DETERMINANTS OF TANNIN-RICH FOOD AND BEVERAGE CONSUMPTION: ORAL PERCEPTION VS.

PSYCHOSOCIAL ASPECTS

Elsa Lamy¹, Cristina Pinheiro^{1,2}, Lénia Rodrigues¹, Fernando Capela e Silva^{1,3}, Orlando Silva Lopes^{1,3}, Sofia Tavares^{4,5}, Rui Gaspar⁶

¹Institute of Mediterranean Agricultural and Environmental Sciences (ICAAM), University of Évora, Évora, Portugal; ²Department of Zootechnics, University of Évora, Évora, Portugal; ³Department of Biology, University of Évora, Évora, Portugal; ⁴Education and Psychology Research Center (CIEP), University of Évora, Évora, Portugal; ⁵Department of Phsychology, University of Évora, Évora, Portugal; ⁶William James Center for Research, ISPA-Instituto Universitário, Lisbon, Portugal

1. INTRODUCTION

Tannins constitute a heterogeneous group of polyphenolic compounds, present in a considerable number of vegetable foods. The term tannin is derived from the properties of these compounds to interact and precipitate macromolecules, such as proteins, make them able to tan animal leather [1]. Subsequently a general definition for tannins emerged, referring them as high molecular weight polyphenols that precipitate protein from solution [2].

Tannins have been found in a variety of plants utilized as human and animal food. Structurally, they can be divided in two different groups: hydrolysable and condensed. The first group is composed by tannins which are esters of phenolic acids (generally gallic acid as in gallotannins or other phenolic acids derived from the oxidation of galloyl residues as in ellagitannins) and a polyol, usually glucose. Condensed tannins are oligomers of catechin and/or epicatechin, usually linked by C-C and occasionally by C-O-C bonds [2]. Condensed tannins, also termed proanthocyanidins, are among the most abundant polyphenols in plants.

Tannins were focus of several studies by their capacity of binding proteins and other macromolecules. The nature of the interactions appears to depend on the nature of tannin, type of macromolecule and the conditions of the medium where the interaction takes place (e.g. pH, ionic strength) [2–5]. Interactions with proteins have been extensively studied, using several different approaches, since these appear to be responsible for the principal adverse properties of tannins: i) both at sensorial level, through the astringency sensation they produce; ii) acting anti-nutritionally, by interacting with food proteins or even endogenous enzymes [1, 2, 4, 6]. Tannin-protein interactions could occur via covalent or ionic bounds, hydrophobic interaction, or hydrogen bonding. Hydrophobic interactions have been considered as the main driving forces toward association [5]. The stability of proteintannin complexes has been postulated to increase with the number of linkages between tannins and proteins and apparently with the number of repeated amino acid sequences [7]. Proteins with high molecular mass, high proline content and lacking secondary structure appear to be the ones with great affinity to complex effectively with tannins [5]. Covalent crosslinks are less common, but also can to occur, particularly when polyphenols oxidize, giving rise to ortho-quinones, which are highly reactive intermediates (Kroll, Rawel, and Rohn 2003; Le Bourvellec and Renard 2012).

Several common human foods including fruits, beverages, vegetables, some grains, cocoa/chocolate and beverages, such as coffee, tea, and wine contain condensed and hydrolysable tannins, leading to an estimated daily intake for humans of more than 1 g of polyphenols per day, as it will be further detailed, in the next sub-chapter [9]. Only a fraction of all the known polyphenols is present in edible food products, and they are responsible for food attributes such as colour formation, astringency, bitterness and aroma [5, 10]. Such influence on food attributes is observed in fresh products, as well as in processed ones. In these last are the processing steps that often involve tissue disruptions and various physicochemical phenomena/interactions (adsorption, oxidation, solubilisation, and migration) that impact on the food quality attributes mentioned [5].

Consumer choices and consumption patterns are influenced by diverse factors. Among biological determinants, sensory attributes of foods and beverage play a key role. Gustation and olfaction are reported to be the principal senses in distinguishing food and beverage sensory properties. Besides these, other mechanical and thermal sensations contribute to the general flavour that characterizes food and drinks. However, nutrient information about an ingested food involves also post-ingestive and post-absorptive systems [11], with receptors involved in taste sensing also expressed in the gastrointestinal tract [12, 13].

Apart from the physiological and biological aspects, food choices and intake also largely depend on psychological and social factors, including beliefs, habits, values and past experiences (Conner and Armitage, 2002).

In this book chapter we will to present the influences of sensory and psychosocial factors on the intake of tannin-rich foods and beverages. The nutritional relevance of tannins, including the principal food and beverages sources of these plant secondary metabolites, and their health positive and negative effects will be briefly reviewed. It will be also included a topic discussing the involvement of oral cavity in the choices of tannin containing products, including the importance of astringency perception and how such perception is linked to individual oral cavity medium and salivary protein profiles. Finally, and due to the importance of hedonics for the final food choices, psychosocial determinants of food intake in general and of polyphenol-rich food consumption in particular (cognitive, affective and behavioural dimensions) will be presented.

As this paper examines the principal factors influencing tannin-rich food and beverage consumption, tannin chemistry per se is not covered and readers are referred to several excellent reviews namely: [15], [16], [17], [18], [19], [20], among others.

2. NUTRITIONAL RELEVANCE OF TANNINS

2.1 Tannins as antinutrients

Tannins are plant secondary metabolites usually considered as natural non-nutrients. Moreover, some of the phytochemicals normally found associated to tannins, including alkaloids and phenolic compounds occur as toxins.

Among the antinutritional and toxic effects described for tannins, decreases in food intake, growth rate, feed efficiency, net metabolizable energy, and protein digestibility are the ones mainly investigated. Other deleterious effects of tannins include damages to mucosal lining of gastrointestinal tract, alteration of excretion of certain cations, and increased excretion of proteins and essential amino acids [21]. Negative effects of foods rich in plant secondary metabolites can be also by reducing food intake, associated to decreases in food organoleptic quality. Many low-molecular weight plant secondary compounds are bitter and high-molecular weight ones, such as tannins, are usually

involved in the interaction with macromolecules, particularly with salivary proteins, resulting as astringent [4].

2.2. Consumption and health benefits of tannin-rich foods and beverages

Nonetheless what was stated above, recent interest in food phenolic and tannins has increased greatly, due to their antioxidant capacity (free radical scavenging and metal chelating activities) and their possible beneficial implications in human health, also reported for these plant metabolites. Beneficial effects such as treatment and prevention of cancer [22], cardiovascular disease [23], and other pathologies [21] have been attributed to phenolic compounds. In fact, there is considerable epidemiologic evidences that diets rich in fruit and vegetables can reduce the incidence of non-communicable diseases, with such positive effects attributed by authors, in great part, to phenolics [e.g. [24]]. They was refereed to exhibit potent free radical-scavenging properties in vitro [25] and, in vivo, they was refereed as having antioxidant capacity. Their involvement in protection against lipid peroxidation was referred [26]. Moreover, they appear to contribute to lower the levels of free radicals within the body [27] and to exert modulatory effects in cells through selective actions on different components of the intracellular signalling cascades vital for cellular functions such as growth, proliferation and apoptosis [27]. A detailed review about the effects of tannins on health is beyond the aim of this chapter and readers can find detailed information in other works e.g. [27], [28], [29], among others.

