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Pressure-induced Shape-shifting of Helical Bacteria[†]

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Many bacterial species are helical in form, including the widespread pathogen *H. pylori*. Motivated by recent experiments on *H. pylori* showing that cell wall synthesis is not uniform¹, we investigate the possible formation of helical cell shape induced by elastic heterogeneity. We show, experimentally and theoretically, that helical morphogenesis can be produced by pressurizing an elastic cylindrical vessel with helical reinforced lines. The properties of the pressurized helix are highly dependent on the initial helical angle of the reinforced region. We find that steep angles result in crooked helices with, surprisingly, reduced end-to-end distance upon pressurization. This work helps to explain the possible mechanisms for the generation of helical cell morphologies and may inspire the design of novel pressure-controlled helical actuators.

1 Introduction

Bacteria span a large range of sizes and a diversity of shapes². In most species, cell morphology is primarily determined by the peptidoglycan cell wall, an intricate polymeric mesh that coats the cell and serves as a stress-bearing structure against turgor pressure³. Importantly, cells with helical morphology are broadly present across prokaryotic species and are among the most common cellular shapes (Fig. 1a)⁴. In addition to species that naturally grow as helices, mutants of rod-shaped and C-shaped species may acquire helical morphology in septation-deficient mutants⁶, when septation is suppresed⁷, or under environmental stresses⁸. These observations might reflect common underlying mechanisms that the cell can adjust to generate different morphologies, allowing the shape-shifting between helix, curved and rod cells. Conversely, the ubiquity of helical cell shapes in bacteria may indicate a convergent selection of the helical design to serve specific biological functions. For instance, Helicobacter pylori, a gastrointestinal pathogen and paradigmatic example of helical cell, shows reduced pathogenicity in mutants lacking helical shape^{5,9}.

Since bacterial cells can transition between rod shape or Cshape to helices, it is natural to ask how cell shape can be tuned

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to accommodate the conditions of the ever-changing environment characteristic of bacterial life forms. Their ability to control cell shape relies on the regulation of the synthesis and mechanical properties of the cell wall. Current models propose a stressdependent^{3,10,11} and/or curvature-dependent^{1,9,12} remodeling and growth of the cell envelopes. Moreover, the interaction of cell envelopes with scaffold proteins, particularly in the form of stretch-resistance fibers analogous to the cytoskeleton in eukaryotes, has been proposed as cell shape regulation model, such as the pioneer work by Wolgemuth¹³. These two mechanisms are not mutually exclusive and very likely work in conjunction^{14,15}. Both processes can, potentially, lead to a complex envelope composed of regions with different rigidities, akin to a composite material^{16,17}.

The underlying microscopic organization of the cell envelope



Fig. 1 a) Electron micrograph of the helical bacterium *Helicobacter pylori*. Scale bar is 0.5 μ m. Image reproduced with permission from⁵. b) Simulated helical cell obtained after pressurizing a spherocylinder, where material is reinforced along a helical path with a reinforcement angle $\alpha = 47.6^{\circ}$ (corresponding to $n_r = 2.5$ turns of the helix). The pressure used is such that $\bar{p} := pr_0/Y = 0.21$ (where r_0 is the unpressurized tube radius and Y the 2d Young modulus). c) Silicone balloon reinforced by an (effectively) inextensible thread (red), pressurized to $p \approx 0.2$ atm.

