Geometry and dynamics of lipid membranes
Supplemental Material

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Contents

I. Theoretical Considerations

In this section, we summarize our past work [1], and use an irreversible thermodynamic framework to determine the equations governing a single-component, area-incompressible lipid membrane. We first describe the geometry and kinematics of an arbitrarily curved and deforming two-dimensional membrane surface. Next, the local balances of mass, linear momentum, and angular momentum are provided. The membrane stresses are determined via an irreversible thermodynamic analysis, and substituted into the linear momentum balance to yield the governing equations of motion.

1. A geometric and kinematic description

We model a lipid membrane as a single differentiable manifold about the membrane mid-plane, implicitly assuming no slip between the two bilayer leaflets. The geometry of arbitrarily curved surfaces is described in detail in several classical texts [2,3] as well as our previous work [1]; only relevant details are presented here. For a general description of the kinematics of lipid membranes, see Ref. [1, Sec. II].

The position $\boldsymbol{x}$ of the membrane surface is parametrized by two general coordinates, θ^1 and θ^2, and is a function of time t. We prescribe Greek indices to span the set $\{1, 2\}$, such that the position field is written as $\boldsymbol{x} = \boldsymbol{x}(\theta^\alpha, t)$. At any point $\boldsymbol{x}$, the surface parametrization induces the vectors $\boldsymbol{a}_\alpha := \partial \boldsymbol{x}/\partial\theta^\alpha = \boldsymbol{x}_{,\alpha}$, where $(\,\cdot\,)_{,\alpha}$ is used to denote partial differentiation with respect to θ^α. The set $\{\boldsymbol{a}_\alpha\}$ spans the tangent plane to the surface at the point $\boldsymbol{x}$. The unit normal $\boldsymbol{n}$ to the tangent plane is calculated as $\boldsymbol{n} := (\boldsymbol{a}_1 \times \boldsymbol{a}_2)/|\boldsymbol{a}_1 \times \boldsymbol{a}_2|$. Any vector $\boldsymbol{u} \in \mathbb{R}^3$ can be decomposed in the $\{\boldsymbol{a}_\alpha, \boldsymbol{n}\}$ basis as $\boldsymbol{u} = u^\alpha \boldsymbol{a}_\alpha + u\,\boldsymbol{n}$, where here and from now on we use the Einstein summation convention, in which indices repeated in a subscript and superscript are summed over.

Distances on the membrane surface are characterized by the covariant metric $a_{\alpha\beta} := \boldsymbol{a}_\alpha \cdot \boldsymbol{a}_\beta$. The contravariant metric, $a^{\alpha\beta}$, is the matrix inverse of the covariant metric. The covariant and contravariant metric components lower and raise indices, respectively, so for example $u_\alpha = a_{\alpha\beta}\, u^\beta$, $u^\alpha = a^{\alpha\beta} u_\beta$, and $\boldsymbol{a}^\alpha = a^{\alpha\beta}\boldsymbol{a}_\beta$. The covariant curvature components $b_{\alpha\beta}$ are calculated as $b_{\alpha\beta} := \boldsymbol{n} \cdot \boldsymbol{x}_{,\alpha\beta}$. The mean curvature H and Gaussian curvature K are given by $H := \frac{1}{2} a^{\alpha\beta} b_{\alpha\beta}$ and $K := \det(b_{\alpha\beta})/\det(a_{\alpha\beta})$, and are related to the principal surface curvatures κ_1 and κ_2 according to $H = (\kappa_1 + \kappa_2)/2$ and $K = \kappa_1\kappa_2$.

The covariant derivative with respect to θ^β, denoted $(\,\cdot\,)_{;\beta}$, produces quantities which transform tensorially under a change of basis: $u^\alpha_{;\beta}$ transforms as tensor components while $u^\alpha_{,\beta}$ does not. The covariant derivative of the vector components u^α with respect to θ^β is given by $u^\alpha_{;\beta} := u^\alpha_{,\beta} + \Gamma^\alpha_{\beta\mu} u^\mu$, where the Christoffel symbols of the second kind, $\Gamma^\alpha_{\beta\mu}$, are given by $\Gamma^\alpha_{\beta\mu} := \frac{1}{2} a^{\alpha\delta}(a_{\delta\beta,\mu} + a_{\delta\mu,\beta} - a_{\beta\mu,\delta})$.

The material time derivative $\mathrm{d}(\,\cdot\,)/\mathrm{d}t$ describes how a quantity associated with a material point changes in time. The membrane velocity $\boldsymbol{v}$ is given by $\boldsymbol{v} := \mathrm{d}\boldsymbol{x}/\mathrm{d}t = \dot{\boldsymbol{x}}$, and is expanded in the $\{\boldsymbol{a}_\alpha, \boldsymbol{n}\}$ basis as $\boldsymbol{v} = v^\alpha \boldsymbol{a}_\alpha + v\,\boldsymbol{n}$. The coordinates θ^α are chosen such that $v\,\boldsymbol{n} = (\partial\boldsymbol{x}/\partial t)|_{\theta^\alpha} = \boldsymbol{x}_{,t}$, i.e. such that a point of constant θ^α only moves in the normal direction. For notational convenience, we introduce the quantities ${w_\alpha}^\beta := v^\beta_{;\alpha} - v\, b_{\alpha\beta}$ and $w_\alpha := v^\beta b_{\alpha\beta} + v_{,\alpha}$, such that the acceleration $\dot{\boldsymbol{v}}$ is given by $\dot{\boldsymbol{v}} = (v_{,t} + v^\alpha w_\alpha)\,\boldsymbol{n} + (v^\alpha_{,t} - v\, w^\alpha + v^\beta {w_\beta}^\alpha)\,\boldsymbol{a}_\alpha$.

2. The balance laws

We now provide a brief summary of the balance law formulation developed in Refs. [1,4] to describe the dynamics of arbitrarily curved and deforming, single-component, incompressible lipid membranes. We obtain the four equations which can be used to solve for the four unknowns in the governing equations—namely, the surface tension and three components of the membrane velocity.

The balance of mass

As lipid membranes can only stretch 2–3% before tearing [5,6], we model them as being area-incompressible, such that their areal mass density ρ is constant. In this case, a mass balance indicates the surface divergence of the membrane velocity is zero, which is written as

$$v^\alpha_{;\alpha} - 2vH = 0\ . \tag{1}$$

Equation (1) is also called the continuity equation or the incompressibility constraint, and is enforced with the Lagrange multiplier $\lambda = \lambda(\theta^\alpha, t)$, which is physically interpreted as the surface tension of the membrane.

The balance of linear momentum

Lipid membranes are acted upon by body forces $\boldsymbol{b}$ on the membrane surface and tractions $\boldsymbol{T}$ on the membrane boundary. As shown in the seminal work on elastic shells by P.M. Naghdi [7], the tractions can be decomposed into stress vectors $\boldsymbol{T}^\alpha$ across curves of constant θ^α, such that the linear momentum balance for a lipid membrane is given by

$$\rho \dot{\boldsymbol{v}} = \rho \boldsymbol{b} + \boldsymbol{T}^\alpha_{;\alpha} \ . \tag{2}$$

The last term in Eq. (2) is analogous to the divergence of the stress tensor in standard continuum mechanics, and describes how stresses applied on the lipid membrane boundary are transmitted through the membrane.

Without loss of generality, the stress vectors $\boldsymbol{T}^\alpha$ can be decomposed in the $\{\boldsymbol{a}_\alpha, \boldsymbol{n}\}$ basis as

$$\boldsymbol{T}^\alpha = N^{\alpha\beta} \boldsymbol{a}_\beta + S^\alpha \boldsymbol{n} \ , \tag{3}$$

where $N^{\alpha\beta}$ are the in-plane stress components and S^α are the out-of-plane shear forces. Substituting Eq. (3) into Eq. (2), using the geometric identities $\boldsymbol{a}_{\beta;\alpha} = b_{\alpha\beta}\, \boldsymbol{n}$ and $\boldsymbol{n}_{;\alpha} = -b^\beta_\alpha\, \boldsymbol{a}_\beta$, and splitting the equation into in-plane and out-of-plane components yields

$$\rho \dot{\boldsymbol{v}} \cdot \boldsymbol{a}^\alpha = \rho b^\alpha + N^{\beta\alpha}_{;\beta} - S^\beta b^\alpha_\beta \tag{4}$$

and

$$\rho \dot{\boldsymbol{v}} \cdot \boldsymbol{n} = p + S^\alpha_{;\alpha} + N^{\alpha\beta} b_{\alpha\beta} \ , \tag{5}$$

where $p = \rho \boldsymbol{b} \cdot \boldsymbol{n}$ is the pressure drop across the membrane surface and $b^\alpha = \rho \boldsymbol{b} \cdot \boldsymbol{a}^\alpha$ are the in-plane body forces. Equations (4) and (5) already show the in-plane and out-of-plane coupling: the in-plane stresses $N^{\alpha\beta}$ couple to the curvature components to give rise to out-of-plane forces, while the out-of-plane shear forces S^α couple to the curvature components and lead to in-plane forces.

The in-plane (4) and shape (5) equations, along with the continuity equation (1), are the four equations governing the evolution of the surface tension and three components of the membrane velocity. However, the functional forms of $N^{\alpha\beta}$ and S^α are not yet determined, and require constitutive laws—which will be determined in the forthcoming sections.

The balance of angular momentum

Moments applied at the membrane boundary are transmitted through the membrane, and captured in the couple–stress components $M^{\alpha\beta}$. A comprehensive description of the angular momentum balance of a material surface is presented in Ref. [7], and those parts appropriate for lipid membranes are summarized in our past work [1]. From an angular momentum balance, we find

$$\sigma^{\alpha\beta} := \left(N^{\alpha\beta} - b^\beta_\mu M^{\mu\alpha} \right) \quad \text{is symmetric} \ , \qquad \text{and} \qquad S^\alpha = -M^{\beta\alpha}_{;\beta} \ . \tag{6}$$

In Eq. (6), $\sigma^{\alpha\beta}$ are the couple-free in-plane stress components, and the second condition is a familiar result from solid mechanics: gradients of moments lead to shear forces. With Eq. (6), we can express the stress vectors (3), and thus the components of the linear momentum balance (4, 5), in a suitable form if $\sigma^{\alpha\beta}$ and $M^{\alpha\beta}$ are known in terms of the fundamental unknowns.

3. The results from irreversible thermodynamics

At this point, we have not yet prescribed the constitutive behavior of the surface under consideration, and $\sigma^{\alpha\beta}$ and $M^{\alpha\beta}$ remain unknown. As discussed in our previous work [1], the theory of irreversible thermodynamics can be used to determine the forms of $\sigma^{\alpha\beta}$ and $M^{\alpha\beta}$ for a variety of two-dimensional materials. We now summarize the developments of Ref. [1], in which the constitutive behavior of lipid membranes is obtained by requiring curvature changes to be elastic and in-plane flows to be irreversible. We begin by positing the existence of a Helmholtz free energy density $\psi = \psi(a_{\alpha\beta}, b_{\alpha\beta}, T)$, where T is the membrane temperature, and find

$$\sigma^{\alpha\beta} = \rho\left(\frac{\partial\psi}{\partial a_{\alpha\beta}} + \frac{\partial\psi}{\partial a_{\beta\alpha}}\right) + \pi^{\alpha\beta} \tag{7}$$

and

$$M^{\alpha\beta} = \frac{\rho}{2}\left(\frac{\partial\psi}{\partial b_{\alpha\beta}} + \frac{\partial\psi}{\partial b_{\beta\alpha}}\right) + \omega^{\alpha\beta} \ . \tag{8}$$

In Eqs. (7) and (8), the first terms on the right-hand side are the elastic components of the stresses and couple-stresses, while $\pi^{\alpha\beta}$ and $\omega^{\alpha\beta}$ are the stress components due to irreversible behavior. As lipid membranes bend elastically, curvature changes are reversible and $\omega^{\alpha\beta} = 0$. The irreversible in-plane flow of lipids leads to viscous stresses, which in the linear irreversible regime are given by $\pi^{\alpha\beta} = \zeta\, \dot{a}_{\mu\nu}\, a^{\alpha\mu}\, a^{\beta\nu}$ for an incompressible surface. Here ζ is the two-dimensional in-plane viscosity, with units of force $\cdot$ time/length, or equivalently mass/time [1, Sec. III.C.1].

(a). The choice of Helmholtz free energy

By specifying the form of the Helmholtz free energy density ψ, we determine $\sigma^{\alpha\beta}$ and $M^{\alpha\beta}$ through Eqs. (7) and (8), respectively. However, for a single-component, area-incompressible lipid membrane, the Helmholtz free energy density does not depend on all components of $a_{\alpha\beta}$ and $b_{\alpha\beta}$. Rather, ψ depends only on the mean curvature H, Gaussian curvature K, and membrane density ρ. For mathematical convenience, we define $\bar{\psi}(\rho, H, K, T) := \psi(a_{\alpha\beta}, b_{\alpha\beta}, T)$; in the case of the lipid membranes under consideration, the Helmholtz free energy is given by

$$\rho\bar{\psi} = k_{\mathrm{b}} H^2 + k_{\mathrm{g}} K + \lambda\left(1 - \frac{\rho}{\rho_0}\right) \ , \tag{9}$$

where k_{b} and k_{g} are the mean and Gaussian bending moduli, ρ_0 is the membrane density in the reference configuration, and λ is a Lagrange multiplier enforcing the incompressibility constraint $\rho = \rho_0$. The constraint $\rho = \rho_0$ is equivalent to Eq. (1), as (see Ref. [1]) $\dot{\rho} = -\rho\,(v^{\alpha}_{;\alpha} - 2vH)$. In Eq. (9), the first two terms energetically penalize lipid membrane bending, as originally put forth by P. Canham [8], W. Helfrich [9], and E. A. Evans [10].

(b). The equations of motion

By substituting the Helmholtz free energy density (9) into Eqs. (7) and (8), calculating $N^{\alpha\beta}$ and S^{α} from Eq. (6), and substituting the result and the acceleration into Eqs. (4) and (5), we obtain the equations of motion. The in-plane equations of motion are given by

$$\begin{aligned}\rho\Big(v^{\alpha}_{,t} - v\, w^{\alpha} + v^{\beta} w_{\beta}{}^{\alpha}\Big) &= \big(\lambda\, a^{\alpha\beta} + \pi^{\beta\alpha}\big)_{;\beta} \\ &= a^{\alpha\beta}\lambda_{,\beta} + \zeta\Big(\Delta v^{\alpha} + K v^{\alpha} + 2\big(v_{,\beta} H - v H_{,\beta}\big)a^{\alpha\beta} - 2b^{\alpha\beta} v_{,\beta}\Big) \ ,\end{aligned} \tag{10}$$

where in-plane body forces ρb^{α} are neglected and $\Delta(\,\cdot\,) := a^{\alpha\beta}(\,\cdot\,)_{;\alpha\beta}$ is the surface Laplacian. We note that for any Helmholtz free energy density depending only on ρ, H, K, and T, no bending forces enter the in-plane equations (10) despite the coupling observed in Eqs. (4) and (5). Equation (10) is the surface analog of the Navier–Stokes equations, in which the pressure is replaced by the negative surface tension. The first term on the right-hand side of Eq. (10) describes in-plane forces due to gradients in tension, while all terms involving the viscosity coefficient ζ are the in-plane viscous forces. The additional viscosity terms, beyond the surface Laplacian of v^{α}, arise due to nonzero membrane curvatures—indicating the coupling between geometry and viscous forces.

The out-of-plane equation, also called the shape equation, is given by

$$\begin{aligned}\rho\Big(v_{,t} + v^{\alpha} w_{\alpha}\Big) &= p + \ \big(\lambda\, a^{\alpha\beta} + \pi^{\alpha\beta}\big) b_{\alpha\beta} - 2\, k_{\mathrm{b}}\, H\big(H^2 - K\big) - k_{\mathrm{b}}\, \Delta_{\mathrm{s}} H \\ &= p + 2\,\lambda\, H + 2\,\zeta\,\Big(b^{\alpha\beta} v_{\alpha;\beta} - 2v\big(2H^2 - K\big)\Big) - 2\, k_{\mathrm{b}}\, H\big(H^2 - K\big) - k_{\mathrm{b}}\, \Delta_{\mathrm{s}} H \ .\end{aligned} \tag{11}$$

In the case of a static membrane ($\boldsymbol{v} = \boldsymbol{0}$) and no mean bending modulus ($k_{\mathrm{b}} = 0$), the shape equation simplifies to the Young–Laplace equation: $p + 2\lambda H = 0$. The quantities in Eq. (11) containing k_{b} arise from the Naghdi–Helfrich bending energy (9), and the $k_{\mathrm{b}}\Delta_{\mathrm{s}}H$ term contains four derivatives of the membrane position—which are the gradients of the shear forces found in standard beam bending problems. The quantity multiplied by the in-plane viscosity ζ in the second line of the shape equation (11), which can be equivalently written as $\pi^{\alpha\beta}b_{\alpha\beta}$, is the contraction of the in-plane viscous stresses $\pi^{\alpha\beta}$ with the curvature components $b_{\alpha\beta}$—and demonstrates how the in-plane and out-of-plane equations are coupled through curvature. It is the ratio of $\pi^{\alpha\beta}b_{\alpha\beta}$ to the elastic bending forces that leads to the new dimensionless Scriven–Love number SL, while the ratio of tension to bending forces leads to the well-known Föppl–von Kármán number Γ [11]. In the subsequent sections, we determine and non-dimensionalize the unperturbed and perturbed governing equations in flat, spherical, and cylindrical geometries.

II. Flat Membrane Patches

We begin by studying nearly planar lipid membranes. First, the unperturbed and perturbed governing equations are presented. The equations are then non-dimensionalized for (i) an initially static planar membrane with no flow and (ii) a flat membrane which initially has an in-plane flow. In both cases, the Föppl–von Kármán number determines the relative importance of surface tension and bending in governing the membrane's dynamical response to a shape perturbation. For a membrane with an initial in-plane flow, the Scriven–Love number quantifies the relative importance of viscous forces in the normal direction and bending forces.

1. The general unperturbed governing equations

The position of a perfectly flat lipid membrane patch is parametrized by the coordinates $\theta^1 = x$ and $\theta^2 = y$, and given by

$$\boldsymbol{x}_{(0)}(x, y) = x\,\boldsymbol{e}_x + y\,\boldsymbol{e}_y \;, \tag{12}$$

where as in the main text a subscript or superscript '(0)' denotes an unperturbed quantity. As shown in Fig. 1(a) in the main text, x and y range from 0 to L, the characteristic length scale of the patch. With the results of Sec. I.I.1, we find

$$\begin{aligned}
&\boldsymbol{a}_\alpha^{(0)} = \boldsymbol{e}_\alpha \;, \qquad && a_{\alpha\beta}^{(0)} = \delta_{\alpha\beta} \;, \qquad && a^{\alpha\beta}_{(0)} = \delta^{\alpha\beta} \;, \qquad && && \boldsymbol{n}_{(0)} = \boldsymbol{e}_z \;, \\
&b_{\alpha\beta}^{(0)} = 0 \;, && H_{(0)} = 0 \;, && K_{(0)} = 0 \;, && \text{and} && \Gamma^{\alpha\,(0)}_{\lambda\mu} = 0 \;,
\end{aligned} \tag{13}$$

where $\delta_{\alpha\beta}$ and $\delta^{\alpha\beta}$ denote the Kronecker delta. Furthermore, for a perfectly flat plane the normal velocity $v_{(0)} = 0$, and therefore the velocity $\boldsymbol{v}$ is given by

$$\boldsymbol{v}_{(0)} \;=\; v^\alpha_{(0)}\boldsymbol{e}_\alpha \;=\; v^x_{(0)}\boldsymbol{e}_x \;+\; v^y_{(0)}\boldsymbol{e}_y \;. \tag{14}$$

In this case, the continuity (1), in-plane (10), and shape (11) equations are given respectively by

$$v^\alpha_{(0),\alpha} \;=\; 0 \;, \tag{15}$$

$$\rho\big(\,v^\alpha_{(0),t} \;+\; v^\beta_{(0)}\,v^\alpha_{(0),\beta}\,\big) \;=\; \delta^{\alpha\beta}\lambda_{(0),\beta} \;+\; \zeta\,\big(v^\alpha_{(0),xx} \;+\; v^\alpha_{(0),yy}\big) \;, \tag{16}$$

and

$$p \;=\; 0 \;. \tag{17}$$

The continuity equation (15) and in-plane equations (16) are identical to the continuity and Navier–Stokes equations of an incompressible two-dimensional Newtonian fluid, in which the pressure is replaced with the negative surface tension. The shape equation (17) indicates that for a perfectly flat membrane there are no out-of-plane viscous, surface tension, or bending forces.

