¹	3.79 (0.83–17.30)	2.29 (0.69–7.59)	1.66 (0.58–4.75)
Age²			
18–34	0.12** (0.02–0.58)	0.64 (0.21–2.00)	0.18** (0.05–0.65)
35–49	0.25 (0.05–1.16)	0.69 (0.20–2.37)	0.36 (0.12–1.06)
BMI³			
< 25.0	0.028** (0.003–0.289)	0.10* (0.01–0.80)	0.28* (0.09–0.93)
25.0–29.9	0.059* (0.005–0.665)	0.15 (0.02–1.38)	0.39 (0.12–1.27)
Non-smoker ⁴	1.96 (0.47–8.15)	1.13 (0.42–3.00)	1.74 (0.57–5.32)
Umami taste recognition	0.50** (0.32 –0.77)	0.72* (0.53–1.00)	0.69* (0.49–0.96)
Model fit statistics -2-log-likelihood 191.5, $\chi^2(14) = 51.6$, $p < 0.001$			

UM1 was the least sensitive, UM2 the semi-sensitive, and UM3 the most sensitive cluster. * $p < 0.05$, ** $p < 0.01$. ¹ Reference category female. ² Reference category 50–79 years old. ³ Reference category ≥ 30.0 . ⁴ Reference category current or former smoker. Modified from original publication II.

The effects of gender, age, BMI, smoking, and TRS on TSS were investigated using two-way ANOVA. None of the two-way interaction was significant. The significant main effects were gender ($F [1, 183] = 6.77$, $p = 0.010$), and age ($F [2, 183] = 4.93$, $p = 0.008$). On an average level, male subjects had 0.236 units lower sensitivity than female subjects. Considering the age, the youngest subjects had 0.335 units and the middle-aged subjects had 0.265 units higher TSS than the oldest subjects.

5.6 Portions of vegetables, fruits, and berries per week

The mean portions of vegetables consumed per week was 21.1 (sd 10.5, $N = 177$). The consumption of vegetables varied between umami taste sensitivity clusters ($F [2] = 3.25$, $p = 0.041$; **Figure 8A**). The median portions of fruits consumed per week was 10.9 (interquartile range [IQR] 3.5–14.0, $N = 177$) and was related to age ($H [2] = 23.92$, $p < 0.001$; **Figure 8B**). The median portions of berries consumed per week was 3.5 (IQR 1.5–7.0, $N = 177$). Berry consumption was related to gender and BMI ($U = 2246.5$, $p = 0.042$, and $H [2] = 7.00$, $p = 0.030$, respectively; **Figure 8C–D**). Other taste modality-specific sensitivities, TSS, or education level were not related to the portions of vegetables, fruits, or berries consumed per week.

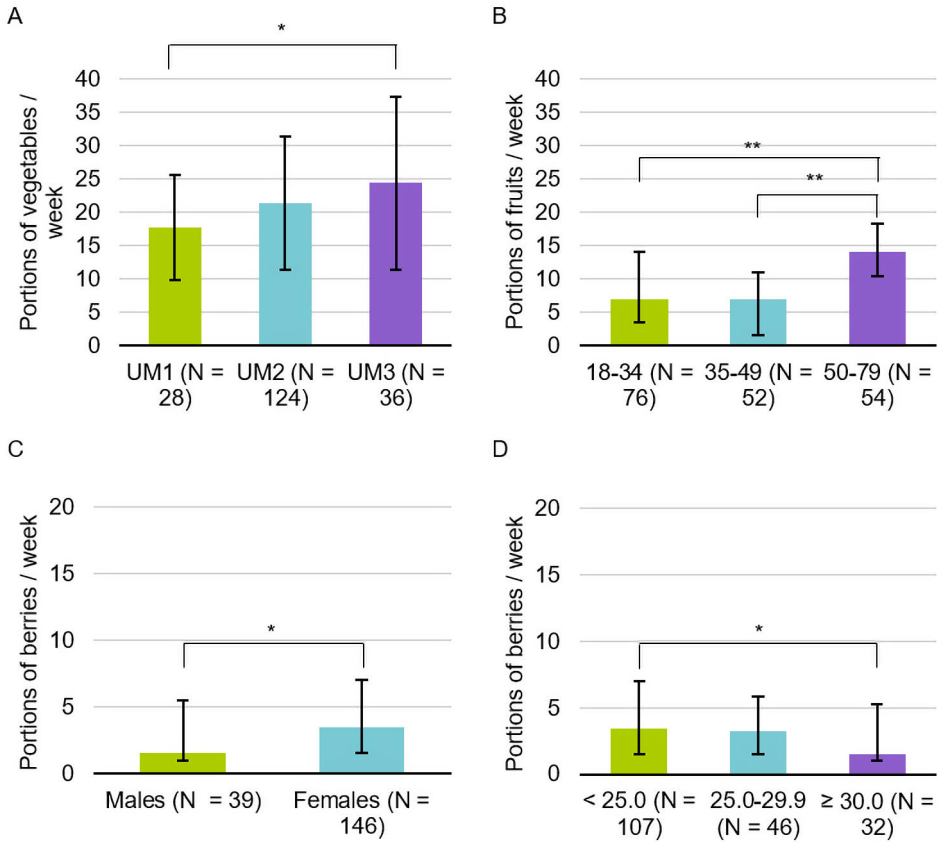


Figure 8. The significant group differences in the number of portions of vegetables (mean and standard deviation), fruits, and berries (median and interquartile range) per week (possible range 0-42). A) vegetable portions by umami taste sensitivity groups, UM1 = the least sensitive, UM2 = the semi-sensitive, UM3 = the most sensitive, B) fruit portions by age groups (years), C) berry portions by gender, D) berry portions by BMI groups. * $p < 0.05$, ** $p < 0.001$ based on Tukey (A) and Mann–Whitney U (B-D) test. Modified from original publication III.

5.7 Habits of masking or modifying taste

The distribution of some consumption habits was narrow in this study; hence, they were not analyzed further. These habits included adding cream to coffee, adding sugar to coffee, adding sweetener to coffee, adding sweetener to tea, adding milk to tea, and adding aromatic salt to a meal. The frequencies of other habits are shown in **Table 13**. The associations between these consumption habits and taste sensitivity as well as subject characteristics were analyzed further. The associations with taste sensitivity were also analyzed separately for every age group.

The more common habit of adding milk to coffee was related to higher bitter taste sensitivity (H [2] = 6.08, $p = 0.048$; **Figure 9A**) as well as to females, younger age, and higher education (U = 1075.5, $p < 0.001$, H [2] = 12.7, $p = 0.002$, and U = 2434.5, $p = 0.048$, respectively; **Figure 10A–C**).

The oldest subjects added sugar to berries more frequently than the youngest subjects, regardless of taste sensitivity (H [2] = 7.83, $p = 0.020$; **Figure 10D**).

Higher sensitivity to bitter, sweet, and salty tastes indicated more frequent habit of adding ketchup to a meal (H [2] = 8.55, $p = 0.014$, H [2] = 7.56, $p = 0.023$, and H [2] = 11.8, $p = 0.003$, respectively; **Figure 9B–D**). For sweet taste sensitivity, this habit was especially noted among 35–49-year-old subjects (H [2] = 8.56, $p = 0.041$) as the subjects who were the most sensitive to sweet used to add ketchup more frequently than the least sensitive subjects (U = 44.5, $p = 0.036$). Additionally, the taste sensitivity score and adding ketchup to a meal had a statistically significant positive correlation ($r = 0.178$, $p = 0.015$).

The most sensitive subjects to sourness added sugar or honey to tea more frequently than the semi-sensitive subjects (H [2] = 7.62, $p = 0.022$; **Figure 9E**). Among the youngest subjects, the least sensitive to umami added sugar or honey to tea more frequently than the semi or most sensitive subjects (H [2] = 11.9, $p = 0.008$; U = 18.0, $p = 0.028$, U = 2.0, $p = 0.013$, respectively). Additionally, the lower educated subjects (U = 3754.0, $p = 0.013$; **Figure 10E**) added sugar or honey to tea more frequently than the higher educated subjects.

Table 13. The distribution of responses [N (%)] for the habits of masking/modifying taste.

	Add milk to coffee	Add sugar/honey to tea	Add salt to vegetable cooking water	Add salt to a meal	Add ketchup to a meal	Add soy sauce to a meal
Always	83 (52.2)	29 (15.7)	37 (19.5)	6 (3.1)	0 (0.0)	0 (0.0)
Often	15 (9.4)	29 (15.7)	47 (24.7)	24 (12.6)	8 (4.2)	6 (22.2)
Occasionally	7 (4.4)	31 (16.8)	40 (21.1)	37 (19.4)	70 (36.5)	42 (22.2)
Rarely	16 (10.1)	44 (23.8)	29 (15.3)	83 (43.5)	72 (37.5)	70 (37.0)
Never	38 (23.9)	52 (28.1)	37 (19.5)	41 (21.5)	42 (21.9)	71 (37.6)
Total N	159	185	190	191	192	189

Modified form original publication III.

Among the oldest subjects, sour taste sensitivity was related to the habit of adding soy sauce to a meal (H [2] = 12.1, $p = 0.007$); the most sensitive to sourness added soy sauce less frequently than the least sensitive ones (U = 29.0, $p = 0.027$).

Moreover, males added soy sauce more frequently than females ($U = 2257.0, p = 0.031$; **Figure 10F**).

None of the potential predictors explained the frequency of adding salt to a meal or adding salt to vegetable cooking water.

Because a subject could also respond that he/she does not drink coffee or tea, the associations between consuming coffee or tea and taste sensitivities were analyzed. Unlike coffee consumers, those who avoided coffee ($N = 33, 17.2\%$ of all respondents) were more likely bitter taste sensitive subjects ($X^2 [2] = 12.9, p = 0.002$) or had a higher TSS ($t [185] = 2.63, p = 0.009$).

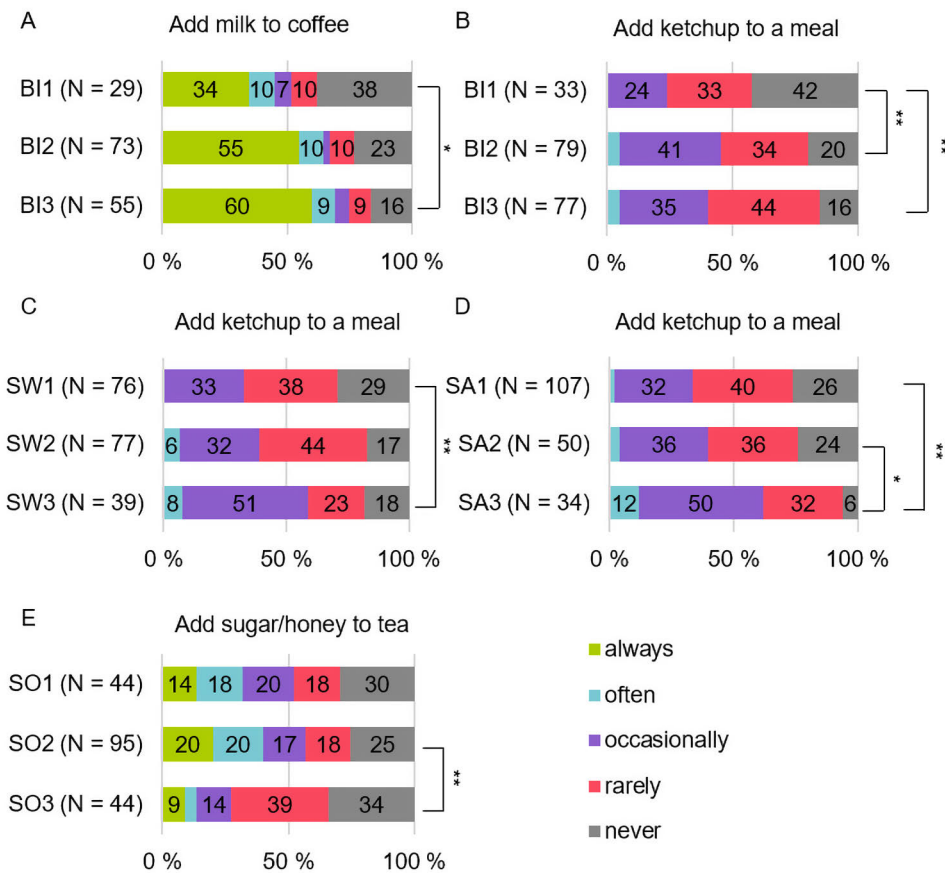


Figure 9. Differences in the frequency to mask/modify tastes by taste sensitivity groups, 1 = the least sensitive subjects, 2 = semi-sensitive subjects, 3 = the most sensitive subjects. A) bitter taste sensitivity vs. the habit of adding milk to coffee, B) bitter taste sensitivity vs. adding ketchup to a meal, C) sweet taste sensitivity vs. adding ketchup to a meal, D) salty taste sensitivity vs. adding ketchup to a meal, E) sour taste sensitivity vs. habit of adding sugar/honey to tea. * $p < 0.05$, ** $p < 0.01$ based on Mann–Whitney U tests. BI, bitter; SW, sweet; SA, salty; SO, sour. Modified from original publication III.

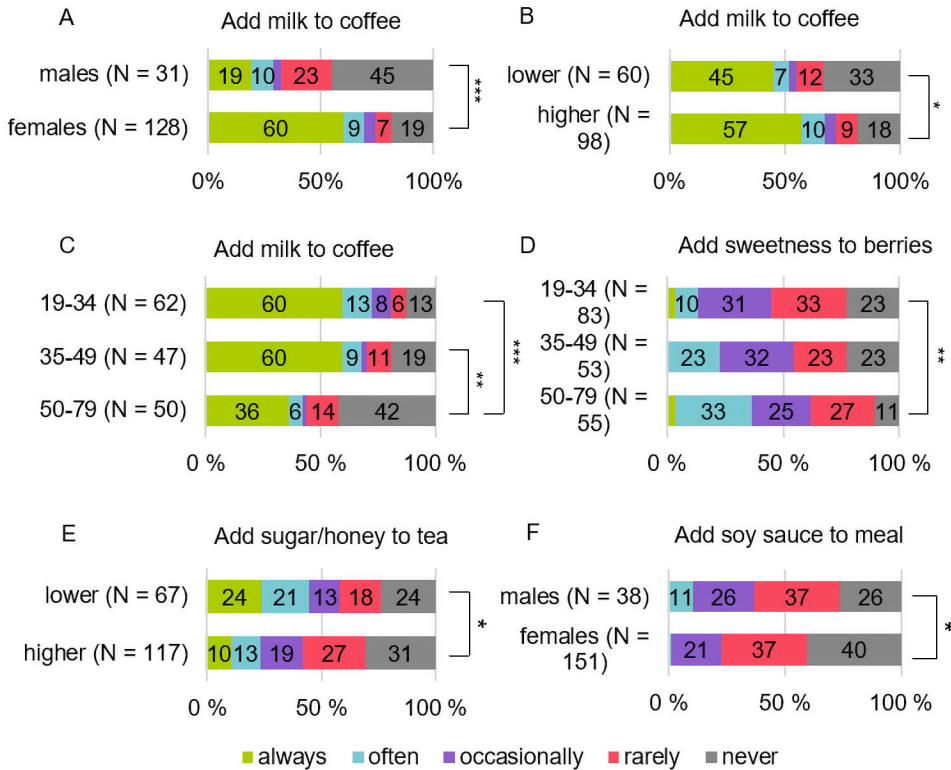


Figure 10. Significant group differences in frequency to mask/modify tastes. A) gender vs. the habit of adding milk to coffee, B) education vs. the habit of adding milk to coffee, C) age (years) vs. the habit of adding milk to coffee, D) age (years) vs. the habit of adding something sweet to berries, E) education vs. the habit of adding sugar/honey to tea, F) gender vs. the habit of adding soy sauce to a meal. * $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$ based on the Mann–Whitney U test. Modified from original publication III.

5.8 Factor analysis of recalled pleasantness

Two or three components were extracted from the principal component analysis applied to the recalled pleasantness of foods and beverages (**Table 14**). Eleven new variables were extracted for further analysis, and labeled as bitter vegetables, strong-tasting vegetables, pungent foods, berries, fruits, salty-and-fatty foods, sweet-and-fatty foods, salty-and-savory foods, bitter-and-astringent alcoholic beverages, bitter-and-astringent non-alcoholic beverages, and sweet beverages.

Table 14. Rotated variable loadings of the extracted pleasantness components PC1–PC3 (correlation coefficients). The bolded coefficient indicates the highest correlation of the item. For simplicity, only coefficients above 0.400 are shown. The labels of new variables are in italics and the mean [sd] of the original pleasantness ratings (1 = extremely unpleasant, 9 = extremely pleasant) in the parentheses.

Foods	PC1	PC2	PC3
Vegetables and pungent items (N = 154)			
<i>Bitter vegetables (6.46 [2.12])</i>			
Red beet	0.725		
Swedish turnip	0.714		
Brussels sprout	0.710		
Carrot	0.530		
Radish	0.509	0.401	
<i>Strong-tasting vegetables (6.37 [2.46])</i>			
Onion		0.765	
Rucola		0.684	
Olive		0.658	
Celery		0.652	
<i>Pungent foods (5.92 [2.37])</i>			
Chili sauce			0.928
Chili			0.842
Wasabi			0.715
Mustard			0.448
Variance explained (%)	28.9	12.8	7.7
Berries and fruits (N = 186)			
<i>Berries (7.20 [1.97])</i>			
Lingonberry	0.833		
Red currant	0.817		
Black currant	0.754		
Sea buckthorn berry	0.658		
Bilberry	0.499		
<i>Fruits (6.73 [2.04])</i>			
Avocado		0.806	
Lemon		0.764	
Rhubarb		0.638	
Grapefruit	0.432	0.475	
Variance explained (%)	33.7	10.4	
Sweet, salty, and fatty (N = 177)			
<i>Salty-and-fatty foods (6.67 [1.99])</i>			
French fries	0.824		
Potato chips	0.769		
Mayonnaise	0.709		

Foods	PC1	PC2	PC3
<i>Sweet-and-fatty foods (7.67 [1.66])</i>			
Ice cream		0.800	
Sweet pastry		0.723	
Milk chocolate		0.642	
Candy		0.547	
<i>Salty-and-savory foods (6.68 [2.52])</i>			
Blue cheese			0.821
Dry-cured salmon			0.744
Soy sauce			0.479
Variance explained (%)	24.0	15.0	11.1
Beverages (N = 170)			
<i>Bitter-and-astringent alcohol beverages (5.84 [2.52])</i>			
White wine	0.757		
Dry cider	0.716		
Red wine	0.699	0.409	
Long drink	0.656		0.438
Strong alcohol	0.610		
Beer	0.548	0.539	
<i>Bitter-and-astringent non-alcoholic beverages (7.04 [2.22])</i>			
Carbonated water		0.782	
Tea		0.668	
Coffee		0.555	
<i>Sweet beverages (4.81 [2.41])</i>			
Soft drink			0.828
Light soft drink			0.754
Sweet cider			0.538
Variance explained (%)	29.9	17.6	10.9

PC refers to Principal Component. N refers to the number of subjects included in the analysis. Modified from original publication III.

5.9 Factors related to recalled pleasantness

The pleasantness variables from factor analysis were subjected to multivariate linear regression with gender, age, BMI, education, and modality-specific taste sensitivities as possible explanatory factors. In another model, the TSS was included instead of the modality-specific sensitivities. A stepwise procedure was applied (see chapter 4.5). The models explained significantly recalled pleasantness except for fruits, and sweet-and-fatty foods. The statistically significant models are shown in **Table 15**. All taste sensitivity variables as well as education were not significant explanatory factors in any model, but gender, age, and BMI were related to recalled pleasantness.

Overall, only small proportions (3.4%–11.4% [$100 \times R^2$ from **Table 15**]) of the pleasantness scores were explained with the models.

Male gender and lower BMI predicted higher pleasantness of bitter vegetables. They equally contributed to the model (standardized β coefficients, -0.172 and -0.166 , respectively). In the third step, sour taste sensitivity was included in the model because its p -value (0.067) was under the selected criterion (0.100). However, the model did not improve by the addition of sour taste sensitivity ($R^2_{\text{change}} = 0.022$, $F_{\text{change}} = 3.42$, $p_{\text{change}} = 0.067$), and the final model comprising only gender and age is reported in **Table 15**.

Gender was the only explanatory factor for pungent food pleasantness and bitter-and-astringent alcohol beverages, as females liked pungent foods more and alcohol less than males. For pungent foods, salty and sweet taste sensitivities were added in the model in the third step (p -values, 0.060 and 0.071 , respectively), but this did not enhance the model (for salty $R^2_{\text{change}} = 0.021$, $F_{\text{change}} = 3.30$, $p_{\text{change}} = 0.071$; for sweet $R^2_{\text{change}} = 0.023$, $F_{\text{change}} = 3.60$, $p_{\text{change}} = 0.060$).

The pleasantness of strong-tasting vegetables, berries, salty-and-savory foods, and bitter non-alcoholic beverages was positively related to age, whereas pleasantness of salty-and-fatty foods was negatively associated with age. Both older age and lower BMI were related to decreased pleasantness of sweet beverages, age having a higher contribution to the model than BMI (standardized β coefficients, -0.311 and 0.224 , respectively). For salty-and-fatty and sweet-and-fatty foods, BMI was included in the models in the second step, but this did not significantly improve the models ($R^2_{\text{change}} = 0.019$, $F_{\text{change}} = 3.41$, $p_{\text{change}} = 0.067$ and $R^2_{\text{change}} = 0.020$, $F_{\text{change}} = 3.56$, $p_{\text{change}} = 0.061$, respectively)

Although the models did not explain statistically significantly the pleasantness of fruits and sweet-and-fatty foods, a trend was noted that higher BMI indicated lower liking of fruits, and female gender indicated higher liking for sweet-and-fatty foods.

Table 15. The results of hierarchical multivariate linear regression with food pleasantness components as dependent variables: unstandardized β coefficients (95% confidence intervals) and model statistics.

Pleasantness variable ¹	Gender ²	Age ³	BMI ³	Model statistics
Bitter vegetables (N = 149)	-0.417 * (-0.802, -0.032)	0.149 (-0.050, 0.347)	-0.210 * (-0.418, -0.003)	F (3, 145) = 3.39, p = 0.020, R^2 = 0.066
Strong-tasting vegetables (N = 149)	0.208 (-0.179, 0.595)	0.395 *** (0.201, 0.588)		F (2, 146) = 8.47, p < 0.001, R^2 = 0.104
Pungent foods (N = 149)	0.596 ** (0.202, 0.990)	0.082 (-0.115, 0.279)		F (2, 146) = 4.67, p = 0.011, R^2 = 0.060
Berries (N = 180)	-0.004 (-0.367, 0.359)	0.330 *** (0.157, 0.502)		F (2, 177) = 7.16, p = 0.001, R^2 = 0.075
Fruits (N = 180)	-0.005 (-0.366, 0.356)	0.075 (-0.104, 0.253)	-0.254 * (-0.446, -0.062)	F (3, 176) = 2.28, p = 0.081, R^2 = 0.037
Salty-and-fatty foods (N = 174)	-0.167 (-0.525, 0.191)	-0.277 ** (-0.456, -0.098)		F (2, 171) = 4.90, p = 0.009, R^2 = 0.054
Sweet-and-fatty foods (N = 174)	0.450 * (0.086, 0.815)	-0.021 (-0.203, 0.161)		F (2, 171) = 3.05, p = 0.050, R^2 = 0.034
Salty-and-savory foods (N = 174)	0.116 (-0.237, 0.470)	0.235 ** (0.059, 0.412)		F (2, 171) = 3.57, p = 0.030, R^2 = 0.040
Bitter-and-astringent alcoholic beverages (N = 165)	-0.604 ** (-0.961, -0.248)	0.078 (-0.100, 0.255)		F (2, 162) = 6.21, p = 0.003, R^2 = 0.071
Bitter-and-astringent non-alcoholic beverages (N = 165)	-0.266 (-0.620, 0.088)	0.227 * (0.051, 0.404)		F (2, 162) = 4.65, p = 0.011, R^2 = 0.054
Sweet beverages (N = 165)	-0.187 (-0.546, 0.172)	-0.379 *** (-0.564, -0.194)	0.291 ** (0.094, 0.489)	F (3, 161) = 6.92, p < 0.001, R^2 = 0.114

* p < 0.05, ** p < 0.01, *** p < 0.001; ¹ N refers to the number of subjects included in the analysis; ² Entered in the analysis as a dummy variable: 0 = male, 1 = female.; ³ Entered in the analysis as a category variable with increasing age/BMI (see Table 5). Modified from original publication III.

5.10 Factors related to use-frequency

New use-frequency variables were computed to comprise the same food and beverage items as the new pleasantness variables. The descriptive data of these new variables and the correlations between use-frequency and pleasantness are shown in **Table 16**. The internal consistency of the new variables was good except for bitter-and-astringent non-alcoholic beverages and sweet beverages (Cronbach's α 0.232

and 0.355, respectively). The correlations were from moderate to strong except for bitter vegetables ($r = 0.238$). For pungent items, the correlation between use-frequency and pleasantness was not significant.

Use-frequency was also analyzed using multinomial linear regression to explore whether gender, age, BMI, education, or taste sensitivity explained use-frequency after controlling for pleasantness. In the models, the equivalent pleasantness score was the single significant explanatory factor for use-frequency except for bitter vegetables, pungent foods, fruits, berries, and salty-and-savory foods. The models for these food categories are shown in **Table 17**.

All models (in Table 16) were statistically significant and explained use-frequency from 8.5% (pungent foods) to 49.2% (salty-and-savory foods). Taste sensitivity was a significant contributor for pungent foods and salty-and-savory foods consumption. Regarding pungent foods, lower bitter taste sensitivity and male gender indicated more frequent consumption, bitter taste sensitivity having a slightly higher contribution (standardized β coefficients of -0.207 and -0.160 , respectively). Additionally, when the TSS was entered in the model instead of taste-modality specific sensitivities, it was a significant factor for pungent foods consumption ($F [df = 3, 144] = 4.00, p = 0.010, R^2 = 0.076, \beta = -0.324$).

More frequent consumption of salty-and-savory foods was explained with higher sour taste sensitivity and lower umami taste sensitivity in addition to male gender and higher pleasantness score, which had the highest contribution to the model (standardized β coefficients, $0.173, -0.158, -0.137$, and 0.664 , respectively).

Higher liking and older age almost equally predicted higher bitter vegetable consumption (standardized β coefficients, 0.280 and 0.249 , respectively). More frequent use of berries was explained with higher pleasantness score, lower BMI, and older age in that order (standardized β coefficients, $0.574, -0.186$, and 0.127 , respectively). Higher liking and lower BMI indicated more frequent consumption of fruits (standardized β coefficients, 0.558 and -0.193 , respectively).

Table 16. The descriptives of use-frequency variables and their correlation with equivalent pleasantness variables.

Use-frequency variable	Descriptives				Correlation		
	N	Mean ¹	SD	Cronbach's α	N	Correlation with pleasantness	Sig. (2-tailed) of correlation
Bitter vegetables	191	2.86	0.60	0.653	154	0.238	0.003
Strong-tasting vegetables	190	3.33	0.83	0.619	153	0.389	<0.001
Pungent foods	187	2.75	0.90	0.727	153	0.065	0.426
Berries	190	3.03	0.84	0.722	184	0.604	<0.001
Fruits	189	2.69	0.72	0.571	183	0.602	<0.001
Salty-and-fatty foods	191	2.64	0.74	0.668	176	0.572	<0.001
Sweet-and-fatty foods	190	3.49	0.69	0.505	175	0.493	<0.001
Salty-and-savory foods	190	2.76	0.81	0.444	175	0.672	<0.001
Bitter-and-astringent alcoholic beverages	191	2.21	0.74	0.785	170	0.726	<0.001
Bitter-and-astringent non-alcoholic beverages	192	4.29	1.07	0.232	170	0.704	<0.001
Sweet beverages	190	2.02	0.71	0.355	168	0.634	<0.001

¹ Range from 1 (more seldom than a few times per year or never) to 6 (daily). Modified from original publication III.

Table 17. The results of hierarchical multivariate linear regression with use-frequency variables as dependent variables: unstandardized β coefficients (95% confidence intervals) and model statistics.

Use-frequency variable ¹	Gender ²	Age ³	BMI ³	Pleasantness	Taste sensitivity ³	Model Statistics
Bitter vegetables (N = 149)	0.176 (-0.059, 0.411)	0.190** (0.074, 0.306)		0.176*** (0.079, 0.274)		F (3, 145) = 8.59, $p < 0.001$, $R^2 = 0.151$
Pungent foods (N = 148)	-0.343* (-0.683, -0.004)	0.067 (-0.111, 0.246)			Bitter: -0.259* (-0.466, -0.052)	F (3, 144) = 4.45, $p = 0.005$, $R^2 = 0.085$
Berries (N = 178)	0.048 (-0.205, 0.301)	0.131* (0.001, 0.262)	-0.207** (-0.342, -0.071)	0.489*** (0.386, 0.592)		F (4, 173) = 28.3, $p < 0.001$, $R^2 = 0.396$
Fruits (N = 177)	-0.075 (-0.292, 0.142)	0.042 (-0.065, 0.149)	-0.182** (-0.298, -0.065)	0.415*** (0.326, 0.504)		F (4, 172) = 27.0, $p < 0.001$, $R^2 = 0.386$
Salty-and-savory foods (N = 172)	-0.266* (-0.484, -0.048)	0.036 (-0.079, 0.151)		0.535*** (0.445, 0.625)	Sour: 0.196** (0.059, 0.334) Umami: -0.219* (-0.392, -0.046)	F (5, 166) = 32.1, $p < 0.001$, $R^2 = 0.492$

* $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$; ¹ N refers to the number of subjects included in the analysis; ² Entered in the analysis as dummy variable: 0 = male, 1 = female.; ³ Entered in the analysis as a category variable with increasing age/BMI/taste sensitivity (see **Tables 5 and 6**). Modified from original publication III.

6 Discussion

In this study, taste perception and food-related behavior were investigated among 205 Finnish adults. This study filled gaps in knowledge by considering all five taste modalities in the taste sensitivity assessment as well as by understanding food-related behavior. Food-related behavior was explored through various angles, including weekly consumption of vegetables, fruits, and berries; tendency to mask or modify the taste of food; and the use-frequency and recalled pleasantness of several foods and beverages.

6.1 Individual taste perception

Hierarchical clustering was applied to intensity evaluations to reveal taste sensitivity groups. This multivariate method enabled the analysis of several concentration levels for determining taste sensitivity. The clustering revealed distinctive sensitivity groups that could be easily labeled as the most, semi-, and least sensitive clusters. Regarding salty taste, the distinction between the taste clusters was not as clear because the members in the semi-sensitive cluster perceived the mildest samples similar to those in the least sensitive cluster and the strongest samples similar to those in the most sensitive cluster. Moreover, the most sensitive salty tasters perceived all samples quite near each other on the intensity scale.

For sour and sweet tastes, the intensity curves of the clusters were near to each other but still the clusters had statistically different taste responsiveness. A previous study also reported less variance in sweet taste perception compared to that of other taste modalities (Rawal et al., 2017).

The most evident difference between sensitivity clusters was with bitter and umami tastes as the least sensitive groups hardly perceived anything in the samples. Previous studies have also shown hyposensitivity to the bitterness of caffeine (Dsamou et al., 2012) and umami taste (Chen et al., 2009; Lugaz et al., 2002; Singh et al., 2010). Taste recognition was related to taste intensity perception only in bitter and umami tastes. Logically, the more sensitive subjects recognized the tastes better. Either the other taste modalities were more familiar to the subjects or the sensitivity span was too narrow to detect differences in recognition.

Sweet taste was the easiest taste modality to recognize, as has also been reported previously (Doty et al., 2017). If the taste of sucrose was not recognized as sweet, it was typically perceived as water. Likewise, if caffeine taste was not recognized as bitter it was reported to be tasteless. Although the bitterness of caffeine was not confused with sourness, the sour taste of citric acid was confused with bitterness. The most common confusions concerned umami and salty tastes: the umami taste of MSG was confused with saltiness, and the saltiness of NaCl was confused with umami. For these confusions there are probably two explanations. First, MSG also possesses a salty taste because of the sodium ion. Second, repeated exposure makes it easier to recognize taste modalities (Hettinger et al., 1999), and some subjects may not have been familiar with umami taste. The effect of unfamiliarity was reduced in this study by allowing the subjects taste all taste modalities before the actual taste test; nonetheless, the possible unfamiliarity may have hindered the identification of umami taste. Umami was also confused with bitterness in the most dilute MSG sample.

In previous studies on taste recognition (other than studies on recognition threshold), umami has been excluded. With other taste modalities, sour–bitter (Doty et al., 2017; Hyde & Feller, 1981) and bitter–sour (Doty et al., 2017) confusions have been the most common. Other reported confusions include salty–bitter and salty–sour (Doty et al., 2017) that were not present in this study.

This study corroborates the need for careful selection of several concentration levels for intensity evaluation, as has also been highlighted earlier with bitter tastants (Keast & Roper, 2007). For the sour and umami tastes, the perceived intensities varied statistically significantly in every sample by the sensitivity clusters. However, only three strongest samples differed significantly between the clusters of sweet and bitter tastes, and, more remarkably, only one sample was perceived differently by all salty clusters.

The sensitivity clusters were of different sizes between taste modalities indicating that a subject can belong to a different sensitivity cluster in different taste modalities. The interactions between the taste sensitivity clusters across all taste modalities were analyzed using multinomial logistic regression. Overall, sensitivity to one taste was predicted well by that to other taste modalities. Furthermore, all cluster-level associations were in the hypothesized direction: more sensitivity in one taste predicted more sensitivity in another taste. No association was noted between sweet and bitter taste sensitivity, bitter and salty taste sensitivity, salty and sour taste sensitivity, umami and sour taste sensitivity, or salty and umami taste sensitivity. The correlation analysis showed low to moderate positive correlations across taste modalities, similar to other studies (Barragán et al., 2018; Coltell et al., 2019; Dinnella et al., 2018; Duffy, 2004; Hwang et al., 2016; Lim et al., 2008; Webb et al., 2015).

The TSS was determined based on the modality-specific taste sensitivities. The most (13.6%) and least sensitive (22.1%) subjects were minorities, but together they were 35.7% of all subjects. For example, those subjects belonging to the least sensitive group may have considerably similar taste experiences with each other (perceive all taste modalities as mild), whereas the experiences may be very versatile between the subjects who belong to the semi-sensitive group (more variation in sensitivity).

6.2 Factors related to taste perception

Age was the main factor related to taste perception as younger subjects were more likely to have stronger taste perception and could correctly recognize more taste modalities. This age factor was observed in the taste sensitivity and recognition scores as well as in all taste modality-specific recognitions. In the modality-specific sensitivities, age was related only to bitter and umami tastes. An age effect was reported for the same tastants as used in this study for the suprathreshold intensity measures and taste recognition (Barragán et al., 2018; Doty et al., 2017; Methven et al., 2012; Mojet et al., 2003; Simchen et al., 2006). Furthermore, in their review, Methven et al. (2012) concluded that, with citric acid, NaCl, and caffeine, intensity perception has been somewhat consistent, whereas the findings varied for sucrose.

Fischer et al. (2013) reported no association between age and taste sensitivity except for sweet taste, after they controlled for multiple putative taste-related factors in a large-scale study ($N = 2374$). In their study, contrary to the findings of many studies, age was positively related to sweet taste sensitivity as well as to other tastes when no adjustment for multiple factors was applied. The weakness of their study was that they used paper discs for taste intensity evaluation instead of whole-mouth stimulation.

Taste deterioration seems to be more evident after the age of 60 years (Methven et al., 2012). Thus, the age range of study participants can affect the results. In this study, the oldest age group was 50–79 years ($M [sd] = 61.8 [8.5]$ years), the majority (43.1%) being 50–59 years old, whereas the elderly group has been older in many studies (e.g., Mojet et al., 2003; Simchen et al., 2006). If a higher cut-off point was selected, the relationship between age and taste could have been more evident. However, decreasing the age range would have rendered the oldest age group too small for statistical analysis.