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Fig. 2 Shape morphology as a function of pressure. a) Spherocylinder with reinforcement along $\alpha = 78.6^{\circ}$ (corresponding to $n_r = 2$ turns) at different pressures p, from left to right: 0, 0.60, 1.10 and 1.30 atm (where Y = 60 mN/m and $r_0 = 200 \text{ nm}$). b) Helix height z as a function of the nondimensionalized pressure $\bar{p} = pr_0/Y$. Roman numbers: Minimal energy configurations at $\bar{p} = 0.47$ for the reinforcement angles $\alpha = 78.6$, 81.4, 84.3 and 85.7 degrees. c) Helical angle ζ as a function of \bar{p} . Symbols are simulation results; solid lines are model predictions.

can be manifested upon changes of the internal (turgor) pressure ¹⁸. For example, in *E. coli* a decrease of the inner turgor pressure mediated by hyper-osmotic shock results, as expected, in a decrease of the cell's length and radius, though the reduction in radius is minimal ¹⁹. This mechanical response has been attributed to the circumferential organization of the cell wall. Conversely, in *H. pylori*, a decrease in turgor pressure results in an increase of length (Fig. S6, ESI⁺, ^{20,21}). This behavior is not observed in previous mechanical models ¹³.

In this work we explore the changes in shape of helical cells by turgor-pressure-dependent deformation of rod-like cells with a single helical reinforcement (Fig. 1b). We find that the resulting shape after pressurization strongly depends on the helical angle of the reinforced fiber (Fig. 2a). For large helical reinforcement angles, i.e. aligned with the long axis of the rod, pressurization results in the formation of crooked helices with a non-intuitive shortening of the end-to-end distance. We develop a theoretical model that explains the shortening quantitatively and captures qualitatively the resulting helical properties upon pressurization. We confirm our theoretical results experimentally using silicone balloons (Fig. 1c).

2 Results

2.1 Computational model

To study the resulting shapes of cells subjected to turgor pressure, we construct a triangular spring mesh in the shape of a spherocylinder (Fig. 2). Under small deformations, this mesh model maps to a continuous material with Poisson's ratio $v = \frac{1}{3}$, and 2D Young modulus *Y* given by $Y = \frac{2}{\sqrt{3}}k$, with *k* the spring constant of the mesh²². We assigned a stiffness to the mesh from the characteristic 3D Young modulus *E* and a thickness *t* of Gram negative cell walls, where Y = Et. Inspired by the experimentally-observed preferential binding of cytoskeleton-like proteins to concave areas of the cell surface ^{1,6,7}, we consider a reinforced helical region on the main cylindrical part to be significantly stiffer. This results in a nearly-undeformable region at the range of pressures explored. In real cells, the reinforcement can be a consequence of the anisotropic remodeling of the cell wall, the interaction with protein scaffolds or a combination of both. We find the configu-

rations of minimal energy using a non-linear conjugate gradient algorithm (Sec. I(B), ESI[†]). Upon pressurization, the resulting difference in the resistance to stretching of the reinforced region with respect to the main body leads to the formation of cells with helical morphology (Fig. 2a).

Naively, we would expect that an increase in the pressure p results in an expansion of the contour length L_c (total length of the tube, caps excluded), the height of the helix z and the radius of the tube r concomitant to the formation of the helix. This is the behaviour observed experimentally in macroscopic models¹³. Though the general intuition is correct for L_c and r, in contrast, a subtle increase of z during the initial steps of the pressurization is later followed by a shortening, such that $z(p) < z_0$ (Fig. 2a and 2b). This result is compatible with the increase of the end-to-end distance after a reduction of the turgor pressure, via hyper-osmotic shocking, observed in *H. pylori* (Fig. S6, ESI⁺, ^{20,21}). We study the shortening behavior in a range of biologically-relevant pressures. We will use a non-dimensional rescaled pressure $\bar{p} := pr_0/Y$, where r_0 is the radius of the non-pressurized tube.

The shape after pressurization is highly dependent on the helical angle of the reinforced line, α , which is defined in the undeformed configuration. The shape changes from a tube with helical bumps on the surface to a coiled helix as α increases from 30° to 86° (Fig. S7, ESI†). For $\alpha > 70^\circ$, the resulting shape is well described by a helix and this is the parameter regime we focus on in this letter. We found that for cylinders with a number of turns of the reinforced line n_r greater than 0.5 turns, the resulting helical shape at different pressure is approximately independent of the initial length (Fig. S13, ESI†). For the sake of simplicity, we study the formation of helices in the n_r independent regime.

