

Flat or crumpled: States of active symmetric membranes

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We set up and study the hydrodynamic theory for inversion-symmetric active fluid and tethered membranes. For some choices of the activity parameter, such membranes are stable and described by linear hydrodynamic equations, which are exact in the asymptotic long wavelength limit, giving stable flat phases with translational quasi-long-range orders. For other choices of the activity parameter, the system is linearly unstable in the long wavelength limit, implying crumpling, or has intermediate wave-vector instabilities, suggesting patterns. We argue that in such an active membrane thermal noises dominate over any active noises, and use those to calculate the correlation functions of membrane conformation fluctuations in the stable case, and the associated correlation functions of the embedding bulk flow velocities. Our work identifies a hitherto unknown activity-induced route, distinct from the well-known thermal crumpling of equilibrium fluid membranes, to destabilize a membrane.

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Considerable success has been achieved by now in applying the principles of thermodynamics and statistical mechanics to membranes in thermal equilibrium in terms of continuum theories, parametrized by a set of elastic constants [1–3]. Such theories have successfully predicted and explained a variety of results, e.g., thermal crumpling of large tensionless lipid membranes at any low but nonzero temperature T [1,2,4,5] and the existence of statistically flat phases orientational long-range order (LRO) at sufficiently low but finite T in tethered membranes [1,6,7]. It is, however, now understood that due to the underlying microscopic active processes in live cells [8], e.g., nonequilibrium fluctuations of cell cytoskeletons [9] or active proteins in lipid membranes [10,11], live cell membranes display unusual dynamical fluctuation properties [12–15]. Similarly, experimental comparisons of fluctuations in healthy, live red blood cell membranes and those in adenosine triphosphate (ATP) depleted red blood cells suggest that active processes should be responsible in live red blood cell membrane fluctuations [16–18]. More recently, by comparing membrane response and fluctuations on single red blood cells, a violation of the fluctuation-dissipation-theorem (FDT) [19] in the flick-

ering of live red blood cells demonstrating the underlying nonequilibrium, active processes was reported in Ref. [20]. The generality of experimental observations on the manifestations of the nonequilibrium nature of cell membrane dynamics has prompted scientists to look for minimal physical descriptions. Such efforts have led to theories of active membranes applicable to various settings [20–32]. We here construct and study the hydrodynamic equations for open, inversion-symmetric, isotropic single-component active fluid or tethered membranes, which are tensionless in the equilibrium limit and embedded in three-dimensional (3D) isotopic fluids.

Our principal results are as follows. (i) The nonequilibrium dynamics of nearly flat symmetric active membranes, fluid or tethered, emerge from their couplings with an embedding active isotropic bath, provided by a 3D active but isotropic fluid. (ii) The linearized hydrodynamic equations predict that such a nearly flat patch can be stable, corresponding to orientational LRO for a fluid membrane, or orientational LRO and in-plane translational quasi-long-range order (QLRO). A *positive active tension*, generated by the interplay between active processes and 3D embedding fluid flows, is responsible for orientational LRO. These results are *exact* in the asymptotic long wavelength limit, with all nonlinear effects being irrelevant. Thus nonlinear effects play *no* role in sustaining the order. (iii) Although these results are reminiscent of those for equilibrium fluid or tethered membranes *with a finite tension* at some effective temperature, in our linear theory the equal-time undulation mode correlation function depends on a dynamic (active, see below) coefficient, indicating the inherent nonequilibrium nature of the system. In contrast, the in-plane displacement correlators depend only on thermody-

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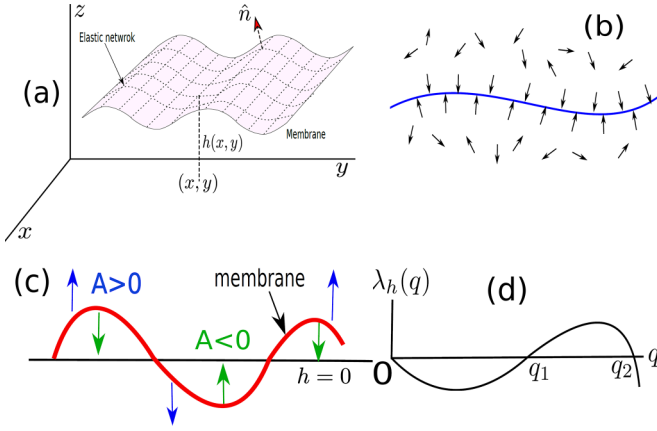