Gender was associated with sour taste sensitivity and recognition as well as with the TSS. Females were more sensitive and recognized sour taste better than males. In this study, the limitation was that the proportion of males was lower than that of females. Previous results on the relationship between gender and taste sensitivity

have been inconsistent, although females seem to be more sensitive to PROP (Tepper et al., 2017).

Interestingly, females also seem to perform superior in odor tests than males (Brand & Millot, 2001). The proposed explanations for gender differences in olfaction include that females encounter and learn more odor cues, have an evolutionary purpose to protect offspring (Brand & Millot, 2001), or have higher verbal fluency (Larsson et al., 2003; Monnery-Patris et al., 2009). These suggestions also serve as an interesting view for future taste research.

BMI status was related to umami taste sensitivity as the subjects with lower BMI were more sensitive. Notably, the number of umami-sensitive and obese subjects was low, resulting very small subpopulation. Previously, only one study considered the association between MSG taste intensity and BMI. No significant association was noted, although higher BMI was related to lower sensitivity to umami measured using a threshold method (Pepino et al., 2010). More research on BMI and taste sensitivity interactions are needed owing to the inconsistent results.

Smoking was not related to taste perception. This result is in agreement with the findings of some previous studies (Konstantinidis et al., 2010; Pepino et al., 2010). Vennemann et al. (2008) found a smoking effect in one of the 16 samples varying in tastants and concentration. Incorrect recognitions for the most dilute QHCl were greater in heavy smokers than in light smokers or non-smokers. Fischer et al. (2013) reported that not salty or sweet taste, but bitter and sour taste, were related to smoking, as smokers were more sensitive than non-smokers. In this thesis, the number of smokers was small, and they had to be combined with former smokers for statistical analysis. This grouping may explain the results, as current taste sensitivity is likely not related to former smoking (Chéruef et al., 2017). Clearly, the effect of smoking on taste perception is yet unknown. Future studies that also consider the number of cigarettes smoked per day are warranted to address this issue.

6.3 Factors associated with food-related behavior

People sensitive to some taste modality have been thought to also perceive intense taste from foods. This sensitivity would lead to the rejection of strong-tasting foods. In contrast, those with low taste sensitivity would seek for strong-tasting foods to reach optimal pleasantness level.

In this study, the taste modality-specific sensitivities and the TSS were related to food consumption, but not pleasantness. Moreover, the background factors explained food consumption behavior as well as pleasantness. The pleasantness of foods was strongly related to the use-frequency of the same food items, as expected.

A possible explanation for the lack of association between taste sensitivity and pleasantness can be a more complex interaction due to individual variation also in

pleasantness patterns. For example, in the case of sweet taste, people can be categorized based on their hedonic responses to increasing concentration of sucrose solutions. The typical categories include sweet likers (liking increases with increasing concentration), sweet dislikers (liking decreases with increasing concentration), and medium likers (the shape of liking–concentration plot is inverted U) (Iatridi et al., 2019). Yang et al. (2019) reported that low sweetness likers were more sensitive to sweetness and also liked less high sweetened ice tea than high sweetness likers, whereas, in other studies, no clear difference in sweetness intensity perception was found between sweet likers and dislikers (Looy et al., 1992; Methven et al., 2016).

Furthermore, many results or the lack of previously reported associations can be explained with the choice of food items that vary between studies and food cultures.

6.3.1 Taste sensitivity and food-related behavior

Sensitivity to bitterness was associated with the consumption of coffee, masking the (bitter) taste of food, and consumption of pungent foods. Pungent foods were consumed less frequently by bitter-sensitive subjects. However, the effect of bitter taste sensitivity was not shown in pungent food pleasantness. A possible association might have existed as caffeine and pungency intensity perception have been correlated positively (Dinnella et al., 2018), and sensitivity to pungency has been shown to be negatively correlated with pungent food liking (Törnwall et al., 2012). Previously, pungency and pungent food consumption were studied relative to PROP sensitivity. PROP tasters seem to perceive pungency stronger than non-tasters (Dinnella et al., 2018; Spinelli et al., 2018; Tepper, 2008), although, in a large-scale study ($N = 1119$), capsaicin was correlated stronger with intensity perception of other tastants ($r = 0.256\text{--}0.349$) than with PROP ($r = 0.199$) (Dinnella et al., 2018). Among Finnish subjects, PROP sensitivity was not related to pungency perception (Törnwall et al., 2012).

The bitter-sensitive subjects masked the taste of food more frequently than the less sensitive subjects by adding milk to coffee and ketchup to a meal. Overall, the bitter-sensitive subjects avoided coffee more likely than the less-sensitive subjects. Otherwise, bitter taste sensitivity was not associated with bitter food-related behavior such as the pleasantness or consumption of bitter-and-astringent alcoholic or non-alcoholic beverages, vegetables, and berries. Similar to PROP sensitivity (Tepper, 2008), caffeine sensitivity could also have been associated with sweet- and fatty food-related behavior.

Sensitivity to umami was associated with umami-tasting food consumption. More sensitive subjects consumed less salty-and-savory foods compared to less sensitive subjects. This result supports the theory that higher sensitivity would lead

to the avoidance of strong-tasting foods. Umami-sensitive subjects also consumed more portions of vegetables per week than the subjects who were less sensitive to umami. This finding may be important in understanding vegetable consumption. As vegetables are naturally umami-tasting (Martin et al., 2014), and the taste can be even intensified by processing (van Stokkom et al., 2016), people sensitive to umami may perceive an intense umami taste from vegetables, suppressing bitterness and making vegetables more palatable.

Some results were unexpected and challenging to rationalize. A more frequent habit of adding sugar or honey to tea and soy sauce to a meal (among the oldest subjects) was related to lower sour taste sensitivity in addition to less frequent consumption of salty-and-savory foods. Furthermore, a more frequent habit of adding sugar or honey to tea was noted in the youngest subjects least sensitive to umami. Additionally, more frequent addition of ketchup to a meal was associated with higher sensitivity to sweet, salty, and bitter tastes. This connection may be related to the high content of sugar and salt in ketchup, masking or intensifying the taste of a meal. No other studies seem to have investigated these issues.

Some of these unexpected results could arise by chance, as the analyses were not computed modality-specifically, i.e. considering only sweet taste sensitivity and sweet foods. This practice was chosen because the taste of a food item is complex and usually involves several taste modalities although scientists are used to labeling food categories as “sweet foods” or “salty foods” according to the dominant taste modality. Thus, the modality-specific approach would have been arbitrary and some results may have been missed because of subjective categorization.

The TSS that was used as a descriptor for the overall taste sensitivity was associated with three consumption variables. Higher overall taste sensitivity was associated with a more frequent habit of adding ketchup to a meal and less frequent consumption of pungent foods and coffee. Thus, if only the overall taste sensitivity was considered in this study, many interesting associations would have been missed. This finding encourages to study modality-specific sensitivities instead of an overall descriptor of taste sensitivity when the associations between taste sensitivity and food-related behavior are considered.

Some more associations could have existed, according to previous studies. First, alcohol liking and consumption have been linked to salty, sour, sweet, and bitter perception (Duffy et al., 2004; Fischer et al., 2013); however, in this study, taste sensitivity was not related to alcoholic beverage pleasantness or consumption. Second, sweet food-related behavior has been linked to sensitivity to sweetness (Jayasinghe et al., 2017). However, the results of this study support the findings of previous studies showing no association between sweet taste sensitivity and sweet foods (Cicerale et al., 2012; Keskitalo et al., 2007; Low et al., 2018).

Because this study was cross-sectional, a cause–effect relationship cannot be concluded; repeated exposure to a taste stimulus could cause decreased taste sensitivity, or *vice versa*. Some longitudinal studies have addressed this issue. A three-month low-sugar diet caused more intense sweetness perception in food products, but pleasantness ratings were not affected (Wise et al., 2016). Repeated exposure to MSG enriched broth decreased umami taste sensitivity in women but not in men (Noel et al., 2018). In the same study, repeated exposure to MSG was associated with diminished intake of and desire for savory foods at an *ad libitum* meal, but it did not affect hedonic ratings of umami-rich foods. The increased salt intake did not affect sensitivity to saltiness (Bertino et al., 1986; Bolhuis et al., 2015). One study found increased preference for higher levels of salt after increased intake (Bertino et al., 1986), whereas another study found no effect of increased intake on pleasantness (Bolhuis et al., 2015). Experience-induced changes in taste function have been suggested to be reversible as has been shown for glucose (Gonzalez et al., 2007) and MSG (Han et al., 2018; Kobayashi et al., 2006).

6.3.2 Background factors and food-related behavior

Background factors were related to recalled pleasantness as well as to consumption behavior. Concerning pungent foods, oddly, females found pungent foods more pleasant, but males consumed them more frequently. Furthermore, pungent food pleasantness and use-frequency were not correlated. In previous studies, males have been shown to like pungent foods more than females (Törnwall et al., 2014) as well as to consume more chili peppers (Spinelli et al., 2018) or then, consumption of spicy foods has not been associated with gender (Ludy & Mattes, 2012). Pungent food-related behavior has also been connected to genetic factors (Törnwall et al., 2012) and personality factors such as food adventurousness (Spinelli et al., 2018; Tepper, 2008; Törnwall et al., 2012). Moreover, the cultural effect is highlighted, as early and repeated exposure to spicy foods already in childhood has been linked to increased liking and consumption of pungent foods (Ludy & Mattes, 2012).

Gender differences were also observed in other food-related behaviors. Males consumed salty-and-savory foods and liked bitter-and-astringent alcohol beverages more than females did. Females found sweet-and-fatty-foods more pleasant than males did, supporting previous findings in Finnish subjects (Törnwall et al., 2014; Tuorila et al., 2017). Concerning vegetables, fruits, and berries, males consumed fewer portions of berries per week and liked bitter vegetables more than females did. Typically, women consume more vegetables, fruits, and berries in Finland (Knaapila et al., 2014; Valsta et al., 2018). In general, females have higher interest in healthy eating (Kiefer et al., 2005).

With increasing age, the preference for strong-tasting foods, especially bitter and umami-tasting foods, seemed to increase. This relationship was shown because of a higher liking score for bitter non-alcoholic beverages, berries, strong-tasting vegetables, and salty-and-savory foods among the older subjects, whereas preference for sweet beverages and salty-and-fatty foods among younger age groups. The preference for strong-tasting foods despite taste sensitivity may be explained with habituation to strong tastes over the years. Younger subjects also liked to add milk to coffee, which may be explained with the changing coffee culture as younger people may have been accustomed to drinking coffee with milk, such as cappuccino and latte. Furthermore, older age was related to more frequent consumption of fruits, berries, and bitter vegetables. In general, in Finland, vegetable consumption decreases and berry and fruit consumption increases with age (Valsta et al., 2018). The higher liking and consumption of berries among the older subjects may be explained with their habit of adding something sweet to berries.

Higher BMI was associated with lower scores for many variables related to vegetables, fruits, and berries and a higher score for sweet beverage pleasantness. These results would substantiate the assumption that people with higher BMI would have a less healthy diet. However, for example, sweet-and-fatty foods were not related to BMI. Previous studies found no association between BMI and sweet food-related behavior (Low et al., 2018), or several food categories (Guido et al., 2016).

Education level as an indicator of socioeconomic position was expected to be associated with food-related behavior because socioeconomic status has been related to dietary habits (Giskes et al., 2009). Furthermore, higher education has been shown to be associated with higher consumption of vegetables, fruits, and berries in Finland (Valsta et al., 2018). However, in this study, only differences between education levels were found in the frequency to add sweetness to tea and milk to coffee.

6.4 Limitations

Despite the strengths that five taste modalities were considered at several concentration levels, a whole-mouth taste stimulation was applied, and a large-scale and heterogeneous study population was used, there are some aspects to be acknowledged when the results are interpreted.

Although the group of subjects was heterogeneous, it was unbalanced for background factors. The majority were females, lean, highly educated, and non-smokers. However, the reference groups were still larger than those in many previous studies. The aim was not to obtain a representative population sample. However, the unbalanced group sizes may have affected the analyses. Furthermore, BMI is only an estimate of body size and was calculated from self-reported height and weight that diminishes the validity.

Concerning design, this study was a part of a large research project, and the subjects also completed other sensory tests. For intensity evaluation, a comprehensible scale that required no extensive training was chosen. Furthermore, the intensity was evaluated without a cross-modal reference, but thorough verbal and written instructions were provided to avoid scale-use bias. Additionally, the concentration levels of samples were chosen carefully to avoid ceiling effect. The widely used gLMS was not applied in this study, because VAS is commonly and successfully used in our sensory laboratory. Furthermore, the study was conducted with mild-tasting samples that probably would not have been well differentiated with gLMS.

Taste sensitivity groups were determined data-drivenly by using hierarchical clustering, and the simultaneous analyses of all samples smoothed out variation in intensity rating that was not a result of the true intensity perception.

Taste sensitivity was determined using one compound per taste modality. With other tastants, the results may have been different. Furthermore, the concentrations of taste samples were lower than those used in many previous studies. As already mentioned above, higher concentrations would have caused a ceiling effect with the scale used; however, they would also have caused unnecessary unpleasant testing experience for the subjects. The strongest concentration was thought to be clearly perceivable for the majority and was based on the ASTM (1981) standard for measuring taste intensity

The study design was planned carefully to avoid excessive fatigue. The session required about 120 min, including discussions and tests related to sight and smell. The subjects could proceed at their own speed within the limits of instructions. Additionally, the participants could quit at any time, but no one did.

The data about food-related behavior were acquired with several questions, but the questionnaires were not validated. The Finnish food culture had to be considered, and thus, for example, the French PrefQuest (Deglaire et al., 2012) could not be applied. The items in the questionnaires were chosen based on the assumption that they would divide subjects' opinions and elicit different dominant taste sensations.

7 Conclusions and Future Prospects

This study showed that people perceive taste differently, especially bitter and umami tastes. However, sensitivity to one taste modality does not necessarily indicate sensitivity to another taste modality. Considering caffeine or MSG as reference compounds, people can vary extremely in their perception. Leaders of trained sensory panels should be aware of this possible variation in taste perception. Furthermore, the ability of people to distinguish between taste modalities or that they are familiar with the names of taste modalities that are used by sensory scientists should not be taken for granted.

During the recruitment of study participants, the characteristics of subjects should be considered more carefully, as gender, age, and BMI may contribute to taste sensitivity and food-related behavior. Although it is convenient to recruit participants from near the research facilities, it often results in a homogeneous study population affecting the results and conclusions.

Moreover, this study highlights the importance of assessing the actual behavior toward food and not just hedonics, as the studied factors were related to food consumption rather than pleasantness. Food consumption behavior was more broadly related to taste modality-specific sensitivity than to the taste sensitivity score. PROP perception is commonly used as a marker for general taste acuity as measuring sensitivity to one compound is much more convenient than using one or several compounds representing each taste modality. However, based on this study, if the relationship between taste sensitivity and food-related behavior is investigated using only a general descriptor of taste sensitivity, some interesting findings may be missed, possibly explaining also some inconsistency in results.

However, other factors such as personality traits, culture, and social dynamics may be more essential for food-related behavior than taste sensitivity. Future studies should consider more comprehensively factors that are related to food choice and consumption to be able to interpret the relationship between taste acuity and food-related behavior. Longitudinal studies would be essential to reveal the cause-and-effect relationship between taste sensitivity and food consumption as well as between taste sensitivity and taste-related intrinsic and extrinsic factors.

Acknowledgements

This thesis was carried out in projects funded by the Academy of Finland at Functional Foods Forum during the years 2015–2020. I am grateful to my supervisor and project leader, Professor Mari Sandell, for trusting in me and providing me this opportunity. Thank you for sharing your broad expertise in and passion about sensory perception. You always remembered to ask how I was and persistently tried to restore my faith in this project when I was too critical.

I also want to thank my other supervisor, Professor Harri Niinikoski, and my follow-up committee, Professor Seppo Salminen, and Research Director Satu Männistö for all the discussion, advice and support that helped in the progression of this work.

The official reviewers, Associate Professor Caterina Dinnella and Research Director Sophie Nicklaus are thanked for the time and the excellent feedback that helped me to improve his thesis.

I am extremely thankful to my co-authors. Senior Researcher Ulla Hoppu, thank you for guiding me in the scientific world. I learned so much from you during our numerous discussions. Your huge support and contribution to this work are the key factors that assisted me in finishing this project. I am also thankful to my other co-author, superhuman, Research Scientist Heikki Aisala. You had always time to read and give the best comments to manuscripts and posters. I am also thankful that you built up the questionnaire in Compusense, gave your important input in designing the testing protocol, and helped me collect the data.

I express my thanks to all the other members of the Food and Senses research group during these years. I am thankful to all of you who contributed to this study. Especially, thank you Pauliina Ojansivu for all the preliminary testing and planning. I also owe huge gratitude to Leo Lepistö who tirelessly contributed to the data collection and spent long days in the sensory lab. Saara, thank you for sharing the office room and the interesting conversations. Without your presence and friendship, this project would have been like a tough piece of meat and not even half as fun as it has been.

Thanks to all other people who have worked at Functional Foods Forum during these years. You have made this the best workplace. Without the coffee breaks and

tyky activities with you, this thesis would not be finished. The support and encouragement you gave me were invaluable.

The financial support of the Academy of Finland, Turku Doctoral Program of Clinical Research, Turku University Foundation, and the Finnish Food Research Foundation are gratefully acknowledged. I would also like to thank all the volunteers for participating in the study.

Special thanks belong to Fc Parsa. You brought me a reason to survive until Thursday and to be constantly alert in the case of tärppi.

The greatest gratitude I owe to my wonderful family. Kiitos Äiti ja Iskä, että olette aina tukeneet päätöksiäni, pitäneet huolta (myös kissoista) ja kannustaneet eteenpäin. Kiitos myös Sanna ja Ville-Matti sekä Jani ja Kirsi hauskanpidosta, huolenpidosta, keskusteluista ja esimerkillisyydestä. Lopuksi, kiitos Jesse, että tulit maustamaan elämäni. Olen suunnattoman kiitollinen kaikista halauksista, mixed plateista, oluista ja ihan jokaisesta hetkestä, jotka olet jakanut kanssani. Erityiskiitos kissojen hoidosta.

Cup&Pint, Turku, some Thursday in February 2020

Sari Puputti

References

- ASTM. (1981). Guidelines for the selection and training of sensory panel members. Philadelphia, PA. *American Society for Testing and Materials*.
- Bachmanov, A. A., Bosak, N. P., Lin, C., Matsumoto, I., Ohmoto, M., Reed, D. R., & Nelson, T. M. (2014). Genetics of taste receptors. *Current Pharmaceutical Design*, *20*(16), 2669–2683. <https://doi.org/10.2174/13816128113199990566>
- Bajec, M. R., & Pickering, G. J. (2008). Thermal taste, PROP responsiveness, and perception of oral sensations. *Physiology and Behavior*, *95*(4), 581–590. <https://doi.org/10.1016/j.physbeh.2008.08.009>
- Bajec, M. R., & Pickering, G. J. (2010). Association of thermal taste and PROP responsiveness with food liking, neophobia, body mass index, and waist circumference. *Food Quality and Preference*, *21*(6), 589–601. <https://doi.org/10.1016/J.FOODQUAL.2010.03.007>
- Barragán, R., Coltell, O., Portolés, O., Asensio, E. M., Sorlí, J. V., Ortega-Azorín, C., González, J. I., Sáiz, C., Fernández-Carrión, R., Ordovas, J. M., Corella, D., Barragán, R., Coltell, O., Portolés, O., Asensio, E. M., Sorlí, J. V., Ortega-Azorín, C., González, J. I., Sáiz, C., ... Corella, D. (2018). Bitter, Sweet, Salty, Sour and Umami Taste Perception Decreases with Age: Sex-Specific Analysis, Modulation by Genetic Variants and Taste-Preference Associations in 18 to 80 Year-Old Subjects. *Nutrients*, *10*(1539), 1539. <https://doi.org/10.3390/nu10101539>
- Bartoshuk, L M, Duffy, V. B., Fast, K., Green, B. G., Prutkin, J., & Snyder, D. J. (2002). Labeled scales (e.g., category, Likert, VAS) and invalid across-group comparisons: what we have learned from genetic variation in taste. *Food Quality and Preference*, *14*, 125–138.
- Bartoshuk, Linda M., Catalanotto, F., Hoffman, H., Logan, H., & Snyder, D. J. (2012). Taste damage (otitis media, tonsillectomy and head and neck cancer), oral sensations and BMI. *Physiology & Behavior*, *107*(4), 516–526. <https://doi.org/10.1016/J.PHYSBEH.2012.06.013>
- Bartoshuk, Linda M. (2000). Comparing Sensory Experiences Across Individuals: Recent Psychophysical Advances Illuminate Genetic Variation in Taste Perception. *Chemical Senses*, *25*(4), 447–460. <https://doi.org/10.1093/chemse/25.4.447>
- Bartoshuk, Linda M, Duffy, V. B., & Miller, I. J. (1994). PTC/PROP Tasting: Anatomy, Psychophysics, and Sex Effects. *Physiology & Behavior*, *56*(6), 1165–1171.
- Bertino, M., Beauchamp, G. K., & Engelman, K. (1986). Increasing Dietary Salt Alters Salt Taste Preference. *Physiology & Behavior*, *38*, 203–213. [https://doi.org/10.1016/0031-9384\(86\)90155-1](https://doi.org/10.1016/0031-9384(86)90155-1)
- Bitnes, J., Martens, H., Ueland, Ø., & Martens, M. (2007). Longitudinal study of taste identification of sensory panellists: Effect of Ageing, Experience and Exposure. *Food Quality and Preference*, *18*(2), 230–241. <https://doi.org/10.1016/j.foodqual.2005.11.003>
- Boesveldt, S., Bobowski, N., McCrickerd, K., Maître, I., Sulmont-Rossé, C., & Forde, C. G. (2018). The changing role of the senses in food choice and food intake across the lifespan. *Food Quality and Preference*, *68*, 80–89. <https://doi.org/10.1016/J.FOODQUAL.2018.02.004>

- Bolhuis, D. P., Gijsbers, L., De Jager, I., Geleijnse, J. M., & De Graaf, K. (2015). Encapsulated sodium supplementation of 4 weeks does not alter salt taste preferences in a controlled low sodium and low potassium diet. *Food Quality and Preference*, *46*, 58–65. <https://doi.org/10.1016/j.foodqual.2015.07.005>
- Brand, G., & Millot, J.-L. (2001). Sex differences in human olfaction: Between evidence and enigma. *Quarterly Journal of Experimental Psychology*, *54B*(3), 259–270. <https://doi.org/10.1080/02724990143000045>
- Breslin, P. A. S. (2013). An Evolutionary Perspective on Food and Human Taste. *Current Biology*, *23*(9), R409–R418. <https://doi.org/10.1016/J.CUB.2013.04.010>
- Breslin, P. A. S., & Spector, A. C. (2008). Mammalian taste perception. *Current Biology*, *18*(4), R148–R155. <https://doi.org/10.1016/J.CUB.2007.12.017>
- Bufe, B., Breslin, P. A. S., Kuhn, C., Reed, D. R., Tharp, C. D., Slack, J. P., Kim, U.-K., Drayna, D., & Meyer. (2005). The Molecular Basis of Individual Differences in Phenylthiocarbamide and Propylthiouracil Bitterness Perception. *Current Biology*, *15*, 322–327. <https://doi.org/10.1016/j.cub.2005.01.047>
- Calò, C., Padiglia, A., Zonza, A., Corrias, L., Contu, P., Tepper, B. J., & Barbarossa, I. T. (2011). Polymorphisms in TAS2R38 and the taste bud trophic factor, gustin gene co-operate in modulating PROP taste phenotype. *Physiology & Behavior*, *104*(5), 1065–1071. <https://doi.org/10.1016/J.PHYSBEH.2011.06.013>
- Catanzaro, D., Chesbro, E. C., & Velkey, A. J. (2013). Relationship between food preferences and PROP taster status of college students. *Appetite*, *68*, 124–131. <https://doi.org/10.1016/J.APPET.2013.04.025>
- Chamoun, E., Carroll, N., Duizer, L., Qi, W., Feng, Z., Darlington, G., Duncan, A., Haines, J., Ma, D., Study, T. G. F. H., Chamoun, E., Carroll, N. A., Duizer, L. M., Qi, W., Feng, Z., Darlington, G., Duncan, A. M., Haines, J., Ma, D. W. L., & The Guelph Family Health Study. (2018). The Relationship between Single Nucleotide Polymorphisms in Taste Receptor Genes, Taste Function and Dietary Intake in Preschool-Aged Children and Adults in the Guelph Family Health Study. *Nutrients*, *10*(8), 990. <https://doi.org/10.3390/nu10080990>
- Chamoun, E., Mutch, D. M., Allen-Vercoe, E., Buchholz, A. C., Duncan, A. M., Spriet, L. L., Haines, J., L, D. W., & L Ma, D. W. (2016). A review of the associations between single nucleotide polymorphisms in taste receptors, eating behaviors, and health. *Critical Reviews in Food Science and Nutrition*, *58*(2), 194–207. <https://doi.org/10.1080/10408398.2016.1152229>
- Chen, Q.-Y., Alarcon, S., Tharp, A., Ahmed, O. M., Estrella, N. L., Greene, T. A., Rucker, J., & Breslin, P. A. (2009). Perceptual variation in umami taste and polymorphisms in TAS1R taste receptor genes. *American Journal of Clinical Nutrition*, *90*, 770S–779S. <https://doi.org/10.3945/ajcn.2009.27462N>
- Chéruef, F., Jarlier, M., & Sancho-Garnier, H. (2017). Effect of cigarette smoke on gustatory sensitivity, evaluation of the deficit and of the recovery time-course after smoking cessation. *Tobacco Induced Diseases*, *15*(15), 1–8. <https://doi.org/10.1186/s12971-017-0120-4>
- Cicerale, S., Riddell, L. J., & Keast, R. S. J. (2012). The Association between Perceived Sweetness Intensity and Dietary Intake in Young Adults. *Journal of Food Science*, *77*(1), H31–H35. <https://doi.org/10.1111/j.1750-3841.2011.02473.x>
- Coltell, O., Sorlí, J. V., Asensio, E. M., Fernández-Carrión, R., Barragán, R., Ortega-Azorín, C., Estruch, R., González, J. I., Salas-Salvadó, J., Lamon-Fava, S., Lichtenstein, A. H., & Corella, D. (2019). Association between taste perception and adiposity in overweight or obese older subjects with metabolic syndrome and identification of novel taste-related genes. *The American Journal of Clinical Nutrition*, *109*(6), 1709–1723. <https://doi.org/10.1093/ajcn/nqz038>

- Cordain, L., Eaton, S. B., Sebastian, A., Mann, N., Lindeberg, S., Watkins, B. A., O'Keefe, J. H., & Brand-Miller, J. (2005). Origins and evolution of the Western diet: health implications for the 21st century. *The American Journal of Clinical Nutrition*, *81*(2), 341–354. <https://doi.org/10.1093/ajcn.81.2.341>
- Cox, D. N., Hendrie, G. A., & Carty, D. (2016). Sensitivity, hedonics and preferences for basic tastes and fat amongst adults and children of differing weight status: A comprehensive review. *Food Quality and Preference*, *48*, 1–9. <https://doi.org/10.1016/J.FOODQUAL.2015.01.006>
- Cruz, A., & Green, B. G. (2000). Thermal stimulation of taste. *Nature*, *403*(6772), 889–892. <https://doi.org/10.1038/35002581>
- de Boer, A., Ter Horst, G. J., & Lorist, M. M. (2013). Physiological and psychosocial age-related changes associated with reduced food intake in older persons. *Ageing Research Reviews*, *12*(1), 316–328. <https://doi.org/10.1016/J.ARR.2012.08.002>
- Deglaire, A., Méjean, C., Castetbon, K., Kesse-Guyot, E., Urbano, C., Hercberg, S., & Schlich, P. (2012). Development of a questionnaire to assay recalled liking for salt, sweet and fat. *Food Quality and Preference*, *23*(2), 110–124. <https://doi.org/10.1016/j.foodqual.2011.08.006>
- Delwiche, J. F., Buletic, Z., & Breslin, P. A. S. (2001). Covariation in individuals' sensitivities to bitter compounds: Evidence supporting multiple receptor/transduction mechanisms. *Perception & Psychophysics*, *63*(5), 761–776. <https://doi.org/10.3758/BF03194436>
- Depoortere, I. (2014). Taste receptors of the gut: Emerging roles in health and disease. *Gut*, *63*, 179–190. <https://doi.org/10.1136/gutjnl-2013-305112>
- Dias, A. G., Rousseau, D., Duizer, L., Cockburn, M., Chiu, W., Nielsen, D., & El-Sohemy, A. (2013). Genetic Variation in Putative Salt Taste Receptors and Salt Taste Perception in Humans. *Chem. Senses*, *38*, 137–145. <https://doi.org/10.1093/chemse/bjs090>
- Dinehart, M. E. E., Hayes, J. E. E., Bartoshuk, L. M. M., Lanier, S. L. L., & Duffy, V. B. B. (2006). Bitter taste markers explain variability in vegetable sweetness, bitterness, and intake. *Physiology & Behavior*, *87*(2), 304–313. <https://doi.org/10.1016/J.PHYSBEH.2005.10.018>
- Dinnella, C., Monteleone, E., Piochi, M., Spinelli, S., Prescott, J., Pierguidi, L., Gasperi, F., Laureati, M., Pagliarini, E., Predieri, S., Torri, L., Barbieri, S., Valli, E., Bianchi, P., Braghieri, A., Caro, A. Del, Monaco, R. Di, Favotto, S., Moneta, E., ... Forestali, A. E. (2018). Individual Variation in PROP Status, Fungiform Papillae Density, and Responsiveness to Taste Stimuli in a Large Population Sample. *Chemical Senses*, *43*, 697–710. <https://doi.org/10.1093/chemse/bjy058>
- Doets, E. L., & Kremer, S. (2015). The silver sensory experience – A review of senior consumers' food perception, liking and intake. *Food Quality and Preference*, *48*, 316–332. <https://doi.org/10.1016/j.foodqual.2015.08.010>
- Doty, R. L., Chen, J. H., & Overend, J. (2017). Taste Quality Confusions: Influences of Age, Smoking, PTC Taster Status, and other Subject Characteristics. *Perception*, *46*, 257–267. <https://doi.org/10.1177/0301006616685577>
- Doty, R. L., Heidt, J. M., MacGillivray, M. R., Dsouza, M., Tracey, E. H., Mirza, N., & Bigelow, D. (2016). Influences of age, tongue region, and chorda tympani nerve sectioning on signal detection measures of lingual taste sensitivity. *Physiology & Behavior*, *155*, 202–207. <https://doi.org/10.1016/J.PHYSBEH.2015.12.014>
- Drewnowski, A., & Hann, C. (1999). Food preferences and reported frequencies of food consumption as predictors of current diet in young women. *The American Journal of Clinical Nutrition*, *70*(1), 28–36. <https://doi.org/10.1093/ajcn/70.1.28>
- Dsamou, M., Palicki, O., Septier, C., Chabanet, C., Lucchi, G., Ducoroy, P., Chagnon, M.-C., & Morzel, M. (2012). Salivary Protein Profiles and Sensitivity to the Bitter Taste of Caffeine. *Chemical Senses*, *37*(1), 87–95. <https://doi.org/10.1093/chemse/bjr070>

- Duffy, V B, Peterson, J. M., Dinehart, M. E., & Bartoshuk, L. M. (2003). Genetic and environmental variation in taste. *Topics in Clinical Nutrition*, *18*, 209–220. <https://doi.org/10.1097/00008486-200310000-00002>
- Duffy, Valerie B., Peterson, J. M., & Bartoshuk, L. M. (2004). Associations between taste genetics, oral sensation and alcohol intake. *Physiology & Behavior*, *82*(2–3), 435–445. <https://doi.org/10.1016/J.PHYSBEH.2004.04.060>
- Duffy, Valerie B. (2004). Associations between oral sensation, dietary behaviors and risk of cardiovascular disease (CVD). *Appetite*, *43*(1), 5–9. <https://doi.org/10.1016/j.appet.2004.02.007>
- Duffy, Valerie B, Hayes, J. E., Davidson, A. C., Kidd, J. R., Kidd, K. K., & Bartoshuk, L. M. (2010). Vegetable Intake in College-Aged Adults Is Explained by Oral Sensory Phenotypes and TAS2R38 Genotype. *Chemosensory Perception*, *3*(3–4), 137–148. <https://doi.org/10.1007/s12078-010-9079-8>
- Fábián, T., Beck, A., Fejérdy, P., Hermann, P., & Fábián, G. (2015). Molecular Mechanisms of Taste Recognition: Considerations about the Role of Saliva. *International Journal of Molecular Sciences*, *16*(12), 5945–5974. <https://doi.org/10.3390/ijms16035945>
- Feeney, E. L., & Hayes, J. E. (2014a). Exploring associations between taste perception, oral anatomy and polymorphisms in the carbonic anhydrase (gustin) gene CA6. *Physiology & Behavior*, *128*, 148–154. <https://doi.org/10.1016/j.physbeh.2014.02.013>
- Feeney, E. L., & Hayes, J. E. (2014b). Regional differences in suprathreshold intensity for bitter and umami stimuli. *Chemosensory Perception*, *7*(3–4), 147–157. <https://doi.org/10.1007/s12078-014-9166-3>
- Feeney, E. L., O'Brien, S. A., Scannell, A. G. M., Markey, A., & Gibney, E. R. (2017). Suprathreshold measures of taste perception in children - Association with dietary quality and body weight. *Appetite*, *113*, 116–123. <https://doi.org/10.1016/j.appet.2017.02.026>
- Feng, P., Huang, L., & Wang, H. (2014). Taste Bud Homeostasis in Health, Disease, and Aging. *Chemical Senses*, *39*(1), 3–16. <https://doi.org/10.1093/chemse/bjt059>
- Feron, G., & Salles, C. (2018). Food oral processing in humans: Links between physiological parameters, release of flavour stimuli and flavour perception of food. *International Journal of Food Studies*, *7*(1), 1–12. <https://doi.org/10.7455/ijfs/7.1.2018.a1>
- Fischer, M. E., Cruickshanks, K. J., Pankow, J. S., Pankratz, N., Schubert, C. R., Huang, G.-H., Klein, B. E. K., Klein, R., & Pinto, A. (2014). The associations between 6-n-propylthiouracil (PROP) intensity and taste intensities differ by TAS2R38 haplotype. *Journal of Nutrigenetics and Nutrigenomics*, *7*(3), 143–152. <https://doi.org/10.1159/000371552>
- Fischer, M. E., Cruickshanks, K. J., Schubert, C. R., Pinto, A., Klein, B. E. K., Klein, R., Nieto, F. J., Pankow, J. S., Huang, G. H., & Snyder, D. J. (2013). Taste intensity in the Beaver Dam Offspring Study. *Laryngoscope*, *123*(6), 1399–1404. <https://doi.org/10.1002/lary.23894>
- Fischer, M. E., Cruickshanks, K. J., Schubert, C. R., Pinto, A., Klein, R., Pankratz, N., Pankow, J. S., & Huang, G.-H. (2013). Factors Related to Fungiform Papillae Density: The Beaver Dam Offspring Study. *Chem. Senses*, *38*, 669–677. <https://doi.org/10.1093/chemse/bjt033>
- Fjell, A. M., Walhovd, K. B., Reinvang, I., Lundervold, A., Salat, D., Quinn, B. T., Fischl, B., & Dale, A. M. (2006). Selective increase of cortical thickness in high-performing elderly—structural indices of optimal cognitive aging. *NeuroImage*, *29*(3), 984–994. <https://doi.org/10.1016/J.NEUROIMAGE.2005.08.007>
- Fox, A. L. (1932). The Relationship between Chemical Constitution and Taste. *Proceedings of the National Academy of Sciences*, *18*(1), 115–120. <https://doi.org/10.1073/pnas.18.1.115>
- Galindo-Cuspinera, V., Waeber, T., Antille, N., Hartmann, C., Stead, N., & Martin, N. (2009). Reliability of Threshold and Suprathreshold Methods for Taste Phenotyping: Characterization

