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Main effects of human saliva on flavour perception and the potential contribution to food consumption

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> Whole saliva is a mixture composed by the secretions of the major and minor salivary glands and the crevicular fluid, bacteria, cells and food debris. Its properties (flow and composition) are highly intra- and inter-individually dependent and reflect the health status of individuals. Saliva plays a key role in the eating process and on the perception of flavour. Flavour corresponds to the combined effect of taste sensations, aromatics and chemical feeling factors evoked by food in the oral cavity. It is a key determinant of food consumption and intake. This review summarises the evidence about the role of saliva in flavour perception and its potential contribution to food intake. All in all, evidence on the relationships between salivary parameters and both food perception and feeding behaviour is presented. This review emphasises that new studies accounting for the effect of salivary constituents on flavour alterations due to diseases (i.e. cancer, obesity and diabetes) are lacking and are expected in the incoming years.

> > Human saliva: Flavour perception: Food consumption: Nutritional status

Flavour corresponds to the combination of sensations that includes taste, aroma and trigeminal sensations. It has a major role in the final perception of food, its enjoyment and thus, is considered the main endogenous factor for food preferences and intake. In this regard, differences in flavour perception across individuals (e.g. low-salt sensitivity) could explain unbalanced food behaviours that lead to food-dependent illnesses (e.g. hypertension). Moreover, different illnesses or therapies (such as chemotherapy or radiotherapy in cancer patients) might alter flavour perception⁽¹⁾ and decrease the enjoyment of food, which might compromise the individual's nutritional status. Thus, understanding the factors affecting flavour perception may provide clues to drive food consumption towards keeping a proper nutritional status.

Apart from food characteristics, flavour perception is strongly influenced by the oral physiology. During the eating process, food is broken down and impregnated by saliva to form a food bolus. Tastants and non-volatile (e.g. trigeminal) compounds are released from food and dissolved in saliva, where they migrate and bind to the taste and trigeminal receptors, depending on their affinity. Aroma (volatile) compounds are released from food into air or saliva and reach, via the airflow, the olfactory receptors located in the nasal cavity (retronasal olfaction). These processes greatly depend on the individual's oral parameters and particularly on the amount and the composition of secreted saliva. Accordingly, it is not surprising that differences in salivary parameters might have an influence on differences on perception across individuals and also on differences within an individual throughout their life (i.e. as a function of alterations in salivary flow or in the chemical composition of saliva due to illnesses or biological changes such as $ageing)^{(2)}$.

The aim of this literature review was to summarise the existing findings on the effects of human saliva on flavour perception and the possible contribution to food consumption.

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Abbreviation: PRP, proline-rich proteins.

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Human saliva: properties and functions

Whole saliva is a complex mixture composed of the secretions of the major (submandibular, sublingual and parotid; 90%) and minor salivary glands (10%), together with the crevicular fluid, cellular debris and bacteria. Its composition and flow are dependent on endogenous (circadian rhythms, age, sex and several disease states) or exogenous factors (diet and pharmaco- $\log(a) = \log(a)^{(3-6)}$. For young healthy individuals, interindividual variability of saliva is considered more important than intra-individual variability⁽⁷⁾. However, salivary flow and composition vary throughout the day. At rest (unstimulated saliva), salivary flow is composed at 70, 20 and 5 % by submaxillary, parotid and sublingual glands, respectively. During mastication (stimulated saliva), the parotid contribution can represent up to 60 %, while those of submaxillary and sublingual glands decrease by 40 and 2 %, respectively. The composition of the secreted fluid varies strongly as a function of the type of gland. For instance, proline-rich proteins (PRP) represent up to 70 % of the protein secreted by the parotid glands and are almost absent from the other glands' secretion. It should be noted that this composition is also susceptible to change as a function of diet. Indeed, numerous studies have reported that the presence of PRP in saliva depends on the consumption of $tannins^{(8)}$. In mouse and rats, the secretion of these proteins can be induced by a tannin-rich diet⁽⁹⁾. The secretion of other salivary proteins, such as α -amylase, has also been reported to be dependent on the diet⁽¹⁰⁾. Therefore, it appears that the composition of saliva is under a dynamic control modulated by the food consumed.

