Shear-driven instabilities of membrane tubes and Dynamin-induced scission

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Motivated by the mechanics of Dynamin-mediated membrane tube fission we analyse the stability of fluid membrane tubes subjected to shear flow in azimuthal direction. We find a novel helical instability driven by the membrane shear flow which has its onset at shear rates that are physiologically accessible under the action of Dynamin and could also be probed using in-vitro experiments on GUVs using magnetic tweezers. We discuss how such an instability may play a role in the mechanism for Dynamin-mediated membrane tube fission.

The covariant hydrodynamics of fluid membranes has been a subject of much interest in the soft matter and biological physics community in recent years, both for the general theoretical features of such systems [1–3] and their application to biologically relevant processes [4–8]. Such systems couple membrane hydrodynamics with bending elasticity and have been shown to display complex visco-elastic behaviour in geometries with high curvature [9].

Membrane tubes are highly curved and are found in many contexts in cell biology, including the endoplasmic reticulum and the necks of budding vesicles [10]. Such tubes can be pulled from a membrane under the action of a localized force (such as from molecular motors) [11–13]. They are stable due to a balance between the forces from bending energy, involving the bending rigidity \( \kappa \), and from the surface tension \( \sigma \) and have equilibrium radius \( r_0 = \sqrt{\frac{\kappa}{2\sigma}} \) [14].

One of the simplest ways to drive flows on the surface of these tubes is to impose a velocity in the azimuthal direction. The analysis of shape changes induced by such flows is the subject of this letter. Two possible mechanisms for realizing such flows via in-vitro and in-vivo experiments are shown in Fig. 1.

The fission of membrane tubes plays an important role in many cellular processes, ranging from endocytosis to mitochondria fission [15–16]. The key component of the biological machinery required to induce membrane fission is a family of proteins called Dynamin which hydrolyse GTP into GDP [17–18]. Dynamin is a protein complex that oligomerizes to form polymers which wrap helically around membrane tubes [17–19]. Although there is clear evidence that Dynamin undergoes a conformational change when it hydrolyses GTP, there is not yet a consensus on the exact method of fission [21–24]. It has been shown experimentally that, upon hydrolysis of GTP, Dynamin (counter)rotates rapidly whilst constricting [18]. The rotation frequency can be of order 10Hz [18], giving a mechanism for the generation of flows in the azimuthal direction.

Another possible way of driving such flows is by pulling a small tube from a Giant Unilamellar Vesicle (GUV) or cell with magnetic tweezers and using magnetic field

FIG. 1. Possible realizations of shear driven instabilities on membrane tubes (shown in orange throughout). a) Dynamin on the neck of a budding vesicle. Under hydrolysis of GTP the protein constricts and (counter)rotates, prior to fission of the tube. This rotation drives a significant shear flow on the neck of the vesicle. b) A GUV with membrane tube pulled by magnetic tweezers; the magnetic bead can be spun in order to drive flows in the azimuthal direction on the tube. c) Sketch of the growth of the helical instability described in this letter, the final stage is a possible pathway to tube fission due to non-linear effects. The basis vectors on the membrane \( \mathbf{e}_i \), where \( i = r, \theta, z \), length of tube, \( L \), and equilibrium radius, \( r_0 \), are labelled. Middle panel shows shear direction.
oscillations to spin an attached bead [26, 28].

The membrane behaves as a viscous fluid with 2D viscosity $\eta_m$. The ratio of this viscosity over the viscosity of the bulk aqueous fluid, $\eta$, gives a length scale, $L_{SD} = \frac{2m}{\eta}$, called the Saffman-Delbrück length [29–31]. This is the distance over which bulk hydrodynamics screens membrane flows in planar geometry. In the case of a membrane tube the screening length is modified due to geometric effects and becomes $\sqrt{L_{SD}D_0}$, [31]. We will consider dynamics on a scale less than this, such that the dominant dissipation mechanism involves the membrane flows. This means that we can neglect bulk flows on sufficiently short length-scales (sufficiently short tubes), so long as we match to physically appropriate conditions at the tube ends. Such approaches have been used to great effect in understanding membrane dynamics on scales shorter than the screening length [7, 8, 32]. For further details see S.I.

We consider a lipid membrane as a manifold equipped with metric $g_{ij}$ and second fundamental form $b_{ij}$ [33]. The coordinate basis is defined by the triad $\{\vec{e}_1, \vec{e}_2, \vec{n}\}$ where $\vec{e}_1$ and $\vec{n}$ are the basis of the tangent bundle and normal bundle of the surface respectively. The surface has velocity, $\vec{V} = \vec{v} + \vec{w} \vec{n}$ where $\vec{v}$ is the velocity tangential to the membrane, $\vec{n}$ is the normal to the membrane, and $\vec{w}$ is the velocity normal to the membrane. We define the mean and Gaussian curvature as $2H = b_{ij} + K = \det b_{ij}$ respectively. We assume the membrane behaves like a zero-Reynolds number fluid in the tangential direction [34] and has bending energy given by the usual Helfrich energy [35]. Surface tension, $\sigma$, is imposed as a Lagrange multiplier imposing membrane area conservation. We will assume zero spontaneous curvature for simplicity. For conciseness we will simply state the equations of motion for the membrane, for details on their derivation see [5, 36] or S.I. We will also show equations using standard index notation, for details of the geometric formalism used see S.I. or [5, 35, 37].

The continuity equation for an incompressible membrane is given by

$$\nabla_i v^i = 2H w$$

which is simply the Euclidean continuity equation modified to account for the normal motion of the membrane.

Force balance normal to the membrane means the normal elastic and viscous forces must sum to zero, leading to the following

$$\kappa [2\Delta_{LB} H - 4H (H^2 - K)] + 2\sigma H$$
$$+ 2\eta_m [b^i_j \nabla_i v^j - 2(2H^2 - K) w] = 0$$

Here $\kappa$ is the bending rigidity of the membrane and $\Delta_{LB}$ is the Laplace-Beltrami operator. Note that we are using a geometrical definition of $\Delta_{LB}$ that is analogous to a curl-curl operator on a manifold, hence the sign difference with the usual Laplacian operator in the shape equation (see S.I. for details). This is a modified form of the shape equation first derived by Zhong-Can & Helrich [14] but with the addition of viscous normal forces given by fluid flow on the membrane. The term coupling the second fundamental form and gradients in tangential velocity can be thought of as the normal force induced by fluid flowing over an intrinsically curved manifold. This term is of fundamental importance in the present study as it drives a shape instability. The other non-standard term $\sim (2H^2 - K) w$ is the dissipative force associated with the normal velocity, inducing flows in the tangential direction on a curved surface.