2. The general perturbed governing equations

A height perturbation is now introduced in the normal direction, such that the membrane position is given by

$$\boldsymbol{x}(x,y,t) \;=\; x\,\boldsymbol{e}_x \,+\, y\,\boldsymbol{e}_y \,+\, \epsilon\,\tilde{h}(x,y,t)\,\boldsymbol{e}_z \;, \tag{18}$$

where ϵ is a small parameter. The height perturbation modifies the geometry of the surface, and to first order in ϵ we find

$$\begin{aligned} &\boldsymbol{a}_\alpha \;=\; \boldsymbol{e}_\alpha \,+\, \epsilon\,\tilde{h}_{,\alpha}\,\boldsymbol{e}_z \;, \qquad a_{\alpha\beta} \;=\; \delta_{\alpha\beta} \;, \qquad \boldsymbol{n} \;=\; \boldsymbol{e}_z - \epsilon\,\tilde{h}_{,\alpha}\,\boldsymbol{e}_\alpha \;, \qquad b_{\alpha\beta} \;=\; \epsilon\,\tilde{h}_{,\alpha\beta} \;, \\ &\Gamma^\alpha_{\lambda\mu} \;=\; 0 \;, \qquad H \;=\; \frac{1}{2}\,\epsilon\,\Delta_{\mathrm{s}}\,\tilde{h} \;, \qquad \text{and} \qquad K \;=\; 0 \;, \end{aligned} \tag{19}$$

where for a flat plane the surface Laplacian of a scalar quantity is given by $\Delta_{\mathrm{s}}\,(\,\cdot\,) = (\,\cdot\,)_{,xx} + (\,\cdot\,)_{,yy}$, namely the two-dimensional Cartesian Laplacian. The in-plane velocities, normal velocity, and surface tension are similarly expanded as

$$v^\alpha = v^\alpha_{(0)} + \epsilon\,\tilde{v}^\alpha \;, \qquad v = \epsilon\,\tilde{h}_{,t} \;, \qquad \text{and} \qquad \lambda = \lambda_{(0)} + \epsilon\,\tilde{\lambda} \;. \tag{20}$$

In Eq. (20), quantities with a 'tilde' accent are assumed to be of the same order as their unperturbed counterparts. For example, $v^\alpha_{(0)}$ and $\tilde{v}^\alpha$ are both the same order, and the smallness of the velocity perturbation is contained in ϵ. In Eq. $(20)_2$, the normal velocity component v is calculated according to $v = \boldsymbol{x}_{,t}\cdot\boldsymbol{n}$ (see Sec. I.I.1). Substituting Eqs. (19) and (20) into Eqs. (1), (10), and (11) and keeping terms of first order in ϵ, the first-order perturbed equations are obtained as

$$\tilde{v}^\alpha_{,\alpha} = 0 \;, \tag{21}$$

$$\rho\big(\,\tilde{v}^\alpha_{,t} \,+\, \tilde{v}^\beta\,v^\alpha_{(0),\beta} \,+\, v^\beta_{(0)}\,\tilde{v}^\alpha_{,\beta}\,\big) \;=\; \delta^{\alpha\beta}\,\tilde{\lambda}_{,\beta} \,+\, \zeta\,\big(\tilde{v}^\alpha_{,xx} \,+\, \tilde{v}^\alpha_{,yy}\big) \;, \tag{22}$$

and

$$\rho\big(\,\tilde{h}_{,tt} \,+\, v^\alpha_{(0)}\,v^\beta_{(0)}\,\tilde{h}_{,\alpha\beta} \,+\, v^\alpha_{(0)}\,\tilde{h}_{,t\alpha}\,\big) \;=\; 2\,\zeta\,\tilde{h}_{,\alpha\lambda}\,\delta^{\lambda\beta}\,v^\alpha_{(0),\beta} \,-\, \frac{1}{2}\,k_{\mathrm{b}}\,\Delta^2_{\mathrm{s}}\,\tilde{h} \,+\, \lambda_{(0)}\,\Delta_{\mathrm{s}}\,\tilde{h} \;. \tag{23}$$

Equation (23) indicates velocity gradients in the base state ($v^\alpha_{(0),\beta} \neq 0$) lead to viscous forces in the normal direction, and bring about the Scriven–Love number. In the remainder of this section, the unperturbed (15)–(17) and perturbed (21)–(23) governing equations are non-dimensionalized for an initially static membrane, and a membrane with an initial base flow.

3. The case of an initially static flat patch: non-dimensionalization

We first non-dimensionalize the unperturbed and perturbed governing equations in the case of an initially flat, static lipid membrane, for which $\boldsymbol{v}_{(0)} = \boldsymbol{0}$. According to Eqs. (15)–(17), $\lambda_{(0)}$ is a constant, which we denote λ_0 and assume to be known from how the membrane patch is constrained at its boundary. The unperturbed solution is written as

$$v^\alpha_{(0)} = 0 \;, \qquad v_{(0)} = 0 \;, \qquad \text{and} \qquad \lambda_{(0)} = \lambda_0 \;. \tag{24}$$

We introduce the surface tension scale Λ as

$$\Lambda := \lambda_0 \;, \tag{25}$$

and assume the size of the patch L sets the characteristic length over which perturbed quantities vary. However, the unperturbed solution does not set a characteristic time or velocity scale, which are instead determined by non-dimensionalizing the perturbed equations.

Substituting the unperturbed solution (24) into the perturbed equations (21)–(23) yields

$$\tilde{v}^\alpha_{,\alpha} = 0 \;, \tag{26}$$

$$\rho\,\tilde{v}^\alpha_{,t} \;=\; \delta^{\alpha\beta}\,\tilde{\lambda}_{,\beta} \,+\, \zeta\,\big(\tilde{v}^\alpha_{,xx} \,+\, \tilde{v}^\alpha_{,yy}\big) \;, \tag{27}$$

and

$$\rho\,\tilde{h}_{,tt} \;=\; -\,\frac{1}{2}\,k_{\mathrm{b}}\,\Delta_{\mathrm{s}}^{2}\,\tilde{h} \;+\; \lambda_0\,\Delta_{\mathrm{s}}\,\tilde{h}~. \tag{28}$$

Note that in a flat geometry with no initial flow, viscous forces do not arise in the shape equation (28) and so the Scriven–Love number will not appear when the equations are non-dimensionalized.

The perturbation in the normal direction, $\epsilon\,\tilde{h}$, is prescribed to be of a length scale Z such that $\epsilon\,\tilde{h}/Z$ is $O(1)$, where $\epsilon := Z/L \ll 1$ is a small parameter and $\tilde{h}$ is $O(L)$. An initial perturbation is assumed to relax over a time scale τ, such that $\tilde{h}_{,t}$ is $O(L/\tau)$. Moreover, the out-of-plane perturbation induces in-plane flows of a characteristic velocity, denoted V, which vary in-plane over the length scale L, such that $\tilde{v}^{\alpha}$ is $O(V)$ and $\tilde{v}^{\alpha}_{,\beta}$ is $O(V/L)$. Finally, $\tilde{\lambda}$ is assumed to be $O(\Lambda)$, where Λ is known (see Eq. (25)). Corresponding dimensionless quantities are then defined as

$$x^* := \frac{x}{L}~, \qquad y^* := \frac{y}{L}~, \qquad \tilde{h}^* := \frac{\tilde{h}}{L}~, \qquad \tilde{v}^{\alpha *} := \frac{\tilde{v}^{\alpha}}{V}~, \qquad \tilde{\lambda}^* := \frac{\tilde{\lambda}}{\Lambda}~, \qquad \text{and} \qquad t^* := \frac{t}{\tau}~, \tag{29}$$

and are all $O(1)$. We now seek to determine V and τ from a scaling analysis of the perturbed equations.

We first substitute Eq. (29) into Eq. (26) to obtain the dimensionless perturbed continuity equation as

$$\tilde{v}^{\alpha *}_{,\alpha^*} \;=\; 0~. \tag{30}$$

Moreover, as the general continuity equation (1) couples in-plane height deformations with in-plane velocity gradients, we assume the time scale τ and velocity scale V are related by

$$\tau \;=\; \frac{L}{V}~. \tag{31}$$

Next, the in-plane equations (27) are considered. Substituting Eq. (29) into Eq. (27) yields

$$\frac{\rho\,V}{\tau}\;\tilde{v}^{\alpha *}_{,t^*} \;=\; \frac{\Lambda}{L}\;\delta^{\alpha^*\beta^*}\;\tilde{\lambda}^*_{,\beta^*} \;+\; \frac{\zeta\,V}{L^2}\left(\tilde{v}^{\alpha *}_{,x^*x^*} \;+\; \tilde{v}^{\alpha *}_{,y^*y^*}\right)~, \tag{32}$$

which upon substitution of Eq. (31) and rearrangement of terms yields

$$Re\;\tilde{v}^{\alpha *}_{,t^*} = \frac{\Lambda L}{\zeta V}\,\delta^{\alpha^*\beta^*}\;\tilde{\lambda}^*_{,\beta^*} + \tilde{v}^{\alpha *}_{,x^*x^*} + \tilde{v}^{\alpha *}_{,y^*y^*}~, \tag{33}$$

where the Reynolds number Re is defined as

$$Re \;:=\; \frac{\rho\,V L}{\zeta}~. \tag{34}$$

For biological lipid membranes, inertial terms are generally negligible ($Re \ll 1$); the surface tension and velocity terms in Eq. (32) are assumed to balance such that, combined with Eq. (31), we find

$$V \;=\; \frac{L\,\Lambda}{\zeta} \qquad\quad \text{and} \qquad\quad \tau \;=\; \frac{\zeta}{\Lambda}~. \tag{35}$$

Given the scaling in Eq. (35), we check to see if inertial terms are negligible, as was previously assumed. For lipid membranes, $\rho \sim 10^{-8}$ pg/nm^2 [12], $\zeta \sim 10$ pN$\cdot\mu$sec/nm [13], and we consider patches with a characteristic length $L \sim 10^2$–10^3 nm. As discussed in the main text, surface tensions are in the range $\Lambda \sim 10^{-4}$–10^{-1} pN/nm [14, 15], for which Re (34) ranges from 10^{-10} to 10^{-5} and is indeed negligible. The in-plane equations (33) then simplify to

$$\tilde{v}^{\alpha *}_{,x^*x^*} \,+\, \tilde{v}^{\alpha *}_{,y^*y^*} \,+\, \delta^{\alpha^*\beta^*}\;\tilde{\lambda}^*_{,\beta^*} \;=\; 0~. \tag{36}$$

Finally, the perturbed shape equation is analyzed. Substituting Eq. (29) into Eq. (28) yields

$$\frac{\rho\,L}{\tau^2}\;\tilde{h}^*_{,t^*t^*} \;=\; -\,\frac{1}{2}\;\frac{k_{\mathrm{b}}}{L^3}\;(\Delta^*_{\mathrm{s}})^2\,\tilde{h}^* \;+\; \frac{\Lambda}{L}\;\Delta^*_{\mathrm{s}}\,\tilde{h}^*~, \tag{37}$$

which consists of inertial, bending, and tension terms, respectively. We define the Föppl–von Kármán number Γ to be the ratio of tension to bending terms, given by

$$\Gamma := \frac{\Lambda L^2}{k_{\mathrm{b}}} \ . \tag{38}$$

With Eq. (38) and the definition of the Reynolds number (34), Eq. (37) can be rewritten as

$$Re\,\Gamma\ \tilde{h}^*_{,t^*t^*} \ = \ -\frac{1}{2}\,(\Delta^*_{\mathrm{s}})^2\,\tilde{h}^* \ + \ \Gamma\,\Delta^*_{\mathrm{s}}\,\tilde{h}^* \ . \tag{39}$$

For lipid and biological membranes, $k_{\mathrm{b}} \sim 100$ pN·nm [14]. Given the previously mentioned values of $\rho \sim 10^{-8}$ pg/nm^2 [12] and $\zeta \sim 10$ pN·μsec/nm [13], as well as the values of $L \sim 10^2$–10^3 nm and $\Lambda \sim 10^{-4}$–10^{-1} pN/nm from our analysis of various experiments (see Tables I and II in the main text), we find $\Gamma \sim 10^{-2}$–10^3 and $Re\,\Gamma = \rho\Lambda^2 L^4/(\zeta^2 k_{\mathrm{b}}) \sim 10^{-12}$–$10^{-2} \ll 1$, for which Eq. (39) simplifies to

$$\Gamma\,\Delta^*_{\mathrm{s}}\,\tilde{h}^* - \frac{1}{2}\,(\Delta^*_{\mathrm{s}})^2\,\tilde{h}^* = 0 \ . \tag{40}$$

The dimensionless continuity, in-plane, and shape equations are given respectively by Eqs. (30), (36), and (40), and are presented as Eqs. (10)–(13) in the main text.

4. The case of a flat patch with a base flow: non-dimensionalization

We next consider a planar membrane with some initial nontrivial in-plane flow ($v^{\alpha}_{(0),\beta} \neq 0$) satisfying the unperturbed equations (15)–(17). The initial in-plane flow sets the characteristic velocity scale V, and as before the base state sets the surface tension scale Λ as well as the length scale L over which shape changes occur. When non-dimensionalizing the perturbed shape equation, the competition between viscous forces and bending forces gives rise to the Scriven–Love number SL; the competition between tension and bending forces leads to the Föppl–von Kármán number Γ, as in the initially static case.

(a). The unperturbed equations

Assuming a known characteristic in-plane velocity scale V, where velocities vary from 0 to V over a length scale L, along with a known surface tension scale Λ, we non-dimensionalize the unperturbed quantities in the base state according to

$$x^* = \frac{x}{L} \ , \qquad y^* = \frac{y}{L} \ , \qquad v^{\alpha *}_{(0)} := \frac{v^{\alpha}_{(0)}}{V} \ , \qquad \text{and} \qquad \lambda^*_{(0)} := \frac{\lambda_{(0)}}{\Lambda} \ . \tag{41}$$

Substituting Eq. (41) into the unperturbed governing equations (15)–(17) yields

$$v^{\alpha *}_{(0),\alpha^*} = 0 \ , \tag{42}$$

$$Re\,v^{\beta *}_{(0)}\,v^{\alpha *}_{(0),\beta^*} \ = \ \frac{\Lambda L}{\zeta V}\ \delta^{\alpha^*\beta^*}\,\lambda^*_{(0),\beta^*} + \ v^{\alpha *}_{(0),x^*x^*} + \ v^{\alpha *}_{(0),y^*y^*} \ , \tag{43}$$

and

$$p = 0 \ , \tag{44}$$

where in Eq. (43) we assume the base flow is at steady state, such that $v^{\alpha}_{(0),t} = 0$. For the biological systems of interest [16,17], the length scale L ranges from 100–1000 nm, the velocity scale V ranges from 10^{-6}–10^{-3} nm/μsec (equivalently 10^{-3}–1 μm/sec), and surface tensions range from 10^{-4}–10^{-1} pN/nm [14–17]. For such characteristic values, Re (34) ranges from 10^{-13} to 10^{-9} and $\zeta V/(\Lambda L)$ ranges from 10^{-7} to 1. Accordingly, inertial terms are neglected in Eq. (43), which simplifies to

$$\frac{\zeta V}{\Lambda L}\Big(v^{\alpha *}_{(0),x^*x^*} + \ v^{\alpha *}_{(0),y^*y^*}\Big) + \ \delta^{\alpha^*\beta^*}\,\lambda^*_{(0),\beta^*} \ = \ 0 \ , \tag{45}$$

When $\zeta V/(\Lambda L) \ll 1$, the tension term dominates Eq. (45), such that $\lambda^*_{(0)}$ is constant and $v^{\alpha *}_{(0),x^*x^*} + v^{\alpha *}_{(0),y^*y^*} = 0$—as is the case in the Couette flow example considered in the main text.

(b). The perturbed equations

Suppose all perturbed quantities vary over the length scale L set by the base state, such that dimensionless perturbed quantities are given by Eq. (29), as was the case for an initially static membrane. Substituting Eq. (29) into the perturbed continuity (21) and in-plane (22) equations yields

$$\tilde{v}^{\alpha *}_{,\alpha^*} = 0 \tag{46}$$

and

$$\delta^{\alpha^*\beta^*}\,\tilde{\lambda}^*_{,\beta^*} + \frac{\zeta V}{\Lambda L}\left(\tilde{v}^{\alpha *}_{,x^*x^*} + \tilde{v}^{\alpha *}_{,y^*y^*}\right) = 0\ , \tag{47}$$

where we neglect inertial terms for simplicity. In the limit where $\zeta V/(\Lambda L) \ll 1$, as is the case for small V, the in-plane equations (47) reveal $\tilde{\lambda}^*_{,\beta^*} = 0$, for which $\tilde{\lambda}^* =$ constant. However, as discussed in the main text, when V tends to zero one must recover the corresponding initially static solution (36), which is not the case. Thus, the result $\tilde{\lambda}^* =$ constant is unphysical, and our assumption that all perturbed quantities vary over the length scale L is incorrect.

We next assume all perturbed quantities vary over some unknown length scale ℓ, which is to be determined via non-dimensionalization. In this case, we define

$$x' := \frac{x}{\ell}\ , \qquad y' := \frac{y}{\ell} \qquad \text{and} \qquad \Delta'_{\mathrm{s}}(\,\cdot\,) := \ell^2\,\Delta(\,\cdot\,)\ , \tag{48}$$

such that the dimensionless continuity (21) and in-plane (22) equations are given by

$$\tilde{v}^{\alpha *}_{,\alpha'} = 0 \tag{49}$$

and

$$\delta^{\alpha^*\beta'}\,\tilde{\lambda}^*_{,\beta'} + \frac{\zeta V}{\Lambda \ell}\left(\tilde{v}^{\alpha *}_{,x'x'} + \tilde{v}^{\alpha *}_{,y'y'}\right) = 0\ . \tag{50}$$

As in the previous example, we ignore inertial terms for simplicity. Given Eq. (50), we choose the length scale ℓ to be given by

$$\ell := \frac{\zeta V}{\Lambda}\ , \tag{51}$$

such that viscous and tension forces balance. The in-plane equations are then identical to their initially static counterparts (33). Next, the perturbed shape equation (23) is non-dimensionalized with Eqs. (29), (41), and (48), yielding

$$2\,\frac{\zeta V}{\ell^2}\,\tilde{h}^*_{,\alpha'\lambda'}\,\delta^{\lambda'\beta^*}\,v^{\alpha *}_{(0),\beta^*} - \frac{1}{2}\,\frac{k_{\mathrm{b}}L}{\ell^4}\,\Delta'^{\,2}_{\mathrm{s}}\,\tilde{h}^* + \frac{\Lambda L}{\ell^2}\,\lambda^*_{(0)}\,\Delta'_{\mathrm{s}}\,\tilde{h}^* = 0\ . \tag{52}$$

Substituting Eq. (51) into Eq. (52), rearranging terms, and defining

$$\ell^* := \frac{\ell}{L} = \frac{\zeta V}{\Lambda L} \tag{53}$$

for notational convenience, we obtain

$$\frac{\zeta^2 V^2}{k_{\mathrm{b}}\Lambda}\left(2\,\ell^*\,\tilde{h}^*_{,\alpha'\lambda'}\,\delta^{\lambda'\beta^*}\,v^{\alpha *}_{(0),\beta^*} + \lambda^*_{(0)}\,\Delta'_{\mathrm{s}}\,\tilde{h}^*\right) - \frac{1}{2}\,\Delta'^{\,2}_{\mathrm{s}}\,\tilde{h}^* = 0\ . \tag{54}$$

When V goes to zero, Eq. (54) simplifies to $\Delta'^{\,2}_{\mathrm{s}}\,\tilde{h}^* = 0$. However, in this limit, one must recover the initially static solution (40), which is again not the case. Thus, the assumption that all perturbed quantities vary over the length scale ℓ is also incorrect.

