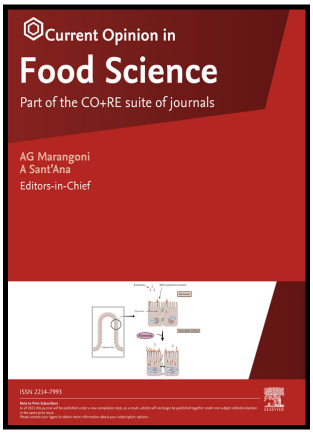

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Taste perception and oral microbiota: recent advances and future perspectives

Short title: Taste and oral microbiota

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Abstract

Human health is to a large extent affected by our food choices. Recent advances in the sensory field have shown relations between taste perception and the oral microbiota, which could open up for a new pathway to change food preferences. Here we summarize the latest insights on taste perception and oral microbiota and discuss upon the knowledge gaps. Although relationships between oral bacteria and taste thresholds have been shown, there are inconsistencies among studies, and the direction of causality needs to be proven. Within-subject longitudinal studies are recommended, and three focus areas are proposed for future research linked to causality, natural fluctuations and perturbation effects. Multidisciplinary collaboration is needed to get a full systemic overview of the complex human host-microbiome regulation and determine to what extent it is possible to modulate taste perception through the oral microbiota.

Introduction

Food choice is a complex human behaviour, motivated by various determinants related to the individual (biological, physiological and psychological factors), the context (situational and socio-cultural factors) and the food itself [1]. Understanding the drivers behind food consumption has great relevance to promote healthier food choices and consequently reduce chronic lifestyle diseases. Humans differ with respect to both dietary needs and individual preferences, where individual sensory perception has been suggested to be one of the regulators of food choices. Sensory perception is multifaceted and involves the interaction of various modalities: vision, audition, kinesthesis, as well as flavour perception a complex combination of chemosensory modalities (smell, taste, and chemesthesis) [2].

Taste is a fundamental driver of food preferences and aversions [3]. Its mechanisms are also the most studied and understood of the flavour modalities, such as the structural mechanisms of basic taste perception. Following food ingestion, chewing and enzymatic digestion of the food starts in the saliva, leading to the formation of various chemical compounds. Taste perception occurs as these compounds reach the receptor cells, located on the tongue, the soft palate and the pharynx [4], as well as in the gut [5]. The chemical activation of the taste receptors triggers a stimulation of the neuronal fibres connected to receptor cells, sending the signal to the brain for processing into a sensory experience in terms of taste quality, intensity and hedonics. Tastants originating from simple carbohydrates, acids, sodium, various plant alkaloids and amino acids, are sensed as sweet, sour, salty, bitter and umami, respectively. Taste stimuli of salty and sour have been described to work through diffusion of ions through ion channels [6]. Additionally, growing evidence for fat receptors suggests that fattiness may also be categorised as a basic taste [7].

There are large between-subject differences when it comes to taste perception [8], and variability in taste receptor expression, abundance and salivary flow rate [9] can partly explain taste sensitivity differences. Emerging research suggests that genetic predisposition and non-genetic factors such as life stage (age) or eating behaviour can influence taste perception (e.g., chewing differences will impact taste release and thus perception) [10]. Single nucleotide polymorphisms (SNPs) of taste receptors have been demonstrated to influence taste perception and individual food preferences [11]. Moreover, previous work has shown that lower sensitivity to a taste is associated with enhanced preferences towards that taste [5]. For instance, supertasters (i.e. individuals with heightened taste responsiveness to 6-n-propylthiouracil, PROP) are expected to have higher aversion to bitter taste, influencing their diet, e.g. lower consumption of bitter foods such as vegetables [12]. However, there is evidence that the relation is not necessarily the same for all tastes [13], and some contradictory results have been reported regarding the relation between sensitivity, preferences and diets [14, 15].

One possible explanation for these discrepancies may be linked to individual differences in the oral microbiota. Traditionally, the oral microbiota has been studied in relation to oral diseases, while now it has also gained attention in healthy individuals linked to sensory perception. An increased interest in the topic is evident, with recent publications suggesting a relevant role of oral microbiota in modulating taste perception and sensitivity [5, 16-27]. More broadly, this also suggests a potential role for the oral microbiota in the food choice loop influencing dietary patterns (Figure 1A). As the field is in its infancy, this short review aims to map the current state of the art and knowledge gaps in the connection between taste perception and oral microbiota in order to identify future research directions.

