

REVIEW

The tongue as a gripper

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ABSTRACT

Frogs, chameleons and anteaters are striking examples of animals that can grab food using only their tongue. How does the soft and wet surface of a tongue grip onto objects before they are ingested? Here, we review the diversity of tongue projection methods, tongue roughnesses and tongue coatings, our goal being to highlight conditions for effective grip and mobility. A softer tongue can reach farther: the frog *Rana pipiens* tongue is 10 times softer than the human tongue and can extend to 130% of its length when propelled in a whip-like motion. Roughness can improve a tongue's grip: the spikes on a penguin *Eudyptes chrysolophus* tongue can be as large as fingernails, and help the penguin swallow fish. The saliva coating on the tongue, a non-Newtonian biofluid, can either lubricate or adhere to food. Frog saliva is 175 times more viscous than human saliva, adhering the tongue to slippery, furry or feathery food. We pay particular attention to using mathematical models such as the theory of capillarity, elasticity and friction to elucidate the parameters for effective tongue use across a variety of vertebrate species. Finally, we postulate how the use of wet and rough surfaces to simultaneously sense and grip may inspire new strategies in emerging technologies such as soft robots.

KEY WORDS: Grip, Soft robotics, Papillae, Saliva

Introduction

Food can be slippery, furry or just plain hard to reach. To propel food into the mouth, animals are aided by teeth, hands, paws or lips. The thesis of this Review is that the tongue also has a dazzling array of prehensile functions. Historically, it has received little attention as a manipulator, and instead has been regarded as an organ of taste or mastication. Tongue surface features such as papillae and saliva, heralded for their use in sensing, can also be used to adhere to food. In this Review, we show how properties of tongues can aid in the attachment to food and its propulsion into the mouth.

Studying the tongue may provide inspiration for the field of 'soft robotics' (see Glossary), where the aim is to use flexible manipulators to simultaneously sense and transport objects. Today's soft robots grip objects using a dry rubber surface, whereas tongues apply a greater variety of techniques, such as surfaces coated with spikes or saliva (Fig. 1). The tongue is typically used to manipulate objects for the purpose of ingestion, so objects of interest are going to get wet. A soft and wet manipulator could be especially helpful in surgical robotics, where grippers often interface with both tissue and fluid. Tongue-inspired manipulators

could also lead to new advancements in human prosthetics, human–robot interaction and enhanced control for autonomous robots.

Well before the age of soft robotics, the vertebrate tongue had long intrigued anatomists. Human tongue tissue, like heart tissue, consists of bundles of muscle fibers bound by connective tissue into a three-dimensional array; it is because of this unique combination of radial and longitudinal bundles that one can peel off the fibers of a bovine steak but not the bovine tongue (Anderson et al., 2005). Doran and Baggett (1971) classified mammalian tongues into two types, intra-oral and extra-oral. An intra-oral tongue is used primarily during mastication for saturating food with saliva. An extra-oral tongue is used for prey capture and food manipulation outside the oral cavity.

In a review, Kier and Smith (1985) described many vertebrate tongues as boneless muscular hydrostats (see Glossary), composed almost entirely of muscle that maintains an 'essentially' constant volume. For a cylindrical tongue of diameter D and length L , the volume may be written $V = \pi D^2 L$. Because volume is conserved, we can write:

$$0 = \frac{dV}{dL} = 2\pi DL + \pi D^2 dL/dD, \quad (1)$$

and therefore:

$$\frac{dL}{dD} = -\frac{2L}{D}. \quad (2)$$

Eqn 2 states that the rate of change of tongue length is inversely proportional to tongue diameter. Moreover, the negative sign means that the diameter must shrink for the tongue to extend. This constraint makes certain tongue shapes able to extend more than others. A thin cylindrical tongue, like that of an anteater, elongates farther for a smaller decrease in diameter than a short, yet wide, tongue.

The mechanics behind high-speed tongues were reviewed by Van Leeuwen et al. (2000), who analyzed the various types of amphibian tongue projection. Iwasaki (2002) reviewed the epithelial features and adaptations found on tongues. Kim and Bush (2012) discussed the various drinking strategies employed in nature, many of which use tongue movement. A study by Lauga et al. (2016) modeled human filiform papillae (see Glossary) as elastic beams that amplify bending deformation when fluids move on the tongue surface. In this Review, we draw from much of the data in these reviews, as well as 15 other papers, YouTube and our own experimental measurements. We include data from 73 species, which are listed in Dataset 1. We restrict our discussion to only vertebrate tongues, and do not discuss the tongues of fish, which function in an aquatic environment using mechanisms likely different from those presented here.

Although many of the biological features of tongues have been described, there lacks a theoretical framework that unifies the variety of tongues under a single goal, that of enhancing grip. The goal of this Review is to provide a physical picture of how tongues grip. We begin by presenting the characteristic size of the tongue

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Glossary**Elastomer**

A rubbery polymer capable of large strains before permanent deformation.

Filiform papillae

Small structures that exist on the ventral surface of most tongues, such as the human tongue. Filiform papillae are typically the smallest of all papillae types, and are devoid of taste buds. These structures are often found in high density, giving the tongue a brush-like texture.

Hyper-redundant

Manipulators that have a large number of degrees of freedom.

Muscular hydrostats

Biological organs devoid of skeletal support, capable of highly controlled movements through multidirectional contraction of muscle tissue.

Poisson's ratio

The ratio of transverse contraction strain to axial extension strain. It reflects the phenomenon where material expands in directions perpendicular to applied compression.

Soft robotics

A subfield of robotics that uses highly compliant materials for actuation, movement and grip, often inspired by biology.

Viscous dissipation

An irreversible process where kinetic energy of a viscous fluid is converted into internal energy, or heat.

Young's modulus

A measure of material stiffness, defined as the ratio of stress (applied force per unit area) and strain (relative change in length from deformation). The larger the Young's modulus, the stiffer the material.

and its elasticity, and how these correlate to different projection mechanisms. We then proceed to the tongue surface, discussing how feature size and shape affect gripping techniques. Lastly, we discuss how saliva can aid in lubrication or adhesion based on its viscosity. We close with a discussion of directions for future research in this emerging area, such as high-speed soft robotic actuators or hydration-enhancing micro-textures for the medical industry.

Tongue projection mechanisms

Tongues accomplish a range of feats – for example, the giant palm salamander can spit out its tongue 50 times faster than a human can blink (Deban et al., 2007), whereas the anteater navigates its sticky, 60 cm snake-like tongue into termite mounds (Naples, 1999). How does the tongue differ between these two extreme scenarios? For

both cases, the tongue must extend, yet herein lies the problem – the tongue is composed of biological muscle that can only contract. To solve this problem, the vertebrate tongue has evolved to convert contractive shortening into tongue elongation through four distinct mechanisms: mechanical pulling, inertial elongation, ballistic projection and hydrostatic elongation (Nishikawa, 1999; Van Leeuwen et al., 2000), which we discuss in turn.