Tannins and other phenolics compounds are present in dietary sources such as fruits and vegetables, cocoa, chocolate, red wine, green and black tea, among others. The most important suppliers, in terms of amounts, are those that, besides having a considerable amount of polyphenols, are widely consumed in large quantities such as green tea, black tea, red wine, coffee and cocoa/chocolate. Fruits and vegetables, on the other hand, despite being consumed in relatively high amounts, have lower levels of these compounds, comparatively to these last referred items. Nevertheless, along with herbs and spices, nuts, algae and olive oil, they are potentially significant for supplying certain types of phenols and polyphenols of restricted botanical occurrence [27].

Condensed tannins (proanthocyanidins – PA) are more widespread in the plant kingdom than hydrolysable tannins. Examples of food sources of condensed tannins are: coffee, tea, wine, grapes, cranberries, strawberries, blueberries, apples, apricots, barley, peaches, dry fruits, mint, basil, rosemary etc. Hydrolyzable tannins can be found, among others, in foods like: Pomegranate, strawberries, raspberries, clove, barley, rice, oat, rye, among others.

Daily consumption of tannin containing food products varies among countries and from region to region. For European countries, such as Poland, France, Spain and Finland, studies report mean daily amounts of polyphenols consumed as: $1756.5 \pm 695.8 \text{ mg} [30], 1193 \pm 510 \text{ mg} [31],$ 820 ± 323 mg [32] and 863 ± 415 mg [33], respectively. For Portugal, only data for polyphenol intake from fresh fruits, was found, which was reported to be 783.9 \pm 31.7 mg gallic acid equivalents per person, per day [34]. It has been reported that tannin consumption in India ranges from 1500- 2500 mg/day, depending on the region, and about 1000 mg/day within the USA [35]. Care is needed for comparisons among countries, in terms of polyphenol intake, since this may be somehow difficult due to the different methodologies employed for polyphenol levels calculations. Only as example, for Spanish individuals, one study reported a mean individual daily consumption of 820 ± 323 mg [32], as it was referred above, whereas other mentioned 2590 and 3016 mg/person/day [36].

Mediterranean region is theoretically a significant consumer of tanninrich foods. In terms of total amounts, this region may not be much different from other world region (Asia consumes considerable levels of polyphenol-rich foods), but Mediterranean diet presents particularities in the types of polyphenols. The ones provided by olives and olive oils are characteristic from Mediterranean diet, and these correspond to more than 10% of polyphenol total intake [32].

Besides regional and cultural influences, intake of polyphenols/tannins is also influenced by sex, with men having higher absolute intakes, comparatively to women [31]. This may reflect differences in particular habits, such as wine and coffee consumption, since differences between sexes were mainly encountered for polyphenols present in those drinks [35].

3. DEVELOPMENT OF FOOD PREFERENCES

Human behaviour is dynamic and constructed. This is the same to say that, food choice is not a stable phenomenon, but changes under different circumstances, experiences and moments of persons live, being this a predominantly learned behaviour (except for the rejection of bitter and the preference of sweet), and with fewer innate rules (except for the physiologic mechanisms involved in hunger, thirst and satiation). Research suggests that people's preferences for particular foods and food acceptance patterns are largely learned (e.g. [37–40]). The

evidence that food preferences of children change over time depending on their experiences and learnings [41] reinforces a continuous construction of the process of food choices. In the early years of life food preferences are determined by familiarity and sweetness. The existence in adulthood of preferences for foods such as coffee, beer, alcoholic beverages and spices, which are typically rejected during infancy, are evidence of this, as these preferences were acquired and have changed throughout life [42].

The development of food preferences (i.e. the acquisition of new preferences, their change or the maintenance of innate preferences that would otherwise disappear) occur through different learning mechanisms: exposure, association of stimulus or consequences, and social learning. Repeated exposure to certain foods seems determinant in the acquisition of dietary acceptance patterns, that is, the more frequent has the food been tasted, more may be its acceptance. This exposure begins early in life [38, 43]. Exposing the baby to the flavours present in the amniotic fluid and breast milk, from the mother's diet (e.g. alcohol, garlic, vanilla), will them become familiar and increase the child's acceptance of foods with similar flavours [43]. Fruits and vegetable acceptance may greatly depend on bitter exposure earlier in life [39]. Later, the family eating behaviour is one of the determinants of child food preferences and choices [43]. Ogden et al., (2013) state the existence of a direct relation between exposure to food and food preferences.

Learning by stimuli association or classical conditioning is another way of developing food preferences. For example, the negative feelings associated with negative health condition, following the ingestion of a particular food, is a very powerful mechanism for developing aversions to taste or food. Human beings reject certain foods and their taste when their intake have caused nauseas. People also learn through the consequences by eating certain products. The eating behaviour (like any other) suffers influences from contingent factors to it. Research has sought to study the association between foods and environmental consequences (i.e. rewards and punishments). Accordingly, studies show that positive attention of an adult associated with food, increases the preference of children for it [44]. Others studies have produced evidence that the use of certain foods as a reward increases the acceptance of these, but not of those whose intake intends to reinforce [44]. Social learning (also known as modelling or observational learning), refers to the influence of observing other peoples' behaviour on their own behaviour. This approach emphasizes the role of significant others (usually parents and peers) and the media in the development of food preferences and habits of children. In this sense, it is argued that children adopt similar eating behaviours to the ones of their parents and significant others. Eating is a social behaviour by what other people may serve (and often do) as models [45]. There are several studies that suggest that food preferences change according to the observation of food intake by others [46], specially models who the child identifies with (e.g. other child) or who is emotionally attached to (e.g. friend, hero). For example, studies have shown that children change their preference for different vegetables when they watch, for four consecutive days, another child eating a vegetable different from one that they initially preferred [47]. Not only the preferences but also behaviours, attitudes and beliefs change by influence of parents' attitudes, television and advertising. Foods that parents buy and have at home and the exposure to their habits and preferences, also influence food choice and intake by children [46, 48].

4. BIOLOGICAL DETERMINANTS OF TANNIN-RICH FOOD CHOICES

4.1 The involvement of oral cavity in the acceptance of tannin containing products

4.1.1 Sensorial attributes: bitterness, astringency and aroma

Factors affecting food choices are diverse, but despite the importance of each of them, sensorial characteristics play a pivotal role in food acceptance, preferences and choices. The palatability of a particular food is related to the pleasure that people experience when ingesting that food, and that is greatly linked to the sensorial aspects of foods. The way food is perceived in the mouth is more than just taste. During consumption, is the flavour of food, caused by the simultaneous stimulation of taste, olfaction (aroma) and texture, that is sensed [49]. The influence of palatability on ingestive behavior has gained attention of several researchers, from where it has been assumed that increases in palatability results in increases in food consumption (reviewed in [50]).

Polyphenol rich foods are essentially characterized by 2 major sensorial aspects: bitterness and astringency, which may negatively affect the food intake by decreasing the palatability. Bitterness is a chemical sensation elicited by the linkage of the bitter molecule to the bitter taste receptor. This last is a membrane protein present in taste receptor cells, clustered in taste buds on the tongue and present in other structures, such as palate, soft palate, and areas in the upper throat (pharynx and laryngopharynx). Bitter taste receptor belongs to the T2Rs family, which are members of the seven transmembrane domain, G-protein coupledreceptor (GPCR) superfamily [51]. At least 25 different T2R have been identified, showing the complexity in bitter taste perception [52]. Some T2R present specificity for one or few bitter compounds, falling in the class of "specialists", whereas there are T2Rs recognizing a diversity of bitter substances, being considered "generalists" [53]. In general, each bitter responsive taste receptor cell expresses multiple types of bitter receptors [54], but not all bitter receptors are expressed by every bitter cell [55]. Bitter taste transduction occurs through activation of a taste cell-specific G protein that activates phospholipase C pathway, generating second messengers inositol phosphate the (IP3), diacylglycerol (DAG) and H+. This results in the release of Ca2+ from intracellular stores.