FIG. 1. Schematic (a) model diagram of a membrane depicted in the Monge gauge that is embedded in an active isotropic fluid. Here, $\mathbf{R} = [\mathbf{r} + \mathbf{u}, h(\mathbf{r}, t)]$, where $h(\mathbf{r}, t)$ is the height above points $\mathbf{r} = (x, y)$ on a reference plane. Further, $\hat{n}$ is the local normal to the membrane. (b) Schematic diagram showing actin filaments grafted normally to the membrane; in the bulk they are in the isotropic phase. (c) Diagram depicting the role of active stress in stabilizing ($A < 0$, green arrows indicating *reduction* in fluctuations) or destabilizing ($A > 0$, blue arrows indicating *enhancement* of fluctuations) the membrane. (d) Plot of $\lambda_h(\mathbf{q})$ versus q showing an unstable intermediate band of wave vectors within the range $q_1 < q < q_2$, $\lambda_h(\mathbf{q}) > 0$, implying linear instability. See text.

namic or equilibrium parameters. (iv) The undulation modes can be linearly unstable at intermediate scales, presumably giving rise to steady patterns, if the membrane is permeable and the associated permeation flow is sufficiently strongly destabilizing. (v) The active tension can also be negative, in which case the undulation modes are linearly unstable at the longest scales, signaling membrane crumpling. Interestingly, the in-plane displacement modes are still linearly stable, but should become *nonlinearly* unstable, possibly due to their nonlinear couplings with the undulation modes, which are irrelevant in the linearly stable case. Our theoretical predictions are general and can be tested in artificial *in vitro* settings. Our theory identifies a previously unexplored activity-induced route to destabilize a membrane, which is distinct from the well-known thermal crumpling phenomenon in equilibrium fluid membranes [4].

We now construct the hydrodynamic equations for a permeable active symmetric tethered membrane embedded in a 3D bulk isotropic fluid. The hydrodynamic equation for an active symmetric fluid membrane can be obtained by ignoring the in-plane displacement modes since these are *not* broken symmetry hydrodynamic modes for fluid membranes. The conformation $\mathbf{R}(\mathbf{s})$ of any membrane in three dimensions is parametrized by a two-dimensional (2D) position vector $\mathbf{s}$ that designates points on the membrane [33,34]. The local membrane velocity is then formally given by $\partial_t \mathbf{R}(\mathbf{s})$. For a nearly flat patch of a membrane without any overhangs, it is convenient to use the Monge gauge [1,19], in which $\mathbf{R} = [\mathbf{r} + \mathbf{u}, h(\mathbf{r}, t)]$, where $h(\mathbf{r}, t)$ is the height above points $\mathbf{r} = (x, y)$ on a reference plane; see Fig. 1(a) for a schematic diagram of the membrane. Here, $\mathbf{u}$ is the relative in-plane displacement of a point whose location in the undistorted membrane is at

$\mathbf{R} = [\mathbf{r}, h = 0]$. This reference plane is, however, completely arbitrary.

We denote the 3D bulk hydrodynamic flow velocity by v'_α , ($\alpha = x, y, z$) and the 2D flow velocity in the membrane by v_i , $i = x, y$. Ignoring any number conservation, h and $\mathbf{u} \equiv u_i$ are the two hydrodynamic variables in the problem along with the total momentum of the system. In the presence of a permeation flow velocity v_{perm} locally normal to the membrane, considered as a permeable fluid film [35], there is a local normal relative velocity ($= v_{\text{perm}}$) between the membrane and the bulk fluid flow at the location of the membrane normally to it. With $\partial_t h \equiv \partial_t R_z$ in the Monge gauge, h obeys

