The Secretion, Components, and Properties of Saliva

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Abstract

Saliva has one of the most difficult roles to perform in the body. It must facilitate the taste and detection of foods nutritious to the body but also defend the mucosa from infection by the ever-present microbiota present in the mouth. It achieves these roles by having a complex composition and versatile physical properties. The protein and ion components make a solution that is 99% water into a viscoelastic solution capable of many roles, such as acting as a lubricant and an antimicrobial, preventing the dissolution of teeth, aiding digestion, and facilitating taste. This review describes the neural regulation of salivary secretion in terms of fluid, protein, and ion secretion. It then describes some of the components and physical properties of saliva and attempts to relate them to the functions that saliva must perform.

NERVES CONTROL THE SECRETION OF SALIVA

Salivary flow is a continuous process in conscious humans that is upregulated by a reflex mostly stimulated by taste and chewing (Chaudhari & Roper 2010, Hector & Linden 1999). Resting, or unstimulated, salivary flow (approximately 0.5 ml min^{-1} in most adults) is the result of low-level autonomic stimulation by the higher centers, including the orbitofrontal cortex and amygdala of the brain working via the salivary centers within solitary tract nuclei in the brain stem to act on salivary glands (Matsuo 1999). When we are asleep, these inputs from the higher centers are reduced and so we have decreased salivary flow (approximately 0.1 ml min^{-1}), which is why our teeth are particularly susceptible to attack at this time by microorganisms that are ever present in the mouth. During times of stress, the higher centers reduce nerve traffic to the salivary centers and then to the salivary glands, which causes dry mouth (Garrett 1987).

Salivary secretion is upregulated above the resting rate by taste and chewing and to a lesser degree by smell stimulation. Chewing of foods stimulates the receptors in the periodontal ligament (Scott et al. 1998) sandwiched between the tooth and the alveolar process of the jaw bone, although interestingly these are not stimulated by empty chewing, i.e., teeth grinding (Anderson et al. 1996). For taste stimulation of salivary secretion, many studies have used citric acid, as it generates by far the largest salivary flows, often at a tenth of the concentration of other stimulants, such as sweet, salty, bitter, and umami (Hodson & Linden 2006). However, citric acid is rarely apparent in the diet in a nonbuffered form, and thus chewing can be considered equally efficient at stimulating saliva production as taste under normal conditions. Because the tasting, chewing, and smelling sensory inputs are integrated in the brain (Rolls 2011) before being sent to the salivary glands, there are few differences in the protein profile between chewing- and taste-stimulated salivas, at least those from the parotid gland. Although saliva collected from the submandibular/sublingual glands does show variations in mucin concentration and other proteins between a chewing- and taste-stimulated secretion, this probably reflects differential activation and secretion by the two glands (Ilangakoon & Carpenter 2011). Few studies collect a truly pure submandibular or sublingual secretion because of the difficulties of the ductal anatomy; the submandibular gland duct passes through the sublingual and can sometimes connect into the sublingual duct(s) before entering the mouth (Proctor et al. 2007). More detailed proteomic analyses have revealed differences in the protein content of parotid saliva when stimulated by the different tastes (Neyraud et al. 2006), although the proteins identified appear to be principally of nonsalivary gland origin.

It is thus well established that the main stimulants of salivary flow above the resting rate are taste and chewing, but surprisingly there is little evidence that the thought of food can affect salivary secretion. The occurrence of mouthwatering at the sight or thought of food, although widely appreciated, is a difficult one to reproduce under controlled conditions. Most experiences of food include an aroma that, as indicated above, can stimulate the submandibular/sublingual gland to secrete saliva. In fact, in some recent experiments subjects exposed to food with no smell component showed no measurable stimulated salivary secretion. Although some reports have shown a conditioned-like salivary reflex (Holland & Matthews 1970), the flows were very small and transient. In dogs and other species, a conditioned salivary reflex can be easily demonstrated. A possible explanation for mouthwatering in humans would be the effect of facial muscles under voluntary control squeezing on the ducts that convey the saliva from the glands to the mouth to cause a transient flow of saliva (Ilangakoon & Carpenter 2011).