The TAS2R38 gene encodes the taste receptor that responds to phenylthiocarbamide (PTC) and 6-n-propylthiouracil (PROP). This has been the bitter taste receptor gene subjected to a higher number of studies, and the perception that different individuals may have different sensitivities for bitter taste arrived from these studies. Polymorphisms at the level of TAS2R38 were referred to be one of the principal reasons for the differences in taste perception [56]. Nevertheless, bitter taste sensitivity is not completely explained by these polymorphisms and approximately 30% of the phenotypic variation is probably due to different factors, among which the characteristics of the medium surrounding receptors, namely saliva composition [57].

Even more than bitter, tannin-rich foods are characterized by their astringent properties. This sensation, is sometimes also referred as taste, and some controversy exists. The activation of nerves related to taste transduction (chorda tympani and glossopharyngeus nerves), by astringent compounds, suggested astringency as a taste [58]. On the other hand, different authors demonstrated that astringents can also be perceived in non-taste oral tissues, besides it increases with repetitive sampling (e.g. [59]), what are features typical of trigeminal sensations. Recently it was suggested that astringency, despite being a trigeminal sensation, may be not only mediated by mechanosensors, but rather to involve a chemosensory detection together with the stimulation of trigeminal mechanosensors [60]. Astringency has been described as "the complex of sensations due to shrinking, drawing or puckering of the epithelium as a result of exposure to substances such as alums or tannins" by the American Society for Testing of Materials. Different qualities of astringency have been reported: i) the prototypic rough and puckering astringency mainly produced by compounds such as flavan-3-ols [61]; ii) a soft and velvety astringent mouthfeel, mainly produced by flavanone glycosides [62].

Both bitterness and astringency appear to contribute to the level of acceptance of tannin-rich foods. Several authors tried to relate either bitterness perception or astringency perception with the consumption of foods rich in these sensorial stimuli. Nevertheless, controversy exists, with different studies reporting different results, mainly due to different experimental factors (individuals' characteristics, such as age, sex, ethnicity, among others; types of foods evaluated; types of sensorial methodologies employed for evaluating taste phenotype).

Consumption of polyphenol containing foods has been related to the sensitivity for the bitter compounds PROP and PTC. Sandell and colleagues [63] reported differences between persons with different polymorphisms at the level of the TAS2R38 bitter taste receptor, with the ones corresponding to high sensitivity consuming fewer vegetables than the ones carrying the polymorphisms corresponding to low sensitivity. As well, lower acceptance of bitter tasting fruits and vegetables in PROP sensitive women was also reported [64]. Other studies, on the contrary, reported small differences in cruciferous vegetable intake [65], as well as in different fruits and berries [66], related to PROP taste sensitivity status. Vegetable intake was also related to variability at the level of other bitter taste receptor, besides TAS2R38, being this issue reviewed in [67].

For children, despite not all studies support a relationship between taste sensitivity and food acceptance, it has been stated that sensory aspects can be more important in determining preferences and choices, comparatively to adults or elderly [68, 69]. Concerning polyphenol-rich foods, bitter sensitive children have been reported as having lower acceptance [70] and consuming lower amounts of bitter vegetables [71], comparatively to high sensitive children. Despite the influence of bitter taste sensitivity, as discussed above, astringency perception has been generally accepted as the principal sensorial determinant of tannin-rich food consumption. The astringency and bitterness of many vegetables and fruits containing phytonutrients are often cited as the reason for consumers rejecting plant based products, despite their known health benefits [64]. It was observed that increased levels of tannins in fruit juices were associated to decreases in liking, particularly in subjects for which sensitivity for astringency was high, suggesting a key role of astringency in tannin-rich items preferences [72]. Nevertheless, the authors of the study reported that in terms of acceptance, no such clear relationship with astringency intensity was observed. Whereas for fruits, astringency is reported as a negative attribute, for other products, such as wine, this is not so linear. Pleasantness of astringent sensations of wine depend on the balance among other factors, including alcohol and sugar content [73].

If the taste perception is recognized to play a central role in food tasting, as described earlier, olfaction, in turn, is known to be involved in food and beverage odour and aroma/flavour perception. However, a distinction should be made between the food/beverage odour detection and aroma detection, since odorants can reach the ciliated olfactory receptor neurons (ORNs) located in the nasal olfactory epithelium via two distinct odour routes. In odour detection, odorants are inhaled/sniffed through the external nostrils towards reaching the receptors in the nasal olfactory epithelium ("orthonasal perception"). In contrast, in aroma detection, volatile compounds are transported via retronasal (i.e., nasopharynx) to gain access to the receptors at the olfactory epithelium ("retronasal perception") [74]. The differential processing of olfactory stimuli presented through the retronasal or orthonasal routes [75] may result from distinct odour flow patterns.

In the sensorial aspects potentially involved in determining acceptance and preference of tannin rich foods, aroma should also be included. The levels and types of tannins present in a food or drink may interfere with aroma perception. In products like wine, it has been reported that the partitioning between air and liquid phases is influenced by the presence of wine non-volatile compounds, among which polyphenols [76](Villamor and Ross, 2013). Interaction between aroma compounds and these plant secondary metabolites, present in wine matrix, can affect perceived aroma intensity and quality [77]. It was reported that the intensities of fruity, citrus, strawberry, cooked fruit and floral aromas, decreased when the level of polyphenols increased [78]. For olive oil, a recent article also reported decreases in volatile release due to the addition of phenols [79]. Another aspect contributing to the effect of tannins on aroma perception is that this can be influenced by saliva composition, as it appears that saliva can bind some volatile compounds, inhibiting them to access receptors at the olfactory epithelium [80]. Since dietary tannins bind salivary proteins (e.g. Soares, Brandão, Mateus, & De Freitas, 2015), as it will be detailed in the next section, the levels of tannins may change the levels of salivary proteins free to interact with volatile compounds, changing aroma perception.

4.1.2. The role of saliva in tannin-rich items ingestion

Two possible mechanisms were proposed to explain astringency and both are based on the interactions between tannins and salivary proteins. The oldest belief is that the precipitates resultant from the interaction tannins-salivary proteins increase friction between mouth surfaces and stimulate mechanoreceptors [82]. Other authors suggest that tannins interact with glycoproteins, which are responsible for the viscous elastic characteristics of the lubricating film that lines the oral cavity, affecting lubrication [82, 83]. At the moment, a more integrative view is considered, in which there is a two-step interaction between salivary proteins and polyphenols (: i) in the first step of interaction, tannins may bind the salivary proteins that constitute dynamic film; ii) in a second step, the remaining tannins, not bound in the first step, can interact with the adsorbed glycoprotein layer, with the consequent oral cavity loss of lubrication and astringency development.

Proline-rich proteins (PRPs) [84], histatins [85], statherins, cystatins [86] and alpha-amylase [87, 88] are the salivary proteins most referred as the ones with considerable affinity for tannins and, consequently, potentially involved in astringency development. These salivary proteins represent a considerable part of the saliva total protein content. The nature of the interaction between these salivary proteins and polyphenols depends on several factors, among which protein characteristics and the type of polyphenol. Salivary proteins such as acidic PRPs and statherins present lower selectivity towards polyphenol structures, comparatively to histatins and cystatins [86]. Among these, salivary PRPs were by far the most studied, being generally considered as the main family of

salivary proteins involved in astringency [89]. Mucins also seem to have a role in astringency. Salivary mucins are glycoproteins with diverse molecular weight (usually divided in low- and high-molecular weight), having gel-forming and non-gel-forming abilities, and which are major contributors of the mucus barrier in the oral cavity. It was observed that polyphenols interact with mucins, altering the lubricant function of these proteins, contributing to astringency [90].