At this point, our two incorrect scaling attempts reveal (i) $\tilde{v}^\alpha$ and $\tilde{\lambda}$ must vary over the length scale ℓ (51), and (ii) $\tilde{h}$ cannot vary over ℓ. We therefore posit that $\tilde{h}$ varies over the patch length scale L, while $\tilde{v}^\alpha$ and $\tilde{\lambda}$ vary over ℓ. The first-order continuity equation (21) is then non-dimensionalized as

$$\tilde{v}^{\alpha *}_{,\alpha'} = 0\ . \tag{55}$$

The in-plane equations are non-dimensionalized by substituting Eqs. (29) and (48) into Eq. (22), yielding

$$\frac{\rho V^2}{\ell}\Big(\frac{\ell}{V\tau}\,\tilde{v}^{\alpha *}_{,t^*} \,+\, \frac{\ell}{L}\,\tilde{v}^{\beta *}\,v^{\alpha *}_{(0),\beta^*} \,+\, v^{\beta *}_{(0)}\,\tilde{v}^{\alpha *}_{,\beta'}\Big) \;=\; \frac{\Lambda}{\ell}\,\delta^{\alpha'\beta'}\,\tilde{\lambda}^*_{,\beta'} \,+\, \frac{\zeta V}{\ell^2}\Big(\tilde{v}^{\alpha *}_{,x'x'} \,+\, \tilde{v}^{\alpha *}_{,y'y'}\Big)\;. \tag{56}$$

In considering the inertial terms in Eq. (56), we first recognize $\ell/L = \zeta V/(\Lambda L)$, which was found in Sec. II.4 (a) to range from 10^{-7} to 1 over the experiments of interest. Accordingly, we choose the time scale τ to be given by

$$\tau = \frac{\ell}{V} = \frac{\zeta}{\Lambda}\;, \tag{57}$$

such that the first and third terms on the left-hand side of Eq. (56) are balanced. By substituting Eqs. (34), (51), (53), and (57) into Eq. (56) and rearranging terms, we obtain

$$Re\,\ell^*\,\Big(\tilde{v}^{\alpha *}_{,t^*} \,+\, \ell^*\,\tilde{v}^{\beta *}\,v^{\alpha *}_{(0),\beta^*} \,+\, v^{\beta *}_{(0)}\,\tilde{v}^{\alpha *}_{,\beta'}\Big) \;=\; \delta^{\alpha'\beta'}\,\tilde{\lambda}^*_{,\beta'} \,+\, \tilde{v}^{\alpha *}_{,x'x'} \,+\, \tilde{v}^{\alpha *}_{,y'y'}\;. \tag{58}$$

As $Re\,\ell^* \ll 1$ for the experimental systems under consideration (see Sec. II.4 (a)), inertial terms are negligible in Eq. (58), and the dimensionless perturbed in-plane equations are given by

$$\tilde{v}^{\alpha *}_{,x'x'} \,+\, \tilde{v}^{\alpha *}_{,y'y'} \,+\, \delta^{\alpha'\beta'}\,\tilde{\lambda}^*_{,\beta'} \;=\; 0\;. \tag{59}$$

Finally, we analyze the perturbed shape equation. Substituting Eqs. (29), (41), and (48) into Eq. (23) leads to

$$\rho\Big(\frac{L}{\tau^2}\,\tilde{h}^*_{,t^*t^*} + \frac{V^2}{L}\,v^{\alpha *}_{(0)}v^{\beta *}_{(0)}\tilde{h}^*_{,\alpha^*\beta^*} + \frac{V}{\tau}\,v^{\alpha *}_{(0)}\tilde{h}^*_{,t^*\alpha^*}\Big) = 2\,\frac{\zeta V}{L^2}\,\tilde{h}^*_{,\alpha^*\lambda^*}\,\delta^{\lambda^*\beta^*}v^{\alpha *}_{(0),\beta^*} - \frac{1}{2}\,\frac{k_{\mathrm{b}}}{L^3}(\Delta^*_{\mathrm{s}})^2\,\tilde{h}^* + \frac{\Lambda}{L}\,\lambda^*_{(0)}\Delta^*_{\mathrm{s}}\,\tilde{h}^*\;. \tag{60}$$

Note that in Eq. (60), all spatial derivatives of the perturbed velocities are with respect to the length ℓ (denoted by $(\,\cdot\,)_{,\alpha'}$), while all spatial derivatives of the perturbed shape are with respect to the length L (denoted with $(\,\cdot\,)_{,\alpha^*}$). With Eqs. (34), (38), (51), (53), and (57), Eq. (60) can be rewritten as

$$\begin{aligned}&\frac{Re\,\Gamma}{\ell^*}\,\Big(\tilde{h}^*_{,t^*t^*} \,+\, (\ell^*)^2\,v^{\alpha *}_{(0)}v^{\beta *}_{(0)}\tilde{h}^*_{,\alpha^*\beta^*} \,+\, \ell^*\,v^{\alpha *}_{(0)}\tilde{h}^*_{,t^*\alpha^*}\Big)\\ &\qquad = 2\,\frac{\zeta V L}{k_{\mathrm{b}}}\,\tilde{h}^*_{,\alpha^*\lambda^*}\,\delta^{\lambda^*\beta^*}\,v^{\alpha *}_{(0),\beta^*} \,+\, \Gamma\,\lambda^*_{(0)}\Delta^*_{\mathrm{s}}\,\tilde{h}^* \,-\, \frac{1}{2}\,(\Delta^*_{\mathrm{s}})^2\,\tilde{h}^*\;.\end{aligned} \tag{61}$$

The coefficient $Re\,\Gamma/\ell^*$ on the left-hand side of Eq. (61) can be expressed as $\rho L^4\Lambda^2/(k_{\mathrm{b}}\zeta^2)$, which ranges from 10^{-12} to 10^{-2} over the experiments considered. Accordingly, inertial terms are negligible in the shape equation (61), which simplifies to

$$2\,\frac{\zeta V L}{k_{\mathrm{b}}}\,\tilde{h}^*_{,\alpha^*\lambda^*}\,\delta^{\lambda^*\beta^*}\,v^{\alpha *}_{(0),\beta^*} \,+\, \Gamma\,\lambda^*_{(0)}\Delta^*_{\mathrm{s}}\,\tilde{h}^* \,-\, \frac{1}{2}\,(\Delta^*_{\mathrm{s}})^2\,\tilde{h}^* \;=\; 0\;. \tag{62}$$

In Eq. (62), the coefficient of the first term is the ratio of viscous forces to bending forces in the out-of-plane direction. We thus define the Scriven–Love number to be given by

$$SL \;:=\; \frac{\zeta V L}{k_{\mathrm{b}}}\;, \tag{63}$$

such that the dimensionless perturbed shape equation is found to be

$$2\,SL\,\tilde{h}^*_{,\alpha^*\lambda^*}\,\delta^{\lambda^*\beta^*}\,v^{\alpha *}_{(0),\beta^*} \,+\, \Gamma\,\lambda^*_{(0)}\,\Delta^*_{\mathrm{s}}\,\tilde{h}^* \,-\, \frac{1}{2}\,(\Delta^*_{\mathrm{s}})^2\,\tilde{h}^* \;=\; 0\;. \tag{64}$$

Equations (55), (59), and (64) are the dimensionless perturbed equations for an initially flat membrane patch with a base flow, provided in Eqs. (17)–(20) in the main text.

(c). The analysis of past experimental data

We now present the experimental data used to calculate the Scriven–Love and Föppl–von Kármán numbers in planar systems with a base flow, and reiterate that the Scriven–Love number does not appear in initially static planar systems. The results of the first three rows of Table I in the main text are detailed in Tables 1–3. In all cases, we assume $k_{\mathrm{b}} = 100$ pN·nm, $\Lambda = 10^{-3}$ pN/nm, and $\zeta = 10$ pN·μsec/nm, as these values were not provided in the experimental studies.

The three situations considered in Tables 1–3 involve vesicles being released from an initially planar membrane during endocytosis. To estimate the velocity scale of in-plane flows on the planar membrane, we approximate the distance moved by lipids near the endocytic site, over the time Δt of the event. Consider an initially flat circular patch of lipids, with radius R_{f}, that eventually forms a vesicle of radius R_{v}. The continuity of the material requires $\pi R_{\mathrm{f}}^2 = 4\pi R_{\mathrm{v}}^2$, such that the in-plane velocity scale $V \sim R_{\mathrm{f}}/\Delta t$ can be approximated as

$$V \sim \frac{2R_{\mathrm{v}}}{\Delta t} \ . \tag{65}$$

In the experiments under consideration, R_{v} and Δt are reported and Eq. (65) is used to approximate the velocity scale V.

Experiment #1: We consider experimental data of ultrafast endocytosis, from Fig. 2 of Ref. [16], which corresponds to Ref. [42, ▲] in the main text.

Quantity	Value	Calculation
V	$8 \cdot 10^{-4}$ nm/μsec	Eq. (65), with $R_{\mathrm{v}} \sim 20$ nm, $\Delta t \sim 50$ msec (Fig. 2)
L	$1 \cdot 10^{2}$ nm	Estimated from Figs. 2(e) and 2(f)
SL	$8 \cdot 10^{-3}$	Eq. (63)
Γ	$1 \cdot 10^{-1}$	Eq. (38)

Table 1: Calculations from Ref. [16], for the first row of Table I in the main text [42, ▲].

Experiment #2: We consider experimental data of ultrafast endocytosis, from Fig. 6 of Ref. [16], which corresponds to Ref. [42, ★] in the main text.

Quantity	Value	Calculation
V	$3 \cdot 10^{-5}$ nm/μsec	Eq. (65), with $R_{\mathrm{v}} \sim 40$ nm, $\Delta t \sim 3$ sec (Fig. 6)
L	$5 \cdot 10^{1}$ nm	Estimated from Fig. 6(g)
SL	$2 \cdot 10^{-4}$	Eq. (63)
Γ	$2 \cdot 10^{-2}$	Eq. (38)

Table 2: Calculations from Ref. [16], for the second row of Table I in the main text [42, ★].

Experiment #3: We consider experimental data of endocytosis, from Figs. 3(a) and 5(a) of Ref. [17], which corresponds to Ref. [43, ■] in the main text.

Quantity	Value	Calculation
V	$6 \cdot 10^{-6}$ nm/μsec	Eq. (65), with $R_{\mathrm{v}} \sim 100$ nm , $\Delta t \sim 30$ sec (Figs. 3(a), 5(a))
L	$1 \cdot 10^{3}$ nm	Estimated from Fig. 5(a)
SL	$6 \cdot 10^{-4}$	Eq. (63)
Γ	$1 \cdot 10^{1}$	Eq. (38)

Table 3: Calculations from Ref. [17], for the third row of Table I in the main text [43, ■].

III. Spherical Membrane Vesicles

We now consider spherical lipid membrane vesicles, following the same general analysis as in the case of nearly planar membranes. The unperturbed and perturbed governing equations are presented, and then non-dimensionalized for two base states: (i) an initially static sphere and (ii) a sphere rotating at constant angular velocity about an axis. In both cases, the Föppl–von Kármán number Γ quantifies the relative importance of surface tension and bending terms in the dynamics of the perturbed membrane. The Scriven–Love number SL again does not appear in the initially static case, as was the case in planar systems without a base flow. However, when a rotating spherical vesicle is perturbed, the Scriven–Love number appears and characterizes the relative importance of viscous and bending forces in the membrane's dynamical response.

1. The unperturbed governing equations

The position of a spherical vesicle of radius R is given by

$$\boldsymbol{x}_{(0)}(\theta,\varphi) \;=\; R\,\boldsymbol{e}_r(\theta,\varphi)\;, \tag{66}$$

where θ is the polar angle and φ is the azimuthal angle, as in a standard spherical coordinate system (see Fig. 4(a) of the main text). We calculate geometric quantities using the results of Sec. II.1, and find

$$\begin{aligned}
&\boldsymbol{a}_1^{(0)} = R\,\boldsymbol{e}_\theta\;, \qquad \boldsymbol{a}_2^{(0)} = R\,\sin\theta\,\boldsymbol{e}_\varphi\;, \qquad \boldsymbol{n}_{(0)} = \boldsymbol{e}_r\;, \qquad a^{(0)}_{\alpha\beta} = R^2\,\mathrm{diag}\,(1,\sin^2\theta)\;,\\
&a^{\alpha\beta}_{(0)} = R^{-2}\,\mathrm{diag}\,(1,\csc^2\theta)\;, \qquad b^{(0)}_{\alpha\beta} = -R\,\mathrm{diag}\,(1,\sin^2\theta)\;, \qquad H_{(0)} = -1/R\;,\\
&K_{(0)} = 1/R^2\;, \qquad \Gamma^{\varphi(0)}_{\varphi\theta} = \Gamma^{\varphi(0)}_{\theta\varphi} = \cot\theta\;, \qquad \text{and} \qquad \Gamma^{\theta(0)}_{\varphi\varphi} = -\sin\theta\,\cos\theta\;,
\end{aligned} \tag{67}$$

where only nonzero Christoffel symbols are presented. The unperturbed membrane velocity, which has no normal component ($v_{(0)} = 0$), is given by

$$\boldsymbol{v}_{(0)} \;=\; v^\alpha_{(0)}\,\boldsymbol{a}^{(0)}_\alpha \;=\; R\,v^\theta_{(0)}\boldsymbol{e}_\theta \,+\, R\,\sin\theta\,v^\varphi_{(0)}\boldsymbol{e}_\varphi\;. \tag{68}$$

With the above calculations, the unperturbed continuity (1), in-plane (10), and shape (11) equations are written as

$$v^\theta_{(0),\theta} \,+\, v^\varphi_{(0),\varphi} \,+\, \cot\theta\,v^\theta_{(0)} \;=\; 0\;, \tag{69}$$

$$\begin{aligned}
&\rho R^2\Big(v^\theta_{(0),t} \,+\, v^\theta_{(0)}\,v^\theta_{(0),\theta} \,+\, v^\varphi_{(0)}\,v^\theta_{(0),\varphi} \,-\, \sin\theta\,\cos\theta(v^\varphi_{(0)})^2\Big)\\
&\qquad = \zeta\Big(v^\theta_{(0)} \,+\, v^\theta_{(0),\theta\theta} \,+\, \csc^2\theta\,v^\theta_{(0),\varphi\varphi} \,-\, \cot\theta\,v^\varphi_{(0),\varphi} \,+\, 2\,\cot\theta\,v^\theta_{(0),\theta}\Big) \,+\, \lambda_{(0),\theta}\;,
\end{aligned} \tag{70}$$

$$\begin{aligned}\rho R^2\Big(v^{\varphi}_{(0),t} + v^{\theta}_{(0)}\,v^{\varphi}_{(0),\theta} + v^{\varphi}_{(0)}\,v^{\varphi}_{(0),\varphi} + 2\cot\theta\,v^{\theta}_{(0)}\,v^{\varphi}_{(0)}\Big)& \\ = \zeta\Big(v^{\varphi}_{(0),\theta\theta} + \csc^2\theta\,v^{\varphi}_{,(0)\varphi\varphi} + 2\cot\theta\,\csc^2\theta\,v^{\theta}_{(0),\varphi} + 3\cot\theta\,v^{\varphi}_{(0),\theta}\Big) &+ \csc^2\theta\,\lambda_{(0),\varphi}\ ,\end{aligned} \tag{71}$$

and

$$-\rho R^2\Big((v^{\theta}_{(0)})^2 + \sin^2\theta\,(v^{\varphi}_{(0)})^2\Big) = p\,R - 2\,\lambda_{(0)}\ . \tag{72}$$

The continuity and in-plane equations (69)–(71) are similar in structure to those of the flat case (15, 16), and the shape equation (72) contains no viscous or bending terms. From now on, to avoid cumbersome algebra, we only consider the base state where

$$v^{\theta}_{(0)} = 0\ , \qquad v^{\varphi}_{(0)} = v^{\varphi}_0\ , \qquad \text{and} \qquad v_{(0)} = 0\ , \tag{73}$$

for constant v^{φ}_0. When $v^{\varphi}_0 = 0$, the base state is static, while if $v^{\varphi}_0 \neq 0$ the sphere is rotating at a constant angular velocity about the z-axis.

2. The perturbed governing equations

The position of a perturbed spherical membrane is given by

$$\boldsymbol{x}(\theta,\varphi,t) = \Big[R + \epsilon\,\tilde r(\theta,\varphi,t)\Big]\,\boldsymbol{e}_r(\theta,\varphi)\ , \tag{74}$$

where $\tilde r$ is $O(R)$ and $\epsilon := \delta R/R$ is a small parameter, as shown in Fig. 4(b) of the main text. To first order in ϵ, the perturbed geometric quantities are calculated as

$$\boldsymbol{a}_1 = (R+\epsilon\,\tilde r)\,\boldsymbol{e}_\theta + \epsilon\,\tilde r_{,\theta}\,\boldsymbol{e}_r\ , \qquad \boldsymbol{a}_2 = (R+\epsilon\,\tilde r)\,\sin\theta\,\boldsymbol{e}_\varphi + \epsilon\,\tilde r_{,\varphi}\,\boldsymbol{e}_r\ ,$$

$$\boldsymbol{n} = \frac{1}{R}\big(R\,\boldsymbol{e}_r - \epsilon\,\tilde r_{,\theta}\,\boldsymbol{e}_\theta - \epsilon\,\tilde r_{,\varphi}\,\csc\theta\,\boldsymbol{e}_\varphi\big)\ , \qquad a_{\alpha\beta} = (R^2 + 2\,\epsilon\,\tilde r\,R)\,\mathrm{diag}\,(1,\,\sin^2\theta)\ ,$$

$$b_{\alpha\beta} = \begin{pmatrix} -R - \epsilon\,\tilde r + \epsilon\,\tilde r_{,\theta\theta} & \epsilon\,\tilde r_{,\theta\varphi} - \epsilon\,\cot\theta\,\tilde r_{,\varphi} \\ \epsilon\,\tilde r_{,\theta\varphi} - \epsilon\,\cot\theta\,\tilde r_{,\varphi} & -\sin^2\theta\,R + \epsilon\big[-\tilde r\,\sin^2\theta + \tilde r_{,\varphi\varphi} + \sin\theta\,\cos\theta\,\tilde r_{,\theta}\big] \end{pmatrix}\ ,$$

$$H = -\frac{1}{R} + \frac{\epsilon}{2R^2}\left(2\tilde r + R^2\Delta_{\mathrm{s}}\tilde r\right)\ , \qquad K = \frac{1}{R^2} - \frac{\epsilon}{R^3}\left(2\tilde r + R^2\Delta_{\mathrm{s}}\tilde r\right)\ , \qquad \Gamma^{\theta}_{\theta\theta} = \epsilon\,\tilde r_{,\theta}/R\ ,$$

$$\Gamma^{\varphi}_{\theta\theta} = -\epsilon\,\tilde r_{,\varphi}\,\csc^2\theta/R\ , \qquad \Gamma^{\theta}_{\theta\varphi} = \Gamma^{\theta}_{\varphi\theta} = \epsilon\,\tilde r_{,\varphi}/R\ , \qquad \Gamma^{\varphi}_{\varphi\theta} = \Gamma^{\varphi}_{\theta\varphi} = \cot\theta + \epsilon\tilde r_{,\theta}/R\ ,$$

$$\Gamma^{\theta}_{\varphi\varphi} = -\sin\theta\,\cos\theta - \epsilon\,\sin^2\theta\,\tilde r_{,\theta}/R\ , \qquad \text{and} \qquad \Gamma^{\varphi}_{\varphi\varphi} = \epsilon\,\tilde r_{,\varphi}/R\ ,$$

where the two-dimensional surface Laplacian for scalar quantities is given by $\Delta_{\mathrm{s}}(\,\cdot\,) := [(\,\cdot\,)_{,\theta\theta} + \cot\theta(\,\cdot\,)_{,\theta} + \csc^2\theta(\,\cdot\,)_{,\varphi\varphi}]/R^2$. The fundamental unknowns are expanded to first order as

$$v^\theta = \epsilon\,\tilde v^\theta\ , \qquad v^\varphi = v^\varphi_0 + \epsilon\,\tilde v^\varphi\ , \qquad v = \epsilon\,\tilde r_{,t}\ , \qquad \text{and} \qquad \lambda = \lambda_{(0)} + \epsilon\tilde\lambda\ , \tag{75}$$

where in the case of an initially static membrane $v^{\varphi}_0 = 0$. In Eq. $(75)_3$, the normal velocity v is again calculated as $v = \boldsymbol{x}_{,t}\cdot\boldsymbol{n}$ (Sec. II.1).

