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Abstract

Sensations experienced in the mouth influence food choices, both immediately and in the long term. Such sensations are themselves influenced by experience with flavors, the chemical environment of the mouth, genetics of receptors for flavors, and individual behavior in the chewing of food. Gustation, the sense of taste, yields information about nutrients, influences palatability, and feeds into the human body's preparation to receive those nutrients. Olfaction, the sense of smell, contributes enormously to defining and identifying food flavors (and is experienced even after placing food inside the mouth). Another vital component of food flavor is texture, which contributes to palatability, especially if a food's texture violates a person's expectations. Next, chemesthesis is the sense of chemically induced irritancy and temperature, for example spiciness and stinging. All of these sensations are potentially modified by saliva, the chemical and physical media of the mouth. As a person experiences the culmination of these oral sensations, modified through an individual's own unique saliva, the flavors in turn influence both what and how a person eats.

Keywords: Taste, smell, texture, chemesthesis, saliva, food choice

1. Introduction

Food must be eaten in order to be nutritious (or deleterious). This fundamental fact may be obvious, but it is also the crux of the dilemmas regarding feeding behavior and health. In the end, all the healthy food in the world will have absolutely no effect on a person who does not make the choice to ingest that food. As the most dominant driver of food choice is flavor, e (IFICF, 2016), the mouth therefore plays a large role in a person's decision to ingest something. In general, "flavor" is experienced by the brain combining sensory experiences including aroma, tastes, textures, and perhaps even visual and audible cues from a food (Small, 2012). Not all fields and researchers agree on how many of these sensory attributes should be included in strict definitions of "flavor," but for this review the term will be used inclusively of the combination of sensations that may contribute to an individual's experiences and expectations of a food. Notably, a number of these potential "flavor" components can be obtained from sensory input before putting a food in the mouth. For example, expectations about a food may be derived from appearance, odors are perceived from a distance, and perception of thickness from stirring or swirling a beverage tracks strongly with in-mouth texture (Christensen & Casper, 1987). However, the full experience of flavor comes together as the food enters the mouth. Additionally, the properties (both physical and chemical) of the foods themselves will dictate the way the food is manipulated by the teeth and tongue. The combination of food sensation and oral manipulations can also influence the pace of feeding. Some foods take longer to chew than others. Some foods have dynamic textures which might influence the pace of consumption. But beyond even those fundamental differences, humans themselves differ in their own personal oral environments and chewing behaviors, which in turn will influence what they are willing to eat.

The purpose of this review is to briefly cover the sensations (gustation, retronasal olfaction, texture, and chemesthesis/trigeminal sensations) and secretions (saliva) of the oral cavity, and discuss how these factors may interact with food choice.

2. Gustation and olfaction

Gustation is the sense of taste, and will be used in this article to avoid confusion with the verb “to taste” (i.e., putting something in the mouth to experience/ingest it) or the more common vernacular meaning of the noun “taste” (referring to flavor in general). While colloquially “taste” often refers to many aspects of flavor, scientifically the sense of gustation is more limited. In general, gustation occurs by tastants first dissolving or suspending into saliva. The saliva passes over taste receptors, which are present on taste cells. The taste cells are organized into taste buds, which are present throughout much of the oral epithelium including the soft palate and the esophagus. However, most of the taste buds are found in the fungiform, foliate, and circumvallate papillae of the tongue (Miller & Bartoshuk, 1991). Tastants bind to the taste receptors, activating taste cells (either directly or through interaction with neighboring taste cells) to send a signal through nerves to the brain.

While scientists tend to agree gustation is limited to only a few qualities, there is little consensus on the total number of these “primary” gustatory qualities. Sweet, sour, salty, and bitter are widely accepted as gustatory percepts, but umami/savoriness, oleogustus (fatty acid taste), starchy taste, and several mineral tastes have also been proposed, with much ambiguity on why the first four are definitely gustatory sensations while the latter might or might not be. Some criteria for defining gustatory sensations have, however, been proposed (Mattes, 2011). They include: the sensation should offer an evolutionary advantage; ligands and receptors should have been identified; the receptors should activate gustatory specific cells and send signals along gustatory specific nerves; the sensation should be unique from other gustatory sensations; and the sensation should evoke some kind of physiological or behavioral response. Still, even among widely accepted tastes, not all fit this list of criteria equally. For example, a wide variety of chemical structures are all detected as bitter, and the receptors for saltiness and sourness are still not firmly established. This ambiguity over defining gustation is a critical reason why the number of gustatory sensations remains debated. For example, the concept of a gustatory component for fat is not new, dating back at least to the 1500s (Fernel, 1581). Yet, separating the textural from the gustatory sensation of fat is challenging, not only due to the physical differences in texture from fat compared to water but also due to the challenges in distributing fatty molecules in an emulsion with water (Running & Mattes, 2014a, 2014b). The issue of a “taste” for fat is then further complicated by the apparent unpleasantness of the fatty acids when used as gustatory stimuli (Running, Craig, & Mattes, 2015; Running, Hayes, & Ziegler, 2017) compared to the assumed pleasantness of high-fat foods. This observed negative hedonic experience of fatty acid taste compared to fattiness in general is precisely why a new term, “oleogustus,” has been proposed to isolate the gustatory experience of fatty acids (Running et al., 2015). In any case, this particular gustatory sensation is a prime example of how strict definitions elude us for what is gustation and what is some other oral sensation.