$$\frac{\partial h}{\partial t} - v_{\text{perm}} = v'_z|_{z=h}. \quad (1)$$

In general, v_{perm} is a function of h and u_{ij} that odd in h , tilt invariant due to the rotational symmetry [1] and also invariant under $u_i \rightarrow u_i + \text{const.}$. Since the permeation flow is locally normal to the membrane, $v_{\text{perm}} = \sqrt{1 + (\nabla h)^2} f_{\text{perm}}(\nabla^2 h, u_{ij})$, where $f_{\text{perm}}(\nabla^2 h, u_{ij})$ is a general function of its arguments and their in-plane space derivatives, and odd in h . For small fluctuations, expanding in h and u_{ij}

$$v_{\text{perm}} = \mu_1 \nabla^2 h + \frac{\mu_1}{2} \nabla^2 h (\nabla h)^2 + \mu_2 \nabla \cdot \mathbf{u} \nabla^2 h + \mu_p \frac{\delta \mathcal{F}}{\delta h}, \quad (2)$$

retaining only the lowest-order nonlinearities. Here, $u_{ij} = \frac{1}{2}(\partial_i u_j + \partial_j u_i + \partial_i h \partial_j h)$ is the strain tensor [1,19], $\mu_p > 0$ is an equilibrium permeation coefficient, and μ_1, μ_2 give the strengths of active permeation, each of which can be positive or negative. Indeed, symmetry arguments, which are used to write down Eq. (2), say nothing about the active parameters whose magnitudes and signs are determined by the microscopic physics of a particular situation. For instance, μ_1 , effectively a nonhydrodynamic tension, can be made negative by strong curvature-dependent active fusion processes on the membrane [36,37], or by curvature-inducing molecules [38]. It can also be positive for certain protein pumps in membranes; see Refs. [22,39]. Here, $\mathcal{F}$ is the Landau-Ginzburg free-energy functional of a tensionless tethered membrane. General symmetry considerations dictate

$$\mathcal{F} = \frac{1}{2} \int d^2 r [K (\nabla^2 h)^2 + \lambda u_{ii}^2 + 2\mu u_{ij} u_{ij}]; \quad (3)$$

with $K > 0$ the bend modulus and λ, μ are the Lamé coefficients [19]. The equation of u_i is

$$\frac{\partial u_i}{\partial t} = v_i. \quad (4)$$

In the extreme Stokesian limit, dropping the fluid inertia, 3D hydrodynamic velocity v'_α is obtained from the force balance condition $\nabla_\beta \sigma'_{\alpha\beta} = 0$, where stress tensor

$$\sigma'_{\alpha\beta} = \eta'(\partial_\alpha v'_\beta + \partial_\beta v'_\alpha) - P' \delta_{\alpha\beta} \quad (5)$$

for an incompressible bulk fluid [40], η' is the shear viscosity and P' is the 3D pressure.

Ignoring inertia, the 2D in-plane velocity v_i satisfies a force balance equation. There are internal forces in the membrane to be balanced by the external forces on the membrane from the embedding 3D bulk fluid. The internal forces per unit area of the membrane are $\nabla_j \sigma_{ij}^{\text{tot}}$, where σ_{ij}^{tot} is the total 2D internal

stress

$$\sigma_{ij}^{\text{tot}} = \eta(\partial_i v_j + \partial_j v_i) + \eta_b \nabla \cdot \mathbf{v} \delta_{ij} - P \delta_{ij} + \sigma_{ij}^{\text{el}} + \sigma_{ij}^a, \quad (6)$$

η and η_b are the 2D shear and bulk viscosities, respectively, and P is a 2D partial pressure. Further, $\sigma_{ij}^{\text{el}} = \delta \mathcal{F} / \delta u_{ij}$ is the elastic stress [19,41]. The last contribution to σ_{ij}^{tot} comes from the active stress $\sigma_{\alpha\beta}^a = A n_\alpha n_\beta$, where $\hat{\mathbf{n}} = (\hat{z}, -\nabla_i h)$ is the local normal to the leading order in h fluctuations with $\hat{z}$ being the unit vector along the z direction. This active stress can locally generate forces $\nabla_j \sigma_{ij}^a$ tangentially and $\nabla_j \sigma_{zj}^a$ normally to the membrane, and can arise, e.g., in a membrane with actin filaments grafted normally to it (or also in a isotopic live bacterial suspension). The actin polymerization or depolymerization can force the membrane [42,43]. Now define a 3D polarization vector $\mathbf{p} \equiv p_\alpha$ that is nonvanishing only at the location of the membrane. Elsewhere in the bulk active fluid being in its isotropic phase, we set $\mathbf{p} = 0$. For a nearly flat membrane, the condition of normal anchoring gives $p_\alpha = -\hat{n}_\alpha$ [44]. A nonzero p_α on the membrane allows us to define an active stress $\sim A p_\alpha p_\beta$ [45–50], which with normal anchoring gives $\sigma_{\alpha\beta}^a$ as defined above, with $A < (>) 0$ corresponding to contractile, e.g., as in actin cytoskeletons (extensile, e.g., in some bacterial suspensions) [50] active stress. See Fig. 1(b) for a schematic representation.