Substituting the geometric quantities provided above, as well as Eq. (75), into the governing equations (1, 10, 11) and keeping only terms of first order in ϵ, the first-order perturbed equations are found to be

$$\tilde v^{\theta}_{,\theta} + \tilde v^{\varphi}_{,\varphi} + \cot\theta\,\tilde v^\theta + \frac{2}{R}\left(\tilde r_{,t} + v^{\varphi}_0\,\tilde r_{,\varphi}\right) = 0\ , \tag{76}$$

$$
\begin{aligned}
&\rho R^2\Big(\tilde{v}^\theta_{,t} \,+\, v^\varphi_0\,\tilde{v}^\theta_{,\varphi} \,-\, 2\,v^\varphi_0 \sin\theta\,\cos\theta\,\tilde{v}^\varphi \,-\, \frac{(v^\varphi_0)^2}{R}\,\sin^2\theta\,\tilde{r}_{,\theta}\Big) \\
&\quad = \zeta\Big(\tilde{v}^\theta \,+\, \tilde{v}^\theta_{,\theta\theta} \,+\, \csc^2\theta\,\tilde{v}^\theta_{,\varphi\varphi} \,+\, \cot\theta\,\tilde{v}^\theta_{,\theta} \,-\, 2\cot\theta\,\tilde{v}^\varphi_{,\varphi} \,-\, \cot^2\theta\,\tilde{v}^\theta\Big) \,+\, \tilde{\lambda}_{,\theta}\ ,
\end{aligned}
\tag{77}
$$

$$
\begin{aligned}
&\rho R^2\Big(\tilde{v}^\varphi_{,t} \,+\, \frac{2\,v^\varphi_0}{R}\,\tilde{r}_{,t} \,+\, v^\varphi_0\,\tilde{v}^\varphi_{,\varphi} \,+\, 2\,v^\varphi_0\cot\theta\,\tilde{v}^\theta \,+\, \frac{(v^\varphi_0)^2}{R}\,\tilde{r}_{,\varphi}\Big) \\
&\quad = \zeta\Big(\tilde{v}^\varphi_{,\theta\theta} \,+ \csc^2\theta\,\tilde{v}^\varphi_{,\varphi\varphi} + 2\cot\theta\,\csc^2\theta\,\tilde{v}^\theta_{,\varphi} \,+\, 3\cot\theta\,\tilde{v}^\varphi_{,\theta}\Big) + \csc^2\theta\,\tilde{\lambda}_{,\varphi}\ ,
\end{aligned}
\tag{78}
$$

and

$$
\begin{aligned}
&\rho R^2\Big(\tilde{r}_{,tt} \,-\, 2\,v^\varphi_0\,R\,\sin^2\theta\,\tilde{v}^\varphi \,+\, (v^\varphi_0)^2\,\big[-\sin^2\theta\,\tilde{r} \,+\, \sin\theta\,\cos\theta\,\tilde{r}_{,\theta} \,+\, \tilde{r}_{,\varphi\varphi}\big] \,+\, v^\varphi_0\,\tilde{r}_{,t\varphi}\Big) \\
&\quad = -2R\tilde{\lambda} + \lambda_{(0)}\Big(2\tilde{r} + R^2\Delta_{\mathrm{s}}\tilde{r}\Big) - \frac{k_{\mathrm{b}}}{2}\Big(R^2\Delta_{\mathrm{s}}^2\,\tilde{r} + 2\Delta_{\mathrm{s}}\tilde{r}\Big) + 2\zeta v^\varphi_0\Big(\cos\theta\big[\csc\theta - \sin\theta\big]\tilde{r}_{,\theta\varphi} - \cos^2\theta\cot^2\theta\tilde{r}_{,\varphi}\Big)\ .
\end{aligned}
\tag{79}
$$

We now non-dimensionalize both the unperturbed (69)–(72) and perturbed (76)–(79) governing equations for the initially static and rotating base states.

3. The case of an initially static spherical vesicle: non-dimensionalization

For a spherical vesicle initially at rest, $v^\varphi_0 = 0$ in Eq. (73). In this case, the unperturbed continuity equation (69) is automatically satisfied, and the equations of motion (70)–(72) simplify to

$$
\lambda_{(0),\theta} = 0\ , \qquad \lambda_{(0)},\varphi = 0\ , \qquad \text{and} \qquad \lambda_{(0)} = \frac{pR}{2}\ , \tag{80}
$$

such that the unperturbed solution is given by

$$
v^\theta_{(0)} = 0\ , \qquad v^\varphi_{(0)} = 0\ , \qquad v_{(0)} = 0\ , \qquad \text{and} \qquad \lambda_{(0)} = \lambda_0 := \frac{pR}{2}\ . \tag{81}
$$

The unperturbed solution sets the surface tension scale Λ as

$$
\Lambda := \frac{pR}{2}\ , \qquad \text{such that} \qquad \lambda^*_{(0)} = \frac{\lambda_{(0)}}{\Lambda} = 1. \tag{82}
$$

We now seek to determine the velocity and time scales via non-dimensionalization of the perturbed equations, as these quantities are not set in the base state.

Substituting the unperturbed solution (81) into the perturbed equations (76)–(79) yields

$$
\tilde{v}^\theta_{,\theta} \,+\, \tilde{v}^\varphi_{,\varphi} \,+\, \cot\theta\,\tilde{v}^\theta \,+\, \frac{2}{R}\,\tilde{r}_{,t} \,=\, 0\ , \tag{83}
$$

$$
\rho R^2\,\tilde{v}^\theta_{,t} \,=\, \zeta\Big(\tilde{v}^\theta \,+\, \tilde{v}^\theta_{,\theta\theta} \,+\, \csc^2\theta\,\tilde{v}^\theta_{,\varphi\varphi} \,+\, \cot\theta\,\tilde{v}^\theta_{,\theta} \,-\, 2\cot\theta\,\tilde{v}^\varphi_{,\varphi} \,-\, \cot^2\theta\,\tilde{v}^\theta\Big) \,+\, \tilde{\lambda}_{,\theta}\ , \tag{84}
$$

$$
\rho R^2\,\tilde{v}^\varphi_{,t} \,=\, \zeta\Big(\tilde{v}^\varphi_{,\theta\theta} \,+ \csc^2\theta\,\tilde{v}^\varphi_{,\varphi\varphi} + 2\cot\theta\,\csc^2\theta\,\tilde{v}^\theta_{,\varphi} \,+\, 3\cot\theta\,\tilde{v}^\varphi_{,\theta}\Big) + \csc^2\theta\,\tilde{\lambda}_{,\varphi}\ , \tag{85}
$$

and

$$
\rho R^2\,\tilde{r}_{,tt} \,=\, -2\,R\,\tilde{\lambda} \,+\, \lambda_0\Big(2\,\tilde{r} \,+\, R^2\Delta_{\mathrm{s}}\tilde{r}\Big) \,-\, \frac{k_{\mathrm{b}}}{2}\Big(R^2\,\Delta_{\mathrm{s}}^2\,\tilde{r} \,+\, 2\,\Delta_{\mathrm{s}}\,\tilde{r}\Big)\ . \tag{86}
$$

As in the flat case, viscous terms do not appear in the perturbed shape equation of an initially static spherical vesicle (86). Therefore, in this case, we will not obtain the Scriven–Love number *SL* upon non-dimensionalization.

At this point, we provide characteristic scales for all unknown quantities. We assume the perturbed velocities $\tilde{v}^\theta$ and $\tilde{v}^\varphi$ are of the same order, which we denote Ω. The surface tension scale in the base state is known (82), and as before $\tilde{\lambda}$ is assumed to be of the same scale. Finally, we assume radial shape perturbations, which are of order R, vary over a time scale τ. This leads to the following dimensionless quantities:

$$\theta^* := \theta\ , \qquad \varphi^* := \varphi\ , \qquad \tilde{r}^* := \frac{\tilde{r}}{R}\ , \qquad \tilde{v}^{\alpha *} := \frac{\tilde{v}^{\alpha}}{\Omega}\ , \qquad \tilde{\lambda}^* := \frac{\tilde{\lambda}}{\Lambda}\ , \qquad \text{and} \qquad t^* := \frac{t}{\tau}\ , \tag{87}$$

which are all $O(1)$ by construction. Substituting Eq. (87) into the perturbed continuity equation (83), we obtain

$$\tilde{v}^{\theta *}_{,\theta^*} + \tilde{v}^{\varphi *}_{,\varphi^*} + \cot\theta^*\,\tilde{v}^{\theta *} + \frac{2}{\Omega\tau}\,\tilde{r}^*_{,t^*} = 0\ . \tag{88}$$

As in-plane flows are required to balance shape changes to the membrane, we find

$$\Omega = \frac{1}{\tau}\ . \tag{89}$$

Next, the in-plane equations are considered. Substituting Eqs. (87) and (89) into the perturbed in-plane equations (84, 85) and rearranging terms yields

$$Re\,\tilde{v}^{\theta *}_{,t^*} = \tilde{v}^{\theta *} + \tilde{v}^{\theta *}_{,\theta^*\theta^*} + \csc^2\theta^*\tilde{v}^{\theta *}_{,\varphi^*\varphi^*} + \cot\theta^*\tilde{v}^{\theta *}_{,\theta^*} - 2\cot\theta^*\tilde{v}^{\varphi *}_{,\varphi^*} - \cot^2\theta^*\tilde{v}^{\theta *} + \frac{\Lambda}{\zeta\Omega}\,\tilde{\lambda}^*_{,\theta^*} \tag{90}$$

and

$$Re\,\tilde{v}^{\varphi *}_{,t^*} = \tilde{v}^{\varphi *}_{,\theta^*\theta^*} + \csc^2\theta^*\,\tilde{v}^{\varphi *}_{,\varphi^*\varphi^*} + 2\cot\theta^*\,\csc^2\theta^*\,\tilde{v}^{\theta *}_{,\varphi^*} + 3\cot\theta^*\,\tilde{v}^{\varphi *}_{,\theta^*} + \frac{\Lambda}{\zeta\Omega}\,\csc^2\theta^*\,\tilde{\lambda}^*_{,\varphi^*}\ , \tag{91}$$

where for spherical vesicles the Reynolds number is given by

$$Re := \frac{\rho\Omega R^2}{\zeta}\ . \tag{92}$$

Assuming viscous forces are of the same order as surface tension forces in the perturbed equations, one obtains

$$\Omega = \frac{\Lambda}{\zeta}\ , \qquad \text{with} \qquad \tau = \frac{\zeta}{\Lambda}\ , \tag{93}$$

such that the base state surface tension sets the scale of angular velocities and also the time scale over which radial perturbations change. In this case, over the range of experiments considered in this work, $O(Re) \leq 10^{-4}$ and inertial terms are indeed negligible.

Finally, substituting Eqs. (87), (89), and (93) into the perturbed shape equation (86), we obtain

$$Re\,\Gamma\,\tilde{r}^*_{,t^*t^*} = \Gamma\Big(2\,\tilde{r}^* + \Delta^*_{\mathrm{s}}\,\tilde{r}^* - 2\tilde{\lambda}^*\Big) - \frac{1}{2}\Big(\Delta^{*2}_{\mathrm{s}}\,\tilde{r}^* + 2\,\Delta^*_{\mathrm{s}}\,\tilde{r}^*\Big)\ , \tag{94}$$

where the Föppl–von Kármán number Γ is defined as

$$\Gamma := \frac{\Lambda R^2}{k_{\mathrm{b}}} \tag{95}$$

and the dimensionless surface Laplacian is given by $\Delta^*_{\mathrm{s}}(\,\cdot\,) := R^2\,\Delta_{\mathrm{s}}(\,\cdot\,)$. As the inertial terms on the left-hand side of Eq. (94) contains a factor of $Re\,\Gamma$ and $Re \ll 1$, inertial terms are always negligible compared to surface tension terms. However, we note that in cases where Γ is large, inertial terms can be comparable to bending terms. The non-dimensional perturbed equations governing initially static spheres are then given by

$$\tilde{v}^{\theta *}_{,\theta^*} + \tilde{v}^{\varphi *}_{,\varphi^*} + \cot\theta^*\,\tilde{v}^{\theta *} + 2\,\tilde{r}^*_{,t^*} = 0\ , \tag{96}$$

$$\tilde{v}^{\theta *} + \tilde{v}^{\theta *}_{,\theta^*\theta^*} + \csc^2\theta^*\tilde{v}^{\theta *}_{,\varphi^*\varphi^*} + \cot\theta^*\tilde{v}^{\theta *}_{,\theta^*} - 2\cot\theta^*\tilde{v}^{\varphi *}_{,\varphi^*} - \cot^2\theta^*\tilde{v}^{\theta *} + \tilde{\lambda}^*_{,\theta^*} = 0\ , \tag{97}$$

$$\tilde{v}^{\varphi *}_{,\theta^*\theta^*} + \csc^2\theta^*\,\tilde{v}^{\varphi *}_{,\varphi^*\varphi^*} + 2\cot\theta^*\,\csc^2\theta^*\,\tilde{v}^{\theta *}_{,\varphi^*} + 3\cot\theta^*\,\tilde{v}^{\varphi *}_{,\theta^*} + \csc^2\theta^*\,\tilde{\lambda}^*_{,\varphi^*} = 0\ , \tag{98}$$

and

$$\Gamma\Big(2\,\tilde{r}^* + \Delta^*_{\mathrm{s}}\,\tilde{r}^* - 2\,\tilde{\lambda}^*\Big) - \frac{1}{2}\Big(\Delta^{*2}_{\mathrm{s}}\,\tilde{r}^* + 2\,\Delta^*_{\mathrm{s}}\,\tilde{r}^*\Big) = 0\ . \tag{99}$$

Note that Eqs. (96)–(99) are presented as Eqs. (25)–(28) in the main text.

4. The case of an initially rotating spherical vesicle: non-dimensionalization

We now turn to the case of a spherical vesicle which, prior to being perturbed, is rotating at constant angular velocity $v_0^\varphi \neq 0$. We first show such a velocity field is a valid solution to the general unperturbed equations of a spherical vesicle, for which the base state sets the characteristic angular velocity, surface tension, and length scales. In this case, we find both the Föppl–von Kármán and Scriven–Love numbers result from non-dimensionalization of the perturbed shape equation: the Föppl–von Kármán number again compares tension to bending forces, while the Scriven–Love number compares viscous forces in the normal direction to bending forces.

(a). The unperturbed equations

We begin by determining the solution of the unperturbed governing equations. Substituting the unperturbed flow field (73) into the unperturbed equations (69)–(72) reveals the continuity equation is automatically satisfied, and the remaining equations simplify to

$$\lambda_{(0),\theta} \;=\; \rho R^2 \sin\theta \cos\theta \, (v_0^\varphi)^2 \ , \tag{100}$$

$$\lambda_{(0),\varphi} \;=\; 0 \ , \tag{101}$$

and

$$\lambda_{(0)} \;=\; \frac{1}{2}\Big(pR + \rho R^2 \sin^2\theta \, (v_0^\varphi)^2\Big) \ . \tag{102}$$

At this point, we recognize that for the spherical vesicles under consideration (see Sec. III.4 (c), as well as Table I of the main text), $\rho \sim 10^{-8}$ pg/nm^2, $R \sim 10^2$–10^4 nm, $v_0^\varphi \leq 10^{-3}$ μsec^{-1}, and $\lambda_{(0)} \sim 10^{-4}$–$10^{-1}$ pN/nm. In this case, $O(\rho R^2 (v_0^\varphi)^2) \sim 10^{-12}$–$10^{-6}$ pN/nm, and inertial terms are negligible relative to tension forces. Equations (100)–(102) then simplify to

$$\lambda_{(0),\theta} \;=\; 0 \ , \qquad \lambda_{(0),\varphi} \;=\; 0 \ , \qquad \text{and} \qquad \lambda_{(0)} \;=\; \frac{pR}{2} \ , \tag{103}$$

such that the unperturbed solution is given by

$$v^\theta_{(0)} = 0 \ , \qquad v^\varphi_{(0)} = v_0^\varphi \ , \qquad v_{(0)} = 0 \ , \qquad \text{and} \qquad \lambda_{(0)} = \lambda_0 := \frac{pR}{2} \ . \tag{104}$$

We note that in this case, the characteristic scales

$$\Omega := v_0^\varphi \qquad \text{and} \qquad \Lambda := \lambda_0 = \frac{pR}{2} \tag{105}$$

are set by the base state.

(b). The perturbed equations

In the base state, quantities are expected to vary over $O(1)$ changes in the angles θ and φ, or equivalently over $O(R)$ lengths on the membrane surface. As in the planar case, the introduction of an angular velocity scale Ω allows for the possibility of a new length scale ℓ—or equivalently, a new angular scale $\Phi = \ell/R$—over which certain quantities can vary. As the governing equations are written in terms of angular derivatives, we will predominantly use the new angular scale Φ in our analysis here. As in the planar case, we first demonstrate why a new angular scale is needed and then show which quantities vary over Φ. Note that due to the geometry of the system, $\Phi \leq 1$.

First, assume all perturbed quantities vary over $O(1)$ changes in θ and φ, such that $\theta^* = \theta$ and $\varphi^* = \varphi$. In this case, all perturbed quantities are scaled according to Eq. (87), where the angular velocity scale Ω and surface tension scale Λ are set by the base state (105). The perturbed continuity equation (76) is non-dimensionalized as

$$\tilde{v}^{\theta*}_{,\theta^*} + \tilde{v}^{\varphi*}_{,\varphi^*} + \cot\theta^* \, \tilde{v}^{\theta*} + 2\,\tilde{r}^*_{,\varphi^*} + \frac{2}{\tau\Omega}\,\tilde{r}^*_{,t^*} \;=\; 0 \ , \tag{106}$$

for which the time scale τ is given by $\tau = 1/\Omega$ such that in-plane and out-of-plane quantities are of the same order. Equation (106) then simplifies to

$$\tilde{v}^{\theta*}_{,\theta^*} + \tilde{v}^{\varphi*}_{,\varphi^*} + \cot\theta^* \, \tilde{v}^{\theta*} + 2\,\tilde{r}^*_{,\varphi^*} + 2\,\tilde{r}^*_{,t^*} = 0 \; . \tag{107}$$

Next, Eq. (87) is substituted into the in-plane equations (77, 78). Neglecting inertial terms for the simplicity of our argument, we then obtain

$$\tilde{v}^{\theta*} + \tilde{v}^{\theta*}_{,\theta^*\theta^*} + \csc^2\theta^* \, \tilde{v}^{\theta*}_{,\varphi^*\varphi^*} + \cot\theta^* \, \tilde{v}^{\theta*}_{,\theta^*} - 2\cot\theta^* \, \tilde{v}^{\varphi*}_{,\varphi^*} - \cot^2\theta^* \, \tilde{v}^{\theta*} + \frac{\Lambda}{\zeta\Omega} \, \tilde{\lambda}^*_{,\theta^*} = 0 \tag{108}$$

and

$$\tilde{v}^{\varphi*}_{,\theta^*\theta^*} + \csc^2\theta^* \, \tilde{v}^{\varphi*}_{,\varphi^*\varphi^*} + 2\cot\theta^* \, \csc^2\theta^* \, \tilde{v}^{\theta*}_{,\varphi^*} + 3\cot\theta^* \, \tilde{v}^{\varphi*}_{,\theta^*} + \frac{\Lambda}{\zeta\Omega} \csc^2\theta^* \, \tilde{\lambda}^*_{,\varphi^*} = 0 \; . \tag{109}$$

Recalling that Ω and Λ are set by the base state (105), we find that in the limit of vanishing Ω, i.e. when v_0^φ tends to zero, the in-plane equations (108, 109) imply $\tilde{\lambda}^* =$ constant. However, in the limit of vanishing base velocity, we must recover the initially static shape equation (99), in which the perturbed surface tension varies over the patch in reaction to the perturbed membrane shape. This is not the case, and thus our assumption that all quantities vary over $O(1)$ changes in θ and φ is unphysical.

