

Surfing locomotion of elastic sheets driven by curvature mismatch

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The locomotion of flexible membranes on top of curved surfaces appears in different contexts and scales, from cells to tissue and to cm-scale organisms. We present an experimental and theoretical study of curvature-driven locomotion, using gel ribbons that surf on a curved fluid-fluid interface via autonomous periodic modulation of their curvature. We derive a mechanical model in which forces and torques emerge from the curvature mismatch between the ribbon and the substrate. Analytic and numerical solutions of the equations of motion successfully predict the experimentally measured velocity profiles. We conclude by highlighting the relevance of this curvature-driven mode of locomotion to other mechanical, as well as biological systems.

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Can membranes, attached to a surface, generate net forces and torques for locomotion without the application of locally tangential stresses? Experimental observations show that cells move and orient themselves in correlation with the substrate's curvature (curvotaxis) [1–6]. Curvature-driven locomotion also occurs on a much larger scale, in a seemingly unrelated physical context: motion driven by capillary forces acting on rigid [7–11] as well as flexible [12] floating objects. For example, on scales of mm-cm, a water lily larva propagates on curved fluid interface by varying its curvature [13]. In what follows, we define and characterize a generic mode of locomotion that does not involve locally tangential stresses and suggest that it can appear in a wide range of systems.

We have constructed a synthetic system that allows for generating and measuring this type of dynamics. It consists of active gel ribbons that periodically change their curvature while being confined to a nonuniformly curved liquid interface. The ribbons periodically “surf” along the curved interface, and we measure their velocity profiles. We suggest that the energy of the system stems from a mismatch between the curvature of the surface and the time-dependent curvature of the ribbon. It typically consists of terms that result from deformations of both the ribbon and the substrate. When the surface's curvature is nonuniform, spatial and angular gradients of the energy lead to forces and torques on the ribbon. We integrate the equations of motion and compute the trajectories of the ribbons, successfully recovering experimental results and predicting more general possible dynamics.

Our experimental system consists of a rectangular glass container, filled with two stratified liquids: a few centimeters of perfluorodecalin ($\rho = 1.91 \text{ g/cm}^3$) covered with a double amount of BZ solution ($\rho = 1.03 \text{ g/cm}^3$). A narrow strip of BZ gel ($L = 0.43 \text{ cm}$, $h = 550 \text{ }\mu\text{m}$, $w = 0.15 \text{ cm}$, see

Supplemental Material [14] for explanations on BZ gels and solution) is placed on the interface between the two liquids. While the strip is immersed in the BZ solution, periodic reaction fronts spontaneously propagate inside the gel and cause it to change color from orange to green. As shown in [15,16], in the green (oxidized) phase, the gel swells compared to its volume in the orange (reduced) state. Our ribbons are asymmetric across their thickness (see Supplemental Material [14]) with enhanced reaction on one side. As a result, the ribbons' reference (spontaneous) curvature $\bar{\kappa}$, periodically oscillates between positive and negative values [see Fig. 1(e) and Movie S1]. When the BZ gel strips are left to float freely on the fluid interface, they perform a periodic motion between the walls and the center of the container [Figs. 1(a) and 1(b) and Movies S2 and S3]. The motion is followed by a camera (see details in Supplemental Material [14]). The gel is initially in its orange phase, “parking” next to one of the container's walls, pointing toward it. As the reaction evolves, the gel moves toward the center of the container, rotates, and as it is fully oxidized, it stops at the center of the container oriented perpendicularly to its original orientation (Fig. 1). When the reaction decays, the ribbon rotates and surfs toward the closest wall, where it stops, completing a full period of the motion.¹ This motion can persist for hundreds of periods, as long as the BZ solution, which supplies the energy to the process, is renewed.

Though we model our system within the framework of elastocapillarity [17–19], we suggest that our modeling is relevant to a much wider class of phenomena. We start by studying the problem, which is described in Fig. 1(d). It consists of a flexible ribbon, which is confined to the interface between two liquids with a density difference, $\Delta\rho$, and interfacial surface tension σ . The ribbon has a *fixed* uniaxial reference curvature, $\bar{\kappa}$, along its long dimension, length L , width $w < L$, thickness $h \ll w$, and Young's modulus Y . The fluid interface is not flat. Near the container's wall,

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¹In a similar experiment that was done with a square container, the gel moved from the center to three out of the four walls and had no preferred orientation in the vicinity of the center (Movie S4).