Saliva has many functions that are needed for proper protection and functioning of the human body. These functions can be of protective nature: maintaining oral mucosal structures, taste buds and taste-sensing cells integrity and microbial homeostasis, healing of several mucosal lesions, wounds and ulcers, removal of desquamated epithelial cells, leucocytes and food debris by swallowing, the formation of tooth pellicle with physico-chemical defense properties, among others. Consequently, disruptions in saliva contribute to conditions such as tooth decay and respiratory tract infections. Another function of saliva is related to its capacity to lubricate the oral cavity allowing speaking and communicating but also to form a food bolus that can be swallowed safely. Saliva plays other essential roles during the food oral processing. Saliva is the medium that bathes the taste receptors in the oral cavity and in which aroma and taste compounds are dissolved when food is eaten⁽⁷⁾. Saliva moistens food and binds food particles into a coherent bolus suitable for swallowing⁽¹¹⁾. In addition to acting as a facilitator of flavour release by solubilising flavour active compounds during food structure breakdown, saliva plays other important roles in chemosensory perception. Saliva contains enzymes and molecules that can interact with food components. During the food oral processing, salivary components destabilise colloidal systems such as emulsions that participate in the formation of soluble and insoluble aggregates and

breakdown compounds through enzymatic action. All these mechanisms participate in food digestion. Flavour compounds are dissolved in saliva depending on their hydrophobicity and can bind to salivary proteins as a function of their affinity. Binding to salivary proteins can lead to scavenging of flavour compounds (e.g. tan-nin–PRP interactions)^(12,13) or facilitate their transport (fatty acids–lipocaline-1 interactions⁽¹⁴⁾), modifying their solubility and profile of release and finally the concentration in the proximity of the receptors⁽¹⁵⁾.

Contribution of saliva to flavour perception

Consequent to the information exposed earlier, it is stated that flavour perception corresponds not exactly to the food characteristics but to the food-saliva mixture⁽¹⁶⁾. In this regard, it has been shown that the concentration of taste compounds dissolved in saliva correlates better to taste perception than the initial concentration of tastants in the food material⁽¹⁷⁾. Thereby, salivary characteristics such as flow rate⁽¹⁸⁾, composition^(19,20) and buffer capacity⁽²¹⁾, modulate flavour perception through different mechanisms. We are now going to summarise the main evidence about the role of saliva in the different flavour modalities.

The role of saliva in taste perception

Taste is possibly, together with astringency, the most studied flavour modality in relation to salivation. In human subjects, it is assumed that the taste system can differentiate five primary sensory qualities (sweet, umami, sour, salty and bitter) that are associated with palatability, thus inducing food acceptance or rejection. Sweet, umami and salt modalities allow recognition of energy-rich food and maintenance of electrolyte balance(22). By contrast, bitter taste likely acts as a warning mechanism against toxic or harmful chemicals $^{(23,24)}$, even if human subjects regularly choose to ingest natural and synthetic bitter-tasting compounds in foods, beverages and medications⁽²³⁾. In addition to bitter taste, the sour taste modality is thought to act as a brake or warning against noxious foods⁽²²⁾. In addition, the ability to taste fatty acids has been recently proposed as a sixth primary sensory quality⁽²⁴⁾ and has been confirmed by different groups^(24–26).

Taste sensitivity varies greatly among individuals, which means that the same stimulus can taste different in two individuals. These differences depend, in part, on cognitive factors, such as cultural and social differences, and in part on physiological factors, from which the role of saliva is increasingly recognised. As shown by Ferry *et al.*⁽²⁷⁾, an efficient mixing with saliva facilitates the release of tastants from the food matrix to the saliva phase and their transport to taste receptors. During this process, some salivary constituents chemically interact with taste substances. Moreover, saliva protects the taste receptors from damage by dryness and bacterial infection⁽²⁸⁾. However, the exact mechanisms of how saliva

influences and modulates taste sensation are still a challenging field of research. Data clearly indicate the major role of several salivary proteins, such as salivary carbonic anhydrase VI (gustin), PRP, cystatins, α -amylases, histatins, salivary albumin and mucins^(29–34). Other proteins, such as glucagon-like peptide-1, salivary Ig-A, zinc- α -2-glycoprotein, salivary lactoperoxidase, salivary prolactin-inducible protein, salivary lipocaline-1 and salivary molecular heat shock proteins (HSP70/HSPA)^(30,35) are also expected to play an important role. Furthermore, factors including salivary flow rate, buffer capacity and ionic composition of saliva should also be considered.