Force balance in the tangential direction gives

$$\eta_m [\Delta_{LB} v^i - 2K v^i + 2(b^{ij} - 2H g^{ij}) \nabla_j w]$$
$$- \nabla_i \sigma = 0$$

which is the modified form of the 2D Stokes equations. The new terms, coupling Gaussian curvature with tangential velocity, and curvature components with the gradients in normal velocity, come from the modified form of the rate-of-deformation tensor which accounts for the curved and changing geometry of the membrane. The term $\sim K v^i$ describes the convergence/divergence of streamlines on a curved surface. The term $\sim (b^{ij} - 2H g^{ij}) \nabla_j w$ describes the forces induced tangentially by the dynamics of the membrane.

We consider a ground-state membrane tube ($w = 0$) of length $L$ in cylindrical coordinates $(r, \theta, z)$ with radius $r_0 = \sqrt{\frac{r}{2\pi}}$ and impose a velocity $v = v_0 \vec{e}_\theta$ at $z = 0$ (which can be interpreted as the edge of an active Dynamin ring, for example). Making use of the azimuthal symmetry the continuity and Stokes equations reduce to an ODE that admits the solution

$$v^{(0)} = (v_0 - \Omega z) \vec{e}_\theta$$

where the exact value of $\Omega$ depends on the boundary condition at $z = L$, but roughly scales as $\Omega \sim \frac{v_0}{L}$ if we either implement torque balance, e.g. at the boundary where a tube joins onto a planar membrane, or simply set $v(L) = 0$, see S.I. for more details.

We can now make a perturbation about this ground state in $r(z, \theta, t) = r_0 + u(\theta, z, t)$, $\vec{v} = \vec{v}^{(0)} + \delta \vec{v}^\theta(\theta, z, t) \vec{e}_\theta + \delta v^z(\theta, z, t) \vec{e}_z$, $\sigma = \sigma_0 + \delta \sigma(\theta, z, t)$ and $w = \partial_t u$. Making use of the discrete Fourier transform, $f(\theta, z, t) = \sum_q q, m \tilde{f}_{q, m}(t) e^{iqz + im\theta}$, where $\tilde{f}_{q, m}$ is the Discrete Fourier Transform of $f(\theta, z)$ with $m \in \mathbb{Z}$ and $q = \frac{2\pi n}{L}$ where $n \in \mathbb{Z} \setminus \{0\}$, we can write Eqs. 1 [2, 3] in Fourier space and linearise in the perturbations. The linear response of the normal force balance is the following

$$F_{q, m} \delta u_{q, m} + \tilde{F}_{q, m} \delta \sigma_{q, m} + \tilde{F}_m \delta v^\theta_{q, m}$$
$$+ \tilde{G}_{q, m} \delta v^z_{q, m} + \tilde{\sigma}_{q, m} \delta \sigma_{q, m} = 0$$

for $m \neq 0$ and

$$F_{q, 0} \delta u_{q, 0} + \tilde{F}_{q, 0} \delta \sigma_{q, 0} + \tilde{G}_{q, 0} \delta v^z_{q, 0} + \tilde{\sigma}_{q, 0} \delta \sigma_{q, 0} = 0$$

for $m = 0$. This equation is of the form of a linear ODE with coefficients that are periodic in $q$. A solution of this equation is

$$u_{q, m}(t) = \sum_{n \neq 0} (\xi_{n, q, m} \cos n z + \eta_{n, q, m} \sin n z) e^{i(qz + nm\theta)}$$

where $\xi_{n, q, m}$ and $\eta_{n, q, m}$ are determined by the initial condition.

The solution for $m = 0$ is

$$u_{q, 0}(t) = \sum_{n \neq 0} (\xi_{n, q, 0} \cos n z + \eta_{n, q, 0} \sin n z) e^{i(qz + nm\theta)}$$

where $\xi_{n, q, 0}$ and $\eta_{n, q, 0}$ are determined by the initial condition.
where
\[ F_{q,m}^u = \frac{4\sigma_0^2}{\kappa} \left[ q^4 + m^4 + 2q^2m^2 - 2m^2 + 1 \right] - \frac{2\eta_m \tilde{q} \Omega}{r_0^2} \]  
\[ F_{q,m}^z = 0; \quad \bar{F}_{q,m} = \frac{2\eta_m}{r_0^2}, \]  
\[ \bar{G}_{q,m} = \frac{2\eta_m}{r_0^2} \]  
where \( \tilde{q} = q r_0 \).

Note the sign of the final term in Eq. [3] suggests that the shear flow could lead to an instability in the \( m \neq 0 \) modes. The force distribution on the tube is shown in Fig. 2. Note that the \( (m \rightarrow -m, \tilde{q} \rightarrow -\tilde{q}) \) symmetry of the force defines a “handedness” which changes upon reversing the direction of the shear rate.

Similar linear response equations can be found for the force balance and continuity in the tangential directions, these can then be used to solve for \( \delta u_{q,m}^z, \delta u_{q,m}^\theta, \) and \( \delta \sigma_{q,m} \) in terms of \( \bar{u}_{q,m} \) and its time derivative. From this we derive the following growth rate equation for \( \bar{u}_{q,m} \), where time is normalised according to \( t = \bar{t} \tau \) with \( \tau = \frac{2\pi r_0}{\sigma_0} \),
\[ \partial_t \bar{u}_{q,m} = \frac{\bar{u}_{q,m}}{\tilde{q}^2(m^2 + 3q^2)} F(m, \tilde{q}) \]  
where
\[ F(m, \tilde{q}) = -4imq^4\frac{\nu_0 \eta_m}{\tau_0 \sigma_0} \]
\[ - 2 \left( m^2 + q^2 \right)^2 \left( 1 + m^4 + q^4 + 2m^2 (q^2 - 1) \right) \]
\[ + m \tilde{q} \left( m^2 (2m^2 - 1) + (4m^2 - 3) q^2 + 2q^4 \right) \tilde{\Omega} \]
and \( \tilde{\Omega} = \frac{2\pi \nu}{\sigma_0} \) is the dimensionless shear rate.