Mechanical pulling (Fig. 2A) is employed by amphibians such as frogs and toads. Such animals have a unique anatomy: in most mammals, the tongue is attached to the throat, but in frogs and toads, it is attached to the front of the lower jaw. Frogs and toads use this attachment point to propel the tongue like a mousetrap. The tongue rotates out of the mouth owing to the longitudinal shortening of the genioglossus muscle, the primary contraction muscle in the tongue. Because the tongue rotation speeds are slow, making the centripetal forces minimal, the tongue unfortunately shrinks by as much as 60% of its resting length during the strike. To compensate for this shortening, animals with mechanical pulling tongues will lunge their body forward to reach prey (Nishikawa, 1999).

Inertial elongation (Fig. 2B) is also used by frogs and toads. It is similar to mechanical pulling in that the genioglossus muscle contracts and causes the tongue to swing outward. In addition, the frog rapidly drops its jaw, giving the tongue an additional boost of speed, reaching velocities of 4 m s^{-1} (Nishikawa and Gans, 1996). Jaw-dropping rates in inertial systems can reach 3700 deg s^{-1} , as we found in the frog *Rana pipiens*, twice the rate found in frogs that use mechanical pulling, such as *Ascaphus truei* (Nishikawa and Cannatella, 1991), which can reach 1800 deg s^{-1} . This additional speed increases centripetal forces that cause the tongue to lengthen, eliminating the need for body lunging.

All 160 species of chameleons and a number of species of salamanders have evolved unique ballistic projection mechanisms capable of generating tongue accelerations of up to 50 times gravity (de Groot and van Leeuwen, 2004; Deban et al., 2007; Deban et al., 1997). The plethodontid ‘lungless’ salamander tongue uses two spiral arrays of protractor muscles to compress the needle-like arms of a horseshoe-shaped cartilage skeleton. The skeleton folds medially as it and the surrounding soft, sticky tissue are projected out of the mouth (Fig. 2C). Chameleons extend their tongues using an energy storage-and-release mechanism. Cylindrical connective tissue sheaths are longitudinally loaded around a central cartilaginous bone; upon release, the loaded sheaths slide over the

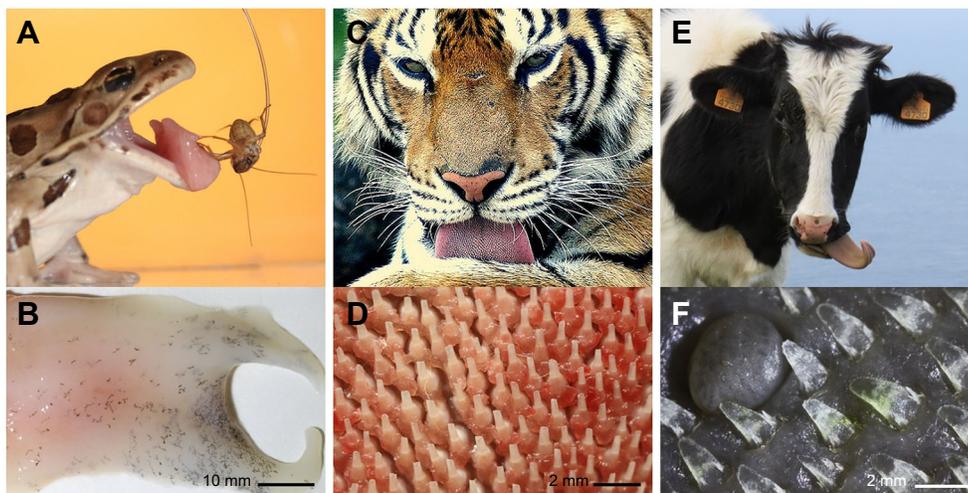


Fig. 1. The diversity of tongues and their surface features. (A) A frog *Rana pipiens* catching a cricket and (B) the frog's tongue. (C) A tiger grooming its fur and (D) the tiger's tongue. (E) A cow extending its tongue and (F) the cow's tongue. Photo credit: (C,E) Wikimedia Commons.

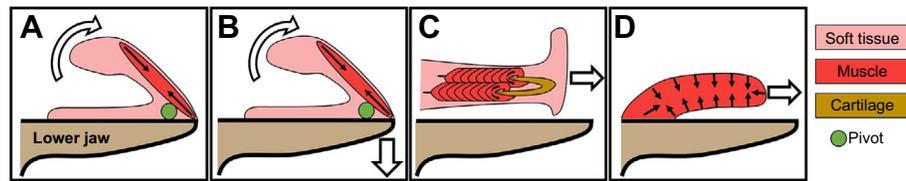


Fig. 2. Tongue projection mechanisms. (A) Mechanical pulling, as seen in the tailed frog *Ascaphus truei* (Nishikawa and Cannatella, 1991). As the genioglossus muscle contracts, the tongue rotates forward. (B) Inertial elongation, as seen in the northern leopard frog, *Rana pipiens*. Rapid jaw opening and contraction of the genioglossus muscle causes the tongue to rotate forward and elongate. (C) Ballistic projection, as seen in the plethodontid salamander. Muscles organized in a spiral array contract over a thin horseshoe-shaped cartilage to propel the tongue at high speeds. (D) Hydrostatic elongation, as seen in humans. Longitudinal and radial muscle fibers contract to extend the tongue.

tip of this bone, projecting both the sheaths and the surrounding soft, sticky tissue. Mammals, to be discussed next, have a comparably more mundane technique called hydrostatic elongation.

Most vertebrates have a tongue that possesses both longitudinal and radial muscle fibers, allowing for a high degree of motion control (Fig. 2D) (Kier, 2012). When the tongue is extended, this motion is called hydrostatic elongation. Tongues of this type share properties with octopus arms and elephant trunks, and are collectively called muscular hydrostats. These muscles elongate by taking advantage of their incompressibility, and transmit force through internal pressure. Contraction of radial muscle causes the tongue to shrink in radius but extend in length. Conversely, when the muscle is relaxed, the tongue is relatively short and can be conveniently stored without interfering with the upper throat.