The 2D force balance equation for the in-plane flow on the membrane reads [51–53]

$$\nabla_j \sigma_{ij}^{\text{tot}} + f_i = 0. \quad (7)$$

Here, f_i is the force per unit area on the 2D membrane due to the shear stress of the bulk flow:

$$f_i = \eta' \left(\frac{\partial v'_i}{\partial z} + \frac{\partial v'_z}{\partial x_i} \right) \Big|_{z=h_+} - \eta' \left(\frac{\partial v'_i}{\partial z} + \frac{\partial v'_z}{\partial x_i} \right) \Big|_{z=h_-}. \quad (8)$$

Normal stress balance at the membrane yields

$$\left(2\eta' \frac{\partial v'_z}{\partial z} - P' \right) \Big|_{z=h_+} - \left(2\eta' \frac{\partial v'_z}{\partial z} - P' \right) \Big|_{z=h_-} - \frac{\delta \mathcal{F}}{\delta h} + \nabla_j \sigma_{zj}^a = 0 \quad (9)$$

balancing the external forces per unit area or the normal stresses by the bulk fluid on the membrane with the internal forces per unit area by the membrane that include elastic restoring forces of the membrane and active forces due to the active stress defined above.

We impose $v'_\alpha(z = \pm\infty) = 0$ as the boundary conditions on v'_α . Lastly, the no-slip boundary condition on the membrane implies $v'_{\alpha=i}(z = h_+) = v'_{\alpha=i}(z = h_-) = v_i$ and the continuity condition $v'_z(z = h_+) = v'_z(z = h_-)$. We now solve for $v'_\alpha(\mathbf{r}, z, t)$ subject to the above conditions. Defining $v'_\alpha(\mathbf{q}, z, t)$ and $v_i(\mathbf{q}, t)$ as the in-plane Fourier transforms of $v_\alpha(\mathbf{r}, z, t)$ and $v_i(\mathbf{r}, t)$, where $\mathbf{q}$ is a wave vector, (see, e.g., Refs. [51–53]) and by using Eqs. (2) and (3), and ignoring nonlinearities, we obtain

$$\frac{\partial h(\mathbf{q}, t)}{\partial t} = \frac{Aq}{4\eta'} h(\mathbf{q}, t) - \mu_1 q^2 h(\mathbf{q}, t) - \frac{Kq^3}{4\eta'} h(\mathbf{q}, t), \quad (10)$$

which is the linearized hydrodynamic equation for the undulation modes. The intermediate calculational details, similar to Refs. [28,52,53], are straightforward, and are given in the Supplemental Material (SM) [54].

To obtain the hydrodynamic equations for $\mathbf{u}$, we decompose $\mathbf{u} = (u_\parallel, u_\perp)$ and $\mathbf{v} = (v_\parallel, v_\perp)$, where $\parallel$ and $\perp$ refer to in-plane directions parallel and perpendicular to $\hat{\mathbf{q}}$. To calculate $v_\perp$ and $v_\parallel$, we resolve Eq. (7) perpendicular and parallel to $\hat{\mathbf{q}}$ giving $v_\perp(\mathbf{q}, t) = -[\mu q / (2\eta')] u_\perp(\mathbf{q}, t)$ to the linear order in (small) fluctuations. Then

$$\frac{\partial u_\perp(\mathbf{q}, t)}{\partial t} = -\frac{\mu q}{2\eta'} u_\perp(\mathbf{q}, t) \quad (11)$$

is the linearized hydrodynamic equation for $u_\perp$. In the long wavelength limit, the equation for $v_\parallel(\mathbf{q}, t)$ reads

$$4\eta' q v_\parallel(\mathbf{q}, t) = -iqP(\rho) - (\lambda + 2\mu) q^2 u_\parallel(\mathbf{q}, t). \quad (12)$$