The role of saliva in taste perception: saltiness

Sodium is an important mineral and essential part of a balanced diet. It is also important for seasoning food, food texture and preservation. Sodium is perceived through epithelial Na⁺ channels allowing the diffusion of sodium through the cell membrane. This diffusion depends on a gradient of concentration between extraand intracellular fluid.

It has been reported that elevated salivary flow rates are correlated to lower sodium release and saltiness perception⁽³⁶⁾. This could be due to the high volume of saliva that implies a limited reabsorption of sodium within the salivary ducts^(19,36). Moreover, Heinzerling *et al.*⁽¹⁸⁾ have validated this hypothesis in a modified-saliva strategy. After excluding parotid saliva and adding artificial saliva in the mouth close to the parotid duct at preset flow rates, they observed significant decreases in perception with increasing salivary flow rates for sodium chloride. Accordingly, it can be stated that young healthy individuals with high salivary flows will perceive less salty taste than individuals with low salivary flow. However, in acutely hospitalised elderly, it has been seen that salty taste was particularly impaired in patients with dry mouth⁽³⁷⁾. This could be due to cognitive problems in these patients or a cognitive mechanism of adaptation in link with the need of a clearance of the extracellular medium. Indeed, the endogenous sodium levels in saliva have been found to define the threshold of salt taste perception(17,38,39). Therefore, it is necessary to exceed the salivary sodium concentration to activate this sensation.

Apart from the ion concentration, it has been observed by protein quantitation using isobaric tags for relative and absolute quantitation and nanoliquid chromatography and tandem MS (nano-liquid chromatography–MS/MS) that the salivary proteome pattern affects human salt taste sensitivity in young individuals⁽⁴⁰⁾. Moreover, proteolysis and carbonic anhydrase 6 have been associated with the liking of saltiness (positively and inversely, respectively)⁽⁴¹⁾.

Finally, it has been observed that to understand saltiness perception, it is important to consider the whole food matrix and the diffusion of salt. Indeed, the efficiency of the mixing of food and saliva and the transport of the tastants to the taste receptors will be dependent on the food structure and on how food is destructured during the eating process. This is the case for the perception of saltiness in starch-thickened foods⁽²⁷⁾. In that case, it was observed that high α -amylase activities were linked to decreased saltiness perception in starches exhibiting a granular structure. Microscopic evidence showed that the enzyme could disrupt such structures, and this was associated with a decreased mixing efficiency and, consequently, a reduced transport of sodium to the saliva phase and to the taste buds.

The role of saliva in taste perception: sweetness

The effect of salivary flow on sweetness sensitivity is not so clear as in the case of salt. Heinzerling *et al.*⁽¹⁸⁾, following the same saliva-modified strategy explained earlier, did not find any correlation between salivary flow and sweetness perception. Moreover, Bonnans and Noble⁽⁴²⁾, studying the temporal perception of sweetness in nineteen individuals (classified in three groups according to their parotid salivary flow (low, medium, high)), did not observe significant differences in any timeintensity parameter of sweetness perception across groups, although the low-flow subjects reached maximum intensity later than the high-flow group. This difference could be due to the type of receptors involved. Indeed, sweet perception involves the binding of sweet molecules onto the heterodimer human taste type 1 receptor 2 and 3 (hT1R2/hT1R3), which does not require a gradient of concentration, similar to in the case of sodium detection. As in the case of salty taste, in acutely hospitalised elderly, it has been seen that sugar taste was particularly impaired in patients with dry mouth $^{(37)}$.

Regarding the effects of saliva composition on sweet perception, it has been seen that saliva pH affects the sweetness sense⁽⁴³⁾. Moreover, salivary proteome and glucose levels have been related to sweet taste sensitivity in young adults⁽⁴⁴⁾ and α -amylase concentrations with taste scores in healthy children⁽⁴⁵⁾. In addition, some relationships between salivary hormones, such as leptin and the sweet taste receptor genes (TAS1R2/TAS1R3) have been related to sweet taste sensitivity in adults⁽⁴⁶⁾ and children⁽⁴⁴⁾. Although it has been found that these associations are sex and BMI-dependent, the mode of action of salivary leptin at the taste receptor level is not clear and should be elucidated in future studies.