Each of the aforementioned mechanisms is associated with tongues of different length. Tongue length is measured from tongue tip to point of attachment (Fig. 3A). The relationship between tongue resting length and body mass is shown in Fig. 3B using data gathered from 12 different literature sources (Anderson et al., 2012; Deban and Nishikawa, 1992; Emura et al., 2013; Igado, 2011; Meijaard, 1997; Muchhala, 2006; Naples, 1999; Nishikawa and Cannatella, 1991; Nishikawa and Roth, 1991; Noel et al., 2017; Pfeiffer et al., 2000; Reis et al., 2010) as well as our own measurements. Tongues of cow, coyote, Great Dane domestic dog, human, racoon, giant otter, fox, mink, rabbit, ring tail cat, hamster, rat and squirrel were gathered from Zoo Atlanta, a local dissection laboratory, and a local supermarket. If tongues are received frozen, they are first defrosted before measuring resting lengths. For mechanical and inertial mechanisms, there is insufficient recorded tongue lengths to plot a trend accurately. Excluding the outliers (anteater, tube-lipped nectar bat and pangolin), the tongue length for ballistic and hydrostatic mechanisms scales as:

$$L_{\text{ballistic}} = 73M^{0.26} (R^2 = 0.73, N = 23), \quad (3)$$

$$L_{\text{hydrostatic}} = 33M^{0.35} (R^2 = 0.81, N = 30). \quad (4)$$

As can be shown by the exponents (0.26 and 0.35), the tongues of at least hydrostatic projectors have a resting length that scales closely with body mass approximately to the one-third power, satisfying isometry. Isometry, a property where body parts have constant proportions across body sizes, is shared by a variety of animals from cockroaches to humans (McMahon and Bonner, 1983). Across a 100,000-fold change in mass, the tongue length increases nearly 30-fold, nearly as expected by isometry. The factor of two difference in pre-factor for Eqns 3 and 4 is likely due to the different kinds of muscle tissue employed for each mechanism. For example, ballistic tongues are covered with a thick and soft epithelial tissue.

Several animals with hydrostatic tongues do not follow the same pre-factor, including the tube-lipped nectar bat *Anoura fistulata*, the pangolin *Manis javanica* and the anteater *Myrmecophaga tridactyla*. The tube-lipped nectar bat drinks nectar from the flower *Centropogon nigricans* using a tongue that is 50% longer than its body, the longest tongue relative to body length of any mammal. The anteater and pangolin use snake-like tongues to gather ants and termites from insect holes. These three unique animals have specialized tongues that are detached from the hyoid bone (Muchhala, 2006; Naples, 1999; Prapong et al., 2009), which is typically used for tongue articulation and swallowing. This adaptation allows these animals to store their extra-long tongues deep within their chest cavity. These three animals fit their own trend: $L_{\text{hydrostatic outliers}} = 177M^{0.32}$ ($R^2 = 0.36$, $N = 3$), which still follows isometry but involves tongue lengths six times longer than other hydrostatic tongues. Such adaptations demonstrate the substantial evolutionary pressures to lengthen the tongue.

A tongue that can stretch out to reach food has a higher chance of grabbing it. Utilizing Kier's theory for volume conservation in muscular hydrostats (Kier and Smith, 1985), we write tongue 'stretch percentage' as:

$$\text{Stretch percentage} = \frac{L + \Delta L}{L} \times 100, \quad (5)$$

where L is the resting tongue length and ΔL is the increase in tongue length (Fig. 3A). A stretch percentage of 100% means that the tongue does not change in length. Using data gathered from literature (de Groot and van Leeuwen, 2004) and YouTube videos to estimate ΔL , we calculated the tongue stretch percentage across vertebrates, which can be seen in Fig. 3C. As shown by the black and red points in the plot, hydrostatic and inertial tongues have stretch percentages ranging from 130% to 250%. In contrast, the mechanical pulling tongue, shown by the purple point, shrinks during muscle contraction. For ballistic mechanisms, which rely on layers of sheathed tissue that extend like a telescope, the stretch percentage can reach well above 800%, as shown by the blue point representing the chameleon *Trioceros jacksonii xantholophus*.

Nishikawa (1999) first mentioned that the frog tongue follows a nearly straight line from mouth to prey, which may help the frog to accurately target its prey. The same straight-line motion appears to be the case for the tip of a bullwhip and an octopus arm, other whip-like mechanisms that reach their targets quickly (Fig. 4). An octopus arm can unfurl along a single plane to snag prey with its suckers. Bullwhips exhibit a propagation of curling waves, ending in the high end-tip velocity and the well-known supersonic crack (Goriely and McMillen, 2002). Although the octopus arm and frog tongue display similar kinematics, the mechanisms by which they unravel are quite different. To unfurl its arm, the octopus employs a wave of

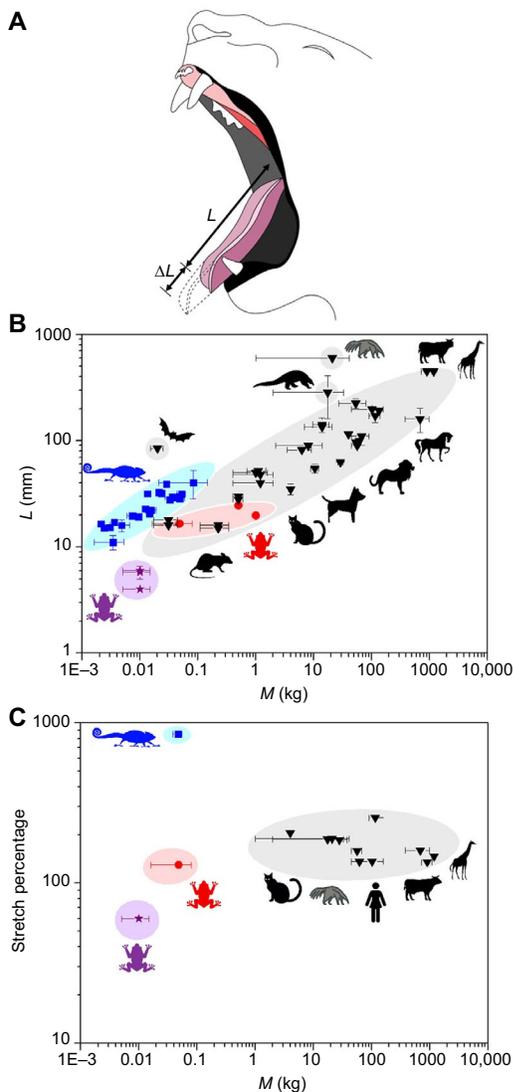


Fig. 3. Feeding mechanics linked with tongue geometry. (A) Schematic diagram of a tongue. Resting length L is measured from the point of attachment to the tip of the tongue. The increase in tongue length is given by ΔL . (B) The relationship between resting tongue length L and body mass M . Included are the four tongue projection mechanisms defined in Fig. 2: mechanical pulling (purple stars), inertial projection (red circles), hydrostatic projection (black inverted triangles) and ballistic projection (blue squares). (C) Stretch percentage across four tongue projection groups. Stretch percentage for ballistic projection (blue square) reaches well over three times that of inertial projection. Horizontal error bars in B and C indicate recorded mass range. The vertical error bars in B indicate s.d. for measured L .

muscle activation from the arm's base to tip, likely to overcome the large drag forces in the water (Yekutieli et al., 2005). In contrast, the frog tongue stretches passively during unraveling, with the ability to extend in length from 36 to 49 mm, a stretch percentage of 130% (Noel et al., 2017). Other papers have noted stretch percentages of 180% for inertial elongators such as *Bufo marinus* (Nishikawa, 1999; Nishikawa and Gans, 1996). This elastic stretching of the tongue also aids in tongue withdrawal, with the tissue 'springing back' like a bungee cord, requiring less effort from the hyoglossus retractor muscle. Despite the differences in tissue extensibility, the bullwhip, octopus arm and frog tongue are all able to project along a straight line with speed and precision; the comparable shape in which these different systems unravel deserves future investigation.