The modes become unstable when the real part of the growth rate changes sign to \( \Re \{ F(m, q) \} > 0 \), which occurs for
\[ |\tilde{\Omega}| > \frac{2 \left( m^2 + \tilde{q}^2 \right)^2 \left( 1 + m^4 + \tilde{q}^4 + 2m^2 (\tilde{q}^2 - 1) \right)}{|m\tilde{q}| (m^2 (2m^2 - 1) + (4m^2 - 3) \tilde{q}^2 + 2\tilde{q}^4)}. \]  

We note that \( \Re \{ F(0, q) \} < 0 \) for all \( \tilde{q} \), meaning that the \( m = 0 \) peristaltic mode is always linearly stable. This is not the case for the \( m = 1 \) mode, which is the first to be driven unstable. The imaginary part of Eq. [3] corresponds to the corkscrew like propagation of the mode. The growth rate and stability diagram for the \( |m| = 1 \) mode is plotted in Fig. 3. Note that the growth rate is a discrete function of \( \tilde{q} \) by the length of the tube. The divergence of the growth rate for small \( \tilde{q} \) is removed by the bulk hydrodynamics, however this is at a length scale much longer than the tube length, see S.I. for more details.

This helical instability is a new type of membrane instability, distinct from the usual peristaltic (Pearling) instabilities found in membrane tubes.

To evaluate the physiological significance of this we first estimate \( \tilde{\Omega} \) from experiment. The rotation frequency of Dynamin is known to be \( \nu \sim 1 - 10 \text{ Hz} \) [18], with tube radius at the start of constriction \( r_0 \sim 10 \text{ nm} \) [17, 21]. Assuming multiplicative coupling between Dynamin rings on the tube, the shear rate is \( \tilde{\Omega} \sim \frac{2\pi r_0 \nu N}{L} \), where \( N \) is the number of Dynamin rings. In the small \( \tilde{q} \) limit \( \tilde{\Omega} \approx 4\tilde{q} \), see inset to Fig. 3. Assuming that the cutoff wavenumber of the tube is associated with a fundamental mode \( \tilde{q}_{\text{min}} = \frac{2\pi r_0}{L} \), gives the critical spinning frequency.
for the onset of instability as
\[ \nu_{\text{crit}} \simeq \frac{4\sigma_0}{N\eta_m}. \] (11)

This doesn’t depend explicitly on \( L \) because increasing the tube length reduces the shear rate but also increases the largest unstable wavelength, and vice versa, in such a way that the two effects cancel. The functional form of this relation can be explained using a scaling analysis of Eq. 2. For \( q \sim 1/L \), the first order correction to the curvature scales like \( H \sim \frac{u}{L^2} \) so that the elastic force-per-unit-area scales like \( f_{el} \sim \frac{\eta_m}{L^2} \), while the off-diagonal components of the two fundamental form scale like \( b \sim \frac{u}{\eta_m L} \) and hence the viscous force-per-unit-area scale like \( f_{vis} \sim \frac{\eta_v L}{\eta_m} \sim \frac{\eta_v N \nu}{L^2} \). Balancing these forces gives a critical frequency \( \nu_{\text{crit}} \sim \frac{\sigma_0}{\eta_m} \).

Typical membranes in the fluid (liquid disordered) phase have viscosities \( \eta_m \sim 10^{-8} - 10^{-7} \text{ Pa m s} \) [39] (higher in the liquid ordered phase). However, much higher values have been associated with tubes pulled from living cells, \( \eta_m \sim 10^{-7} - 10^{-5} \text{ Pa m s} \). If we assume the surface tension takes a physiologically typical value of \( \sigma_0 \sim 10^{-5} \text{ N m}^{-1} \) and \( N \sim 1-10 \) [40] then this gives a critical frequency of \( \nu_{\text{crit}} \sim 0.1 - 100 \text{Hz} \), which suggests that it may be possible for Dynamin to drive this instability under physiological conditions.

A natural way for the instability to progress is fission of the tube, which is of particular significance given that the exact mechanism for Dynamin mediated fission is unknown. This effect may be amplified due to friction with the cytoskeleton [41] impeding the supply of membrane to the growing instability. As the instability grows the surface tension will increase, either narrowing the tube or causing Pearling [38]. An increase in tension has been shown to accelerating spontaneous tube fission [42] and friction impeding membrane flow has been shown experimentally to scission tubes [41]. This picture of fission, promoted by membrane hydrodynamics just outside the active Dynamin site, is consistent with the experimental observation that the location of fission is near the edge of the active Dynamin site rather than directly under it [42]. The time-scale over which the instability grows is of the order of \( \tau = \frac{\eta_m}{\sigma_0} \sim 10^{-3} \text{ s} \) (the units of the growth rate axis on Fig. 3), which is sufficiently fast to be consistent with the Dynamin-induced fission process.

Although we have provided evidence that a membrane instability can be driven by the rotation of Dynamin, our study is based on the simplified geometry of a cylindrical tube, rather than the neck of a budding vesicle, a location where Dynamin might typically act in-vivo. While our approach becomes analytically intractable for such complex membrane geometries we can gain some intuition into how the driving force per unit area of the instability changes with the geometry of the neck region by considering the term in the normal force balance equation that is responsible for driving the instability. Given the helical symmetry of the instability we infer that this driving force-per-unit-area goes like the mixed derivative in the shape, \( f_{\text{driving}} \sim \eta_m b^i \nabla_i v^j \). The term which acts like the shear rate on the tube now depends on \( z \) and we must calculate it numerically, see S.I.. In the case of a catenoid neck this leads to an amplification of the driving force by (only) a factor of 2 near the active site (\( z = 0 \)), for details see S.I. Whilst a relatively small effect this is qualitatively consistent with the experimental observation that Dynamin fission of a tube in-vitro often occurs near the GUV neck [42] and that fission on the necks of a budding vesicles in-vivo occurs faster than it does on long tubes [21, 43].

A second possibility for the non-linear growth is a stable non-equilibrium shape driven by the membrane flow. In this case it is worth noting an analogy between the membrane tube instability that we discuss here and elastic rods under torsion that deform non-linearly into plectonemes [44]. We suggest that it may also be possible for the unstable membrane tube to develop fluid plectonemes, similar to those actually seen in experiments on long tubes covered in Dynamin [18, 43]. We intend to explore this in future work.

A possible experiment to better understand the non-linear evolution of the instability and determine whether hydrodynamic effects alone are sufficient to induce fission would involve a short tube pulled from a GUV or cell by magnetic tweezers that then spins its end, Fig. 1b. This would also enable to test our predictions more quantitatively. The instability should also arise in a longer tube, however the quantitative nature of our predictions would likely require modifications due to screening of membrane flow by the ambient fluid. In this case we expect that the unstable wavelength would then be set by the screening length \( \sqrt{LSD} \) rather than the tube length [21, 45] and that Eq (11) would continue to hold at the scaling level.