Finally, saliva can also modify sweet taste by acting on the food matrix. The hydrolysis of polymers, such as starch by salivary α -amylase, can lead to smaller sugars that can be detectable by the sweet receptors in the mouth^(47,48).

The role of saliva in taste perception: sourness

In adults, it has been seen that individuals with high salivary flows can neutralise the acidity of sour solutions more efficiently than individuals presenting low salivary flows⁽⁴⁹⁾. Authors hypothesised that this could be due to a higher dilution effect or buffering capacity when the flow is greater. Interestingly, this group also presented a steeper slope of rising perception and a quicker NS Proceedings of the Nutrition Society

rising phase, which was translated in that high-flow subjects exhibited higher perceived intensity for acid solutions than low-flow subjects⁽⁴⁹⁾. However, the effects of saliva on sourness seem very study-dependent. For example, Heinzerling et al.⁽¹⁸⁾ found an inverse correlation between salivary flow and sourness perception. Conversely, Bonnans and Noble⁽⁴²⁾ did not observe significant differences in any time-intensity parameter sourness perception studying the temporal perception of sourness in individuals with the different parotid flow. The different acids and concentrations tested in the different studies could be at the origin of the variability of the results, as sourness is not only related to $pH^{(49)}$, but also to titratable acidity(49,50). Indeed, sour tastants have to diffuse through the membrane to be perceived inhibition of proton-sensitive channel. via the Therefore, differences in membrane permeability of the tastant as a function of the structure of the molecules can be at the origin of the divergent results.

The role of saliva in taste perception: bitterness

In human subjects, twenty-five receptors belonging to the T2R receptor family have been reported. Each of these receptors binds from two to about fifty compounds, allowing the detection of more than 1000 compounds. Mutation in these receptors can greatly influence the perception of bitterness as reported for 6-n-propylthiouracil sensitivity⁽⁵¹⁾. Regarding the effect of saliva, in middleaged adults, no relationships have been shown between bitterness perception and salivary flow⁽¹⁸⁾. However, in healthy children, Marquezin *et al.*⁽⁴⁵⁾ found a significant correlation between bitter taste sensitivity and unstimulated salivary flow rate.

Moreover, it has been observed that salivary protein profiles are linked to bitter taste acceptance in infants⁽⁵²⁾. The best predictors of bitter taste acceptance are a secretory component, zinc- α -2-glycoprotein, carbonic anhydrase 6, lactoperoxidase, prolactin-inducible protein and S-type cystatins. Additionally, a trend has been shown between bitter sensitivity and saliva interferon- α ⁽⁵³⁾, two specific basic PRP⁽⁵⁴⁾, amylase fragments, immunoglobulins and serum albumin and/or serum albumin fragments, cystatin SN⁽⁵⁵⁾, gustin (carbonic anhydrase VI) gene polymorphism, salivary zinc and BMI in human subjects⁽²⁹⁾. Finally, a relationship between salivary leptin levels and bitter perception dependent on sex and BMI was found by Rodrigues *et al.*⁽⁴⁴⁾. Actually, it has been suggested that sex and BMI variables might influence saliva composition which may affect bitter taste response ⁽⁴⁴⁾.

The role of saliva in taste perception: umami

Although some studies have addressed the role of umami taste in oral and overall health (as a potent stimulant of saliva flow or to remedy hypogeusia)^(56–59), the role of saliva (flow or composition) in umami perception has been little explored. To the author's knowledge, only one study had investigated the possible relationship

between endogenous glutamate levels in the whole saliva and umami responses⁽²⁰⁾. They observed that individual differences in salivary glutamate concentrations in stimulated whole saliva may influence perceived pleasantness, but not intensity, of suprathreshold in sodium monoglutamate solutions⁽²⁰⁾.