How does a frog tongue's stretch relate to its material properties? During inertial tongue projection, rotational kinetic energy (U_k) from rapid jaw opening is transferred into elastic potential energy (U_e). When the tongue is fully extended, there likely remains some kinetic energy in the form of waves along the tongue. We assume a bounding case of complete transfer to elastic energy, $U_k=U_e$. The elastic potential energy in the tongue tissue may be written as:

$$U_e = \frac{EA_0\Delta L^2}{2L}, \quad (6)$$

where E is Young's modulus (see Glossary) and A_0 is the tongue cross-sectional area. Rotational kinetic energy (U_k) can be calculated from high-speed videos. To maximize the tongue reach, ΔL for a fixed amount of kinetic energy, the Young's modulus (E) should be as low as possible. In other words, to stretch far, the tongue should be soft.

Softness of materials is characterized by the material's stiffness or Young's modulus: the lower the Young's modulus, the easier it is to stretch the tissue. The Young's modulus of a material is valid for small deformations, where force necessarily changes linearly with displacement. Beyond this linear regime, the Young's modulus must be used with care because biological tissue is often anisotropic and viscoelastic in nature. As detailed by McKee et al. (2011), tissue stiffness can span several orders of magnitude based on the direction and location that it is measured. In addition, the Young's modulus of a tissue can vary between *vivo* and *ex vivo*, owing to muscle activation by the animal.

The two most common ways to measure Young's modulus are by tensile stretching and indentation. Tensile stretching involves measuring the bulk muscle stiffness in a chosen direction, whereas indentation involves measuring the surface stiffness of skin, a value known as the epithelial tissue stiffness. For example, within the elastic regime at low deformations, the human tongue has an estimated bulk Young's modulus of 294 kPa (Hashimoto and Suga, 1986) and an epithelial Young's modulus of 15.2 ± 3.9 kPa, which we measured using flat-plate indentation *ex vivo*. Thus, the tongue epithelial tissue is nearly 20 times softer than the bulk tissue. For inertial elongators, a low bulk Young's modulus is important to maximize tongue reach. The northern leopard frog *Rana pipiens* has a measured tongue tensile stiffness of 4.2 kPa *ex vivo*, 70 times softer than the human tongue.

How the tongue surface affects grip

Interaction between the tongue and its target is dependent on the skin of the tongue, known as the epithelial tissue. The epithelial surface of the tongue is covered in microstructures called papillae (Fig. 5A–F). The two dominant types of papillae are fungiform and filiform. Fungiform papillae often take the shape of discs or mushrooms, and contain high concentrations of nerve endings and taste buds; owing to the low density of fungiform papillae on the tongue, we will not consider their role on grip in this Review. Here, we focus primarily on the filiform papillae, which hereon will be referred to simply as papillae. Using data from the literature (Abd-Elnaeim et al., 2002; Fouda et al., 2015; Kleinteich and Gorb, 2016; Kobayashi et al., 1998; Kumar and Bate, 2004; Lauga et al., 2016; Mascitti and Osvaldo Kravetz, 2002; Okada and Schraufnagel, 2005; Verissimo et al., 2015; Zweers et al., 1995) along with our own measurements, we found that papillae sizes range over three orders of magnitude (Fig. 5G) and can have varying levels of keratinization, with some as rigid as fingernails. Large, rigid

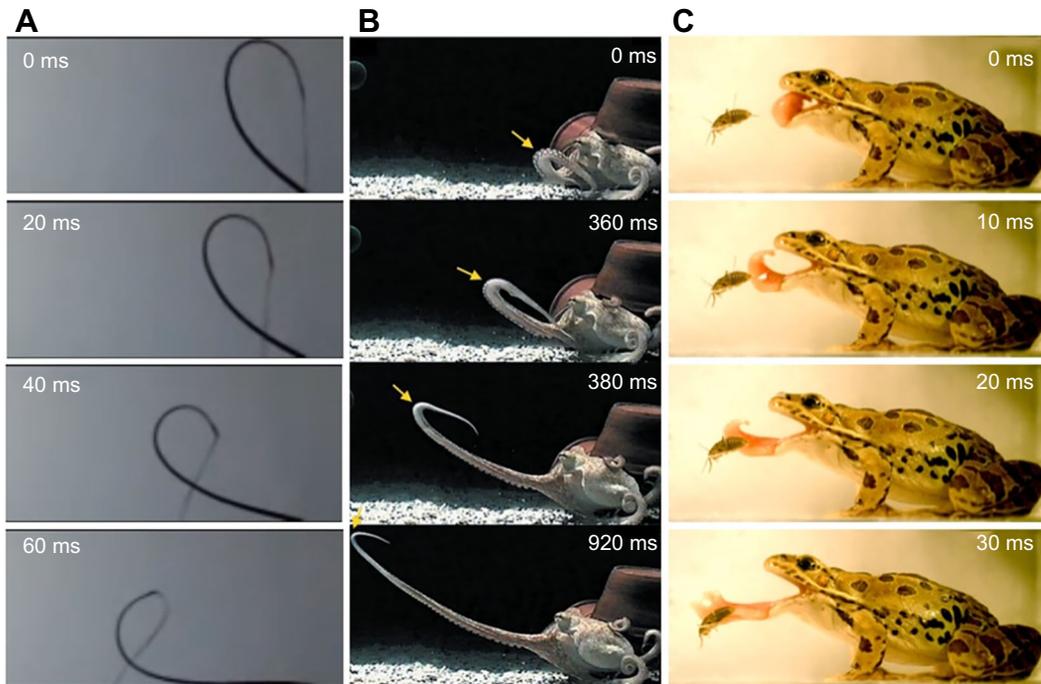


Fig. 4. Whip-like motion found in hyper-redundant (see Glossary) appendages. (A) Multiple exposures of a bullwhip exhibiting propagating waves during motion, kinematically similar to (B) an octopus arm and (C) inertial tongue projection in the frog *Rana pipiens*. Photo credit: (A) YouTube (user WorldWideWhips) and (B) Sumbre et al. (2001).

papillae are more than 1 mm long and help improve grip, like the claws on a cat. In contrast, papillae from 10 to 500 μm lengths are softer and are primarily used to hold saliva on the surface of the tongue, enhancing saturation and lubrication of food. Small papillae can also grip onto viscous saliva, which in turn helps adherence to prey.