Here, ρ is the 2D membrane density. Now assume the total particle number $\int d^2r \rho$ is constant only on average due to possible nonnumber conserving events, e.g., birth-death of the particles (assumed active). Then ρ is not a conserved density and hence is not a hydrodynamic variable. In fact, fluctuations $\delta\rho$ about the mean concentration ρ_0 relax quickly. In the spirit of coarse-grained hydrodynamic approaches, we then replace $\chi(\rho)$ by $\chi(\rho_0)$, a constant. This ensures that P drops out of Eq. (12). Solving for $v_\parallel(\mathbf{q}, t)$ we get

$$\frac{\partial u_\parallel(\mathbf{q}, t)}{\partial t} = -\frac{\lambda + 2\mu}{4\eta'} q u_\parallel(\mathbf{q}, t) \quad (13)$$

to the linear order in (small) fluctuations.

Notice that Eqs. (11) and (13) are *always* linearly stable since $\mu > 0$ and $\lambda + 2\mu > 0$ for the thermodynamic stability of $\mathcal{F}$. In contrast, Eq. (10) is linearly unstable or stable in the long wavelength limit, when the active parameter A is positive (i.e., extensile) or negative (i.e., contractile); see Fig. 1(c) for a schematic diagram depicting the role of active stress in stabilizing ($A < 0$) or destabilizing ($A > 0$) the membrane: $A > 0$ enhances the distortion of a local patch in the membrane, pushing it locally further from the mean membrane position, whereas $A < 0$ suppresses the distortions, bringing the patch closer to the mean position. Even when $A < 0$, if μ_1 is large negative ensuring a sufficient scale separation between $A < 0$ and $\mu_1 < 0$, on one hand, and μ_1 and K , on the other, h dynamics displays linear instability for an intermediate range of wave vectors. This instability is due to the destabilizing nature of the active permeation flow. Qualitatively, the forces on the membranes due to the active proteins which couple with the local curvature, can enhance (suppress) the local curvature, destabilizing (stabilizing) it; see Fig. 2(a) for a pictorial representation. See Fig. 1(d) for a schematic plot of $\lambda_h \equiv -|A|q/(4\eta') + |\mu_1|q^2 - Kq^3/(4\eta')$ versus q with $\mu_1 < 0$, where λ_h is the effective damping in Eq. (10); $A < 0$. The threshold μ_c of μ_1 for linear instability can be obtained by setting $\lambda_h(q) = 0$ and $\partial \lambda_h / \partial q = 0$, giving $\mu_c \equiv -\sqrt{(|A|K)/2\eta'}$. Taking $A/(4\eta'a) \sim 1 \text{ min}^{-1}$ [55], $a \sim 100 \text{ nm}$ as the typical mesh size in actin cortex [56], we get $A/(4\eta') \sim 100 \text{ nm/min}$; see also Ref. [57] for related general discussions. Then using $\eta' \sim 10^{-3} \text{ kg/(m.sec)}$ and $K \sim 10^{-20} \text{ J}$ [58], we get a rough estimate $\mu_c \sim 10^{-17} \text{ m/s}^2$.

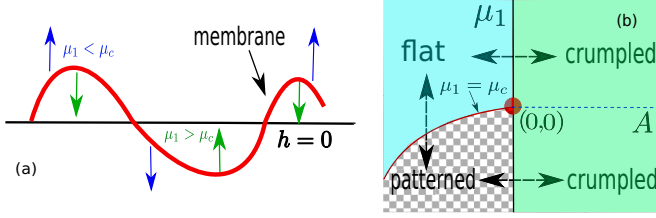


FIG. 2. (a) Schematic diagram showing active permeation flow stabilizing ($\mu_1 > \mu_c$; green arrows) or destabilizing ($\mu_1 < \mu_c$; blue arrows) the membrane. (b) Different phases of symmetric active membranes in the $A - \mu_1$ plane. Three distinct transitions are shown by double arrows, with a triple point at $(0, 0)$ (filled red circle).