A finite helix can be defined by four parameters: the radius of the tube *r*, the radius of the helix *R*, the pitch *L*, and the number of turns of the helix central axis *n*. Other variables of interest can be derived from these four parameters, e.g. $L_c = 2\pi n \sqrt{R^2 + L^2}$ (not including the caps). We analyze the response of the helical parameters as a function of pressure (Fig. S8, ESI†). We find that *R* increases when the shell is pressurized to low pressures. However, contrary to *r* and L_c , its dependency with \bar{p} can be non-monotonic. In the large α regime, *R* shows a well-defined



Fig. 3 p_z^* as a function of the number of reinforced turns n_r . Dashed lines are exponential fits for $n_r < 0.5$ (red) and $n_r > 0.5$ (blue). The intersection between both fits occurs at $n_r^* \simeq 0.5$. *Insets*. Minimal energy configurations for $n_r = 0.40$ and $n_r = 0.59$ showing the soft transition between C-shape to helix ($\bar{p} = 0.47$). Data for different aspect ratios L_{c_0}/r_0 , with constant r_0 , and fixed reinforcement helical angle ($\alpha = 84.3^\circ$).

maximum that precedes its decrease when higher pressures are applied. The helical pitch L does not coincide with the pitch of the reinforced line and follows a similar trend to that observed for z, more precisely, an increase of less than 15% during the initial steps of the pressurization before a reduction with further increase of \bar{p} . A proxy for the shape and crookedness of the helix is given by the helical angle $\zeta = \operatorname{atan}(L/R)$. For every reinforcement angle, ζ decreases monotonically with *p*, where steep α leads to smaller helical angles for a given pressure (Fig. 2c). Surprisingly, we note that *n* is higher than the original number of turns of the reinforced string $n(p) > n_r$, with a deviation increasing with α . This behavior is consistent with the observed absence of coupling between the pitch of the helix and that imposed by the reinforced line. Nonetheless, *n* shows hardly any variation prior or during the shortening transition. Therefore, initial shortening is mostly dependent on the expansion of R. We note however that n shows a significant increase at high pressures. This change of trend is approximately coincident with the the critical pressure at which maximum R is obtained.

We also examined if surface torsion τ is involved in the shortening transition (Fig. S9 and Sec. II(B), ESI†). We find that τ grows super-linearly with pressure and that its absolute value for a given pressure is decreasing with α . Furthermore, we find that τ has a smooth dependency on \bar{p} and no change of τ during pressurization can be associated with a reduction of z, thus discarding torsion as a major determinant of the shortening transition. We observe a very similar response of the helical parameters and the torsion upon pressurization in vessels with wider reinforced strings (Fig. S10, ESI†).

We studied the response of shells molded in the shape of helices in the relax configuration. Shells with uniform mechanical properties does not show shortening when pressurized (Fig. S11, ESI†). By reinforcing the inner most region of negative Gaussian curvature, we observe a decrease in length and reduction of the helical angle (Fig. S12, ESI[†]).

We have shown the pressure-induced formation of helices with steep reinforcement angles α . However, the angle α is a function of the number of turns of the reinforced string n_r and the contour length of the tube in its undeformed configuration L_{c_0} . We performed simulations with different initial lengths L_{c_0} considering a fixed reinforcement angle ($\alpha = 84.3^{\circ}$), hence varying n_r . Only the longer tubes show a length-independent behaviour (Fig. S13). We analyze the response of the critical pressure leading to maximum extension, p_7^* , as a function of n_r . We observe two clearly distinguishable regimes. For initial lengths that result in $n_r < 0.5$ we find an exponential decrease of p_7^* , whilst for lengths resulting in $n_r > 0.5$ turns, the critical pressure is mostly insensitive to n_r (Fig. 3). From visual inspection of the resulting shapes, we note a transition separating a C-shaped-regime for $n_r < 0.5$ from a helix-dominated regime for $n_r > 0.5$. Thus, $n_r \approx 0.5$ is a transition point between a C-shaped morphology upon pressurization and a helical shape.