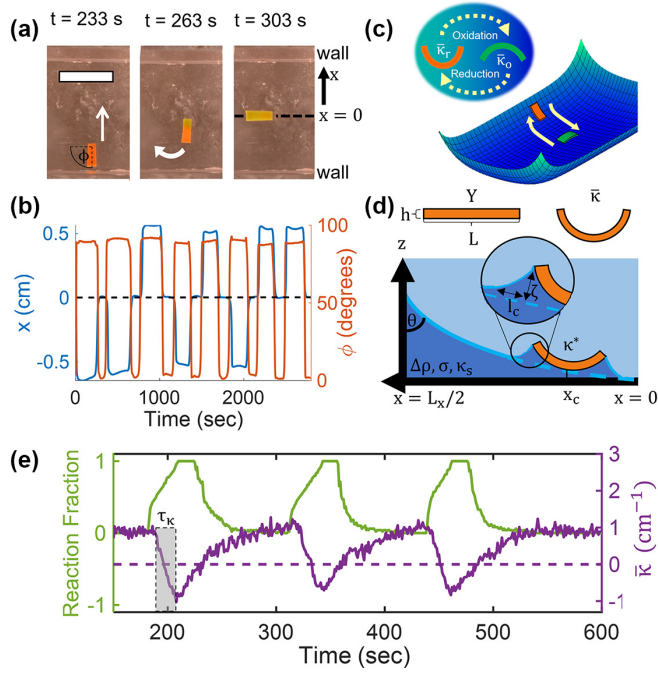


FIG. 1. Basic observations: (a) A BZ gel ribbon is placed on the interface between perfluorodecalin and BZ solution in a rectangular glass aquarium ($L_x = 2.05$ cm, $L_y = 3$ cm). Images of half a period of motion. The angle ϕ , as well as the two containers' walls, are indicated. scale bar: 1 cm. (b) The position (x , blue line) and orientation (ϕ , orange line) of the ribbon as functions of time. (c) An illustration of the two stationary states of a gel ribbon on top of the curved interface. The gel moves to the place where its curvature best fits the curvature of the interface. (d) An illustration of an elastic ribbon of length L , thickness h , Young's modulus Y , and reference curvature $\bar{\kappa}$ floating on a fluid interface with curvature $\kappa_s(x)$. The density difference is $\Delta\rho$ and the surface tension is σ . θ is the contact angle and l_c is the capillary length. The ribbon pulls up fluid to a maximal height ζ . The location of the ribbon's center is denoted by x_c and the origin is at the center of the container. (e) The reaction fraction (green line) and the curvature of a BZ gel ribbon (purple line) as functions of time. The ribbon is fully immersed in BZ solution (not confined to an interface) and changes its curvature periodically (from $\bar{\kappa}_r \cong 1$ cm $^{-1}$ to $\bar{\kappa}_o \cong -0.8$ cm $^{-1}$ in ~ 20 seconds and back in ~ 40 seconds) as the reaction propagates inside it.

it develops a meniscus, with a characteristic height function $z(x, y)$, which determines the surface curvature tensor field $\mathbf{b}_s$. Far from the container's corners, $z(x, y) = z(x) \approx l_c \cot(\theta) e^{-(x-L_x/2)/l_c}$ and the curvature is uniaxial $\kappa_s(x)$. Here, the container's walls are located at $x = \pm L_x/2$, i.e., $x = 0$ is at the center of the container, θ is the contact angle and $l_c = (\sigma/\Delta\rho g)^{1/2}$, the capillary length. When the ribbon is confined to the interface between two fluids, both the strip and the interface are deformed. The ribbon pulls up some liquid to a maximal height ζ [see Fig. 1(d)]—a deformation that costs gravitational energy. On the other hand, the liquid pulls back and bends the ribbon off its reference curvature—a deformation that costs elastic bending energy. The actual curvature of the ribbon and its motion are dictated by the balance between these competing energies. Using the theory of non-Euclidean sheets [20–22], we write the elastic energy

of the ribbon which, in general, consists of a stretching term E_s and a bending term E_B :