However, dimensionally $\mu_1 \sim \text{permeation coefficient} \times \text{surface tension}$. Using the typical values of the parameters [58], we get $\mu_1 \sim 10^{-17} \text{ m/s}^2$, close to μ_c . Notwithstanding these suggested representative values, *in vitro* set ups, however, allow experimentally controlling these active parameters by a variety of methods, e.g., controlled addition of active proteins and adding or removing of ATP [20,59–62], permitting to explore wider ranges of these parameters.

To calculate the correlation functions, we now must include noises in the governing dynamical equations. Let g_h , $g_\perp$, and $g_\parallel$ be the noises added in Eqs. (10), (11), and (13), all of which are assumed to be Gaussian-distributed with zero mean. The noises have two sources: thermal and active noises. The thermal noises that survive in the equilibrium limit of the dynamics are controlled by the FDT [19], which relates the noise variances to the damping coefficients. This gives zero-mean long-range noises with variances [51]

$$\langle g_h(\mathbf{q}, t) g_h(-\mathbf{q}, 0) \rangle = \frac{2k_B T_{\text{eff}} \delta(t)}{4\eta' q}, \quad (14)$$

$$\langle g_\perp(\mathbf{q}, t) g_\perp(-\mathbf{q}, 0) \rangle = \frac{2k_B T_{\text{eff}} \delta(t)}{2\eta' q}, \quad (15)$$

$$\langle g_\parallel(\mathbf{q}, t) g_\parallel(-\mathbf{q}, 0) \rangle = \frac{2k_B T_{\text{eff}} \delta(t)}{4\eta' q}, \quad (16)$$

where T_{eff} is an effective temperature and k_B is the Boltzmann constant. Furthermore, there should be additive active noises, which are expected to be short range [63–66], and hence subdominant to the thermal noises in the long wavelength limit. We thus conclude that although the model is *active*, the noises are essentially *thermal*. This forms a major conclusion of this work. Do we then have the FDT in the linearized hydrodynamics? To know this, we must calculate the correlation function of the fields by using Eqs. (14) and (15). We consider the linearly stable case with no intermediate wave vector instabilities. In the long wavelength limit, we get

$$\langle |h(\mathbf{q}, t)|^2 \rangle = \frac{k_B T}{|A| q^2}, \quad \langle |u_a(\mathbf{q}, t)|^2 \rangle = \frac{k_B T}{\tilde{a} q^2}. \quad (17)$$

Here, $a = \perp, \parallel$ and correspondingly $\tilde{a} = 2\mu, \lambda + 2\mu$, respectively. Our results in Eq. (17) remind us of the known equilibrium results for a fluid membrane with a finite tension A , and a 2D crystal with Lamé coefficients μ, λ . Nonetheless, A is an *active* dynamical coefficient and not a thermodynamic coefficient, unlike μ and λ . The fact that A appears in a static or time-independent quantity $\langle |h(\mathbf{q}, t)|^2 \rangle$ [see Eq. (17) above], is a reminder to us that in spite of the apparent equilibrium-like behavior the underlying dynamics is actually a nonequilibrium dynamics. Lastly, Eqs. (10), (11), (13), and (17) show that all of $h, u_\perp, u_\parallel$ have the dynamic exponent $\tilde{z} = 1$ and roughness or spatial scaling exponent $\chi = 0$ in two dimensions, the physically relevant dimension. Here, $\tilde{z} = 1$ means the fluctuations relax much faster than the diffusive relaxations.

