An experimental biomimetic tongue–palate system has been developed to probe human in-mouth texture perception. Model tongues are made from soft elastomers patterned with fibrillar structures analogous to human filiform papillae. The palate is represented by a rigid flat plate parallel to the plane of the tongue. To probe the behaviour under physiological flow conditions, deflections of model papillae are measured using a novel fluorescent imaging technique enabling sub-micrometre resolution of the displacements. Using optically transparent Newtonian liquids under steady shear flow, we show that deformations of the papillae allow their viscosity to be determined from 1 Pa s down to the viscosity of water (1 mPa s), in full quantitative agreement with a previously proposed model (Lauga et al. 2016 Front. Phys. 4, 35 (doi:10.3389/fphy.2016.00035)). The technique is further validated for a shear-thinning and optically opaque dairy system.

1. Introduction

While a key element of the eating experience, a detailed understanding of how humans perceive food texture currently remains elusive. The ability to discriminate accurately between small differences in food structure—likely witnessed by anyone who has compared, for example, full fat milk with semi-skimmed milk—is well observed [1,2]. From a food-processing perspective, classic texture characterization techniques actually fail to reproduce the same resolution as reported by human subjects ([3], N. Godinot 2006, unpublished data). Consequently, efforts to replace fat and sugar, nutrients that also play a structural role in processed food, have only met with partial success [4], frustrating attempts to create food that is both more nutritionally balanced and also preferred by consumers. Furthermore, from a medical perspective, applying a better understanding of texture perception to dysphagia, a potentially life-threatening condition for sufferers, could lead to even more effective treatment options [5].

Past work on characterizing physical texture in-mouth has frequently focused on approximating the tongue–palate system by smooth-walled parallel planes, between which a food matrix undergoes steady shearing flow [6]. This gave insight into the relevant shear rates and relative importance of competing physical effects such as bulk rheology and surface lubrication [7].

The tongue is, however, not smooth but covered at its upper surface with both fungiform and filiform papillae. For humans, fungiform papillae are mushroom-shaped structures of typical diameter approximately 400 μm and height approximately 100 μm, and are distributed with a surface density [8] of about 2 papillae mm$^{-2}$. They have been shown to be involved in texture perception. Using psychophysical experiments, the acuity of the oral mechanosensory system has indeed been linked to variations among tasters of their fungiform papillae density [9]. Experimental investigations in surface-averaged measurement devices have also evidenced that the fungiform-like topography...
did impact the tribological properties of the tongue–palate system [8]. The role of filiform papillae for texture perception has, however, not been thoroughly studied. Filiform papillae are distributed over the tongue with a surface density [10] of about 5 papillae mm$^{-2}$. They are fibril-like structures with a typical length of about 250 μm and a radius of about 34 μm [11], with no chemical receptors at their base [12]. Such high aspect ratios make them ideal candidates for mechano-sensing via fluid–structure interactions with liquids entering the oral cavity. Recently, theoretical investigations of isolated filiform papillae-like posts in the presence of viscous flows suggested that local deflections of a single papilla could generate stresses relevant for sensory input [13]. Such a mechanism for sensing stresses, while not yet causally shown, is hinted at in new observations in mice [14], which indicate that filiform papillae are co-located with nerve endings expressing Piezo2, a mechanosensitive ion channel whose involvement in touch mammalian cells has been evidenced recently [15].

Deflections of ciliated organs have been identified in mechanosensation processes for other biological systems [16–18] and shown to provide an enhanced sensitivity that recent biomimetic systems have been able to reproduce, such as in the case of the fish lateral line [19]. From this biomimetic principle, sensors have thus been developed to measure liquid or air flow velocities near a boundary [20–22]. Within the context of in-mouth texture perception, no analogous biomimetic approaches have however been reported so far.

The present work is therefore dedicated to developing a novel biomimetic tongue–palate system and to investigating the local deflections of filiform papillae present in a shearing flow. We first detail the fabrication of the experimental set-up. We then measure the deflections of papillae over a large range of shear stresses and provide a full experimental validation of the model of Lauga et al. [13]. Finally, we discuss our results and the implications for the perception of texture of food products.

2. Material and methods

The functioning of the human tongue–palate system was mimicked by placing an elastomer-based artificial tongue at the bottom of a rheometer cell, on the one hand, and using the upper rigid rotating disc of the rheometer as an equivalent of the palate, on the other hand.