Of the major salivary glands, the parotid is the largest and contributes the greatest flow (as much as 60% of the total) when stimulated by taste or chewing (Matsuo 2000) but contributes a smaller amount to resting salivary flow. It secretes a serous secretion that contains no mucins but is rich in amylase and proline-rich proteins (PRPs), the functions of which are discussed below.

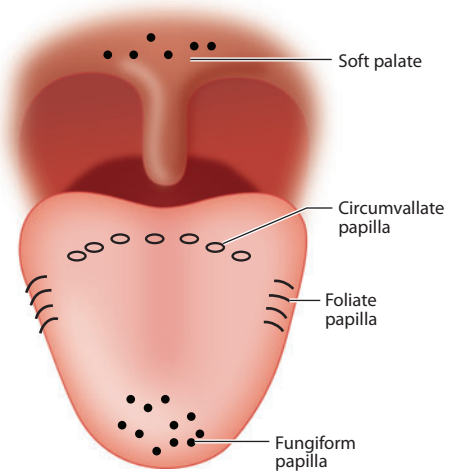

Figure 1

Taste buds occur on the tongue in three main areas, which are associated with the circumvallate, foliate and fungiform papillae (small areas of keratinized epithelium often appear as red dots). The taste buds in the foliate and circumvallate papillae are located within crypts that are constantly bathed by the serous minor salivary glands (von Ebner's glands). Occasional taste buds may also be found in the soft palate.

Studies in rat indicate that the parotid gland is the most responsive to variations in the diet, such that during times of nutrient starvation, glands can become smaller and atrophic but can then regenerate during resumption of feeding (Hall & Schneyer 1964). The submandibular and sublingual glands are less responsive to changes in diet and contribute more to the resting salivary flow rate.

In addition to the major salivary glands (which exist as bilateral pairs), there are hundreds of minor salivary glands located in the submucosa throughout the oral cavity. These glands secrete small volumes (<1 μl min^{-1} per gland) of mucin-rich saliva and are generally considered not to secrete reflexively, i.e., no increase in salivary flow in response to food unlike the major glands. Although only contributing approximately 10% of salivary flow, the minor glands are important in maintaining a mucin-rich layer adjacent to the mucosa. A small subset of the minor glands are the von Ebner's glands at the base of crypts that surround the foliate and circumvallate (but not fungiform) papillae on the tongue, where the majority of the taste buds are located (**Figure 1**). These infrequently studied glands (Eliasson & Carlen 2010) appear more serous than mucous and contain some proteins of interest to food processing, e.g., lipocalin and lingual lipase, both of which have been speculated to play a role in detecting fat. However, the salivary output of these glands is so small that the role of lipocalin and lingual lipase could only be to maintain their immediate environment of the taste buds in the crypts rather than the digestion of fat.

Taste buds are mostly located on the tongue in three main areas: the fungiform, foliate, and circumvallate papilla. The taste maps of the tongue often reproduced in textbooks are now largely discounted; there is abundant evidence to show most areas of the tongue are able to detect most tastes. Most taste buds are located on the posterior part of the tongue at the foliate and circumvallate papilla, although there is considerable variation in the number of taste buds between people, which has sometimes been correlated with supertaster status (a heightened ability to detect and discriminate tastes) (Hayes et al. 2008). There is still a lack of clarity as to the role of saliva in mediating taste. Initially, it appeared that the main role of saliva was to hydrate tastants to allow

their delivery to the taste buds. There do not appear to be specific proteins mediating specific tastes. Both sourness and umami are ionic in nature and freely diffuse to the taste buds. Sweet and bitter tastants are usually more complex structures, and research suggests that there are not specific salivary proteins that aid their diffusion to the taste buds. The role of counter-ions is also largely ignored, although we know that bicarbonate ions do affect taste, particularly the sourness tastants (Matsuo 2000).