$$E_{el}[\mathbf{a}, \mathbf{b}] = Y \int [h E_s(\mathbf{a} - \bar{\mathbf{a}}) + h^3 E_B(\mathbf{b} - \bar{\mathbf{b}})] dA, \quad (1)$$

where $\mathbf{a}$ is the metric tensor and $\mathbf{b}$ is the curvature tensor of the ribbon. $\bar{\mathbf{a}}$ and $\bar{\mathbf{b}}$ are the reference metric and curvature tensors, respectively. For our system, in which the reference curvatures of both the ribbon and the surface (far from the container's corners), $\bar{\kappa}$ and κ_s respectively, are uniaxial, we have (see Supplemental Material [14])

$$\tilde{E}_{el} = Y h^3 L (\kappa(x, \phi) - \bar{\kappa})^2, \quad (2)$$

where $\tilde{E}_{el}$ is the elastic energy up to numerical factors, ϕ is a rotational degree of freedom, with $\phi = \pi/2$ is along $\hat{x}$ [see Fig. 1(a)], and $\kappa(x, \phi)$ is the actual ribbon's curvature. For a ribbon, oriented perpendicularly to the wall, the energy associated with the deformation of the substrate to a profile $\xi(x)$ above the unperturbed interface, $z(x)$, is approximately (see Supplemental Material [14], Eqs. S4–S11) $\tilde{E}_{sub} = \Delta\rho g \int (\xi(x') - z(x'))^2 dx' \approx \Delta\rho g (L + l_c) L^4 (\kappa - \kappa_s(x_c))^2$. For a ribbon oriented along the $\hat{\phi}$ direction, we get after simplifications (See Supplemental Material [14], Eqs. S9–S11)

$$\begin{aligned} \tilde{E}_{sub} &\cong \Delta\rho g l_c L^4 |\mathbf{b}(x, y, \phi) - \mathbf{b}_s(x, y)|^2 \\ &\cong \Delta\rho g l_c L^4 (\kappa - (\kappa_{s,x} \sin(\phi))^2 + \kappa_{s,y} \cos(\phi))^2. \end{aligned} \quad (3)$$

The total energy, up to numerical constants, is therefore $\tilde{E} = \tilde{E}_{el} + \tilde{E}_{sub}$, and the selected curvature $\kappa^*(x, \phi)$ is determined by its minimization with respect to κ . Substituting $\kappa^*(x, \phi)$ into the energy expression yields a *space and orientation dependent potential energy*.

In the one-dimensional case, i.e., when $\mathbf{b}$ has only one nonzero entry, we find

$$\kappa^*(x) = \frac{\bar{\kappa} \kappa_s(x) + 1}{(\bar{\kappa} + 1)} \bar{\kappa}, \quad (4)$$

where $\bar{\kappa} = \Delta\rho g l_c / Y \cdot (L/h)^3 = (\Delta\rho g \sigma / Y^2)^{1/2} \cdot (L/h)^3$ represents the ratio between the stiffness of the substrate and that of the ribbon, a ratio, which appears in other, static, elastocapillary problems [23–25]. It can be shown (see Supplemental Material [14]) that $\bar{\kappa} = (\frac{L}{l_c}) (\frac{L}{L_{ec}})^2$ where $L_{ec} = \sqrt{\frac{Y h^3}{\sigma}}$ is the elastocapillary length [26]. For stiff ribbons, $\bar{\kappa} \ll 1$ and $\kappa^* \approx \bar{\kappa}$ - the system behaves like rigid floating bodies that have been studied before [8, 27]. If the ribbon is very flexible, namely, $\bar{\kappa} \gg 1$, $\kappa^*(x) \approx \kappa_s(x)$. In this limit, the substrate energy is negligible, and the dynamics is dominated by the elastic energy of the ribbon. By taking the spatial and angular derivatives of the energy, we obtain the force, $\vec{F}$, and torque, $\vec{M}$, that act on the ribbon, with $F \sim (\kappa - \kappa_s) \frac{d\kappa_s}{dx}$. Far from the wall $\frac{d\kappa_s}{dx}$ is small, and it increases monotonically toward the wall. Contrarily, $\kappa - \kappa_s$ decreases when the ribbon approaches its equilibrium point. The multiplication of these two terms guarantees that the maximal force is obtained at some intermediate point. Using the fact that the system is overdamped, we derive the equation of motion of the ribbon: In this case, the linear and angular velocities, $\vec{v}$ and $\vec{\omega}$, are proportional to