- with PROP and Sodium Chloride. *Chemosensory Perception*, 2, 214–228. <https://doi.org/10.1007/s12078-009-9059-z>
- Giskes, K., Avendaño, M., Brug, J., & Kunst, A. E. (2009). A systematic review of studies on socioeconomic inequalities in dietary intakes associated with weight gain and overweight/obesity conducted among European adults. *Obesity Reviews*, 11(6), 413–429. <https://doi.org/10.1111/j.1467-789X.2009.00658.x>
- Gondivkar, S. M., Indurkar, A., Degwekar, S., & Bhowate, R. (2009). Evaluation of gustatory function in patients with diabetes mellitus type 2. *Oral Surgery, Oral Medicine, Oral Pathology, Oral Radiology, and Endodontology*, 108(6), 876–880. <https://doi.org/10.1016/j.tripleo.2009.08.015>
- Gonzalez, K. M., Peo, C., Livdahl, T., & Kennedy, L. M. (2007). Experience-Induced Changes in Sugar Taste Discrimination. *Chemical Senses*, 33(2), 173–179. <https://doi.org/10.1093/chemse/bjm078>
- Green, B. G., & George, P. (2004). “Thermal Taste” Predicts Higher Responsiveness to Chemical Taste and Flavor. *Chemical Senses*, 29(7), 617–628. <https://doi.org/10.1093/chemse/bjh065>
- Green, Barry G., Dalton, P., Cowart, B., Shaffer, G., Rankin, K., & Higgins, J. (1996). Evaluating the “labeled magnitude scale” for measuring sensations of taste and smell. *Chemical Senses*, 21(3), 323–334. <https://doi.org/10.1093/chemse/21.3.323>
- Green, Barry G., Shaffer, G. S., & Gilmore, M. M. (1993). Derivation and evaluation of a semantic scale of oral sensation magnitude with apparent ratio properties. *Chemical Senses*, 18(6), 683–702. <https://doi.org/10.1093/chemse/18.6.683>
- Guido, D., Perna, S., Carrai, M., Barale, R., Grassi, M., Rondanelli, M., & Perna, S. (2016). Multidimensional evaluation of endogenous and health factors affecting food preferences, taste and smell perception. *The Journal of Nutrition, Health & Aging*, 20(10), 971–981. <https://doi.org/10.1007/s12603-016-0703-4>
- Han, P., Mohebbi, M., Unrath, M., Hummel, C., & Hummel, T. (2018). Different Neural Processing of Umami and Salty Taste Determined by Umami Identification Ability Independent of Repeated Umami Exposure. *Neuroscience*, 383, 74–83. <https://doi.org/10.1016/J.NEUROSCIENCE.2018.05.004>
- Hardikar, S., Hoechenberger, R., Villringer, A., & Ohla, K. (2017). Higher sensitivity to sweet and salty taste in obese compared to lean individuals. *Appetite*, 111, 158–165. <https://doi.org/10.1016/j.appet.2016.12.017>
- Hartley, I., Liem, D., Keast, R., Hartley, I. E., Liem, D. G., & Keast, R. (2019). Umami as an ‘Alimentary’ Taste. A New Perspective on Taste Classification. *Nutrients*, 11(1), 182–200. <https://doi.org/10.3390/nu11010182>
- Hayes, J. E., Bartoshuk, L. M., Kidd, J. R., & Duffy, V. B. (2008). Supertasting and PROP Bitterness Depends on More Than the TAS2R38 Gene. *Chemical Senses*, 33, 255–265. <https://doi.org/10.1093/chemse/bjm084>
- Hayes, J. E., Feeney, E. L., & Allen, A. L. (2013). Do polymorphisms in chemosensory genes matter for human ingestive behavior? *Food Quality and Preference*, 30(2), 202–216. <https://doi.org/10.1016/J.FOODQUAL.2013.05.013>
- Hayes, J. E., Sullivan, B. S., & Duffy, V. B. (2010). Explaining variability in sodium intake through oral sensory phenotype, salt sensation and liking. *Physiology & Behavior*, 100(4), 369–380. <https://doi.org/10.1016/J.PHYSBEH.2010.03.017>
- Heinzerling, C. I., Stieger, M., Bult, J. H. F., & Smit, G. (2011). Individually Modified Saliva Delivery Changes the Perceived Intensity of Saltiness and Sourness. *Chemosensory Perception*, 4(4), 145–153. <https://doi.org/10.1007/s12078-011-9099-z>
- Henkin, R. I., Levy, L. M., & Fordyce, A. (2013). Taste and smell function in chronic disease: A review of clinical and biochemical evaluations of taste and smell dysfunction in over 5000 patients at

- The Taste and Smell Clinic in Washington, DC. *American Journal of Otolaryngology*, 34(5), 477–489. <https://doi.org/10.1016/J.AMJOTO.2013.04.006>
- Henkin, R. I., Martin, B. M., & Agarwal, R. P. (1999). Efficacy of exogenous oral zinc in treatment of patients with carbonic anhydrase VI deficiency. *American Journal of the Medical Sciences*, 318(6), 392–405. [https://doi.org/10.1016/S0002-9629\(15\)40664-0](https://doi.org/10.1016/S0002-9629(15)40664-0)
- Hettinger, T. P., Gent, J. F., Marks, L. E., & Frank, M. E. (1999). A confusion matrix for the study of taste perception. *Perception & Psychophysics*, 61(8), 1510–1521.
- Holt, S. H. ., Cobiac, L., Beaumont-Smith, N. ., Easton, K., & Best, D. . (2000). Dietary habits and the perception and liking of sweetness among Australian and Malaysian students: A cross-cultural study. *Food Quality and Preference*, 11(4), 299–312. [https://doi.org/10.1016/S0950-3293\(99\)00076-2](https://doi.org/10.1016/S0950-3293(99)00076-2)
- Hoogeveen, H. R., Dalenberg, J. R., Renken, R. J., ter Horst, G. J., & Lorist, M. M. (2015). Neural processing of basic tastes in healthy young and older adults — an fMRI study. *NeuroImage*, 119, 1–12. <https://doi.org/10.1016/J.NEUROIMAGE.2015.06.017>
- Hwang, L.-D., Breslin, P. A. S., Reed, D. R., Zhu, G., Martin, N. G., & Wright, M. J. (2016). Is the Association Between Sweet and Bitter Perception due to Genetic Variation? *Chemical Senses*, 41, 737–744. <https://doi.org/10.1093/chemse/bjw083>
- Hyde, R. J., & Feller, R. P. (1981). Age and sex effects on taste of sucrose, NaCl, citric acid and caffeine. *Neurobiology of Aging*, 2(4), 315–318. [https://doi.org/10.1016/0197-4580\(81\)90041-5](https://doi.org/10.1016/0197-4580(81)90041-5)
- Iatridi, V., Hayes, J. E., & Yeomans, M. R. (2019). Reconsidering the classification of sweet taste liker phenotypes: A methodological review. *Food Quality and Preference*, 72, 56–76. <https://doi.org/10.1016/j.foodqual.2018.09.001>
- Jayasinghe, S. N., Kruger, R., Walsh, D. C. I., Cao, G., Rivers, S., Richter, M., & Breier, B. H. (2017). Is Sweet Taste Perception Associated with Sweet Food Liking and Intake? *Nutrients*, 9(750), 1–19. <https://doi.org/10.3390/nu9070750>
- Kaminski, L. C., Henderson, S. A., & Drewnowski, A. (2000). Young women’s food preferences and taste responsiveness to 6-n-propylthiouracil (PROP). *Physiology & Behavior*, 68(5), 691–697. [https://doi.org/10.1016/S0031-9384\(99\)00240-1](https://doi.org/10.1016/S0031-9384(99)00240-1)
- Keast, R. S., & Costanzo, A. (2015). Is fat the sixth taste primary? Evidence and implications. *Flavour*, 4(1), 5. <https://doi.org/10.1186/2044-7248-4-5>
- Keast, R. S. J., & Roper, J. (2007). A Complex Relationship among Chemical Concentration, Detection Threshold, and Suprathreshold Intensity of Bitter Compounds. *Chemical Senses*, 32(3), 245–253. <https://doi.org/10.1093/chemse/bjl052>
- Keskitalo, K., Tuorila, H., Spector, T. D., Cherkas, L. F., Knaapila, A., Silventoinen, K., & Perola, M. (2007). Same genetic components underlie different measures of sweet taste preference. *The American Journal of Clinical Nutrition*, 86(6), 1663–1669. <https://doi.org/10.1093/ajcn/86.5.1663>
- Kiefer, I., Rathmanner, T., & Kunze, M. (2005). Eating and dieting differences in men and women. *Journal of Men’s Health and Gender*, 2(2), 194–201. <https://doi.org/10.1016/j.jmhg.2005.04.010>
- Kim, U.-K., Breslin, P. A. S., Reed, D., & Drayna, D. (2004). Genetics of Human Taste Perception. *Journal of Dental Research*, 83(6), 448–453. <https://doi.org/10.1177/154405910408300603>
- Kim, U. kyung, Jorgenson, E., Coon, H., Leppert, M., Risch, N., & Drayna, D. (2003). Positional cloning of the human quantitative trait locus underlying taste sensitivity to phenylthiocarbamide. *Science*, 299, 1221–1225. <https://doi.org/10.1126/science.1080190>
- Knaapila, A., Hwang, L.-D., Lysenko, A., Duke, F. F., Fesi, B., Khoshnevisan, A., James, R. S., Wysocki, C. J., Rhyu, M., Tordoff, M. G., Bachmanov, A. A., Mura, E., Nagai, H., & Reed, D.

- R. (2012). Genetic Analysis of Chemosensory Traits in Human Twins. *Chemical Senses*, *107*(9), 935–939. <https://doi.org/10.1093/chemse/bjs070>
- Knaapila, A. J., Sandell, M. A., Vaarno, J., Hoppu, U., Puolimatka, T., Kaljonen, A., & Lagström, H. (2014). Food neophobia associates with lower dietary quality and higher BMI in Finnish adults. *Public Health Nutrition*, *18*(12), 2161–2171. <https://doi.org/10.1017/S1368980014003024>
- Kobayashi, C., Kennedy, L. M., & Halpern, B. P. (2006). Experience-Induced Changes in Taste Identification of Monosodium Glutamate (MSG) Are Reversible. *Chemical Senses*, *31*(4), 301–306. <https://doi.org/10.1093/chemse/bjj033>
- Kolkka-Palomaa, M., Jääskeläinen, S. K., Laine, M. A., Teerijoki-Oksa, T., Sandell, M., & Forssell, H. (2015). Pathophysiology of primary burning mouth syndrome with special focus on taste dysfunction: A review. *Oral Diseases*, *21*(8), 937–948. <https://doi.org/10.1111/odi.12345>
- Konstantinidis, I., Chatziavramidis, A., Printza, A., Metaxas, S., & Constantinidis, J. (2010). Effects of smoking on taste: Assessment with contact endoscopy and taste strips. *Laryngoscope*, *120*(10), 1958–1963. <https://doi.org/10.1002/lary.21098>
- Landis, B. N., Welge-Luessen, A., Brämerson, A., Bende, M., Mueller, C. A., Nordin, S., & Hummel, T. (2009). “Taste Strips” – A rapid, lateralized, gustatory bedside identification test based on impregnated filter papers. *Journal of Neurology*, *256*(2), 242–248. <https://doi.org/10.1007/s00415-009-0088-y>
- Lanier, S. A., Hayes, J. E., & Duffy, V. B. (2005). Sweet and bitter tastes of alcoholic beverages mediate alcohol intake in of-age undergraduates. *Physiology & Behavior*, *83*(5), 821–831. <https://doi.org/10.1016/j.physbeh.2004.10.004>
- Larsson, M., Lövdén, M., & Nilsson, L. G. (2003). Sex differences in recollective experience for olfactory and verbal information. *Acta Psychologica*, *112*(1), 89–103. [https://doi.org/10.1016/S0001-6918\(02\)00092-6](https://doi.org/10.1016/S0001-6918(02)00092-6)
- Lawless, H. T., Horne, J., & Spiers, W. (2000). Contrast and Range Effects for Category, Magnitude and Labeled Magnitude Scales in Judgements of Sweetness Intensity. *Chemical Senses*, *25*(1), 85–92. <https://doi.org/10.1093/chemse/25.1.85>
- Lawless, H. T., Stevens, D. A., Chapman, K. W., & Kurtz, A. (2005). Metallic Taste from Electrical and Chemical Stimulation. *Chemical Senses*, *30*(3), 185–194. <https://doi.org/10.1093/chemse/bji014>
- Lawless, Harry T., & Heymann, H. (2010a). Measurement of Sensory Thresholds. In D. R. Heldman, D. A. Golden, R. W. Hartel, H. Heymann, J. H. Hotchkiss, M. G. Johnson, J. Montecalvo, S. S. Nielse, & J. L. Silva (Eds.), *Sensory Evaluation of Food, Principals and Practices* (Second, pp. 125–147). Springer, New York, NY, USA.
- Lawless, Harry T., & Heymann, H. (2010b). Physiological and Psychological Foundations of Sensory Function. In D. R. Heldman, D. A. Golden, R. W. Hartel, H. Heymann, J. H. Hotchkiss, M. G. Johnson, J. Montecalvo, S. S. Nielse, & J. L. Silva (Eds.), *Sensory Evaluation of Food, Principals and Practices* (Second, pp. 19–56). Springer, New York, NY, USA.
- Liang, P., Jiang, J., Ding, Q., Tang, X., & Roy, S. (2018). Memory Load Influences Taste Sensitivities. *Frontiers in Psychology*, *9*, 2533. <https://doi.org/10.3389/fpsyg.2018.02533>
- Lim, J., Urban, L., & Green, B. G. (2008). Measures of Individual Differences in Taste and Creaminess Perception. *Chemical Senses*, *33*, 493–501. <https://doi.org/10.1093/chemse/bjn016>
- Lipchock, S. V., Spielman, A. I., Mennella, J. A., Mansfield, C. J., Hwang, L.-D., Douglas, J. E., & Reed, D. R. (2017). Caffeine Bitterness is Related to Daily Caffeine Intake and Bitter Receptor mRNA Abundance in Human Taste Tissue. *Perception*, *46*(3–4), 245–256. <https://doi.org/10.1177/0301006616686098>

- Looy, H., Callaghan, S., & Weingarten, H. P. (1992). Hedonic Response of Sucrose Likers and Dislikers to Other Gustatory Stimuli. *Physiology & Behavior*, *52*, 219–225.
- Loper, H. B., La Sala, M., Dotson, C., & Steinle, N. (2015). Taste perception, associated hormonal modulation, and nutrient intake. *Nutrition Reviews*, *73*(2), 83–91. <https://doi.org/10.1093/nutrit/nuu009>
- Low, J. Y., Lacy, K. E., McBride, R., & Keast, R. S. J. (2016). The Association between Sweet Taste Function, Anthropometry, and Dietary Intake in Adults. *Nutrients*, *8*(5), 241–255. <https://doi.org/10.3390/nu8040241>
- Low, J. Y. Q., Lacy, K. E., McBride, R. L., & Keast, R. S. J. (2018). The Associations Between Oral Complex Carbohydrate Sensitivity, BMI, Liking, and Consumption of Complex Carbohydrate Based Foods. *Journal of Food Science*, *83*(8), 2227–2236. <https://doi.org/10.1111/1750-3841.14276>
- Ludy, M.-J., & Mattes, R. D. (2012). Comparison of sensory, physiological, personality, and cultural attributes in regular spicy food users and non-users. *Appetite*, *58*(1), 19–27. <https://doi.org/10.1016/J.APPET.2011.09.018>
- Lugaz, O., Pillias, A.-M., & Faurion, A. (2002). A New Specific Ageusia: Some Humans Cannot Taste L-Glutamate. *Chemical Senses*, *27*, 105–115. <https://doi.org/10.1093/chemse/27.2.105>
- Ly, A., & Drewnowski, A. (2001). PROP (6-n-Propylthiouracil) Tasting and Sensory Responses to Caffeine, Sucrose, Neohesperidin Dihydrochalcone and Chocolate. *Chemical Senses*, *26*(1), 41–47. <https://doi.org/10.1093/chemse/26.1.41>
- Martin, C., Visalli, M., Lange, C., Schlich, P., & Issanchou, S. (2014). Creation of a food taste database using an in-home “taste” profile method. *Food Quality and Preference*, *36*, 70–80. <https://doi.org/10.1016/j.foodqual.2014.03.005>
- Martin, L. J., & Sollars, S. I. (2017). Contributory role of sex differences in the variations of gustatory function. *Journal of Neuroscience Research*, *95*(1–2), 594–603. <https://doi.org/10.1002/jnr.23819>
- Masi, C., Dinnella, C., Monteleone, E., & Prescott, J. (2015). The impact of individual variations in taste sensitivity on coffee perceptions and preferences. *Physiology & Behavior*, *138*, 219–226. <https://doi.org/10.1016/j.physbeh.2014.10.031>
- McDaid, O., Stewart-Knox, B., Parr, H., & Simpson, E. (2007). Dietary zinc intake and sex differences in taste acuity in healthy young adults. *Journal of Human Nutrition and Dietetics*, *20*(2), 103–110. <https://doi.org/10.1111/j.1365-277X.2007.00756.x>
- Melis, M., Atzori, E., Cabras, S., Zonza, A., Calò, C., Muroli, P., Nieddu, M., Padiglia, A., Sogos, V., Tepper, B. J., & Tomassini Barbarossa, I. (2013). The Gustin (CA6) Gene Polymorphism, rs2274333 (A/G), as a Mechanistic Link between PROP Tasting and Fungiform Taste Papilla Density and Maintenance. *PLoS ONE*, *8*(9), e74151. <https://doi.org/10.1371/journal.pone.0074151>
- Methven, L., Xiao, C., Cai, M., & Prescott, J. (2016). Rejection thresholds (R_{JT}) of sweet likers and dislikers. *Food Quality and Preference*, *52*, 74–80. <https://doi.org/10.1016/j.foodqual.2016.03.012>
- Methven, Lisa, Allen, V. J., Withers, C. A., & Gosney, M. A. (2012). Ageing and taste. *Proceedings of the Nutrition Society*, *71*(4), 556–565. <https://doi.org/10.1017/S0029665112000742>
- Meyerhof, W., Batram, C., Kuhn, C., Brockhoff, A., Chudoba, E., Bufer, B., Appendino, G., & Behrens, M. (2010). The Molecular Receptive Ranges of Human TAS2R Bitter Taste Receptors. *Chemical Senses*, *35*(2), 157–170. <https://doi.org/10.1093/chemse/bjp092>

- Mojet, J., Heidema, J., & Christ-Hazelhof, E. (2003). Taste perception with age: generic or specific losses in supra-threshold intensities of five taste qualities? *Chemical Senses*, *28*, 397–413. <https://doi.org/10.1093/chemse/28.5.397>
- Monnery-Patris, S., Rouby, C., Nicklaus, S., & Issanchou, I. (2009). Development of olfactory ability in children: Sensitivity and identification. *Developmental Psychobiology*, *51*(3), 268–276. <https://doi.org/10.1002/dev.20363>
- Naik, B. S., Shetty, N., & Maben, E. V. S. (2010). Drug-induced taste disorders. *European Journal of Internal Medicine*, *21*(3), 240–243. <https://doi.org/10.1016/J.EJIM.2010.01.017>
- Nakamura, Y., Sanematsu, K., Ohta, R., Shirosaki, S., Koyano, K., Nonaka, K., Shigemura, N., & Ninomiya, Y. (2008). Diurnal variation of human sweet taste recognition thresholds is correlated with plasma leptin levels. *Diabetes*, *57*(10), 2661–2665. <https://doi.org/10.2337/db07-1103>
- Noel, C. A., Finlayson, G., & Dando, R. (2018). Prolonged Exposure to Monosodium Glutamate in Healthy Young Adults Decreases Perceived Umami Taste and Diminishes Appetite for Savory Foods. *The Journal of Nutrition*, *148*(6), 980–988. <https://doi.org/10.1093/jn/nxy055>
- Noel, C. A., Sugrue, M., & Dando, R. (2017). Participants with pharmacologically impaired taste function seek out more intense, higher calorie stimuli. *Appetite*, *117*, 74–81. <https://doi.org/10.1016/J.APPET.2017.06.006>
- Nordin, S., Brämerson, A., Bringlöv, E., Kobal, G., Hummel, T., & Bende, M. (2007). Substance and tongue-region specific loss in basic taste-quality identification in elderly adults. *European Archives of Oto-Rhino-Laryngology*, *264*, 285–289. <https://doi.org/10.1007/s00405-006-0169-9>
- Padiglia, A., Zonza, A., Atzori, E., Chillotti, C., Calò, C., Tepper, B. J., & Barbarossa, I. T. (2010). Sensitivity to 6-n-propylthiouracil is associated with gustin (carbonic anhydrase VI) gene polymorphism, salivary zinc, and body mass index in humans. *The American Journal of Clinical Nutrition*, *92*(3), 539–545. <https://doi.org/10.3945/ajcn.2010.29418>
- Pavlos, P., Vasilios, N., Antonia, A., Dimitrios, K., Georgios, K., & Georgios, A. (2009). Evaluation of young smokers and non-smokers with Electrogustometry and Contact Endoscopy. *BMC Ear, Nose, and Throat Disorders*, *9*, 9. <https://doi.org/10.1186/1472-6815-9-9>
- Pepino, M. Y., Finkbeiner, S., Beauchamp, G. K., & Mennella, J. A. (2010). Obese Women Have Lower Monosodium Glutamate Taste Sensitivity and Prefer Higher Concentrations Than Do Normal-weight Women. *Obesity*, *18*(5), 959–965. <https://doi.org/10.1038/oby.2009.493>
- Piochi, M., Pierguidi, L., Torri, L., Spinelli, S., Monteleone, E., Aprea, E., Arena, E., Borgogno, M., Cravero, M. C., Galassi, L., Gatti, E., Lozano, L., Musi, V., Piasentier, E., Valli, E., & Dinnella, C. (2019). Individual variation in fungiform papillae density with different sizes and relevant associations with responsiveness to oral stimuli. *Food Quality and Preference*, *78*, 1–9. <https://doi.org/10.1016/J.FOODQUAL.2019.103729>
- Piochi, Maria, Dinnella, C., Prescott, J., & Monteleone, E. (2018). Associations between human fungiform papillae and responsiveness to oral stimuli: effects of individual variability, population characteristics, and methods for papillae quantification. *Chemical Senses*, *43*(5), 313–327. <https://doi.org/10.1093/chemse/bjy015>
- Platte, P., Herbert, C., Pauli, P., Breslin, P. A. S., & Garbutt, J. (2013). Oral Perceptions of Fat and Taste Stimuli Are Modulated by Affect and Mood Induction. *PLoS ONE*, *8*(6), e65006. <https://doi.org/10.1371/journal.pone.0065006>
- Rawal, S., Huedo-Medina, T., Hoffman, H. J., Swede, H., & Duffy, V. B. (2017). Structural Equation Modeling of Associations among Taste-Related Risk Factors, Taste Functioning and Adiposity HHS Public Access. *Obesity*, *25*(4), 781–787. <https://doi.org/10.1002/oby.21785>

- Sadananda Naik, B., Shetty, N., Maben, E. V. S. V. S., Naik, B. S., Shetty, N., & Maben, E. V. S. V. S. (2010). Drug-induced taste disorders. *European Journal of Internal Medicine*, *21*(3), 240–243. <https://doi.org/10.1016/j.ejim.2010.01.017>
- Sandell, M. A., & Breslin, P. A. S. (2006). Variability in a taste-receptor gene determines whether we taste toxins in food. *Current Biology*, *16*(18), R792–R794. <https://doi.org/10.1016/j.cub.2006.08.049>
- Sandell, M., Hoppu, U., Lundén, S., Salminen, M., Puolimatka, T., Laaksonen, O., Laitinen, K., & Hopia, A. (2015). Consumption of lingonberries by TAS2R38 genotype and sensory quality of texture-designed lingonberry samples. *Food Quality and Preference*, *45*, 166–170. <https://doi.org/10.1016/j.foodqual.2015.06.015>
- Sandell, M., Hoppu, U., Mikkilä, V., Mononen, N., Kähönen, M., Männistö, S., Rönnemaa, T., Viikari, J., Lehtimäki, T., & Raitakari, O. T. (2014). Genetic variation in the hTAS2R38 taste receptor and food consumption among Finnish adults. *Genes & Nutrition*, *9*(6), 433–440. <https://doi.org/10.1007/s12263-014-0433-3>
- Sartor, F., Donaldson, L. F., Markland, D. A., Loveday, H., Jackson, M. J., & Kubis, H.-P. (2011). Taste perception and implicit attitude toward sweet related to body mass index and soft drink supplementation. *Appetite*, *57*, 237–246. <https://doi.org/10.1016/j.appet.2011.05.107>
- Sasano, T., Satoh-Kuriwada, S., & Shoji, N. (2015). The important role of umami taste in oral and overall health. *Flavour*, *4*(1), 1–10. <https://doi.org/10.1186/2044-7248-4-10>
- Schiffstein, H. N. J. (2012). Labeled Magnitude Scales: A critical review. *Food Quality and Preference*, *26*, 151–158. <https://doi.org/10.1016/j.foodqual.2012.04.016>
- Schiffman, S. S. (2018). Influence of medications on taste and smell. *World Journal of Otorhinolaryngology - Head and Neck Surgery*, *4*(1), 84–91. <https://doi.org/10.1016/j.wjorl.2018.02.005>
- Sharafi, M., Rawal, S., Fernandez, M. L., Huedo-Medina, T. B., & Duffy, V. B. (2018). Taste phenotype associates with cardiovascular disease risk factors via diet quality in multivariate modeling. *Physiology & Behavior*, *194*, 103–112. <https://doi.org/10.1016/J.PHYSBEH.2018.05.005>
- Shen, Y., Kennedy, O. B., & Methven, L. (2016). Exploring the effects of genotypical and phenotypical variations in bitter taste sensitivity on perception, liking and intake of brassica vegetables in the UK. *Food Quality and Preference*, *50*, 71–81. <https://doi.org/10.1016/j.foodqual.2016.01.005>
- Shen, Y., Kennedy, O. B., & Methven, L. (2017). The effect of genotypical and phenotypical variation in taste sensitivity on liking of ice cream and dietary fat intake. *Food Quality and Preference*, *55*, 79–90. <https://doi.org/10.1016/J.FOODQUAL.2016.08.010>
- Shigemura, N., Shirosaki, S., Sanematsu, K., Yoshida, R., & Ninomiya, Y. (2009). Genetic and Molecular Basis of Individual Differences in Human Umami Taste Perception. *PLoS ONE*, *4*(8), e6717. <https://doi.org/10.1371/JOURNAL.PONE.0006717>
- Simchen, U., Koebnick, C., Hoyer, S., Issanchou, S., & Zunft, H.-J. F. (2006). Odour and taste sensitivity is associated with body weight and extent of misreporting of body weight. *European Journal of Clinical Nutrition*, *60*(6), 698–705. <https://doi.org/10.1038/sj.ejcn.1602371>
- Singh, P. B., Schuster, B., & Seo, H.-S. (2010). Variation in umami taste perception in the German and Norwegian population. *European Journal of Clinical Nutrition*, *64*(10), 1248–1250. <https://doi.org/10.1038/ejcn.2010.133>
- Snyder, D. J., & Bartoshuk, L. M. (2016). Oral sensory nerve damage: Causes and consequences. *Reviews in Endocrine and Metabolic Disorders*, *17*(2), 149–158. <https://doi.org/10.1007/s11154-016-9377-9>
- Sollai, G., Melis, M., Pani, D., Cosseddu, P., Usai, I., Crnjar, R., Bonfiglio, A., & Tomassini Barbarossa, I. (2017). First objective evaluation of taste sensitivity to 6-n-propylthiouracil

- (PROP), a paradigm gustatory stimulus in humans. *Scientific Reports*, 7, 40353. <https://doi.org/10.1038/srep40353>
- Spinelli, S., De Toffoli, A., Dinnella, C., Laureati, M., Pagliarini, E., Bendini, A., Braghieri, A., Gallina Toschi, T., Sinesio, F., Torri, L., Gasperi, F., Endrizzi, I., Magli, M., Borgogno, M., di Salvo, R., Favotto, S., Prescott, J., & Monteleone, E. (2018). Personality traits and gender influence liking and choice of food pungency. *Food Quality and Preference*, 66, 113–126. <https://doi.org/10.1016/J.FOODQUAL.2018.01.014>
- Stillman, J. A., Morton, R. P., Hay, K. D., Ahmad, Z., & Goldsmith, D. (2003). Electrogustometry: strengths, weaknesses, and clinical evidence of stimulus boundaries. *Clinical Otolaryngology and Allied Sciences*, 28(5), 406–410. <https://doi.org/10.1046/j.1365-2273.2003.00729.x>
- Subar, A. F., Freedman, L. S., Tooze, J. A., Kirkpatrick, S. I., Boushey, C., Neuhauser, M. L., Thompson, F. E., Potischman, N., Guenther, P. M., Tarasuk, V., Reedy, J., & Krebs-Smith, S. M. (2015). Addressing Current Criticism Regarding the Value of Self-Report Dietary Data. *The Journal of Nutrition*, 145(12), 2639–2645. <https://doi.org/10.3945/jn.115.219634>
- Tepper, B. J. (2008). Nutritional Implications of Genetic Taste Variation: The Role of PROP Sensitivity and Other Taste Phenotypes. *Annual Review of Nutrition*, 28, 367–388. <https://doi.org/10.1146/annurev.nutr.28.061807.155458>
- Tepper, B. J., Melis, M., Koelliker, Y., Gasparini, P., Ahijevych, K. L., & Barbarossa, I. T. (2017). Factors influencing the phenotypic characterization of the oral marker, PROP. *Nutrients*, 9(12), 1–15. <https://doi.org/10.3390/nu9121275>
- Than, T. T., Delay, E. R., & Maier, M. E. (1994). Sucrose threshold variation during the menstrual cycle. *Physiology & Behavior*, 56(2), 237–239. [https://doi.org/10.1016/0031-9384\(94\)90189-9](https://doi.org/10.1016/0031-9384(94)90189-9)
- Tordoff, M. G. (2001). Calcium: Taste, Intake, and Appetite. *Physiological Reviews*, 81(4), 1567–1597. <https://doi.org/10.1152/physrev.2001.81.4.1567>
- Törnwall, O., Silventoinen, K., Hiekkalinna, T., Perola, M., Tuorila, H., & Kaprio, J. (2014). Identifying flavor preference subgroups. Genetic basis and related eating behavior traits. *Appetite*, 75, 1–10. <https://doi.org/10.1016/j.appet.2013.11.020>
- Törnwall, O., Silventoinen, K., Kaprio, J., & Tuorila, H. (2012). Why do some like it hot? Genetic and environmental contributions to the pleasantness of oral pungency. *Physiology & Behavior*, 107(3), 381–389. <https://doi.org/10.1016/j.physbeh.2012.09.010>
- Tuorila, H., Keskitalo-Vuokko, K., Perola, M., Spector, T., & Kaprio, J. (2017). Affective responses to sweet products and sweet solution in British and Finnish adults. *Food Quality and Preference*, 62, 128–136. <https://doi.org/10.1016/J.FOODQUAL.2017.06.021>
- Valsta, L., Lundqvist, A., Kaartinen, N., Raulio, S., Sääksjärvi, K., & Männistö, S. (2018). Ruokatottumukset. In P. Koponen, K. Borodulin, A. Lundqvist, K. Sääksjärvi, & S. Koskinen (Eds.), *Terveys, toimintakyky ja hyvinvointi Suomessa, FinTerveys 2017 -tutkimus* (pp. 33–37). THL, Helsinki, Finland. <http://urn.fi/URN:ISBN:978-952-343-105-8>
- Van Der Klaauw, N. J., & Smith, D. V. (1995). Taste Quality Profiles for Fifteen Organic and Inorganic Salts. *Physiology & Behavior*, 58(2), 295–306.
- van Stokkom, V. L., Teo, P. S., Mars, M., de Graaf, C., van Kooten, O., & Stieger, M. (2016). Taste intensities of ten vegetables commonly consumed in the Netherlands. *Food Research International*, 87, 34–41. <https://doi.org/10.1016/J.FOODRES.2016.06.016>
- Vandenberghe-Descamps, M., Labouré, H., Prot, A., Septier, C., Tournier, C., Feron, G., & Sulmont-Rossé, C. (2016). Salivary Flow Decreases in Healthy Elderly People Independently of Dental Status and Drug Intake. *Journal of Texture Studies*, 47(4), 353–360. <https://doi.org/10.1111/jtxs.12191>

- Vennemann, M. M., Hummel, T., & Berger, K. (2008). The association between smoking and smell and taste impairment in the general population. *Journal of Neurology*, *255*, 1121–1126. <https://doi.org/10.1007/s00415-008-0807-9>
- Wasalathanthri, S., Hettiarachchi, P., & Prathapan, S. (2014). Sweet taste sensitivity in pre-diabetics, diabetics and normoglycemic controls: a comparative cross sectional study. *BMC Endocrine Disorders*, *14*(1), 67. <https://doi.org/10.1186/1472-6823-14-67>
- Webb, J., Bolhuis, D. P., Cicerale, S., Hayes, J. E., & Keast, R. (2015). The Relationships Between Common Measurements of Taste Function. *Chemosensory Perception*, *8*(1), 11–18. <https://doi.org/10.1007/s12078-015-9183-x>
- Welge-Lüssen, A., Dörig, P., Wolfensberger, M., Krone, F., & Hummel, T. (2011). A study about the frequency of taste disorders. *Journal of Neurology*, *258*(3), 386–392. <https://doi.org/10.1007/s00415-010-5763-5>
- Williams, J. A., Bartoshuk, L. M., Fillingim, R. B., & Dotson, C. D. (2016). Exploring Ethnic Differences in Taste Perception. *Chemical Senses*, *41*, 449–456. <https://doi.org/10.1093/chemse/bjw021>
- Wise, P. M., Nattress, L., Flammer, L. J., & Beauchamp, G. K. (2016). Reduced dietary intake of simple sugars alters perceived sweet taste intensity but not perceived pleasantness. *American Journal of Clinical Nutrition*, *103*(1), 50–60. <https://doi.org/10.3945/ajcn.115.112300>
- Wise, Paul M., & Breslin, P. A. S. (2013). Individual differences in sour and salt sensitivity: detection and quality recognition thresholds for citric acid and sodium chloride. *Chemical Senses*, *38*(4), 333–342. <https://doi.org/10.1093/chemse/bjt003>
- World Health Organization. Obesity and Overweight. Retrieved February 15, 2019, from <https://www.who.int/news-room/fact-sheets/detail/obesity-and-overweight>
- Yang, Q., Kraft, M., Shen, Y., MacFie, H., & Ford, R. (2019). Sweet Liking Status and PROP Taster Status impact emotional response to sweetened beverage. *Food Quality and Preference*, *75*, 133–144. <https://doi.org/10.1016/j.foodqual.2019.02.016>
- Zhang, J., Jin, H., Zhang, W., Ding, C., O’Keeffe, S., Ye, M., & Zuker, C. S. (2019). Sour Sensing from the Tongue to the Brain. *Cell*, *179*(2), 392–402.e15. <https://doi.org/10.1016/j.cell.2019.08.031>

Appendix

Appendix 1. Recalled pleasantness of food and beverage items that were included in the factor analysis.