Salivary glands are composed of two main cell types: the acini, which make the saliva; and the ductal cells, which modify and convey the saliva to the mouth. The secretion of saliva is a well-studied mechanism (for a review, see Turner & Sugiya 2002) that involves the active secretion of salt (as sodium and chloride ions) by the acinar cells into the ductal lumen of the gland upon receiving a neural signal from the brain. Water, but not protein, derived from the blood system passes around via the tight junctions, and through, via aquaporin channels, the acinar cells to form saliva that is isotonic with respect to serum. In the parotid and submandibular glands, the salt is mostly recovered by the striated ducts, which are impermeable to water. Their striated description derives from their corrugated basal membrane, which is packed with mitochondria. Recovery of salt from the saliva changes the primary isotonic saliva (as secreted by the acini) into a hypotonic saliva. This has important implications for the maintenance of taste buds and for their sensitivity to salt detection (Matsuo 2000). By existing in hypotonic saliva, taste buds are able to detect salt at much lower thresholds than found in serum, and this is the reason that tears, sweat, and blood taste salty. However, the reabsorption of salt is an energy-expensive process (hence the large numbers of mitochondria within the striated ducts) that is not upregulated during stimulated salivary secretion; the result is that stimulated saliva has a higher sodium and chloride concentration than resting saliva, but it is unclear whether this greatly affects taste.

Salivary glands are densely innervated by parasympathetic and sympathetic nerves of the autonomic nervous system. Unlike the rest of the body, the two parts of the autonomic system work together rather than antagonistically. Parasympathetic nerve impulses produce a high-flow, low-protein saliva, whereas sympathetic impulses produce a low-flow, high-protein saliva. However, these are not absolutes. Parasympathetic stimuli seem particularly important for the secretion of mucins, and adrenergic stimuli can invoke some salivary flow (Proctor 1998). As mentioned above, the fluid component of saliva is mediated by the secretion of salt into the ductal lumen, following the stimulation of muscarinic receptors on acinar cells through intracellular calcium. In contrast, protein secretion into saliva is usually mediated by the sympathetic nerve stimulation of β- (and to some extent α-) adrenergic receptors acting via intracellular cyclic adenosine monophosphate (AMP) changes to cause the fusion of secretory granules with the apical membrane of cells (Castle & Castle 1998). However, not all proteins are secreted in this way; a notable exception is secretory IgA. This is the main antibody in saliva and is actively carried across acinar and ductal cells via a transporter protein called the polymeric immunoglobulin receptor (pIgR). Although this process can be upregulated by neural activity (Carpenter et al. 1998), it does not involve storage of IgA within cells. Instead, IgA, which is made by plasma cells located in the gland, binds to the pIgR on acinar and ductal cells on the basolateral surface. Once endocytosed into the cell, the vesicle is transported across the cell to the apical membrane, where the membrane receptor is cleaved to release secretory IgA (the secretory component is the cleaved part of the pIgR). The pIgR is specific to IgA, and so even though there are equal numbers of IgG-, IgA-, and IgM-producing plasma cells within the gland (Mega et al. 1992), IgA becomes the single-most-abundant antibody in saliva because it is preferentially bound by the pIgR (Brandtzaeg 1998). Little or no diffusion of immunoglobulins into saliva occurs, except under conditions of inflammation or disease.