Oral microbiota and taste: current knowledge

Substantial evidence has shown a crucial role of the human microbiota in health and disease. Approximately the same order of magnitude of bacteria as human cells are in the human body [28], with the oral cavity as the second most densely populated site after the gastrointestinal tract. At health, the communities are thought to be in homeostasis, even after daily perturbations (e.g., by food, drinks, toothbrushing, medicines, etc.). However, when a perturbation becomes too high (e.g., frequent sugar intake), or the host is compromised by for instance disease, the microbiomes can be unbalanced (dysbiosis), impacting their modulator role on the host.

Diet is an important daily factor that can affect the oral microbiota, but recent studies suggest that the microbes might also influence dietary preferences by affecting taste sensitivity (Figure 1B). This potential link was examined in healthy individuals classified as supertasters or non-tasters [19], where the supertasters had lower detection thresholds for sweet, bitter, salt and sour tastes and had higher density of fungiform papillae. Higher abundance of certain bacteria (*Actinomyces*, *Oribacterium*, *Campylobacter*, *Solobacterium* and *Catonella*) was found on the tongue of supertasters, though their overall microbiota composition and alpha diversity were not different. Further links to food intake were explored by the same researchers [20], showing correlations between i) bacteria and taste recognition thresholds (i.e. certain taxa and salt/sour thresholds), ii) bacteria and dietary intake (e.g. *Prevotella* related to fiber intake, *Clostridia* related to protein/fat intake), and iii) taste recognition thresholds and dietary intake (low bitterness threshold linked to total energy and carbohydrate intake). Esberg et al [22] recently showed that sucrose intake and genetic variants related to taste perception (TAS1R1 and GNAT3) differed between subject groups having different salivary microbiota profiles. They also found that groups with higher sucrose intake were either characterized by lower species diversity, including aciduric- and caries-associated species, or by higher species diversity with fewer aciduric species. Relationship between salivary microbiota profiles and sucrose intake was confirmed in a following study [29]. Genetic variation in bitter taste receptor (TAS2R38) has also been related to different microbiota in the saliva [30]. Further, impairment to sense lipids (linoleic acid, LA) has been related to bacterial signatures of circumvallate papillae [16-18]. Higher abundance of the TM7 bacterial family was shown in the taster group compared to the non-tasters, and taxa of the *Porphyromonadaceae* family were associated with higher LA sensitivity, also within an obese subgroup [18] and diabetic subgroup [17]. Indeed, bacterial signatures were different between diabetic low- and high-lipid tasters, where lower LA taste perception was found in patients taking antidiabetic drug [17]. The association between bacterial phyla in saliva and in tongue biofilm and taste sensitivity, showed highest positive correlation between Bacteroidetes on the tongue and sensitivity to bitterness, while Actinobacteria in the saliva was negatively correlated to saltiness [23]. In contrast, Mameli et al [26] reported that the ability to identifying bitter taste was lower in children and adolescents with the highest abundance of Bacteroidetes in the saliva compared to those with the lowest of Bacteroidetes. Associations between tongue microbiota (several bacteria taxa and *Candida*) and poor taste were demonstrated in a large cohort of 356 older adults [24]. However, not when the data were adjusted for age and oral health status, which were the most important factors affecting the microbiota.

The mechanistic evidence that supports the role of the oral microbiota in taste sensitivity and dietary preferences remains scarce, though two dominating mechanisms have been suggested (Figure 1A): i) The oral microbiota can influence taste perception by creating a physical barrier through biofilm formation, that can limit the access of tastants to their receptors. In this sense, reduced tongue plaque through regular tongue brushing has been shown to improve taste sensitivity for saltiness and sourness in nursed elderly [31] and to heighten taste sensitivity of four of the basic tastes, except umami, in Thai older adults [32]. ii) The metabolic activity of the oral microbiota could mediate sensitivity either through consumption of tastants derived from food or saliva or through production of bioactive metabolites. Most knowledge on the metabolic capacity of the oral microbiota is derived from studies in relation to oral diseases. Takahashi [33] has summarized the overall knowledge on the metabolic pathways of the oral bacteria: Saccharolytic bacteria, such as *Streptococcus*, *Actinomyces* and *Lactobacillus*, can degrade carbohydrates into organic acids, while proteolytic/amino acid-degrading bacteria, such as *Prevotella* and *Porphyromonas*, can degrade proteins into amino acids, SCFAs, ammonia, sulphur compounds and indole/skatole. Higher numbers of saccharolytic lactobacilli have been shown in the saliva of patients with impaired sour taste perception, suggesting that acids produced by the bacteria could cause adaption to sour taste, increasing its taste threshold [34]. More efficient lactic acid production has also been observed in low sucrose-sensitive individuals compared to high-sensitive [25], suggested to be caused by higher abundance of lactogenic streptococci, though microbiota analysis was lacking in the study. In the review by Schwartz et al [27], bacterial conversion of aroma precursors into aroma compounds was addressed; they suggested that bacteria may utilize and thereby change the concentration of saliva glutamate (umami taste), which may in turn influence the perception and preference towards glutamate. Recently a novel hypothesis for explaining the variability in the perception of fatty taste in obese subjects has been postulated, involving differences in methanogenesis activity of the oral microbiota [16]. It was suggested that an oral microbiota with enhanced methanogenesis activity will release methylamine that inhibits potassium channels in taste receptor cells causing higher fatty taste signal.