Category (N of subjects included in the analyses)	Item	Mean Pleasantness	Sd
Vegetables, vegetable dishes, and pungent sauces (N = 154)	Swedish turnip	5.88	2.029
	Carrot	8.06	1.068
	Tomato	8.01	1.318
	Red beet	6.91	1.838
	Brussels sprout	5.75	2.236
	Onion	6.97	2.081
	Rucola	7.07	2.013
	Selery	5.11	2.550
	Radish	5.68	2.192
	Cucumber	8.05	1.298
	Chili	6.09	2.236
	Olive	6.31	2.658
	Wasabi	5.16	2.618
	Chili sauce	6.19	2.235
	Mustard	6.24	2.241
	Cabbage casserole	6.89	2.225
	Puréed vegetable soup	7.51	1.805
	Mushroom	7.27	2.175
Cooked new potatoes	8.26	1.347	
Pea soup	7.01	1.824	
Fruits and berries (N = 186)	Banana	7.86	1.497
	Grapefruit	6.37	2.312
	Watermelon	7.92	1.512
	Orange	7.98	1.317
	Lemon	6.68	1.759
	Rhubarb	6.85	1.835
	Avocado	7.03	2.178
	Lingonberry	6.64	2.216

	Bilberry	8.60	0.834
	Black currant	7.49	1.664
	Red currant	6.97	1.772
	Strawberry	8.62	0.997
	Seabuckthorn	6.31	2.198
<hr/>			
Sweet, salty, and fatty foods (N = 177)	Blue cheese	6.67	2.849
	Dark chocolate	7.24	1.866
	Milk chocolate	7.93	1.606
	Salmiak	7.39	2.119
	Candy	7.06	1.852
	Sweet pastry	7.47	1.752
	Ice cream	8.22	1.109
	Mayonnaise	6.35	1.954
	Soy sauce	6.16	2.106
	Ketchup	6.53	1.812
	French fries	6.90	1.758
	Potato chips	6.76	2.200
	Dry-cured salmon	7.21	2.458
<hr/>			
Alcohol and non-alcoholic beverages (N = 170)	Coffee	7.02	2.516
	Tea	7.59	1.514
	Carbonated water	6.49	2.411
	Soft drink	5.59	2.314
	Light soft drink	4.54	2.579
	Red wine	6.68	2.536
	White wine	6.74	2.286
	Beer	5.36	2.954
	Sweet cider	4.31	2.174
	Dry cider	5.81	2.185
	Long drink	5.24	2.455
Strong alcohol	4.48	2.329	

Original Publications

Puputti, S., Aisala, H., Hoppu, U., & Sandell, M. (2018)
Multidimensional measurement of individual differences in taste
perception.
Food Quality and Preference



Contents lists available at ScienceDirect

Food Quality and Preference

journal homepage: www.elsevier.com/locate/foodqual

Multidimensional measurement of individual differences in taste perception

Sari Puputti^a, Heikki Aisala^{a,b}, Ulla Hoppu^a, Mari Sandell^{a,*}^a Functional Foods Forum, University of Turku, FI-20014 Turku, Finland^b Food Chemistry and Food Development, Department of Biochemistry, University of Turku, FI-20014 Turku, Finland

ARTICLE INFO

Keywords:

Taste
Individual differences
Sensitivity
Hierarchical clustering
Intensity
Perception

ABSTRACT

Individual taste sensitivity has been claimed to affect food consumption and health. The methods used to assess taste sensitivity are various and thus, cause conflicting results. Thresholds, PROP intensity or fungiform papillae density only partly describe taste function. They may not relate to the actual taste perception in food because of compounds, concentration levels, or the measurement levels used. The objective of the study was to measure individual taste function extensively. With hierarchical clustering, we aimed to reveal taste sensitivity groups among people. Another aim was to investigate the associations between taste qualities. In addition, an overall taste sensitivity score was determined to analyze the generalized taste sensitivity.

The sensory study was carried out with Finnish volunteers (N = 205, age 19–79, 80% females). Citric acid, caffeine, sucrose, NaCl, and MSG were used as the prototypic taste compounds. The subjects rated the intensity of five concentration levels of each tastant.

Hierarchical clustering made it possible to analyze the complex data. The results of clustering were distinctive for taste modalities and the number of subjects in the clusters varied. In general, the clusters could be labeled as more sensitive, semi-sensitive, and less sensitive tasters. In bitter and umami tasted one cluster consisted of hyposensitive subjects. The membership in a taste cluster could be partly predicted by the sensitivity to other taste modalities. This study showed that a minority may be hyper- or hyposensitive to all taste modalities. On the other hand, the majority, the semi-sensitive tasters, can be a very heterogeneous group.

1. Introduction

Taste is an important contributor to food liking and consumption. The traditionally accepted taste qualities are sweet, salty, sour, bitter and umami. Interindividual variation in taste perception may be partly explained by physiological differences or cognitive processing of the taste signals in the brain (Bachmanov & Beauchamp, 2007). Taste sensitivity may affect eating behavior and health, although the evidence is scarce and focuses on taste genetics (Cox, Hendrie, & Carty, 2015; Hayes, Feeney, & Allen, 2013; Hayes, Sullivan, & Duffy, 2010; Monteleone et al., 2017; Sandell et al., 2014, 2015).

Individual perception of taste is challenging to measure. Traditionally five different methods have been used to define taste sensitivity: detection and recognition threshold (DT and RT, respectively), suprathreshold intensity measure, 6-n-propylthiouracil (PROP) taster status and fungiform papillae (FP) count (Webb, Bolhuis, Cicerale, Hayes, & Keast, 2015). DT and RT focus on very low concentrations which are not relevant in a food context. These thresholds do not correlate with suprathreshold intensities (Keast & Roper, 2007; Mojet, Christ-Hazelhof, & Heidema, 2005). Thus explaining food

selection with individual DT or RT can be misleading (Low, Lacy, McBride, & Keast, 2016). Taste sensitivity to PROP has been used to classify people as supertasters, medium tasters, and non-tasters. Some have found PROP bitterness intensity to correlate with other tastant perception (Bajec & Pickering, 2008; Fischer et al., 2014; Hayes, Bartoshuk, Kidd, & Duffy, 2008). However, PROP tasting measures sensitivity to only one bitter compound, and its role as an indicator for global taste function has been questioned (Fischer et al., 2014; Lim, Urban, & Green, 2008; Webb et al., 2015). FP has been considered to relate to taste function by housing the taste receptor cells. Nonetheless, FP density is a physical feature and does not imply how an individual perceives taste in reality (Feeney & Hayes, 2014; Fischer et al., 2013). Thus, considering the actual perception of food, the suprathreshold intensity measure may be the most relevant method to define taste sensitivity.

Most of the publications on individual taste perception have focused on RT, DT, or PROP. The few existing results from other tastants suggest moderate correlations between intensities. Lim et al. (2008) found correlations (Pearson's r 0.33–0.43) between sucrose, NaCl, QHCl and citric acid intensities. However, they represented the taste stimuli by

* Corresponding author.

E-mail address: mari.sandell@utu.fi (M. Sandell).

rolling cotton swabs across the tip of the tongue, which is not as reliable method as whole-mouth sipping because the intensity perception may vary across regions on the tongue (Feeney & Hayes, 2014; Williams, Bartoshuk, Fillingim, & Dotson, 2016). Nonetheless, Webb et al. (2015) also found suprathreshold intensities to correlate (Pearson's $r = 0.34\text{--}0.56$) between all taste qualities. Moreover, Hwang et al. (2016) reported a moderate association between bitterness and sweetness. These results support the idea of generalized taste sensitivity or hypergeusia as suggested by Hayes and Keast (2011).

This study is part of a larger research project focusing on individual differences in sensory perception. The object of this study was to investigate the differences in taste perception between individuals. The hypothesis was that people can be classified into different sensitivity groups based on their intensity ratings. Another objective was to investigate the commonality between individual sensitivities taking different taste qualities in various concentrations into account. In addition, the idea of generalized taste sensitivity was analyzed. To achieve these objectives in a large research, we needed simple and rapid methods to measure several stimuli intensities. Thus we used line scales for rating the stimuli, and hierarchical clustering to perform data-driven clustering of subjects into taste-specific sensitivity groups.

2. Materials and methods

2.1. Participants

The sensory test was carried out in the sensory laboratory of Functional Foods Forum (University of Turku) in accordance with the ISO8589 standard. Altogether 206 adults (19–79 years) participated in the sensory tests. The test location determined that most of the participants lived in Turku or the surrounding areas in South-West Finland. The exclusion criteria were pregnancy or a lactating state. One person was later excluded because of taste loss after an accident. All the subjects were not able to complete all the sections of the research mainly because of a lack of time, technical issues or hypersensitivity to caffeine. These subjects were only excluded on an analysis by analysis basis rather than being entirely excluded. The number of excluded subjects was small varying from zero (age and gender as background information) to seven (smoking as background information). The final number of subjects are marked in Tables 2 and 3, and Figs. 1 and 2.

The subjects were recruited by advertisements around the University, on the University web pages and at public events. They were instructed to avoid eating, drinking anything other than water, chewing gum and smoking one hour prior the test. The subjects were not trained but before every section, they received both verbal and written instructions. All of the subjects provided written informed consent and were rewarded after every visit. The study was reviewed by the Southwest Finland Hospital District's Ethics Committee (145/1801/2014).

2.2. Taste stimuli

Five taste qualities were involved: sour, bitter, sweet, salty, and umami. One prototypic tastant for every quality was chosen. Five dilutions of every tastant were prepared in active-carbon filtered water, as is described in Table 1. Afterward, the mildest dilution of every tastant was excluded from the analyses being too mild for the test conditions based on inconsistent evaluation by many participants. The solutions were prepared less than four days before use except for MSG, which was prepared less than two days before, following good laboratory practices. Samples were stored under refrigeration in glass bottles and allowed to return to room temperature before serving.

The concentration levels were chosen based on our previous experience. The strongest samples were in line with ASTM standard for measuring taste intensity. Additionally, they are easily perceivable for the majority of individuals with normal taste function in our

experience. We decided the other samples would be milder (concentration increase 0.25log). Stronger samples could have caused a ceiling effect when using line scales.

The sample presentation was designed to prevent excessive fatigue and the effect of positional bias. The samples were served in two sets of 14 samples during one session. The first set involved the mildest dilutions: the E and D dilutions of each tastant, the C dilution of NaCl and citric acid, and two blank samples (active-carbon filtered water) in random order. The rest of the dilutions and a blank sample in random order formed the second set. The C dilution of NaCl and citric acid were assigned to the first set because the salty and sour tastes are easier to rinse off than bitter or umami taste which may easily retain in the mouth. Thus, they could have interfered the evaluation of the mildest samples. In addition, the C dilution of sucrose was assigned to the second set because it was expected to be the most easily recognizable taste.

The subjects received 5 ml of each sample in a glass beaker marked with three-digit codes. They were advised to sip the entire sample, spin it around the mouth for five seconds and then spit it out into an adjacent basin. The instructions included rinsing the mouth with active-carbon filtered water and, if needed, eating a piece of cream cracker between samples. Samples were evaluated once.

2.3. Tasting procedure

Participants were familiarized with the tasting procedure and the taste qualities by tasting the strongest dilution of every tastant. If a taste quality was incorrectly identified, the subject tasted the sample again. The participants rated the intensities of taste samples using line scales anchored both verbally and numerically (0–10): 0 = “no sensation”, 2 = “very mild”, 4 = “quite mild”, 6 = “quite strong”, 8 = “very strong”, 10 = “extremely strong”. The subjects were instructed to rate the intensity above zero if they perceived something else than pure water. The subjects were also instructed verbally that value five on the scale should be a clearly detectable taste sensation and value ten as strong in intensity that the subject would not like to taste it again. After the intensity rating, the subjects indicated the taste quality they recognized (the results not included here).

Compusense five Plus software (Compusense, Guelph, Canada) was used for data collection in the sensory laboratory. Background information was collected with Webropol (Webropol Inc, Helsinki, Finland) online questionnaires. All communication was in Finnish.

2.4. Statistics

Hierarchical clustering was used for data-driven segmentation of the subjects. The clustering was performed on the standardized intensity ratings using the squared Euclidean distance measure and Ward's method. A three-cluster solution was retained for every taste quality. Retaining more clusters could have led to overfitting and have resulted in too small clusters for further statistical analyses.

The least sensitive cluster was labeled with 1, the most sensitive cluster with 3, and the middle cluster with 2. The overall taste sensitivity score was the mean of all clusters (range 1–3). The score was calculated for each participant based on the clusters to which he/she belonged. Those who scored 1.0–1.4 were considered hyposensitive tasters because they belonged to cluster 1 in the majority of the taste qualities (and to cluster 2 at most in the others). Hypersensitive tasters scored 2.6–3.0 being in cluster 3 in three taste qualities at least (and in cluster 2 at least in the others). Semi-sensitive tasters scored 1.6–2.4. Only those subjects who had evaluated all the samples were taken into account ($N = 199$, six missing).

The differences in intensity ratings between the clusters were analyzed with one-way MANOVA and Tukey's or Tamhane's (when equal variances not assumed) test as a *post hoc* test. Multinomial logistic regression was used to study the associations between taste clusters. For

Table 1

The samples and their presenting order. All samples were evaluated in a single session.

Taste	Prototypic tastant	Sample A (mM)	Sample B (mM)	Sample C (mM)	Sample D (mM)	Sample E (mM)
Sour	Citric acid ^a	3.33 ²	1.87 ²	1.05 ¹	0.57 ¹	0.33 ¹
Bitter	Caffeine ^a	3.60 ²	2.03 ²	1.14 ²	0.62 ¹	0.36 ¹
Sweet	Sucrose ^b	58.4 ²	32.9 ²	18.5 ²	10.5 ¹	5.84 ¹
Salty	Sodium chloride ^a	34.2 ²	19.2 ²	10.8 ¹	5.99 ¹	3.42 ¹
Umami	L-glutamic acid, monosodium salt ^a	10.7 ²	6.01 ²	3.38 ²	1.87 ¹	1.07 ¹

^a Produced by Sigma-Aldrich, St. Louis, USA.^b Produced by Alfa Aesar GmbH&Co KG, Karlsruhe, Germany.¹ The sample was served in the first sample set for evaluation.² The sample was served in the second sample set for evaluation.

every taste quality, one model was made using all the other taste qualities as predictors. The largest cluster was selected as a reference category. The criterion for significance was set to be $p \leq .05$. All statistical analyses were computed with IBM SPSS Statistics 23.0 (IBM Corporation, Armonk, USA).

3. Results

3.1. The subject characteristics

The final 205 subjects (41.7 ± 15.2 years, age range 19–79) were predominantly women (80.0%), highly educated (63.9%) and non-smokers (74.2%) (Table 2). Gender and smoking were associated ($\chi^2_{df=1} = 8.08, p = .004$); men had more frequently smoking history. A third of the men used to be smokers. Altogether six individuals reported smoking every day and 11 individuals occasionally.

3.2. Hierarchical clustering

Hierarchical clustering was applied to reveal three sensitivity groups for each taste quality. The clusters represent a less sensitive (cluster 1), a semi-sensitive (cluster 2) and a more sensitive (cluster 3) group. The following sections overview the results in detail for each taste quality. The clusters are reviewed starting with the less sensitive cluster and the differences between the clusters are emphasized. All results are also shown in Table 3 and in Fig. 1. One-way MANOVA was applied to observe cluster differences in intensities. Although some variables failed to meet all assumptions for MANOVA (homogeneity of variance-covariance), the four test statistics (Pillai's Trace, Wilk's Λ , Hotelling's Trace, and Roy's Largest Root) were significant.

3.2.1. Sour

The sour taste clusters had statistically significant differences in every concentration level ($p < .001$). Cluster 1, or SO1 (SO = sour), consisted of 25.2% of the participants (51 of 202). They rated all

Table 2

Subject characteristics (n = 205).

Variable	Mean or n	Sd or %	Data missing (n)
Age (years)	41.7	15.2	0
Gender			0
Female	164	80.0	
Male	41	20.0	
Education ^a			3
Low	73	36.1	
High	129	63.9	
Smoking			7
Currently/formerly	51	25.8	
Non-smoker	147	74.2	

^a Low education includes comprehensive school, high school and lower vocational degree whereas high education includes a polytechnic degree or any university degree.

intensities milder than the overall mean (n = 202), SO2 (cluster 2) or SO3 (cluster 3) members. In SO1, the mean of the strongest sample (A) was 5.29 indicating it was clearly perceivable but not very strong.

SO2 was the largest cluster with 102 members (50.5%). Their intensity ratings were similar to the overall sample mean and between the ratings of SO1 and SO3. Sample A was rated as a little below very strong (7.21).

SO3 with 49 members (24.3%) was equal to the size of SO1. They rated sample A as 8.52 on average, which was more than very strong. SO3 rated samples A–C more intense than SO1 rated sample A. Additionally SO3 rated sample B as more intense than SO2 rated sample A.

3.2.2. Bitter

Moreover, the bitter clusters were significantly different in every sample except for the mildest sample D between the clusters B1 (B1 = bitter) and B2. B1 was the smallest group with 35 (17.4%) members. They perceived sample A as very mild (2.38) and barely detected any taste in the mildest samples.

The other clusters were about equal in size with 87 members (43.3%) in B2 and 79 members (39.3%) in B3. Except for sample D, B2 rated the other samples much more intense than B1. Sample A was rated between quite and very strong (6.90) by B2.

B3 perceived all the samples as much more intense than the other clusters or the overall mean. They gave the mean rating of 8.14 (very strong) for sample A. B3 members perceived all samples much stronger than B1 perceived sample A. The perception of samples B and C by B3 were as strong as the perception of sample A and B by B2, respectively. Additionally, B3 rated sample D much stronger than B2 rated sample C.

3.2.3. Sweet

The clusters of sweet taste perception differed in every concentration except for the mildest in the case of clusters SW1 (SW = sweet) and SW2. The more sensitive SW3 was the smallest cluster (n = 41) the other two being equal in size (n = 83 in SW1 and n = 80 in SW2).

SW1 rated all the samples as milder than the overall sample mean (n = 204). In this cluster, sample A was clearly perceivable (4.74) but the lower concentrations were perceived more or less as mild. SW2 rated sample A as 6.81 on average which is more intense than the overall mean. SW2 perceived samples B and C as strong as SW1 perceived samples A and B, respectively.

SW3 perceived all the samples stronger than the overall mean. They perceived sample A as very strong (7.99). SW3 rated the two mildest samples as intense as SW1 rated the two strongest samples. When SW2 and SW3 were compared, SW2 rated a sample as strong as SW3 the one step milder sample.

3.2.4. Salty

The result of clustering based on salty taste perception is distinctive from the other taste clusterings. The largest cluster with 57.1% of 203

Table 3

Cluster and the whole sample mean intensities \pm SD (95% confidence intervals for the mean intensities in the brackets) for every sample (A–D, see Table 1) and the distribution of subjects between the clusters (n).

Taste	Test statistics ¹	Sample	Cluster 1	Cluster 2	Cluster 3	All
Sour	$p < .001$, $F_{df=8,392} = 75.1$, Wilk's $\Lambda = 0.156$, partial $\eta^2 = 0.605$	A	5.29 \pm 1.06 (4.99–5.58) c	7.21 \pm 1.22 (6.97–7.45) b	8.52 \pm 0.91 (8.26–8.78) a	7.04 \pm 1.60 (6.81–7.26)
		B	4.02 \pm 1.48 (3.60–4.43) c	6.35 \pm 1.41 (6.08–6.63) b	7.81 \pm 1.23 (7.46–8.16) a	6.12 \pm 1.94 (5.85–6.39)
		C	2.15 \pm 0.78 (1.93–2.37) c	4.41 \pm 1.35 (4.15–4.68) b	6.07 \pm 1.23 (5.72–6.42) a	4.24 \pm 1.83 (3.99–4.50)
		D	1.14 \pm 1.07 (0.84–1.44) c	2.14 \pm 1.29 (1.89–2.39) b	4.56 \pm 1.16 (4.22–4.89) a	2.47 \pm 1.73 (2.23–2.71)
		n (%)	51 (25.2)	102 (50.5)	49 (24.3)	202 (100)
Bitter	$p < .001$, $F_{df=8,390} = 87.1$, Wilk's $\Lambda = 0.129$, partial $\eta^2 = 0.641$	A	2.38 \pm 1.69 (1.80–2.96) c	6.90 \pm 1.52 (6.58–7.23) b	8.14 \pm 1.52 (7.80–8.49) a	6.60 \pm 2.55 (6.25–6.96)
		B	1.20 \pm 1.45 (0.70–1.70) c	5.07 \pm 1.90 (4.67–5.48) b	7.12 \pm 2.02 (6.67–7.57) a	5.20 \pm 2.79 (4.82–5.59)
		C	0.65 \pm 1.22 (0.23–1.07) c	2.19 \pm 1.80 (1.81–2.58) b	5.71 \pm 2.05 (5.26–6.18) a	3.31 \pm 2.71 (2.93–3.69)
		D	0.59 \pm 0.75 (0.33–0.85) b	0.71 \pm 0.79 (0.54–0.88) b	3.50 \pm 2.08 (3.03–3.97) a	1.78 \pm 1.99 (1.51–2.06)
		n (%)	35 (17.4)	87 (43.3)	79 (39.3)	201 (100)
Sweet	$p < .001$, $F_{df=8,396} = 60.5$, Wilk's $\Lambda = 0.203$, partial $\eta^2 = 0.550$	A	4.74 \pm 1.27 (4.46–5.02) c	6.81 \pm 1.21 (6.54–7.08) b	7.99 \pm 1.18 (7.62–8.36) a	6.20 \pm 1.78 (5.96–6.45)
		B	2.93 \pm 1.21 (2.66–3.19) c	5.14 \pm 1.29 (4.85–5.43) b	6.39 \pm 1.53 (5.91–6.87) a	4.49 \pm 1.90 (4.23–4.75)
		C	1.68 \pm 0.96 (1.47–1.89) c	2.49 \pm 1.36 (2.19–2.79) b	5.02 \pm 1.14 (4.66–5.38) a	2.67 \pm 1.69 (2.45–2.90)
		D	0.79 \pm 0.83 (0.61–0.97) b	1.10 \pm 1.01 (0.88–1.32) b	2.45 \pm 1.81 (1.88–3.02) a	1.25 \pm 1.30 (1.06–1.43)
		n (%)	83 (40.7)	80 (39.2)	41 (20.1)	204 (100)
Salty	$p < .001$, $F_{df=8,394} = 68.5$, Wilk's $\Lambda = 0.175$, partial $\eta^2 = 0.582$	A	4.73 \pm 1.65 (4.43–5.03) b	7.56 \pm 1.30 (7.20–7.93) a	7.47 \pm 1.63 (6.92–8.03) a	5.93 \pm 2.09 (5.64–6.22)
		B	2.63 \pm 1.45 (2.36–2.89) b	5.86 \pm 1.58 (5.41–6.30) a	5.23 \pm 2.28 (4.46–6.00) a	3.90 \pm 2.22 (3.59–4.21)
		C	1.65 \pm 1.26 (1.42–1.88) c	3.08 \pm 2.06 (2.49–3.65) b	5.01 \pm 1.26 (4.59–5.44) a	2.60 \pm 1.96 (2.33–2.87)
		D	1.44 \pm 1.12 (1.23–1.65) b	1.05 \pm 0.87 (0.81–1.30) b	4.21 \pm 1.15 (3.82–4.60) a	1.83 \pm 1.54 (1.62–2.05)
		n (%)	116 (57.1)	36 (17.7)	51 (25.1)	203 (100)
Umami	$p < .001$, $F_{df=8,394} = 54.4$, Wilk's $\Lambda = 0.226$, partial $\eta^2 = 0.525$	A	2.01 \pm 1.11 (1.60–2.42) c	5.53 \pm 1.34 (5.30–5.75) b	8.01 \pm 1.11 (7.64–8.37) a	5.47 \pm 2.14 (5.18–5.77)
		B	2.33 \pm 1.37 (1.82–2.85) c	4.22 \pm 1.85 (3.91–4.54) b	7.06 \pm 1.67 (6.51–7.61) a	4.48 \pm 2.24 (4.17–4.79)
		C	1.14 \pm 1.09 (0.73–1.55) c	3.26 \pm 1.67 (2.97–3.54) b	6.34 \pm 1.48 (5.85–6.82) a	3.52 \pm 2.19 (3.22–3.82)
		D	0.85 \pm 0.70 (0.58–1.11) c	2.51 \pm 1.75 (2.21–2.80) b	3.89 \pm 2.39 (3.10–4.67) a	2.52 \pm 1.98 (2.25–2.79)
		n (%)	30 (14.8)	135 (66.5)	38 (18.7)	203 (100)

Different lower cases indicate statistically significant ($p \leq .05$) differences between the clusters in a sample.

¹ One-way MANOVA for the differences in cluster intensities.

participants, SA1 (SA = salty) was also the least sensitive. The group perceived the samples milder than the overall mean except for sample D. Sample A was perceived on an average level as 4.73 and the rest as quite mild.

To SA2 belonged 25.1% ($n = 51$) of the subjects. They perceived sample C as 3.08 which was equal to SA1's perception of sample B (2.63) and was less than SA3's perception of sample D (4.21). The perception of the mildest sample was as hard for SA2 as for SA1. SA3 had only 36 (17.7%) members. They had rated samples A and B as equally intense as SA2. The ratings for the other samples are at the same level, around five. SA3 differed from SA1 and the overall mean in every sample.

3.2.5. Umami

The majority, 66.5% (135 of 203) of participants were in UM2 (UM = umami). The other clusters were about the same size UM1 having 30 (14.8%) and UM3 38 (18.7%) members. The members in UM1 had difficulties in perceiving any of the samples. They rated both samples A and B as equally mild level (2.01 and 2.33, respectively). Samples C and D were barely detectable (1.14 and 0.85, respectively) and rated as milder than the overall mean.

As the largest cluster, UM2's ratings were at the same level with the overall mean. UM2 perceived the mildest sample as intense as UM1 perceived the strongest sample. UM3 was the most sensitive cluster with every rating above the overall mean. They rated sample A as very strong (8.01). Additionally, the mean of sample D was above the mean of UM1's sample A and as intense as UM2's sample B.

3.3. Taste cluster interactions

The following sections overview the results of logistic regression in detail for each taste quality as a dependent variable. The largest cluster was set as a reference category in every case. The odd ratios for models are shown in Table 4. The low number of subjects in UM1 and UM3 caused small subpopulations in some cases. This diminishes the

statistical power (confidence intervals are very wide) and limits the applicability of comparisons.

3.3.1. Sour

Logistic regression revealed that 63.8% of the sour cluster membership was classified correctly when all the other tastes were predictors. The more sensitive bitter tasters, rather than the semi-sensitive tasters, were significantly less likely to be a less sensitive sour taster than a semi-sensitive taster. Additionally, it was significantly more likely for the subject to perceive sourness intensely if the subject tasted saltiness or sweetness intensely. Those who perceived umami samples very weakly (UM1), also perceived sour samples 3.55 times more likely as milder (SO1) than the average cluster (SO2).

3.3.2. Bitter

Fifty-three point eight percent of the bitter cluster membership was predicted correctly by the other taste clusters. The significant predictors were sour and umami. The less sensitive sour tasters were 5.26 times more likely than the semi-sensitive tasters to be a semi-sensitive bitter taster (BI2) than a more sensitive bitter taster (BI3). When comparing UM1 and UM2, the subjects who perceived the umami samples as very mild, were 2.98 times more likely to perceive also the bitter samples as very mild rather than as on an average level.

3.3.3. Sweet

The other taste clusters predicted the sweet cluster membership correctly in 59.3% of the cases. Salty, umami and sour were the statistically significant predictors. In the case of salty taste, the members of both minority clusters (SA2 and SA3) were more likely to belong to the SW3 than to SW1. The more sensitive sour and umami tasters were more likely than the semi-sensitive tasters to be a more sensitive sweet taster rather than a less sensitive taster. Moreover, if a subject perceived the umami samples as very mild, he/she was 4.76 times more likely to be a less sensitive sweet taster rather than a semi-sensitive taster.

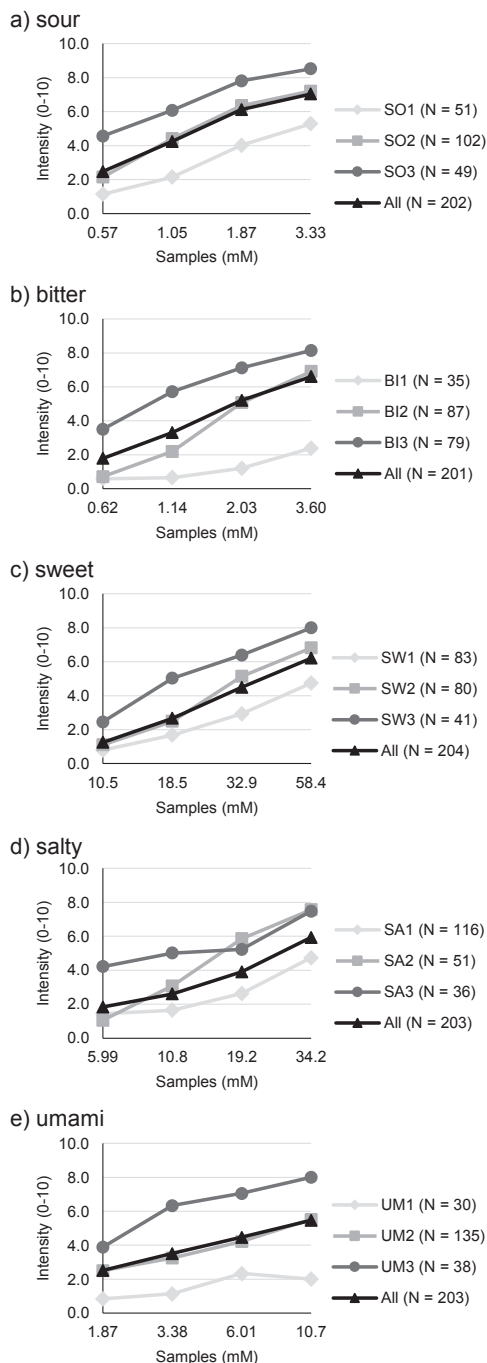


Fig. 1. The mean intensities in different clusters and in the whole sample for all the concentration levels, a) sour, b) bitter, c) sweet, d) salty, e) umami. Review Table 3 for the exact values for means (and SD).

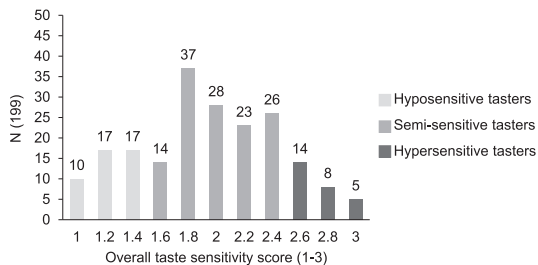


Fig. 2. Frequencies of overall taste sensitivity scores (n = 199).

3.3.4. Salty

Of the salty cluster distribution, 63.3% was predicted correctly by the other taste clusters. The significant predictors were the most intensively perceiving clusters of sour and sweet (SO3 and SW3). The more sensitive sour tasters, rather than the semi-sensitive tasters, were 2.79 times more likely to be a more sensitive salty taster rather than a less sensitive taster. When compared to the less sensitive sweet tasters, the more sensitive tasters were 7.80 times more likely to belong to SA3 and 5.80 times more likely to belong to SA2 than SA1.

3.3.5. Umami

The umami cluster membership was predicted as 68.8% correct by the other taste clusters. SO1, SW2, and SW3 were the significant predictors. The less sensitive sour tasters were 3.26 more likely than the semi-sensitive tasters to be a less sensitive umami taster rather than a semi-sensitive taster. Likewise, being a less sensitive sweet taster predicted a five times greater probability of tasting the umami samples as very mild. In contrast, SW2 membership predicted a 3.27 times greater probability of belonging to UM3 than UM2. Additionally, SW3 members were 4.19 times more likely than SW1 members to belong to UM3 rather than UM2.

3.4. Overall taste sensitivity score

Fig. 2 illustrates the distribution of the overall taste sensitivity score. A minority (27 of 199 subjects, 13.6%) scored above 2.4, therefore being hypersensitive tasters. Additionally, only 5 subjects belonged to the most sensitive cluster in every taste quality. The hyposensitive tasters who scored 1.0–1.4 accounted for 22.1% of the participants. There were 10 very insensitive participants, who belonged to the least sensitive cluster in every taste quality. Thus a clear majority (64.3%) were semi-sensitive tasters scoring 1.6–2.4.

4. Discussion

4.1. Hierarchical clustering

To our knowledge, this was the first time a hierarchical clustering was applied to an analysis of individual taste sensitivity. To group people, the more common application of hierarchical clustering has been in market research for consumer segmentation (e.g. den Uijl, Jager, de Graaf, Waddell, & Kremer, 2014; Piqueras-Fiszman & Jaeger, 2016). Hierarchical clustering of intensity ratings revealed distinctive groups showing dissimilarities in people's taste perception. The intensity curves appeared as expected with rising intensity within the concentration level. With the exception of salty taste, the labeling of clusters as more sensitive tasters, semi-sensitive tasters, and less sensitive tasters is reasonable.

In the case of salty taste, none of the clusters can be labeled easily as semi-sensitive tasters. The majority belonged to the least sensitive tasters. Additionally, there were two sensitive clusters. The first (SA2) perceived the stimuli as clearly more intense as the concentration

Table 4
Taste interactions by the multinomial logistic regression model. The statistically significant odd ratios (OR) are bolded.

Explaining factors	Dependent factor, OR (95% confidence intervals)									
	SO1	SO3	BI1	BI3	SW2	SW3	SA2	SA3	UM1	UM3
SO1			0.88 (0.32–2.40)	0.19** (0.06–0.63)	0.47 (0.18–1.24)	0.90 (0.22–3.60)	0.42 (0.13–1.31)	0.45 (0.08–2.38)	3.26* (1.02–10.45)	0.34 (0.07–1.67)
SO3			0.39 (0.07–2.06)	1.24 (0.56–2.74)	2.46 (0.83–7.28)	4.81* (1.42–16.36)	1.44 (0.58–3.56)	2.79* (1.05–7.40)	2.26 (0.33–15.22)	1.12 (0.48–2.63)
BI1	0.87 (0.32–2.36)	0.36 (0.06–1.98)			0.61 (0.21–1.80)	0.24 (0.02–2.34)	1.09 (0.32–3.77)	1.06 (0.17–6.63)	2.65 (0.90–7.84)	0.57 (0.11–2.93)
BI3	0.19** (0.06–0.63)	1.22 (0.55–2.71)			1.16 (0.50–2.70)	1.76 (0.62–4.95)	0.94 (0.42–2.11)	2.29 (0.86–6.14)	-	0.90 (0.39–2.08)
SW2	0.44 (0.17–1.17)	2.57 (0.85–7.78)	0.61 (0.21–1.79)	1.10 (0.47–2.55)			2.32 (0.93–5.77)	3.36 (0.95–11.87)	0.20* (0.05–0.80)	3.27* (1.01–10.64)
SW3	1.00 (0.25–4.02)	5.05* (1.46–17.42)	0.22 (0.02–2.05)	1.72 (0.62–4.81)			5.80** (1.88–17.89)	7.80** (1.83–33.31)	-	4.19* (1.13–15.47)
SA2	0.40 (0.13–1.26)	1.43 (0.58–3.51)	1.14 (0.33–3.94)	1.00 (0.45–2.22)	2.25 (0.91–5.56)	5.56** (1.82–16.94)			0.25 (0.03–2.26)	1.48 (0.60–3.66)
SA3	0.44 (0.08–2.36)	2.79* (1.05–7.37)	1.08 (0.18–6.53)	2.48 (0.93–6.62)	3.51 (0.99–12.36)	7.87** (1.85–33.58)			0.87 (0.80–9.38)	1.56 (0.55–4.38)
UM1	3.55* (1.18–10.70)	2.91 (0.43–19.82)	2.98* (1.05–8.46)	-	0.21* (0.05–0.84)	-	0.19 (0.02–1.63)	0.61 (0.05–6.89)		
UM3	0.39 (0.81–1.91)	1.13 (0.48–2.64)	0.61 (0.12–3.16)	0.96 (0.42–2.18)	3.12 (0.95–10.23)	4.03* (1.08–14.99)	1.47 (0.59–3.66)	1.47 (0.52–4.20)		
correctly predicted, %	63.8		53.8		59.3		63.3		68.8	

The reference categories were SO2 (sour), BI2 (bitter), SW1 (sweet), SA1 (salty), UM2 (umami). “-” indicates too wide confidence intervals for appropriate comparisons. * p < .05 ** p < .01

increased. The second (SA3) perceived the sample intensities as being quite near to each other. This phenomenon is hard to explain. It has been reported, that some individuals can taste NaCl as sweet in low concentrations (Galindo-Cuspinera et al., 2009; Wise & Breslin, 2013). Thus the individuals in SA3 could perceive the most dilute samples as clearly sweet making them rate the stimuli more intense than the others.