2.1. Artificial tongue fabrication

Elastomer tongues were obtained by a combination of micromilling and moulding techniques as sketched in figure 1. A Plexiglas mould shaped as a circular pool with a raised and polished bottom (see figure 1a, upper panel, for a sectional view along its diameter) was first fabricated with an inner diameter $\Phi_i = 50$ mm and an outer diameter $\Phi_o = 64$ mm. Cylindrical holes of diameter 100 μm and depth 450 μm were then drilled in the bottom of the pool (figure 1a, lower panel) using a three-axis computer desktop CNC Mini-Mill machine (Mini-tech Machinery Corp., USA). These holes were distributed on a square grid with a 1 μm resolution, with a surface density of 10 holes cm$^{-2}$. With this density, hydrodynamics interactions between papillae are negligible [23]. In a third step, an isopropanol solution containing green fluorescent beads of diameter 1–5 μm (GFM, Cospheric, 1.3 g ml$^{-1}$) at a concentration of 50 mg l$^{-1}$ was poured onto the mould and left for 15 min at room temperature (figure 1b, upper panel). This duration was sufficient to allow sedimentation of the beads to the bottom of the cylindrical holes. The supernatant solvent was then carefully pipetted and the pool dried for 15 min in a oven at $T = 65°C$ (figure 1b, lower panel). Following this procedure, some beads could however remain adsorbed on the raised flat bottom of the pool. These unwanted beads were simply and efficiently removed using a commercial adhesive tape applied to the flat raised surface of the mould and carefully peeled off.

The artificial tongues were made of two optically transparent and commercially available cross-linked polydimethylsiloxane (PDMS) elastomers, Sylgard 184 and Sylgard 527 (Dow Corning, USA), mixed in a 31 : 69 mass ratio. Prior to final mixing, both melts were first blended separately with their respective cross-linker agent, in a 10 : 1 stoichiometric ratio for Sylgard 184 and in a 50 : 50 ratio for Sylgard 527. Air bubbles present in the final mixture were removed by 10 min of centrifugation at 3000 r.p.m. followed by 2 min in a low-pressure vacuum. This mixture was then poured into the Plexiglas mould (figure 1c, upper panel). Given the large aspect ratio of the micro-holes, air micro-bubbles could occasionally be trapped within the microstructures during pouring. These were removed by placing the mould filled with PDMS for an additional 10 min in a low-pressure vacuum. The mixture was then cured for at least 12 h in an oven at $T = 65°C$. Finally, the polymerized tongue (with dimensions $\Phi_i = 50$ mm, $\Phi_o = 64$ mm, depth 4.5 mm, backing layer width 2.5 mm) was carefully unmoulded to avoid rupture of the papillae (figure 1c, lower panel). We checked that the papillae were intact and that the fluorescent beads were still present at their tip using either fluorescence microscopy (figure 2a) or scanning electron microscopy (SEM) imaging (figure 2b). Note that in some cases, such as the one shown in figure 2a, a small number of beads remained on the edges of the papillae.
2.2. Geometrical and mechanical characterizations of the tongues

As the bead deposition process can yield variations in the final length $L$ of the papillae, we measured $L$ of all papillae considered in this work, using either optical microscopy or confocal imaging. For the former, $L$ was taken as the difference in height between the apex of the papillae and their base. The results of all combined measurements gave $L = 435 \pm 7 \mu m$.

Young’s modulus $E$ of the artificial tongues was measured with Johnson–Kendall–Roberts (JKR) tests [24,25], performed between an elastomer block ($50 \times 50 \times 20 \mathrm{~mm}$, thickness $15 \mathrm{~mm}$) prepared with the same ratio of Sylgard 184 and 527, and a planoconvex glass lens (optical grade; Melles-Griot 01LPX017, BK7, radius of curvature $R = 9.33 \mathrm{~mm}$). JKR tests were done with a custom-made set-up described elsewhere [6]. They consist in measuring the area of the circular contact between the lens and the elastomer as a function of the applied normal load, yielding a relationship from which $E$ can be deduced [27]. Our measurements yielded $E = 0.80 \pm 0.16 \mathrm{MPa}$.