Inter-individual differences in salivary protein composition is well known. Moreover, for the same individual, several factors, such as age, sex, pathological conditions, among others, affect salivary protein composition. Due to the influence salivary proteins may have in astringency perception, differences in salivary proteome may result in differences in acceptance and preferences of tannin-rich foods. A study from Dinnella et al. [72], already referred in this chapter, pointed for the different sensitivities for astringency in persons with different salivary protein profiles. Moreover, saliva composition appears to change after a certain time consuming polyphenols: we observed that modification in saliva composition in different animal models [87, 91, 92], whereas other authors reported it also for humans [93]. Such differences can be responsible for changes in acceptance and preferences of tannin-rich items, after individuals have repeated contacts with such compounds. A recent study, in rodents, highlight that changing salivary protein composition, changes in orosensory and postingestive feedback will occur [94].

4.2 Influence of post-ingestive mechanisms

So far, gustation, olfaction and mechanical sensations have been reported to be the principal senses in distinguishing food sensory properties. However, is now well known that nutrient information about an ingested food involves also post-ingestive and post-absorptive systems [11]. In fact, receptors to detect basic tastes such as, umami [95], sweet [95–97] and bitter [13, 98] are found in the gastrointestinal tract and in other extra-gustatory tissues. The diverse studies suggest that taste cells in the oral cavity and taste like cells in the gastrointestinal tract share many common characteristics, expressing taste receptors and signal transducers to pass on nutrients, including proteins, carbohydrates and lipids [99–101] and non-nutrients, including phenolic compounds [101] information to the particular sensory nerves that innervate each tissue [95, 99].

At the beginning of this sub-chapter, we referred that palatability does not relies in isolated sensorial aspects of food, but it reflects emotional aspects that such sensorial characteristics evoke. In this context, palatability greatly depends on the post-ingestive effects a food produces. As it was presented in sub-chapter 2, choices are learned by making associations of sensorial aspects (conditioned stimuli) with postingestive consequences (unconditioned stimuli) [102]. That is one of the reasons why the typical sensations of tannin-rich foods and drinks, such as bitterness or astringency, often thought of as aversive, are accepted. Avoidance of high tannin diets is the result of both conditioned and unconditioned avoidance [103].

Post-ingestive aspects related to tannin consumption are diverse and depend on the type of tannins. Condensed tannins are mainly considered "antinutritional" because they can reduce non-heme iron absorption, causing decreases in endogenous nitrogen. Moreover, they may reduce digestibility, mainly due to their capacity to bind other macromolecules, among which food proteins and endogenous enzymes [4]. Hydrolysable tannins, at high levels, are also related to toxicity [21]. Salivary proteins are involved in modulating post-ingestive feedback associated with chronic exposure to tannin-rich diets [94]. In rodent models such effect is well demonstrated, since after a few days of tannin consumption, saliva composition changes (e.g. [104]), with the increase in production of proteins with high affinity for tannins, preventing them to exert effects at gastro-intestinal tract level.

5. PSYCHOSOCIAL ASPECTS OF FOOD CHOICES (WHAT MOTIVATES POLYPHENOL-RICH FOOD CONSUMPTION?)

Answering the central questions in the food choice and intake domain -"Who eats what, when, where and, most of all, why?" – is not an easy endeavour. Apart from the physiological and biological aspects mentioned in the previous sections, food choices and intake also largely depend on psychological and social factors. Beliefs, habits, values and past experiences for example, have a major influence on the foods selected [105]. These multi-determined behaviours are dependent on individual and contextual factors and are dynamic, in the sense that they can be (socially and individually) "constructed" and learned, and can change with time.

Given this, they should be explained from different scientific areas, not only from a biological/physiological perspective but also from psychosocial perspectives. The latter is the focus of the next section, where we will present the determinants in general, associated with food choice and intake from a psychosocial perspective, focusing afterwards on tannin rich foods. Despite the major component of psychology in the development of food preferences, the sub-chapter referring to that (sub-chapter 3) was presented before, to help comprehension of the aspects focused at sub-chapter 4.

5.1 Multi-level and multi-dimensional determinants of food related preferences, choices and behaviours

Various models attempted to explain food preferences, choice and intake, for many decades now. This has allowed the identification of a wide diversity of determinants in different levels of analysis - from a micro level of intra and inter-individual analysis, to a macro level of intra and inter-groups analysis – from the perspective of various disciplines (biology, psychology, economy, etc.). In order to organize the literature in this regard, Connor et al. [105] grouped these into three main categories: food related factors, environmental factors and individual factors. In terms of the relationship between them, the first two determine the processes that occur at the individual level (psychological, physiological, including sensory), which translate into preferences, choices and eating behaviours.

Given that in previous sections there was a focus on food related factors (characteristics of food, sensitivity to certain components of food, taste, etc), our focus will be now on environmental and individual factors.

5.1.1 The surrounding environment

The environmental factors category includes a set of external influences on the individual, resulting from factors that take place in their surrounding environment, which includes the social, cultural, economic, and other contexts. In this regard, religion for example, is a determinant factor for certain types of foods and beverages, as for example cow for the Hindu religion and alcohol for the Muslim religion, translating into rejection of these products. The availability of certain food products also determines preferences for these, over other products. This is the case of Mediterranean diet that for many years has induced preferences towards products available in these regions, such as tomato or certain types of fish, for example. Also, the marketing and advertising industry has always had the goal of directing people's preferences towards certain desired targets. This shows that the social and cultural environment is a strong determinant of preferences, choices and eating behaviours [106].

In accordance, concerning the social context, [107], showed that eating with family or other know people, increased the energy intake associated with food consumption in 18%, compared with people eating alone or in the presence of strangers. The role of other people in this regard is of much importance as they may help in choosing what is adequate or "ideal" to eat in a certain situation and contribute to maintain regular eating pattern and an adequate diet [108]. The presence of other people can also compensate for disabilities that the individual may have and may be a barrier to the intake of preferred foods. In addition, eating with others may also serve as a positive social reinforcement to eat certain types of food and drink certain beverages, in certain contexts (e.g. barbecues), which may allow either decreasing risks (e.g. of eating food with allergens) or increasing them (e.g. consumption of high calorie foods). Finally, various studies on the social context of food choice and intake (see [108]) also showed that: loneliness is the main reason for reduction both in food consumption and satisfaction with food [109, 110]; low levels of satisfaction with social relationships (i.e. their quality, rather than quantity) predicted reduced food intake and adequacy of food regimens [110, 111]; social interaction while food intake occurs, is predictive of improvements is food regimens.

Another important factor in this category is the availability of resources with regard to food choice and purchase. Studies with the elderly population, for example, have shown that the loss of a spouse, especially for man, has a high impact over food choices and reduces satisfaction with food related life [108]. In accordance, low financial resources may limit the purchase of certain food products; physical and mental disabilities, transportation constraints, architectural barriers, living in a rural area, may all limit mobility and access to food stores, supermarkets, etc were preferred foods are available. All these factors may serve as barriers preventing people from having access to preferred food products and determine the purchase of more or less suitable alternatives, which in turn may influence and alter habitual preferences.