Despite the colloquial meaning of the word “taste,” much of a food’s overall flavor actually comes from odor: specifically, retronasal olfaction. These are the odors that pass through the back of the mouth into the airway and up into the nasal passages. When nasal passages are inflamed or otherwise blocked, this movement of air is restricted and results in lack of sensation. This is why when a person develops a respiratory infection, they can no longer “taste” anything—in reality, the sense of gustation is intact, but the sense of olfaction is limited. Loss of the retronasal olfaction reduces the sensation of the food to gustation, texture, and chemesthesis, and as a result the ability to identify flavors is severely limited.

The importance of odor on flavor identification is likely because the olfactory system can detect multitudes of distinct odors, especially compared to the very restricted list of gustatory sensations described above. To date, over 400 olfactory receptors have been identified, each of which is expressed on its very own set of individual olfactory neurons (Chess, Simon, Cedar, & Axel, 1994; Mainland et al., 2014; Zhang & Firestein, 2009). These neurons extend from the olfactory epithelium, and small piece of tissue in the uppermost part of the nasal passages, directly into the brain's olfactory bulb, where the signals are processed. When odorants dissolve into the mucus coating the olfactory epithelium, they stimulate the odor neurons by interacting with the receptors. The brain interprets the pattern of which neurons were activated, and the aroma is perceived (Buck & Axel, 1991; Hasin-Brumshtein, Lancet, & Olender, 2009). With the hundreds of olfactory receptors, and the subsequent plethora of activation combinations, humans can detect thousands of unique odors.

3. Texture and chemesthesis

Texture of foods is derived from physical structure, including the dynamic structural changes that occur as food interacts with oral surfaces and saliva (Koç, Vinyard, Essick, & Foegeding, 2013). The physical nature of the food stimulates the sense of touch in the mouth, and the mouth is relatively sensitive to these sensations. Mechanoreceptors on the tongue can have small receptive fields (around 2.4 mm^2) and respond to low levels of force (0.15 mN, which is similar the force exerted by gravity on half a grain of rice) (Trulsson & Essick, 1997). The texture of foods also directly influences the processes of chewing and swallowing, thus influencing the time food spends in the mouth as well as overall eating rate. Understanding the dynamics of food texture in the mouth require consideration of the food's original structure. While gustation and olfaction often emphasize biochemical reactions, such as receptor-ligand pairs and inter/intra-cellular trafficking of signaling molecules, the study of food texture requires some mechanical and engineering perspective in order to model and interpret breakdown of food's physical structures. Inevitably, this physical breakdown of the food in turn influences the other senses in the mouth, as taste, odor, and chemesthetic compounds are released or re-adhere to the structures altered by chewing (Dijksterhuis & Piggott, 2000). Importantly, human mouth behavior may also have a role in the perception of food texture. Recently categories of mouth behavior have been proposed, which include chewers, crunchers, smooshers, and suckers (Jeltema, Beckley, & Vahalik, 2015), based on the preferred mouth movements of an individual and/or the foods that best allow those movements. For examples, “smooshers” seem to prefer to squeeze their food between the tongue of palate, and this behavior correlates with preference for more semi-solid foods such as yogurts or oatmeal. However, whether these food preferences drive the mouth behavior or the mouth behavior drives the food preferences is unclear. Nevertheless, numerous studies have confirmed that individuals certainly do differ in their mouth behaviors, including number of chews, shape of the chewing movement, amount of muscle effort in chewing, chewing rhythm, and more (Brown, Langley, Martin, & MacFie, 1994; Devezeaux de Lavergne, van de Velde, & Stieger, 2017). Furthermore, many of these parameters are more consistent within-subject than would be expected for wide differences in food properties such as hardness or fracturability. For example, individuals who used fewer chews before swallowing a carrot also tended to have fewer chews before swallowing apples, pork, salami, shortcake, and toast (Brown et al., 1994). Thus, the chewing behavior appears to be entrenched or innate in some way that is determined by the individual rather than the food.