The experimental evidence suggest that helical shape may involve the relaxation of the cross-linking bonds of the cell wall^{1,9,23}. Simulations where the helical region is weakened instead of reinforced indicate that weakening is also a feasible mechanism for the formation of helices. Helical parameters during pressurization show a similar response to that observed by reinforcing, including the shortening for large reinforcement angles and the formation of crooked helices (Fig. 4 and Fig. S14, ESI†).

2.2 Experimental verification

Our numerical model predicts a substantial reduction of z at large reinforcement angles α as a result of the formation of highly crooked helices. To further test this observation, we performed experiments using custom-made silicone balloons with a nonextensible embroidery thread wrapped and embedded on the silicone body (Sec. III, ESI†). We explore pressure-induced formation of helices in the large α regime (Fig 5). Silicone shows a hyper-elastic stress-strain response and thus a quantitative comparison with simulation is not possible. Yet, we find qualitative agreement between the experiment and our computational results (Fig. S20, ESI†). We observe a similar response of the helical radius *R* to that observed in the simulations: the increase of *R* with pressure until reaching a critical point from where subse-



Fig. 4 Pressurization of tubes with helical weakening. a) Height of the helix, z. b) Helical angle, ζ . Lines connecting dots are a guide to the eye. The weakening is adjusted by reducing the 2D Young modulus Y of the helical domain by 1/3. Lines connecting dots are a guide to the eye.



Fig. 5 Shape morphology of pressurized silicone models reinforced along a helical path. The string, visible as a red line, is initially set at $\alpha = 73^{\circ}$, and is effectively inextensible. The nondimensionalized pressures used are, from left to right, $\bar{p} = 0$, 0.38, 0.76, 1.14 and 1.52.

quent increase in p reduces the helical radius. This is linked to the development of the helix into a more compact structure, resulting in rapid decrease of z. Remarkably, the magnitude of the deformations for the indicated helical parameters are on the same scale to that obtained from the numerical simulation.

2.3 Continuum theory

To explain the physics behind the formation of helices, the shortening transition and its dependency on α , we model the system analytically by using continuum elasticity. Inspired by the observation that the radius of the tube *r* and the contour length of the central axis L_c have little dependency on the reinforcement angle (Fig. S15 and Fig. S16, ESI⁺), we assume a separation of the overall swelling of the system and other deformations. Namely, we use an empirical expression for r and L_c as functions of p independent of the reinforcement angle α (Sec. II(A), ESI[†]). The reinforced line always lies along the shortest path with the fixed number of turns on the surface connecting the two ends of the helix to minimize the elastic energy penalty. The analytical expression for this path is provided in Sec. II(B), ESI[†] (Equation S32). Since the springs in the reinforced region are so stiff that the results do not change with further increase of reinforced spring constant, we assume this reinforced line is unstretchable. This would be equivalent to a constraint that the inner-most part of the helix has a fixed length L_f . We consider the energy per unit length Φ of a hollow rod subjected to uniform bending and twisting under a linear elasticity framework²⁴:

$$\Phi = \frac{EI}{2}\kappa^2 + \frac{\mu J}{2}\tau^2.$$
 (1)