All these examples show that, although food preferences, choice and intake are determined by the characteristics of food, other factors are also determinants of these, namely considering factors external to the individual or not related to the food itself. One example and a strong determinant in this regard, is the social environment. The mere presence of other people may be a determinant for the emergence of behaviours that otherwise would not emerge, if the person was alone. In addition to contextual factors, individual factors also play an important role. This will be discussed next, followed by a developmental approach to food choice and intake, which takes into consideration the interaction between the individual and her/his environment. From all the aspects mentioned, social factors may be the most effective means for enhancing liking among human beings. For example, when an adult shows pleasure while consuming a food, this positive response can influence a child's hedonic response [106].

Taking into account what was stated about social influence in food and beverages consumption, the effect of these factors in the context of tannin-rich food and beverages intake can be easy to identify.

For many drinks, such as coffee, tea, and wine, the positive value generally associated with the social context of consumption can be an important mechanism for acceptance [112].

5.1.2 The individual

In addition to external influences, there are intra-individual processes (cognitive, affective, behavioural, sensorial and physiological) that in interaction with environmental processes (e.g. social environment) and the characteristics of food products (e.g. taste, mechanical sensation), also determine preferences, choices and behaviours. This interaction can translate for example into food intolerances and allergies, illnesses and other positive and/or negative effects.

In this regard, individual level factors such as age, gender, individual's personality traits (temporally stable characteristics of an individual) and other factors, may have an influence over preferences, choices and behaviours. For example, there are individuals that are much influenced by emotions when eating, others have a particular vulnerability to food related stimulus in their surrounding environment (e.g. advertising), some are impulsive while others are (cognitively and behaviourally) restrained. Moreover, different levels of knowledge, learning and experience with regard to food related issues (e.g. food risks and benefits) may induce different types of beliefs, emotions, and behaviours with regard to food (e.g. food safety practices and hygiene, at home). In this regard, the role of attitudes towards certain types of foods (e.g. with regard to their perceived benefits) is evident as these may determine a positive, neutral or negative tendency towards certain food products. (e.g. negative attitudes towards fruit may decrease the probability of someone choosing fruit, when in the supermarket). These attitudes may function for example as a moderator of the relationship between sensitivity to certain components of food and preference for them. For example, if people have a high sensitivity to the astringent properties of certain food products, having a negative attitude towards these products (e.g. certain vegetables) may increase the probability of rejection of these, while this effect would not be so strong if attitudes were positive.

In addition to variables such as attitudes, personality characteristics and others, one of the strongest influences on food choices and intake is a person's habit. Habits can be defined as goal-directed automatic behaviours that are mentally represented and can be triggered by environmental cues (see e.g. [113–115]. In other words, a pre-condition for habitual behaviour to be performed automatically (e.g. buy tea) is the existence of an active goal (e.g. buy snacks and beverages for the afternoon work breaks) due to the presence of relevant environmental cues (e.g. being in the tea and cookies section at the supermarket), with goal being defined as "an internal representation of a desired state, such as a behaviour or an outcome" [116]. Under the "right" situational conditions (environmental cues), behaviour can be automatically performed, without the person even being consciously aware of this. Therefore, the person may find herself arriving at the counter to pay for groceries, with a pack of tea bags, sometimes without even remembering grabbing it. This automaticity effect is particularly strong in stable/familiar contexts (frequently encountered on a daily basis) and when people are in heavy cognitive load situations (exhaustion, time pressure, distraction or information overload; when under stress; etc) [114, 115, 117, 118]. This means that there is a predisposition for our preferences, choices and food intake to be stable, i.e. we prefer, choose and consume mainly what we used to prefer, choose or eat.

However, this does not mean that these preferences, choices and eating habits cannot be changed. Under certain conditions, for example when the context changes (the habitually selected products are not available; the price and/or the necessary financial resources to buy these change; the person's mobility to go to the stores is constrained; the person finding herself in a social context in which these habits are seen in a negative way, thus not supporting them), habits can change. In addition to this more "natural" way of changing habitual preferences, choices and eating habits, these can also be changed in a more "artificial" way. One possibility referred in the literature in this regard is the development of implementation intentions [119]. These involve a planning process specifying that "when situation Y arises, I will perform response X" (e.g. "when I am at the fruit section in the supermarket, I will buy red grapes"), linking a critical situation (situation Y – being in the fruit

section in the supermarket) with a goal directed behaviour (response X – buying red grapes). To achieve this planning the person needs to define the "when", "where" and "how" the responses will allow the attainment of the goal. The associated cognitive process demands that the expectation of encountering situation Y makes its mental representation cognitively more accessible. This heightened accessibility in turn, facilitates the selective attention involved in the detection of the presence of situation Y in the surrounding environment and thus the individual readily responds to it (response X) whenever situation Y it is detected [113]. The power of these implementation intentions comes from the fact that they can artificially and temporarily simulate the automaticity that is characteristic of habitual behaviours [113].

From this it can be seen that habitual preferences, choices and eating behaviours are stable and tend to maintain themselves overtime. Still, it can also be seen that these are changeable either through natural changes in a person's environment or context (social, economic, cultural, architectural, etc) or through "artificial" changes induced by interventions direct to habits change. Perceptions and food preferences change along with time and throughout repeated exposure. This is true for bitter taste and/or astringent foods, as well for other food sensorial attributes (e.g. textures). It is possible come to like of a food innately rejected. Also, repeated exposure can enhance hedonic evaluation of bitter beverage products [120].

CONCLUSIONS

The understanding of the process of food choices is not easy and requires a multidisciplinary view. Different types of determinants act together to modulate preferences and choices. As well as for other types of foods, also for tannin-rich foods these different factors need to be considered.

Tannins are a chemically diverse group of compounds that are present, at variable levels, in most vegetable foods, so their intake is almost universal. Differences at chemical level result in different techniques for measuring their levels. This may be one of the reasons why it is difficult to quantify the intake levels of these compounds among different populations.

At sensorial level, tannins are considered as responsible for astringency and bitter taste, which are usually regarded as aversive stimuli. Nevertheless, the foods and beverages containing them are not completely refused and some are even preferred for some people. Sensorial aspects, as well as psychosocial determinants of the choices of these compounds have been reviewed, but future multidisciplinary research work need to be developed. A deep knowledge about the factors affecting consumption of tannin-rich foods is desirable, in order to promote different habits and a potential higher intake of these plant secondary metabolites, which besides having some negative consequences, have recognized positive health effects.

AKNOWLEDGEMENTS

This chapter is funded by FEDER Funds through the Operational Programme for Competiveness Factors-COMPETE and National Funds through FCT-Foundation for Science and Technology under the Strategic Projects PEstOE/AGR/UI0115/2014 (ICAAM—University of Évora). Authors acknowledge also the financial support from the Portuguese Science Foundation (FCT) in the form of Elsa Lamy FCT investigator IF/01778/2013 and Rui Gaspar Grant contract FCT No. UID/PSI/04810/2013. The Portuguese Science Foundation (FCT) played no role in the development of the present work or upon its submission for publication.