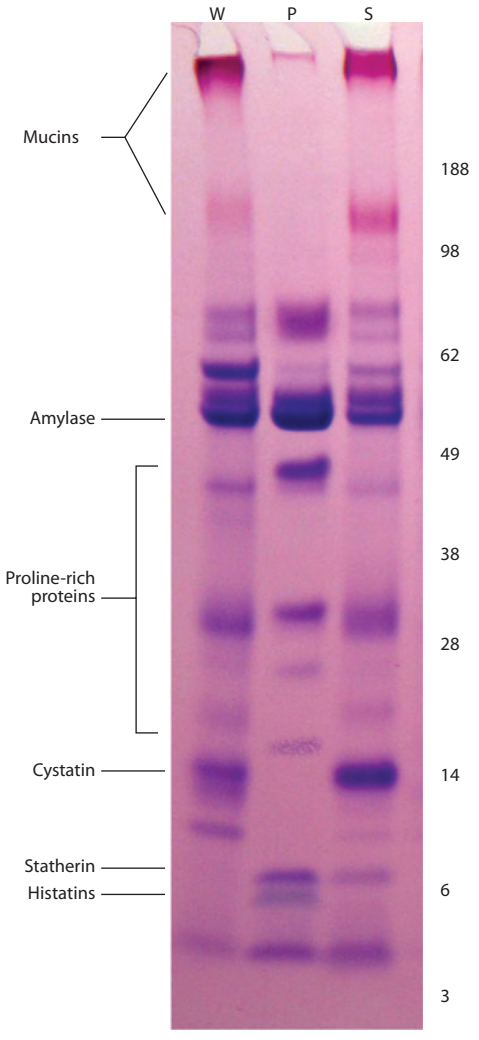

Figure 2

The protein components of whole-mouth (W), parotid (P), and submandibular/sublingual (S) salivas. Proteins have been separated according to size, with the largest at the top, and then stained with Coomassie Brilliant Blue and Periodic acid–Schiff's reagent to show proteins and glycoproteins. Parotid saliva is serous, amylase rich, and mucin free. In contrast, submandibular/sublingual saliva is mucin and cystatin rich. Although whole-mouth saliva should be the sum of the separate salivas (i.e., P+S), it lacks certain proteins, most notably the proline-rich proteins and statherin and histatin, which readily interact with bacteria and hard and soft tissues in the mouth. Numbers indicate apparent molecular weight in kiloDaltons.

COMPONENTS OF SALIVA

Most proteins in saliva are made by the salivary glands, but there are large differences between the glands as to which proteins they synthesize (**Figure 2**). Some proteins are universal to all glands, such as the secretory component, which is the transporter of IgA (the main antibody in saliva). Mucins (Muc5b and Muc7 gene products) are common to the submandibular and sublingual glands as well as most minor glands but are not expressed by the parotid and von Ebner's glands (which

are serous glands). Basic PRPs appear to be exclusive to the parotid glands, whereas acidic PRPs appear in submandibular and parotid glands. PRPs are highly polymorphic, and although encoded by only six genes, more than 50 different proteins exist, mostly because of gene rearrangements but also because of some post-secretory processing (Azen 1993). The result of this is a huge variety of proteins not only between individuals but also within the same individual at different times of the day (because of the contribution of different glands). Why there is such diversity between glands is not immediately obvious. It could relate to the locations in the mouth where each gland deposits saliva. The parotid gland delivers the least saliva at rest but the most during periods of chewing, thus the delivery of parotid saliva adjacent to the upper molars might be important to aid the chewing of food. In contrast, the submandibular and sublingual exit into the mouth under the tongue. Given that they contribute the most to resting saliva, it may be suggested that this position is the best to distribute the saliva across the mouth by the action of the tongue. However, these are only speculations; several studies have shown that the loss of one gland caused by, for example, salivary stones obstructing ducts has little impact on functions of the mouth. This reflects the multifunctional properties of saliva.

Amylase is the single most abundant protein in saliva. It is generally thought to be involved in the initial digestion of starch-containing foods. However, this seems unlikely because its activity is greatly reduced as soon as it reaches the acidic environment of the stomach. Pancreatic amylase is much more likely to be involved in starch digestion (Butterworth et al. 2011). So why then is there so much amylase in saliva? It may be more important in the post-mastication clearance of food from the mouth. Although best known as an enzyme specific to maltose conversion to glucose, amylase is very efficient at converting many nonsoluble complex polysaccharides into smaller soluble units. This has two advantages: the dissolution of food particles stuck on teeth and the reduction of the availability of substrates for microbial growth.

Many of the protein families in saliva (**Figure 3**) have unusual amino acid sequences. In addition to the PRPs already mentioned, there are histidine-rich proteins (known as histatins) and cysteine-rich proteins (known as cystatins). The histatins appear to be particularly effective at controlling fungal growth in the mouth (Helmerhorst et al. 1999). However, the presence of so many histidines with a ring structure creates a strong affinity for polyphenols (Wroblewski et al. 2001), which is similar to the way that the proline ring structure aids in the binding of proline to polyphenols (Jobstl et al. 2004).

The high proline content of PRPs leads to an extended structure (Boze et al. 2010), which is also mirrored in mucins that are both proline and serine rich. The serine amino acid is the main site for the O-linked glycosylation, which may account for more than 50% of mucin structure. The glycosylation, and particularly the terminal sialic acids, are important to bacterial binding, which aids in aggregation and clearance of bacteria from the mouth.