Here τ is the twist rate and κ is the local curvature of the helix central axis. The parameter $\mu = \frac{E}{2(1+\nu)}$ is the second Lamé coefficient, and *I* and *J* are the moments of inertia and twist, respectively. For a thin-walled tube, $I = \pi r^3 t$ and $J = 2\pi r^3 t$, in which *r* is the radius of the tube and *t* is the wall thickness. The bending and twisting magnitude of a helix deformed from a cylinder are $\tau = \frac{2\pi n}{L_c} (\sin \zeta - n_r/n)$ and $\kappa = \frac{2\pi n}{L_c} \cos \zeta$, see Sec. II(B) (ESI†). Again, $\zeta = \arctan(L/R)$ is the helical angle, n_r is the number of turns of the reinforced area in the zero pressure case and *n* is the number of turns of the helix. The state of the system at any pressure can be determined by minimizing the energy given the empirical functions r(p) and $L_c(p)$ under the constraint that the length of the inner-most path of the helix is fixed. This framework allows us to predict, analytically, the helix parameters as a function of pressure (Sec. II(C), ESI†). A comparison between simulation results and the analytical formulation can be found in Fig. 2 and in ESI† (Fig. S9 and Fig. S17). It is worth noting that in the simulation we observe wrinkles formed near the reinforced string (Fig. S18, ESI†). As a consequence of restrained stretching, regions adjacent to the reinforcement string are wrinkled in a direction perpendicular to the string and show well-defined periodicity. The agreement between simulation and theory suggests that energy changes associated with wrinkling are negligible.

In Fig. 6, we show a phase diagram representing the change in z with respect to the rescaled pressure, as a function of α and \bar{p} . The diagram clearly shows the regions of lengthening and shortening in z. We can predict analytically the critical pressure of the transition from lengthening to shortening for a given helical angle.

Due to the constraint that the reinforced path is not stretchable, we have:

$$L_f = \sqrt{z^2 + (2\pi n)^2 \cdot (R - r)^2}.$$
 (2)

Since the value of L_f is held fixed when pressure increases, it is then clear that the helix height $z \le L_f$ and the maximum of z is achieved when R = r. This corresponds to a configuration where the reinforced line becomes completely straight. Such straightening behavior of the reinforced string is observed in the simulation: at low pressures, for every α , the reinforced string is straightened, increasing its alignment with the long axis of the tube (Fig. S19, ESI†). This initial alignment results in the positioning of the reinforced string to the internal (concave) side of the incipient helix. By requiring R = r we can derive the criteria for the critical pressure at the maximum height under the proper approximations (Sec. II(D), ESI†),

$$\cot^{2}(\alpha) = \frac{(L_{c}(p)/L_{c_{0}})^{2} - 1}{(r(p)/r_{0})^{2} + 1},$$
(3)

where L_{c_0} and r_0 are the contour length and the tube radius in the undeformed state, and L_c and r are functions of pressure. The right hand side depends on the material properties of the tube, which turns out to be non-linear for the triangular mesh. Equation 3 also reveals that the state of maximum height may not be achievable when α is small, as observed in the simulation. A comparison between Eq. 3 and simulation results can be found in Fig. 6.

3 Discussion and Conclusions

How bacterial shape is generated is an important question in microbiology. Here, we have shown that reinforced rod-shaped cells with the mechanical properties of bacterial cell walls can transit to helical shape upon pressurization. Simulations indicate that large deformations can occur in response to turgor pressure. In particular, large reinforcement angles lead to crooked three-dimensional helices with reduced pitch and large radius,



Fig. 6 Heatmap of the helix height (z) as a function of the angle of reinforcement and the nondimensionalized pressure. The white region corresponds to the region of maximal height observed in the simulation. The black line is the theoretical prediction for the critical pressure at the maximum height $p_z^*(\alpha)$ following Eq. 3.

which can result in the shortening of the cellular end-to-end distance. During pressurization, the localization of the reinforced region is reallocated to the internal side of the helix. Then, the experimentally-observed filamentous proteins on the concave region of the cell may reflect strong interactions with the cell wall combined with a resistance to stretching rather than a curvaturedependent binding affinity^{6,25}.