Next, we attempt to find a consistent scaling result by introducing a new angular scale Φ over which all perturbed quantities vary. In this case, we define the new quantities

$$\theta' := \frac{\theta}{\Phi} \; , \qquad \varphi' := \frac{\varphi}{\Phi} \qquad \text{and} \qquad \Delta'_{\mathrm{s}}(\,\cdot\,) := \Phi^2 R^2 \, \Delta_{\mathrm{s}}(\,\cdot\,) \; , \tag{110}$$

such that all angular derivatives are non-dimensionalized with θ' and φ' rather than θ^* and φ^*. All other perturbed quantities are non-dimensionalized as in Eq. (87). The dimensionless continuity equation is obtained by substituting Eqs. (87) and (110) into Eq. (76), and is found to be

$$\tilde{v}^{\theta*}_{,\theta'} + \tilde{v}^{\varphi*}_{,\varphi'} + \Phi\cot\theta^* \, \tilde{v}^{\theta*} + 2\,\tilde{r}^*_{,\varphi'} + \frac{2\Phi}{\tau\Omega} \, \tilde{r}^*_{,t^*} = 0 \; . \tag{111}$$

As $\Phi \leq 1$ due to geometric constraints, and it is possible that $\Phi \ll 1$, Eq. (111) requires the time scale τ to be given by

$$\tau = \frac{\Phi}{\Omega} \tag{112}$$

such that in-plane and out-of-plane motions are of the same order. Accordingly, Eq. (111) simplifies to

$$\tilde{v}^{\theta*}_{,\theta'} + \tilde{v}^{\varphi*}_{,\varphi'} + \Phi\cot\theta' \, \tilde{v}^{\theta*} + 2\,\tilde{r}^*_{,\varphi'} + 2\,\tilde{r}^*_{,t^*} = 0 \; . \tag{113}$$

The in-plane equations (77, 78) are similarly non-dimensionalized, and can be expressed as

$$\Phi^2 \, \tilde{v}^{\theta*} + \tilde{v}^{\theta*}_{,\theta'\theta'} + \csc^2\theta' \, \tilde{v}^{\theta*}_{,\varphi'\varphi'} + \Phi\cot\theta' \, \tilde{v}^{\theta*}_{,\theta'} - 2\,\Phi\cot\theta' \, \tilde{v}^{\varphi*}_{,\varphi'} - \Phi^2\cot^2\theta' \, \tilde{v}^{\theta*} + \frac{\Lambda\Phi}{\zeta\Omega} \, \tilde{\lambda}^*_{,\theta'} = 0 \tag{114}$$

and

$$\tilde{v}^{\varphi*}_{,\theta'\theta'} + \csc^2\theta' \, \tilde{v}^{\varphi*}_{,\varphi'\varphi'} + 2\,\Phi\cot\theta' \, \csc^2\theta' \, \tilde{v}^{\theta*}_{,\varphi'} + 3\,\Phi\cot\theta' \, \tilde{v}^{\varphi*}_{,\theta'} + \frac{\Lambda\Phi}{\zeta\Omega} \csc^2\theta' \, \tilde{\lambda}^*_{,\varphi'} = 0 \; , \tag{115}$$

where inertial terms are neglected to simplify our argument. To ensure surface tension gradients are of the same order as in-plane viscous forces, even in the limit of small Ω, we must have

$$\Phi = \frac{\zeta\Omega}{\Lambda} \qquad \text{and} \qquad \tau = \frac{\zeta}{\Lambda} \; , \tag{116}$$

with the latter satisfying Eq. (112). Finally, the shape equation (79) is non-dimensionalized with Eqs. (87) and (110), and is given by

$$\begin{aligned} &\Phi^2 \, \Lambda \Big(2\,\Phi^2 \, \tilde{r}^* + \Delta'_{\mathrm{s}} \, \tilde{r}^* - 2\,\Phi^2 \, \tilde{r}^* \Big) - \frac{k_{\mathrm{b}}}{2R^2} \Big(\Delta'^2_{\mathrm{s}} \, \tilde{r}^* + 2\,\Phi^2 \, \Delta'_{\mathrm{s}} \, \tilde{r}^* \Big) \\ &\qquad + 2\,\zeta\,\Omega\,\Phi^2 \Big(\cos\theta' \big[\csc\theta' - \sin\theta' \big] \tilde{r}^*_{,\theta'\varphi'} - \Phi \, \cos^2\theta' \cot^2\theta' \, \tilde{r}^*_{,\varphi'} \Big) = 0 \; . \end{aligned} \tag{117}$$

Thus, in the limit where Ω tends to zero, for which (see Eq. (116)) Φ tends to zero as well, Eq. (117) simplifies to

$$\Delta_{\mathrm{s}}^{\prime 2}\, \tilde{r}^{*} \;=\; 0 \;. \tag{118}$$

However, one must recover the initially static shape equation (99) when Ω goes to zero. As this is not the case, our choice of scaling here is again incorrect.

As in the planar case, at this point we recognize that $\tilde{v}^{\theta}$, $\tilde{v}^{\varphi}$, and $\tilde{\lambda}$ must vary over $O(\Phi)$ changes in θ and φ, while $\tilde{r}$ does not. We assume $\tilde{r}$ varies over $O(1)$ changes in θ and φ. With this choice, the first-order continuity equation (76) is non-dimensionalized as

$$\tilde{v}^{\theta *}_{,\theta'} \,+\, \tilde{v}^{\varphi *}_{,\varphi'} \,+\, \Phi\big(\cot\theta^{*}\, \tilde{v}^{\theta *} \,+\, 2\, \tilde{r}^{*}_{,\varphi^{*}}\big) \,+\, \frac{2\Phi}{\tau\Omega}\, \tilde{r}^{*}_{,t^{*}} \;=\; 0 \;, \tag{119}$$

which once more requires the time and angular velocity scales to be given by Eq. (116). In Eq. (119), and throughout the rest of this section, spatial derivatives of the perturbed velocities and surface tensions are with respect to θ' and φ', while those of the perturbed velocities are with respect to θ^{*} and φ^{*}. Upon substitution of Eq. (116) into Eq. (119), we obtain

$$\tilde{v}^{\theta *}_{,\theta'} \,+\, \tilde{v}^{\varphi *}_{,\varphi'} \,+\, \Phi\big(\cot\theta^{*}\, \tilde{v}^{\theta *} \,+\, 2\, \tilde{r}^{*}_{,\varphi^{*}}\big) \,+\, 2\, \tilde{r}^{*}_{,t^{*}} \;=\; 0 \;, \tag{120}$$

which is provided as the perturbed continuity equation in the main text (35). The perturbed in-plane equations are non-dimensionalized as

$$\begin{aligned} &\mathit{Re}\,\Phi\Big(\tilde{v}^{\theta *}_{,t^{*}} \,+\, \tilde{v}^{\theta *}_{,\varphi'} \,-\, 2\,\Phi \sin\theta^{*}\cos\theta^{*}\, \tilde{v}^{\varphi *} \,-\, \Phi \sin^{2}\theta^{*}\, \tilde{r}^{*}_{,\theta^{*}}\Big) \\ &\quad=\; \tilde{v}^{\theta *}_{,\theta'\theta'} + \csc^{2}\theta^{*} \tilde{v}^{\theta *}_{,\varphi'\varphi'} \,+\, \Phi\cot\theta^{*}\big(\tilde{v}^{\theta *}_{,\theta'} \,-\, 2\, \tilde{v}^{\varphi *}_{,\varphi'}\big) \,+\, \Phi^{2}\, \tilde{v}^{\theta *}\big(1-\cot^{2}\theta^{*}\big) \,+\, \tilde{\lambda}^{*}_{,\theta'} \end{aligned} \tag{121}$$

and

$$\begin{aligned} &\mathit{Re}\,\Phi\Big(\tilde{v}^{\varphi *}_{,t^{*}} \,+\, 2\,\tilde{r}^{*}_{,t^{*}} \,+\, \tilde{v}^{\varphi *}_{,\varphi'} \,+\, 2\,\Phi\cot\theta^{*}\, \tilde{v}^{\theta *} \,+\, \Phi\, \tilde{r}^{*}_{,\varphi^{*}}\Big) \\ &\quad=\; \tilde{v}^{\varphi *}_{,\theta'\theta'} + \csc^{2}\theta^{*}\, \tilde{v}^{\varphi *}_{,\varphi'\varphi'} \,+\, \Phi\cot\theta^{*}\big(2\csc^{2}\theta^{*}\, \tilde{v}^{\theta *}_{,\varphi'} \,+\, 3\, \tilde{v}^{\varphi *}_{,\theta'}\big) \,+\, \csc^{2}\theta^{*}\, \tilde{\lambda}^{*}_{,\varphi'} \;, \end{aligned} \tag{122}$$

where the choice of Φ in Eq. (116) ensures viscous forces and tension forces are the same order. As $\mathit{Re} \ll 1$ and $\Phi \leq 1$, Eqs. (121) and (122) simplify to

$$\tilde{v}^{\theta *}_{,\theta'\theta'} + \csc^{2}\theta^{*} \tilde{v}^{\theta *}_{,\varphi'\varphi'} \,+\, \Phi\cot\theta^{*}\big(\tilde{v}^{\theta *}_{,\theta'} \,-\, 2\, \tilde{v}^{\varphi *}_{,\varphi'}\big) \,+\, \Phi^{2}\, \tilde{v}^{\theta *}\big(1-\cot^{2}\theta^{*}\big) \,+\, \tilde{\lambda}^{*}_{,\theta'} \;=\; 0 \tag{123}$$

and

$$\tilde{v}^{\varphi *}_{,\theta'\theta'} + \csc^{2}\theta^{*}\, \tilde{v}^{\varphi *}_{,\varphi'\varphi'} \,+\, \Phi\cot\theta^{*}\big(2\csc^{2}\theta^{*}\, \tilde{v}^{\theta *}_{,\varphi'} \,+\, 3\, \tilde{v}^{\varphi *}_{,\theta'}\big) \,+\, \csc^{2}\theta^{*}\, \tilde{\lambda}^{*}_{,\varphi'} \;=\; 0 \;, \tag{124}$$

which are presented as Eqs. (36) and (37) in the main text. Finally, the perturbed shape equation (79) is considered, which upon substitution of Eqs. (110), and (116) is given by

$$\begin{aligned} &\frac{\mathit{Re}\,\Gamma}{\Phi}\Big(\tilde{r}^{*}_{,t^{*}t^{*}} \,+\, \Phi\, \tilde{r}^{*}_{,t^{*}\varphi^{*}} \,+\, \Phi^{2}\Big[-2\sin^{2}\theta^{*}\, \tilde{v}^{\varphi *} \,-\, \sin\theta^{*}\, \tilde{r}^{*} \,+\, \sin\theta^{*}\cos\theta^{*}\, \tilde{r}^{*}_{,\theta^{*}} \,+\, \tilde{r}^{*}_{,\varphi^{*}\varphi^{*}}\Big]\Big) \\ &\quad=\; 2\, \frac{\zeta\Omega R^{2}}{k_{\mathrm{b}}}\, \Big(\cos\theta^{*}\big[\csc\theta^{*} - \sin\theta^{*}\big]\tilde{r}^{*}_{,\theta^{*}\varphi^{*}} \,-\, \cos^{2}\theta^{*}\cot^{2}\theta^{*} \tilde{r}^{*}_{,\varphi^{*}}\Big) \\ &\qquad+\, \Gamma\Big(2\,\tilde{r}^{*} \,+\, \Delta^{*}_{\mathrm{s}}\, \tilde{r}^{*} - 2\,\tilde{\lambda}^{*}\Big) \,-\, \frac{1}{2}\Big(\Delta^{*2}_{\mathrm{s}}\, \tilde{r}^{*} \,+\, 2\,\Delta^{*}_{\mathrm{s}}\, \tilde{r}^{*}\Big) \;. \end{aligned} \tag{125}$$

For the systems under consideration, $\mathit{Re}/\Phi \,\leq\, 10^{-3} \,\ll\, 1$, such that inertial forces are always negligible relative to tension forces. Equation (125) shows the ratio of viscous forces to bending forces gives rise to the Scriven–Love number, defined as

$$\mathit{SL} \;=\; \frac{\zeta\Omega R^{2}}{k_{\mathrm{b}}} \;. \tag{126}$$

Substituting Eq. (126) into Eq. (125) and neglecting inertial terms leads to

$$2\, \mathit{SL}\, \Big(\cos\theta^{*}\big[\csc\theta^{*} - \sin\theta^{*}\big]\tilde{r}^{*}_{,\theta^{*}\varphi^{*}} \,-\, \cos^{2}\theta^{*}\cot^{2}\theta^{*} \tilde{r}^{*}_{,\varphi^{*}}\Big) + \Gamma\Big(2\,\tilde{r}^{*} + \Delta^{*}_{\mathrm{s}}\, \tilde{r}^{*} - 2\,\tilde{\lambda}^{*}\Big) - \frac{1}{2}\Big(\Delta^{*2}_{\mathrm{s}}\, \tilde{r}^{*} \,+\, 2\,\Delta^{*}_{\mathrm{s}}\, \tilde{r}^{*}\Big) \;=\; 0 \;, \tag{127}$$

provided in the main text as Eq. (38). Note that in the limit where Ω goes to zero, SL goes to zero as well (126) and the shape equation (127) simplifies to its initially static counterpart, Eq. (99).

(c). The analysis of past experimental data

We now present our calculation of the Scriven–Love and Föppl–von Kármán numbers, for initially rotating spherical vesicles, as the Scriven–Love number does not arise for initially static spheres. Details for rows 4–8 of Table I in the main text are presented as Tables 4–8 below. When values of the bending modulus k_{b} and surface tension scale Λ are not provided, we assume $k_{\mathrm{b}} = 100$ pN·nm and $\Lambda = 10^{-3}$ pN/nm. In all cases, we use $\zeta = 10$ pN·μsec/nm. Furthermore, in all experiments considered, the shear rate $\dot{\gamma}$ is provided. As described in the main text, we choose $\Omega = \dot{\gamma}$, and calculate the velocity scale V as

$$V \;=\; \dot{\gamma}\, R \; . \tag{128}$$

Experiment #1: We consider experimental data of GUVs in a shear flow, from Figs. 2, 4, and 6 of Ref. [18], which corresponds to Ref. [44, $\bowtie$] in the main text. Note the bending modulus k_{c} in Ref. [18] is related to k_{b} in the present work according to $k_{\mathrm{b}} = 2\, k_{\mathrm{c}}$.

Quantity	Value	Calculation
V	$6 \cdot 10^{-1}$ nm/μsec	Eq. (128), with $\dot{\gamma} \sim 10^{-5}$ μsec^{-1} (Fig. 2)
R	$6 \cdot 10^{4}$ nm	Fig. 4
k_{b}	30 pN·nm	Fig. 4, text on page 7136
Λ	$4 \cdot 10^{-3}$ pN/nm	Fig. 6
SL	$1 \cdot 10^{4}$	Eq. (126)
Γ	$5 \cdot 10^{5}$	Eq. (95)

Table 4: Calculations from Ref. [18], for the fourth row of Table I in the main text [44, $\bowtie$].

Experiment #2: We consider experimental data of white blood cells in a shear flow within a blood vessel, where experimental data on blood flow is obtained from Table 1 of Ref. [19], and that of white blood cells from Fig. 1 of Ref. [20]. These experiments correspond to Refs. [45, 46, $\clubsuit$] in the main text. Note that to calculate the shear rate in a blood vessel, we used the result $\dot{\gamma} \sim Q/R_{\mathrm{t}}^3$ for laminar flow in a tube of radius R_{t}, with flow rate Q.

Quantity	Value	Calculation
V	3 nm/μsec	Eq. (128), with $\dot{\gamma} \sim 5 \cdot 10^{-4}$ μsec^{-1} (Table 1 of Ref. [19])
R	$6 \cdot 10^{3}$ nm	Estimated from Fig. 1 of Ref. [20]
SL	$2 \cdot 10^{3}$	Eq. (126)
Γ	$4 \cdot 10^{2}$	Eq. (95)

Table 5: Calculations from Refs. [19, 20], for the fifth row of Table I in the main text [45, 46, $\clubsuit$].

Experiment #3: We consider experimental data of GUVs in a shear flow, from Fig. 2 and Video 1 of Ref. [21], which corresponds to Ref. [47, $\diamondsuit$] in the main text. We approximated the shear rate as $\dot{\gamma} \sim V_{\mathrm{s}}/10\,\mu$m, where V_{s} is the free streaming velocity and 10 μm is the height of the post about which the vesicle is formed. From Video 1 of the Supporting information, we calculate $V_{\mathrm{s}} \sim 1$ nm/μsec, such that $\dot{\gamma} \sim 10^{-4}$ $\mu\mathrm{sec}^{-1}$.

Quantity	Value	Calculation
V	$6 \cdot 10^{-1}$ nm/μsec	Eq. (128), with $\dot{\gamma} \sim 10^{-4}$ $\mu\mathrm{sec}^{-1}$ (Fig. 2(a) and Video 1)
R	$6 \cdot 10^{3}$ nm	Fig. 2(d)
SL	$4 \cdot 10^{2}$	Eq. (126)
Γ	$4 \cdot 10^{2}$	Eq. (95)

Table 6: Calculations from Ref. [21], for the sixth row of Table I in the main text [47, ♢].

Experiment #4: We consider experimental data of GUVs in a shear flow, from line 18 in Table 1 of Ref. [22], which corresponds to Ref. [48, ♡] in the main text. Note the bending modulus κ_{c} in Ref. [22] is related to k_{b} in the present work according to $k_{\mathrm{b}} = 2\,\kappa_{\mathrm{c}}$.

Quantity	Value	Calculation
V	$3 \cdot 10^{-2}$ nm/μsec	Eq. (128), with $\dot{\gamma} \sim 2 \cdot 10^{-6}$ $\mu\mathrm{sec}^{-1}$ (Table 1, line 18)
R	$1 \cdot 10^{4}$ nm	Table 1, line 18
k_{b}	170 pN·nm	Page 394, below Eq. (9)
SL	$2 \cdot 10^{1}$	Eq. (126)
Γ	$6 \cdot 10^{2}$	Eq. (95)

Table 7: Calculations from Ref. [22], for the seventh row of Table I in the main text [48, ♡].

Experiment #5: We consider experimental data of the lipid membranes surrounding retrovirus particles in a shear flow within a blood vessel, where experimental data on blood flow is again obtained from Table 1 of Ref. [19], and that of retrovirus particles from Fig. 1 of Ref. [23]. These experiments correspond to Refs. [45, 49, ♠] in the main text. The shear rate calculation is identical to that of Experiment #2 (see Table 5).