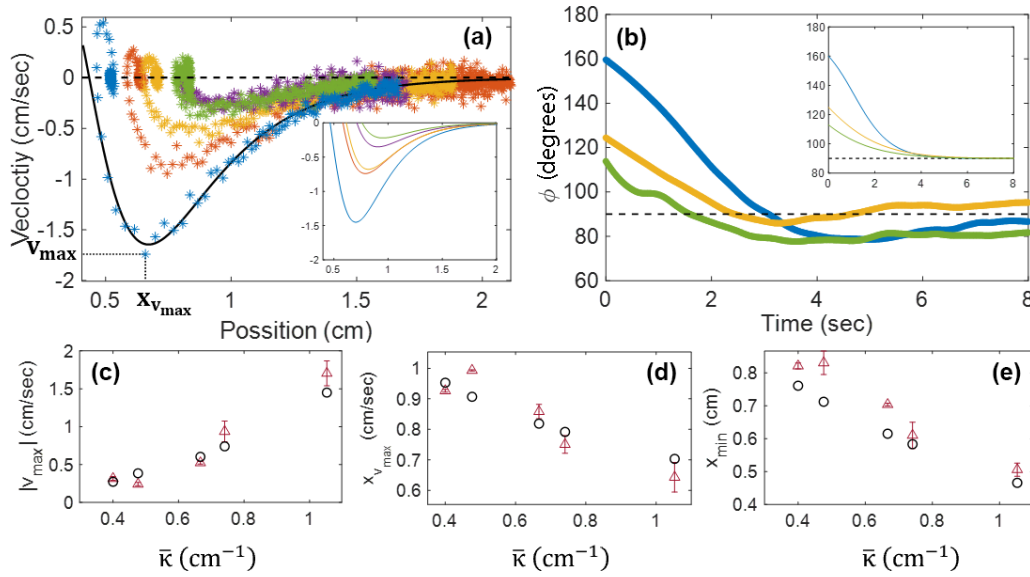


FIG. 2. Velocity profiles (a) and orientation (b) of five different ribbons ($w = 0.3$ cm, $L = 0.7$ cm) floating on water and attracted to a wall ($x = 0$). The reference curvatures and thicknesses are 1.05 cm^{-1} and 290 μm (blue), 0.74 cm^{-1} and 290 μm (orange), 0.67 cm^{-1} and 290 μm (yellow), 0.48 cm^{-1} and 380 μm (purple), and 0.4 cm^{-1} and 380 μm (green). The solid black line in (a) is a fit with Eq. (5) to the measured trajectory of the ribbon with the largest curvature (blue symbols), with $\tilde{D} = 49$ ($\text{dyn} \cdot \text{sec})/\text{cm}^2$ and $\theta = 31^\circ$. Insets: Theoretical velocity and orientation curves of the ribbons [Eq. (5)] with the relevant experimental parameters and the average values of the contact angle and drag coefficients: $\theta = 28^\circ$, $\tilde{D} = 55$ ($\text{dyn} \cdot \text{sec})/\text{cm}^2$, and $\tilde{I} = 0.75$ $\text{dyn} \cdot \text{sec}$. The absolute value of the maximal velocity (c), the location of the maximal velocity (d) and the stopping points (e) for the data in panel (a), as measured experimentally (red triangles) and computed using Eq. (5) (black circles).

$\vec{F}$ and $\vec{M}$, respectively:

$$\begin{aligned}\vec{v}(x, y, \phi) &= \vec{F}(x, y, \phi)/D = -\vec{\nabla} \tilde{E}(x, y, \phi)|_{\kappa=\kappa^*}/\tilde{D} \\ \vec{\omega}(x, y, \phi) &= \vec{M}(x, y, \phi)/I = -\frac{\partial \tilde{E}}{\partial \phi} \hat{z}|_{\kappa=\kappa^*}/\tilde{I}.\end{aligned}\quad (5)$$

D and I depend on the ribbon's dimensions and fluid viscosity. Since $\tilde{E}$ is approximated and misses numerical factors, the proportion coefficients that are used in the following data analysis, $\tilde{D}$ and $\tilde{I}$, are proportional, but not identical to D and I (see Supplemental Material [14]).