The role of saliva in taste perception: fattiness

Fat perception is a complex sensation dependent on different sensory cues, such as texture, olfaction and taste⁽⁶⁰⁾. Many researchers state that orally expressed lipases might hydrolyse TAG and, consequently, release NEFA. However, fatty acids are poorly soluble in aqueous solvents, which could preclude their access to their sensory receptors. Thus, it has been hypothesised that salivary proteins could play a role in the transport of fatty acids in the mouth. The salivary lipocalin-1 presents a hydrophobic pocket at the centre of its structure. This pocket is called the calice. Fatty acids can be embedded in this pocket as a function of the length of the aliphatic chain and the number of insaturation⁽⁶¹⁾. In this hypothesis, fatty acids are transported by lipocalin-1 to taste buds to mediate fat taste perception (and even creaminess)⁽⁶²⁾. In this regard, relationships between salivary parameters (lipolysis, lipocalin, antioxidant status, protein amount, lysozyme activity and salivary flow) and fat-liking or perception have been found by different authors^(7,60,63). Mejean *et al.*⁽⁴¹⁾ have recently found a positive association between the liking for fat and salivary flow and proteolysis. Moreover, a recent paper has shown that the basal NEFA concentration in human saliva is related to the salivary lipolytic activity⁽⁶⁴⁾, and authors have hypothesised that this could have an effect on the taste perception of fatty acids, although this role needs to be elucidated in the future. However, the salivary enzyme(s) responsible for this lipolytic activity has(ve) still not been identified. As a result, this hypothesis is questioned by some researchers who believe that a lingual lipase cannot make a noticeable contribution due to its very low concentration in saliva and argue that fatty sensation is likely detected through an oral tactile mechanism⁽⁶⁵⁾. For example, a study performed by Chen and Eaton⁽⁶⁶⁾ showed no significant increase in fattiness/creaminess sensation after consumption of a rich NEFA fluid of controlled viscosity suggesting that NEFA may have a limited role in fatty sensation. There is no doubt that research findings from various studies are somewhat contradicting and further studies are needed to clarify the possible influences of saliva properties (i.e. lingual lipase) on the oral sensation of oil/fat related sensory features.

The role of saliva in trigeminal perception

Trigeminal perception addresses the sensations resulting from irritation caused by chemical stimuli in the mouth. It involves both the activation of chemico- and mecano-receptors and includes so-called astringency, cooling and/or heating sensations. Astringency has been the modality most extensively studied since it plays a key role in food acceptability.

Astringency is a trigeminal sensation⁽⁶⁷⁾ that is described as a drying-out, roughening and puckery sensation felt in the mouth. This sensation is generally felt during the consumption of plant-based food and beverages such as red wines, teas and some fruit. It is produced by the binding and precipitation of salivary proteins and phenolic compounds, such as tannins. However, the molecular mechanisms behind this perception are still unclear. Astringency is generally described as a tactile sensation, and it is known that salivary PRP have a particular affinity for tannins⁽¹²⁾. There are two main hypotheses explaining the tactile origin of astringency. One hypothesis postulates that the precipitation of salivary proteins, and in particular of PRP, from saliva reduces its lubricating properties, leading to an increase in friction force within the oral cavity⁽⁶⁸⁾. In agreement with this hypothesis, it has been observed that the experimental aggregation threshold of PRP by tannins is close to the perception threshold of the tannins studied⁽¹³⁾. The second hypothesis proposes that this sensation is due to the direct interaction of tannins with the mucosal pellicle, leading to the loss of its lubricating properties and to the increase in friction force at the surface of the oral mucosa⁽⁶⁹⁾. In this second hyptothesis, PRP play a protective role and prevent the sensation of astringency through binding, aggregation and ultimately, precipitation of tannins. Recently, Ployon et al.⁽⁷⁰⁾ have shown that tannins aggregate the mucosal pellicle, while the presence of PRP precludes this aggregation. This observation supports the second hypothesis described earlier. accordance with this finding. Schwarz and Hofmann⁽⁷¹⁾ suggested that astringency might be related to the amount of unbound astringent compounds rather than to the precipitation of polyphenol-protein complexes. The authors measured the *in vitro* binding activity of salivary proteins (in unstimulated saliva) to different astringent stimuli and related the data to sensory threshold concentrations. It was observed that the astringent stimuli perceived at low concentrations (i.e. low thresholds) did not show protein-binding activity. Moreover, low salivary levels of proteins could be correlated to an increased astringency perception⁽⁷²⁾, while subjects who were able to rapidly restore their initial protein contents were observed to be less sensitive to astringency $^{(33)}$.