Large, rigid papillae aid in soft tissue grip

Large papillae arise in cats and hoofed animals, but are found at their largest in birds. The tongues of some penguins, geese and flamingos have 1-cm-long backwards-slanted spines to help push slippery plants and prey down the throat. Hoofed animals such as deer use conical papillae to tear plant matter. Cows do not have upper front teeth, necessitating an even rougher grip than deer. This grip is accomplished by the cow’s trident-shaped papillae. We hypothesize that the sharpness of the papillae enhances grip into soft tissues. In this section, we will use the example of the tongue of the penguin *Aptenodytes fosteri* (emperor penguin), as shown in Fig. 5A, interacting with a fish to investigate how papillae may interact with a soft object.

Consider a fish resting on the penguin papillae as it slides into the throat to the right, as shown in Fig. 6A. The fish applies a normal force F_N onto the sharp tip of a single papilla, causing deformation of the fish’s skin. For a sharp penguin papilla, the tip shape can be approximated as a cone; the indentation distance δ into the tissue may be written as:

$$\delta = \sqrt{\frac{\pi F_N \sin \theta}{2 \tan \alpha} \frac{1 - \nu^2}{E}}, \tag{7}$$

where α is the half angle opening of the cone, θ is the angle between papilla and tongue surface, and ν and E are the Poisson’s ratio (see Glossary) and Young’s modulus of the fish tissue, respectively

(McKee et al., 2011). Eqn 7 is used to measure the Young’s modulus of *ex vivo* biological tissues, where the tissue is assumed to be linearly elastic and homogeneous at small deformations. Clearly, penetration depth increases with sharper papillae and increased applied force. Papillae are indeed quite sharp: we find that a domestic cat papilla has a cone angle of 7 deg and a deer papilla a cone angle of 9 deg. A cow has trident-shaped papilla, with the central spike having a cone angle of 15 deg and the cone angles of the adjoining spikes reaching 9 deg. By comparison, a cat claw has a cone angle of 8 deg. Although the cat papilla and cat claw have similar cone angles, it is important to note that the conical tip radius of the cat claw is 0.09 mm, sharper than the cat papillae of radius 0.14 mm. The smaller tip radius makes the claw more likely to puncture tissue.

The backwards-slanted papillae work like a one-way valve, allowing food to slide into but not out of the mouth. If the fish in Fig. 6A slides to the right, the papilla rotates clockwise and slides out of its insertion point. Conversely, if the fish slides to the left, the papilla rotates counter-clockwise and its tip digs deeper, resisting the motion. The rotation of the papillae is further resisted by connective tissue at the papillae’s base, which apply a resistive torque T_{joint} . We measured the resistive torque of a cat papilla in tongue tissue *ex vivo*. Fig. 6B shows that the relationship between angle θ and torque is highly nonlinear, in particular, the torque increases exponentially as the papillae are rotated counter-clockwise. This behavior further prevents prey from falling out of the mouth. The mechanism for this trend is unknown, but it may have to do with the papillae’s unique shape at the base. Our finite element analysis of the tissue deformation shows high stresses at the papilla base that may give rise to this resistance (Fig. 6C). Stiffening of the tongue’s muscular tissue would further increase joint torque and prevent prey from falling out of the mouth.

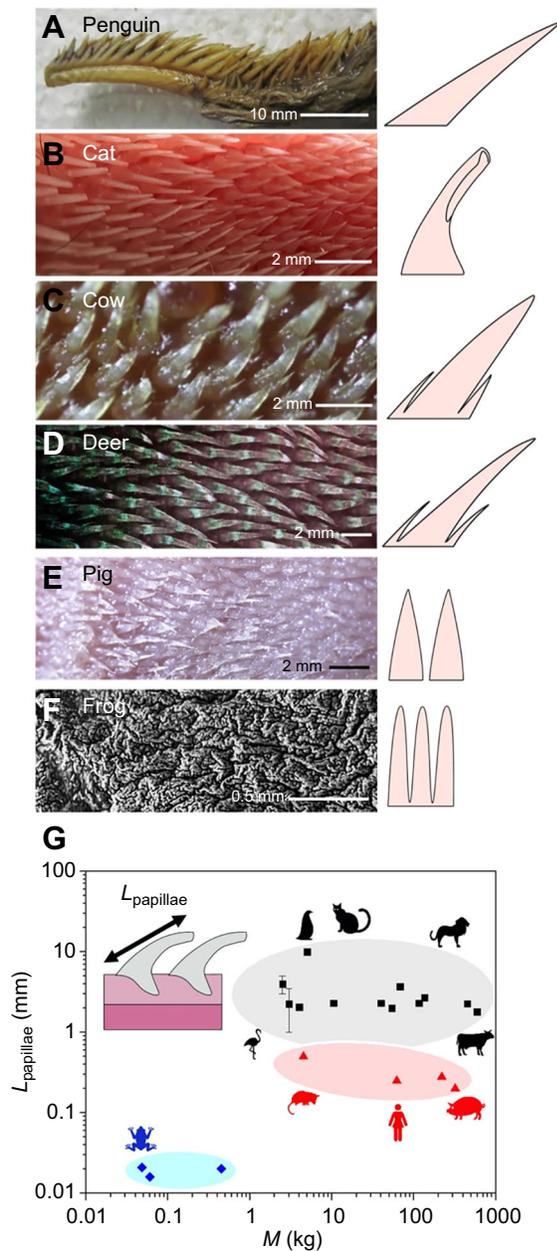


Fig. 5. A tongue's surface projections, or papillae, range over three orders of magnitude in length. Papillae photographs (left) and schematics (right) of (A) nestling penguin *Aptenodytes fosteri*, (B) domestic cat *Felis catus*, (C) cow *Bos taurus*, (D) deer *Odocoileus virginianus*, (E) pig *Sus domesticus* and (F) frog *Lithobates catesbeianus*, arranged from the longest to shortest papillae. Rigid papillae (A–D) tilt towards the throat, whereas soft papillae (E, F) do not. (G) Relationship between papillae length and body mass. Large, rigid papillae (black squares) greater than 1 mm are used for grip and tissue penetration. Soft papillae smaller than 1 mm are used for holding saliva on the tongue to enhance food saturation (red triangles) and adhesion (blue diamonds). (G, inset) Papillae length L_{papillae} measured from tongue surface to papilla tip. Photo credit: (A) Pablo Tubaro and Yolie Davies, Bernardino Rivadavia Natural Sciences Argentine Museum.

Small, soft papillae grip saliva on tongue

Although tongues of human, pig and frog appear smooth, microscopy reveals that these tongues are covered in tiny, flexible papillae of lengths much less than 1 mm. The primary purpose of such short papillae is to hold saliva on the tongue. Saliva has a number of functions, including lubricating and protecting oral

tissue, aiding in taste, and providing enzymes to enhance food breakdown and digestion (Humphrey and Williamson, 2001). Without saliva, food would be difficult to swallow and oral tissue would dry out, a risk for animals far from a water source. Short papillae are not keratinized and act instead like a soft toothbrush, utilizing surface tension of saliva to keep the tongue surface wet. The papillae counteract the effects of evaporation and gravity that would otherwise drain the tongue of its saliva.