Quantity	Value	Calculation
V	$3 \cdot 10^{-3}$ nm/μsec	Eq. (128), with $\dot{\gamma} \sim 5 \cdot 10^{-4}$ $\mu\mathrm{sec}^{-1}$ (Table 1 of Ref. [19])
R	$5 \cdot 10^{1}$ nm	Estimated from Fig. 1 of Ref. [23]
SL	$1 \cdot 10^{-1}$	Eq. (126)
Γ	$2 \cdot 10^{-2}$	Eq. (95)

Table 8: Calculations from Refs. [19, 23], for the eighth row of Table I in the main text [45, 49, ♠].

IV. Cylindrical Membrane Tubes

The final geometry we consider is that of lipid membrane tubes, following the same procedure as in the previous two cases. We present the general unperturbed and perturbed governing equations, and then non-dimensionalized them in two cases: (i) a static membrane tube and (ii) a tube with a base flow. For lipid membrane tubes, the surface tension scale in the base state can be set by either bending forces or the pressure drop across the membrane. Moreover, tubes can have an axial length scale, over which quantities vary, that is much longer than the tube radius. This leads to the possibility of different velocity scales in the axial and angular direction. Importantly, we find that unlike the planar and spherical geometries, the Scriven–Love number *SL* emerges in both the initially static case and the situation with a base flow, thus showing that geometry plays a significant role in the dynamics of lipid membranes.

1. The general unperturbed governing equations

The position of an unperturbed cylindrical membrane tube of radius R is given by

$$\boldsymbol{x}_{(0)}(\theta, z) \;=\; R\,\boldsymbol{e}_r(\theta) \;+\; z\,\boldsymbol{e}_z \;, \tag{129}$$

where θ and z are the polar angle and axial position, respectively, of a standard cylindrical coordinate system, as shown in Fig. 5(a) of the main text. Relevant geometric quantities are calculated as

$$\begin{aligned}
&\boldsymbol{a}_1^{(0)} = R\,\boldsymbol{e}_\theta \;, \qquad \boldsymbol{a}_2^{(0)} = \boldsymbol{e}_z \;, \qquad \boldsymbol{n}_{(0)} = \boldsymbol{e}_r \;, \qquad a^{(0)}_{\alpha\beta} = \operatorname{diag}(R^2, 1) \;, \qquad a^{\alpha\beta}_{(0)} = \operatorname{diag}(R^{-2}, 1) \;, \\
&b^{(0)}_{\alpha\beta} = \operatorname{diag}(-R, 0) \;, \qquad H_{(0)} = -1/(2R) \;, \qquad K_{(0)} = 0 \;, \qquad \text{and} \qquad \Gamma^{\alpha(0)}_{\lambda\mu} = 0 \;.
\end{aligned} \tag{130}$$

Furthermore, for a cylindrical tube the surface Laplacian of a scalar quantity is given by $\Delta_{\mathrm{s}}\,(\,\cdot\,) = R^{-2}(\,\cdot\,)_{,\theta\theta} + (\,\cdot\,)_{,zz}$. An unperturbed membrane tube has no normal velocity component, so $v_{(0)} = 0$ and the membrane velocity $\boldsymbol{v}_{(0)}$ is given by

$$\boldsymbol{v}_{(0)} \;=\; v^\alpha_{(0)}\boldsymbol{a}^{(0)}_\alpha \;=\; R\,v^\theta_{(0)}\boldsymbol{e}_\theta \;+\; v^z_{(0)}\boldsymbol{e}_z \;. \tag{131}$$

Given the above geometric quantities, we find the unperturbed continuity, in-plane θ, in-plane z, and shape equations, (1), (10), and (11), are respectively given by

$$v^\theta_{(0),\theta} \;+\; v^z_{(0),z} \;=\; 0 \;, \tag{132}$$

$$\rho\,R^3\left(v^\theta_{(0),t} \;+\; v^\theta_{(0)}\,v^\theta_{(0),\theta} \;+\; v^z_{(0)}\,v^\theta_{(0),z}\right) \;=\; \zeta\,R\left(v^\theta_{(0),\theta\theta} \;+\; R^2\,v^\theta_{(0),zz}\right) \;+\; R\,\lambda_{(0),\theta} \;, \tag{133}$$

$$\rho\,R^2\left(v^z_{(0),t} \;+\; v^\theta_{(0)}\,v^z_{(0),\theta} \;+\; v^z_{(0)}\,v^z_{(0),z}\right) \;=\; \zeta\left(v^z_{(0),\theta\theta} \;+\; R^2\,v^z_{(0),zz}\right) \;+\; R^2\,\lambda_{(0),z} \;, \tag{134}$$

and

$$-\rho\,R^3\,(v^\theta_{(0)})^2 \;=\; pR^2 \;-\; R\,\lambda_{(0)} \;+\; \frac{k_{\mathrm{b}}}{4R} \;+\; 2\,\zeta\,R\,v^z_{(0),z} \;. \tag{135}$$

While the continuity (132) and in-plane (133, 134) equations are similar in structure to those of a flat plane (15, 16), the cylindrical shape equation (135) differs from its flat (17) and spherical (72) counterparts in that it balances inertia, pressure, surface tension, and viscous forces. In the simplest case when there is no flow, if $p = 0$ then $\lambda_{(0)} = k_{\mathrm{b}}/(4R^2)$, as first discussed in Ref. [24]. On the other hand, if there is no flow and bending forces are negligible, we obtain the Young–Laplace equation $\lambda_{(0)} = pR$.

2. The general perturbed governing equations

We introduce a height perturbation in the normal direction, such that the membrane position is given by

$$\boldsymbol{x}(\theta, z, t) \;=\; \Big[R \;+\; \epsilon\,\tilde{r}(\theta, z, t)\Big]\boldsymbol{e}_r(\theta) \;+\; z\,\boldsymbol{e}_z \;. \tag{136}$$

In this case, the small parameter ϵ is defined as

$$\epsilon := \frac{\delta R}{R} \ll 1 , \tag{137}$$

where as in the spherical case δR is the characteristic size of the radial perturbation and $\tilde{r}$ is $O(R)$, as shown in Fig. 5(b) in the main text. To first order in ϵ, the perturbed geometric quantities are given by

$$\begin{aligned}
\boldsymbol{a}_1 &= \big(R + \epsilon\,\tilde{r}\big)\,\boldsymbol{e}_\theta + \epsilon\,\tilde{r}_{,\theta}\,\boldsymbol{e}_r , & \boldsymbol{a}_2 &= \boldsymbol{e}_z + \epsilon\,\tilde{r}_{,z}\,\boldsymbol{e}_r , \\
\boldsymbol{n} &= \boldsymbol{e}_r - \frac{\epsilon}{R}\,\tilde{r}_{,\theta}\,\boldsymbol{e}_\theta - \epsilon\,\tilde{r}_{,z}\,\boldsymbol{e}_z , & a_{\alpha\beta} &= \mathrm{diag}\,\big(R^2 + 2\epsilon\,\tilde{r}R,\ 1\big) , \\
b_{\alpha\beta} &= -\mathrm{diag}\,\big(R + \epsilon\,\tilde{r},\ 0\big) - \epsilon\,\tilde{r}_{,\alpha\beta} , & \Gamma^\theta_{\theta\theta} &= \epsilon\,\tilde{r}_{,\theta}/R , \\
\Gamma^\theta_{\theta z} &= \Gamma^\theta_{z\theta} = \epsilon\,\tilde{r}_{,z}/R , & \Gamma^z_{\theta\theta} &= -\epsilon\,R\,\tilde{r}_{,z} , \\
H &= -\big(R - \epsilon\,\tilde{r} - \epsilon\,R^2\,\Delta_\mathrm{s}\,\tilde{r}\big)/(2R^2) , \quad \text{and} & K &= -\epsilon\,\tilde{r}_{,zz}/R .
\end{aligned} \tag{138}$$

The fundamental unknowns are expanded to first order as

$$v^\theta = v^\theta_{(0)} + \epsilon\,\tilde{v}^\theta , \qquad v^z = v^z_{(0)} + \epsilon\,\tilde{v}^z , \qquad v = \epsilon\,\tilde{r}_{,t} , \qquad \text{and} \qquad \lambda = \lambda_{(0)} + \epsilon\,\tilde{\lambda} , \tag{139}$$

where as before quantities with a 'tilde' are assumed to be the same order as their unperturbed counterparts. By substituting Eqs. (138) and (139) into Eqs. (1), (10), and (11) and keeping only first order terms, we find the first-order perturbed governing equations as

$$R\,\tilde{v}^\theta_{,\theta} + R\,\tilde{v}^z_{,z} + v^\theta_{(0)}\,\tilde{r}_{,\theta} + v^z_{(0)}\,\tilde{r}_{,z} + \tilde{r}_{,t} = 0 , \tag{140}$$

$$\begin{aligned}
&\rho R^2 \Big(R\,\tilde{v}^\theta_{,t} + v^\theta_{(0)}\,\big(2\,\tilde{r}_{,t} + v^\theta_{(0)}\,\tilde{r}_{,\theta} + 2\,v^z_{(0)}\,\tilde{r}_{,z}\big) + R\,v^\theta_{(0)}\,\tilde{v}^\theta_{,\theta} + R\,v^z_{(0)}\,\tilde{v}^\theta_{,z}\Big) \\
&\qquad = \zeta\,\Big(\tilde{r}_{,t\theta} + R\,\tilde{v}^\theta_{,\theta\theta} + R^3\,\tilde{v}^\theta_{,zz} + v^\theta_{(0)}\,\tilde{r}_{,\theta\theta} + v^z_{(0)}\,\tilde{r}_{,\theta z}\Big) + R\,\tilde{\lambda}_{,\theta} ,
\end{aligned} \tag{141}$$

$$\begin{aligned}
&\rho R^2 \Big(\tilde{v}^z_{,t} + v^\theta_{(0)}\,\tilde{v}^z_{,\theta} + v^z_{(0)}\,\tilde{v}^z_{,z} - R\,(v^\theta_{(0)})^2\,\tilde{r}_{,z}\Big) \\
&\qquad = \zeta\,\Big(-R\,\tilde{r}_{,tz} + \tilde{v}^z_{,\theta\theta} + R^2\,\tilde{v}^z_{,zz} - R\,v^\theta_{(0)}\,\tilde{r}_{,\theta z} - R\,v^z_{(0)}\,\tilde{r}_{,zz}\Big) + R^2\,\tilde{\lambda}_{,z} ,
\end{aligned} \tag{142}$$

and

$$\begin{aligned}
&\rho R^2\Big(\tilde{r}_{,tt} + v^\theta_{(0)}\,\tilde{r}_{,t\theta} + v^z_{(0)}\,\tilde{r}_{,tz} - 2\,R\,v^\theta_{(0)}\,\tilde{v}^\theta - (v^\theta_{(0)})^2\,\big(\tilde{r} - \tilde{r}_{,\theta\theta}\big) + 2\,v^\theta_{(0)}\,v^z_{(0)}\,\tilde{r}_{,\theta z} + (v^z_{(0)})^2\,\tilde{r}_{,zz}\Big) \\
&\quad = 2\,\zeta\,R\,\tilde{v}^z_{,z} + \lambda_{(0)}\,\Big(\tilde{r} + R^2\,\Delta_\mathrm{s}\tilde{r}\Big) - R\,\tilde{\lambda} - \frac{k_\mathrm{b}}{4R^2}\Big(3\,\tilde{r} + 4\,\tilde{r}_{,\theta\theta} + R^2\,\Delta_\mathrm{s}\,\tilde{r} + 2\,R^4\,\Delta^2_\mathrm{s}\,\tilde{r}\Big) .
\end{aligned} \tag{143}$$

In what follows, we non-dimensionalize the unperturbed (132)–(135) and perturbed (140)–(143) governing equations for tubes which are either static or have a flow in the base state.

3. The case of an initially static membrane tube: non-dimensionalization

We begin by non-dimensionalizing the unperturbed and perturbed equations governing a lipid membrane tube initially at rest, for which $\boldsymbol{v}_{(0)} = \boldsymbol{0}$. According to Eqs. (132)–(135), the unperturbed solution is given by

$$v^\theta_{(0)} = 0 , \qquad v^z_{(0)} = 0 , \qquad v_{(0)} = 0 , \qquad \text{and} \qquad \lambda_{(0)} = \lambda_0 := pR + \frac{k_\mathrm{b}}{4R^2} . \tag{144}$$

The shape equation $(144)_4$ indicates the base state surface tension scale can be set by either bending or pressure forces, however in all cases, we chose the surface tension scale Λ as

$$\Lambda := \lambda_0 = pR + \frac{k_\mathrm{b}}{4R^2} , \qquad \text{such that} \qquad \lambda^*_{(0)} := \frac{\lambda_{(0)}}{\Lambda} = 1 . \tag{145}$$

The perturbed governing equations for an initially static membrane tube are found by substituting Eq. (144) into Eqs. (140)–(143), yielding

$$R\,\tilde{v}^{\theta}_{,\theta} \,+\, R\,\tilde{v}^{z}_{,z} \,+\, \tilde{r}_{,t} \,=\, 0 \;, \tag{146}$$

$$\rho R^3\,\tilde{v}^{\theta}_{,t} \,=\, \zeta\left(\tilde{r}_{,t\theta} \,+\, R\,\tilde{v}^{\theta}_{,\theta\theta} \,+\, R^3\,\tilde{v}^{\theta}_{,zz}\right) \,+\, R\,\tilde{\lambda}_{,\theta} \;, \tag{147}$$

$$\rho R^2\,\tilde{v}^{z}_{,t} \,=\, \zeta\left(-\,R\,\tilde{r}_{,tz} \,+\, \tilde{v}^{z}_{,\theta\theta} \,+\, R^2\,\tilde{v}^{z}_{,zz}\right) \,+\, R^2\,\tilde{\lambda}_{,z} \;, \tag{148}$$

and

$$\rho R^2\,\tilde{r}_{,tt} \,=\, 2\,\zeta\,R\,\tilde{v}^{z}_{,z} \,+\, \lambda_0\left(\tilde{r} \,+\, R^2\,\Delta_{\mathrm{s}}\,\tilde{r}\right) \,-\, R\,\tilde{\lambda} \,-\, \frac{k_{\mathrm{b}}}{4R^2}\left(3\,\tilde{r} \,+\, 4\,\tilde{r}_{,\theta\theta} \,+\, R^2\,\Delta_{\mathrm{s}}\,\tilde{r} \,+\, 2\,R^4\,\Delta_{\mathrm{s}}^2\,\tilde{r}\right) . \tag{149}$$

At this point, we introduce the relevant dimensionless quantities. The small parameter ϵ is given by Eq. (137), such that $\tilde{r}$ is $O(R)$. We assume a perturbation in the radial direction causes gradients in the angular direction over $O(1)$ changes in θ, however as detailed in Sec. V A of the main text, perturbations may vary over axial distances L which are much larger than the tube radius R. We therefore define the parameter

$$\delta \,:=\, \frac{R}{L} \tag{150}$$

to characterize the length scale over which quantities vary in the axial direction, relative to the cylinder radius. We emphasize that δ is not the aspect ratio of the tube: L is the length scale over which quantities are expected to vary in the axial direction, and two tubes with the same aspect ratio can have different values of δ (see Fig. 6 of the main text). Here and from now on, we refer to tubes with $\delta \sim 1$ as thick tubes, while those with $\delta \ll 1$ are referred to as thin tubes. We also denote the currently unknown characteristic angular velocity scale as Ω and axial velocity scale as V. Finally, we introduce the unknown time scale τ over which radial perturbations vary, and define the dimensionless quantities

$$\theta^* := \theta \;, \quad z^* := \frac{z}{L} \;, \quad \tilde{r}^* := \frac{\tilde{r}}{R} \;, \quad \tilde{v}^{\theta *} := \frac{\tilde{v}^{\theta}}{\Omega} \;, \quad \tilde{v}^{z *} := \frac{\tilde{v}^{z}}{V} \;, \quad \tilde{\lambda}^* := \frac{\tilde{\lambda}}{\Lambda} \;, \quad \text{and} \quad t^* := \frac{t}{\tau} \;. \tag{151}$$

In Eq. (151), we once again assume the base state surface tension scale Λ (145) also sets the scale of $\tilde{\lambda}$. With Λ and L known, we seek to determine Ω, V, and τ through appropriate non-dimensionalization of the perturbed governing equations (146)–(149) for thick and thin tubes.

(a). The case of a thick tube ($L \sim R$)

For thick tubes, the axial length scale over which gradients are expected is equal to the tube radius, written as $L = R$. We substitute Eq. (151) into the perturbed continuity equation (146) to obtain

$$\Omega\;\tilde{v}^{\theta *}_{,\theta^*} \,+\, \frac{V}{R}\,\tilde{v}^{z *}_{,z^*} \,+\, \frac{1}{\tau}\,\tilde{r}^{*}_{,t^*} \,=\, 0 \;. \tag{152}$$

Assuming both axial and angular in-plane velocity gradients account for the changes in membrane shape, we require

$$\Omega \,=\, \frac{V}{R} \,=\, \frac{1}{\tau} \;, \tag{153}$$

such that Eq. (152) simplifies to

$$\tilde{v}^{\theta *}_{,\theta^*} \,+\, \tilde{v}^{z *}_{,z^*} \,+\, \tilde{r}^{*}_{,t^*} \,=\, 0 \;. \tag{154}$$

The continuity equation (154) connects out-of-plane deformations and in-plane flows, and along with Eq. (153) indicates the time scale τ over which height perturbations vary is equal to the time scales $1/\Omega$ and R/V of angular and axial in-plane flows, respectively. Equation (154) is provided as Eq. (49) in the main text.

We next substitute Eqs. (151) and (153) into the perturbed in-plane equations, (147) and (148), and rearrange terms to obtain

$$Re\,\tilde{v}^{\theta*}_{,t^*} \;=\; \tilde{r}^*_{,t^*\theta^*} \,+\, \tilde{v}^{\theta*}_{,\theta^*\theta^*} \,+\, \tilde{v}^{\theta*}_{,z^*z^*} \,+\, \frac{\Lambda R}{\zeta V}\,\tilde{\lambda}^*_{,\theta^*} \tag{155}$$

and

$$Re\,\tilde{v}^{z*}_{,t^*} \;=\; -\tilde{r}^*_{,t^*z^*} \,+\, \tilde{v}^{z*}_{,\theta^*\theta^*} \,+\, \tilde{v}^{z*}_{,z^*z^*} \,+\, \frac{\Lambda R}{\zeta V}\,\tilde{\lambda}^*_{,z^*}\ , \tag{156}$$

where for cylindrical tubes the Reynolds number is given by

$$Re \;:=\; \frac{\rho V R}{\zeta}\ . \tag{157}$$

We choose for the axial velocity scale V to satisfy $\zeta V = \Lambda R$, such that surface tension and viscous forces balance in the in-plane equations, (155) and (156). As a result, the time and velocity scales are given by

$$\tau \;=\; \frac{\zeta}{\Lambda}\ , \qquad \Omega \;=\; \frac{\Lambda}{\zeta}\ , \qquad \text{and} \qquad V \;=\; \frac{\Lambda R}{\zeta}\ . \tag{158}$$

In this case, the Reynolds number (157) can be written as $Re = \rho\Lambda R^2/\zeta^2$, which ranges from 10^{-12} to 10^{-7} over the experiments considered, and in all cases $Re \ll 1$. Accordingly, Eqs. (155) and (156) simplify to

$$\tilde{r}^*_{,t^*\theta^*} \,+\, \tilde{v}^{\theta*}_{,\theta^*\theta^*} \,+\, \tilde{v}^{\theta*}_{,z^*z^*} \,+\, \tilde{\lambda}^*_{,\theta^*} \;=\; 0 \tag{159}$$

and

$$-\,\tilde{r}^*_{,t^*z^*} \,+\, \tilde{v}^{z*}_{,\theta^*\theta^*} \,+\, \tilde{v}^{z*}_{,z^*z^*} \,+\, \tilde{\lambda}^*_{,z^*} \;=\; 0\ , \tag{160}$$

which are Eqs. (50) and (51) in the main text.