In order to verify our model predictions, we conducted a series of experiments with uniformly curved flexible PVS ribbons ($L = 0.7$ cm, $h = 290$ – 380 μm , $w = 0.3$ cm, see Supplemental Material [14]) with $0.4 < \bar{\kappa} < 1.1 \text{ cm}^{-1}$. The ribbons were placed on the surface of distilled water approximately 2 cm from the wall and their motion was tracked (Movie S5), yielding $x(t)$, the location of the center of the ribbon, and $\phi(t)$, its orientation. The velocity curves [Fig. 2(a)] are indeed characterized by an acceleration toward the wall, a maximal velocity, v_{max} , obtained at $x_{v_{\text{max}}}$, and then deceleration until the ribbon stops at x_{min} [28]. Our model (solid line) is successful in describing the entire motion for $\bar{\kappa} = 1.05 \text{ cm}^{-1}$ and $h = 290$ μm , as well as curves that correspond to other experimental data (inset), using fixed, best fitting, parameters: $\theta = 28^\circ$ and $\tilde{D} = 55$ ($\text{dyn} \cdot \text{sec})/\text{cm}^2$ (the std in θ and $\tilde{D}$ are 4° and 16 ($\text{dyn} \cdot \text{sec})/\text{cm}^2$, respectively. Direct measurements of θ yield $\theta = 30^\circ \pm 2$, see Supplemental Material [14]). Both experimental and theoretical curves show that as $\bar{\kappa}$ increases, v_{max} increases [Fig. 2(c)], while $x_{v_{\text{max}}}$ and x_{min} decrease [Figs. 2(d) and 2(e)]. The model provides good

predictions for the dependence of the trajectories on L and Y as well (see Supplemental Material [14]) and successfully describes the evolution of the ribbon orientation as well [Fig. 2(b)]. Movie S6 shows the entire dynamics.

We now analyze the motion of the active BZ gel strips. Here, the reference curvature varies in time, $\bar{\kappa} = \bar{\kappa}(t)$, with a typical period of ~ 150 s [Fig. 1(e), Movie S1], [note that the BZ gel ribbons are two orders of magnitude softer than the PVS ribbon ($Y \cong 2 \cdot 10^4$ dyn/cm^2 [29]), therefore, their velocity is much lower]. We superimpose a sequence of full trajectories [Fig. 3(a)], in which the strip approaches the walls and retracts back to the center of the container. Since the acceleration toward the wall takes place while $\bar{\kappa}$ is approximately constant (the gel is in its reduced phase), the attraction profiles look like the ones we measured for the PVS ribbons. In contrast, the repulsion stage, in which the gel moves while $\bar{\kappa}(t)$ is changing, demonstrates more symmetric profiles, with maximal velocity which is 2 times smaller than the attraction. In this case, the gel “chases” after its new equilibrium point that moves toward the center of the container. Here, the speed is governed by the curvature rate of change $\dot{\bar{\kappa}}$. We analyze the attraction trajectory, using Eq. (5) and $\bar{\kappa} = \bar{\kappa}_r = 1 \text{ cm}^{-1}$ [see Fig. 1(e)] and seven attractive trajectories, we extract the average values of D , θ , and l_c and use them, together with $\bar{\kappa}(t)$ for numerical derivation of the velocity curves (Figs. S3 and S6). The simulation recovers successfully the measured trajectories, and the movie that presents the theoretically computed motion (Movie S7) resembles the experimentally measured motion (Movie S2). As for the angular velocity, the computation captures only part of the profile's characteristics. Though, as in the experiments, there is a difference between