REFERENCES

- 1. Riedl KM, Hagerman AE (2001) Tannin-protein complexes as radical scavengers and radical sinks. J Agric Food Chem 49:4917–23
- 2. Haslam E (1998) Practical Polyphenolics: From Structure to Molecular Recognition and Physiological Action.
- 3. Hagerman AE, Butler LG (1981) The specificity of proanthocyanidin-protein interactions. J Biol Chem 256:4494–7
- 4. Ann E. Hagerman (1992) Phenolic Compounds in Food and Their Effects on Health I. 506:236–247

- 5. Le Bourvellec C, Renard CMGC (2012) Interactions between Polyphenols and Macromolecules: Quantification Methods and Mechanisms. Crit Rev Food Sci Nutr 52:213–248
- 6. Horigome T, Kumar R, Okamoto K (1988) Effects of condensed tannins prepared from leaves of fodder plants on digestive enzymes in vitro and in the intestine of rats. Br J Nutr 60:275–85
- Canon F, Paté F, Meudec E, Marlin T, Cheynier V, Giuliani A, Sarni-Manchado P (2009) Characterization, stoichiometry, and stability of salivary protein-tannin complexes by ESI-MS and ESI-MS/MS. Anal Bioanal Chem 395:2535–45
- KROLL J, RAWEL HM, ROHN S (2003) Reactions of Plant Phenolics with Food Proteins and Enzymes under Special Consideration of Covalent Bonds. Food Sci Technol Res 9:205–218
- 9. Scalbert A, Williamson G (2000) Dietary intake and bioavailability of polyphenols. J Nutr 130:2073S–85S
- 10. Kemperman RA, Bolca S, Roger LC, Vaughan EE (2010) Novel approaches for analysing gut microbes and dietary polyphenols: challenges and opportunities. Microbiology 156:3224–31
- 11. Berthoud H-R (2002) Multiple neural systems controlling food intake and body weight. Neurosci Biobehav Rev 26:393–428
- Wu S V., Rozengurt N, Yang M, Young SH, Sinnett-Smith J, Rozengurt E (2002) Expression of bitter taste receptors of the T2R family in the gastrointestinal tract and enteroendocrine STC-1 cells. Proc Natl Acad Sci 99:2392–2397
- Rozengurt E (2006) Taste receptors in the gastrointestinal tract. I. Bitter taste receptors and alpha-gustducin in the mammalian gut. Am J Physiol Gastrointest Liver Physiol 291:G171–7
- 14. M Conner CA (2002) The social psychology of food. Open University Press, Buckingham, UK
- 15. Bors W, Michel C (2002) Chemistry of the antioxidant effect of polyphenols. Ann N Y Acad Sci 957:57–69
- 16. Bravo L (1998) Polyphenols: chemistry, dietary sources, metabolism, and nutritional significance. Nutr Rev 56:317–33

- 17. Butler LG (1992) Antinutritional effects of condensed and hydrolyzable tannins. Basic Life Sci 59:693–8
- Ferreira D, Gross GG, Hagerman AE, Kolodziej H, Yoshida T (2008) Tannins and related polyphenols: perspectives on their chemistry, biology, ecological effects, and human health protection. Phytochemistry 69:3006–8
- 19. Reed JD (1995) Nutritional toxicology of tannins and related polyphenols in forage legumes. J Anim Sci 73:1516–28
- 20. Scalbert A, Mila I, Expert D, Marmolle F, Albrecht AM, Hurrell R, Huneau JF, Tomé D (1999) Polyphenols, metal ion complexation and biological consequences. Basic Life Sci 66:545–54
- 21. Chung KT, Wong TY, Wei CI, Huang YW, Lin Y (1998) Tannins and human health: a review. Crit Rev Food Sci Nutr 38:421–64
- 22. Huang W-Y, Cai Y-Z, Zhang Y (2010) Natural phenolic compounds from medicinal herbs and dietary plants: potential use for cancer prevention. Nutr Cancer 62:1–20
- Habauzit V, Morand C (2011) Evidence for a protective effect of polyphenols-containing foods on cardiovascular health: an update for clinicians. Ther Adv Chronic Dis 3:87–106
- 24. Oyebode O, Gordon-Dseagu V, Walker A, Mindell JS (2014) Fruit and vegetable consumption and all-cause, cancer and CVD mortality: analysis of Health Survey for England data. J Epidemiol Community Health 68:856–62
- 25. Moukette BM, Pieme CA, Njimou JR, Biapa CPN, Marco B, Ngogang JY (2015) In vitro antioxidant properties, free radicals scavenging activities of extracts and polyphenol composition of a non-timber forest product used as spice: Monodora myristica. Biol Res 48:15
- 26. Pandurangan AK, Periasamy S, Anandasadagopan SK, Ganapasam S, Srinivasalu SDC (2012) Green tea polyphenol protection against 4nitroquinoline 1-oxide-induced bone marrow lipid peroxidation and genotoxicity in Wistar rats. Asian Pac J Cancer Prev 13:4107–12

- 27. Crozier A, Jaganath IB, Clifford MN (2009) Dietary phenolics: chemistry, bioavailability and effects on health. Nat Prod Rep 26:1001
- 28. Garcia-Muñoz C, Vaillant F (2014) Metabolic fate of ellagitannins: implications for health, and research perspectives for innovative functional foods. Crit Rev Food Sci Nutr 54:1584–98
- Quideau S, Deffieux D, Douat-Casassus C, Pouységu L (2011) Plant polyphenols: chemical properties, biological activities, and synthesis. Angew Chem Int Ed Engl 50:586–621
- Grosso G, Stepaniak U, Topor-Mądry R, Szafraniec K, Pająk A (2014) Estimated dietary intake and major food sources of polyphenols in the Polish arm of the HAPIEE study. Nutrition 30:1398–1403
- Pérez-Jiménez J, Fezeu L, Touvier M, Arnault N, Manach C, Hercberg S, Galan P, Scalbert A (2011) Dietary intake of 337 polyphenols in French adults. Am J Clin Nutr 93:1220–8
- 32. Tresserra-Rimbau A, Medina-Remón A, Pérez-Jiménez J, et al (2013) Dietary intake and major food sources of polyphenols in a Spanish population at high cardiovascular risk: the PREDIMED study. Nutr Metab Cardiovasc Dis 23:953–9
- Ovaskainen M-L, Törrönen R, Koponen JM, Sinkko H, Hellström J, Reinivuo H, Mattila P (2008) Dietary intake and major food sources of polyphenols in Finnish adults. J Nutr 138:562–6
- Pinto P, Cardoso S, Pimpão RC, Tavares L, Ferreira RB, Santos CN (2013) Daily polyphenol intake from fresh fruits in Portugal: contribution from berry fruits. Int J Food Sci Nutr 64:1022–9
- 35. Chun OK, Chung SJ, Song WO (2007) Estimated dietary flavonoid intake and major food sources of U.S. adults. J Nutr 137:1244–52
- 36. Saura-Calixto F, Serrano J, Goñi I (2007) Intake and bioaccessibility of total polyphenols in a whole diet. Food Chem 101:492–501
- Beauchamp GK, Mennella JA (2009) Early flavor learning and its impact on later feeding behavior. J Pediatr Gastroenterol Nutr 48 Suppl 1:S25–30