PROPERTIES AND FUNCTIONS

The properties of saliva (summarized in **Figure 4**) are modified by the glycoproteins and ions within saliva to allow the various and many functions of saliva to be performed. Water is a Newtonian fluid because the viscosity doesn't change with increasing shear. In contrast, saliva, despite being composed of 99% water, is described as a non-Newtonian fluid because the viscosity decreases with increasing shear. In practice, this allows saliva to be easily spread on the oral surfaces as well as to be retained and not easily washed off oral surfaces. This is an important function for saliva because the oral mucosal surfaces are the main site for the interaction with the microorganisms in the mouth (Dewhirst et al. 2010). The highest shear rates in the mouth occur during eating and swallowing. These high shear rates aid in maintaining a constant flow of saliva from where it enters the mouth (ductal openings) to the back of the throat (for swallowing). The constant

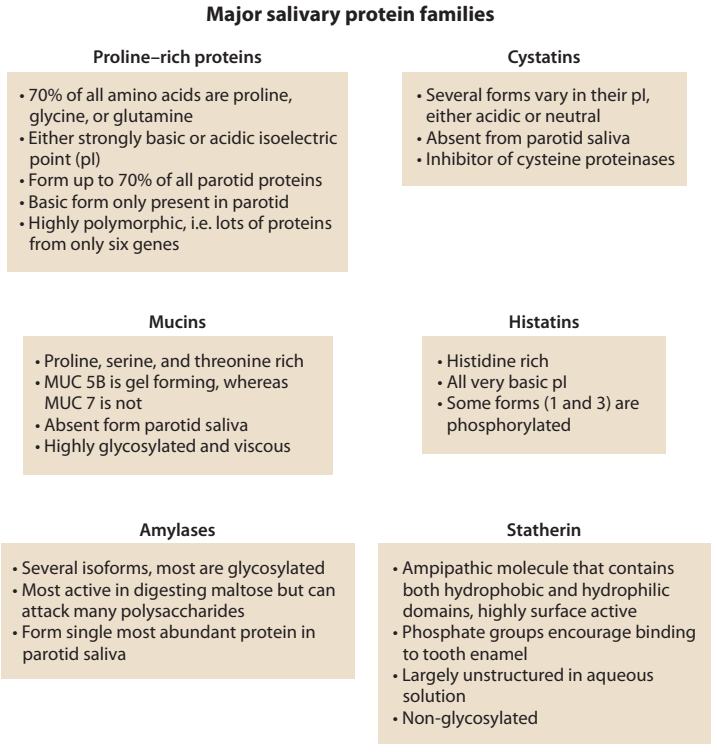

Figure 3

The unusual amino acid composition of many salivary proteins reflects the unique properties that they need to perform the many functions of saliva. Proline-rich proteins, histatins, and mucins have elongated structures to aid binding. Cystatins are protease inhibitors. Statherin has important roles in binding calcium. Only amylase, which is the single-most-abundant protein, has a more typical amino acid composition.

movement of saliva is important for the removal of bacteria, the pH buffering of saliva, and oral health generally.

Mucins are high-molecular-weight glycoproteins with an elongated structure that contribute significantly to the viscoelastic behavior of saliva. They can self-aggregate to form very large structures, leading to the viscous nature of whole-mouth saliva or submandibular/sublingual saliva. Parotid saliva, which contains no mucins but still has many glycoproteins, has a viscosity closer to that of water. However, parotid saliva still has strong viscoelastic qualities, not least of which are its surface active properties (Proctor et al. 2005), which allow the wetting of both hydrophobic and hydrophilic surfaces. This is particularly important because of the different properties of foods. Some may be dry, e.g., biscuits, whereas others may be oily, e.g., chips/fries. All these foods need to be coated in a layer of saliva to enable bolus formation and be safely swallowed (Chen 2009).

Bolus formation is another important function of saliva that is largely under-studied. As well as the wetting properties mentioned above, saliva incorporation into food is important to allow the food particles to stick together. The physical breakdown of food by chewing results in ever smaller particles. Once they have been sufficiently processed, a bolus is formed by the action of the tongue and must be sufficiently well-lubricated (by saliva) to pass through the throat. Touch receptors in the throat determine if the bolus is ready to be swallowed (Prinz & Lucas 1995).

Statherin, another salivary protein, seems to be a very important molecule for saliva in terms of physical properties. As well as being the most surface-active component in saliva (Proctor et al.