Sour and umami had similar cluster formations. The most populated clusters were the average clusters (SO2 and UM2) whereas the more and the less sensitive clusters had an equal number of subjects. In the case of bitter and umami, the less sensitive group had difficulties in perceiving anything in the samples and therefore they could be labeled as hyposensitive clusters. The insensitivity to umami can be explained by the fact that many of the participants were unfamiliar with the modality beforehand. On the other hand, previous studies have shown hyposensitivity to umami (Chen et al., 2009; Lugaz, Pillias, & Faurion, 2002; Singh, Schuster, & Seo, 2010). Our results support the findings regarding caffeine hyposensitivity by Dsamou et al. (2012). However in contrast, the sweet clusters were quite near each other, although the difference between cluster intensities was also statistically significant in every sweet sample. This is in line with a previous study showing less variance in sweetness than in other taste qualities (Rawal, Hayes, Wallace, Bartoshuk, & Duffy, 2013).

The cluster intensities were significantly different in every sample in the case of sour and umami. Similarly, the A–C samples in bitter and sweet were perceived significantly different in every cluster. However, in salty taste, only sample C differed significantly between all the clusters. Therefore, in theory, only one concentration level would have been enough to make the distinction between clusters. However, this study supports the earlier findings (Keast & Roper, 2007), that it is critical to choose appropriate concentration level in intensity measures.

4.2. Taste cluster interactions

We found that the taste clusters were linked together. We are not familiar with any other studies that have taken all taste qualities into account and analyzed the connections between different sensitivity groups. Overall, the cluster membership of a taste quality was predicted substantially well by other taste clusters.

Sour was the only modality that all other taste modalities explained significantly. Increased sensitivity to bitter taste was linked to the average level perception of sourness. Similarly, being sensitive to sweetness predicted more sensitivity to sourness and vice versa. Possibly citric acid can be perceived as bitter or sweet in low concentrations (Kim, Breslin, Reed, & Drayna, 2004; Wise & Breslin, 2013), which can explain the connections found in our study. According to Kim et al. (2004) and Wise and Breslin (2013), NaCl can also be perceived as sweet in low concentrations, which can explain the associations between salty and sweet clusters. Interestingly, insensitivity to umami predicted insensitivity to bitterness but bitter insensitivity was not a significant predictor of umami insensitivity. Bitter and umami perceptions are linked to heritage, although to different receptor coding genes (Newcomb, Xia, & Reed, 2012). On the other hand, sweet and umami receptors are genetically related (Kim et al., 2004) which is supported by associations between umami and sweet clusters in our study. Additionally, high sensitivity to saltiness and sourness were associated, as well as low sensitivity to umami and sourness. These associations are hard to explain in any other way than with general taste sensitivity.

Webb et al. (2015) found significant correlations between all suprathreshold taste modalities. They used the same prototypic compounds as in this study, but the concentrations were much stronger for sucrose and NaCl in their study. Our findings are in line with Lim et al. (2008) who found correlations between the sweetness of sucrose, the

saltiness of NaCl, and the sourness of citric acid with higher concentrations than here. Our study showed no link between the bitterness of caffeine and sweetness of sucrose. Likewise, umami and saltiness were not associated. The discrepancy between the studies can be explained by the use of different methods such as concentration levels or scales (gLMS vs. line scale).

4.3. Overall taste sensitivity score

These results support the idea of generalized taste sensitivity. Only a minority belonged to the extreme groups in overall taste sensitivity score but together they made 35.7% of all the participants. On the other hand, the semi-sensitive tasters were a very heterogeneous group. In theory, hypersensitive people, as well as hyposensitive, share similar taste worlds but among the semi-sensitive tasters, the worlds can be various.

There are several internal and external factors, such as age, gender, weight status and genotype, that can impact our taste function (e.g. Hansen, Reed, Wright, Martin, & Breslin, 2006; Hyde & Feller, 1981; Mojet, Heidema, & Christ-Hazelhof, 2003; Mojet et al., 2005; Newcomb et al., 2012; Simchen, Koebnick, Hoyer, Issanchou, & Zunft, 2006; Simpson et al., 2012) and can explain these results on individual taste sensitivity. Here our focus was on investigating the differences in taste perception between participants and not the reasons that would explain the dissimilarities between different groups.

4.4. Strengths and limitations

The individual perception was measured without guiding a subject with an anchored reference stimulus or a cross-modal reference, such as weights. With untrained panelists, scale usage is always an issue, regardless of the reference used. Instead of using a reference the participants were given thorough written and verbal instructions on how to use the scale. However, a limitation is that we were not able to tell if the differences in interindividual ratings were true or the result of scale-use bias. Nonetheless, if it was solely about scale-use bias, the associations between clusters would have been more strongly shown in the logistic regression analysis. Using hierarchical clustering made it possible to take all the samples into account simultaneously, and thus, to smooth out the individual variation in sample rating. Additionally, retaining three-cluster-models reduced the effect of the limitation that every sample was rated only once by a subject. Altogether, resources were saved by using hierarchical clustering.

One weakness of this study is that we used only one prototypic taster for every modality. The results could be different with other stimuli. On the other hand, we took all the taste qualities into account and used whole-mouth stimulation. The compounds used are the same as is suggested in ISO8586 and ASTM standards.

Finally, the population sample was unbalanced for gender, the age distribution was quite wide, and smokers were included in the analyses. All these factors may affect taste sensitivity; they possibly affected also the results reported here. Thus, general conclusions should be drawn cautiously from these results. However, our aim was to achieve a large sample size rather than a representative population sample. Thus, we wanted to include all volunteers in this study, and the next step is to explore the factors explaining the differences in perception between the sensitivity groups.

5. Conclusions

We presented a new insight into the individual perception by revealing the differences in subjective intensity measures between data-driven sensitivity groups. These results encourage the careful selection of the concentration levels used in intensity measures. Additionally, the capability of caffeine and MSG as reference compounds should be reassessed. Furthermore, the study shows that different taste modalities

are related, but sensitivity to one taste does not indicate sensitivity to another taste for certain. When investigating the associations between taste function and other factors, such as food consumption, it should be kept in mind that it is possible for several subpopulations of tasters to exist.

Acknowledgements

Academy of Finland is acknowledged for funding (MS252005, 256176, 263747, 309408). We would like to thank Mrs. Pauliina Ojansivu (Functional Food Forum, University of Turku, Finland) for screening the sensory evaluation methods and Mr. Leo Lepistö (Functional Food Forum, University of Turku, Finland) for helping in collecting the data. In addition, we are very grateful to all the participants.


References

- Bachmanov, A. A., & Beauchamp, G. K. (2007). Taste receptor genes. *Annual Review of Nutrition*, 27, 389–414. <http://dx.doi.org/10.1146/annurev.nutr.26.061505.111329>.
- Bajec, M. R., & Pickering, G. J. (2008). Thermal taste, PROP responsiveness, and perception of oral sensations. *Physiology and Behavior*, 95(4), 581–590. <http://dx.doi.org/10.1016/j.physbeh.2008.08.009>.
- Chen, Q.-Y., Alarcon, S., Tharp, A., Ahmed, O. M., Estrella, N. L., Greene, T. A., ... Breslin, P. A. (2009). Perceptual variation in umami taste and polymorphisms in TAS1R taste receptor genes. *American Journal of Clinical Nutrition*, 90, 770S–779S. <http://dx.doi.org/10.3945/ajcn.2009.27462N>.
- Cox, D. N., Hendrie, G. A., & Carty, D. (2015). Sensitivity, hedonics and preferences for basic tastes and fat amongst adults and children of differing weight status: A comprehensive review. *Food Quality and Preference*, 1–9. <http://dx.doi.org/10.1016/j.foodqual.2015.01.006>.
- den Uijl, L. C., Jager, G., de Graaf, C., Waddell, J., & Kremer, S. (2014). It is not just a meal, it is an emotional experience – A segmentation of older persons based on the emotions that they associate with mealtimes. *Appetite*, 83, 287–296. <http://dx.doi.org/10.1016/j.appet.2014.09.002>.
- Dsamou, M., Palicki, O., Septier, C., Chabanet, C., Lucchi, G., Ducoroy, P., ... Morzel, M. (2012). Salivary protein profiles and sensitivity to the bitter taste of caffeine. *Chemical Senses*, 37(1), 87–95. <http://dx.doi.org/10.1093/chemse/bjr070>.
- Feeney, E. L., & Hayes, J. E. (2014). Regional differences in suprathreshold intensity for bitter and umami stimuli. *Chemosensory Perception*, 7(3–4), 147–157. <http://dx.doi.org/10.1007/s12078-014-9166-3>.
- Fischer, M. E., Cruickshanks, K. J., Pankow, J. S., Pankratz, N., Schubert, C. R., Huang, G.-H., ... Pinto, A. (2014). The associations between 6-N-propylthiouracil (PROP) intensity and taste intensities differ by TAS2R38 haplotype. *Journal of Nutrigenetics and Nutrigenomics*, 7(3), 143–152. <http://dx.doi.org/10.1002/aur.1474>. Replication.
- Fischer, M. E., Cruickshanks, K. J., Schubert, C. R., Pinto, A., Klein, R., Pankratz, N., ... Huang, G.-H. (2013). Factors related to fungiform papillae density: The beaver dam offspring study. *Chemical Senses*, 38, 669–677. <http://dx.doi.org/10.1093/chemse/bjt033>.
- Galindo-Cuspinera, V., Waeber, T., Antile, N., Hartmann, C., Stead, N., & Martin, N. (2009). Reliability of threshold and suprathreshold methods for taste phenotyping: Characterization with PROP and sodium chloride. *Chemosensory Perception*, 2(4), 214–228. <http://dx.doi.org/10.1007/s12078-009-9059-z>.
- Hansen, J. L., Reed, D. R., Wright, M. J., Martin, N. G., & Breslin, P. A. S. (2006). Heritability and genetic covariation of sensitivity to PROP, SOA, quinine HCl, and caffeine. *Chemical Senses*, 31(5), 403–413. <http://dx.doi.org/10.1093/chemse/bjj044>.
- Hayes, J. E., Bartoshuk, L. M., Kidd, J. R., & Duffy, V. B. (2008). Supertasting and PROP bitterness depends on more than the TAS2R38 gene. *Chemical Senses*, 33(3), 255–265. <http://dx.doi.org/10.1093/chemse/bjm084>.
- Hayes, J. E., Feeney, E. L., & Allen, A. L. (2013). Do polymorphisms in chemosensory genes matter for human ingestive behavior? *Food Quality and Preference*, 30(2), 202–216. <http://dx.doi.org/10.1016/j.foodqual.2013.05.013>.
- Hayes, J. E., & Keast, R. S. J. (2011). Two decades of supertasting: Where do we stand? *Physiology and Behavior*, 104(5), 1072–1074. <http://dx.doi.org/10.1016/j.physbeh.2011.08.003>.
- Hayes, J. E., Sullivan, B. S., & Duffy, V. B. (2010). Explaining variability in sodium intake through oral sensory phenotype, salt sensation and liking. *Physiology and Behavior*, 100(4), 369–380. <http://dx.doi.org/10.1016/j.physbeh.2010.03.017>.
- Hwang, L.-D., Breslin, P. A. S., Reed, D. R., Zhu, G., Martin, N. G., & Wright, M. J. (2016). Is the association between sweet and bitter perception due to genetic variation? *Chemical Senses*, 41, 737–744. <http://dx.doi.org/10.1093/chemse/bjw083>.
- Hyde, R. J., & Feller, R. P. (1981). Age and sex effects on taste of sucrose, NaCl, citric acid and caffeine. *Neurobiology of Aging*, 2(4), 315–318. [http://dx.doi.org/10.1016/0197-4580\(81\)90041-5](http://dx.doi.org/10.1016/0197-4580(81)90041-5).
- Keast, R. S. J., & Roper, J. (2007). A complex relationship among chemical concentration, detection threshold, and suprathreshold intensity of bitter compounds. *Chemical Senses*, 32(3), 245–253. <http://dx.doi.org/10.1093/chemse/bjl052>.
- Kim, U.-K., Breslin, P. A. S., Reed, D., & Drayna, D. (2004). Genetics of human taste perception. *Journal of Dental Research*, 83(6), 448–453. <http://dx.doi.org/10.1177/>

- 154405910408300603.
- Lim, J., Urban, L., & Green, B. G. (2008). Measures of individual differences in taste and creaminess perception. *Chemical Senses*, *33*, 493–501. <http://dx.doi.org/10.1093/chemse/bjn016>.
- Low, J. Y., Lacy, K. E., McBride, R., & Keast, R. S. J. (2016). The association between sweet taste function, anthropometry, and dietary intake in adults. *Nutrients*, *8*(5), 241–255. <http://dx.doi.org/10.3390/nu8040241>.
- Lugaz, O., Pillias, A.-M., & Faurion, A. (2002). A new specific ageusia: Some humans cannot taste l-glutamate. *Chemical Senses*, *27*, 105–115.
- Mojet, J., Christ-Hazelhof, E., & Heidema, J. (2005). Taste perception with age: Pleasantness and its relationships with threshold sensitivity and supra-threshold intensity of five taste qualities. *Food Quality and Preference*, *16*(5), 413–423. <http://dx.doi.org/10.1016/j.foodqual.2004.08.001>.
- Mojet, J., Heidema, J., & Christ-Hazelhof, E. (2003). Taste perception with age: Generic or specific losses in supra-threshold intensities of five taste qualities? *Chemical Senses*, *28*, 397–413. <http://dx.doi.org/10.1093/chemse/28.5.397>.
- Monteleone, E., Spinelli, S., Dinnella, C., Endrizzi, I., Laureati, M., Pagliarini, E., ... Tesini, F. (2017). Exploring influences on food choice in a large population sample: The Italian Taste project. *Food Quality and Preference*, *59*, 123–140. <http://dx.doi.org/10.1016/j.foodqual.2017.02.013>.
- Newcomb, R. D., Xia, M., & Reed, D. R. (2012). Heritable differences in chemosensory ability among humans. *Flavour*, *1*(1), 9. <http://dx.doi.org/10.1186/2044-7248-1-9>.
- Piqueras-Fiszman, B., & Jaeger, S. R. (2016). Consumer segmentation as a means to investigate emotional associations to meals. *Appetite*, *105*, 249–258. <http://dx.doi.org/10.1016/j.appet.2016.05.034>.
- Rawal, S., Hayes, J. E., Wallace, M. R., Bartoshuk, L. M., & Duffy, V. B. (2013). Do polymorphisms in the TAS1R1 gene contribute to broader differences in human taste intensity? *Chemical Senses*, *38*(8), 719–728. <http://dx.doi.org/10.1093/chemse/bjt040>.
- Sandell, M., Hoppu, U., Lundén, S., Salminen, M., Puolimatka, T., Laaksonen, O., ... Hopia, A. (2015). Consumption of lingonberries by TAS2R38 genotype and sensory quality of texture-designed lingonberry samples. *Food Quality and Preference*, *45*, 166–170. <http://dx.doi.org/10.1016/j.foodqual.2015.06.015>.
- Sandell, M., Hoppu, U., Mikkilä, V., Mononen, N., Kähönen, M., Männistö, S., ... Raitakari, O. T. (2014). Genetic variation in the hTAS2R38 taste receptor and food consumption among Finnish adults. *Genes & Nutrition*, *9*(6), 433. <http://dx.doi.org/10.1007/s12263-014-0433-3>.
- Simchen, U., Koebnick, C., Hoyer, S., Issanchou, S., & Zunft, H.-J. F. (2006). Odour and taste sensitivity is associated with body weight and extent of misreporting of body weight. *European Journal of Clinical Nutrition*, *60*(6), 698–705. <http://dx.doi.org/10.1038/sj.ejcn.1602371>.
- Simpson, E. E. A., Rae, G., Parr, H., O'Connor, J. M., Bonham, M., Polito, A., ... Stewart-Knox, B. (2012). Predictors of taste acuity in healthy older Europeans. *Appetite*, *58*(1), 188–195. <http://dx.doi.org/10.1016/j.appet.2011.09.007>.
- Singh, P. B., Schuster, B., & Seo, H.-S. (2010). Variation in umami taste perception in the German and Norwegian population. *European Journal of Clinical Nutrition*, *64*(10), 1248–1250. <http://dx.doi.org/10.1038/ejcn.2010.133>.
- Webb, J., Bolhuis, D. P., Cicerale, S., Hayes, J. E., & Keast, R. (2015). The relationships between common measurements of taste function. *Chemosensory Perception*, *8*(1), 11–18. <http://dx.doi.org/10.1007/s12078-015-9183-x>.
- Williams, J. A., Bartoshuk, L. M., Fillingim, R. B., & Dotson, C. D. (2016). Exploring ethnic differences in taste perception. *Chemical Senses*, *41*, 449–456. <http://dx.doi.org/10.1093/chemse/bjw021>.
- Wise, P. M., & Breslin, P. A. S. (2013). Individual differences in sour and salt sensitivity: Detection and quality recognition thresholds for citric acid and sodium chloride. *Chemical Senses*, *38*(4), 333–342. <http://dx.doi.org/10.1093/chemse/bjt003>.

Puputti, S., Aisala, H., Hoppu, U., & Sandell, M. (2019)
Factors explaining individual differences in taste sensitivity and taste
modality recognition among Finnish adults.
Journal of Sensory Studies

Factors explaining individual differences in taste sensitivity and taste modality recognition among Finnish adults

Sari Puputti¹  | Heikki Aisala^{1,2} | Ulla Hoppu¹ | Mari Sandell^{1,3}

¹Functional Foods Forum, University of Turku, Turku, Finland

²Food Chemistry and Food Development, Department of Biochemistry, University of Turku, Turku, Finland

³Monell Chemical Senses Center, Philadelphia, Pennsylvania

Correspondence

Sari Puputti, Functional Foods Forum, University of Turku, FI-20014 University of Turku, Turku, Finland.
Email: sari.puputti@utu.fi

Funding information

Biotieteiden ja Ympäristön Tutkimuksen Toimikunta, Grant/Award Number: MS309408

Abstract

The objective of this study was to investigate the factors affecting interindividual variation in the sense of taste among Finnish adults. Two components of taste function were examined with five established taste modalities: taste sensitivity and capability to identify taste modalities. The potential explanatory factors for taste function included gender, age, BMI, and smoking. In total, 205 volunteers participated in the study at the sensory evaluation laboratory of Functional Foods Forum. Older age (>50 years) and male gender predicted a less sensitive sense of taste in general. For umami sensitivity, high BMI along with older age predicted lower sensitivity. Additionally, taste recognition and sensitivity were related in bitter and umami tastes. Older age was also associated with a poorer capability in taste recognition. Sour–bitter, umami–salty, and salty–umami were the most frequent taste confusions.

Practical applications

These results showed individual differences in taste perception among adult. This study can help to understand diversity in personal eating practices and food choices, which can be utilized in personal nutritional guidance and well-being applications. We suggest that umami should be included in studies concerning taste function. There is high variation in umami perception and as umami may increase food palatability, it can be an important element in improving diet especially among elderly people. In sensory research, panelists' interindividual variation in taste perception can be wide and should be acknowledged by careful design of studies.

1 | INTRODUCTION

Eating is an essential part of an individual's well-being and daily-life practices. The more palatable a food is, the more likely it will be eaten. Thus, food quality perceived with our senses is an essential factor contributing to our nutrition and health. Therefore, it is important to investigate what type of sensory worlds individuals live in.

Humans perceive at least five taste modalities according to current knowledge: sweet, salty, sour, bitter, and umami. In the oral cavity, taste stimuli are detected by taste receptor cells organized in taste

buds of gustatory papillae. When the receptor cells interact with taste molecules, signals are transmitted to the brain via cranial nerves (Bachmanov & Beauchamp, 2007). Interindividual variations in taste perception may be due to physiological differences in the gustatory system, cognitive processing of taste signals in the brain, genetics, or environmental influence. The most variation seemingly occurs in bitter and umami perception (Knaapila et al., 2012; Lugaz, Pillias, & Faurion, 2002; Puputti, Aisala, Hoppu, & Sandell, 2018). Additionally, among the general population, accuracy in recognizing taste qualities as sweet, salty, sour, bitter, and umami may vary (Doty, Chen, & Overend, 2017; Hettinger, Gent, Marks, & Frank, 1999).

This is an open access article under the terms of the Creative Commons Attribution License, which permits use, distribution and reproduction in any medium, provided the original work is properly cited.

© 2019 The Authors. *Journal of Sensory Studies* published by Wiley Periodicals, Inc.

The intrinsic factors that possibly affect the sense of taste, include gender, age, genetics, and ethnicity (Dias et al., 2013; Doets & Kremer, 2015; Fischer et al., 2013; Martin & Sollars, 2017; Methven et al., 2012; Williams, Bartoshuk, Fillingim, & Dotson, 2016). The extrinsic factors possibly affecting taste function comprise health and health-behavior-related factors, such as smoking, weight, diseases, and medication (Doets & Kremer, 2015; Doty, Shah, & Bromley, 2008; Fischer et al., 2013; Hardikar, Hoechenberger, Villringer, & Ohla, 2017; Pepino, Finkbeiner, Beauchamp, & Mennella, 2010). In contrast, there are also studies showing no associations between these factors and taste function (Fischer et al., 2013; Konstantinidis, Chatziavramidis, Printza, Metaxas, & Constantinidis, 2010; Methven et al., 2012; Mojet, Heidema, & Christ-Hazelhof, 2003; Pepino et al., 2010). Thus, more studies that encompass all taste modalities are needed to better understand the factors affecting interindividual variations in taste perception. The additional knowledge gained from such studies could increase the success of efforts to provide personal nutritional guidance and prevent food-intake-related diseases, such as obesity or cardiovascular diseases. Gaining deeper knowledge of the variation in our sensory experiences could help us with interpreting individual experiences.

This study is part of a more extensive research project concerning individual differences in sensory perception and eating behavior. Previously, we reported the extent of interindividual variations in taste sensitivity measured using the intensity judgments of a series of taste solutions (Puputti et al., 2018). Hierarchical clustering of the intensity judgments revealed hypo-, semi-, and hypersensitive tasters in the study population. Hence, the objective here was to further investigate with the same study participants if the variation in taste sensitivity can be explained by personal characteristics and by the capability to identify taste modalities. Additionally, more insight into an individual's capability to recognize taste modalities and the subject characteristics affecting taste recognition was obtained. Gender and age were the included intrinsic factors, whereas BMI and smoking were chosen as the extrinsic factors describing health behavior.

2 | MATERIALS AND METHODS

2.1 | Participants

The participants were recruited by announcements at the University of Turku and public events. In total, 206 Finnish volunteers (19–79 years

old) participated in the study. The exclusion criteria included pregnancy and being in a lactating state. Additionally, one person was excluded afterward because of self-reported ageusia after a head trauma. Moreover, all communication was in Finnish, leading to the exclusion of some potential participants. Otherwise, all volunteers were selected for inclusion in the study without prerequisites for a balanced sample regarding any variable, such as an even distribution of gender. After being given a full account of the research aims, written informed consent was obtained from the subjects. They were rewarded with food products after every visit. The study was approved by the Southwest Finland Hospital District's Ethics Committee (145/1801/2014), and it was performed in accordance with the ethical standards as laid down in the 1964 Declaration of Helsinki and its later amendments.

2.2 | Sensory evaluation procedure

The taste modalities included sour, bitter, sweet, salty, and umami. Each taste quality was represented by one prototypic tastant, as described in Table 1. Five concentration levels (A = the strongest, E = the mildest; concentration increased by factor 1.78) of each tastant were prepared by dilution in active-carbon filtered water following good laboratory practices. The sample solutions were stored under refrigeration less than 4 days and monosodium salt of L-glutamic acid (MSG) less than 2 days before use. The samples were allowed to settle at room temperature before serving them in two blocks of 14 samples during one session (28 samples in total). The first block included the mildest concentration levels and two blanks (active-carbon filtered water), and the second block included the strongest concentration levels and one blank. The sample presentation order was randomized inside the blocks. This presentation design was planned to prevent the effect of positional bias and excessive fatigue. The samples were evaluated once.

The concentration levels in Table 1 were chosen based on the ASTM International standard (ASTM, 1981) for measuring taste intensity and on previous experience in the sensory evaluation laboratory of Functional Foods Forum. For this reason, the strongest concentration was expected to be readily perceivable for the majority with normal taste function. Additionally, stronger concentration levels could have caused a severe ceiling effect with the line scales that were used for taste intensity judgments.

The study participants were instructed not to wear intensely scented cosmetics and fragrances during the test day. Furthermore,

TABLE 1 Taste samples

Taste	Prototypic tastant	Sample A (mM)	Sample B (mM)	Sample C (mM)	Sample D (mM)	Sample E (mM)
Sour	Citric acid ^a	3.33	1.87	1.05	0.57	0.33
Bitter	Caffeine ^a	3.60	2.03	1.14	0.62	0.36
Sweet	Sucrose ^b	58.4	32.9	18.5	10.5	5.84
Salty	Sodium chloride (NaCl) ^a	34.2	19.2	10.8	5.99	3.42
Umami	L-glutamic acid, monosodium salt (MSG) ^a	10.7	6.01	3.38	1.87	1.07

^aProduced by Sigma-Aldrich, St. Louis, MO.

^bProduced by Alfa Aesar GmbH&Co KG, Karlsruhe, Germany.

eating, drinking other than water, chewing gum, and smoking were forbidden 1 hr before the test. The subjects were given thorough verbal and written instructions on how to evaluate the samples. Additionally, the subjects tasted the strongest dilution of each tastant to become familiar with the taste qualities and the tasting procedure.

Five milliliters of sample was served in a glass beaker marked with a random three-digit code. The subjects were instructed to sip the sample, spin it around their mouth and tongue for 5 s, and spit it out. Between the samples, the subjects were advised to rinse their mouths with active-carbon filtered water. Furthermore, a cream cracker was provided for additional mouth neutralization.

First, the intensity of a sample was rated on a continuous line scale (from 0 to 10). The scale was anchored both numerically and verbally as follows: 0 = "no sensation," 2 = "very mild," 4 = "quite mild," 6 = "quite strong," 8 = "very strong," and 10 = "extremely strong." Moreover, the subjects were instructed to rate the intensity above zero if they perceived something else than pure water. In addition, a five on the scale should have been a clear taste sensation. The subjects were asked to make a mark on the line scale at any point they preferred. These intensity judgments were used to determine taste sensitivity as described in Section 2.3. Second, the subjects were asked about the recognition of the taste quality with a forced choice question. The response options were "sweet," "salty," "sour," "bitter," "umami," "water," and, "something else." The application of these results is described in Section 2.4.

The sensory tests were performed in the sensory evaluation laboratory of Functional Foods Forum (ISO8589), the University of Turku. The responses were collected with Compusense five plus software (Compusense, Inc., Guelph, Canada).

2.3 | Taste sensitivity: Modality-specific and general

The taste sensitivities of the subjects were determined previously in Puputti et al. (2018). The standardized intensity ratings (rescaled to population mean zero and standard deviation one) were analyzed with hierarchical clustering leading to data-driven segmentation. A three-cluster segmentation was retained for each taste modality (Table 2). For each taste modality, the least sensitive cluster was marked with 1 (e.g., SW1 for sweet cluster 1) and called hyposensitive tasters, the middle cluster was marked with 2 (e.g., SW2) and called semisensitive tasters, and the most sensitive cluster was marked with 3 (e.g., SW3) and called hypersensitive tasters.

In addition to the taste modality-specific sensitivity, general taste sensitivity was analyzed with the taste sensitivity score (Puputti et al., 2018). The score was determined as the mean of the taste modality-specific sensitivity cluster memberships (score range 1.0–3.0). Thus, the closer the score was to three, the more sensitive the individual.

2.4 | Taste recognition: Modality-specific and general

Because there were five concentration levels for each taste modality, a subject could correctly recognize (e.g., a sucrose solution as sweet)

TABLE 2 Subject characteristics ($n = 205$)

Variable	<i>n</i>	%	Data missing (<i>n</i>)
Age	205		0
19–34 years	88	42.9	
35–49 years	59	28.8	
50–79 years	58	28.3	
Gender	205		0
Female	164	80.0	
Male	41	20.0	
BMI	198		7
<25.0	111	56.1	
25.0–29.9	51	24.9	
≥30.0	36	17.6	
Smoking	198		7
Currently/formerly	51	25.8	
Nonsmoker	147	74.2	
Sour sensitivity	202		3
SO1	51	25.2	
SO2	102	50.5	
SO3	49	24.3	
Bitter sensitivity	201		4
BI1	35	17.4	
BI2	87	43.3	
BI3	79	39.3	
Sweet sensitivity	204		1
SW1	83	40.7	
SW2	80	39.2	
SW3	41	20.1	
Salty sensitivity	203		2
SA1	116	57.1	
SA2	51	25.1	
SA3	36	17.7	
Umami sensitivity	203		2
UM1	30	14.8	
UM2	135	66.5	
UM3	38	18.7	

Taste sensitivity groups: 1 = the least sensitive, 2 = the semisensitive, 3 = the most sensitive.

zero to five samples within a taste modality. Only the subjects, who had evaluated all five samples per taste modality were included in the analyses of the recognition results.

In addition to the modality-specific recognition, the general capability to recognize taste modalities was analyzed with a taste recognition score. The score was determined by taking the average of the total correct recognitions of all taste qualities. Thus, the theoretical score range was from 0.0 (all samples incorrectly identified) to 5.0 (all samples correctly identified). Only the subjects who had evaluated all samples were analyzed ($n = 199$).

2.5 | Predictors

Webropol online questionnaires (Webropol, Inc., Helsinki, Finland) were used for the data collection of subject characteristics and health behavior. Gender was changed to a dummy variable: 0 = male and 1 = female. Age was divided into three categories: the youngest 19–34 years old ($M [SD] = 27.8 [4.1]$ years), the middle-aged 35–49 years old ($M [SD] = 42.5 [4.3]$ years), and the oldest 50–79 years old ($M [SD] = 61.8 [8.5]$ years). BMI was calculated from self-reported height and weight according to the formula $\text{kg}/(\text{m})^2$. The participants were divided into three categories based on BMI: the lean individuals BMI <25.0 ($M [SD] = 21.8 [2.0]$) including three underweight persons (BMI <18.5), the overweight individuals BMI = 25.0–29.9 ($M [SD] = 27.2 [1.4]$), and the obese individuals BMI ≥ 30.0 ($M [SD] = 34.9 [4.6]$). Smoking habit was determined with the response options “yes, daily,” “yes, occasionally,” “not now but used to,” and “no.” For the analyses, the first three alternatives were combined into current/former smokers because of the low number of subjects in those categories. Six females (3.8% of females) and no males smoked every day, while seven females (4.4% of females) and four males (10.3% of males) smoked occasionally. One-third of males ($n = 13$) and 13.2% ($n = 21$) of females were former smokers. The group sizes are in Table 2.

2.6 | Statistics

Chi-squared test or Fisher's exact test was applied to analyze the associations between the categorical variables. The taste modality-specific sensitivity was predicted with multinomial logistic regression. The model included gender, age, BMI, smoking, and correct recognitions as the explanatory factors. *T*-test and ANOVA with Tukey as a post-hoc test were applied to explore the effects of the predictor variables (gender, age group, BMI group, and smoking status) on the taste sensitivity score and the taste recognition score. At first, two-way ANOVA was applied with all possible interactions and main effects. Because none of the two-way interactions was statistically significant, they were excluded, leaving only the main effects. The criterion for significance was set to be $p < .05$. All statistical analyses were computed with IBM SPSS Statistics 23.0 (IBM Corporation, Armonk, NY).

Some of the participants did not complete every section of the study because of time constraints, technical issues, or self-reported hypersensitivity to caffeine. Missing data were dealt with in each analysis rather than entirely excluding the subjects with missing data. The number of subjects with missing data was small, ranging from zero (gender) to seven (BMI and smoking status). The subject numbers included in the analyses are provided in tables and figures.

3 | RESULTS

3.1 | Subject characteristics

The subject characteristics are described in Table 2. Gender and smoking were associated ($\chi^2 [1] = 8.1, p = .004$), as fewer females

than males had a history of smoking. The clear majority of females, 78.6%, reported being nonsmokers, whereas 56.4% of males had no history of smoking. Additionally, BMI was associated with smoking ($\chi^2 [2] = 13.9, p = .001$). The lean individuals were predominantly nonsmokers (81.1% of the lean individuals) as were the overweight individuals (76.5% of them), whereas half of the obese participants were current or former smokers.

Furthermore, age and BMI were associated ($\chi^2 [4] = 24.2, p < .001$). The majority (75.3%) of the youngest individuals whereas under half of the middle-aged or the oldest individuals were lean. Otherwise, the background variables were not associated.

3.2 | Taste recognitions

The distributions of responses for the taste modality recognition are shown in Figure 1. As expected, the correct recognition rate increased with concentration. The majority recognized the taste of three or four strongest dilutions correctly in each taste quality. For the mildest dilutions of citric acid, sourness was confused with bitterness. Moreover, bitter was also the most frequently chosen incorrect response for the other citric acid samples, though the frequency was under the chance level (the odds of guessing any response option was $1/7 = 0.1429$).

Although the sour taste of citric acid was confused with bitter taste, the caffeine bitterness was seldom confused with sourness. The most frequent incorrect response was water, which was chosen above the chance level for the three most dilute samples. Additionally, if sucrose dilutions were not recognized as sweet, they were perceived as water.

The salty taste of NaCl was confused with umami in the three most dilute samples, and additionally, the most dilute sample was perceived as water by 35.3% of the participants. In addition to salty-umami confusion, umami-salty confusion also appeared. Salty was selected frequently for the three strongest samples of MSG. The majority perceived the most dilute sample as umami or water. Furthermore, bitter was selected by 14.4% of the subjects.

Associations between the correct recognitions and subject characteristics are presented in Table 3. Gender was associated with sour taste recognition ($t [200] = -2.2, p = .032$) with females identifying sour taste better. Age was related to taste recognition in every taste modality ($F_{\text{sour}}[2, 199] = 6.1, p = .003$; $F_{\text{bitter}}[2, 199] = 9.7, p < .001$; $F_{\text{sweet}}[2, 200] = 3.6, p = .030$; $F_{\text{salty}}[2, 200] = 4.0, p = .020$; $F_{\text{umami}}[2, 199] = 8.5, p < .001$). In general, the oldest participants made fewer correct recognitions. However, for the sweet taste, the only difference was that the middle-aged participants correctly recognized more samples than the youngest participants. Umami recognition was also associated with BMI ($F [2, 192] = 3.8, p < .025$); the lean participants correctly recognized more samples than the overweight participants. The other subject characteristics were not significantly associated with modality-specific recognition.