Our theory predicts three distinct phases in this model. (i) In the linearly stable case, all of $\langle h^2(\mathbf{r}, t) \rangle$, $\langle u_\perp^2(\mathbf{r}, t) \rangle$, $\langle u_\parallel^2(\mathbf{r}, t) \rangle$ scale as $\ln(L/a_0)$, giving positional QLRO, where L is the linear system size and a_0 is a microscopic cutoff. Likewise, equal-time correlation functions $\langle h(\mathbf{r}, t) h(0, t) \rangle$, $\langle u_\perp(\mathbf{r}, t) u_\perp(0, t) \rangle$, $\langle u_\parallel(\mathbf{r}, t) u_\parallel(0, t) \rangle$ all behave as $\ln(r/a_0)$, growing logarithmically with $r \equiv |\mathbf{r}|$, another hallmark of QLRO. Furthermore, $\langle (\nabla h)^2 \rangle$ is independent of L for large L , giving orientational LRO a statistically flat phase. (ii) In the unstable case ($A > 0$), independent of μ_1 , clearly both $\langle h^2(\mathbf{r}, t) \rangle$ and $\langle (\nabla h)^2 \rangle$ diverge as soon as L exceeds a threshold determined by the zero of λ_h for a finite q . This implies a crumpled phase of the membrane with both positional and orientational short-range order, different from the well-known thermal crumpling phenomenon of equilibrium fluid membranes at any finite T . Thermal crumpling occurs in tensionless fluid membranes, whereas in the present case it is due to a negative “active tension” $A > 0$. What happens if $A = 0$? Since A can be varied by varying the strength of the active stress, let us assume it has been tuned to zero, which is the transition point between the “ordered” statistically flat phase ($A < 0$) and “disordered” crumpled phase ($A > 0$). At this transition point, assuming $\mu_1 > 0$, we obtain

$$\langle h^2(\mathbf{r}, t) \rangle \sim L, \quad \langle (\nabla h)^2 \rangle \sim \text{independent of } L, \quad (18)$$

corresponding to positional short-range order and orientational long-range order. Thus at the transition point, the membrane is clearly *less* ordered than in the “ordered” flat phase, but more ordered than the “disordered” crumpled phase. Further, $\langle \mathbf{u}^2(\mathbf{x}, t) \rangle \sim \ln(L/a_0)$ at $A = 0$, giving in-plane positional QLRO. With $A = 0$, there is no active tension and the membrane is tensionless, nonetheless with $\mu_1 > \mu_c (= 0 \text{ now})$, we define effective wave-vector-dependent bend modulus $K_{\text{eff}} \equiv K + \mu_1/q$, which diverges strongly for small q , rendering thermal crumpling ineffective. (iii) One can observe yet another transition if $A < 0$ (i.e., long wavelength stability) and μ_1 , another active parameter, is varied: as μ_1 becomes less than μ_c , patterns are formed with a preferred wave vector $q_c = \sqrt{|A|/K}$. The phase boundary between the flat and patterned phases is given by $\mu_1 = \mu_c \equiv -\sqrt{|A|K}/(2\eta')$. With relevant values of $\mu_1 \sim \mu_c$, a typical experimental realization should be close to the threshold of patterned states. See Fig. 2(b) for a phase diagram in the $A - \mu_1$ plane.

Membrane density fluctuations $\delta\rho$, a nonhydrodynamic variable, are controlled by $v_{\parallel}$, or $u_{\parallel}$, with $\langle|\delta\rho(\mathbf{q}, t)|^2\rangle$ is *finite* in the long wavelength limit for $A < 0$, $\mu_1 > 0$, but has divergences if $A > 0$, or at finite q , if $\mu_1 < \mu_c$; see the SM [54]. This may be experimentally explored by particle tracking [67].

We now discuss the nonlinear effects so far neglected in our studies above. There are two distinct sources of nonlinearities in the present model: those that exist in equilibrium and appear from $\mathcal{F}$ and another class which appear in the nonequilibrium dynamics and have their origin in the underlying active processes. These nonlinear terms appear both in the dynamics of h and $\mathbf{u}$; see the SM [54] for details. However, symmetries of h and $\mathbf{u}$ demand that every additional factors of h and $\mathbf{u}$ must be associated with one or more additional gradient operators. Then scaling and renormalization arguments together with the linear theory scaling exponents $\chi = 0$, $\tilde{z} = 1$ ensure that all these nonlinear terms are *irrelevant* in the linearly stable states; see the SM [54]. This means the scaling of the correlation functions in the linearly stable case as reported above are in fact *exact* in the asymptotic long wavelength limit. Indeed, since all the potential nonlinear terms are *irrelevant* and hence vanish in the long wavelength limit, the theory is *effectively linear* in that limit and the nonlinearities play no role in sustaining the order. This is unlike most ordered active matter systems [68–72], where nonlinear effects are essential, with rare exceptions being those studied in Refs. [73,74].