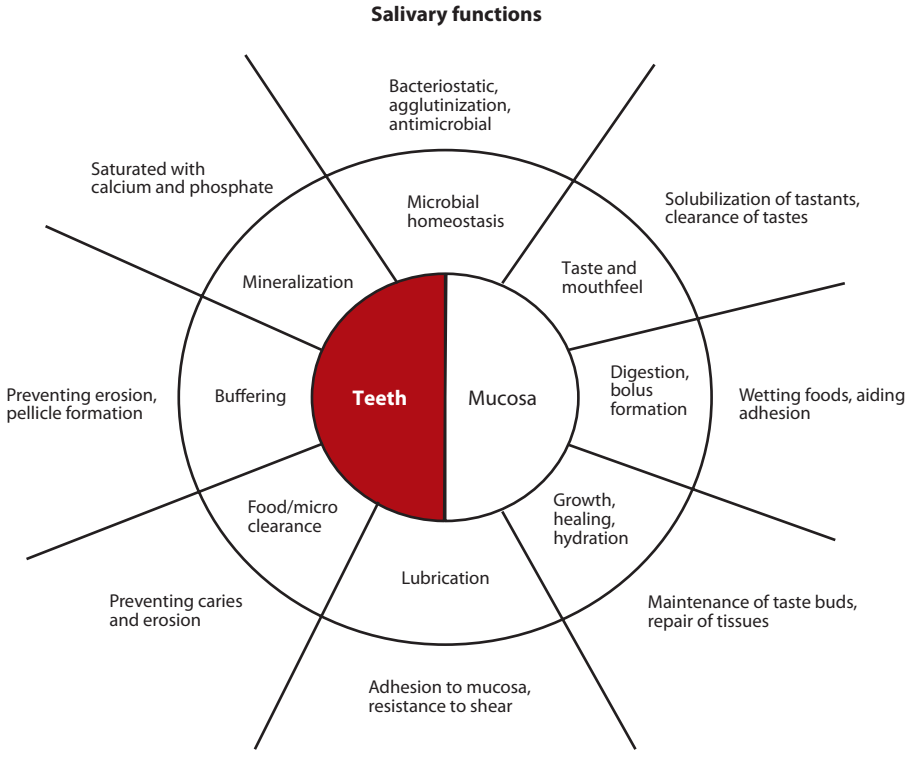

Figure 4

The functions of saliva can be divided according to the surface, i.e., the teeth or mucosa. Some functions, such as lubrication and microbial homeostasis, are common to both surfaces, whereas most other functions are unique to the surface. Some proteins have been assigned to different functions, but the list is not definitive and is based on available research.

2005), it has also been shown to be an important boundary lubricant (Douglas et al. 1991, Harvey et al. 2011). The lubrication or tribological qualities of saliva are central to many of its food-processing roles (Bongaerts et al. 2007). For example, statherin is a major component (Li et al. 2004) of the enamel pellicle, which is a subset of salivary proteins that stick tightly to the tooth surface. Statherin also functions as a lubricant of the teeth, which is crucial to preventing the teeth from chipping and wearing during chewing (Harvey et al. 2011, Young et al. 2001). The ionic components of saliva, and particularly calcium, are also influenced by protein components within saliva. Saliva is supersaturated with calcium with respect to hydroxyapatite, which is the main mineral component of teeth. This is to prevent the dissolution of teeth when exposed to oral fluids, foods, and particular dietary acids. Most calcium in saliva is protein bound to statherin or to other phospho-containing proteins (such as acidic PRPs). This has the beneficial effect of preventing the excessive precipitation of calcium onto the teeth, especially at bacteria-covered sites (such as the gingival enamel margin) that cause calculus (Hay et al. 1986).

SUMMARY

The components of saliva are many, and its secretion by salivary glands is complex. The multifunctionality of salivary proteins has also slowed the investigation of the function of each

protein. However, this complexity is presumably necessary to allow us to eat as wide a variety of foods as possible. The roles of saliva in eating are being investigated by more and more experimenters. Further analyses may help to reveal why there is such diversity in food preference and how that preference changes with increasing age.

DISCLOSURE STATEMENT

The author is not aware of any affiliations, memberships, funding, or financial holdings that might be perceived as affecting the objectivity of this review.

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