In summary, we have developed a hydrodynamic theory that predicts an instability on fluid membrane tubes that is driven purely by a shear in the membrane flow. Such flows are shown to first drive a helical instability, which is quite distinct from any previously identified instabilities of fluid membrane tubes. We predict that this instability is physiologically accessible to active Dynamin but has not previously been considered in models of its function [43, 46]. This instability may provide a mechanism for Dynamin-mediated tube fission mechanism, e.g. due to increasing tension in the subsequent non-linear growth regime.

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SUPPLEMENTARY INFORMATION

Differential Geometry

Here we present a “users guide” to the style of geometric notation used in the main paper. We do not focus on mathematical rigour here, for a more formal treatment see [33].

If we define a manifold $\mathcal{M}^n$ where the derivative of a curve at point $p \in \mathcal{M}^n$ gives an element of the tangent space $X_p \in T_p(\mathcal{M}^n)$, we can express this in terms of a coordinate basis

$$X_p = X^i \left( \frac{\partial}{\partial x^i} \right)_p$$

(S1)

where Einstein summation over mixed indices is implicit.

If we choose a family of curves on $\mathcal{M}^n$ with continuous derivatives we can extend the definition of the tangent space to the tangent bundle on $\mathcal{M}^n$, $T(\mathcal{M}^n) = \bigcup_p T_p(\mathcal{M}^n)$. This extends the definition of a vector to a vector field on the manifold, $X \in T(\mathcal{M}^n)$.

The dual of $T(\mathcal{M}^n)$ can be defined as the cotangent space $T^*(\mathcal{M}^n)$. An element of this space, a 1-form, is defined in the following way

$$\omega \in T^*(\mathcal{M}^n)$$

(S2)

In coordinate notation

$$\omega(X) = \omega_i x^i = \omega^j \delta^i_j = \omega^i.$$  

(S3)

In general a type $(p, q)$ tensor field, $T$ is defined in the following way

$$T(X_1, ..., X_p, \omega_1, ..., \omega_q) \to \mathbb{R}$$

(S4)

where $X_1, ..., X_p \in T(\mathcal{M}^n)$ and $\omega_1, ..., \omega_q \in T^*(\mathcal{M}^n)$.

We can define a type $(2, 0)$ metric tensor on the manifold as

$$g(\cdot, \cdot) : g(X, Y) \to \mathbb{R}$$

(S5)

where $X, Y \in T(\mathcal{M}^n)$.

$$g(\cdot, \cdot) = ds^2 = g_{ij} dx^i dx^j = \bar{e}_i \cdot \bar{e}_j dx^i dx^j$$

(S6)

which allows a mapping between vectors and 1-forms.

The exterior or wedge product between two 1-forms is defined as the totally asymmetric tensor product

$$\omega_1 \wedge \omega_2 = \omega_1 \otimes \omega_2 - \omega_2 \otimes \omega_1.$$  

(S7)

A $p$-form, $\alpha$, can be defined from $p$ 1-forms as

$$\alpha = \omega_1 \wedge ... \wedge \omega_p.$$  

(S8)

This has the following property

$$\omega_1 \wedge ... \wedge \omega_r \wedge ... \wedge \omega_s \wedge ... \omega_p = -\omega_1 \wedge ... \wedge \omega_s \wedge ... \wedge \omega_r \wedge ... \omega_p$$

(S9)

for any two $s, r$. Or in coordinate notation

$$a_{i...r...s...j} = -a_{i...s...r...j}$$

(S10)

where $\alpha = \alpha_{i...j} dx^i \wedge ... \wedge dx^j$.

This along with the metric leads to the natural geometric definition of the volume form $vol^n := \sqrt{g} dx^1 \wedge ... \wedge dx^n$, where $g := \det(g_{ij})$.

The exterior derivative, $d$, of a smooth function $f$ is just its differential $df = \frac{\partial f}{\partial x^i} dx^i$. The exterior derivative, $d$, of a $p$ form is a $p + 1$ form

$$d\alpha = d\alpha_{i...j} \wedge dx^i \wedge ... \wedge dx^j.$$  

(S11)
The Hodge star operator, \( \star : \tau^*(\mathcal{M})^{(k)} \to \tau^*(\mathcal{M})^{(n-k)} \), is defined by the Hodge inner product of two differential forms \( \alpha \) and \( \beta \)

\[
\alpha \wedge \star \beta = (\alpha \cdot \beta) \text{ vol}^n
\]  
(S12)
in coordinate notation we have

\[
\star \alpha = \epsilon_{i_1 \ldots i_n} \sqrt{\text{det} g} g^{j_1 \ldots j_k} g^{i_1 j_1} \ldots g^{i_k j_k} \text{d}x^{i_{k+1}} \wedge \ldots \wedge \text{d}x^n
\]  
(S13)
where \( \epsilon \) is the totally asymmetric tensor.

A diffeomorphism is a map between two manifolds that is smooth, one-to-one, onto and has a smooth inverse. The Lie derivative is a natural object to use in continuum mechanics as it describes how a vector field \( X \) changes along the flow generated by a vector field \( Y \). If \( \phi(t) = \phi_t \) is a diffeomorphism parametrised by \( t \) and describing the local flow generated by \( X \), where \( t \) is defined such that \( \lim_{t \to 0} \phi_t(X) = X \), then we define the Lie derivative of a vector field \( Y \) with respect to a vector field \( X \) as follows

\[
[\mathcal{L}_X Y]_x = \lim_{t \to 0} \frac{\phi_{-t} Y_{\phi_0(x)} - Y_x}{t} = X(Y) - Y(X)
\]  
(S14)
as such \( \mathcal{L}_X Y \) is a vector field on \( \mathcal{M}^n \). Similar identities can be derived for more general tensors \([33]\).

We will define the Laplace-Beltrami operator as

\[
\Delta_{\text{LB}} = -\star d \star d
\]  
(S15)
which for scalar \( \phi \) and vector \( v \) is the following in index notation

\[
\Delta_{\text{LB}} \phi = -\frac{1}{\sqrt{|g|}} \partial_i \left( \sqrt{|g|} g^{ij} \partial_j \phi \right)
\]
and

\[
\Delta_{\text{LB}} v^q = -\frac{1}{\sqrt{|g|}} \epsilon_{npr} k_l^p q^m g^{nm} \partial_m \left( \sqrt{|g|} g^{kq} g^{ij} \partial_j (v^r g_{rl}) \right)
\]  
(S16)
where the later formula is not usually given in the literature as it is simpler to work with exterior calculus identities (which is how we will proceed).