Discussion and perspectives

The suggested involvement of the oral microbiota in taste perception is quite new and deserves further attention as it could give new tools to support healthy eating. In particular, the causality behind the highlighted connections is still poorly understood and needs further investigation.

It is known that bacteria interact with their host directly or indirectly through their metabolism. The scientific evidence for this is complex, but often involves some kind of perturbation, showing a changed response at either gene, bacteria or community level. Perturbation of the oral microbiota community have been demonstrated in several studies, e.g., by mouthwash [35], but to our knowledge changes in taste perception of the same host have not been explored. However, the abovementioned effect of tongue brushing causing enhanced taste sensitivity [32], demonstrates that the microbiota load on the tongue, does play a part in taste modulation. Further, there seems to be a general assumption that high consumption of a tastant causes reduced sensitivity to that taste, though studies report effects in both ways. Whether or how the oral microbiome is involved in this feed-back loop needs to be elucidated, though variation between individuals in microbiota load or composition is likely to influence the microbiotas' metabolic capability to modulate tastants. For instance, an oral microbiota with enhanced capability to metabolize sucrose (available as tastant) would result in higher lactic acid production, a feature observed in low sucrose-sensitive individuals compared to high sucrose-sensitive individuals [25]. The enhanced production of lactic acid would both deplete sucrose and hinder the perception of sweetness by mixture suppression effect [36]. Thus, between-subject variation in the oral microbiota may be one of several factors causing between-subject variation in taste perception. Indeed, age and oral health status were found to be confounders in the relationship between oral microbiota and taste in older adults [24]. To have better control of these and other confounders in future studies, one recommended approach would be to study temporal variations within subjects.

Limited studies exist on the within-subject stability of either the oral microbiota or the taste perception. Understanding their normal fluctuations in both short-term perspectives (e.g., time of day, variations in dietary intake, seasonal variation, hormone levels) and long-term perspectives (e.g., during life-stages), would be important to identify regulatory factors. Studies on within-subject variations could be based on following subjects categorized by known confounders (e.g., by gender, body mass index status, diet preferences, taste sensitivity). Studies following a steady, trained sensory panel may be useful to obtain precise and reliable data on sensory sensitivity and microbiota fluctuations.

Intervention studies including specific perturbations, such as diet changes, could be used to study causality effects between taste perception and oral microbiota community. However, as many factors are involved, only small effects can be anticipated and therefore meta-analysis of multiple studies should be considered. Ethical and practical considerations in these types of studies are important, as controlled studies are complex to conduct with humans. The individual variation in microbiota composition is high, potentially leading to low statistical power. In the study by Cattaneo et al [19], only a few bacterial genera were detected as different between supertasters and non-tasters, although no differences were detected at the community level. Moreover, the choice of statistical method has been shown to have an impact on true- and false discovery rates in intervention studies [37] and recall rates may be low in studies with a small sample size [38]. This implies that findings at lower levels in the bacterial phylogeny (genus or species) are highly uncertain and need to be corroborated with further studies. Further, a possible laboratory approach is to use oral *in vitro* simulations [25] by inoculating a certain stimulus with oral microbiota from different subject groups, to demonstrate how metabolization may be connected to microbiota. Note that this approach would also disengage the effect of the oral microbiome from a potential effect of the gut microbiome, which has been related to taste perception [5, 39]. Indeed, a role for the gut microbiome in terms of taste perception complicates this research field but should preferentially also be included in the human studies. Differences between the role of the saliva and tongue microbiota in relation to taste perception should also be further explored, though it is plausible to assume that metabolites closest to the taste buds, might influence more on the taste perception. Current advances in the omics field also open new possibilities to integrate data from the microbiota (taxa, genetic potential or expression) with proteomics and metabolomics to determine potential mechanisms when connections between the oral microbiota and taste perception are demonstrated.