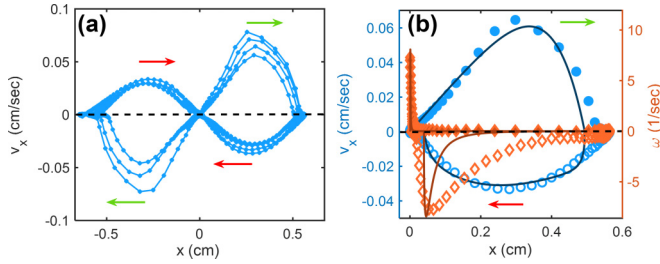


FIG. 3. Velocity profiles of BZ ribbons. (a) Velocity of a BZ gel ribbon ($L = 0.43$ cm, $h = 550$ μ m, $w = 0.15$ cm) as a function of its position, during seven complete cycles of the motion. The origin is in the center of the container, and the walls are at $x = \pm 1.025$ cm. (b) The linear (blue circles) and angular (orange diamonds) velocity profiles as measured over one cycle. The full and empty symbols correspond to the attraction and repulsion profile, respectively. Theoretical linear and angular velocity profiles (dark blue and brown lines), using the parameters obtained in Fig. 1(e) and Supplemental Material Fig. S6: $\bar{\kappa}_r = 1$ cm^{-1} , $\bar{\kappa}_o = -0.8$ cm^{-1} , $\dot{\bar{\kappa}} = 0.09$ $\text{cm}^{-1}/\text{sec}$, $\bar{D} = 35$ ($\text{dyn} \cdot \text{sec})/\text{cm}^2$, $l_c = 0.26$ cm, $\theta = 27^\circ$, the measured L, h, Y , and $\bar{I} = 1.75$ $\text{dyn} \cdot \text{sec}$ as a free parameter. The theoretical angular velocity is divided by a factor of 2.2.

the attractive and repulsive trajectories, the repulsive profile is more localized compared to the measured one, and the maximal velocities are higher by a factor of two. Since our model contains many approximations, we view the results presented in Fig. 3 as support for the theoretical model.

As a last stage of our analysis, we study the interplay between the intrinsic time scale, $\tau_{\bar{\kappa}} = \frac{|\bar{\kappa}_o - \bar{\kappa}_r|}{\dot{\bar{\kappa}}}$, the time of the gel oxidation process, and the time of the motion itself τ_v . We solved numerically the equations of motion while changing $\tau_{\bar{\kappa}}$ over three orders of magnitude (0.05–50 sec). The velocity profiles are shown in Fig. 4(a). While the attraction profiles ($v_x > 0$) are the same, the repulsion profiles ($v_x < 0$) strongly depend on $\dot{\bar{\kappa}}$. Each of them is composed of two parts: As long as the reference curvature keeps changing, the velocity increases concavely. At this stage, the velocity reaches its maximal value. Once $\bar{\kappa}$ becomes constant, the velocity decays convexly in a profile that is common to all samples and is described by Eq. (5). For $\dot{\bar{\kappa}} = 0.072$ $\text{cm}^{-1}/\text{sec}$ (the cyan curve), which most closely corresponds to the experimental parameters [$\tau_{\bar{\kappa}} \approx 20$ s, see Fig. 1(e)], the velocity profile is similar

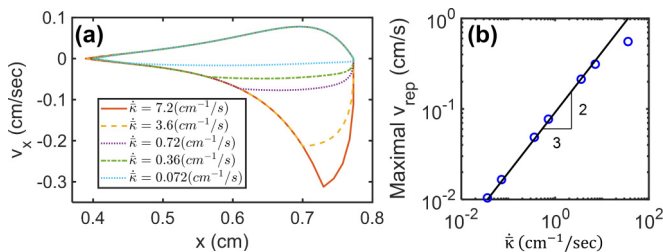


FIG. 4. The effect of the reaction rate on the repulsion profile. (a) Numerical velocity profiles for different curvature change rates, $\dot{\bar{\kappa}}$. (b) A log-log plot of the maximal repulsion velocity as a function of $\dot{\bar{\kappa}}$. The numerical data is consistent with the dimensional analysis predictions: $v_{\max} \sim \dot{\bar{\kappa}}^{2/3}$ (solid line). The best power law fit to the data is $\dot{\bar{\kappa}}^{0.64}$.

to the experimental curves. As $\dot{\bar{\kappa}}$ increases, the velocity profile becomes asymmetric and the maximal velocity increases. Plotting the maximal velocity as a function of $\dot{\bar{\kappa}}$ [Fig. 4(b)], we find a power law dependence, which indicates that for every profile, the relation $\tau_v \approx \tau_{\bar{\kappa}}$ holds. This leads (see Supplemental Material [14]) to the relation $v_{\text{rep}} \sim \left(\frac{\rho g L^4 l_c^2}{D}\right)^{1/3} \dot{\bar{\kappa}}^{2/3}$, which is consistent with our data. Note that this scaling is expected to break at high values of $\dot{\bar{\kappa}}$, when Eq. (5) becomes valid.