- 38. Birch LL, Fisher JO (1998) Development of eating behaviors among children and adolescents. Pediatrics 101:539–49
- 39. Forestell CA, Mennella JA (2007) Early determinants of fruit and vegetable acceptance. Pediatrics 120:1247–54
- 40. Mennella JA, Griffin CE, Beauchamp GK (2004) Flavor programming during infancy. Pediatrics 113:840–5
- Ogden J, Cordey P, Cutler L, Thomas H (2013) Parental restriction and children's diets. The chocolate coin and Easter egg experiments. Appetite 61:36–44
- 42. Drewnowski A (1997) Taste preferences and food intake. Annu Rev Nutr 17:237–53
- 43. Fisher JO, Mitchell DC, Smiciklas-Wright H, Birch LL (2002) Parental influences on young girls' fruit and vegetable, micronutrient, and fat intakes. J Am Diet Assoc 102:58–64
- 44. Birch LL, Zimmerman SI, Hind H (1980) The Influence of Social-Affective Context on the Formation of Children's Food Preferences. Child Dev 51:856
- 45. Cutting TM, Fisher JO, Grimm-Thomas K, Birch LL (1999) Like mother, like daughter: familial patterns of overweight are mediated by mothers' dietary disinhibition. Am J Clin Nutr 69:608–13
- 46. Ogden J (2010) The Psychology of eating. From healthy to disordered behavior.
- Birch LL, Anzman-Frasca S (2011) Learning to prefer the familiar in obesogenic environments. Nestle Nutr Workshop Ser Pediatr Program 68:187–96; discussion 196–9
- Brown R, Ogden J (2004) Children's eating attitudes and behaviour: a study of the modelling and control theories of parental influence. Health Educ Res 19:261–71
- Sáenz-Navajas M-P, Campo E, Culleré L, Fernández-Zurbano P, Valentin D, Ferreira V (2010) Effects of the nonvolatile matrix on the aroma perception of wine. J Agric Food Chem 58:5574–85

- 50. Sørensen LB, Møller P, Flint A, Martens M, Raben A (2003) Effect of sensory perception of foods on appetite and food intake: a review of studies on humans. Int J Obes Relat Metab Disord 27:1152–66
- 51. Montmayeur JP, Matsunami H (2002) Receptors for bitter and sweet taste. Curr Opin Neurobiol 12:366–71
- Adler E, Hoon MA, Mueller KL, Chandrashekar J, Ryba NJ, Zuker CS (2000) A novel family of mammalian taste receptors. Cell 100:693–702
- Behrens M, Reichling C, Batram C, Brockhoff A, Meyerhof W (2009) Bitter taste receptors and their cells. Ann N Y Acad Sci 1170:111–5
- Mueller KL, Hoon MA, Erlenbach I, Chandrashekar J, Zuker CS, Ryba NJP (2005) The receptors and coding logic for bitter taste. Nature 434:225–9
- 55. Voigt A, Hübner S, Lossow K, Hermans-Borgmeyer I, Boehm U, Meyerhof W (2012) Genetic labeling of Tas1r1 and Tas2r131 taste receptor cells in mice. Chem Senses 37:897–911
- 56. Bufe B, Breslin PAS, Kuhn C, Reed DR, Tharp CD, Slack JP, Kim U-K, Drayna D, Meyerhof W (2005) The molecular basis of individual differences in phenylthiocarbamide and propylthiouracil bitterness perception. Curr Biol 15:322–7
- Hayes JE, Bartoshuk LM, Kidd JR, Duffy VB (2008) Supertasting and PROP bitterness depends on more than the TAS2R38 gene. Chem Senses 33:255–65
- Schiffman SS, Suggs MS, Sostman AL, Simon SA (1992) Chorda tympani and lingual nerve responses to astringent compounds in rodents. Physiol Behav 51:55–63
- Des Gachons CP, Mura E, Speziale C, Favreau CJ, Dubreuil GF, Breslin PAS (2012) Opponency of astringent and fat sensations. Curr Biol 22:R829–30
- 60. Schöbel N, Radtke D, Kyereme J, et al (2014) Astringency is a trigeminal sensation that involves the activation of G protein-coupled signaling by phenolic compounds. Chem Senses 39:471–87

- 61. Scharbert S, Holzmann N, Hofmann T (2004) Identification of the astringent taste compounds in black tea infusions by combining instrumental analysis and human bioresponse. J Agric Food Chem 52:3498–508
- 62. Hufnagel JC, Hofmann T (2008) Quantitative reconstruction of the nonvolatile sensometabolome of a red wine. J Agric Food Chem 56:9190–9
- 63. Sandell M, Hoppu U, Mikkilä V, Mononen N, Kähönen M, Männistö S, Rönnemaa T, Viikari J, Lehtimäki T, Raitakari OT (2014) Genetic variation in the hTAS2R38 taste receptor and food consumption among Finnish adults. Genes Nutr 9:433
- 64. Drewnowski A, Gomez-Carneros C (2000) Bitter taste, phytonutrients, and the consumer: a review. Am J Clin Nutr 72:1424– 35
- 65. Sacerdote C, Guarrera S, Smith GD, et al (2007) Lactase persistence and bitter taste response: instrumental variables and mendelian randomization in epidemiologic studies of dietary factors and cancer risk. Am J Epidemiol 166:576–81
- 66. Duffy VB, Hayes JE, Davidson AC, Kidd JR, Kidd KK, Bartoshuk LM (2010) Vegetable Intake in College-Aged Adults Is Explained by Oral Sensory Phenotypes and TAS2R38 Genotype. Chemosens Percept 3:137–148
- Hayes JE, Feeney EL, Allen AL (2013) Do polymorphisms in chemosensory genes matter for human ingestive behavior? Food Qual Prefer 30:202–216
- 68. Cooke LJ, Wardle J (2005) Age and gender differences in children's food preferences. Br J Nutr 93:741–6
- Kamphuis CBM, de Bekker-Grob EW, van Lenthe FJ (2015) Factors affecting food choices of older adults from high and low socioeconomic groups: a discrete choice experiment. Am J Clin Nutr 101:768–74
- 70. Keller KL, Steinmann L, Nurse RJ, Tepper BJ (2002) Genetic taste sensitivity to 6-n-propylthiouracil influences food preference and reported intake in preschool children. Appetite 38:3–12

- Bell KI, Tepper BJ (2006) Short-term vegetable intake by young children classified by 6-n-propylthoiuracil bitter-taste phenotype. Am J Clin Nutr 84:245–51
- 72. Dinnella C, Recchia A, Tuorila H, Monteleone E (2011) Individual astringency responsiveness affects the acceptance of phenol-rich foods. Appetite 56:633–42
- 73. Boselli E, Boulton RB, Thorngate JH, Frega NG (2004) Chemical and sensory characterization of DOC red wines from Marche (Italy) related to vintage and grape cultivars. J Agric Food Chem 52:3843– 54
- 74. Genovese A, Piombino P, Gambuti A, Moio L (2009) Simulation of retronasal aroma of white and red wine in a model mouth system. Investigating the influence of saliva on volatile compound concentrations. Food Chem 114:100–107
- 75. Heilmann S, Hummel T (2004) A new method for comparing orthonasal and retronasal olfaction. Behav Neurosci 118:412–9
- Villamor RR, Ross CF (2013) Wine Matrix Compounds Affect Perception of Wine Aromas. Annu Rev Food Sci Technol 4:1–20
- 77. Polásková P, Herszage J, Ebeler SE (2008) Wine flavor: chemistry in a glass. Chem Soc Rev 37:2478–89
- 78. Goldner MC, Lira P di L, Baren C van, Bandoni A (2011) Influence of polyphenol levels on the perception of aroma in Vitis vinifera cv. Malbec wine. South African J Enol Vitic 32:21–27
- Genovese A, Caporaso N, Villani V, Paduano A, Sacchi R (2015) Olive oil phenolic compounds affect the release of aroma compounds. Food Chem 181:284–94
- Piombino P, Genovese A, Esposito S, et al (2014) Saliva from obese individuals suppresses the release of aroma compounds from wine. PLoS One 9:e85611
- Soares S, Brandão E, Mateus N, De Freitas V (2015) Sensorial Properties of Red Wine Polyphenols: Astringency and Bitterness. Crit Rev Food Sci Nutr. doi: 10.1080/10408398.2014.946468