The nonlinearities are, however, expected to be important in two other situations: (i) With $A > 0$, the linearized h dynamics given by Eq. (10) is linearly unstable. However, the dynamics of $u_{\perp}$, $u_{\parallel}$ remain linearly stable, as both μ and $\lambda + 2\mu$ are assumed to be always positive. Thus the undulation modes get linearly unstable, but the in-plane displacements remain linearly stable, a situation that is physically unacceptable. After all, with the undulation modes getting bigger in the linearly unstable regime, the strain u_{ij} must also get bigger, eventually affecting the in-plane displacements. This apparent contradiction between this physically acceptable expectation and the linear stability of Eqs. (11) and (13) even when $A > 0$ can be reconciled by the nonlinear effects. As shown in the SM [54], these nonlinearities in Eqs. (11) and (13) involve $\nabla_i h$, which also gets bigger with $A > 0$, which, in turn, makes fluctuations in $\mathbf{u}$ grow, leading to *nonlinear instabilities*. (ii) The exponential growth of h in the unstable case with $A > 0$ (or with $\mu_1 < \mu_c$) ultimately must saturate due to the nonlinear effects. This is outside the scope of the present work.

As the membrane fluctuates, it stirs the embedding bulk fluid, generating bulk flows. This can be measured, which calls for calculation of v'_{α} as a function of z . Solving the 3D

Stokes equation for $z > 0$, $z < 0$, we find [54]

$$\langle|v'_{\perp}(\mathbf{q}, z, t)|^2\rangle = \frac{\mu^2}{4\eta^2} q^2 \langle|u_{\perp}(\mathbf{q}, t)|^2\rangle \exp(-2qz), \quad (19)$$

$$\langle|v'_z(\mathbf{q}, z, t)|^2\rangle = \left[\frac{A^2 q^2}{16\eta^2} (1 - qz)^2 \langle|h(\mathbf{q}, t)|^2\rangle + q^2 z^2 \frac{(\lambda + 2\mu)^2}{16\eta^2} \right] \exp(-2qz) \quad (20)$$

for $z > 0$. Correlation of $v'_{\parallel}(\mathbf{q}, z, t)$ can be calculated from those of $v'_z(\mathbf{q}, z, t)$. A similar procedure yields v'_{α} for $z < 0$ [54]. Thus the correlations of $v_{\alpha}(\mathbf{q}, z, t)$ are expressed in terms of the correlations of $h(\mathbf{q}, t)$ and $\mathbf{u}(\mathbf{q}, t)$. Since the latter correlations diverge in the unstable case, the bulk flow should also accordingly be stirred strongly. This can be measured by tracking passive tracer particles [67], giving valuable information about the membrane itself.

We have thus presented a comprehensive hydrodynamic theory of a nearly flat active tethered membrane immersed in a bulk isotropic active fluid. This theory makes quantitative, experimentally testable predictions on the nature of order and scaling of the in-plane and out of plane fluctuations characterized by orientational LRO and positional QLRO, by using the linearized hydrodynamic theory for the linearly stable ordered phase, which are *exact* in the asymptotic long wavelength limit. In the case of long wavelength instability, the membrane is crumpled with positional and orientational short-range order. For long wavelength stability but strong destabilizing permeation flows, our theory speculates pattern formation. It will be interesting to explore its connections with the observed finite-size structures in membranes [75]. While our theory applies strictly to inversion-symmetric isotropic membranes, it should provide a stepping stone for a more general theory, accounting for asymmetry, anisotropy, and spontaneous curvature, relevant for biomembranes. The nature of transitions and the role of fluctuations at the various transitions in this model remain theoretically interesting questions. We expect experiments on *in vitro* set ups involving, say, a graphene sheet coated with identical lipid layers on both sides and immersed in an active fluid bath (e.g., a solution of live orientable bacteria or actin filaments) in its isotropic phase, or in reconstituted membrane-tethered actin cortices [30,76] can verify broad features of our theory.

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