We presented and studied the locomotion, driven by curvature modulation of ribbons made of active BZ gel, confined to a curved fluid interface. The autonomous, periodic alternation of their reference curvature leads to locomotive “surfing” of the ribbons along the interface. Our theoretical model suggests that the motion is driven by gradients in the energy that stem from geometrical incompatibility between the surface and the ribbon. In the current work, the motion stems only from uniaxial bending of the ribbon, and the substrate energy stems from capillary interactions. We suggest, however, that our work has a far-reaching impact. It can be extended in both the type of incompatibility and the type of substrate material:

Types of incompatibilities. In our experiments, the mismatch in the uniaxial curvature introduces a single dimensionless number, $\bar{O}$, characterizing the ratio between the surface stiffness and the ribbon’s bending stiffness. For a two-dimensional sheet, with a non-negligible width w , the reference curvature is typically a two-dimensional tensor $\bar{\mathbf{b}}$. Furthermore, in this case, the stretching energy term [Eq. (1)] could play a role, as a conflict between $\mathbf{a}_s$ and $\bar{\mathbf{a}}$ is possible. Hence, the total energy will be composed of three terms: a substrate deformation term, $E_{\text{sub}} \sim \rho g l_c w L^4 (\mathbf{b} - \mathbf{b}_s)^2$, a bending term, $E_b \sim Y h^3 L w (\mathbf{b} - \bar{\mathbf{b}})^2$, and a stretching term, $E_{\text{st}} \sim Y h w L (\mathbf{a} - \bar{\mathbf{a}})^2$. In this case, we expect an additional two dimensionless numbers. For a square sheet ($w = L$) with a reference metric that determines a reference Gaussian curvature $\bar{K}$, we find (see Supplemental Material [14] for details): $\bar{O} = \frac{\Delta \rho g l_c}{Y} \bar{\kappa}^{-2} = \sqrt{\frac{\Delta \rho g \sigma}{Y^2}} \frac{\bar{K}^{-1}}{L h}$, describing the ratio between the stretching stiffness and the substrate (fluid) stiffness, and $A = \frac{h^2}{L^4 \bar{K}^2} = \frac{h^2}{L^4 \bar{K}} = \frac{\bar{O}}{\bar{O}}$, characterizing the ratio between the bending and stretching stiffnesses, and is familiar from studies of free frustrated sheets [21]. By substituting the values of h, L , and κ , one can determine which of these terms dominates. For example, the case studied in [30] corresponds to the limit $A \ll \bar{O} \ll \bar{O}$. The two-dimensional phase space, which arises from this analysis, is much richer than the one we discuss in this work and requires a deeper investigation.

Substrate material. Considering a flexible sheet with reference curvature $\bar{\kappa}$, confined to an *elastic* substrate with reference curvature κ_s . If $\bar{\kappa} \neq \kappa_s$, both the sheet and the substrate will be deformed and an optimal curvature, κ^* , will be selected. Gradients in κ_s will lead to net forces and torques on the sheet. Different dimensionless numbers, equivalent to $\bar{O}$ and $\bar{O}$ could be computed for such a system, based on the form of the substrate energy. An important example of such a mode of locomotion is possibly that of cells and small tissue fragments [4] that are observed to move [1,3] and orient themselves [2,4] in correlation with the substrate’s curvature. We suggest that the formalism presented here provides tools for a quantitative study and analysis of such curvotaxis phenomena.

The locomotive principle presented in this work is in action even for infinitely rigid substrates. In such a case, the energy of the system is composed only of the elastic, bending, and stretching of the sheet. Surprisingly, the elastic term alone converts gradients in κ_s into forces and torques on the sheet, despite the fact that in such cases all forces are locally normal to the sheet. Locomotion driven by curvature incompatibility is, therefore, a general phenomenon that can occur in different physical and biological systems. It has a broad range of pa-

rameters that can lead to various types of dynamics. Our work calls for further study of the interesting phenomena associated with this type of motion.

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Data availability. The data that support the findings of this article are not publicly available. The data are available from the authors upon reasonable request.

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