Figure 2 illustrates the taste recognition score distribution. The mean score was 3.09 ($SD 0.70$), and the score range was 1.2–4.8. Thus, the average number of correct recognitions was 15, the minimum six, and the maximum 24 of 25 samples. Gender, BMI group, and

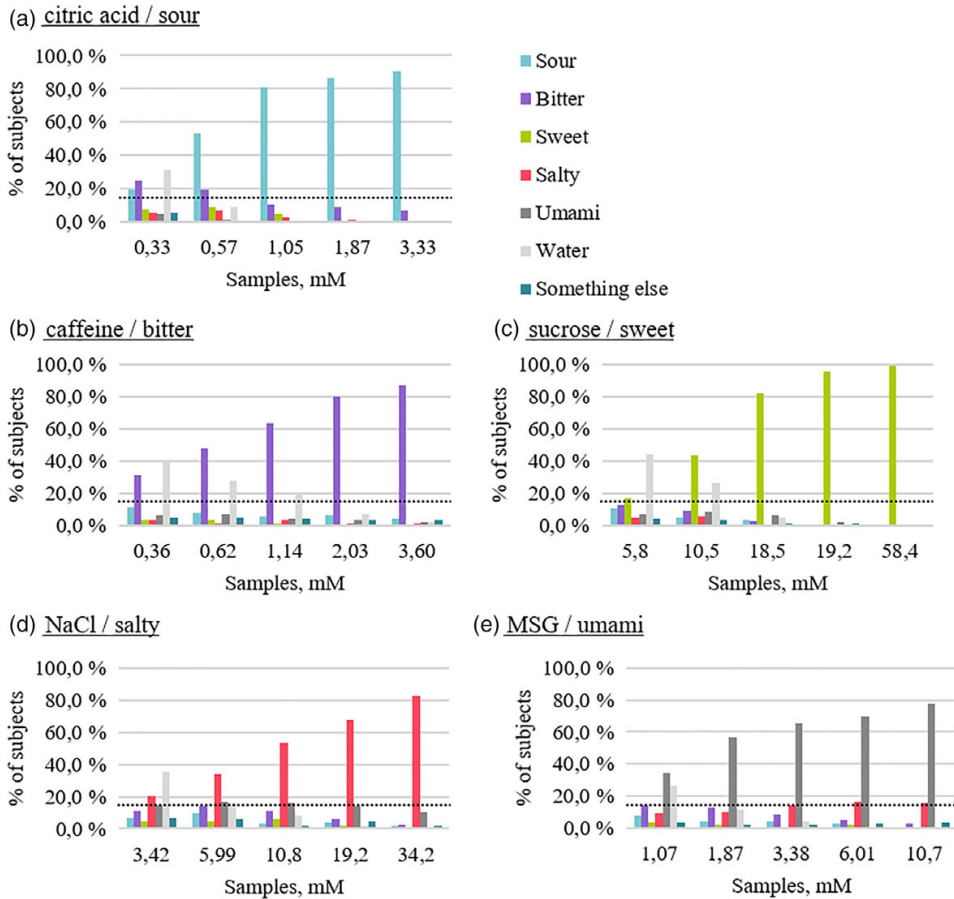


FIGURE 1 Distributions of taste recognitions for all samples: (a) sour citric acid ($n = 203$ – 204), (b) bitter caffeine ($n = 202$), (c) sweet sucrose ($n = 203$ – 204), (d) salty NaCl ($n = 203$ – 204), and (e) umami monosodium salt of L-glutamic acid (MSG; $n = 202$ – 204). The dotted line is the chance level (14.3%) for guessing correctly

smoking status were not related to the taste recognition score (ANOVA). Instead, age was significantly associated with the taste recognition score ($F [2, 185] = 13.2, p < .001$). Tukey's test indicated that both the youngest ($M [SD] = 3.25 [0.66]$) and the middle-aged ($M [SD] = 3.22 [0.65]$) participants had higher scores than the oldest participants ($M [SD] = 2.67 [0.64]$).

3.3 | Predicting taste sensitivity

3.3.1 | Subject characteristics within sensitivity groups

The subject characteristics divided into the sensitivity clusters are presented as Supporting Information in the online version of the article. Gender and age were unequally distributed between the sour clusters ($\chi^2 [2] = 10.1, p = .006$; $\chi^2 [4] = 9.9, p = .042$, respectively). Proportionally more males were in the hyposensitive cluster (40.0%) than in the hypersensitive cluster (7.5%) while females were more

equally divided between these clusters (21.6 and 28.4% of females, respectively). Similar to the sour clusters, the age groups were unequally distributed between the bitter, salty, and umami sensitivity clusters ($\chi^2 [4] = 28.4, p < .001$; $\chi^2 [4] = 9.80, p = .044$; $\chi^2 [4] = 22.4, p < .001$, respectively) as the youngest group was more sensitive than the oldest group. The BMI groups were also unequally distributed for the umami clusters ($\chi^2 [4] = 17.2, p = .002$); proportionally fewer lean people and more obese people belonged to the least sensitive cluster than to the hypersensitive cluster. Otherwise, there were no associations.

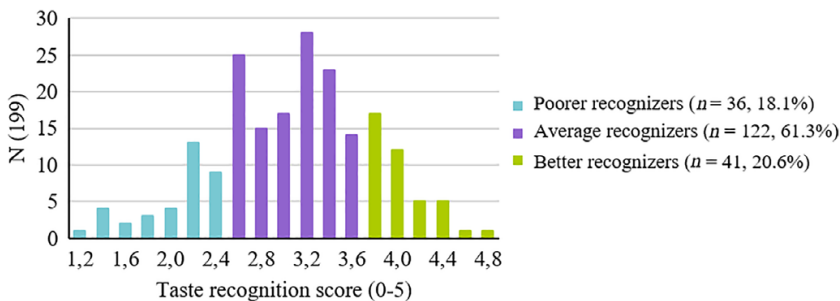
3.3.2 | Predicting taste-specific sensitivity with logistic regression

A logistic regression model adjusted with age, gender, BMI, smoking status, and correct taste recognition rate was applied to predict taste sensitivity. An odds ratio indicates a relative risk ratio between the comparison group and the reference group of the predictor variable

TABLE 3 Associations between correct taste recognition and subject characteristics

	Sour		Bitter		Sweet		Salty		Umami	
	Mean (SD)	n (%)	Mean (SD)	n (%)	Mean (SD)	n (%)	Mean (SD)	n (%)	Mean (SD)	n (%)
Gender										
Female	3.40 (1.02)	162 (80.2)	3.08 (1.37)	162 (80.2)	3.33 (0.90)	162 (79.8)	2.64 (1.19)	162 (79.8)	3.09 (1.39)	161 (79.7)
Male	3.00 (1.18)	40 (19.8)	3.15 (1.39)	40 (19.8)	3.59 (0.89)	41 (20.2)	2.39 (1.07)	41 (20.2)	2.85 (1.37)	41 (20.3)
Data missing		3		3		2		2		3
Age										
19–34 years	3.47a (0.91)	88 (43.6)	3.44a (1.34)	88 (43.6)	3.23b (0.88)	88 (43.3)	2.78a (1.09)	88 (43.3)	3.34a (1.27)	88 (43.3)
35–49 years	3.50a (1.00)	58 (28.7)	3.17a (1.18)	59 (29.2)	3.63a (0.91)	59 (29.1)	2.63ab (1.14)	59 (29.1)	3.19a (1.36)	59 (29.1)
50–79 years	2.91b (1.24)	56 (27.7)	2.45b (1.41)	55 (27.2)	3.38ab (0.89)	56 (27.6)	2.23b (1.25)	56 (27.6)	2.42b (1.42)	56 (27.6)
Data missing		3		3		2		2		2
BMI										
<25.0	3.39 (0.94)	109 (55.9)	3.26 (1.35)	108 (55.4)	3.40 (0.87)	109 (55.6)	2.63 (1.21)	109 (55.6)	3.31a (1.35)	108 (55.4)
25.0–29.9	3.08 (1.21)	51 (26.2)	2.92 (1.52)	51 (26.2)	3.35 (0.77)	51 (26.0)	2.61 (1.15)	51 (26.0)	2.71b (1.38)	51 (26.2)
≥30.0	3.49 (1.12)	35 (17.9)	2.94 (1.26)	36 (18.5)	3.39 (1.15)	36 (18.4)	2.50 (1.13)	36 (18.4)	2.86 ab (1.46)	36 (18.5)
Data missing		10		10		9		9		10
Smoking										
Nonsmoker	3.35 (1.05)	146 (74.9)	3.05 (1.40)	145 (74.4)	3.34 (0.80)	146 (74.5)	2.63 (1.19)	146 (74.5)	3.04 (1.39)	145 (74.4)
Currently/ formerly	3.27 (1.09)	49 (25.1)	3.30 (1.33)	50 (25.6)	3.54 (1.15)	50 (25.5)	2.52 (1.16)	50 (25.5)	3.14 (1.41)	50 (25.6)
Data missing		10		10		9		9		10
All subjects	3.32 (1.06)	203	3.09 (1.37)	202	3.38 (0.90)	203	2.59 (1.17)	203	3.04 (1.39)	202

Notes: Variables with statistically significantly different means between variable groups are bolded. T-test or ANOVA for comparing group means; different letters after the mean value indicate statistically significant differences according to Tukey's test.

**FIGURE 2** Taste recognition score distribution

to fall in the comparison group rather than in the reference group of the dependent variable when adjusted with the other factors in the regression model.

The model fitted well for each taste modality with Goodness-of-Fit test statistics above the significance level. The models significantly explained taste sensitivity except for the sweet and salty tastes ($-2\text{-log-likelihood} = 220.9$, $\chi^2 [14] = 22.5$, $p = .069$, and $-2\text{-log-likelihood} = 220.8$, $\chi^2 [14] = 21.7$, $p = .085$, respectively). However, there was a trend for saltiness such that the oldest subjects were more likely than the youngest or the middle-aged subjects to be hyposensitive and not semisensitive.

Gender was the only significant predictor of sour sensitivity when adjusted for the other factors (Table 4). Females were more likely to be hypersensitive. The main effect of age group was insignificant, but

there was a trend such that the oldest rather than the youngest participants were more likely hyposensitive than semi or hypersensitive.

Age and correct bitter taste recognition had significant main effects on bitter sensitivity (Table 5). When compared to the oldest subjects, the youngest subjects were 3.45 (1/OR in Table 5) times more likely to be hypersensitive than semisensitive. A higher recognition rate predicted more sensitivity. For example, a one unit increase in correct recognition increased the odds of being hypersensitive rather than hyposensitive by a factor of 4.17 (1/OR in Table 5).

Age, BMI, and umami recognition had significant main effects on umami sensitivity (Table 6). The oldest rather than the youngest participants were 8.33 times more likely to be hyposensitive than hypersensitive and 5.56 times more likely to be hyposensitive than semisensitive. Considering BMI, the obese subjects were more likely

TABLE 4 Results of a multinomial logistic regression predicting sour sensitivity with subject characteristics and sour recognition

Sour (n = 195)	SO1, ref. SO3 OR (95 % CL)	SO2, ref. SO3 OR (95 % CL)	SO1, ref. SO2 OR (95 % CL)	Model fit statistics
Male ^a	6.09* (1.52–24.44)	4.28* (1.16–15.84)	1.42 (0.61–3.31)	–2-log-likelihood
Age ^b				241.5, χ^2 (14) = 24.6, $p = .039$
18–34	0.29* (0.09–0.92)	0.83 (0.30–2.26)	0.35* (0.14–0.88)	Nagelkerke pseudo- R^2
35–49	0.37 (0.12–1.18)	0.55 (0.19–1.60)	0.68 (0.28–1.67)	0.135
BMI ^c				Goodness-of-fit
<25.0	0.42 (0.12–1.53)	0.42 (0.14–1.26)	1.01 (0.37–2.77)	ns
25.0–29.9	0.84 (0.21–3.40)	0.61 (0.17–2.15)	1.38 (0.48–3.93)	
Nonsmoker ^d	1.41 (0.49–4.07)	1.24 (0.50–3.03)	1.14 (0.48–2.69)	
Sour taste recognition	0.87 (0.56–1.34)	0.86 (0.59–1.27)	1.01 (0.72–1.41)	

Notes: Odds ratios (95% confidence levels) for all pairs of sensitivity groups and model fit statistics are displayed. Variables having a significant main effect in the model are bolded. SO1 was the least sensitive, SO2 the semisensitive, and SO3 the most sensitive cluster.

^aReference category female.

^bReference category 55–79 years old.

^cReference category ≥ 30.0 .

^dReference category current or former smoker.

* $p < .05$.

TABLE 5 Results of a multinomial logistic regression predicting bitter sensitivity with subject characteristics

Bitter (n = 194)	BI1, ref. BI3 OR (95 % CL)	BI2, ref. BI3 OR (95 % CL)	BI1, ref. BI2 OR (95 % CL)	Model fit statistics
Male ^a	2.83 (0.78–10.31)	1.01 (0.40–2.52)	2.80 (0.87–9.07)	–2-log-likelihood
Age ^b				Goodness-of-fit
18–34	0.30 (0.08–1.13)	0.29** (0.11–0.72)	1.07 (0.32–3.53)	198.8, χ^2 (14) = 85.5, $p < .001$
35–49	0.58 (0.15–2.30)	0.94 (0.37–2.43)	0.62 (0.19–2.06)	Nagelkerke pseudo- R^2 0.409
BMI ^c				Goodness-of-fit
<25.0	0.43 (0.10–1.85)	0.68 (0.26–1.80)	0.64 (0.17–2.36)	ns
25.0–29.9	0.66 (0.14–3.16)	0.62 (0.21–1.87)	1.06 (0.27–4.20)	
Nonsmoker ^d	1.99 (0.50–7.85)	0.91 (0.40–2.05)	2.19 (0.61–7.81)	
Bitter taste recognition	0.24*** (0.15–0.39)	0.69* (0.51–0.93)	0.35*** (0.23–0.54)	

Notes: Odds ratios (95% confidence levels) for all pairs of sensitivity groups and model fit statistics are displayed. Variables having a significant main effect in the model are bolded. BI1 was the least sensitive, BI2 the semisensitive, and BI3 the most sensitive cluster.

^aReference category female.

^bReference category 55–79 years old.

^cReference category ≥ 30.0 .

^dReference category current or former smoker.

* $p < .05$. ** $p < .01$. *** $p < .001$.

to be less sensitive than the lean subjects. Additionally, when compared to the overweight participants, the obese participants were more likely to be hyposensitive than hypersensitive. As the correct recognition rate increased, the probability of being more sensitive increased. For example, as the recognition rate increased by one unit, a participant was 2 times (1/OR in Table 6) more likely to be hypersensitive than hyposensitive.

3.3.3 | Predicting general taste sensitivity

Two-way ANOVA was applied to investigate the effects of gender, age group, BMI group, smoking status, and the taste recognition score

on the taste sensitivity score but none of the two-way interactions was significant. Of the main effects, gender (F [1, 183] = 6.77, $p = .010$) and age (F [2, 183] = 4.93, $p = .008$) were significant. Males had on average level 0.236 units lower sensitivity score than females. Additionally, the youngest had 0.335 units and the middle-aged participants 0.265 units higher score than the oldest participants.

4 | DISCUSSION

The factors affecting taste sensitivity were investigated in this study. Age was the main predictor of taste sensitivity and recognition. The

TABLE 6 Results of a multinomial logistic regression predicting umami sensitivity with subject characteristics

Umami (n = 194)	UM1, ref. UM3 OR (95 % CL)	UM2, ref. UM3 OR (95 % CL)	UM1, ref. UM2 OR (95 % CL)	Model fit statistics
Male ^a	3.79 (0.83–17.30)	2.29 (0.69–7.59)	1.66 (0.58–4.75)	–2-log-likelihood
Age ^b				191.5, χ^2 (14) = 51.6, $p < .001$
18–34	0.12** (0.02–0.58)	0.64 (0.21–2.00)	0.18** (0.05–0.65)	Nagelkerke pseudo-R ²
35–49	0.25 (0.05–1.16)	0.69 (0.20–2.37)	0.36 (0.12–1.06)	0.284
BMI ^c				Goodness-of-fit
<25.0	0.028** (0.003–0.289)	0.10* (0.01–0.80)	0.28* (0.09–0.93)	ns
25.0–29.9	0.059* (0.005–0.665)	0.15 (0.02–1.38)	0.39 (0.12–1.27)	
Nonsmoker ^d	1.96 (0.47–8.15)	1.13 (0.42–3.00)	1.74 (0.57–5.32)	
Umami taste recognition	0.50** (0.32–0.77)	0.72* (0.53–1.00)	0.69* (0.49–0.96)	

Notes: Odds ratios (95% confidence levels) for all pairs of sensitivity groups and model fit statistics are displayed. Variables having a significant main effect in the model are bolded. UM1 was the least sensitive, UM2 the semisensitive, and UM3 the most sensitive cluster.

^aReference category female.

^bReference category 55–79 years old.

^cReference category ≥ 30.0 .

^dReference category current or former smoker.

* $p < .05$. ** $p < .01$.

older subjects were more likely to perceive the taste samples milder and to correctly recognize fewer samples than the younger subjects. This phenomenon was observed for the taste sensitivity score, the taste recognition score, and all taste modalities except for the sweet taste. This result supports earlier findings conducted with water solutions of the same compounds in supra-threshold intensities (Methven et al., 2012; Mojet et al., 2003; Simchen, Koebnick, Hoyer, Issanchou, & Zunft, 2006) and findings considering detection and recognition thresholds (Methven et al., 2012). Interestingly, Methven et al. (2012) noted that results for NaCl, citric acid, and caffeine intensity rating in relation to age have been fairly consistent, whereas results for sucrose have been variable. Mojet et al. (2003) found an age-effect for sucrose as well as for the other taste qualities regardless of the prototypic compound within a taste quality. In contrast to this study by Mojet et al. (2003), we used lower concentrations of taste solutions except for caffeine.

In many studies on the age-effect on taste sensitivity, the elderly group was older than that in this study (Methven et al., 2012; Mojet et al., 2003; Simchen et al., 2006). Although deterioration is a continuous process, the age-effect seems more evident after turning 60 years old (Methven et al., 2012). Hence, the age effect could have been even more obvious in this study if a higher cut-off point for the oldest group was used. However, this shift would have made the group too small for further statistical analysis.

Contrary to many studies, Fischer et al. (2013) found no age effect when age was adjusted with multiple factors that possibly affect taste sensitivity. However, they presented the tastants with paper discs, used stronger intensities of tastants than we did, and did not include the umami taste. Overall, there are various methods used to study the effect of aging on taste sensitivity. It seems evident that sensitivity and capability to recognize taste modalities decrease with age based

on our and earlier findings (Methven et al., 2012). Age-related changes in central processing of the brain might cause weaker sense of taste (Doets & Kremer, 2015). The evidence of physiological changes in taste buds caused by healthy aging is controversial, but the decreased amount and changed composition of saliva that occur in older age may reduce taste function (Doets & Kremer, 2015; Sasano, Satoh-Kuriwada, & Shoji, 2015). According to Sasano et al. (2015), increased sensitivity to umami may promote salivary secretion. As the role of umami sensitivity seems to be a highly relevant factor in adequate and palatable nutrition among the elderly, umami should be an essential part of sensory studies.

In addition to age, gender appeared to be a significant predictor of the taste sensitivity score and sour sensitivity and recognition. Males were less sensitive than females. Mojet et al. (2003) found no overall gender effect using mostly higher concentrations than we did. Simchen et al. (2006) used similar concentrations as we did and found males to be less sensitive to sucrose, NaCl, and citric acid. However, contrary to our study, they used quinine hydrochloride for bitter taste and umami was excluded. Additionally, Fischer et al. (2013) found a similar gender effect with stronger concentrations impregnated on paper discs (umami was not included). Many studies have reported gender differences in taste function, but the underlying mechanisms require further investigation. Currently, research suggests differences in the gustatory system (Martin & Sollars, 2017). The sex hormones probably have a significant influence.

The BMI group was associated with umami sensitivity. A high BMI predicted low sensitivity. This result should be interpreted cautiously because of the low number of obese subjects and hyposensitive umami tasters. This result disagrees with that of Pepino et al. (2010), as in their study, a higher BMI was associated only with higher MSG thresholds (lower sensitivity), not with supra-threshold intensities.

Hardikar et al. (2017) observed that obese individuals perceived sour, sweet, and salty as more intense than lean individuals. They did not include umami in their research. Additionally, they used very high concentrations for the supra-threshold intensity measurement; thus, the results might not be comparable. Additionally, Simchen et al. (2006) found an age \times BMI interaction effect on the taste score, which was determined without umami.

Smoking status was not associated with taste sensitivity or recognition. This is in line with Pepino et al. (2010). However, Fischer et al. (2013) found that smokers perceived sourness and bitterness as more intense than nonsmokers. Vennemann, Hummel, and Berger (2008) found that only heavy smoking, not smoking in general, affected taste recognition using strong concentrations and a different method than we did. They did not note if they introduced the taste qualities to the subjects before the actual test. Konstantinidis et al. (2010) found no effect of smoking on taste function measured with taste strips and as an intensity measure of a drop of taste solutions. However, they reported that smoking might affect fungiform papillae morphology, especially the microcirculation in them.

The effect of smoking on taste function has been poorly studied. The conventional procedure is to exclude smokers from sensory studies; thus, data are scarce. More research is needed to better understand the relationship between taste intensity perception and past smoking, current smoking, and never smoking habits, in addition to the number of cigarettes smoked per day. In this study, only a few subjects were current smokers. For the statistical analyses, they were combined in the same category with former smokers, albeit a former smoking habit may not affect current taste sensitivity (Chéruef, Jarlier, & Sancho-Garnier, 2017). Thus, this might explain our results and general conclusions should not be made. However, we wanted to analyze, if the smoking status explained taste perception in this study population.

Taste sensitivity and recognition were related only for the bitter and umami tastes; the more sensitive subjects had more correct recognitions. This was an expected result because we reported earlier (Puputti et al., 2018) that the subjects least sensitive to bitterness or umami perceived the taste modality as very mild, the intensity curves distinct from the curves for the semi and most sensitive groups. For the other taste modalities, the least sensitive group was not very distinct from the more sensitive groups, which resulted in similar recognition capabilities. Finally, the taste recognition score was not related to the taste sensitivity score that represented the general taste sensitivity.

The most common taste confusions were umami-salty and salty-umami confusions. These confusions may partly be explained by the salty taste of MSG which was used for the umami solutions. Although the subjects tasted umami before the actual taste test, poor capability in umami recognition may be a consequence of unfamiliarity to umami among the subjects, as prior experience affects the ease of taste recognition (Hettinger et al., 1999). Furthermore, the sour taste of citric acid was confused with bitterness to some extent; however, the bitterness of caffeine was not confused with sourness; rather, it was

perceived as water. Similarly, if a sucrose solution was not perceived as sweet, it was reported to be tasteless.

Studies on taste recognition/confusion are difficult to compare because various compounds, methods, and response alternatives have been used. Doty et al. (2017) reported sour-bitter and bitter-sour confusions as being the most common; nevertheless, umami was not part of their research, they used a different method, and the concentrations were much stronger than those used in our study. In their study, saltiness was also mixed with bitterness and sourness, but these confusions were not common in our study. In agreement with our study, the sweetness of sucrose was the most frequently correctly recognized taste modality. Hyde and Feller (1981) also reported sour-bitter confusions (umami was not included in their study). Our results support the finding of Doty et al. (2017) that recognition is associated with age. While in our study age was the only factor related to recognition, they also found a PTC taster status effect, gender effect on salty-bitter confusion, and smoking status effect on bitter-sour confusion—surprisingly, past smokers were better at distinguishing between bitter and sour than never smokers.

In general, a wide variety of sensory evaluation methods have been used to assess taste function (Webb, Bolhuis, Cicerale, Hayes, & Keast, 2015). Additionally, testing procedures, such as choice of taste compounds, concentration levels of taste solutions, judgment scales, and method of taste stimulation (e.g., whole-mouth sip of solution, a drop of a solution on the tongue, spraying a solution, placing a taste strip impregnated with a taste solution on the tongue), differ highly among studies. This partly explains the conflicting results and conclusions.

Even though five taste modalities were included, the number of subjects was high for a sensory study and a whole-mouth multi-concentration taste test was applied in this study, there are some limitations to consider when interpreting the results. First, only one prototypic compound was used. On the other hand, Mojet et al. (2003) found no compound-specific differences within taste modalities between genders or age groups. The selection of the compounds was based on the ISO8586 and ASTM International standards.

Second, this study was part of a more extensive research project, and the participants also completed other tests on their visit. As a result, we decided on a comprehensible scale for intensity ratings that is commonly used in consumer studies and sensory laboratories and that required no time-consuming training of the participants. We decided to measure intensity without any reference stimulus or a cross-modal reference, such as weights or tones. Instead, thorough written and verbal instructions on how to use the scale were given. The possible problem of scale usage was addressed by analyzing the standardized ratings with hierarchical clustering. If the scale-use bias or ceiling effect were serious issues in this case, the logistic regression analysis would have indicated stronger associations between the taste clusters in our previous work (Puputti et al., 2018).

Third, the sample population was unbalanced for gender, BMI, and smoking. However, a representative population sample was not our aim, and all volunteers were welcome to participate. Moreover, although the numbers in the groups of men, obese, and smokers were

smaller than their reference groups, the numbers were larger than those in many earlier studies.

One concern might also be possible fatigue arising from long testing session. The session took approximately 120 min including discussions between the laboratory staff and the participants (making clear the aim of the study and telling the instructions for every test section). In addition to the taste samples mentioned in Section 2.2, the participants concluded other sensory tests related to sight and smell. The procedure was carefully designed to minimize excessive fatigue and to keep up the interest. The participants could proceed at their own pace as long as they followed the instructions, and they had the possibility to quit testing any moment (no one did). The participants were very enthusiastic and motivated because they could learn by experience about their senses.

5 | CONCLUSIONS

This study considered both taste sensitivity and recognition, and included five taste modalities—also umami, that is, neglected many times. Our findings support the previous data that a weakened taste sensitivity and recognition are associated with older age. Additionally, males were less sensitive than females, similar to some previous findings. To further understand the role of smoking in taste function, additional studies are required. We showed that umami should not be neglected in taste research. These results also add to the understanding of the variation in the capability to recognize taste qualities. The sweet taste was the most accurately recognized, whereas sour–bitter, umami–salty, and, salty–umami were the most frequent confusions. In consumer studies, it should not be taken for granted that people know what is meant with sourness, bitterness, or with other taste modalities. Leaders of trained panels must acknowledge that panelists' perception of taste can vary enormously. As gender and age seem to associate with taste perception, their balance in consumer or trained panels should be designed carefully. It is convenient to recruit participants near the research facilities (e.g., campus area). Often this has resulted in a specific panel: young women who are students or highly educated. Undoubtedly, this can cause limitations to a study. In addition to taste function, gender and age are related to eating behavior. Therefore, a better understanding of the connection between these personal characteristics, taste function, and food intake could promote successful guidance in personal nutrition and enhanced prevention of food-intake-related diseases.

ACKNOWLEDGMENTS

This work was supported by the Academy of Finland (MS309408). The authors would like to thank Pauliina Ojansivu (Functional Food Forum, the University of Turku, Finland) for screening the sensory evaluation methods and Leo Lepistö (Functional Food Forum, the University of Turku, Finland) for helping with collecting the data. In addition, we are very grateful to all the study participants.

CONFLICT OF INTEREST

The authors declare that they have no conflict of interest.

ORCID

Sari Puputti  <https://orcid.org/0000-0002-4624-0064>

REFERENCES

- ASTM. (1981). *Guidelines for the selection and training of sensory panel members*. Philadelphia, PA: American Society for Testing and Materials.
- Bachmanov, A. A., & Beauchamp, G. K. (2007). Taste receptor genes. *Annual Review of Nutrition*, 27, 389–414. <https://doi.org/10.1146/annurev.nutr.26.061505.111329>
- Chéruef, F., Jarlier, M., & Sancho-Garnier, H. (2017). Effect of cigarette smoke on gustatory sensitivity, evaluation of the deficit and of the recovery time-course after smoking cessation. *Tobacco Induced Diseases*, 15(15), 1–8. <https://doi.org/10.1186/s12971-017-0120-4>
- Dias, A. G., Rousseau, D., Duizer, L., Cockburn, M., Chiu, W., Nielsen, D., & El-Sohemy, A. (2013). Genetic variation in putative salt taste receptors and salt taste perception in humans. *Chemical Senses*, 38, 137–145. <https://doi.org/10.1093/chemse/bjs090>
- Doets, E. L., & Kremer, S. (2015). The silver sensory experience—A review of senior consumers' food perception, liking and intake. *Food Quality and Preference*, 48, 316–332. <https://doi.org/10.1016/j.foodqual.2015.08.010>
- Doty, R. L., Chen, J. H., & Overend, J. (2017). Taste quality confusions: Influences of age, smoking, PTC taster status, and other subject characteristics. *Perception*, 46, 257–267. <https://doi.org/10.1177/0301006616685577>
- Doty, R. L., Shah, M., & Bromley, S. M. (2008). Drug-induced taste disorders. *Drug Safety*, 31(3), 199–215.
- Fischer, M. E., Cruickshanks, K. J., Schubert, C. R., Pinto, A., Klein, B. E. K., Klein, R., ... Snyder, D. J. (2013). Taste intensity in the beaver dam off-spring study. *Laryngoscope*, 123(6), 1399–1404. <https://doi.org/10.1002/lary.23894>
- Hardikar, S., Hoechenberger, R., Villringer, A., & Ohla, K. (2017). Higher sensitivity to sweet and salty taste in obese compared to lean individuals. *Appetite*, 111, 158–165. <https://doi.org/10.1016/j.appet.2016.12.017>
- Hettinger, T. P., Gent, J. F., Marks, L. E., & Frank, M. E. (1999). A confusion matrix for the study of taste perception. *Perception & Psychophysics*, 61(8), 1510–1521.
- Hyde, R. J., & Feller, R. P. (1981). Age and sex effects on taste of sucrose, NaCl, citric acid and caffeine. *Neurobiology of Aging*, 2(4), 315–318. [https://doi.org/10.1016/0197-4580\(81\)90041-5](https://doi.org/10.1016/0197-4580(81)90041-5)
- Knaapila, A., Hwang, L.-D., Lysenko, A., Duke, F. F., Fesi, B., Khoshnevisan, A., ... Reed, D. R. (2012). Genetic analysis of chemosensory traits in human twins. *Chemical Senses*, 107(9), 935–939. <https://doi.org/10.1093/chemse/bjs070>
- Konstantinidis, I., Chatziavramidis, A., Printza, A., Metaxas, S., & Constantinidis, J. (2010). Effects of smoking on taste: Assessment with contact endoscopy and taste strips. *Laryngoscope*, 120(10), 1958–1963. <https://doi.org/10.1002/lary.21098>
- Lugaz, O., Pillias, A.-M., & Faurion, A. (2002). A new specific Ageusia: Some humans cannot taste L-glutamate. *Chemical Senses*, 27, 105–115. <https://doi.org/10.1093/chemse/27.2.105>. https://oup.silverchair-cdn.com/oup/backfile/Content_public/Journal/chemse/27/2/10.1093_chemse_27.2.105/1/105.pdf?Expires=1490448298&Signature=O7SkfMf61QdZ0KkxTUH6jOyCt1Lpvt5DrbjTL6-sOdaqwulmEapFwcw3c3OrY1w-QsbBIRLAs2tsi96Ta69DzvwoZROwGKx-VnhEEYby-uN5j
- Martin, L. J., & Sollars, S. I. (2017). Contributory role of sex differences in the variations of gustatory function. *Journal of Neuroscience Research*, 95(1–2), 594–603. <https://doi.org/10.1002/jnr.23819>

- Methven, L., Allen, V. J., Withers, C. A., Gosney, M. A., Schiffman, S. S., Essed, N. H., ... Murphy, C. (2012). Ageing and taste. *Proceedings of the Nutrition Society*, 71(4), 556–565. <https://doi.org/10.1017/S0029665112000742>
- Mojet, J., Heidema, J., & Christ-Hazelhof, E. (2003). Taste perception with age: Generic or specific losses in supra-threshold intensities of five taste qualities? *Chemical Senses*, 28, 397–413. <https://doi.org/10.1093/chemse/28.5.397>
- Pepino, M. Y., Finkbeiner, S., Beauchamp, G. K., & Mennella, J. A. (2010). Obese women have lower monosodium glutamate taste sensitivity and prefer higher concentrations than do normal-weight women. *Obesity*, 18(5), 959–965. <https://doi.org/10.1038/oby.2009.493>
- Puputti, S., Aisala, H., Hoppu, U., & Sandell, M. (2018). Multidimensional measurement of individual differences in taste perception. *Food Quality and Preference*, 65, 10–17. <https://doi.org/10.1016/J.FOODQUAL.2017.12.006>
- Sasano, T., Satoh-Kuriwada, S., & Shoji, N. (2015). The important role of umami taste in oral and overall health. *Flavour*, 4(1), 1–10. <https://doi.org/10.1186/2044-7248-4-10>
- Simchen, U., Koebnick, C., Hoyer, S., Issanchou, S., & Zunft, H.-J. F. (2006). Odour and taste sensitivity is associated with body weight and extent of misreporting of body weight. *European Journal of Clinical Nutrition*, 60(6), 698–705. <https://doi.org/10.1038/sj.ejcn.1602371>
- Vennemann, M. M., Hummel, T., & Berger, K. (2008). The association between smoking and smell and taste impairment in the general population. *Journal of Neurology*, 255, 1121–1126. <https://doi.org/10.1007/s00415-008-0807-9>
- Webb, J., Bolhuis, D. P., Cicerale, S., Hayes, J. E., & Keast, R. (2015). The relationships between common measurements of taste function. *Chemosensory Perception*, 8(1), 11–18. <https://doi.org/10.1007/s12078-015-9183-x>
- Williams, J. A., Bartoshuk, L. M., Fillingim, R. B., & Dotson, C. D. (2016). Exploring ethnic differences in taste perception. *Chemical Senses*, 41, 449–456. <https://doi.org/10.1093/chemse/bjw021>

SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section at the end of this article.



How to cite this article: Puputti S, Aisala H, Hoppu U, Sandell M. Factors explaining individual differences in taste sensitivity and taste modality recognition among Finnish adults. *J Sens Stud*. 2019;e12506. <https://doi.org/10.1111/joss.12506>

Puputti, S., Hoppu, U., & Sandell, M. (2019)
Taste sensitivity is associated with food consumption behavior but
not with recalled pleasantness.
Foods



Article

Taste Sensitivity is Associated with Food Consumption Behavior but not with Recalled Pleasantness

Sari Puputti ¹, Ulla Hoppu ¹ and Mari Sandell ^{1,2,*}

¹ Functional Foods Forum, University of Turku, Turku 20014, Finland; sari.puputti@utu.fi (S.P.); ulla.hoppu@utu.fi (U.H.)

² Monell Chemical Senses Center, 3500 Market Street, Philadelphia, PA 19104, USA

* Correspondence: mari.sandell@utu.fi; Tel.: +358-40-352-4149

Received: 20 August 2019; Accepted: 25 September 2019; Published: 27 September 2019



Abstract: As taste perception varies between individuals, it might be important in explaining food consumption behavior. Previous studies have focused on sensitivity to the bitter tastant PROP (6-n-propylthiouracil) concerning eating with little attention paid to other tastants. For the first time, connections between food consumption behavior, pleasantness, and taste sensitivity are studied with five taste modalities. Sensitivity to bitterness, sourness, umami, saltiness, and sweetness as well as an overall taste sensitivity score was determined with intensity evaluation for 199 Finnish adults. Recalled pleasantness and food consumption behavior were enquired with online questionnaires. Consumption concerned intake of vegetables, fruits, and berries; use-frequency of specific foods; and tendency to mask or modify tastes of foods. All modality-specific taste sensitivities were related to some consumption behavior but none to recalled pleasantness. A higher taste sensitivity score indicated avoidance of coffee, lower consumption of pungent foods, and a more frequent habit of adding ketchup to a meal. In conclusion, it may be more informative to study the influence of taste sensitivity on food consumption behavior with taste modalities separately rather than with a general indicator of taste sensitivity. Additionally, these results highlight the importance of studying actual behavior toward food and not just liking.