2.3. Biomimetic experimental set-up of the oral cavity

Artificial tongues were placed at the bottom of the cell of an Anton Paar MCR 302 rheo-microscope that combines both rheology measurements and imaging capabilities. Figure 3a shows a sketch of the experimental set-up used for this work. Rather than moving the tongue, as is the case for humans, the artificial tongue is maintained in a fixed position in the laboratory frame, while the palate is moving. The palate’s equivalent consists of a rigid and flat circular rotating plate (Anton Paar PP40; diameter $40 \mathrm{cm}$). For all experiments, the temperature was kept at $T = 25^\circ \mathrm{C}$.

Imaging of the deflections of papillae were performed with reflection fluorescence microscopy using a long working distance microscope objective positioned directly beneath the artificial tongue (figure 3a, lower part). Only a small portion of the entire artificial tongue, which extends radially from the centre of the cell to its perimeter, could be imaged. In practice, papillae under study were thus brought into this field of view by rotating the artificial tongue. The microscope objective was mounted on a manual translation stage that provided positioning in two directions, vertically and radially from the centre of the rheometer’s cell within the aperture. For our experiments, a $5 \times$ air objective (Edmund Optics, Plan-Apo) was used. Illumination was obtained with a high-power blue LED ($3W$, $\lambda = 465 \pm 5 \mathrm{~nm}$; Sodial(r)), the beam of which was focused on the tip of the papillae. The light emitted by the fluorescent beads was collected by a combination of a dichroic filter and an emission filter (MD498 and MF525-39, respectively; Thorlabs, Inc.) onto a high-resolution, fast and sensitive camera (sCMOS pco.edge 5.5; full resolution $2560 \times 2160$ pixels, 16 bits) that can operate at a frame rate of 100 frames s$^{-1}$ (fps) at full resolution. With the $5\times$ objective, images had a resolution of $1.05 \mu m$ per pixel. In practice, only small portions of the images of size $200 \times 300$ pixels$^2$, with a single papilla present in the field of view, were recorded at 100 fps.

Finally, both the rheometer data and images were acquired simultaneously using a TTL trigger signal sent by the rheometer (controlled by its dedicated software Rheocompass 1.19; Anton Paar) to the camera, once rotation of the upper plate was initiated.

2.4. Sample preparation

In addition to Millipore deionized water ($\eta_0 = 1 \mathrm{mPa s}$), different water/glycerol solutions were used to calibrate the tongue-palate measurement system. These were prepared by mixing pure glycerol (Sigma-Aldrich) with Millipore deionized water at different mass ratios to obtain a logarithmic variation of the solutions’ dynamic viscosity $\eta$ ranging from $1 \mathrm{mPa s}$ to $1 \mathrm{Pa s}$. For each glycerol solution, $\eta$ was measured with the rheomicroscope, operating at $T = 25^\circ \mathrm{C}$ in a plate–plate geometry with the PP40 Anton Paar rotation plate, a $1 \mathrm{mm}$ gap, and without the artificial tongue. It is known that glycerol solutions can be hygroscopic, but no significant change in viscosity was actually measured for the duration of the experiments. A model dairy product was also used in this work, consisting of a commercial semi-skimmed milk mixed with $0.5\%$ w/w xanthan gum hydrated overnight at room temperature. A small amount of sodium azide (Sigma-Aldrich) was added to prevent any bacterial development. The resulting liquid was non-Newtonian and possessed a rheological shear-thinning behaviour that was fully characterized with standard rheological measurements.

In addition, it was completely opaque to visible light.

2.5. Modelling the deflection of an isolated papilla

Following Lauga et al. [13], the tongue–palate system was modelled with two parallel plates separated by a gap $H$. The upper plate playing the role of the palate was rigid and moved laterally (with respect to the lower plate) at a velocity $U$. The lower plate...
mimicking the tongue was also considered rigid but covered with soft elastic cylinders of radius $a$ and length $L$, as equivalents of filiform papillae (figure 3b). In the absence of any fluid–structure hydrodynamic interactions between papillae, an assumption that is true in the limit of low surface density of papillae, Lauga and co-authors derived a scaling relationship between the maximum deflection of the tip of a single cylindrical papilla subjected to a shear laminar liquid flow $\delta$ and the shear rate $\dot{\gamma}$. At steady state, $\delta$ reads

$$\delta = K \frac{U^3}{\tau^2 E/H} = \frac{K}{\dot{\gamma}} \frac{U^3}{\tau^2} \quad \text{with} \quad K = \frac{L^3}{\mu E},$$

(2.1)

where $K$ is a numerical factor whose value can only be determined experimentally. With the geometry of our experimental set-up, one has $U = \omega r$, with $\omega$ the tool angular rotation velocity and $r$ the radial position of the papilla with the origin taken at the centre of rotation of the upper tool.