One final point of note is that we will use the \( \flat, \sharp \) notation to denote raising and lowering of indices for conciseness. For example, if \( v \in T(\mathcal{M}^n) \), then

\[
v^\flat = g_{ij} v^i \text{d}x^j = v_i \text{d}x^i.
\]  
(S17)

**Hydrodynamics on moving fluid membranes**

We need to construct force balance and mass conservation equations on a moving membrane which we will denote by Riemannian manifold \( \Gamma \). As \( \Gamma \) will be embedded in \( \mathbb{R}^3 \) we denote vector fields living in \( \mathbb{R}^3 \) with an arrow above them, for example \( \vec{x} \), and vector fields living in the tangent bundle of \( \Gamma \) by bold typeface, e.g. \( \mathbf{x} \).

The position of \( \Gamma \) will be denoted by \( \vec{X}(x_1, x_2) \), which depends local on two coordinates of \( \mathbb{R}^3 \). This allows for the definition of a basis on \( \Gamma \), \( \vec{e}_i = \partial_i \vec{X} \). \( \Gamma \) is equipped with a metric \( ds^2 = g_{ij} \text{d}x^i \text{d}x^j \), where \( g_{ij} = \vec{e}_i \cdot \vec{e}_j \), this and its inverse act to raise and lower indices respectively (the action by the metric of raising and lowering of indices will sometimes be denoted by the \( \sharp, \flat \) signs respectively). The triad \( (\vec{e}_1, \vec{e}_2, \vec{n}) = \left( \frac{\vec{e}_1 \times \vec{e}_2}{|\vec{e}_1 \times \vec{e}_2|} \right) \) forms a local frame on \( \Gamma \). We also denote the second fundamental form on \( \Gamma \) as \( \text{d}\vec{B} = b_{ij} \text{d}x^i \text{d}x^j \) where \( b_{ij} = \vec{n} \cdot (\partial_j \vec{e}_i) \). The connections along the tangent and normal bundles are defined in the following way

\[
\partial_i \vec{e}_j = C^k_{ij} \vec{e}_k; \quad \partial_i \vec{n} = -b_{ij} \vec{e}_j
\]  
(S18)
where \( C^k_{ij} = \frac{1}{2} g^{im} (\partial_j g_{mk} + \partial_k g_{jm} - \partial_m g_{jk}) \) are Christoffel symbols. We will also define the mean curvature, \( H \), and Gaussian curvature, \( K \), in the following manner

\[
2H = b_i^j; \quad K = \det (b_i^j).
\]  
(S19)

Formally, the rate-of-deformation tensor for a manifold is defined as the Lie-Derivative of the metric along the velocity field \( \mathbf{v} = \mathbf{v} + w \mathbf{n} \), this can be shown to be equal to \([5, 37]\)

\[
d = \mathcal{L}_\mathbf{v} (g) = \frac{1}{2} \left( \nabla \mathbf{v}^\flat + \left( \nabla \mathbf{v}^\flat \right)^T \right) - bw
\]  
(S20)
where $\nabla$ is the covariant derivative. The first two terms are covariant versions of the standard rate-of-deformation tensor, whereas the third term describes the coupling between curvature, $b$, and the velocity normal to the membrane, $w$.

We can find the continuity equation (incompressibility condition) for the membrane by taking the trace of the rate-of-deformation tensor, $d$,

$$\nabla \cdot v = 2Hw.$$  \hspace{1cm} (S21)

The membrane also has associated curvature energies given by the Helfrich energy

$$E_{\text{Hel}} = \int_{\Gamma} dA \sqrt{\kappa H^2}$$  \hspace{1cm} (S22)

the time derivative of which depends only on $w$, $\partial_t E_{\text{Hel}} = \dot{E}[w]$ [9]. Defining the Rayleigh dissipation functional for the membrane in the following way

$$W_\Gamma = \int_{\Gamma} \eta_m d : dA$$  \hspace{1cm} (S23)

accounts for the fluid behaviour of the membrane. From this a complete dissipation functional for the system can be defined as

$$G = W_\Gamma + \dot{E} + \int_{\Gamma} \sigma (\nabla \cdot v - 2Hw) dA$$  \hspace{1cm} (S24)

imposing incompressibility of membrane with Lagrange multiplier, $\sigma$, which corresponds to surface tension. Performing functional variation with respect to the components of the surface velocity yields the force balance equations in the main text, see [5] for details.

**Ground-state flows**

We consider a problem of a membrane tube with spinning velocity $v_0$ at $z = 0$, attached to a flat membrane at $z = L$ where $L \ll L_{SD}$ such that we can solve for the ground-state using only the membrane equations. We treat this flat membrane as an effective “impedance” acting at the end of the tube, as such we do not balance the shape equations at $z = L$.

We may want to consider a tube attached to a sheet of membrane that has some friction associated to some underlying molecular interactions. For example, consider that the tube has been pulled from the plasma membrane [10]. We model this using D’arcy’s equation on the sheet

$$\frac{1}{r} \partial_r (r \partial_r v) - \frac{v}{r^2} - \frac{\lambda}{\eta_m} v = 0$$  \hspace{1cm} (S25)

where $\lambda$ is a friction coefficient associated with the adhesions. The solution to this equation is of the form $v = AK_1 \left( \sqrt{\frac{\lambda}{\eta_m}} r \right)$, where $K_i(x)$ is a modified Bessel equation of the second kind of order $i$. We solve both geometries for some velocity $v_L$ and then balance torques to find the ground-state velocity of the tube.

This leads a velocity profile on the tube (where the flow just follows the standard Stokes equations) of the form

$$v = (v_0 - \Omega z) \bar{e}_\theta$$  \hspace{1cm} (S26)

where

$$\Omega = \frac{v_0 \sqrt{\frac{K_2}{\eta_m \pi r_0}}}{1 + L \sqrt{\frac{\pi}{\eta_m \pi r_0^3}}} \text{ where } K_i = K_i \left( \sqrt{\frac{\lambda}{\eta_m}} r_0 \right).$$

In the limit $\lambda \to 0$ we recover the solution with no friction, where

$$\Omega = \frac{2v_0}{2L \pi r_0^3}.$$  

In both of this and the $\lambda \to \infty$ limit the shear rate is of a similar order of magnitude, scaling like $\Omega \sim v_0 / L$.