Keywords: taste sensitivity; behavior; food; perception; consumption; pleasantness

1. Introduction

The taste of food is a key factor in food choice. As taste perception varies between individuals, individual taste perception might be important regarding food choice, personal nutrition, and, further, quality of life and development of chronic diseases. Thus, wellbeing may be improved and chronic diseases controlled by considering the taste of foods that are consumed regularly. Then again, the consumption of vegetables, fruits, and berries (VFB) is essential for health and wellbeing. Nevertheless, VFB are consumed less than recommended; in Finland, only every tenth man and every fifth woman ate VFB the recommended amount (500 g per day) in 2017, and the consumption has decreased during recent years [1]. This unfavorable behavior may be partly due to the taste of VFB that does not attract all people. At the same time, consuming more calories than expending, especially consuming energy-dense foods and beverages, is increasing the prevalence of overweight individuals and obesity as well as associated morbidity [2]. To promote a healthier diet, individual motives behind food choices must be investigated.

People can perceive at least five taste modalities: sour, bitter, sweet, salty, and umami. These tastes are perceived individually, and most variation seems to occur in umami and bitter perception [3–5].

Individual taste sensitivity can be measured using several psychophysical methods [6]. Threshold sensitivity measures the lowest concentration of a tastant that is either detected (detection threshold) or identified correctly (recognition threshold). The threshold concentrations are typically very low and thus, may be irrelevant in explaining food liking or consumption [7,8]. Another commonly used measurement of taste perception is intensity rating. The subjects evaluate the intensity of sensation elicited by a tastant at a certain concentration level. The concentration is typically above the threshold. The third commonly used measure is a PROP (6-n-propylthiouracil) taster status. It is a phenotype related to a bitter receptor genotype *TAS2R38* at least. Sensitivity to PROP has been applied to classify subjects as supertasters, medium tasters, and non-tasters [9]. In addition, PROP bitterness intensity has been found to correlate with intensity perception of other tastes [10–13], suggesting that the PROP taster status might represent general taste sensitivity, although some have challenged this view [5,6,11,14]. Considering the taste perception of food, intensity measures of PROP or other tastants may be more relevant measures of individual taste sensitivity than the threshold measures [8].

Little is known about the association between taste sensitivity and food pleasantness or food consumption behavior, such as consumption frequency, or habits to mask tastes in food (for example, masking the bitter taste of coffee with milk or sugar). Higher sweet sensitivity indicated a lower intake of sweet foods and a lower liking of some sweet beverages [7]. However, in other studies, sweet sensitivity was not related to sweet food-related behavior [15,16], such as to the importance of adding sugar in coffee or tea [16]. Lipchock et al. (2017) [17] reported that daily coffee consumers were more sensitive to caffeine, the bitter compound found in coffee than those who consumed coffee rarely or not at all. Furthermore, salty and sour taste perception correlated with alcohol intake, but they were not significant predictors of alcohol intake in a multivariate-adjusted model [18]. Research has focused on PROP taste [19–23] and taste genetics [21,24–27] concerning food consumption behavior and liking. Thus, it is essential to investigate using other tastants whether taste sensitivity is related to food pleasantness and consumption.

This study is part of a large research project concerning individual differences in sensory perception and food-related behavior. Previously, we reported inter-individual variations in color [28] and taste perception [5,29]. The study population was segmented into taste sensitivity groups for each taste modality (sour, bitter, sweet, salty, and umami) based on intensity judgments of aqueous solutions [5]. The objective of this study was to investigate further whether taste sensitivity is associated with food consumption behavior and recalled pleasantness of certain foods and beverages typical to the Finnish food culture. The studied consumption habits included weekly intake of VFB (as a number of portions), habits regarding the masking or modifying the taste of food, and use-frequency of specific foods and beverages. In addition to taste sensitivity, sex, age, education, and BMI were studied as possible explanatory factors for food consumption and pleasantness.

2. Materials and Methods

2.1. Participants

The participants were recruited by announcements at the University of Turku and at public events. In total, 206 Finnish-speaking volunteers (19–79 years) participated in the study. The exclusion criteria included pregnancy and being in a lactating state. Additionally, one person was excluded afterward because of self-reported ageusia after head trauma. Smoking was not an exclusion criterion, but as only six subjects reported themselves to be daily smokers, they were excluded from this study. Otherwise, all volunteers ($N = 199$) were selected for the study without prerequisites for a balanced sample regarding any subject characteristic. After a full account of research aims, written informed consent was provided by all of the subjects. They were rewarded with food products after every visit. The study was approved by the Southwest Finland Hospital District's Ethics Committee (145/1801/2014), and it has been performed in accordance with the 1964 Declaration of Helsinki and its later amendments.

2.2. Taste Sensitivity

The measuring of taste sensitivity was reported in detail earlier in Puputti et al. [5]. In summary, taste sensitivity was determined using four concentration levels of prototypical elicitors of sour, bitter, sweet, salty, and umami sensations (Table 1). The intensity judgments were evaluated on line scale (range from 0 = not at all to 10 = extremely strong) and were analyzed with hierarchical clustering. Three sensitivity groups were formed for each taste modality. Thus, for each taste, there was a group of the least sensitive (cluster 1), the semi-sensitive (cluster 2), and the most sensitive tasters (cluster 3). In addition to the taste modality-specific sensitivity, general taste sensitivity was analyzed using a taste sensitivity score. The score was determined as the mean of the taste modality-specific cluster memberships (score range 1.0–3.0). The closer the score was to 3, the more sensitive the participant.

Table 1. Taste samples.

Taste	Prototypic Tastant	Sample A (mM)	Sample B (mM)	Sample C (mM)	Sample D (mM)
Sour	Citric acid ¹	3.33	1.87	1.05	0.57
Bitter	Caffeine ¹	3.60	2.03	1.14	0.62
Sweet	Sucrose ²	58.4	32.9	18.5	10.5
Salty	Sodium chloride (NaCl) ¹	34.2	19.2	10.8	5.99
Umami	L-glutamic acid, monosodium salt (MSG) ¹	10.7	6.01	3.38	1.87

¹ Produced by Sigma-Aldrich, St. Louis, USA; ² Produced by Alfa Aesar GmbH&Co KG, Karlsruhe, Germany.

The sensory test was executed in the sensory evaluation laboratory (ISO8589) of Functional Foods Forum, University of Turku. The subjects were instructed to refrain from food, beverages other than water, chewing gum, and smoking for at least 1 h prior to testing. The responses were collected with Compusense *five* plus software (Compusense Inc., Guelph, ON, Canada).

2.3. Questionnaires

Webropol online questionnaires (Webropol Inc, Helsinki, Finland) were used for the data collection of subject characteristics, food consumption behavior, and recalled pleasantness of foods and beverages. Sex was changed to a dummy variable: 0 = male, 1 = female. Age was not normally distributed, so it was divided into three categories: the youngest, 19–34 years old (M (SD) = 27.8 (4.1) years); the middle-aged, 35–49 years old (M (SD) = 42.5 (4.3) years); and the oldest, 50–79 years old (M (SD) = 61.9 (8.6) years). BMI was calculated from self-reported height and weight according to the formula kg/(m)². BMI also had a non-normal distribution and the participants were divided into three categories: the lean subjects (BMI < 25.0, M (SD) = 21.8 (2.0)) including three underweight persons (BMI < 18.5), the overweight subjects (BMI = 25.0–29.9, M (SD) = 27.2 (1.5)), and the obese subjects (BMI ≥ 30.0, M (SD) = 34.7 (4.2)).

2.3.1. Portions of VFB per Week

The frequency of consumption of vegetables, fruits, and berries was inquired about separately for each food category, with the response options being “every day,” “5–6 days per week,” “3–4 days per week,” “1–2 days per week,” and “more seldom than once per week”. Additionally, the typical number of portions of vegetables, fruits, and berries consumed per day was inquired about using a category scale (0–6 portions), with an additional response option of “I cannot say.” One portion was described as one carrot, tomato, or apple, or 100 mL of berries or grated vegetables. From the answers to these questions, a new variable called portions per week (range 0–42) was computed separately for vegetables, fruits, and berries as portions per day multiplied by use-frequency (mean).

2.3.2. Masking and Modifying Taste

The frequency of certain consumption habits was thought to describe the tendency to mask or modify taste of food. The questions started with “How frequently do you . . . ?” and dealt with masking bitterness: (1) add milk to coffee, (2) add cream to coffee, (3) add sugar to coffee, (4) add sweetener to coffee, (5) add sugar or honey to tea, (6) add sweetener to tea, (7) add milk to tea; modifying taste with salt or condiments: (8) add salt to water when cooking vegetables, (9) add salt to a meal when eating it, (10) add aromatic salt (mixture of salt and seasoning) to a meal when eating it, (11) add ketchup to a meal when eating it, (12) add soy sauce to a meal when eating it; and masking bitterness, sourness and astringency of berries: (13) add sugar, honey or something else sweet to berries. The response options were “always,” “often,” “sometimes,” “rarely,” “never,” and when appropriate “I don’t drink coffee/drink tea/prepare food.” The responses “I don’t drink coffee/drink tea/prepare food” were removed (marked as missing) before statistical analysis but two new dichotomous variables were also formed: drink coffee vs. do not drink coffee, and drink tea vs. do not drink tea.

2.3.3. Recalled Pleasantness and Use-frequency of Foods and Beverages

Recalled pleasantness and use-frequency of specific foods and beverages ($N = 58$) belonging to the Finnish food culture and eliciting diverse sensory experiences were inquired about to investigate liking and consumption habits. The selection of certain items was also based on the assumption that their sensory profiles divide consumers’ opinions strongly. Pleasantness ratings were investigated with a 9-point hedonic scale (1 = extremely unpleasant, 9 = extremely pleasant). The response option “I cannot say” was included in the case of an unfamiliar food or beverage. These responses were removed (marked as missing) before statistical analyses. Consumption frequencies of the same food and beverage items were inquired about using a 6-point category scale with the response options “daily,” “a few times per week,” “once per week,” “once or twice per month,” “a few times per year,” and “more seldom or never.”

2.4. Statistics

A chi-squared test or Fisher’s Exact Test (FET) was applied to analyze the associations between the categorical variables. A t-test or ANOVA (Tukey as a *post hoc* test or Tamhane’s test if variances were not equal) was applied to compare differences between groups. If the assumptions for the parametric methods were not met, the Kruskal-Wallis and/or the Mann-Whitney U test was applied. Bonferroni correction was applied for multiple comparisons when appropriate. Associations between the taste sensitivity score and the variables concerning the habits of masking/modifying taste and the weekly portions of fruits and berries were analyzed with the Spearman rank correlation whereas the association between the taste sensitivity score and the weekly portions of vegetables was analyzed with the Pearson correlation.

Recalled pleasantness ratings for food and beverage categories were subjected to factor analysis. The categories comprised vegetables (bitter, pungent, mild), vegetable dishes, and pungent condiments ($N = 20$); fruits and berries ($N = 13$); sweet, salty, and fatty foods ($N = 13$); and alcoholic and non-alcoholic beverages ($N = 12$) (original items are listed in Supplementary Material Table S1). The principal component method was applied for component extraction and varimax rotation to gain more interpretable results. The number of factors was decided based on an Eigenvalue greater than 1, the scree plots inspection, and meaningful component content. Variables possessing communality (estimate of variance in a variable accounted for by the extracted components) under 0.300 were removed from the model to create a better model. Component scores for further analyses were obtained by the regression method.

The associations between the background factors, taste sensitivity, and the pleasantness components from factor analysis were analyzed using the hierarchical multivariate linear regression. In the first block, sex and age were entered into the model. In the second model, BMI group and/or

education were added to the model if they possessed a significant contribution to the model after controlling for sex and age. In the third block, sour, bitter, sweet, salty and/or umami sensitivity in one model or the taste sensitivity score in another model were entered into the final model if they possessed a significant contribution after controlling for the previously entered predictors. For the second and third block, the forward method was applied to obtain the simplest model. The criterion for including a variable was the significance of the regression coefficient at a $p \leq 0.1$ level. This hierarchical approach enabled the investigation of whether BMI and education in the second block enhanced the prediction model and whether taste sensitivities in the third block enhanced the previous model.

Following the categories of the pleasantness components, new use-frequency variables were calculated as the mean of the consumption frequency of the pleasantness component items. Thus, the pleasantness components and the new use-frequency components comprised the same food or beverage items. The correlations between pleasantness and use-frequency were analyzed using the Pearson correlation. The hierarchical multivariate linear regression approach was also applied to the new use-frequency components to investigate whether factors other than the pleasantness score explained consumption. The process was similar to the pleasantness component analysis except that the third block consisted of the equivalent pleasantness component because it was expected to have a major contribution to the model. Consequently, taste sensitivities were added in the fourth block. The forward method was applied for blocks 2–4.

The criterion for significance was set to be $p < 0.05$. All statistical analyses were completed with IBM SPSS Statistics 25.0 (IBM Corporation, Armonk, NY, USA).

Some of the subjects did not complete every section of the study because of time constraints, technical issues, or self-reported hypersensitivity to caffeine. Missing data were dealt with in each analysis rather than entirely excluding the subjects with missing data. The subject numbers included in the analyses are provided in the text, tables, and figures.

3. Results

3.1. Subject Characteristics

The subjects' ($N = 199$) characteristics are presented in Table 2. Age and BMI were related ($X^2(4) = 25.3, p < 0.001$) as the majority (77.1%) of the youngest individuals were lean whereas under half of the middle-aged (44.4%) or the oldest individuals (40.0%) were lean. The latter two were more likely to be overweight (33.3% of the middle-aged and 40.0% of the oldest individuals) than the youngest individuals (10.8%). Otherwise, sex, age, BMI, or education were not related. The mean taste sensitivity score was 1.94 (SD 0.50). The connections between taste sensitivities and background factors are reported in our previous publication [29]. In summary, increased age indicated lower taste sensitivity except for sweet taste. Male sex was related to lower sensitivity to sour taste and higher BMI to lower sensitivity to umami. Additionally, males had a lower taste sensitivity score than females, and the oldest subjects had a lower score than the younger subjects.

3.2. Portions of VFB per Week

The mean number of portions of vegetables consumed per week was 21.1 (SD 10.5, $N = 177$). The median number of portions of fruits per week was 10.9 (interquartile range IQR 3.5–14.0, $N = 177$) and of berries 3.5 (IQR 1.5–7.0, $N = 177$). The number of vegetable portions consumed varied depending on umami taste sensitivity ($F(2) = 3.25, p = 0.041$) (Figure 1A). Older age was related to the increased consumption of fruits ($H(2) = 23.92, p < 0.001$) (Figure 1B). Consumption of berries varied between sexes and BMI groups ($U = 2246.5, p = 0.042$, and $H(2) = 7.00, p = 0.030$, respectively) (Figure 1C,D). Education or other taste sensitivity variables were not related to the portions of VFB consumed per week.

Table 2. Subjects’ characteristics (N = 199).

Variable	n	%	Data Missing (n)
Age	199		0
19–34 years	86	43.2	
35–49 years	56	28.1	
50–79 years	57	28.6	
Sex	199		0
Female	158	79.4	
Male	41	20.6	
BMI	192		7
<25.0	110	57.3	
25.0–29.9	49	24.6	
≥30.0	33	17.2	
Education ¹	196		3
Low	73	37.2	
High	123	62.8	
Sour sensitivity	197		2
Least sensitive	49	24.9	
Semi-sensitive	101	51.3	
Most sensitive	47	23.9	
Bitter sensitivity	196		3
Least sensitive	35	17.9	
Semi-sensitive	83	42.3	
Most sensitive	78	39.8	
Sweet sensitivity	199		0
Least sensitive	80	40.2	
Semi-sensitive	79	39.7	
Most sensitive	40	20.1	
Salty sensitivity	198		1
Least sensitive	112	56.6	
Semi-sensitive	51	25.8	
Most sensitive	35	17.7	
Umami sensitivity	198		1
Least sensitive	29	14.6	
Semi-sensitive	132	66.7	
Most sensitive	37	18.7	

¹ Low education included comprehensive school, high school, and lower vocational degree, whereas high education included a polytechnic degree or any university degree.

3.3. Masking and Modifying Taste

The distribution of responses for some of the consumption habits was very narrow in this study population; thus, they were not analyzed further. These variables included adding cream to coffee, adding sugar to coffee, adding sweetener to coffee, adding sweetener to tea, adding milk to tea, and adding aromatic salt to a meal. The distributions for other habits are presented in Table 3. The associations were also studied separately in every age group.

Table 3. Distribution of responses [N (%)] for habits of masking/modifying taste.

	Add Milk to Coffee	Add Sugar/Honey to Tea	Add Salt to Vegetable Cooking Water	Add Salt to a Meal When Eating It	Add Ketchup to a Meal When Eating It	Add Soy Sauce to a Meal When Eating It
always	83 (52.2)	29 (15.7)	37 (19.5)	6 (3.1)	0 (0.0)	0 (0.0)
often	15 (9.4)	29 (15.7)	47 (24.7)	24 (12.6)	8 (4.2)	6 (22.2)
occasionally	7 (4.4)	31 (16.8)	40 (21.1)	37 (19.4)	70 (36.5)	42 (22.2)
rarely	16 (10.1)	44 (23.8)	29 (15.3)	83 (43.5)	72 (37.5)	70 (37.0)
never	38 (23.9)	52 (28.1)	37 (19.5)	41 (21.5)	42 (21.9)	71 (37.6)
Total N	159	185	190	191	192	189

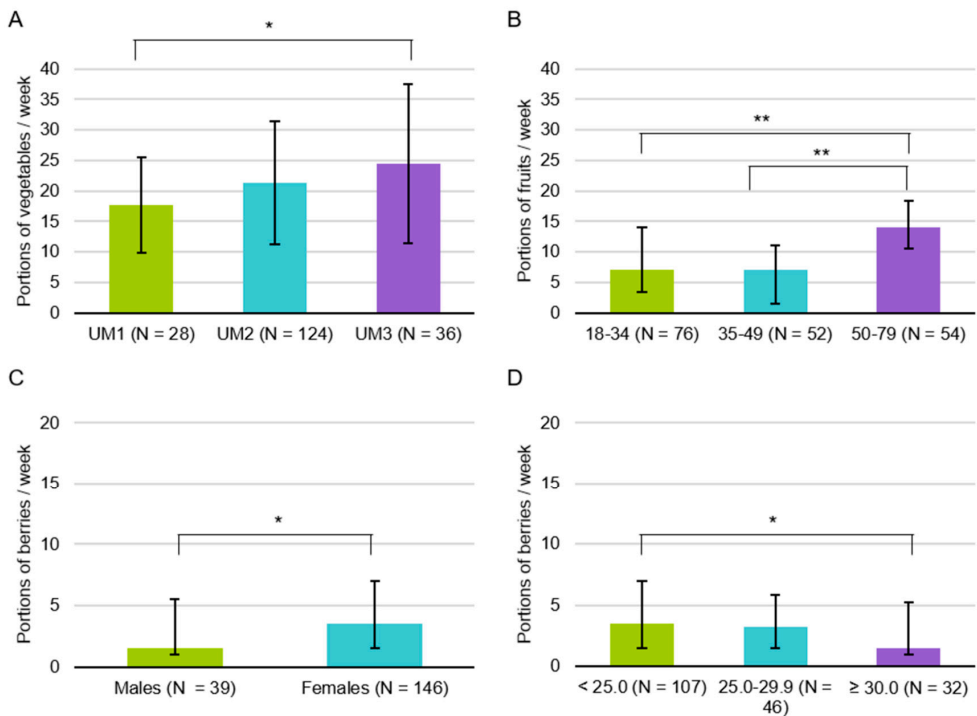


Figure 1. The significant group differences in the number of portions of vegetables (mean and standard deviation), fruits, and berries (median and interquartile range) per week (possible range 0–42). (A) vegetable portions by umami sensitivity groups, UM1 = the least sensitive, UM2 = the semi-sensitive, UM3 = the most sensitive, (B) fruit portions by age groups (years), (C) berry portions by sex, (D) berry portions by BMI groups. * $p < 0.05$, ** $p < 0.001$ based on the Tukey (A) and Mann-Whitney U (B–D) test.

The more common habit of adding milk to coffee was related to female sex, younger age, higher education ($U = 1075.5$, $p < 0.001$, $H(2) = 12.7$, $p = 0.002$, and $U = 2434.5$, $p = 0.048$, respectively) (Figure 2A–C), and higher bitter sensitivity ($H(2) = 6.08$, $p = 0.048$) (Figure 3A).

The oldest subjects added sugar to berries more frequently than the youngest participants despite their taste sensitivity ($H(2) = 7.83$, $p = 0.020$) (Figure 2D).

Bitter, sweet, and salty sensitivity were related to adding ketchup to a meal when eating it ($H(2) = 8.55$, $p = 0.014$, $H(2) = 7.56$, $p = 0.023$, and $H(2) = 11.8$, $p = 0.003$, respectively) (Figure 3B–D). For sweet sensitivity, this was shown especially among 35–49-year-old subjects ($H(2) = 8.56$, $p = 0.041$) when the most sensitive to sweet used ketchup more frequently than the least sensitive ($U = 44.5$, $p = 0.036$). Additionally, the taste sensitivity score and adding ketchup to a meal had a statistically significant correlation ($r = 0.178$, $p = 0.015$).

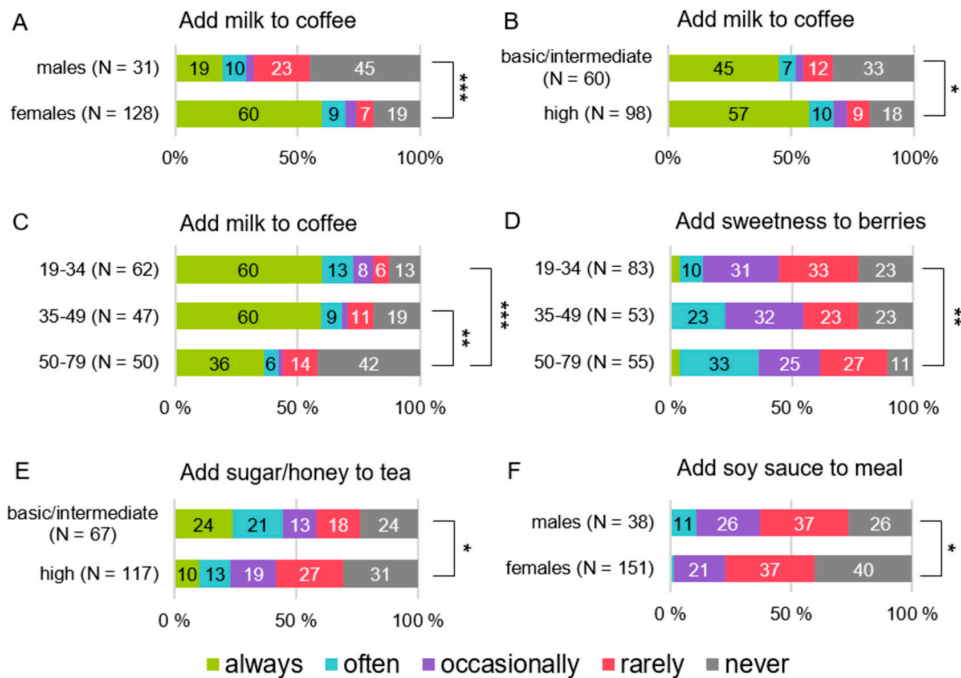


Figure 2. Significant group differences in frequency to mask/modify tastes. (A) sex vs. the habit of adding milk to coffee, (B) education vs. the habit of adding milk to coffee, (C) age (years) vs. the habit of adding milk to coffee, (D) age (years) vs. the habit of adding something sweet to berries, (E) education vs. the habit of adding sugar/honey to tea, (F) sex vs. the habit of adding soy sauce to a meal when eating it. * $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$ based on the Mann-Whitney U test.

Rather than the most sensitive subjects, those semi-sensitive to sourness ($H(2) = 7.62, p = 0.022$) (Figure 3E) and the lower educated subjects ($U = 3754.0, p = 0.013$) (Figure 2E) added sugar or honey to tea more frequently. Among the youngest subjects, the least sensitive to umami added sugar or honey to tea more frequently than the semi or most sensitive subjects ($H(2) = 11.9, p = 0.008; U = 18.0, p = 0.028, U = 2.0, p = 0.013$, respectively).

Males added soy sauce to a meal when eating it more frequently than females ($U = 2257.0, p = 0.031$) (Figure 2F). Among the oldest subjects, sour sensitivity was related to the habit of adding soy sauce to a meal ($H(2) = 12.1, p = 0.007$); the most sensitive to sourness added soy sauce less frequently than the least sensitive ($U = 29.0, p = 0.027$).

None of the potential predictors explained the frequency of adding salt to a meal when eating it or adding salt to vegetable cooking water.

Because a subject could also respond that he/she does not drink coffee or tea, the associations between consuming coffee or tea and taste sensitivities were analyzed. Those who avoided coffee ($N = 33, 17.2\%$ of all respondents) were more likely bitter sensitive subjects ($X^2(2) = 12.9, p = 0.002$) or had a higher taste sensitivity score ($t(185) = 2.63, p = 0.009$) than coffee drinkers.

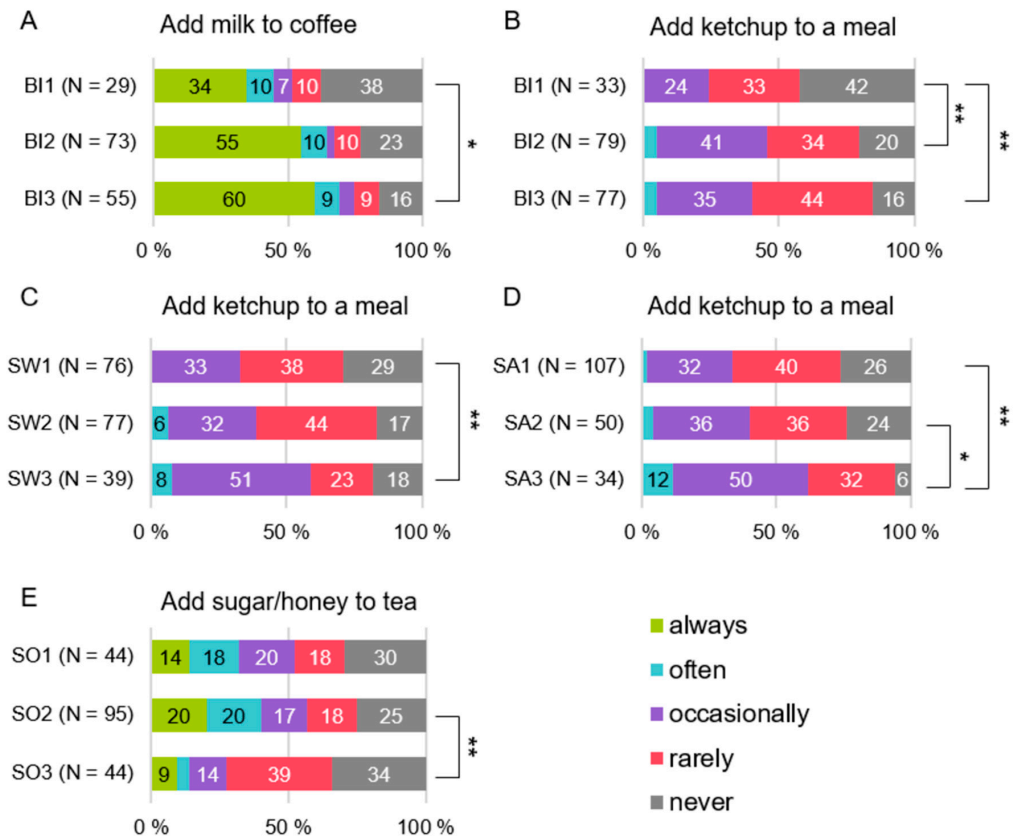


Figure 3. Differences in the frequency to mask/modify tastes by taste sensitivity groups, 1 = the least sensitive subjects, 2 = semi-sensitive subjects, 3 = the most sensitive subjects. (A) bitter sensitivity vs. the habit of adding milk to coffee, (B) bitter sensitivity vs. adding ketchup to a meal when eating it, (C) sweet sensitivity vs. adding ketchup to a meal when eating it, (D) salty sensitivity vs. adding ketchup to a meal when eating it, (E) sour sensitivity vs. habit of adding sugar/honey to tea. BI—bitter; SW—sweet; SA—salty; SO—sour. * $p < 0.05$, ** $p < 0.01$ based on Mann-Whitney U tests.

3.4. Factor Analysis of Recalled Pleasantness

Table 4 presents the components extracted from the principal component analysis applied for the food and beverage pleasantness ratings. For further analysis, 11 composite pleasantness variables were extracted and labeled as bitter vegetables, strong-tasting vegetables, pungent foods, berries, fruits, salty-and-fatty foods, sweet-and-fatty foods, salty-and-savory foods, bitter-and-astringent alcoholic beverages, bitter-and-astringent non-alcoholic beverages, and sweet beverages.

Table 4. Rotated variable loadings of the extracted pleasantness components (correlation coefficients). The bolded coefficient indicates the highest correlation of the item. For simplicity, only coefficients above 0.400 are shown. The labels of new variables are in italics and the mean [SD] of the original pleasantness ratings (1 = extremely unpleasant, 9 = extremely pleasant) in the parentheses.

	PC1	PC2	PC3
Vegetables and pungent items (N = 154)			
<i>Bitter vegetables (6.46 [2.12])</i>			
Red beet	0.725		
Swedish turnip	0.714		
Brussels sprout	0.710		
Carrot	0.530		
Radish	0.509	0.401	
<i>Strong-tasting vegetables (6.37 [2.46])</i>			
Onion		0.765	
Rucola		0.684	
Olive		0.658	
Celery		0.652	
<i>Pungent foods (5.92 [2.37])</i>			
Chili sauce			0.928
Chili			0.842
Wasabi			0.715
Mustard			0.448
Variance explained (%)	28.9	12.8	7.7
Berries and fruits (N = 186)			
<i>Berries (7.20 [1.97])</i>			
Lingonberry	0.833		
Red currant	0.817		
Black currant	0.754		
Sea buckthorn berry	0.658		
Bilberry	0.499		
<i>Fruits (6.73 [2.04])</i>			
Avocado		0.806	
Lemon		0.764	
Rhubarb		0.638	
Grapefruit	0.432	0.475	
Variance explained (%)	33.7	10.4	
Sweet, salty, and fatty (N = 177)			
<i>Salty-and-fatty foods (6.67 [1.99])</i>			
French fries	0.824		
Potato chips	0.769		
Mayonnaise	0.709		
<i>Sweet-and-fatty foods (7.67 [1.66])</i>			
Ice cream		0.800	
Sweet pastry		0.723	
Milk chocolate		0.642	
Candy		0.547	
<i>Salty-and-savory foods (6.68 [2.52])</i>			
Blue cheese			0.821
Dry-cured salmon			0.744
Soy sauce			0.479
Variance explained (%)	24.0	15.0	11.1

Table 4. Cont.

	PC1	PC2	PC3
Beverages (N = 170)			
<i>Bitter-and-astringent alcohol (5.84 [2.52])</i>			
White wine	0.757		
Dry cider	0.716		
Red wine	0.699	0.409	
Long drink	0.656		0.438
Strong alcohol	0.610		
Beer	0.548	0.539	
<i>Bitter-and-astringent non-alcoholic (7.04 [2.22])</i>			
Carbonated water		0.782	
Tea		0.668	
Coffee		0.555	
<i>Sweet beverages (4.81 [2.41])</i>			
Soft drink			0.828
Light soft drink			0.754
Sweet cider			0.538
Variance explained (%)	29.9	17.6	10.9

PC refers to Principal Component. N refers to the number of subjects included in the analysis.

3.5. Explaining Recalled Pleasantness

The associations between the pleasantness variables from factor analysis and subject characteristics were analyzed with multivariate linear regression in three steps. First, sex and age were entered. Second, BMI and education level were entered if they made a significant contribution to the model. Lastly, taste sensitivities were entered if they contributed significantly after controlling for the previously-added variables. The final models are presented in Table 5. Overall, the models explained only a relatively small proportion of the pleasantness scores: from 3.4% for sweet-and-fatty foods to 11.4% for sweet beverages. None of the taste sensitivity factors was a significant contributor to the models.

Increased pleasantness of bitter vegetables was related to male sex and lower BMI. Their contribution to the model was approximately equal (standardized β coefficients -0.172 and -0.166 , respectively). Sour sensitivity was included in the model in block 3 as its p -value (0.067) was under the selected criterion (0.100). However, adding sour sensitivity did not enhance the model significantly when compared to the model including only sex and BMI (R^2 change 0.022, $F_{\text{change}} = 3.42$, $p_{\text{change}} = 0.067$). Thus, the model comprising sex and BMI is reported in Table 5.

Female sex predicted a higher liking score for pungent foods. In the third step, sweet and salty sensitivities were added into the model (p -values 0.060 and 0.071, respectively) but their inclusion did not enhance the model comprising sex and age (for sweet R^2 change 0.023, $F_{\text{change}} = 3.60$, $p_{\text{change}} = 0.060$; for salty R^2 change 0.021, $F_{\text{change}} = 3.30$, $p_{\text{change}} = 0.071$).

Liking of strong-tasting vegetables, as well as berries, was explained by age as older age increased the pleasantness scores. A lower BMI was the only significant predictor of increased fruit liking.

Younger subjects had higher liking scores for salty-and-fatty foods, whereas older age predicted higher salty-and-savory foods liking. The model for sweet-and-fatty foods liking was just above the significance level, although females liked sweets more than males did. BMI was entered in the prediction models of salty-and-fatty foods and sweet-and-fatty foods but the inclusion did not enhance the models significantly (R^2 change 0.019, $F_{\text{change}} = 3.41$, $p_{\text{change}} = 0.067$ and R^2 change 0.020, $F_{\text{change}} = 3.56$, $p_{\text{change}} = 0.061$, respectively).

Table 5. The results of hierarchical multivariate linear regression, food pleasantness components as dependent variables: unstandardized β coefficients (95% confidence intervals) and model statistics.

Pleasantness Component ¹	Sex ²	Age ³	BMI ³	Model Statistics
Bitter vegetables (N = 149)	-0.417 * (-0.802, -0.032)	0.149 (-0.050, 0.347)	-0.210 * (-0.418, -0.003)	F _{df = 3, 145} = 3.39, p = 0.020, R ² = 0.066
Strong-tasting vegetables (N = 149)	0.208 (-0.179, 0.595)	0.395 *** (0.201, 0.588)		F _{df = 2, 146} = 8.47, p < 0.001, R ² = 0.104
Pungent foods (N = 149)	0.596 ** (0.202, 0.990)	0.082 (-0.115, 0.279)		F _{df = 2, 146} = 4.67, p = 0.011, R ² = 0.060
Berries (N = 180)	-0.004 (-0.367, 0.359)	0.330 *** (0.157, 0.502)		F _{df = 2, 177} = 7.16, p = 0.001, R ² = 0.075
Fruits (N = 180)	-0.005 (-0.366, 0.356)	0.075 (-0.104, 0.253)	-0.254 * (-0.446, -0.062)	F _{df = 3, 176} = 2.28, p = 0.081, R ² = 0.037
Salty-and-fatty foods (N = 174)	-0.167 (-0.525, 0.191)	-0.277 ** (-0.456, -0.098)		F _{df = 2, 171} = 4.90, p = 0.009, R ² = 0.054
Sweet-and-fatty foods (N = 174)	0.450 * (0.086, 0.815)	-0.021 (-0.203, 0.161)		F _{df = 2, 171} = 3.05, p = 0.050, R ² = 0.034
Salty-and-savory foods (N = 174)	0.116 (-0.237, 0.470)	0.235 ** (0.059, 0.412)		F _{df = 2, 171} = 3.57, p = 0.030, R ² = 0.040
Bitter-and-astringent alcoholic (N = 165)	-0.604 ** (-0.961, -0.248)	0.078 (-0.100, 0.255)		F _{df = 2, 162} = 6.21, p = 0.003, R ² = 0.071
Bitter-and-astringent non-alcoholic (N = 165)	-0.266 (-0.620, 0.088)	0.227 *(0.051, 0.404)		F _{df = 2, 162} = 4.65, p = 0.011, R ² = 0.054
Sweet beverages (N = 165)	-0.187 (-0.546, 0.172)	-0.379 *** (-0.564, -0.194)	0.291 ** (0.094, 0.489)	F _{df = 3, 161} = 6.92, p < 0.001, R ² = 0.114

* $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$; ¹ N refers to the number of subjects included in the analysis; ² Entered in the analysis as dummy variable: 0 = male, 1 = female.; ³ Entered in the analysis as a category variable with increasing age/BMI (see Table 1).