2.6. Localizing the positions of papillae

Accurate radial positions $r$ of papillae from the rotation axis of the rheoscope were determined as sketched in figure 4. A specific tool was designed in the form of a flat disc whose lower surface was engraved with a pattern of periodic concentric circular grooves of wavelength $\lambda = 500 \, \mu m$ (figure 4c).

Once the artificial tongue was placed on the rheometer bottom cell, the patterned tool was inserted into the rheometer in place of the rotating tool, and brought (in air, i.e. without any liquid) nearly in contact with the tip of the papillae. When imaged from below through the elastomer, one thus obtains an image of both papillae tips and concentric grooves as sketched in figure 4c. The position of the papilla of interest was then simply determined as the sum of the radius of the circular groove closest to the papilla and the distance of the papilla to the groove. The latter was obtained using image analysis, yielding a resolution on $r$ of typically less than 10 $\mu m$.

2.7. Setting the size of the tongue–palate gap $H$

Accurate positioning of the upper plate was done in two successive steps. The first one consisted in making full contact (without any liquid solution) between the upper tool and the surface of the bottom cell without the artificial tongue, to set a zero gap reference height. The second step consisted in positioning the artificial tongue on the bottom cell, still without any liquid solution, and progressively lowering the upper tool, in 10 $\mu m$ increments, until contacts occurred with the tips of the papillae. Contacts were identified by visualizing the displacement of papillae within the field of view, subsequent to a manual rotation of the upper plate. Knowing the zero gap reference height, the length of the papilla and contact heights allowed us to set $H$ to its desired value with a resolution of the order of 10 $\mu m$.

2.8. Papilla displacement measurements

Displacements of the extremity of a papilla were determined using digital image correlation techniques. These consist in correlating images of the tip fluorescent bead markers when a flow is present with a reference image of the papilla at rest (figure 5). Prior to this, all images were filtered with a Gaussian filter of standard deviation 1 pixel to remove high-frequency noise. An Otsu’s criteria automatic thresholding method was then used to set to a null value all pixels with intensity lower than the threshold. Both processes were done with Matlab R2017a (Mathworks, Inc., USA).
The cross-correlation was performed in Fourier space using Matlab’s built-in two-dimensional fast Fourier transform-based algorithm to yield the correlation function $C(\Delta x, \Delta y)$, where $\Delta x$ and $\Delta y$ are the shifts along both the x- and y-axes of the image. Direct determination of its maximum provides the displacement vector $(\Delta x, \Delta y)$ (of magnitude $\delta = \sqrt{\Delta x^2 + \Delta y^2}$) with 1 pixel resolution, i.e. 1.05 µm with the 5 x objective used here. Sub-pixel accuracy on the maximum location is commonly obtained by fitting $C(\Delta x, \Delta y)$ around its maximum with a two-dimensional functional form, such as a polynomial or a Gaussian surface. For this work, we rather chose to interpolate $C(\Delta x, \Delta y)$ on a 100 times finer mesh, as described by Roesgen [28]. This interpolation method has the advantage of drastically reducing any pixel-locking effect, which is known to increase the error on the measured displacements. The method can however be computationally demanding, but the calculation time can be significantly reduced, as shown by Guizar-Sicairos et al. [29], by limiting the interpolation to a region close to the maximum of $C$. Figure 6 shows the results of such correlation-based displacement measurements with a typical example of a single papilla that progressively bends from its initial rest position to its final position in steady flow. Taking into account all physical and numerical noise, the method was found to yield a resolution on the displacement $\delta$ of approximately 71 nm with an oversampling factor of 100. Such a resolution is in particular directly evidenced in the graph in figure 6 in the steady-state regime.

Finally, note that the use of the correlation technique developed here is limited to small deformations of the papillae, i.e. for $\delta/L < 10\%$. Indeed, for larger deformations, one observes shadow-related masking and loss of focus of the fluorescent bead pattern, which can significantly increase the error on the measured displacement.