Helical cells display a large variability of the helical parameters, ranging from nearly straight to highly sinuous 1,26 . This variability might be attained by precise tuning of the cell wall parameters, namely the helical angle of the reinforced region and the stiffness of reinforced and non-reinforced regions. Interestingly, we find that that helical shapes can be formed by both reinforcement and weakening.

It is generally assumed that a given bacterial species has a characteristic distinct shape. However, bacterial shape is not written in stone and the cell can modify its morphology in response to the environment²⁶. Changes in morphology can be plastic, by means of cell wall growth, and operating at slow time scales^{9,27}. At faster time scales, cell shape can be elastically altered by variations of turgor pressure^{18,28}. In short, both envelope synthesis (plastic deformation) and elastic deformations contribute to bacterial shape.

Our computational results show an example of how cell growth, in combination with elastic deformations, is a potential mechanism to trigger shape transitions. We observe that a number of reinforced turns $n_r \approx 0.5$ turns marks a transition between C-shaped cell and helical cells. Therefore, C-shaped cells ($n_r < 0.5$ turns) growing in length and keeping a constant α will develop a helical shape as a result of the increase on n_r (Sec. I(E), ESI†). This agrees with the experimental observations of C-shaped cells acquiring helical morphology upon inhibition of cell division^{6,7}. Thus, under conditions favouring growth, bacteria

can plastically shift from crescent to helical shape¹³.

Nevertheless, the cell could exploit turgor pressure to elastically and dynamically modify its shape. Human-made soft robots composed of elastomers reinforced with helical fibers, known as McKibben actuators, have been designed to produce a variety of extension, bending and/or twist deformations in response of pneumatic pressures^{29–31}. Are helical bacteria exploiting turgor pressure to operate as biological McKibben actuators? Variations of turgor pressure could be used to tune cell shape for a specific biological function. In the example of Helicobacter pylori, the digestive process leads to variations of the external ionic conditions³² (Sec. IV, ESI[†]) and hence to (transient) variations of turgor pressure. The underlying changes on the helical shape could promote the passive penetration through the mucus of the gut, for instance by means of contraction and expansion combined with variations of the helical radius. The mechanism would resemble that found for the self-burial of the coiled seeds in plants in response to changes of the environmental humidity³³. Alternatively, the cell could use an active mechanism for altering its shape²⁸: since the ionic conditions of the intracellular medium can be regulated, the cell could, to some extent, alter its osmolarity to adjust cell morphology and the ensuing drilling of the gut. Shifts in turgor pressure in combination with the anisotropic properties of the cell wall have been proposed as drivers of the Venus fly trap snap or the rapid folding of the leaves in Mimosa pudica^{34,35}. It is plausible to think that bacteria could use similar mechanisms to that used by plants to drive morphological adaptations and dynamical changes of shape. Our numerical observations, validated with macroscopic experimental models, are provoking for verification in live bacterial cells. Carefully-designed experiments combining fluorescence microscopy with microfluidics devices have permitted to visualize the response of bacteria to changes in turgor pressure^{19,36}. Hence, it is feasible to characterize the instantaneous change of the cell helical properties in response to osmotic shocks. The cross-fertilization between experiments and simulations will aid in the understanding of the mechanisms driving cell morphology.

Appendix

In this appendix we list the main parameters and observables used in this work.

Table 1 Geometric parameters and observables

Parameter	Description
z	Helix height
r	Tube radius
L	Helical pitch (tube)
R	Helix radius
α	Helical angle (reinforced string)
ζ	Helical angle (tube)
L_c	Contour length (tube, caps not included)
L_{f}	Contour length (reinforced string)
'n	Number of turns (tube)
n _r	Number of turns (reinforced)
τ	Torsion of the tube's surface
κ	Curvature tube's central axis

Table 2 Mechanical parameters

Parameter	Description
р	Pressure
E	3D Young's modulus
Y	2D Young's modulus
t	Shell thickness
Ι	Moment of inertia
J	Moment of twist

Conflicts of interest

There are no conflicts to declare.

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