Male sex predicted higher liking scores for bitter-and-astringent alcoholic beverages and older age for bitter non-alcoholic beverages. Sweet beverage pleasantness was explained by age and BMI as younger age and higher BMI increased the pleasantness score. Based on the standardized β coefficients, age had a higher contribution to the model than BMI (-0.311 and 0.224).

3.6. Use-frequency

The descriptive data of the composite use-frequency variables and their correlation with equivalent pleasantness variables are presented in Table 6. Except for the bitter vegetable and pungent foods variables, all correlations were strong (correlation coefficients 0.389–0.726) and significant ($p < 0.001$). The correlation between bitter vegetable liking and consumption was significant, but the correlation coefficient was only 0.238. Pungent food consumption was not correlated with liking. Cronbach's alphas indicated a good internal consistency of the new use-frequency items except for bitter-and-astringent non-alcoholic beverages and sweet beverages.

Table 6. The descriptives of use-frequency components and their correlation with equivalent pleasantness components.

Use-frequency Variable	Descriptives				Correlation		
	N	Mean ¹	SD	Cronbach's α	N	Correlation with Pleasantness	Sig. (2-tailed) of Correlation
Bitter vegetables	191	2.86	0.60	0.653	154	0.238	0.003
Strong-tasting vegetables	190	3.33	0.83	0.619	153	0.389	<0.001
Pungent items	187	2.75	0.90	0.727	153	0.065	0.426
Berries	190	3.03	0.84	0.722	184	0.604	<0.001
Fruits	189	2.69	0.72	0.571	183	0.602	<0.001
Salty-and-fatty foods	191	2.64	0.74	0.668	176	0.572	<0.001
Sweet-and-fatty foods	190	3.49	0.69	0.505	175	0.493	<0.001
Salty-and-savory foods	190	2.76	0.81	0.444	175	0.672	<0.001
Bitter-and-astringent alcoholic	191	2.21	0.74	0.785	170	0.726	<0.001
Bitter-and-astringent non-alcoholic	192	4.29	1.07	0.232	170	0.704	<0.001
Sweet beverages	190	2.02	0.71	0.355	168	0.634	<0.001

¹ Range from 1 (more seldom than a few times per year or never) to 6 (daily).

The use-frequency components were also subjected to multivariate linear regression to reveal which factors predicted consumption other than the pleasantness score. The equivalent pleasantness score was the sole contributor to the model for every use-frequency component other than bitter vegetables, pungent foods, berries, fruits, and salty-and-savory foods. For these components, the regression models are presented in Table 7.

In addition to a higher pleasantness score, older age predicted an increased consumption of bitter vegetables. The contribution of bitter vegetable pleasantness score was only slightly higher than the contribution of age (standardized β coefficients of 0.280 and 0.249, respectively). The pleasantness score of pungent foods was not an important contributor to the consumption of pungent foods. Instead, male sex and low sensitivity to bitter taste were significant predictors for increased consumption of pungent foods (standardized β coefficients of -0.160 and -0.207 , respectively). When the taste sensitivity score was applied in the model instead of the separate taste sensitivities, it had a significant contribution to the pungent foods consumption ($F(df = 3, 144) = 4.00, p = 0.010, R^2 = 0.076, \beta = -0.324$); the less sensitive subjects consumed higher amounts of the pungent items.

The order of significance for factor contributions to berry consumption was pleasantness score (standardized β coefficient 0.574), BMI (-0.186), and age (0.127). The fruit pleasantness score had a higher contribution (standardized β coefficient 0.558) to the fruit consumption model than BMI (-0.193). The pleasantness score had the highest contribution (standardized β coefficient 0.664) to the salty-and-savory foods consumption model followed by sour sensitivity (0.173), umami sensitivity (-0.158), and sex (-0.137).

Table 7. The results of hierarchical multivariate linear regression, use-frequency components as dependent variables: unstandardized β coefficients (95% confidence intervals) and model statistics.

Use-frequency Component ¹	Sex ²	Age ³	BMI ³	Pleasantness	Bitter Sensitivity ³	Sour Sensitivity ³	Umami Sensitivity ³	Model Statistics
Bitter vegetables (N = 149)	0.176 (−0.059, 0.411)	0.190 ** (0.074, 0.306)		0.176 *** (0.079, 0.274)				F (3, 145) = 8.59, p < 0.001, R ² = 0.151
Pungent foods (N = 148)	−0.343 * (−0.683, −0.004)	0.067 (−0.111, 0.246)			−0.259 * (−0.466, −0.052)			F (3, 144) = 4.45, p = 0.005, R ² = 0.085
Berries (N = 178)	0.048 (−0.205, 0.301)	0.131 * (0.001, 0.262)	−0.207 ** (−0.342, −0.071)	0.489 *** (0.386, 0.592)				F (4, 173) = 28.3, p < 0.001, R ² = 0.396
Fruits (N = 177)	−0.075 (−0.292, 0.142)	0.042 (−0.065, 0.149)	−0.182 ** (−0.298, −0.065)	0.415 *** (0.326, 0.504)				F (4, 172) = 27.0, p < 0.001, R ² = 0.386
Salty-and-savory foods (N = 172)	−0.266 * (−0.484, −0.048)	0.036 (−0.079, 0.151)		0.535 *** (0.445, 0.625)		0.196 ** (0.059, 0.334)	−0.219 * (−0.392, −0.046)	F (5, 166) = 32.1, p < 0.001, R ² = 0.492

* $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$; ¹ N refers to the number of subjects included in the analysis; ² Entered in the analysis as dummy variable: 0 = male, 1 = female; ³ Entered in the analysis as a category variable with increasing age/BMI/taste sensitivity (see Table 1).

4. Discussion

In this study, the associations between taste sensitivity, food consumption behavior, and recalled pleasantness were investigated with 199 adult participants. To the authors' knowledge, this is the first time that the perception of five taste modalities has been investigated in relation to food consumption and pleasantness. Thus far, research has been focused on the relationship between PROP and food-related behavior, whereas other tastants or taste qualities have gained only little attention. Additionally, large-scale studies with a varied group of subjects are scarce.

The consumption habits regarding some items were related to taste sensitivity. However, taste sensitivity was not related to the recalled pleasantness of the foods and beverages. As was expected, pleasantness was the main predictor of the use-frequency components, except for pungent foods. These results highlight the importance of studying the actual behavior toward food and not just liking.

4.1. Taste Sensitivity, Food Consumption, and Pleasantness

Bitter sensitivity was related to masking bitter tastes and pungent food consumption. Earlier studies on pungency or spicy foods behavior have focused on PROP taste. Higher sensitivity to PROP has been reported to predict a more intense pungency perception [12,23,30]. In a large scale study, the pungency of pure capsaicin correlated with PROP bitterness and taste intensities of other tastants, although the correlation coefficients were rather weak, at least for PROP (0.199) [12]. In the same study, PROP tasters perceived pungency in a food matrix more strongly than non-tasters. PROP bitterness perception was not related to the perception of oral pungency in another sample of Finnish subjects [31]. Intensity perception of oral pungency and liking of oral pungency or spicy foods have been shown to associate negatively when the subjects were grouped into pungency likers, medium-likers, and non-likers, although the correlation between intensity and liking was only -0.16 [31]. If bitter and pungent sensitivities correlated, bitter sensitivity could also associate negatively with pungent food liking. However, this theory was not supported in our study, as bitter sensitivity did not explain pungent food pleasantness. However, bitter sensitivity explained pungent food consumption, as bitter sensitive subjects reported eating pungent items less frequently.

Masking a bitter taste in food or modifying the taste of food by bitter sensitive subjects was shown in the habits of adding milk to coffee, and adding ketchup to a meal when eating it. Additionally, the habit of consuming coffee was less common among bitter sensitive subjects. However, the pleasantness or use-frequency of bitter non-alcoholic beverages, including coffee, was not related to bitter sensitivity. The relationship between coffee consumption and bitter sensitivity has been shown earlier with other kinds of study design. Lipchock et al. [17] showed, though with a small sample size, that daily coffee drinkers rated the intensity of pure caffeine higher than those who consumed coffee irregularly or not at all. Among Italian subjects, PROP sensitivity was not related to coffee liking, but interestingly, the PROP non-tasters added sugar to coffee more frequently than medium or supertasters although they perceived the coffee as milder than others did [32].

Some findings were surprising and challenging to explain. Sour sensitivity was related to the habits of adding sugar/honey to tea and soy sauce to a meal as well as to the consumption frequency of foods with salty and savory dominant tastes. Umami sensitivity was also related to the habit of adding sweetness to tea. Adding ketchup to a meal was also more common among the most sensitive to salt and sweetness. Ketchup is typically a strong-tasting sauce that contains spices, vinegar, sugar, and salt. The considerable amounts of sugar and salt in ketchup may explain why salty and sweet sensitivities were related to ketchup consumption. Concerning these results, there are no other published studies to compare so far. Thus, more large-scale studies are needed.

Umami sensitivity was related to umami-tasting foods: salty-and-savory foods, and weekly vegetable consumption. The result that lower umami sensitivity was related to more frequent consumption of umami-containing foods supports the idea that lower sensitivity to a taste demands higher concentrations of equivalent tastants to reach liking and increased consumption. This idea may depend on a food matrix or a taste as the relationship was opposite regarding ketchup and bitter, salty,

or sweet sensitivity. In the case of vegetables, the most sensitive to umami consumed more portions of vegetables per week than the least sensitive. As umami is also part of vegetable taste profiles [33] and umami intensity is affected by the processing of vegetables [34], umami sensitive people might perceive a more intense umami taste from vegetables, making them more palatable.

The descriptor of overall taste sensitivity, the taste sensitivity score, was related to three items only: consumption of pungent foods, coffee, and adding ketchup to a meal. These findings indicate that studying taste modality-specific sensitivities rather than general indicators of taste sensitivity might give better insights into the relationship between taste perception and food-related behavior.

Based on earlier studies, other associations may have existed. First, in our results, bitter (caffeine) sensitivity was not related to either vegetable liking or consumption, a tendency that has earlier been explained with PROP sensitivity [21,23] and one which, in turn, has been shown to associate with caffeine perception [32,35]. Therefore, there could have been some association with bitter sensitivity and vegetable-related behavior in this study, too.

Second, taste sensitivity was not related to alcohol pleasantness or intake. An earlier study found that perceived NaCl and sour taste intensities correlated positively with yearly alcohol intake [18]. In multiple regression analysis, they were not significant predictors of intake, but PROP intensity perception predicted alcohol intake as lower sensitivity indicated higher intake [18]. It must be noted that in our study, the consumption of alcoholic beverages was low, which may contribute to the results.

Third, sweet sensitivity could have been related to sweet-and-fatty foods or sweet beverage/sweet item liking and/or consumption. Jayasinghe et al. [7] reported that among New Zealand women, a higher sweet sensitivity indicated lower consumption frequency of baking/sweets (e.g., chocolates, biscuits, cakes) which were reported to be consumed more often than once per day. Furthermore, total sweet food intake was lower (on average seven times per day) among sweet sensitive subjects, as well as liking of fruit drinks and fruit juices when liking of 16 sweet beverages was measured. On the contrary, Low et al. [8] found that sweet taste sensitivity was not related to intake of total sugars, added sugar, or sugar-sweetened foods. Additionally, sweetness sensitivity was not related to sweet food liking or consumption in other studies [15,36]. Furthermore, among young adults, sweet perception was not related to sweet food behaviors including intake of confectionery, fruits, or vegetables, or the importance of adding sugar to tea or coffee or avoiding sugar-sweetened or fizzy drinks [16].

Tepper [23] reviewed links between PROP tasting and food-related behavior. The links were not confirmed as there were discrepancies in results between studies. A vast range of methods can explain some discrepancies. Some studies show that the association between PROP tasting and food consumption behavior may depend on sex, age, fungiform papillae density, or personality trait [21,23]. It seems that PROP tasters can perceive more intensively or differentiate some other properties more easily than non-tasters, but this might not always translate into hedonics or consumption of foods [23]. However, earlier studies have found that PROP sensitivity might negatively affect behavior related to pungent, bitter, and creamy foods [23]. In a more recent study, a higher PROP bitterness perception was related to a lower liking and consumption of not only bitter but other vegetables among young adults [21]. Catanzaro et al. [19] found no significant association between PROP tasting and recalled liking of foods that have been reported to be related to PROP taster status. In their study, PROP intensity correlated statistically significantly with the liking of dark chocolate and chili peppers, but the correlation coefficients were only -0.155 and -0.144 , respectively.

This study was cross-sectional; thus, no cause and effect relationship can be concluded. A study by Wise et al. [37] has indicated that reduced sugar consumption causes a more intense sweetness perception in a food matrix but does not affect pleasantness ratings. In the case of salt, salt perception did not change but preference for higher levels of salt increased with increasing salt intake [38]. In a more recent study, perception or pleasantness was not affected by the intake of salt [39]. Noel et al. [40] showed that repeated exposure to MSG in broth diminished umami intensity perception, as well as desire for and intake of savory foods at an ad libitum meal.

4.2. Background Factors, Food Consumption, and Pleasantness

Sex and age, as well as BMI in some cases, were related to pleasantness components, but they explained only a relatively small proportion of pleasantness in regression models. They were also related to many food consumption variables.

In our study, females liked pungent foods more but males consumed them more. Earlier, pungent food liking [41] and chili pepper consumption [30] were related to the male sex, and spicy food consumption has been shown to be independent of sex [42]. Törnwall et al. [31] also found that genetic factors could explain 18–58% of liking and perception of pungency and spicy foods. Additionally, some personality factors, such as food adventurousness, can explain spicy food consumption and liking [23,30,31]. We found no connection between pungent food pleasantness and consumption, although it would be logical that those who like pungency would consume it more than those who dislike it. Ludy and Mattes [42] found this logic with a small sample size, as regular spicy food users liked chili pungency and spicy foods more than non-users. They also found that many of the users had been already introduced to spicy foods in childhood, indicating the relevance of early and repeated exposure to food-related behavior. It should be noted that in our study, a limited number of pungent foods was included.

There were also other sex-related differences. Males liked bitter-and-astringent alcohol more and consumed salty-and-savory items more frequently, while females favored sweet-and-fatty foods. Earlier studies have also found that Finnish females liked sweet-and-fatty foods or sweet foods more than males did [41,43]. Valsta et al. [1] reported that women had consumed more VFB than men during recent years. We found only that females ate more portions of berries per week. In use-frequency components, sex did not have a significant role in explaining the consumption of VFB, but males had higher scores for bitter vegetable pleasantness.

As age increased, the pleasantness score increased for strong-tasting vegetables, berries, salty-and-savory foods, and bitter non-alcoholic beverages, whereas the younger subjects liked salty-and-fatty foods and sweet beverages more. Valsta et al. [1] showed that in Finland, the number of people consuming the recommended amount of vegetables decreases and the number of people consuming the recommended amount of fruits and berries increases by age. In accordance with Valsta et al. [1], we found the consumption of fruits (portions per week) and berries (use-frequency) to increase by age, but we also found an increase by age in the use-frequency (components) of bitter vegetables.

The older subjects seemed to like and consume more strong tastes as bitterness was not a barrier for liking, and those foods with a strong umami taste were considered pleasant. The younger subjects' avoidance of bitterness was supported by the frequency with which they added milk to coffee. The oldest subjects who were also less sensitive to sour used to add soy sauce to a meal when eating it more frequently than more sensitive subjects. One explanation could be that the oldest subjects try to compensate for their weakened taste sensitivity by adding soy sauce to food. The oldest subjects also added sugar to berries more frequently than the younger participants despite their taste sensitivity, which might explain why older age was related to a higher liking and consumption of berries. Among Finnish consumers, increased berry liking has been linked to female sex and older age as well as some personality traits [44]. In this study population, the older subjects were less taste sensitive [29] which could explain the liking of strong and bitter-tasting foods and beverages. However, taste sensitivity was not a significant predictor in regression analysis. Another possible explanation might be becoming accustomed to strong tastes after repeated exposure with age. Then again, cultural and social aspects could explain why the younger participants liked more salty-and-fatty foods and sweet beverages. Coffee culture in Finland has evolved, and younger participants might be becoming used to consuming their coffee with milk, such as in cappuccinos or lattes.

BMI was related to the consumption frequency of berries (both weekly portions and use-frequency component), the pleasantness of bitter vegetables, and the pleasantness and consumption frequency of fruits; the lower the BMI, the higher the score for these variables. In contrast, those subjects with a higher BMI liked sweet beverages more. These results reflect the assumption that people with a lower

BMI might have a healthier diet. However, BMI was not a significant predictor for salty-and-fatty or sweet-and-fatty food consumption or pleasantness. In a recent study, Low et al. [36] found no correlation between BMI and sweet food liking or consumption. In the study by Guido et al. [45], BMI was not related to the preference variables formed with factor analysis: vegetables, fruits, spicy, and milk products. Likewise, there were no differences between lean and obese subjects in the liking of foods with different predominant taste qualities. In an earlier study, the lean subjects liked salty/savory and sweet foods more than the obese subjects did [46].

Education level was related only to the habits of adding milk to coffee and sugar or honey to tea. Education could have been related more extensively to food consumption because education is one indicator of socioeconomic position, which can have an impact on dietary habits [47]. Valsta et al. [1] also reported differences in VFB consumption between education levels as the better-educated people consumed more of these than the lower educated ones. In this study, no relationship was found between education and the consumption of VFB. This might be due to the larger proportion of better-educated participants in this study.

4.3. Limitations

This study considered five taste modalities to explain food consumption and food pleasantness among Finnish adults. The subjects formed a large heterogeneous group of consumers and a wide variety of variables about food consumption behavior was collected. However, there are some limitations to acknowledge. The sample population was unbalanced for background factors. Additionally, the taste sensitivity groups were different in size as a result of the data-driven determination. Although the number of males and obese subjects were smaller than their reference groups, the numbers were higher than those in many earlier studies. A representative population sample was not our aim, but the characteristics of the sample population should be kept in mind when interpreting the results.

The questionnaires about food consumption behavior and pleasantness were not validated. Existing questionnaires, such as the French PrefQuest [48], are not valid globally, as food consumption is strongly connected to culture. Thus, such a questionnaire could not be applied to study food consumption behavior or pleasantness among Finnish people, and we had to develop a new one. The food items in this study were chosen based on the expectation that they would divide people's opinions and elicit different taste sensations.

Concerning the taste sensitivity determination, only one prototypic compound per taste quality was used. With other compounds, the results might have been different. On the other hand, Mojet et al. [49] found no compound-specific differences within taste modalities between sexes or age groups. No references were used to guide the intensity evaluations, but thorough written and verbal instructions were given on how to use the scale. It is not guaranteed that individual ratings were the results of true intensity perception only and not results of scale-use bias. The sensitivity groups were formed via hierarchical clustering, and simultaneous analyses of individual's evaluations made it possible to smooth out variation in sample rating.

5. Conclusions

Taste sensitivity was related to some food consumption behavior; not to recalled pleasantness but to use-frequency, and tendency to mask or modify tastes. Thus, the focus of research should be in studying actual behavior toward food and not just liking. All taste modality-specific sensitivities were related to some aspect of food consumption behavior. The taste sensitivity score – describing overall taste sensitivity – was related only to pungent food consumption, coffee drinking, and the habit of adding ketchup to food. These findings imply that it would be more informative to study the associations between taste sensitivity and food-related behavior with all taste modalities separately rather than with any general indicator of taste sensitivity. Sex, age, and BMI were related to several food consumption habits and pleasantness, but only a small proportion of food pleasantness was explained by them. Additionally, pleasantness was the main factor explaining consumption frequency.

Clearly, factors other than taste sensitivity are also important for food liking and consumption. Culture and social dynamics may have a significant role in how an individual perceives and approaches foods and beverages. Fortunately, food choice and intake can be affected by encouraging healthier choices, and after several exposures people can learn to like, for example, vegetables, fruits, and berries, rather than the preference being determined by biology. There are substantial cultural differences in the ways and frequency of how foods and beverages are consumed. Thus, more studies are needed to fully understand the importance of taste perception in actual behavior toward food.

Supplementary Materials: The following are available online at <http://www.mdpi.com/2304-8158/8/10/444/s1>, Table S1: Recalled pleasantness of all food and beverage items that were included in the factor analysis.

Author Contributions: Conceptualization, M.S., U.H. and S.P.; methodology, M.S., U.H. and S.P.; formal analysis, S.P.; investigation, S.P.; resources, M.S.; writing—original draft preparation, S.P.; writing—review and editing, M.S. and U.H.; supervision, M.S.; funding acquisition, M.S.

Funding: This research was funded by the Academy of Finland, MS309408.

Acknowledgments: The authors are very grateful to all the study participants.

Conflicts of Interest: The authors declare no conflict of interest.

References

1. Valsta, L.; Lundqvist, A.; Kaartinen, N.; Raulio, S.; Sääksjärvi, K.; Männistö, S. Ruokatottumukset. In *Terveys, Toimintakyky ja Hyvinvointi Suomessa FinTerveys 2017-Tutkimus*; Koponen, P., Borodulin, K., Lundqvist, A., Sääksjärvi, K., Koskinen, S., Eds.; THL: Helsinki, Finland, 2018; pp. 33–37.
2. World Health Organization. Obesity and Overweight. Available online: <https://www.who.int/news-room/fact-sheets/detail/obesity-and-overweight> (accessed on 15 February 2019).
3. Knaapila, A.; Hwang, L.-D.; Lysenko, A.; Duke, F.F.; Fesi, B.; Khoshnevisan, A.; James, R.S.; Wysocki, C.J.; Rhyu, M.; Tordoff, M.G.; et al. Genetic Analysis of Chemosensory Traits in Human Twins. *Chem. Senses* **2012**, *107*, 935–939. [CrossRef] [PubMed]
4. Lugaz, O.; Pillias, A.-M.; Faurion, A. A New Specific Ageusia: Some Humans Cannot Taste L-Glutamate. *Chem. Senses* **2002**, *27*, 105–115. [CrossRef] [PubMed]
5. Puputti, S.; Aisala, H.; Hoppu, U.; Sandell, M. Multidimensional measurement of individual differences in taste Perception. *Food Qual. Prefer.* **2018**, *65*, 10–17. [CrossRef]
6. Webb, J.; Bolhuis, D.P.; Cicerale, S.; Hayes, J.E.; Keast, R. The Relationships Between Common Measurements of Taste Function. *Chemosens. Percept.* **2015**, *8*, 11–18. [CrossRef] [PubMed]
7. Jayasinghe, S.N.; Kruger, R.; Walsh, D.C.I.; Cao, G.; Rivers, S.; Richter, M.; Breier, B.H. Is Sweet Taste Perception Associated with Sweet Food Liking and Intake? *Nutrients* **2017**, *9*, 750. [CrossRef] [PubMed]
8. Low, J.Y.; Lacy, K.E.; McBride, R.; Keast, R.S.J. The Association between Sweet Taste Function, Anthropometry, and Dietary Intake in Adults. *Nutrients* **2016**, *8*, 241. [CrossRef]
9. Bartoshuk, L.M. Comparing Sensory Experiences Across Individuals: Recent Psychophysical Advances Illuminate Genetic Variation in Taste Perception. *Chem. Senses* **2000**, *25*, 447–460. [CrossRef]
10. Bajec, M.R.; Pickering, G.J. Thermal taste, PROP responsiveness, and perception of oral sensations. *Physiol. Behav.* **2008**, *95*, 581–590. [CrossRef]
11. Fischer, M.E.; Cruickshanks, K.J.; Pankow, J.S.; Pankratz, N.; Schubert, C.R.; Huang, G.-H.; Klein, B.E.K.; Klein, R.; Pinto, A. The associations between 6-n-propylthiouracil (PROP) intensity and taste intensities differ by TAS2R38 haplotype. *Lifestyle Genom.* **2014**, *7*, 143–152. [CrossRef]
12. Dinnella, C.; Monteleone, E.; Piochi, M.; Spinelli, S.; Prescott, J.; Pierguidi, L.; Gasperi, F.; Laureati, M.; Pagliarini, E.; Predieri, S.; et al. Individual Variation in PROP Status, Fungiform Papillae Density, and Responsiveness to Taste Stimuli in a Large Population Sample. *Chem. Senses* **2018**, *43*, 697–710. [CrossRef]
13. Hayes, J.E.; Bartoshuk, L.M.; Kidd, J.R.; Duffy, V.B. Supertasting and PROP Bitterness Depends on More Than the TAS2R38 Gene. *Chem. Senses* **2008**, *33*, 255–265. [CrossRef] [PubMed]
14. Lim, J.; Urban, L.; Green, B.G. Measures of Individual Differences in Taste and Creaminess Perception. *Chem. Senses* **2008**, *33*, 493–501. [CrossRef] [PubMed]

15. Keskitalo, K.; Tuorila, H.; Spector, T.D.; Cherkas, L.F.; Knaapila, A.; Silventoinen, K.; Perola, M. Same genetic components underlie different measures of sweet taste preference. *Am. J. Clin. Nutr.* **2007**, *86*, 1663–1669. [CrossRef] [PubMed]
16. Cicerale, S.; Riddell, L.J.; Keast, R.S.J. The Association between Perceived Sweetness Intensity and Dietary Intake in Young Adults. *J. Food Sci.* **2012**, *77*, H31–H35. [CrossRef] [PubMed]
17. Lipchock, S.V.; Spielman, A.I.; Mennella, J.A.; Mansfield, C.J.; Hwang, L.-D.; Douglas, J.E.; Reed, D.R. Caffeine Bitterness is Related to Daily Caffeine Intake and Bitter Receptor mRNA Abundance in Human Taste Tissue. *Perception* **2017**, *46*, 245–256. [CrossRef] [PubMed]
18. Duffy, V.B.; Peterson, J.M.; Bartoshuk, L.M. Associations between taste genetics, oral sensation and alcohol intake. *Physiol. Behav.* **2004**, *82*, 435–445. [CrossRef] [PubMed]
19. Catanzaro, D.; Chesbro, E.C.; Velkey, A.J. Relationship between food preferences and PROP taster status of college students. *Appetite* **2013**, *68*, 124–131. [CrossRef] [PubMed]
20. Dinehart, M.E.E.; Hayes, J.E.E.; Bartoshuk, L.M.M.; Lanier, S.L.L.; Duffy, V.B.B. Bitter taste markers explain variability in vegetable sweetness, bitterness, and intake. *Physiol. Behav.* **2006**, *87*, 304–313. [CrossRef] [PubMed]
21. Duffy, V.B.; Hayes, J.E.; Davidson, A.C.; Kidd, J.R.; Kidd, K.K.; Bartoshuk, L.M. Vegetable Intake in College-Aged Adults Is Explained by Oral Sensory Phenotypes and TAS2R38 Genotype. *Chemosens. Percept.* **2010**, *3*, 137–148. [CrossRef]
22. Kaminski, L.C.; Henderson, S.A.; Drewnowski, A. Young women’s food preferences and taste responsiveness to 6-n-propylthiouracil (PROP). *Physiol. Behav.* **2000**, *68*, 691–697. [CrossRef]
23. Tepper, B.J. Nutritional Implications of Genetic Taste Variation: The Role of PROP Sensitivity and Other Taste Phenotypes. *Annu. Rev. Nutr.* **2008**, *28*, 367–388. [CrossRef] [PubMed]
24. Sandell, M.; Hoppu, U.; Lundén, S.; Salminen, M.; Puolimatka, T.; Laaksonen, O.; Laitinen, K.; Hopia, A. Consumption of lingonberries by TAS2R38 genotype and sensory quality of texture-designed lingonberry samples. *Food Qual. Prefer.* **2015**, *45*, 166–170. [CrossRef]
25. Hoppu, U.; Laitinen, K.; Jaakkola, J.; Sandell, M. The hTAS2R38 genotype is associated with sugar and candy consumption in preschool boys. *J. Hum. Nutr. Diet.* **2015**, *28*, 45–51. [CrossRef] [PubMed]
26. Sandell, M.; Hoppu, U.; Mikkilä, V.; Mononen, N.; Kähönen, M.; Männistö, S.; Rönnemaa, T.; Viikari, J.; Lehtimäki, T.; Raitakari, O.T. Genetic variation in the hTAS2R38 taste receptor and food consumption among Finnish adults. *Genes Nutr.* **2014**, *9*, 433–440. [CrossRef] [PubMed]
27. Hayes, J.E.; Feeney, E.L.; Allen, A.L. Do polymorphisms in chemosensory genes matter for human ingestive behavior? *Food Qual. Prefer.* **2013**, *30*, 202–216. [CrossRef] [PubMed]
28. Hoppu, U.; Puputti, S.; Aisala, H.; Laaksonen, O.; Sandell, M.; Hoppu, U.; Puputti, S.; Aisala, H.; Laaksonen, O.; Sandell, M. Individual Differences in the Perception of Color Solutions. *Foods* **2018**, *7*, 154. [CrossRef]
29. Puputti, S.; Aisala, H.; Hoppu, U.; Sandell, M. Factors explaining individual differences in taste sensitivity and taste modality recognition among Finnish adults. *J. Sens. Stud.* **2019**. [CrossRef]
30. Spinelli, S.; De Toffoli, A.; Dinnella, C.; Laureati, M.; Pagliarini, E.; Bendini, A.; Braghieri, A.; Gallina Toschi, T.; Sinesio, F.; Torri, L.; et al. Personality traits and gender influence liking and choice of food pungency. *Food Qual. Prefer.* **2018**, *66*, 113–126. [CrossRef]
31. Törnwall, O.; Silventoinen, K.; Kaprio, J.; Tuorila, H. Why do some like it hot? Genetic and environmental contributions to the pleasantness of oral pungency. *Physiol. Behav.* **2012**, *107*, 381–389. [CrossRef]
32. Masi, C.; Dinnella, C.; Monteleone, E.; Prescott, J. The impact of individual variations in taste sensitivity on coffee perceptions and preferences. *Physiol. Behav.* **2015**, *138*, 219–226. [CrossRef]
33. Martin, C.; Visalli, M.; Lange, C.; Schlich, P.; Issanchou, S. Creation of a food taste database using an in-home “taste” profile method. *Food Qual. Prefer.* **2014**, *36*, 70–80. [CrossRef]
34. van Stokkom, V.L.; Teo, P.S.; Mars, M.; de Graaf, C.; van Kooten, O.; Stieger, M. Taste intensities of ten vegetables commonly consumed in the Netherlands. *Food Res. Int.* **2016**, *87*, 34–41. [CrossRef] [PubMed]
35. Ly, A.; Drewnowski, A. PROP (6-n-Propylthiouracil) Tasting and Sensory Responses to Caffeine, Sucrose, Neohesperidin Dihydrochalcone and Chocolate. *Chem. Senses* **2001**, *26*, 41–47. [CrossRef] [PubMed]
36. Low, J.Y.Q.; Lacy, K.E.; McBride, R.L.; Keast, R.S.J. The Associations Between Oral Complex Carbohydrate Sensitivity, BMI, Liking, and Consumption of Complex Carbohydrate Based Foods. *J. Food Sci.* **2018**, *83*, 2227–2236. [CrossRef] [PubMed]

37. Wise, P.M.; Nattress, L.; Flammer, L.J.; Beauchamp, G.K. Reduced dietary intake of simple sugars alters perceived sweet taste intensity but not perceived pleasantness. *Am. J. Clin. Nutr.* **2016**, *103*, 50–60. [CrossRef] [PubMed]
38. Bertino, M.; Beauchamp, G.K.; Engelman, K. Increasing Dietary Salt Alters Salt Taste Preference. *Physiol. Behav.* **1986**, *38*, 203–213. [CrossRef]
39. Bolhuis, D.P.; Gijbbers, L.; De Jager, I.; Geleijnse, J.M.; De Graaf, K. Encapsulated sodium supplementation of 4 weeks does not alter salt taste preferences in a controlled low sodium and low potassium diet. *Food Qual. Prefer.* **2015**, *46*, 58–65. [CrossRef]
40. Noel, C.A.; Finlayson, G.; Dando, R. Prolonged Exposure to Monosodium Glutamate in Healthy Young Adults Decreases Perceived Umami Taste and Diminishes Appetite for Savory Foods. *J. Nutr.* **2018**, *148*, 980–988. [CrossRef]
41. Törnwall, O.; Silventoinen, K.; Hiekkalinna, T.; Perola, M.; Tuorila, H.; Kaprio, J. Identifying flavor preference subgroups. Genetic basis and related eating behavior traits. *Appetite* **2014**, *75*, 1–10. [CrossRef]
42. Ludy, M.-J.; Mattes, R.D. Comparison of sensory, physiological, personality, and cultural attributes in regular spicy food users and non-users. *Appetite* **2012**, *58*, 19–27. [CrossRef]
43. Tuorila, H.; Keskitalo-Vuokko, K.; Perola, M.; Spector, T.; Kaprio, J. Affective responses to sweet products and sweet solution in British and Finnish adults. *Food Qual. Prefer.* **2017**, *62*, 128–136. [CrossRef]
44. Laaksonen, O.; Knaapila, A.; Niva, T.; Deegan, K.C.; Sandell, M. Sensory properties and consumer characteristics contributing to liking of berries. *Food Qual. Prefer.* **2016**, *53*, 117–126. [CrossRef]
45. Guido, D.; Perna, S.; Carrai, M.; Barale, R.; Grassi, M.; Rondanelli, M.; Perna, S. Multidimensional evaluation of endogenous and health factors affecting food preferences, taste and smell Perception. *J. Nutr. Health Aging* **2016**, *20*, 971–981. [CrossRef] [PubMed]
46. Cox, D.N.; Van Galen, M.; Hedderley, D.; Perry, L.; Moore, P.B.; Mela, D.J. Sensory and hedonic judgments of common foods by lean consumers and consumers with obesity. *Obes. Res.* **1998**, *6*, 438–447. [CrossRef] [PubMed]
47. Giskes, K.; Avendaño, M.; Brug, J.; Kunst, A.E. A systematic review of studies on socioeconomic inequalities in dietary intakes associated with weight gain and overweight/obesity conducted among European adults. *Obes. Rev.* **2009**, *11*, 413–429. [CrossRef] [PubMed]
48. Deglaire, A.; Méjean, C.; Castetbon, K.; Kesse-Guyot, E.; Urbano, C.; Hercberg, S.; Schlich, P. Development of a questionnaire to assay recalled liking for salt, sweet and fat. *Food Qual. Prefer.* **2012**, *23*, 110–124. [CrossRef]
49. Mojet, J.; Heidema, J.; Christ-Hazelhof, E. Taste perception with age: Generic or specific losses in supra-threshold intensities of five taste qualities? *Chem. Senses* **2003**, *28*, 397–413. [CrossRef]



© 2019 by the authors. Licensee MDPI, Basel, Switzerland. This article is an open access article distributed under the terms and conditions of the Creative Commons Attribution (CC BY) license (<http://creativecommons.org/licenses/by/4.0/>).



**UNIVERSITY
OF TURKU**

ISBN 978-951-29-7992-9 (PDF)
ISSN 0355-9483 (Print)
ISSN 2343-3213 (Online)