3. Results and discussion

3.1. Testing the response of a single papilla

We first performed a series of experiments using Newtonian liquids of different viscosities to test the validity of the linear scaling prediction of equation (2.1) (see Material and methods), which relates $\delta$ to $\eta$ and $\dot{\gamma} = r\omega/H$ in the steady-state flow regime. This was done using different water/glycerol solutions with the same artificial tongue and the exact same papilla positioned at $r < \Phi_1/2 - H$ to avoid any hydrodynamic boundary effect. Note that the radial position of the papilla $r$ could change slightly between experiments because of inherent manual repositioning of the tongue, and it was thus systematically determined as explained earlier (see Localizing the positions of papillae). The water/glycerol solutions were prepared according to the protocol described in the Material and methods section, with $\eta$ ranging from $10^{-2}$ Pa s to 1 Pa s (see figure 7, upper inset, for the measured relationship $\eta$-water/glycerol mass ratio).

The experiments consisted in first accurately positioning the upper plate at a distance $H = 4$ mm above the base of the papillae, and second in pipetting a volume of 7.5 ml of the water/glycerol solution within the artificial tongue. The upper plate was then set into rotation at a constant angular velocity $\omega$, causing the papillae to deflect. The steady-state flow regime and thus the maximum bending of the papillae was typically attained in less than 1 s. In practice, each experiment consisted of 11 successive 10 s long measurements. The first one was performed without any flow (papilla at rest) to provide an unperturbed reference state, while the 10 subsequent measurements were done with increasing $\omega$. Analyses of the displacements were performed in the steady-state regime.

The main panel of figure 7 shows for a given papilla the results of these experiments with $\delta$ as a function of $\dot{\gamma}$ for three distinct viscosities, $\eta = 23$ mPa s, $\eta = 119$ mPa s and $\eta = 966$ mPa s. Each single point corresponds to a single measurement and its error bar is taken as the standard deviation of $\delta$ over the 10 s duration of the experiment at steady state. For all three viscosities shown here, $\delta$ is found to be proportional to $\dot{\gamma}$ over almost two decades in $\dot{\gamma}$, in agreement with the prediction of equation (2.1). In addition, all three curves can be rescaled on the same master curve once the axis is multiplied by $\eta$, as shown in the lower inset of figure 7. At a fixed shear
rate, $\delta$ is thus directly proportional to the local viscosity $\eta$ of the probed solution over almost two decades in $\eta$.

The experiments we have considered so far were limited to the case where $H = 4$ mm is much larger than the typical size $L$ of the papillae. In the last stages of food texture perception, however, i.e. immediately prior to swallowing, the tongue can significantly approach the palate (and even eventually be in close contact), and $H$ can be of the order of $L$. We have thus also investigated how $\delta$ varied with $H$ for a single papilla. This was done with a water/glycerol solution of viscosity $\eta = 459 \pm 62$ mPa s at two different angular velocities $\omega$.

As shown in figure 8, for both $\omega$, $\delta \propto 1/H$ for $H \in [0.5–5]$ mm. These measurements fully validate the predictions of equation (2.1), even when $H \approx L$.

3.2. Comparing the response among papillae

Our measurements have focused so far on the response of a single papilla to changes in viscosity. Additional experiments were thus performed to see how robust the measured linear response behaviour is among papillae located at different radial positions and across different artificial tongues. For this, three different papillae on the same artificial tongue were considered, as well as one papilla on another tongue. Similar to before, the papillae were chosen sufficiently far away from the boundaries of the tongue ($r < \Phi/2 - H$). Each series of experiments were not only done with the exact same protocol as before, but were also repeated three times with the same papilla, without any repositioning of the tongue. In addition, for one viscosity, these measurements were repeated three times by changing the solution. A total of nine measurements were thus obtained per angular velocity $\omega$. In addition to the 10 water/glycerol solutions used before, Millipore deionized water ($\eta_0 = 1$ mPa s) and a 45/55 w/w mixture of water/glycerol ($\eta = 4$ mPa s) were used for these experiments. Figure 9 shows the results of all experiments combined in a log–log scale, with $\delta$ as a function of the shear stress $\sigma = \eta \dot{\gamma}$ varying over nearly three orders of magnitude (and with $\eta$ varying exactly over three orders of magnitude from $10^{-3}$ Pa s to 1 Pa s). For each point at a fixed $\omega$, error bars were taken as the standard deviation over all nine measurements performed. Further checks of the linearity of equation (2.1) were obtained by fitting data points at a fixed $\eta$ with a power law of exponent $\beta$ (for the sake of clarity, fits are not displayed on the figure). As shown in the inset of figure 9, for all viscosities, $\beta$ is found to be very close to unity, in full agreement with equation (2.1). Note that the blue-coloured points in figure 9 are slightly shifted upwards with respect to the other coloured symbols. The blue-coloured points do correspond to measurements obtained with a different tongue, in contrast with the other points obtained with different papillae on the same tongue. For this new tongue, while the linear behaviour was still measured, the value of the $\kappa$ parameter (see equation (2.1)) is slightly larger. We checked that the values of both $L$ and $a$ were unchanged within experimental errors. This measured shift is thus likely to be due to variations in the apparent elastic modulus of the papillae, presumably as a result of the fluorescent particle inclusion process. For absolute measurement purposes, such small scatter thus implies that a calibration has to be systematically performed for each new tongue.