Finally, we non-dimensionalize the shape equation (149) by substituting Eqs. (151), (153), and (158) and rearranging terms to obtain

$$\frac{\rho\Lambda^2R^4}{\zeta^2k_{\mathrm{b}}}\,\tilde{r}^*_{,t^*t^*} \;=\; 2\,\frac{\zeta V R}{k_{\mathrm{b}}}\,\tilde{v}^{z*}_{,z^*} \,+\, \frac{\Lambda R^2}{k_{\mathrm{b}}}\Big(\tilde{r}^* \,+\, \Delta^*_{\mathrm{s}}\,\tilde{r}^* \,-\, \tilde{\lambda}^*\Big) \,-\, \frac{1}{4}\Big(3\,\tilde{r}^* \,+\, 4\,\tilde{r}^*_{,\theta^*\theta^*} \,+\, \Delta^*_{\mathrm{s}}\,\tilde{r}^* \,+\, 2\,\Delta^{*2}_{\mathrm{s}}\,\tilde{r}^*\Big)\ , \tag{161}$$

where for thick tubes $\Delta^*_{\mathrm{s}}\,(\,\cdot\,) = R^2\Delta_{\mathrm{s}}\,(\,\cdot\,)$. In Eq. (161), the coeffient $\zeta V R/k_{\mathrm{b}}$ compares viscous to bending forces while the coefficient $\Lambda R^2/k_{\mathrm{b}}$ compares tension to viscous forces. We accordingly obtain the Scriven–Love and Föppl–von Kármán numbers as

$$SL \;=\; \frac{\zeta V R}{k_{\mathrm{b}}} \qquad \text{and} \qquad \Gamma \;=\; \frac{\Lambda R^2}{k_{\mathrm{b}}}\ , \tag{162}$$

for which Eq. (161) can be written as

$$Re\,\Gamma\,\tilde{r}^*_{,t^*t^*} \;=\; 2\,SL\,\tilde{v}^{z*}_{,z^*} \,+\, \Gamma\big(\tilde{r}^* \,+\, \Delta^*_{\mathrm{s}}\,\tilde{r}^* \,-\, \tilde{\lambda}^*\big) \,-\, \frac{1}{4}\big(3\,\tilde{r}^* \,+\, 4\,\tilde{r}^*_{,\theta^*\theta^*} \,+\, \Delta^*_{\mathrm{s}}\,\tilde{r}^* \,+\, 2\,\Delta^{*2}_{\mathrm{s}}\,\tilde{r}^*\big)\ . \tag{163}$$

Note that given the relations in Eq. (158), in this case $SL = \Gamma$. Moreover, as we found $Re \ll 1$ in the biological systems considered, inertial forces are negligible compared to tension forces. Equation (163), with the inertial terms neglected, is presented as Eq. (52) in the main text.

(b). The case of a thin tube $(L \gg R)$

For a thin tube, the length scale L over which axial gradients occur is much larger than the cylinder radius R. We begin by substituting Eq. (151) into the perturbed continuity equation (146), which yields

$$\Omega\;\tilde{v}^{\theta*}_{,\theta^*} \,+\, \frac{V}{L}\;\tilde{v}^{z*}_{,z^*} \,+\, \frac{1}{\tau}\;\tilde{r}^*_{,t^*} \;=\; 0\ . \tag{164}$$

Again assuming both axial and angular in-plane velocity gradients account for the changing membrane shape, we find

$$\Omega = \frac{V}{L} = \frac{1}{\tau} , \tag{165}$$

such that Eq. (164) simplifies to

$$\tilde{v}^{\theta *}_{,\theta^*} + \tilde{v}^{z*}_{,z^*} + \tilde{r}^{*}_{,t^*} = 0 , \tag{166}$$

which is identical to the dimensionless continuity equation for a thick tube (154).

Substituting Eqs. (150), (151), and (165) into the in-plane equations (147, 148) and rearranging terms yields

$$Re\, \delta\, \tilde{v}^{\theta *}_{,t^*} = \tilde{r}^{*}_{,t^*\theta^*} + \tilde{v}^{\theta *}_{,\theta^*\theta^*} + \delta^2\, \tilde{v}^{\theta *}_{,z^*z^*} + \frac{\Lambda L}{\zeta V}\, \tilde{\lambda}^{*}_{,\theta^*} \tag{167}$$

and

$$Re\, \delta\, \tilde{v}^{z *}_{,t^*} = -\delta^2\, \tilde{r}^{*}_{,t^*z^*} + \tilde{v}^{z *}_{,\theta^*\theta^*} + \delta^2\, \tilde{v}^{z *}_{,z^*z^*} + \delta^2\, \frac{\Lambda L}{\zeta V}\, \tilde{\lambda}^{*}_{,z^*} , \tag{168}$$

with Reynolds number $Re = \rho V R/\zeta$. Given Eqs. (167) and (168), there are now two choices for the velocity scale V: we could choose (i) $V = \delta^2 \Lambda L/\zeta$, such that viscous terms and tension gradients balance in the z-direction (168), or (ii) $V = \Lambda L/\zeta$, such that viscous terms balance surface tension gradients in the θ-direction (167). We consider both scaling relations below, ignoring inertial terms for clarity of argument.

In the first case, $V = \delta^2 \Lambda L/\zeta$ and all viscous terms are negligible in the θ-equation (167)—which simplifies to $\tilde{\lambda}^{*}_{,\theta^*} = 0$, implying $\tilde{\lambda}^*$ is independent of θ^*. In the in-plane z-equation, on the other hand, the leading order viscous term balances the surface tension gradient, and we obtain $\tilde{v}^{z*}_{,\theta^*\theta^*} + \tilde{\lambda}_{,z^*} = 0$. As $\tilde{\lambda}^*$ is independent of θ^*, $\tilde{v}^{z^*}_{,\theta^*\theta^*}$ is independent of θ^* as well, and $\tilde{v}^{z*}$ is at most quadratic in θ^*. However, due to the cylindrical geometry $\tilde{v}^{z^*}$ must be periodic in θ^*, which implies $\tilde{v}^{z^*}$ is not a function of θ^*. As a result, the z-equation simplifies to $\tilde{\lambda}^{*}_{,z^*} = 0$, such that $\tilde{\lambda}^*$ is independent of both θ^* and z^*, regardless of how local a perturbation we apply. As such a result is unphysical, this choice of velocity scaling is incorrect, and we turn to the second option.

In the second case, $V = \Lambda L/\zeta$ and the θ-equation simplifies to

$$Re\, \delta\, \tilde{v}^{\theta *}_{,t^*} = \tilde{r}^{*}_{,t^*\theta^*} + \tilde{v}^{\theta *}_{,\theta^*\theta^*} + \tilde{\lambda}^{*}_{,\theta^*} . \tag{169}$$

However, $Re\, \delta = \rho \Lambda R^2/\zeta^2$, which was previously shown to be much less than one, such that inertial terms can be neglected. In the z-equation, to leading order we have

$$\tilde{v}^{z *}_{,\theta^*\theta^*} = 0 , \tag{170}$$

which due to the periodicity requirement enforces $\tilde{v}^{z*}$ to be independent of θ^*, such that $\tilde{v}^{z*} = \tilde{v}^{z*}(z^*, t^*)$. In this case, taking the partial derivative of the continuity equation (166) with respect to θ^* yields $\tilde{v}^{\theta *}_{,\theta^*\theta^*} + \tilde{r}^{*}_{,t^*\theta^*} = 0$. We then find Eq. (169) simplifies to

$$\tilde{\lambda}^{*}_{,\theta^*} = 0 , \tag{171}$$

such that $\tilde{\lambda}^*$ is independent of θ^* and can be written as $\tilde{\lambda}^* = \tilde{\lambda}^*(z^*, t^*)$. Thus, we find that for a thin tube, the choice of scaling

$$V = \frac{\Lambda L}{\zeta} \tag{172}$$

results in both the axial velocity $\tilde{v}^{z*}$ and the surface tension $\tilde{\lambda}^*$ being axisymmetric—a physically reasonable result for a thin tube. Equations (170) and (171) are presented as Eqs. (58) and (59) in the main text.

Finally, with $V = \Lambda L/\zeta$ (172) and $\delta \ll 1$ for a thin tube, the dimensionless shape equation (149) can be written as

$$\Gamma\, Re\, \delta\, \tilde{r}^{*}_{,t^*t^*} = 2\, SL\, \delta \tilde{v}^{z*}_{,z^*} + \Gamma \left(\tilde{r}^* + \tilde{r}^{*}_{,\theta^*\theta^*} - \tilde{\lambda}^*\right) - \frac{1}{4}\left(3\, \tilde{r}^* + 5\, \tilde{r}^{*}_{,\theta^*\theta^*} + 2\, \tilde{r}^{*}_{,\theta^*\theta^*\theta^*\theta^*}\right) , \tag{173}$$

with the Scriven–Love and Föppl–von Kármán numbers once again given by Eq. (162). We note that given the scaling of the velocity (172), in this regime $SL\, \delta = \Gamma$. Furthermore, as $Re\, \delta = \rho \Lambda R^2/\zeta \ll 1$, inertial terms are negligible relative to tension and viscous terms. Equation (173), with the inertial terms removed, is given as Eq. (60) in the main text. Interestingly, in Eq. (173) and its thick tube analog, Eq. (163), we see the emergence of the Scriven–Love number SL in perturbed, initially static tubes. As the Scriven–Love number did not appear in the equations governing initially static flat patches (40) or spherical vesicles (99), the cylindrical equations demonstrate how geometry plays an important role in the dynamics of lipid membranes.

(c). The analysis of past experimental data

At this point, we provide the calculation of quantities in rows 9–11 of Table I in the main text, which correspond to three different experiments in Ref. [25]. As we will see, for two of these experiments, $\Gamma \geq {}^3\!/_4$—which, as discussed in the main text, can lead to membrane pearling [26, 27]. Such an instability involves shape changes over an axial length scale $L = R$. Therefore, we use the thick tube results in our analysis of the aforementioned experiments.

Before analyzing each case, we highlight the importance of determining the pressure drop p across the membrane surface, in order to correctly calculate the scale of the surface tension. A force balance on the membrane [1, 28] shows the pulling force required to maintain a static membrane tube can be written as

$$\begin{aligned} f_{\mathrm{pull}} \;&=\; \frac{\pi k_{\mathrm{b}}}{R} \;+\; p\,\pi R^2 \\ &=\; 4\pi R\lambda \;-\; 3\pi R^2\, p \\ &=\; \pi R\lambda \;+\; \frac{3\pi k_{\mathrm{b}}}{4R}\;, \end{aligned} \tag{174}$$

where the three expressions are equivalent given the unperturbed shape equation $(144)_4$. Many experimental studies assume the pressure drop $p = 0$, in which case

$$\lambda_0 \;=\; \frac{k_{\mathrm{b}}}{4R^2} \qquad\text{and}\qquad f_{\mathrm{pull}} \;=\; 2\pi\sqrt{k_{\mathrm{b}}\lambda_0}\;. \tag{175}$$

However, the pull force expression in Eq. (175) can only be used when the pressure drop p is known to be zero; in general Eq. (174) must be used. Experimental studies generally do not verify there is no pressure drop before using Eq. (175), and Ref. [25] is the only study we found which provides sufficient data to calculate the pressure drop, and ascertain whether the pressure drop is nonzero. Thus, the surface tension scale can be calculated appropriately according to Eq. (174). In Tables 9–11, we calculate the Scriven–Love and Föppl–von Kármán numbers in three different experiments in Ref. [25], which correspond to rows 9–11 in Table 1 of the main text.

Experiment #1: We consider experimental data in which a lipid membrane tube is pulled from a cell bleb, and a pipette injecting pure water is brought closer to and farther from the membrane tether in order to vary the osmotic pressure drop across the membrane. The data is obtained from Fig. S2(e), in the Supplementary Information of Ref. [25], which corresponds to Ref. [50, ✠] in the main text. To calculate the surface tension scale, we first recognize that as the pipette is brought closer to the tether, both the pressure drop and pull force increase, in accordance with Eq. (174). Assuming $p = 0$ when the pipette–tether distance is maximal, we find $f_{\mathrm{pull}} = 11$ pN $= \pi k_{\mathrm{b}}/R$, such that for the reported value of k_{b} we find $R = 110$ nm. Next, we consider the point where the membrane tears, for which (assuming R does not change) $f_{\mathrm{pull}} = 79\,\mathrm{pN} = \pi k_{\mathrm{b}}/R + p\pi R^2$. Thus, $p\pi R^2 = 68$ pN, such that $p = 1.8\cdot 10^{-3}$ pN/nm^2 = 1.8 kPa. With R and p known, we calculate Λ, through Eq. $(174)_1$ and obtain $\Lambda \approx 0.2$ pN/nm. Once the radius R and tension scale Λ are known, V, SL, and Γ are calculated. Note the bending modulus κ in Ref. [25] is related to k_{b} in the present work according to $k_{\mathrm{b}} = 2\kappa$.

Quantity	Value	Calculation
V	2 nm/μsec	Eq. (158)$_3$
R	$1 \cdot 10^2$ nm	Eq. (174)$_1$, with $p = 0$, at max pipette distance
k_b	380 pN·nm	Fig. S2 caption
Λ	$2 \cdot 10^{-1}$ pN/nm	Fig. S2(e), Eq. (174)
SL	7	Eq. (162)
Γ	7	Eq. (162)

Table 9: Calculations from Ref. [25], for the ninth row of Table I in the main text [50, ✠].

Experiment #2: We consider experimental data in which a lipid membrane tether is pulled from a cell bleb, and then held stationary while the pull force relaxes. The data is obtained from Fig. S2(c), in the Supplementary Information of Ref. [25], which corresponds to Ref. [50, ⊛] in the main text. The tube is pulled from $t \approx 18$ seconds to $t \approx 22$ seconds, at which point the tube is kept at a fixed length and the pull force f_pull is allowed to relax, decreasing over time. The tube radius R does not change during this relaxation (Fig. S2(c), blue curve), and according to Eq. (174)$_1$ the decrease in the pull force implies a decrease in the pressure drop p as well. At $t \approx 45$ seconds, the pull force has relaxed, at which point we assume the pressure drop $p \approx 0$. We seek to calculate the pressure drop at $t \approx 22$ seconds, when the tube is initially held stationary. To this end, we recognize $f_\mathrm{pull} = 30$ pN at $t \approx 45$ seconds, and we approximate $f_\mathrm{pull} = 60$ pN at $t \approx 22$ seconds. Following the same set of calculations as in Experiment #1, and correspondingly Table 9, we find $p \approx 6 \cdot 10^{-3}$ pN/nm^2 = 6 kPa and $\Lambda \sim 0.3$ pN/nm, and then calculate all other values. Note the bending modulus κ in Ref. [25] is related to k_b in the present work according to $k_\mathrm{b} = 2\kappa$.

Quantity	Value	Calculation
V	1 nm/μsec	Eq. (158)$_3$
R	$4 \cdot 10^1$ nm	Eq. (174)$_1$, with $p = 0$, at $t = 45$ sec
k_b	380 pN·nm	Fig. S2 caption
Λ	$3 \cdot 10^{-1}$ pN/nm	Fig. S2(c), Eq. (174)
SL	1	Eq. (162)
Γ	1	Eq. (162)

Table 10: Calculations from Ref. [25], for the tenth row of Table I in the main text [50, ⊛].

Experiment #3: We consider experimental data in which a lipid membrane tube is pulled from a GUV, and the membrane tension is altered via pipette aspiration. The data is obtained from Fig. S1, in the Supplementary Information of Ref. [25], which corresponds to Ref. [50, ¶] in the main text. The data in Fig. S1(d) shows $f_\mathrm{pull} \sim \sqrt{\lambda_0}$, indicating the pressure drop is negligible such that Eq. (175) holds. The slope of the curve in Fig. S1(d) indicates $k_\mathrm{b} = 250$ pN·nm. In Fig. S1(b), at $t = 100$ sec, $\Lambda \approx 0.15$ pN/nm and $f_\mathrm{pull} \approx 33$ pN, for which $R = 20$ nm (175). Note the bending modulus κ in Ref. [25] is related to k_b in the present work according to $k_\mathrm{b} = 2\kappa$.

Quantity	Value	Calculation
V	$4 \cdot 10^{-1}$ nm/μsec	Eq. $(158)_3$
R	$2 \cdot 10^{1}$ nm	Eq. $(175)_2$
k_{b}	250 pN·nm	Slope of Fig. S1(d), with Eq. $(175)_2$
Λ	$2 \cdot 10^{-1}$ pN/nm	Fig. S1(b)
SL	$1/4$	Eq. (162)
Γ	$1/4$	Eq. (162)

Table 11: Calculations from Ref. [25], for the eleventh row of Table I in the main text [50, ¶].

4. The case of a membrane tube with a base flow: non-dimensionalization

We end by considering a cylindrical membrane tube which is traveling with constant axial velocity v_0 prior to being perturbed. We first show a constant axial velocity is a solution of the unperturbed membrane equations, and then present the corresponding non-dimensionalized perturbed equations. Unlike the planar and spherical cases, the governing equations differ based on the base state velocity and tube length; the dimensionless perturbed equations in each regime are systematically presented below.

(a). The unperturbed equations

The equations governing an unperturbed lipid membrane tube are provided in Eqs. (132)–(135), and admit general solutions involving gradients of the in-plane velocities and surface tension. In biological systems, however, a common base state is one in which there is no angular velocity and constant axial velocity [25, 29–32]. The corresponding solution to Eqs. (132)–(135), with a constant base velocity, is given by

$$v^{\theta}_{(0)} \,=\, 0 \,, \qquad v^{z}_{(0)} \,=\, v_0 \,, \qquad v_{(0)} \,=\, 0 \,, \qquad \text{and} \qquad \lambda_{(0)} \,=\, \lambda_0 \,:=\, pR + \frac{k_{\mathrm{b}}}{4R^2} \,, \tag{176}$$

where v_0 is the constant axial velocity in the base flow. The base state sets the axial velocity scale V and surface tension scale Λ as

$$V \,:=\, v_0 \qquad \text{and} \qquad \Lambda \,:=\, \lambda_0 \,=\, pR + \frac{k_{\mathrm{b}}}{4R^2} \,. \tag{177}$$

As in the planar and spherical cases, the introduction of a velocity scale in the base state leads to a new length scale over which in-plane quantities vary. In what follows, we follow a similar procedure to the planar and spherical situations to demonstrate the need for a new length scale, and then non-dimensionalize the governing equations in different regimes.

(b). The perturbed equations

For a perturbed tube, we first assume quantities continue to vary over a known length scale L in the axial direction, where $L = R$ in thick tubes and $L \gg R$ in thin tubes. The continuity equation (140) simplifies to $\tilde{v}^{\theta *}_{,\theta^*} + \tilde{v}^{z*}_{,z^*} + \tilde{r}^*_{,z^*} + \tilde{r}^*_{,t^*} = 0$, and reveals $\Omega = V/L = 1/\tau$. Ignoring inertial terms for the sake of argument, the in-plane equations contain only viscous and tension terms, however the tension forces are $O(\Lambda L/(\zeta V))$ relative to the viscous forces. Thus, as V tends to zero, the in-plane equations require $\tilde{\lambda}^*$ to be constant. Such a result is unphysical, as when V goes to zero we expect the surface tension to behave as in the initially static case, for which it responds to shape perturbations according to Eqs. (163) and (173) in thick and thin tubes, respectively, with inertial terms removed. We thus do not expect axial gradients to occur over a length scale L.