Related to texture perception is chemesthesis. Chemesthesis is the chemical stimulation of temperature, touch, and irritation, and is also often referred to as “trigeminal” sensation due to the activity of the trigeminal nerve in carrying these signals from the mouth to the brain. In the oral cavity, this includes sensations like the spiciness of chilis, cooling of mint, and sting of carbonation. The trigeminal nerve informs the brain of these chemesthetic signals as well as physical touch and actual thermal changes. Just as this nerve is shared among these different sensory stimuli, several receptors are also shared. For example, the TRPM8 protein in humans responds to both cool temperatures and menthol, and TRPV1 response to both capsaicin and heat (Roper, 2014). Thus, the overlap in words used to describe the sensations, whether chemical or physical/thermal in nature, makes sense (e.g., coffee and chili peppers can both be "hot"). Perception of intensity from chemesthesis can vary widely among individuals, but this variability is best documented for spiciness. Consistently, those who eat more spicy foods and like spicy foods rate the intensity of spiciness as lower than those who do not eat and do not like spicy foods (Cowart, 1987; Nolden & Hayes, 2017; Prescott & Stevenson, 1996; Tornwall, Silventoinen, Kaprio, & Tuorila, 2012). Likely, this association of eating/liking with intensity is a combination of innate and learned influences (Allen, McGeary, & Hayes, 2014; Byrnes & Hayes, 2013, 2015, 2016; Guimaraes & Jordt, 2007; Tornwall et al., 2012).

4. Saliva

Saliva is the biochemical media of the mouth, as well as a physical lubricant for oral surfaces. When salivation is impaired, gustation, olfaction, oral touch, chemesthesis, chewing, and swallowing are also impaired (Mese & Matsuo, 2007; Satoh-Kuriwada et al., 2009). In a single day, humans may swallow around 0.6-1.5 L of their own saliva (Aliko et al., 2015; Humphrey & Williamson, 2001), yet only about 0.7-1 mL of saliva is present in the mouth at any given time (Lagerlof & Dawes, 1984). The amount of saliva in the mouth is increased by stimulation with tastes and textures, with the strongest stimulations coming from sour taste and chewing (Dawes & Jenkins, 1964; Proctor & Carpenter, 2014; Watanabe & Dawes, 1988a, 1988b). Odor can also stimulate saliva, but the effect is generally weaker than taste and texture (Engelen et al., 2003).

Saliva is not just one fluid. Instead, it is a mixture from several functionally different salivary glands. "Major" salivary glands include the parotid, submandibular, and sublingual glands and contribute the larger volume of saliva to the mouth, whereas "minor" glands are distributed as lingual, buccal, palatine, and labial glands and secrete a relatively small volume of saliva (Humphrey & Williamson, 2001). Importantly, the terms “major” and “minor” refer to the anatomical size of the glands and thus their volume of secretions, rather than the functional importance of those secretions. Indeed, many minor glands are crucial to maintaining adequate protection of oral surfaces (Eliasson & Carlen, 2010; Humphrey & Williamson, 2001). Further, minor glands in the posterior of the tongue (von Ebner’s glands) secrete directly into the clefts of the circumvallate and foliate papillae, where the densest population of taste buds in the mouth are located. Beyond the major and minor glandular distinction, saliva can also be categorized as serous, mucous, or mixed saliva. Serous saliva is thinner and more watery, while mucous saliva is thicker and has more gel-like properties. In general, serous saliva appears to be more involved in solubilizing and processing foods, which mucous saliva is designed more to protect the oral surfaces (Carpenter, 2013; Eliasson & Carlen, 2010; Humphrey & Williamson, 2001). The parotid glands (major) and von Ebner’s glands (minor) secrete serous saliva. The other major glands secrete mucous or mixed saliva, and the other minor glands secrete mucous saliva.