The most widely used evaporation equation is one proposed by Carrier (1918), where the rate of evaporation e from a pool of water scales as:

$$e \sim \frac{A_s V_b \Delta P}{Y} \tag{8}$$

Intuitively, evaporation increases with the tongue's exposed surface area A_s and breathing velocity V_b , and decreases with the latent heat of evaporation of saliva Y , which has units of kJ kg^{-1} . To retain humidity, animals from frogs to mammals close their mouths. Opening the mouth and letting the tongue hang out like a dog's can help animals regulate heat. It is an open question as to how papillae regulate evaporation. Papillae can increase evaporation if they extend beyond the height of the saliva, increasing surface area, but these heights have yet to be measured *in vivo*.

To keep the tongue wet, papillae retain saliva using surface tension forces. At what point does gravity overcome surface tension and cause fluid to drain? The dimensionless Bond number (Bo) measures the relative importance between gravitational forces, which scale as $\rho g h_0$, and surface tension forces, which scale as σ/a (Bush and Hu, 2006), where ρ and σ are the density and surface tension of the water (which we assume to be near to saliva), g is gravitational acceleration, h_0 is the height of the saliva within the array and a is the spacing between papillae. Surface tension can prevent drainage of the saliva if the Bond number is less than 1:

$$Bo = \frac{\rho g h_0 a}{\sigma} = \frac{\text{Gravitational force}}{\text{Surface tension force}} < 1. \tag{9}$$

If we assume the saliva reaches the tips of the papillae, and values of papillae height and spacing are given by Lauga et al. (2016) as 0.25 and 0.1 mm, respectively, then the Bond number for saliva in human papillae is 0.003, meaning that the papillae do an excellent job of keeping the saliva in place.

Although eating dry foods can absorb saliva, the tongue can easily wet itself again. Consider a dyed water drop impacting a dry tongue of the pig *Sus scrofa* (Fig. 7). Tracking of the drop shows that it spreads (in mm) with a time course $z=1.6t^{0.5}$ ($R^2=0.99$). The spreading is driven by a process called imbibition, or rough wetting. It is defined as the motion of liquid through a rough surface, such as fluid spreading across a paper towel. Imbibition is driven by a balance between capillary pressure and viscous dissipation (see Glossary). Bico et al. (2001) analyzed rough wetting, and developed the following relationship to determine how the fluid front z moves in time:

$$z = \left(\frac{2 \cos \theta_f - \cos \theta_c}{3\beta} \frac{\sigma L_{\text{papillae}}}{\eta} \right)^{1/2}, \tag{10}$$

where θ_f is the contact angle on a flat surface, θ_c is the critical contact angle of imbibition, η is the saliva viscosity and β is a numerical factor to adjust for the presence of texture. This scaling

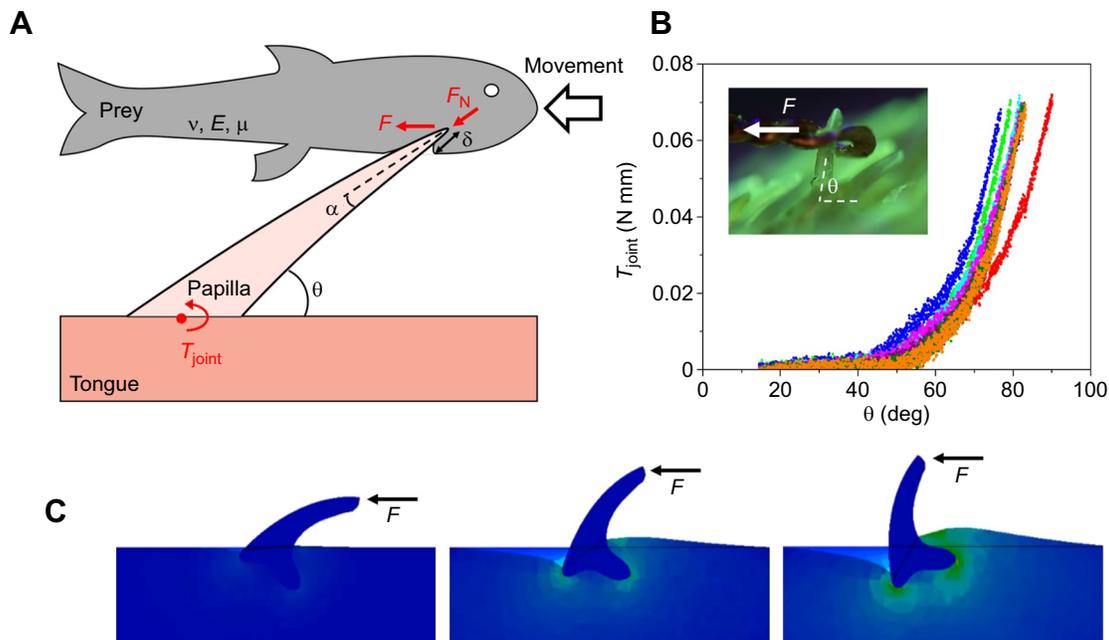


Fig. 6. Sharp, rigid papillae enhance soft tissue grip through angled indentation. (A) Schematic of a fish resting on a penguin papilla (n.b. not to scale) showing applied normal force F_N , applied force from movement F , tissue Poisson's ratio ν , Young's modulus E , friction coefficient μ , papilla cone half-angle α and tongue surface angle θ and papilla–tongue joint resistive torque T_{joint} . (B) Joint resistive torque T_{joint} for an *ex vivo* domestic cat papilla. Each color represents a single trial with the same papilla. (C) Finite element analysis of a rigid cat papilla rotated by applying horizontal force F . High strain areas around the base of the papillae are shown in green, and low strain areas in blue.

exponent (0.5) from our pig tongue experiment in Fig. 7 matches well with the $\frac{1}{2}$ exponent predicted by Eqn 10. The front moves at a peak velocity of 1.6 mm s^{-1} , and with decaying speed as the drop spreads. According to the measured scaling, if a dry pig tongue were exposed to only a single drop of fluid with no forced flow, it would take nearly an hour of wicking for the tongue, of length 190 mm, to become fully wet. To increase the spreading rate of saliva, animals use their tongue to compress food against the roof of the mouth. To ensure that the tongue does not dry out during mastication, the saliva secretion rate must be greater than or equal to the saliva wicked into food. Virot et al. (2017) found that measured chewing frequency is greater than a limit set by saliva secretion rate and food bolus size, suggesting that additional saliva may be secreted to ensure tongue desiccation does not occur.