Conclusions

We propose that future studies should focus on (Figure 1C) determining 1) the causality between the oral microbiota and taste perception, e.g. focusing on microbial and metabolic changes in relation to taste sensitivity following within-subject perturbations, 2) the natural pattern of within-subject fluctuations in oral microbiota and taste sensitivity along the day, seasons and life stages, and 3) if dietary and/or behavioural interventions can be used to modify the oral microbiota to move taste perception in a direction that can enhance healthier food choices. Moreover, we believe multidisciplinary collaboration between researchers within oral health, sensory science, medicine, microbiology and omics is needed to resolve these complex knowledge gaps.

Conflict of interest statement

The authors declare no competing interests.

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Figure Caption

Figure 1. Suggested role of the oral microbiota in the food choice loop. A) Food choice loop, showing how different factors, such as the oral microbiota, can influence taste perception and consequently food choices. Potential mechanisms of the oral microbiota are indicated: i. The involvement of the oral microbiota in food digestion (metabolic activity) that can modulate the level of tastants. ii. The oral microbiota can create a physical barrier through biofilm formation, that can limit the access of tastants to their receptors. B) Current areas where association with the oral microbiota has been demonstrated. C) Three suggested future directions for research. Created with BioRender.com.

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CRediT author statement

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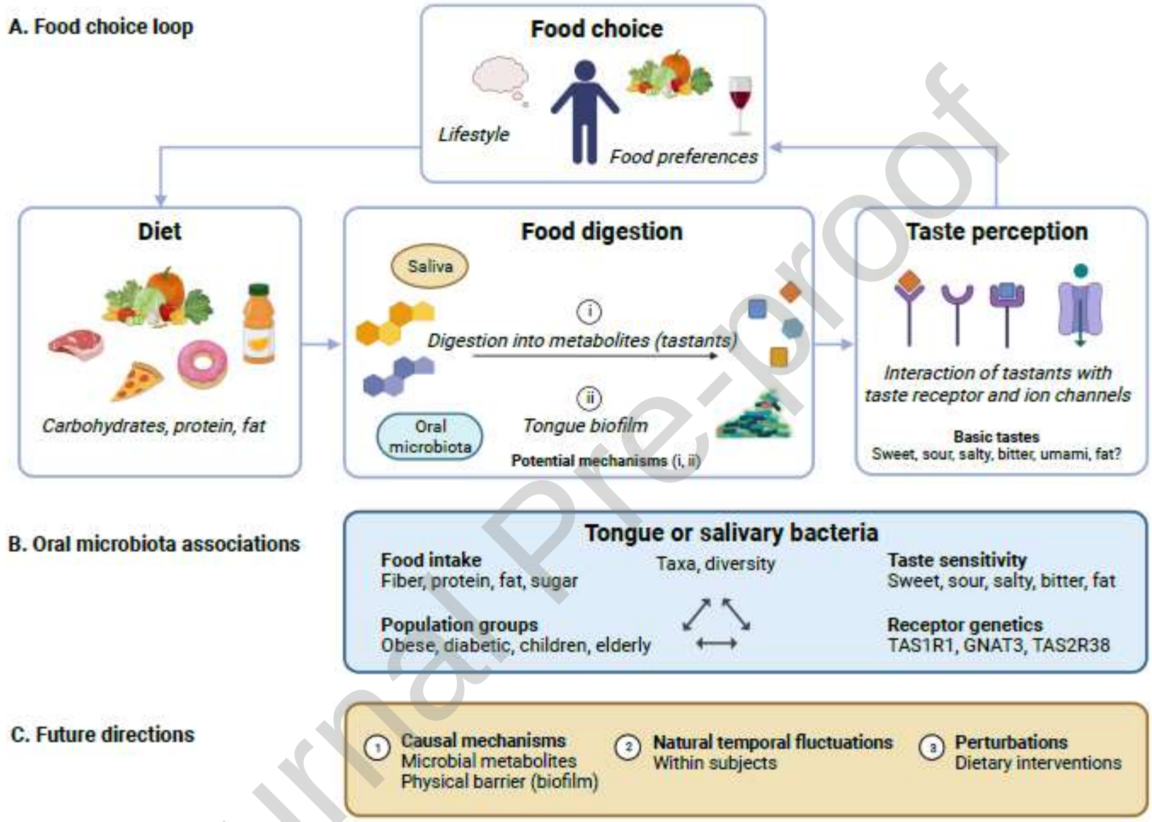

Fig 1

Highlights

- Recent literature suggests a connection between oral microbiota and taste sensitivity
- Interactions between oral microbiota and taste sensitivity may influence food choices
- Evidence on causal effects and the mechanisms behind the associations are missing
- Mapping individual variation in taste sensitivity and oral microbiota is needed