Although there is evidence that astringency arises from tactile stimulation, it can be argued that not all astringent compounds have the same impact on saliva. Rossetti *et al.*⁽⁷³⁾ reported that the effect of catechins on the lubricating properties of stimulated saliva was dependent on the type of catechin. Epigallocatechin gallate interacted with salivary proteins, reducing saliva lubricity and increasing the friction coefficient, while epicatechin had no effect on lubrication. Perceived astringency, however, was comparable for both types of catechins. This observation could be explained by the involvement of trigeminal receptors to astringent compounds. Indeed, two different experiments using rat cell models, have reported that tannins or their metabolites can activate both

trigeminal transient receptor potential channels⁽⁷⁴⁾ and a protein G coupled receptor⁽⁶⁷⁾. Therefore, astringency could be the result of the activation of both trigeminal mechano- and chemo-receptors.

Finally, it should be noted that the astringency sensation is always felt alongside bitterness⁽⁷⁵⁾, which involves perception by specific tannin-taste buds present on the taste papillae⁽⁷⁶⁾.

The role of saliva in aroma perception

Aroma perception is an important factor driving food preferences and choices since it allows for thousands of different sensory notes in foods (e.g. peach, orange, banana, strawberry, apple, etc.) to be distinguished. When volatiles are released from food into the saliva phase, interactions may occur between volatile compounds and salivary components (e.g. mucins and enzymes). These interactions might result in chemical and biochemical reactions, which could affect the volatile concentration and retronasal aroma perception^(77,78). However, due to the higher complexity of this flavour modality to be measured, most of the studies on this topic have been carried out in well-controlled in vitro situations that could not have represented the complexity and dynamics occurring at the human mouth level. To the authors' knowledge, all the studies carried out in *vitro* or *ex vivo* have shown effects of human saliva on aroma compounds⁽⁷⁹⁻⁸⁵⁾, although these effects have been dependent on the pretreatment of the saliva samples and on the food matrix and analytical techniques employed. Generally, it can be assumed that salivary proteins, such as mucins and α -amylase can 'trap' aroma compounds depending on their structure⁽⁸⁴⁾. Moreover, enzymes present in saliva can metabolise some aroma compounds⁽⁸²⁾ or glycosidic aroma precursors⁽⁸¹⁾ modifying the temporal aroma perception^(81,86).

In relation to interindividual variability of saliva properties on aroma compounds, two studies should be mentioned. The first one has shown how differences in saliva composition (such as protein content and total antioxidant capacity) could be responsible for differences in aroma release⁽⁸²⁾</sup>. The second one⁽⁸⁷⁾ showed that saliva from obese individuals presented a diminished aroma release compared with normo-weight subjects, and this fact was again related to the total protein content and the total antioxidant capacity determined in the saliva samples. It can be hypothesised that the saliva from obese individuals might suppress sensitivity to perceive aromas, which could impel these individuals to eat more to be satiated. Therefore, these ex vivo studies have supposed a first step showing that saliva might exert an important role in aroma perception. However, in vivo studies on this topic are still scarce. This could be explained by the fact that the measurement of in vivo aroma release in real time requires sophisticated instruments (such as proton transfer reaction-mass spectrometers) that are not available in many laboratories. Moreover, the calculation of aroma perception thresholds is much more complex than in the case of taste,

since a large amount of aroma notes exist compared with the six basic tastes and measurement requires equipment, such as an olfactoscan that is only available in specialised laboratories. However, some interesting work has been released in recent years. Feron et al.⁽⁸⁸⁾ have studied the relationships between in vivo aroma release and saliva properties during cheese consumption. They showed that salivary flow, lysozyme and sodium levels determined in stimulated saliva samples were the most significant salivary parameters explaining their aroma release data⁽⁸⁸⁾. In particular, salivary flow was negatively correlated to aroma release, which can be explained by a higher dilution of aroma compounds in saliva or by a quicker aroma clearance in the human mouth. The involvement of the other two variables in the aroma release data is not clear at present. Moreover, in a recent study, Guichard *et al.*⁽⁸⁹⁾ found that aroma perception in model cheeses is explained by salivary composition. Lipolytic activity together with sodium content was identified as the salivary parameters that have a greater noticeable impact on aroma perception of cheese products⁽⁸⁹⁾. Individuals with low sodium content in saliva perceived salt-congruent aromas as more intense, while individuals with high lipolytic activity perceived fatcongruent aromas as more intense.

Potential contribution of saliva to food intake

The evidence earlier indicates that saliva influences flavour perception, which is considered a driver of food intake. In this section, the existing evidence on the effects of saliva on food intake will be reviewed.