Next, we assume all quantities vary over some unknown length scale ℓ in the axial direction. As the base flow is only in the z-direction, we assume angular gradients are unchanged, i.e. quantities still vary over $O(1)$ changes in the angle θ. The dimensionless form of the continuity equation is unchanged, but now implies $\Omega = V/\ell = 1/\tau$, where ℓ is a yet to be determined characteristic length scale. The in-plane equations, however, reveal surface tension forces are $O(\Lambda\ell/(\zeta V))$ relative to viscous forces, and motivate the choice

$$\ell \, = \, \frac{\zeta V}{\Lambda} \ , \tag{178}$$

such that in-plane viscous and tension forces are of the same order. We accordingly define the new dimensionless variable

$$z' := \frac{z}{\ell} \ . \tag{179}$$

However, in this case, when V tends to zero the shape equation (143) simplifies to $\tilde{r}^*_{,z'z'z'z'} = 0$—disagreeing with the corresponding result from an initially static tube. As a result, our assumption that all quantities vary over the length scale ℓ (178) is again unphysical.

As in the planar and spherical geometries, we obtain a proper scaling for membrane tubes with a base flow by positing that different quantities vary over different axial distances. In particular, the in-plane quantities $\tilde{v}^\theta$, $\tilde{v}^z$, and $\tilde{\lambda}$ vary over $O(\ell)$ changes in the axial position, with ℓ given by Eq. (178), while out-of-plane shape changes $\tilde{r}$ vary over $O(L)$ changes in z. Thus, $O(\tilde{v}^z_{,z}) = V/\ell$ while $O(\tilde{r}_{,z}) = R/L$. Unlike the previous two cases, however, all quantities are assume to vary over $O(1)$ changes in θ.

With the aforementioned scaling of in-plane and out-of-plane quantities, the governing equations are respectively non-dimensionalized as

$$\Omega\,\tilde{v}^{\theta*}_{,\theta^*} \, + \, \frac{V}{\ell}\,\tilde{v}^{z*}_{,z'} \, + \, \frac{V}{L}\,\tilde{r}^*_{,z^*} \, + \, \frac{1}{\tau}\,\tilde{r}^*_{,t^*} \, = \, 0 \ , \tag{180}$$

$$\frac{\rho R^2}{\zeta}\Big(\frac{1}{\tau}\,\tilde{v}^{\theta*}_{,t^*} \, + \, \frac{V}{\ell}\,\tilde{v}^{\theta*}_{,z'}\Big) \, = \, \frac{1}{\tau\Omega}\,\tilde{r}^*_{,t^*\theta^*} \, + \, \tilde{v}^{\theta*}_{,\theta^*\theta^*} \, + \, \frac{R^2}{\ell^2}\,\tilde{v}^{\theta^*}_{,z'z'} \, + \, \frac{V}{\Omega L}\,\tilde{r}^*_{,\theta^* z^*} \, + \, \frac{\Lambda}{\zeta\Omega}\,\tilde{\lambda}^*_{,\theta^*} \ , \tag{181}$$

$$\frac{\rho\ell^2}{\zeta}\Big(\frac{1}{\tau}\,\tilde{v}^{z*}_{,t^*} \, + \, \frac{V}{\ell}\,\tilde{v}^{z*}_{,z'}\Big) \, = \, -\frac{\ell^2}{\tau L V}\,\tilde{r}^*_{,t^* z^*} \, + \, \frac{\ell^2}{R^2}\,\tilde{v}^{z*}_{,\theta^*\theta^*} \, + \, \tilde{v}^{z*}_{,z'z'} \, - \, \frac{\ell^2}{L^2}\,\tilde{r}^*_{,z^* z^*} \, + \, \frac{\Lambda\ell}{\zeta V}\,\tilde{\lambda}^*_{,z'} \ , \tag{182}$$

and

$$\begin{aligned} &\frac{\rho R^4}{k_{\mathrm{b}}}\Big(\frac{1}{\tau^2}\,\tilde{r}^*_{,t^*t^*} \, + \, \frac{V}{\tau L}\,\tilde{r}^*_{,t^*z^*} \, + \, \frac{V^2}{L^2}\,\tilde{r}^*_{,z^*z^*}\Big) \\ &\quad = \, 2\,\frac{\zeta V R^2}{k_{\mathrm{b}}\ell}\,\tilde{v}^{z*}_{,z'} \, + \, \frac{\Lambda R^2}{k_{\mathrm{b}}}\Big(\tilde{r}^* \, + \, \Delta^*_{\mathrm{s}}\tilde{r}^* \, - \, \tilde{\lambda}^*\Big) \, - \, \frac{1}{4}\Big(3\tilde{r}^* \, + \, 4\tilde{r}^*_{,\theta^*\theta^*} \, + \, \Delta^*_{\mathrm{s}}\tilde{r}^* \, + \, 2\Delta^{*2}_{\mathrm{s}}\,\tilde{r}^*\Big) \ . \end{aligned} \tag{183}$$

At this point, we recognize there are three length scales in the problem: (i) the in-plane axial length scale ℓ, (ii) the cylinder radius R, and (iii) the out-of-plane axial length scale L. To non-dimensionalize Eqs. (180)–(183), we require the relative sizes of ℓ, R, and L. The ratio R/L is captured by δ (150), and we now define the dimensionless quantity

$$\ell^* \, := \, \frac{\ell}{R} \, = \, \frac{\zeta V}{\Lambda R} \ . \tag{184}$$

In what follows, we simplify Eqs. (180)–(183) for different values of ℓ^* and δ. We note that ℓ^* can be thought of as a dimensionless velocity, as for fixed tube radius and normal stress jump, changing V changes ℓ^*. We frequently refer to regimes of different ℓ^* by corresponding values of the velocity from here on.

(c). The case where ℓ is much greater than L

We begin by considering the case where the axial length scale ℓ corresponding to in-plane quantities is larger than the axial length scale L for out-of-plane variables. As L is at least as large as the tube radius R, in this regime $\ell \gg L \geq R$, or equivalently $\ell^* \gg \delta^{-1} \geq 1$. Such a case can arise, for example, when $V \sim 10^{-2}$

nm/μsec = 10 μm/sec, $\Lambda \sim 10^{-4}$ pN/nm, and $R = L \sim 100$ nm. The continuity equation (180) indicates that for out-of-plane shape changes to be accommodated by in-plane angular and axial flows,

$$\Omega \,=\, \frac{V}{L} \,=\, \frac{1}{\tau} \,. \tag{185}$$

The governing equations (180)–(183) can then be written as

$$\tilde{v}^{\theta *}_{,\theta^*} + \frac{L}{\ell}\,\tilde{v}^{z*}_{,z'} + \tilde{r}^*_{,z^*} + \tilde{r}^*_{,t^*} \,=\, 0 \,, \tag{186}$$

$$Re\,\delta\Big(\tilde{v}^{\theta *}_{,t^*} + \frac{L}{\ell}\,\tilde{v}^{\theta *}_{,z'}\Big) \,=\, \tilde{r}^*_{,t^*\theta^*} + \tilde{v}^{\theta *}_{,\theta^*\theta^*} + \frac{R^2}{\ell^2}\,\tilde{v}^{\theta *}_{,z'z'} + \tilde{r}^*_{,\theta^* z^*} + \frac{L}{\ell}\,\tilde{\lambda}^*_{,\theta^*} \,, \tag{187}$$

$$\frac{Re}{\delta}\,\Big(\tilde{v}^{z*}_{,t^*} + \frac{L}{\ell}\,\tilde{v}^{z*}_{,z'}\Big) \,=\, -\tilde{r}^*_{,t^*z^*} + \frac{L^2}{R^2}\,\tilde{v}^{z*}_{,\theta^*\theta^*} + \frac{L^2}{\ell^2}\,\tilde{v}^{z*}_{,z'z'} - \tilde{r}^*_{,z^*z^*} + \frac{L^2}{\ell^2}\,\tilde{\lambda}^*_{,z'} \,, \tag{188}$$

and

$$\begin{aligned} &Re\,\Gamma\,\delta^2\ell^*\Big(\tilde{r}^*_{,t^*t^*} + \tilde{r}^*_{,t^*z^*} + \tilde{r}^*_{,z^*z^*}\Big) \\ &\qquad = 2\,\frac{SL}{\ell^*}\,\tilde{v}^{z*}_{,z'} + \Gamma\Big(\tilde{r}^* + \Delta^*_{\mathrm{s}}\tilde{r}^* - \tilde{\lambda}^*\Big) - \frac{1}{4}\Big(3\tilde{r}^* + 4\tilde{r}^*_{,\theta^*\theta^*} + \Delta^*_{\mathrm{s}}\tilde{r}^* + 2\Delta^{*2}_{\mathrm{s}}\,\tilde{r}^*\Big) \,, \end{aligned} \tag{189}$$

where the Scriven–Love and Föppl–von Kármán numbers are given by Eq. (162), and the Reynolds number (157) is at most 10^{-8} in all cases considered. As $Re \ll 1$ and $L/\ell \ll 1$ in this case, Eqs. (186)–(188) can be simplified to

$$\tilde{v}^{\theta *}_{,\theta^*} + \tilde{r}^*_{,z^*} + \tilde{r}^*_{,t^*} \,=\, 0 \,, \tag{190}$$

$$-\tilde{v}^{z*}_{,z'\theta^*} + \tilde{\lambda}^*_{,\theta^*} \,=\, 0 \,, \tag{191}$$

and

$$-\tilde{r}^*_{,t^*z^*} + \frac{1}{\delta^2}\,\tilde{v}^{z*}_{,\theta^*\theta^*} - \tilde{r}^*_{,z^*z^*} \,=\, 0 \,, \tag{192}$$

where to obtain the θ equation (191) we take the partial derivative of Eq. (186) with respect to θ^*, substitute into Eq. (187), and simplify. The shape equation (189) can be written as

$$2\,\frac{SL}{\ell^*}\,\tilde{v}^{z*}_{,z'} + \Gamma\Big(\tilde{r}^* + \Delta^*_{\mathrm{s}}\tilde{r}^* - \tilde{\lambda}^*\Big) - \frac{1}{4}\Big(3\,\tilde{r}^* + 4\,\tilde{r}^*_{,\theta^*\theta^*} + \Delta^*_{\mathrm{s}}\tilde{r}^* + 2\,\Delta^{*2}_{\mathrm{s}}\,\tilde{r}^*\Big) \,=\, 0 \,. \tag{193}$$

As we will see, Eq. (193) is the shape equation for all other regimes as well. Eqs. (190)–(193) are the governing equations presented as Eqs. (68) and (80)–(82) in the main text, corresponding to Regime IV.

(d). The case where ℓ is less than L

We next consider the case where $\ell \le L$, for which $\ell^* \le \delta^{-1}$. The continuity equation (180) then implies

$$\Omega \,=\, \frac{V}{\ell} \,=\, \frac{\Lambda}{\zeta} \,=\, \frac{1}{\tau} \,, \tag{194}$$

and the governing equations (180)–(183) simplify to

$$\tilde{v}^{\theta *}_{,\theta^*} + \tilde{v}^{z*}_{,z'} + \ell^*\delta\,\tilde{r}^*_{,z^*} + \tilde{r}^*_{,t^*} \,=\, 0 \,, \tag{195}$$

$$\frac{Re}{\ell^*}\,\Big(\tilde{v}^{\theta *}_{,t^*} + \tilde{v}^{\theta *}_{,z'}\Big) \,=\, \tilde{r}^*_{,t^*\theta^*} + \tilde{v}^{\theta *}_{,\theta^*\theta^*} + \frac{1}{(\ell^*)^2}\,\tilde{v}^{\theta *}_{,z'z'} + \ell^*\delta\,\tilde{r}^*_{,\theta^* z^*} + \tilde{\lambda}^*_{,\theta^*} \,, \tag{196}$$

$$Re\,\ell^*\,\Big(\tilde{v}^{z*}_{,t^*} + \tilde{v}^{z*}_{,z'}\Big) \,=\, -\ell^*\delta\,\tilde{r}^*_{,t^*z^*} + (\ell^*)^2\,\tilde{v}^{z*}_{,\theta^*\theta^*} + \tilde{v}^{z*}_{,z'z'} - (\ell^*\delta)^2\,\tilde{r}^*_{,z^*z^*} + \tilde{\lambda}^*_{,z'} \,, \tag{197}$$

and

$$\frac{Re\,\Gamma}{\ell^*}\Big(\tilde{r}^*_{,t^*t^*} + \ell^*\delta\,\tilde{r}^*_{,t^*z^*} + (\ell^*\delta)^2\,\tilde{r}^*_{,z^*z^*}\Big) \\ = 2\,\frac{SL}{\ell^*}\,\tilde{v}^{z*}_{,z'} + \Gamma\Big(\tilde{r}^* + \Delta^*_{\mathrm{s}}\tilde{r}^* - \tilde{\lambda}^*\Big) - \frac{1}{4}\Big(3\tilde{r}^* + 4\tilde{r}^*_{,\theta^*\theta^*} + \Delta^*_{\mathrm{s}}\tilde{r}^* + 2\Delta^{*2}_{\mathrm{s}}\,\tilde{r}^*\Big)\ , \tag{198}$$

where $SL/\ell^* = \Gamma$. The governing equations are analyzed in three different regimes: small velocities, where $\ell^* \ll 1$, moderate velocities, where $\ell^* \sim 1$, and large velocities with a thin tube, where $1 \ll \ell^* \ll \delta^{-1}$. The case of large velocities with a thick tube, i.e. when $1 \le \delta^{-1} \ll \ell$, was analyzed in part IV.4 (c).

Regime I: The equations when the base flow is slow. In the first regime, $\ell^* \ll 1$, or equivalently $V \ll \Lambda R/\zeta$, as would be the case if $\Lambda \sim 10^{-2}$ pN/nm, $R \sim 100$ nm, and $V \sim 10^{-4}$ nm/μsec. As $\ell^* \ll 1$ and $\delta \le 1$ by construction, $\ell^*\delta \ll 1$ as well, and Eqs. (195)–(197) simplify to

$$\tilde{v}^{\theta*}_{,\theta^*} + \tilde{v}^{z*}_{,z'} + \tilde{r}^*_{,t^*} = 0\ , \tag{199}$$

$$\tilde{v}^{\theta*}_{,z'z'} = 0\ , \tag{200}$$

and

$$\tilde{v}^{z*}_{,z'z'} + \tilde{\lambda}^*_{,z'} = 0\ . \tag{201}$$

Equations (199)–(201) are presented as Eqs. (69)–(71) in the main text. To simplify the shape equation (198), we recognize $Re/\ell^* = \rho\Lambda R^2/\zeta^2$, which is independent of the velocity scale V and is negligible. Thus, in this regime, the shape equation is once again given by Eq. (193), or equivalently Eq. (68) of the main text.

Regime II: The equations when the base flow is moderate. In the second regime, $V \sim \Lambda R/\zeta$, such that $\ell^* \sim 1$, e.g. for a thick tube when $V \sim 10^{-3}$ nm/μsec, $\Lambda \sim 10^{-4}$ pN/nm, and $R = L \sim 100$ nm, or for a thin tube when $V \sim 10^{-3}$ nm/μsec, $\Lambda \sim 10^{-3}$ pN/nm, $R \sim 10$ nm, and $L \sim 10^3$ nm. In either case, the governing equations are easily obtained by substituting $\ell^* \sim 1$ into Eqs. (195)–(198). The continuity and in-plane equations are found to be

$$\tilde{v}^{\theta*}_{,\theta^*} + \tilde{v}^{z*}_{,z'} + \delta\,\tilde{r}^*_{,z^*} + \tilde{r}^*_{,t^*} = 0\ , \tag{202}$$

$$\tilde{r}^*_{,t^*\theta^*} + \tilde{v}^{\theta*}_{,\theta^*\theta^*} + \tilde{v}^{\theta*}_{,z'z'} + \delta\,\tilde{r}^*_{,\theta^*z^*} + \tilde{\lambda}^*_{,\theta^*} = 0\ , \tag{203}$$

and

$$-\delta\,\tilde{r}^*_{,t^*z^*} + \tilde{v}^{z*}_{,\theta^*\theta^*} + \tilde{v}^{z*}_{,z'z'} - \delta^2\,\tilde{r}^*_{,z^*z^*} + \tilde{\lambda}^*_{,z'} = 0\ , \tag{204}$$

while the shape equation is once again found to be given by Eq. (193). Equations (202)–(204) are provided as Eqs. (73)–(75) in the main text.

Regime III: The equations when the base flow is fast and the tube is thin. In the third regime, $V \gg \Lambda R/\zeta$ and $\delta \ll 1$, such that $1 \ll \ell^* \ll \delta^{-1}$. Such could be the case, for example, if $V \sim 10^{-2}$ nm/μsec, $\Lambda \sim 10^{-3}$ pN/nm, $R \sim 10$ nm, and $L \sim 10^3$ nm, i.e. if the thin tube example from Regime II had an order of magnitude larger velocity. In this case, Eqs. (195)–(197) simplify to

$$\tilde{v}^{\theta*}_{,\theta^*} + \tilde{v}^{z*}_{,z'} + \tilde{r}^*_{,t^*} = 0\ , \tag{205}$$

$$\tilde{r}^*_{,t^*\theta^*} + \tilde{v}^{\theta*}_{,\theta^*\theta^*} + \tilde{\lambda}^*_{,\theta^*} = 0\ , \tag{206}$$

and

$$\tilde{v}^{z*}_{,\theta^*\theta^*} = 0\ . \tag{207}$$

In this regime, the shape equation is given by Eq. (193). However, following an analogous procedure to the case of a thin, initially static tube, we can show $\tilde{v}^{z*}$ is axisymmetric, thus implying

$$\tilde{\lambda}^*_{,\theta^*} = 0\ , \tag{208}$$

such that $\tilde{\lambda}^*$ is also axisymmetric. Equations (205), (207), and (208) are given as Eqs. (76)–(78) in the main text.

(e). The analysis of past experimental data

We end by calculating the Scriven–Love and Föppl–von Kármán numbers in an instance where a lipid membrane tube is being pulled at a constant velocity, corresponding to the last row in Table I of the main text. For this base state, the pull force is once again given by Eq. (174), which simplifies to Eq. (175) when there is no pressure drop across the membrane.

Experiment #1: We consider the same experimental data as was analyzed in Experiment #2 of Sec. IV.3 (c), in which a lipid membrane tether is pulled from a cell bleb, and then held stationary while the pull force relaxes. In this case, however, we consider the data when the tether is being pulled. The data is once again obtained from Fig. S2(c), in the Supplementary Information of Ref. [25], which corresponds to Ref. [50, ♫] in the main text. As was the case in Experiment #2 of Sec. IV.3 (c), we assume $p \approx 0$ at time $t \approx 45$ seconds, for which $R \sim 40$ nm. The velocity scale V can be calculated from Fig. S2(c) as $V \sim 4 \cdot 10^{-3}$ nm/μsec $= 4\,\mu$m/sec, and k_{b} is reported to be 380 pN·nm. To approximate the surface tension scale at $t \approx 18$ seconds when the tether pulling starts, we estimate $f_{\text{pull}} \approx 100$ pN at that time. In this case, Eq. (174) indicates $p \sim 1 \cdot 10^{-2}$ pN/nm^2 = 10 kPa and $\Lambda \sim 0.6$ pN/nm. Note the bending modulus κ in Ref. [25] is related to k_{b} in the present work according to $k_{\mathrm{b}} = 2\kappa$.

Quantity	Value	Calculation
V	$4 \cdot 10^{-3}$ nm/μsec	Fig. S2(c)
R	$4 \cdot 10^{1}$ nm	Fig. S2(c), Table 10
k_{b}	380 pN·nm	Fig. S2 caption
Λ	$6 \cdot 10^{-1}$ pN/nm	Fig. S2(e), Eq. (174)
SL	$4 \cdot 10^{-3}$	Eq. (162)
Γ	2	Eq. (162)

Table 12: Calculations from Ref. [25], for the twelfth row of Table I in the main text [50, ♫].

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