Multifunctionality of feline papillae

An exception to the conical nature of large papillae is found in felines, from house cats to tigers. Felines exhibit a unique U-shaped cavity in their papillae. These papillae, which we call cavo papillae, wick up saliva and redistribute it in the fur to enhance grooming. The saliva in the cavo papillae is wicked onto the hairs through surface tension. The function of this unique cavity shape is still unknown, but it may aid in detangling, scent distribution or even cooling, as felines lack sweat glands on their epidermis, with the exception of paws (Fenner, 1991). Cats do not use their fluid-holding papillae during lapping; only the smooth tongue tip is used to pull water up, taking advantage of fluid inertia to 'bite off' the vertical water column (Reis et al., 2010).

How viscous saliva enhances adhesion

The function of saliva ranges from lubrication (Bongaerts et al., 2007) to adhesion, depending on the saliva viscosity. Saliva is composed of many different ingredients, including electrolytes, proteins, enzymes and mucins. It is the mucins that have the greatest

effect on viscosity (Park et al., 2007). Mucins are high-molecular-weight long-chain glycoproteins – it is these proteins that also give saliva the stringy effect, or fibrosity, allowing long threads of saliva to be stretched like hot cheese (Davis, 1971), a characteristic of certain non-Newtonian fluids (Fig. 8A). Such long threads can commonly be seen in a baby's drool or when handling a frog tongue. Mucin also gives saliva properties similar to those of paint, which is watery when spread with a brush, but solid-like when left on walls. This property is called shear-thinning, where viscosity decreases with shear rate. Schwarz (1987) speculated that this shear-thinning property causes saliva to act as a protective lubricant during rapid loading such as chewing, by ensuring a constant layer thickness even under high compression.

To measure saliva shear viscosity, a sample can be placed inside a cone-plate rheometer and viscosity measured across several orders of magnitude of shear rate. For both human and frog saliva, the viscosity is found to fit the Carreau–Yasuda model (Helton and Yager, 2007; Noel et al., 2017):

$$\eta = \eta_{\infty} + (\eta_0 - \eta_{\infty})(1 + (\lambda\dot{\gamma})^a)^{(n-1)/a}. \quad (11)$$

As shown in Fig. 8B, at low shear rates, frog saliva viscosity η_0 plateaus at 70 Pa s, whereas, at high shear rates, frog saliva viscosity drops to 1.2 Pa s. The duality of this saliva viscosity makes catching and releasing prey a simple matter for the frog: viscous saliva adheres the tongue to prey, and watery saliva allows the insect to slide off the tongue. When insects enter the mouth, the frog's eyeballs press down on the insect, creating fast-shear in the saliva layer and a subsequent drop in saliva viscosity. Human saliva behaves similarly, even though the shear-thinning property is not used to catch insects. Carnivorous pitcher plant fluid, although not animal-based, also exhibits shear-thinning properties that fit the Carreau–Yasuda model (Ermi et al., 2011), as illustrated in Fig. 8B.

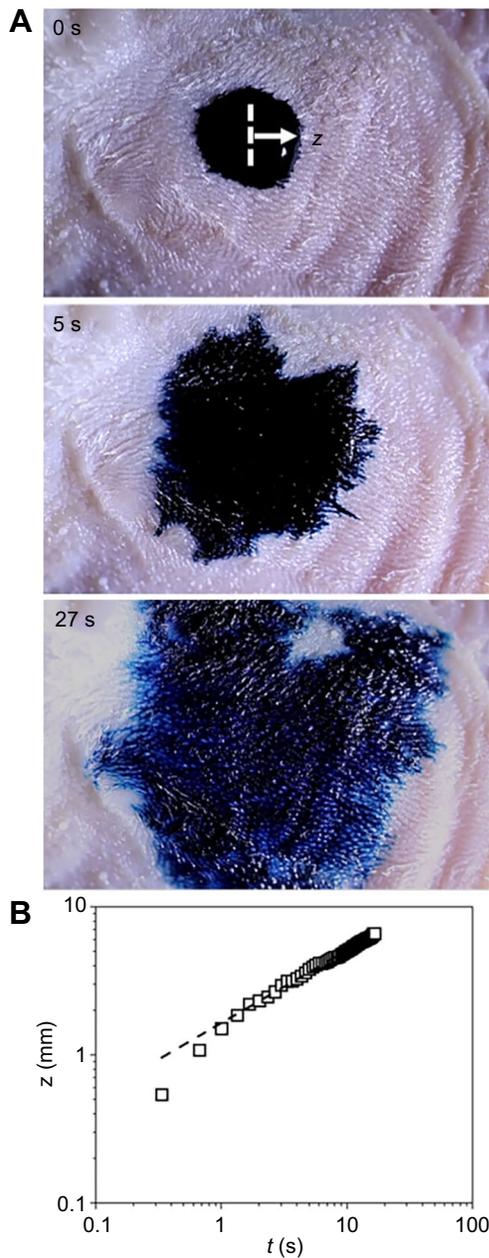


Fig. 7. Drop spreading on a pig tongue *ex vivo*. (A) Multiple exposures of a drop of blue dye spreading. The fluid front z was measured from drop center to the drop edge. (B) Time course of position of fluid front z . Fluid imbibes through the papillae with a front that moves with time $t^{1/2}$, following a balance between capillary pressure and viscous dissipation.

Highly viscous saliva aids in adhesion during prey capture, and can be understood using the mechanics of thin film separation, known as Stefan adhesion. When two rigid plates of radius R_0 , separated by a thin layer of fluid of thickness h_0 , are pulled apart at rate V , the resulting force F_{adh} to initially separate the plates is a function of fluid viscosity η and plate geometry:

$$F_{\text{adh}} = \frac{3\pi\eta R_0^4 V}{2h_0^3}. \quad (12)$$

To increase adhesion force, frogs can increase separation velocity, increase fluid viscosity or decrease saliva film thickness. The Stefan equation is only valid when the saliva layer is thin, the

fluid is an incompressible Newtonian fluid and the flat plates are rigid – the last two assumptions do not hold for frog tongues. Nevertheless, in earlier work (Noel et al., 2017), we showed that Eqn 12 still gives a good estimate for the pull-off force of a plate from a frog tongue.

Although many animals secrete saliva through glands in their oral cavity, amphibians secrete saliva through glands on their tongue. Frog tongues have saliva glands located in between papillae (Hammerman, 1969), allowing the tongue to become saturated with saliva. The necessity of saliva glands on the tongue can be seen by comparing Eqn 10 for human and frog saliva. In a low shear-rate scenario, frog saliva is 175 times the viscosity of human saliva and human papillae are 12 times taller than frog papillae. If we assume the surface tension of both salivas is close to that of water, and the pre-factor $\frac{2 \cos \theta_f - \cos \theta_c}{3\beta \cos \theta_c}$ of human and frog saliva is comparable, then we find frog saliva would spread only 2% of the distance that human saliva moves in the same amount of time. Thus, glands in frogs must deliver the saliva close to the area of intended adhesion.