A recent study⁽⁹⁰⁾ has investigated the relationship among salivary lipolysis and α -amylase activities, as well as zinc concentration with food preferences and choices in people presenting different BMI (n 42). The data showed that α -amylase and lipolysis activities were 1.8 and 2.4-fold higher in overweight than in normal weight subjects, respectively. Conversely, overweight subjects showed a 33 % reduced salivary zinc concentration compared with normal weight subjects. A positive correlation between lipolysis activity and individual preference for high-fat foods and fat content consumption was found. Moreover, it was hypothesised that the higher lipolysis activity found in obese subjects could not ameliorate the sensitivity to fat perception in these subjects who might experience an altered gustin activity due to a reduced concentration of salivary zinc. This condition might influence the high-fat food taste preference and consumption frequency in obese subjects who need more fatty foods to compensate the low oral fat sensitivity. All in all, the data suggested that high salivary lipolysis activity in overweight subjects could be an adaptive response to the low fat-taste perception related to the reduced zinc concentration. Nevertheless, it cannot be ruled out that factors other than diet might influence salivary α -amylase activity in overweight subjects. Mejean et al.⁽⁴¹⁾ recently evaluated the association between salivary flow and composition and the liking of fat, saltiness and sweetness and the usual nutrient intake in an adult

French population (n 282 adults). Authors found that total antioxidant capacity determined in the saliva samples was positively associated with simple carbohydrate intake and inversely to complex carbohydrate consumption. Moreover, other correlations found were that amylolysis was positively associated with both total and simple carbohydrate intake and inversely with the liking of sweetness; salivary flow was positively associated with the liking of fat; proteolysis was positively associated with the liking of saltiness and fat; and carbonic anhydrase VI was inversely associated with the liking of saltiness. Associations between food consumption patterns and saliva composition have also been found in children with eating difficulties⁽⁹¹⁾. Regarding other salivary parameters, it has been found that salivary leptin and TAS1R2/TAS1R3 polymorphisms are related to sweet taste sensitivity and carbohydrate intake in young individuals⁽⁴⁶⁾.

A recent systematic literature review has summarised the existing scientific evidence about the association between a reduced salivary function and food consumption in elderly people. Salivary hypofunction was associated with a decrease in the objective chewing and swallowing abilities and taste perception. Moreover, most of the selected studies showed a relationship between salivary hypofunction and food consumption (in terms of appetite loss, unbalanced dietary intake and malnutrition), although since all the studies were cross-sectional, no causality could be established⁽²⁾.

These studies, although scarce, are very valuable since they have been pioneers in showing the associations between salivary composition and food liking or nutrient intake, which suggests the influence of saliva characteristics in food behaviour. Future longitudinal studies controlling for confounding factors to assess the interplay among salivary components, food intake and nutritional status are needed.

Conclusions

Saliva is the first biological fluid in contact with food and therefore of high importance for the eating process. Since the characteristics of saliva vary greatly across individuals and throughout life, understanding the differences in salivary properties might explain the differences in flavour perception. The studies mentioned earlier mostly support this hypothesis and describe the different ways in which salivary parameters can contribute to flavour perception (taste, aroma and trigeminal sensation) together with its potential contribution to food intake. Aroma is the flavour modality least studied, probably due to its higher complexity and degree of specialisation required to measure the complex mechanisms occurring in the release of aroma *in vivo*.

It is important to have in mind that due to saliva being a complex and dynamic fluid, its flow and composition may qualitatively and quantitatively vary under different conditions of stimulation or as a consequence of variations on the physiological status (due to illnesses or the ageing process). Therefore, the interactions between saliva and flavour or health status occur in both directions according to a vicious circle. Saliva can modify flavour, but the flavour stimuli can also modify saliva secretions; accordingly, several illnesses (e.g. obesity and cancer) might modify the salivary parameters, which in turn will affect food behaviour and nutritional status. Moreover, saliva controls the oral health environment; thus, unbalanced saliva secretions might compromise oral microbiota or tooth status, which in turn, will affect food intake. Therefore, this review puts in the spotlight that more work has to be done in this area to clarify the role of saliva in food behaviour, and mainly longitudinal studies controlling for cofounding factors are needed. This information could be used by nutritionists and/or health practitioners together with the food industry to develop food strategies to increase people's quality of life.

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Conflict of Interest

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Authorship

All authors contributed to this review.

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