While saliva is over 99% water, the proteins and smaller molecules present in saliva significantly influence the behavior of foods in the mouth. Enzymes like salivary α-amylase can break down starch in a matter of seconds, substantially altering texture of food and presumably changing the time it takes before an individual decides to swallow (Bridges, Smythe, & Reddrick, 2017; Mandel, Peyrot des Gachons, Plank, Alarcon, & Breslin, 2010). Small molecules in saliva are released to control ion concentrations in the mouth, such as bicarbonate to neutralize acids which in turn influences sour taste (Helm et al., 1982; Norris, Noble, & Pangborn, 1984). Beyond that, proteins in saliva have been proposed to modify astringency (Dinnella, Recchia, Fia, Bertuccioli, & Monteleone, 2009; Dinnella, Recchia, Vincenzi, Tuorila, & Monteleone, 2010), saltiness (Stolle et al., 2017), bitterness (Dsamou et al., 2012; Morzel et al., 2014), and fattiness/oleogustus perception (Mounayar, Septier, Chabanet, Feron, & Neyraud, 2013; Neyraud, Palicki, Schwartz, Nicklaus, & Feron, 2012; Poette et al., 2014; Schmale, Ahlers, Blaker, Kock, & Spielman, 1993; Schmale, Holtgrevegrez, & Christiansen, 1990; Spielman, D'Abundo, Field, & Schmale, 1993). Additionally, composition of saliva can cause instability in emulsions (mixtures of oil and water) leading to different sensory perceptions of those emulsions among individuals (Dresselhuis, de Hoog, Stuart, Vingerhoeds, & van Aken, 2008; Vingerhoeds, Blijdenstein, Zoet, & van Aken, 2005). Furthermore, work in rats even indicates that exposure to bitterness and astringency can change saliva in ways that subsequently alter the acceptability or intensity of those bitter/astringent compounds (Martin et al., 2018; Torregrossa et al., 2014). In future years more research will hopefully confirm or clarify these linkages between diet, flavor, and saliva, and perhaps yield ways in which we could monitor or alter saliva to improve healthy dietary behaviors.

5. Eating behavior

All of these oral factors can, in isolation or combination, influence food choices and eating behavior. For gustation, sweetness, umami, and saltiness are often thought to enhance the palatability of food while bitterness, sourness, and oleogustus (the rancid, unpleasant taste of fatty acids, particularly polyunsaturated fatty acids, not the delicious fatty texture) seem to reduce palatability. However, these outcomes are not assured. Certainly, sweetness by itself is accepted even in infants, while sourness and bitterness are rejected (Maone, Mattes, Bernbaum, & Beauchamp, 1990; Tatzer, Schubert, Timischl, & Simbruner, 1985). Excess consumption of salt among many cultures would seem to indicate that it is palatable, and the positive effect of adding monosodium glutamate (prototypical stimulus for umami) to items such as soups imply this sensation is liked. However, people do not generally drink sugar water, or salt water, or umami water—instead, we consume foods as mixtures of flavors. Thus, the context of the food itself is critical for understanding the role of flavor in palatability. While fatty foods are often well-liked, when fat breaks from an emulsion and pools on the top of the food, the food can be rejected. Further, our own work on oleogustus indicates that the gustatory sensation from fatty acids is unpalatable. (Running et al., 2015; Running et al., 2017). Similarly, bitterness in isolation is rated as unpleasant, yet bitter foods such as coffee, chocolate, and tea have become firmly embedded in many diets. Some of this may be due to post-ingestive feedback, as these products may have psychoactive (i.e., stimulatory caffeine) or energy contributions that make them appealing. Associations of these eating consequences with the flavor of the food can be learned, thus contributing to the wide array of responses of humans to the sensations experienced in the mouth. Overall, the combination of sensation, saliva, and experience with flavors influences human food choices.

In researching these phenomena, the goal is to identify which of these factors are modifiable, and how, in order to lead to improvements in human diets. With so many potential factors influencing food choices, there is clearly much room for new work. Combining data and approaches across these research fields, such as how mouth behavior or movements might influence dissolution of tastants, or how salivary composition might change over time to alter chemesthetic ligand activity, will hopefully lead to more targeted understanding of these phenomena at the individual level. Moreover, a better grasp of which factors are changeable, and how difficult changes would be to induce, is critical. For example, if a “smooshing” mouth behavior leads to preference for softer foods, does this in turn lead to excess energy intake because soft foods are quickly processed in the mouth? More importantly, can we change that mouth behavior to reduce the excess intake? Is there an ideal life stage to make such interventions? Could the flavor of the food be modified to help alter the mouth behavior? Will alterations in the mouth behavior change the secretion of saliva, and will that in turn alter the flavor experienced? Answers to such questions will be integral as we explore how the oral environment is more than just the gateway that accepts or rejects food. After all, many of the compounds that are active from an oral sensory perspective, such as sweet sugars, slimy soluble dietary fiber, or bitter polyphenols, also influence human health. Presumably, our ability to detect many of these sensations is evolutionarily linked to those health outcomes. As modern technologies evolve our diets more quickly than we as humans can evolve, understanding the role of the oral environment in feeding will be paramount to maintaining healthy eating behaviors and food supplies.

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