**Geometry and flows on tubes with small deformations**

We now consider a perturbation to the geometry of the tube of the form $r(\theta, z, t) = r_0 + u(\theta, z, t)$. We will assume that this perturbation is small with respect to the radius, $u/r_0 \ll 1$. We take the normal to be outward in the radial
direction, and project forces in the normal along this axis. All components of differential forms are given in the basis $d\theta, dz$ hence the different dimensions in components.

To linear order the metric and its inverse on the membrane are

$$\begin{align*}
[g_{ij}] &= \begin{bmatrix} r_0^2 + 2r_0u & 0 \\ 0 & 1 \end{bmatrix}; & g^{-1} &= \begin{bmatrix} \frac{1}{r_0} - \frac{2u}{r_0^2} & 0 \\ 0 & 1 \end{bmatrix}
\end{align*}$$

(S27)

The second fundamental form (and its mixed index version) are given by the following at linear order

$$[b_{ij}] = \left[ \frac{\partial^2 u}{\partial z \partial u} - \frac{u}{r_0} \right] \begin{bmatrix} 0 \\ 0 \\ \frac{1}{r_0} \end{bmatrix}; \quad [b_{ij}^*] = \left[ \frac{\partial^2 u}{\partial z \partial u} - \frac{u}{r_0} \right] \begin{bmatrix} \frac{1}{r_0} \\ 0 \end{bmatrix}$$

(S28)

which gives mean and Gaussian curvature

$$2H = b_{ij}^* b_{ij} = \frac{\partial^2 u}{r_0^2} - \frac{u}{r_0^2} + \frac{2}{r_0} \partial_z u$$

(S29)

$$K = \det \begin{bmatrix} b_{ij}^* \\ b_{ij} \end{bmatrix} = \det \begin{bmatrix} b^*_k g^{kj} \end{bmatrix} = - \frac{\partial^2 u}{r_0^2}$$

The Christoffel symbols are the following

$$\begin{align*}
C^\theta_{ij} &= \begin{bmatrix} \frac{\partial u}{\partial r_0} & \frac{\partial u}{\partial r_0} & 0 \\ 0 & \frac{\partial u}{\partial r_0} & 0 \\ \frac{1}{r_0} & \frac{1}{r_0} & 0 \end{bmatrix}; & C^z_{ij} &= \begin{bmatrix} -r_0 \partial_z u & 0 \\ 0 & 0 \end{bmatrix}
\end{align*}$$

(S30)

which can be used to find the covariant derivative of the velocity field on the membrane $v = (v + \delta v^\theta) \bar{e}_\theta + \delta v^z \bar{e}_z$

$$\nabla v = \begin{bmatrix} \frac{1}{r_0} \partial_\theta \delta v^\theta & \partial_\theta \delta v^z \\ \frac{1}{r_0} \partial_z \delta v^\theta & \partial_z \delta v^z \end{bmatrix}.$$}

(S31)

We will make use of this to calculate the viscous part of the normal membrane response in the shape equation

$$b^* : \nabla v = -\frac{1}{r_0^2} \partial_\theta \delta v^\theta - \frac{\Omega}{r_0} \partial_z \delta v^u. \quad \text{(S32)}$$

We also note here the Hodge duals of the fundamental forms as this provides a natural way to compute Laplacians on manifolds

$$\begin{align*}
* \text{vol}^2 &= 1; & 1 &= \text{vol}^2 \\
* d\theta &= \left( \frac{1}{r_0} - \frac{u}{r_0^2} \right) dz; & * dz &= -(r_0 + u) d\theta
\end{align*}$$

(S33)

we find the Laplacian of the mean curvature $- \star d \star dH = 0$ in order to derive the bending rigidity dominated response. After some lengthy algebra and taking the Fourier representation $u = \sum_{q,m} q(m) e^{iqz + im\theta}$ with similar transforms for $\sigma = \sigma_0 + \delta \sigma$ and the surface velocity components, we can write the shape equation as a linear response theory. This gives Eq. 6 in the main text.

In order to write the surface stokes equations for our perturbed system we need to find the surface Laplacian $- \star d \star d v^b$ of our velocity. This gives

$$(- \star d \star d v^b)^{\theta} = \begin{bmatrix} \frac{\partial \sigma_0 \delta v^z}{r_0^2} - \frac{\partial^2 \delta v^\theta}{r_0} - \frac{\partial^2 u (v_0 - \Omega z)}{r_0^2} + \frac{\Omega \partial_z u}{r_0^2} \left( \frac{\partial}{\partial \theta} \right) \\
\frac{\partial \sigma_0 \delta v^\theta}{r_0} + \frac{\partial \sigma_0 (v_0 - \Omega z)}{r_0^2} - \frac{\partial^2 \delta v^z}{r_0^2} \left( \frac{\partial}{\partial z} \right) \end{bmatrix}$$

(S34)

We note that $-2K v = \frac{2\sigma_0}{r_0^2} u (\frac{\partial}{\partial \theta})$ and $(b - 2Hg)^{\theta} \cdot \nabla w = \frac{2}{r_0} \partial_z \partial_t u (\frac{\partial}{\partial \theta})$. Putting this together into the 2D stokes equation and taking the Fourier transform we find

$$\begin{align*}
\theta : & \quad \eta_m \left[ \frac{mq}{r_0} \delta v^z_{q,m} + \frac{iq}{r_0} \bar{u}_{q,m} + q^2 \delta v^\theta_{q,m} - \frac{q^2 v_0}{r_0} \bar{u}_{q,m} \right] - \frac{im}{r_0} \delta \sigma_{q,m} = 0
\end{align*}$$

(S35)
\[ z : \eta_m \left[ \frac{m^2}{r_0^3} \delta v_{q,m}^z - \frac{mq v_0}{r_0^2} \bar{u}_{q,m} - \frac{mq}{r_0} \delta v_{q,m}^\theta + \frac{iq}{r_0} \partial_t \bar{u}_{q,m} \right] - iq \delta \sigma_{q,m} = 0 \] (S36)

along with the continuity equation

\[ \frac{im}{r_0} \delta v_{q,m}^\theta + iq \delta v_{q,m}^z + \frac{1}{r_0} \partial_t \bar{u}_{q,m} = 0. \] (S37)

From this point it is just a matter of algebra to find the response function in terms of \( \bar{u}_{q,m} \) and \( \partial_t \bar{u}_{q,m} \).