3.3. Testing the response of a food-related complex fluid

So far, all of our previous measurements have been performed with simple liquids that are optically transparent. A food-related product, such as a dairy product, can however be made of sub-micrometric to micrometric particles that scatter visible light and that can make it completely opaque. We thus also tested our imaging set-up with a model dairy product (see Sample preparation for details) sheared between the artificial tongue and the palate (figure 10). The rheological properties of this product were also measured in plane–plane geometry (inset of figure 10, red solid line). Shear-thinning behaviour was evidenced, in agreement with previous measurements [30] (inset of figure 10, black dashed line).

Owing to its reflection-based imaging through the cylindrical papillae, measurements of the bending of papillae in
steady flow were easily achieved with the same resolution on displacement as for optically transparent liquids. Figure 10 shows the results of such measurements with $\delta$ as a function of the angular velocity $\omega$, for the only papilla that was probed, and with a single experiment per angular velocity. For comparison, the same papilla was also used with a pure glycerol Newtonian solution. For this glycerol solution, one recovers the expected linear behaviour contained in equation (2.1), as shown in figure 10 with the power-law fit of the data of exponent $\beta \sim 1$. For the model dairy product, however, one clearly measures a drastic deviation from the linear behaviour, characteristic of a shear-thinning rheological behaviour. Indeed, $\delta$ is found to vary with $\omega$ as a power law of exponent $\beta \sim 0.3$, over almost three decades in $\omega$.

3.4. Discussion

Several key aspects of the current work can be highlighted. First of all, classical methods to manufacture micro-pillars of moderate aspect ratios (i.e. typically not more than 10) usually involve moulding of elastomers either in resin-based substrates fabricated with microphotolithography processes or in sacrificial wax-based templates [20]. In our work, we have used a micro-drilling-based technique of a plastic Plexiglas sample that provides micrometric accuracies in all three directions that is simple, easy to implement and highly reproducible. To follow the displacement of the tip of the pillar, the classical approach is to embed the extremity of the pillar with a marker either in the form of a reflective coating [20,22] or in the form of a fluorescent dye such as rhodamine, as done recently [31]. An alternative method, which does not require any tip marking, has also been implemented and consists in using the optical properties of transparent PDMS-based cylindrical pillars that act as wave guides [20]. Illumination light propagates from the base of the pillars to their extremity, where it is focused, yielding a bright spot that can be detected optically. The same wave guide effect has been reported by Bruecker [31], with fluorescent light of tips covered with rhodamine. In this case, the fluorescent light is emitted both at the tip and at the base of the pillar as the primary fluorescence light propagates down to the base with the wave guide effect. In our work, we propose an alternative method where fluorescent microbeads are embedded by sedimentation in the plastic mould and then cast within PDMS at the top of the cylindrical pillars. This method avoids any possible diffusion of the fluorescent markers [31] and yields a robust and reusable marking mechanism. Compared with the wave guide mechanisms for which flexion of the pillars lowers the intensity of the reflected light from the tip [22], our method offers stable intensity patterns that are independent of the amplitude of the deformation. Moreover, it can be used regardless of the optical index mismatch between the surrounding fluid and the pillar.

Once the tip has been marked, image analysis methods are generally used to locate the position of the tip. These can rely either on morphological analysis [20] or on image auto- and cross-correlation techniques [20,31], which can yield sub-pixel resolution of the measured displacements. In our case, we have used fluorophores in the form of microbeads embedded at the extremity of the pillars. They form a well-defined intensity pattern that increases the resolution of the correlation technique. Moreover, the minimum measurable displacement is only set by the noise of the correlation method, in contrast with the work of Bruecker [31], for which a minimal displacement of the order of the pillar radius was required. Last, the use of an interpolation-based method [28] to locate with sub-pixel accuracy the location of the tip position, rather than using functional fits of the two-dimensional correlation function, avoids any pixel-biased effects and reduces significantly computational time [29].