Perspectives

Among the eight different biological attachment systems found in nature (Gorb, 2008), tongues use three of these mechanisms to grasp food: wet adhesion, hooks and friction. Each of these mechanisms can be used for different gripping scenarios: a high-speed frog tongue can employ wet adhesion in the form of high-viscosity films; cat tongues can grip raw meat using hooks to deform and grip the soft substrate. Part of the gripping process involves the tongues staying wet themselves. To do so, tongues use epithelial microstructures to hold onto biofluids, a method that may have application in the biomedical field with regards to tissue hydration, such as artificial skin grafts or wet dressings for eczema.

It is an exciting time to study tongues because recent technologies are making it possible to build devices that approach the mobility and sensing of biological tongues. This area is called soft robotics, and it has a growing number of workers, despite the fact that general principles for designing such robots do not yet exist (Kim et al., 2013; Rus and Tolley, 2015). The primary difficulty in soft robotics is that there are no governing equations of motion. Hard robots such as the industrial robot arms used in car factories are composed of a number of segments, with actuation at the joints. The motion of the effector can be programmed using the individual joint angles incorporated into a kinematic chain. In comparison, soft robots experience high deformations if they move too quickly or if they impact upon their targets. Nevertheless, nature has yielded a vast array of soft appendages, as evident in the diversity of animal tongues.

Tongue movements, in particular the inertial and ballistic projectors, are capable of providing high speed, strength and precision. Debray (2011) and Hatakeyama and Mochiyama (2013) mimicked the chameleon tongue projection using a combination of a solenoid and elastic band. The recent development of additive manufacturing and silicone casting processes may make other tongue-inspired robots possible. A spiralized muscle could be replicated to simulate the radial contraction found in ballistic tongues, and could introduce a new field of high-speed soft projectors. Future tongue-inspired robots may rely on technologies such as shape memory alloy to mimic muscle fibers (Kim et al., 2009), or fluidic elastomer (see Glossary) actuators to simulate high-speed response in fish (Marchese et al., 2014).

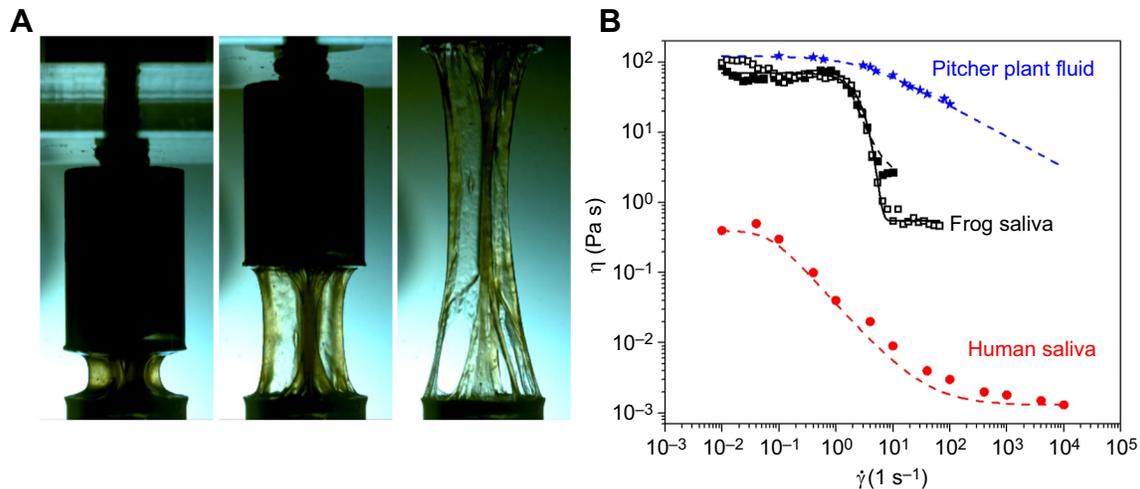


Fig. 8. Saliva exhibits viscoelastic, shear-thinning properties. (A) Frog saliva from *Rana pipiens*, stretched between two plates, shows high fibrosity in the form of fluid threads. (B) Shear viscosity η of human saliva (red circles), frog saliva (open and filled black squares) and pitcher plant fluid (blue stars). All biofluids decrease in shear viscosity η with increasing shear rate $\dot{\gamma}$. The Carreau–Yasuda model for shear-thinning fluids (dashed lines) is used to fit experimental data. Data have been replotted from the following sources: frog saliva (Noel et al., 2017), human saliva (Helton and Yager, 2007) and pitcher plant fluid (Erni et al., 2011).

Although most tongues are wet, future work may show that many of the techniques outlined in this Review do not require the use of saliva. The use of sharp papillae to grab relies primarily upon friction forces and the softness of the target object. Technology such as 3D printing will enable many of the different-shaped papillae on tongues to be fabricated and tested. Such papillae may even help improve the grip of current robots, such as the universal gripper, a bag of granular material that grips by the jamming and liquification of the grains (Brown et al., 2010).

The design criteria for the large papillae is still poorly understood, although analogous systems have been studied. Asbeck et al. (2006) examined the spring and shape of spines best used for wall climbers. Previous investigators have also studied how beetle claws catch on rigid surface asperities that support applied force (Asbeck et al., 2006; Dai et al., 2002), yet these frameworks may change when considering the interaction with compliant surfaces. In tigers, for example, papillae that dig into meat will experience high forces. How do the papillae rend the meat without being torn from the tongue themselves? Detailed studies of the interaction between rigid papillae and soft tissues are still to be done.

Although this Review did not discuss the sensing capabilities of the tongue, they are necessary for many of the coordinated movements discussed here. Tongues may have their own proprioception, measurement of their position and shape in space. New manufacturing techniques such as 3D printing of embedded sensors in soft elastomers (Muth et al., 2014) may provide soft robots with the ability to both sense and move simultaneously. It would be interesting to study how the number of sensors changes with the different tongue movement mechanisms.

One of the challenges in studying tongues is their scarcity among biological collections. We were able to procure 20 samples in the USA, through online and local sources, but samples abroad are also needed to provide comparative data. The soft organs of animals are not preserved as easily as bones, resulting in many taxidermists discarding tongues when they prepare an animal. We encourage the biology community to find new ways to preserve and measure the material properties of tissues such as the tongue. We also encourage future workers in this area to create an infrastructure to improve the

collection and inventory of animal tongues. There are other unique tongues in the animal world that demand a closer look, such as the fake lure on the alligator snapping turtle tongue, and the woodpecker tongue that wraps around the skull and exhibits small spikes to pierce prey.

To study the motion of soft appendages, one need not necessarily look to the octopus or the elephant trunk. In fact, the tongues of most mammals perform great feats of mobility and attachment. The tongue is truly a multifunctional tool, and has only received less attention because it is less accessible than an animal's external appendages. This Review discussed mechanical principles that may be useful in understanding the diversity of tongue gripping mechanisms. Manufacturing techniques in soft robotics may be useful in building physical models to answer biological questions. Such techniques may help in understanding functions of the tongue not discussed here, such as taste and touch.

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Competing interests

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Supplementary information

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