We can solve the 2D Stokes flow to find

\[ \delta \sigma_{q,m} = \frac{q \eta_m (\tilde{q} \partial_t \bar{u}_{q,m} + 2imq v_0 \bar{u}_{q,m} + mq v_0 - i \Omega) \bar{u}_{q,m}}{(m^2 + \tilde{q}^2)} \] (S38)

\[ \delta v_{q,m}^\theta = \frac{i (m^3 + 2mq^2) \partial_t \bar{u}_{q,m} - m^2 q^2 v_0 r_0 \bar{u}_{q,m} + \tilde{q}^3 (qv_0 - i \Omega) \bar{u}_{q,m}}{(m^2 + \tilde{q}^2)^2} \] (S39)

\[ \delta v_{q,m}^z = \frac{q \left( \left( m^3 v_0 - \tilde{q}^2 m v_0 + im \tilde{q} r_0 \Omega \right) \bar{u}_{q,m} + iq^2 r_0 \partial_t \bar{u}_{q,m} \right)}{(m^2 + \tilde{q}^2)^2} \] (S40)

these can then be substituted into Eq. [6] which gives a first order equation governing the growth of \( \bar{u}_{q,m} \).

Notes on screening by bulk flows

There are two places where the screening by bulk hydrodynamics must be considered, the first is in the dynamics of the ground state on the tube. The second is to find out where the crossover between membrane and bulk dissipation in the instability growth happens.

**Flows on a fixed membrane tube**

We will first consider hydrodynamics on a static membrane tube (i.e. we assume that the cylindrical geometry is stable to perturbations in shape). In the limit of small inertia the 3D velocity field, \( \vec{u} \), satisfies the continuity and Stokes equations

\[ \nabla \cdot \vec{u} = 0; \quad \eta \nabla^2 \vec{u} = \nabla P \] (S41)

where \( P \) is the pressure and \( \eta \) the viscosity. This is coupled to the membrane velocity at the boundary with a no-slip condition.

Stress balance at the membrane is imposed by the 2D continuity and Stokes equations and, for surfaces of zero Gaussian curvature, can be written as

\[ \nabla_i v^i = 0; \quad \eta_m \Delta_{LB} v_i - \nabla_i \sigma = t_i^+ + t_i^- \] (S42)

where \( \eta_m \) is the (2D) membrane viscosity, \( \sigma \) is the surface tension, \( v = v^i e_i \) is the tangential membrane velocity and \( \Delta_{LB} \) is the Laplace-Beltrami operator (formally this corresponds to \( \Delta_{LB} = \delta d \) where \( d \) is the exterior derivative and \( \delta \) is the co-differential). The combined operator \( \delta d \) is the generalization of the curl-curl operator to a manifold and acts like a Laplacian [5, 9]. The symbols \( t_i^\pm \) are the traction forces from the bulk fluid acting on the membrane (\( \pm \) denoting interior and exterior respectively) [3, 5].

We will consider a system of a membrane tube with radius \( r_0 = \sqrt{\frac{\kappa}{2 \sigma_0}} \), where \( \kappa \) is the bending rigidity of the membrane and \( \sigma_0 \) is the equilibrium surface tension. This is the radius which minimizes the Helfrich Hamiltonian for a fluid membrane

\[ F = \int_{\Gamma} dA_{\Gamma} \left( 2\kappa H^2 + \sigma_0 \right) \] (S43)

where \( \Gamma \) and \( dA_{\Gamma} \) denote the manifold describing the neutral surface of the membrane and its associated area element, and \( H \) is the mean curvature [14]. For typical membrane tubes fissioned by Dynamin \( r_0 \approx 10 \text{nm} \) [21].
We use standard cylindrical coordinates \((r, \theta, z)\) and take the boundary condition for flow on the membrane to be \(\mathbf{v}|_{z=0} = v_0 \mathbf{e}_\theta\), we treat this as an approximation to the flow induced by Dynamin.

We can then solve the \((S41) \& (S42)\), making use of symmetry \(\mathbf{v} = v(\theta) \mathbf{e}_\theta\), \(\mathbf{u} = u(r, z) \mathbf{e}_\theta\) they reduce to

\[
\frac{1}{r} \partial_r (r \partial_r u_\theta) + \partial_z^2 u_\theta - \frac{u_\theta}{r^2} = 0
\]

\[
\eta M \partial_z^2 v + t_\theta^+ + t_\theta^- = 0
\]

where \(t_\theta^\pm = \lim_{r \to r_0} \eta r \partial_r \left( \frac{\partial u_\theta^\pm}{r} \right)\). We can now solve this numerically by direct methods (taking a Neumann boundary condition for the bulk flow at \(z = 0\) and \(u = 0\) at large distance and \(r = 0\)) [45]. The flow field computed by this method can be seen in Fig.S1.

To understand how the flow field on the membrane varies with Saffman-Delbrück length it is helpful to examine the analytic solutions to the coupled membrane bulk system in Fourier space. The flow field on the membrane in response to a point force in the \(\theta\) direction, \(F_\theta\), was found analytically by Henle & Levine [31], and in the limit \(r_0 \ll L_{SD}\) this gives

\[
v \approx v_0 \mathbf{e}_\theta \exp \left[-\sqrt{2} \frac{|z|}{\sqrt{L_{SD} r_0}} \right].
\]

In the original paper our boundary condition corresponds to \(v_0 = \frac{F_\theta}{4\pi \eta m \sqrt{L_{SD}}}\). Note that this is \(\theta\) independent as the \(m = 0\) Fourier mode dominates the bulk dynamics in this limit, so each cross-section of the tube rotates with a constant velocity. This means that the flow on a tube is screened like \(v \sim e^{-\lambda |z|}\) where \(\lambda = \frac{\sqrt{2}}{\sqrt{L_{SD} r_0}}\). This approximate analytical expression can be compared to numerical solutions where we find that it reproduces the correct power law relation between \(\lambda\) and \(L_{SD}\), see Fig.S2.

For flows with large \(L_{SD}/r_0 \sim 10^3 \to 10^4\) this gives a screening length of order \(100 r_0\) so as long as we consider flows where \(L \lesssim 10 r_0\) then membrane dissipation should dominate.