Second of all, these marking and image correlation methods allow us to probe the deflection of the tip with a spatial resolution of about 70 nm, for deflections up to several tens of micrometres. We were thus able to probe the theoretical predictions of Lauga et al. [13] (see equation (2.1)) in a steady flow by two orders of magnitude of the tip displacement $\delta$. This was done by varying both the viscosity by three orders of magnitude and the shear rate by two orders of magnitude. To the best of our knowledge, exploring this relationship over such a large range of shear stress has never been reported and thus constitutes a rigorous validation of the theoretical model of Lauga et al. [13]. Indeed, even though numerous linear relationships between the deflection at steady state and the fluid velocity have been reported [16,20,21], no systematic variation of viscosities has been performed. Our work demonstrates that the artificial papilla system can be used as a sensitive micro-rheometer to measure viscosities in a way similar to that operated by the tongue–palate system.

Finally, interestingly, the use of fluorescent microbeads as markers enables measurements of optically opaque liquids such as dairy food products. Our system has indeed been successfully used to probe rheological properties of yogurts
and chocolate mousses (not shown). As a model dairy, we have used a mixture of milk and xanthan gum that exhibits, as do many food products, a shear-thinning behaviour. We show that in this case the deflections of papillae are weakly dependent on the shear rate. From a biological point of view, our measurements thus imply that the sensory input, which is most likely related to the bending of papillae, is weakly dependent on the in-mouth shear stress. Texture perception of food products appears therefore robust across varying chewing conditions. Such a feature echoes tactile perception mechanisms in other contexts. In human tactile digital perception, for instance, it is known that such robustness (to variations in the finger/object frictional properties, for example) provides the human hand with the ability to maintain a stable grasp at all times [32]. Similarly, for rodents, which use their facial whiskers to detect objects in their immediate vicinity, the vibrations of whiskers elicited upon contact provide a detection mechanism that is robust over a large range of exploration conditions [33]. The present work suggests that the in-mouth texture perception of food products that have shear-thinning rheological properties is equally robust to variations in the exploratory chewing conditions.

4. Conclusion and perspectives

In this work, we have developed and calibrated a novel biomimetic sensor of the human tongue–palate system, based on the deflections of cylindrical soft asperities reminiscent of the filiform papillae. For a given tongue, the same papilla can actually be reused more than typically 100 times without modifications of its mechanical response. Its operation time is rather limited by photobleaching of its fluorescent microbeads. Our biomimetic sensor is therefore simple to set up and long-lasting.

We have shown that the deflection of papillae was proportional to the applied shear stress. We have provided a rigorous validation of the elastohydrodynamic model developed by Lauga and coauthors. Since tongue tissue can be treated as a simple homogenous fluid where papillae are fully immersed in the liquid and do not take into account any dewetting phenomena of the tongue that could occur during chewing and ingestion. For future work, two main aspects will be addressed. First, the present experiments have focused on shear-induced deflections of the papillae. It is known however from psychophysical studies [35] and ultrasound imaging of oral manipulation of fluids [36] that in-mouth texture perception also involves squeeze flows corresponding to an upward motion of the tongue, whose consequences for papilla deflections have been theoretically modelled by Lauga et al. [13]. Experimental investigations of this exploration condition remain to be performed. Second, in this work, we have only considered the case of tongues covered with a low surface density of papillae, for which hydrodynamics interactions between papillae are negligible. Human tongues, however, possess a much higher density of filiform papillae (approx. 5 papillae mm$^{-2}$), at which non-trivial coupled elastohydrodynamic effects are likely to occur [37]. The effect of the surface density of papillae on their deflections under shear will be the core of a forthcoming paper that will address them both experimentally and theoretically [23]. This work is of relevance to the psychophysics community since it will also help to better understand the textural coding of complex fluids in the oral cavity and allow the design of future psychophysics studies associated with their soft matter physics interpretation. Finally, this work has focused on a first mechanotransduction step involved in liquid food texture perception by the oral cavity. Eventually, deflections of papillae are chemically transduced into a series of action potentials by mechanoreceptors embedded at their base [14]. This second step of the mechanotransduction processes will further participate in signal encoding and amplification and remains to be further investigated.

**Data accessibility.** This article has no additional data.

**Competing interests.** We declare we have no competing interests.

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