- Rossetti D, Yakubov GE, Stokes JR, Williamson A-M, Fuller GG (2008) Interaction of human whole saliva and astringent dietary compounds investigated by interfacial shear rheology. Food Hydrocoll 22:1068–1078
- Schwarz B, Hofmann T (2008) Is there a direct relationship between oral astringency and human salivary protein binding? Eur Food Res Technol 227:1693–1698
- 84. Williamson MP (1994) The structure and function of proline-rich regions in proteins. Biochem J 297 (Pt 2:249–60
- 85. Yan Q, Bennick A (1995) Identification of histatins as tannin-binding proteins in human saliva. Biochem J 311 (Pt 1:341–7
- Soares S, Mateus N, de Freitas V (2012) Interaction of different classes of salivary proteins with food tannins. Food Res Int 49:807– 813
- Da Costa G, Lamy E, Capela e Silva F, Andersen J, Sales Baptista E, Coelho A V (2008) Salivary amylase induction by tannin-enriched diets as a possible countermeasure against tannins. J Chem Ecol 34:376–87
- Soares S, Mateus N, Freitas V de (2007) Interaction of different polyphenols with bovine serum albumin (BSA) and human salivary alpha-amylase (HSA) by fluorescence quenching. J Agric Food Chem 55:6726–35
- Canon F, Giuliani A, Paté F, Sarni-Manchado P (2010) Ability of a salivary intrinsically unstructured protein to bind different tannin targets revealed by mass spectrometry. Anal Bioanal Chem 398:815–22
- 90. Davies HS, Pudney PDA, Georgiades P, Waigh TA, Hodson NW, Ridley CE, Blanch EW, Thornton DJ (2014) Reorganisation of the salivary mucin network by dietary components: insights from green tea polyphenols. PLoS One 9:e108372
- Lamy E, Graça G, da Costa G, Franco C, E Silva FC, Baptista ES, Coelho AV (2010) Changes in mouse whole saliva soluble proteome induced by tannin-enriched diet. Proteome Sci 8:65

- 92. Lamy E, da Costa G, Santos R, Capela e Silva F, Potes J, Pereira A, Coelho A V, Baptista ES (2011) Effect of condensed tannin ingestion in sheep and goat parotid saliva proteome. J Anim Physiol Anim Nutr (Berl) 95:304–12
- 93. Varoni EM, Vitalini S, Contino D, Lodi G, Simonetti P, Gardana C, Sardella A, Carrassi A, Iriti M (2013) Effects of red wine intake on human salivary antiradical capacity and total polyphenol content. Food Chem Toxicol 58:289–94
- 94. Torregrossa A-M, Nikonova L, Bales MB, Villalobos Leal M, Smith JC, Contreras RJ, Eckel LA (2014) Induction of salivary proteins modifies measures of both orosensory and postingestive feedback during exposure to a tannic acid diet. PLoS One 9:e105232
- 95. Iwatsuki K, Ichikawa R, Uematsu A, Kitamura A, Uneyama H, Torii K (2012) Detecting sweet and umami tastes in the gastrointestinal tract. Acta Physiol (Oxf) 204:169–77
- 96. Nakagawa Y, Nagasawa M, Yamada S, Hara A, Mogami H, Nikolaev VO, Lohse MJ, Shigemura N, Ninomiya Y, Kojima I (2009) Sweet taste receptor expressed in pancreatic beta-cells activates the calcium and cyclic AMP signaling systems and stimulates insulin secretion. PLoS One 4:e5106
- Laffitte A, Neiers F, Briand L (2014) Functional roles of the sweet taste receptor in oral and extraoral tissues. Curr Opin Clin Nutr Metab Care 17:379–85
- Sternini C (2007) Taste receptors in the gastrointestinal tract. IV. Functional implications of bitter taste receptors in gastrointestinal chemosensing. Am J Physiol Gastrointest Liver Physiol 292:G457– 61
- 99. Steinert RE, Beglinger C (2011) Nutrient sensing in the gut: interactions between chemosensory cells, visceral afferents and the secretion of satiation peptides. Physiol Behav 105:62–70
- 100. Stewart JE, Seimon R V, Otto B, Keast RSJ, Clifton PM, Feinle-Bisset C (2011) Marked differences in gustatory and gastrointestinal sensitivity to oleic acid between lean and obese men. Am J Clin Nutr 93:703–11

- Breer H, Eberle J, Frick C, Haid D, Widmayer P (2012) Gastrointestinal chemosensation: chemosensory cells in the alimentary tract. Histochem Cell Biol 138:13–24
- Le Magnen J (1999) Effects of the duration of pre- and postprandial fasting on the acquisition of appetite (first published in French in 1957). Appetite 33:21–6
- 103. Lichtenstein G and Cassini (2001) Behavioural mechanisms underlaying food aversion in guinea pigs. Etología 9:29–34
- 104. Lamy E, Baptista ES, Coelho AV, Silva FC e (2010) Morphological alterations in salivary glands of mice (Mus musculus) submitted to tannin enriched diets: comparison with sialotrophic effects of sympathetic agonists stimulation. Arq Bras Med Veterinária e Zootec 62:837–844
- 105. Connor M, Armitage CJ, Conner M (2002) The Social Psychology of Food.
- 106. Rozin P (1990) Acquisition of stable food preferences. Nutr Rev 48:106–13; discussion 114–31
- 107. Hetherington MM, Anderson AS, Norton GNM, Newson L (2006) Situational effects on meal intake: A comparison of eating alone and eating with others. Physiol Behav 88:498–505
- 108. Dean M, Raats MM, Grunert KG, Lumbers M (2009) Factors influencing eating a varied diet in old age. Public Health Nutr 12:2421–7
- 109. Murphy SP, Davis MA, Neuhaus JM, Lein D (1990) Factors influencing the dietary adequacy and energy intake of older Americans. J Nutr Educ 22:284–291
- 110. Walker D, Beauchene RE (1991) The relationship of loneliness, social isolation, and physical health to dietary adequacy of independently living elderly. J Am Diet Assoc 91:300–4
- 111. Revenson TA, Johnson JL (1984) Social and demographic correlates of loneliness in late life. Am J Community Psychol 12:71–85

- Lesschaeve I, Noble AC (2005) Polyphenols: factors influencing their sensory properties and their effects on food and beverage preferences. Am J Clin Nutr 81:330S–335S
- 113. Aarts H, Dijksterhuis A (2000) Habits as knowledge structures: Automaticity in goal-directed behavior. J Pers Soc Psychol 78:53–63
- 114. Aarts H, Verplanken B, Knippenberg A (1998) Predicting Behavior From Actions in the Past: Repeated Decision Making or a Matter of Habit? J Appl Soc Psychol 28:1355–1374
- 115. Verplanken B, Aarts H, Van Knippenberg A (1997) Habit, information acquisition, and the process of making travel mode choices. Eur J Soc Psychol 27:539–560
- 116. Aarts H, Custers R (2010) Habit, Action, and Consciousness.
- 117. Ouellette JA, Wood W Habit and intention in everyday life : The multiple processes by which past behavior predicts future behavior. Psychol Bull 124:54–74
- 118. Verplanken B, Orbell S (2003) Reflections on Past Behavior: A Self-Report Index of Habit Strength1. J Appl Soc Psychol 33:1313–1330
- 119. Schweiger Gallo I, Gollwitzer PM (2007) Implementation intentions: a look back at fifteen years of progress. Psicothema 19:37–42
- 120. Stein LJ, Nagai H, Nakagawa M, Beauchamp GK (2003) Effects of repeated exposure and health-related information on hedonic evaluation and acceptance of a bitter beverage. Appetite 40:119–29