**Membrane flow instability with bulk dissipation**

If we assume that we are still in a regime where our ground-state is valid when neglecting bulk flows, we can then check that the perturbations dynamics do not depend on bulk dissipation at this length-scale. To find the dissipative forces associated with the perturbations we make use of a standard decomposition for the Stokes equations in 3D in terms of three scalar functions \(f^\pm(r, \theta, z)\), \(g^\pm(r, \theta, z)\) and \(h^\pm(r, \theta, z)\) [34]. These are related to the velocity and pressure fields in the following way

\[
\bar{u}^\pm = \nabla f^\pm + \nabla \times (g^\pm \mathbf{e}_z) + \frac{1}{r} \partial_r \left( \nabla h^\pm \right) + \partial_z h^\pm \mathbf{e}_z
\]

\[
P^\pm = -2\eta \partial_z^2 h^\pm.
\]

**FIG. S1.** Flow field for the ground-state of the spinning membrane tube with radius \(r_0 = 1.0\), and Saffman-Delbrück length \(L_{SD}/r_0 = \frac{2m}{\eta r_0} = 10^6\). The boundary condition on the tube at \(z = 0\) is \(v(0) = v_0\) where \(v_0 = 10^3 \text{s}^{-1}\).
FIG. S2. Flow-field decay rate, $\lambda$ (with units Length$^{-1}$) against Saffman-Delbrück length $L_{SD}$ for tube spinning velocity at $z = 0$ given by $\frac{r_0}{v_0} = 10^3$ s$^{-1}$.

FIG. S3. The growth rate $\alpha(\tilde{q})$ for the $|m| = 1$ modes, in units of $\tau^{-1} = \frac{\sigma_0}{\eta m}$, plotted against $|\tilde{q}|$ with dissipation due to bulk flows included. Plotted for different values of dimensionless shear rate $\hat{\Omega} = \frac{\eta m \Omega}{\sigma_0}$ within physiological range. We assume the bulk viscosity is that of water ($\eta \sim 10^{-3}$ Pa s).

We can write these functions in Fourier space in terms of modified Bessel functions

$$
\begin{bmatrix}
  f^+ \\
  g^+ \\
  h^+
\end{bmatrix} = \sum_{q,m} \begin{bmatrix}
  F^+_{q,m} \\
  G^+_{q,m} \\
  H^+_{q,m}
\end{bmatrix} P^+_{q,m}(r) e^{i q z + i m \theta}
$$

(S47)

where $P^+_{q,m}(r) = K_m(qr)$ and $P^-_{q,m}(r) = I_m(qr)$ where $I_m, K_m$ are modified Bessel functions of the first and second kind respectively.

We now solve the bulk stokes equations subject to linearised boundary conditions at the membrane

$$
\mathcal{F} \left( \hat{u}^\pm \cdot \hat{e}_r \right) = \partial_t \hat{u}_{q,m}; \quad \mathcal{F} \left( \hat{u}^\pm \cdot \hat{e}_\theta \right) = \delta v^\theta_{q,m}; \quad \mathcal{F} \left( \hat{u}^\pm \cdot \hat{e}_z \right) = \delta v^z_{q,m}
$$

(S48)

where $\mathcal{F}$ is the Fourier transform in $z$ and $\theta$. From this we find the Fourier coefficients, $F^\pm_{q,m}, G^\pm_{q,m}, H^\pm_{q,m}$. Here we make use of Mathematica to solve the combined system and evaluate the growth rate $\alpha(q) = \frac{\partial u_{q,m}}{u_{q,m}}$ numerically for the $|m| = 1$ modes, Fig.S3.

The cross over to bulk dissipation is at much longer wavelengths that the length of the tube (in fact the bulk hydrodynamics would need to be considered in the ground-state before we reach the point where it is relevant for the instability damping).
Effects of more realistic geometry

To try and understand the effect of the instability in more complex geometry (in particular with non-zero Gaussian curvature in the ground state), we need to consider the term driving the instability as the full calculation becomes intractable very quickly. All the forces acting normal to the membrane which drive the instability are due to the term $b_{ij} \nabla_i v^j$, in particular the driving force (per area) is set by the linear response coefficient of the mixed second derivative of the shape, $k_{\theta z}(z)$ which is now a function of $z$ due to change in geometry (specifically the non-constant gradient in the flow field ground state). The driving force per unit area scales like

$$f_{\text{driving}} \sim 2 \eta_m k_{\theta z}(z) \frac{\partial^2 u}{\partial \theta \partial z}$$

so we will consider how $k_{\theta z}(z)$ changes as we change the geometry of our ground-state.

For some general axisymmetric ground-state parametrized by the vector $\vec{X} = (r(z) \cos \theta, r(z) \sin \theta, z)$ with ground-state flow field $v_0(z) \vec{e}_\theta$ we find (up to linear order in perturbations)

$$b_{ij} \nabla_i v^j = a_{z 0 0 0} \delta v_z + a_{z 1 0 0} \partial_z \delta v_z + k_{\theta z} \frac{\partial^2 u}{\partial \theta \partial z} + b_{z 0 0 1} \partial_\theta \delta v_\theta + k_\theta \partial_\theta u$$

where

$$a_{z 0 0 0} = \frac{-r'(z) - 2r'(z)^3 - r'(z)^5 + r(z)^2 r'(z) r''(z)^2}{r(z)^2 (1 + r'(z)^2)^{5/2}}$$

$$a_{z 1 0 0} = \frac{r''(z)}{(1 + r'(z)^2)^{3/2}}$$

$$k_{\theta z} = \left[ -v_0(z)r'(z) - v_0(z)r'(z)^3 + r(z)v_0'(z) + r(z)r'(z)^2 v'(z) + r(z)v_0(z)r'(z)r''(z) \right] \times \left( r(z)^2 (1 + r'(z)^2)^{5/2} \right)^{-1}$$

$$b_{z 0 0 1} = \frac{1}{r(z)^2 \sqrt{1 + r'(z)^2}}$$

$$k_\theta = \frac{v_0(z)}{r(z)^3 \sqrt{1 + r'(z)^2}}$$

Neck (Catenoid)

To consider the effect of the instability in a more realistic in-vivo situation, for example on the neck of a budding vesicle, we look at the ground state flows and $k_{\theta z}$ on a catenoid, $r(z) = r_0 \cosh \left( \frac{z}{r_0} \right)$. The ground state surface flow is solved numerically with boundary conditions $v(0) = 1$, $v(2) = 0$ taking $r_0 = 1$ and $L = 2$ for simplicity. From this we can evaluate $k_{\theta z}$ and compare to the case of a tube. This is shown in Fig.4. Note the amplification of $k_{\theta z}$ by a factor of 2 near the centre of the catenoid when compared to the tube. The consequences of this for dynamin are discussed in the main paper.
FIG. S4. Plot of the catenoid and the linear response coefficient for the helical shape perturbations on such a surface.