Activating Membranes

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We present a general dynamical theory of a membrane coupled to an actin cortex containing polymerizing filaments with active stresses and currents, and demonstrate that active membrane dynamics [S. Ramaswamy *et al.*, Phys. Rev. Lett. 84, 3494 (2000)] and spontaneous shape oscillations emerge from this description. We also consider membrane instabilities and patterns induced by the presence of filaments with polar orientational correlations in the tangent plane of the membrane. The dynamical features we predict should be seen in a variety of cellular contexts involving the dynamics of the membrane-cytoskeleton composite and cytoskeletal extracts coupled to synthetic vesicles.

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The plasma membrane of a living cell displays striking dynamical structures in the form of growing tubules, ruffles, ridges, and spontaneously generated waves [1–3]. The generality of these observations prompts us to search for a minimal physical description, independent of system-specific detail, unlike Refs. [4,5]. We show that the essential mechanism lies in the interaction of the membrane with the cytoskeleton, driven by molecular motors and adenosine triphosphate (ATP), which can be viewed as a fluid containing orientable, self-driven filaments [6]. Our work is significantly different from a recent paper on membrane waves driven by actin and myosin [7], as we explain in this Letter. Our predictions are general and testable in extracts and artificial settings as well.

Our main results are the following: (i) Active membrane dynamics [8–10] emerges naturally from a complete hydrodynamic theory of a membrane forced by a fluid containing orientable motile elements carrying active stresses. The membrane acquires a tension from the intrinsic stresses on the filaments and a sustained normal velocity from their nonequilibrium directed motion. (ii) Within a mode-truncated description, we find an instability to a spontaneously oscillating state. (iii) Including an in-plane polar orientation field in the membrane gives rise to height bands just past the onset of spontaneous alignment, traveling instabilities deep in the ordered phase, with a growth rate $\sim q_x^{1/2} q_y$, where x is the direction of mean ordering of the filaments, for a small in-plane wave vector (q_x, q_y), and possibly tubules or ridges in a regime where the polarization focuses onto points or lines.

We now construct the dynamics of a fluid membrane coupled to a bulk solvent [11,12] containing active orientable particles [13] described by a vector order parameter $\mathbf{P}(\mathbf{r})$ and a nematic order parameter $\mathbf{Q}(\mathbf{r})$, as functions of three-dimensional position $\mathbf{r}$. The membrane conformation $\mathbf{R}(\vec{u})$ is parametrized by $\vec{u} = (u_1, u_2)$, where $\vec{u}$ is a two-dimensional position vector labeling points in the membrane. The local membrane velocity is denoted by $\mathbf{V}_m(\vec{u}, t)$. If we impose that all surface points labeled by $\vec{u}$ retain their coordinates (i.e., we use a convected coordinate system [14,15]), $\mathbf{V}_m \equiv \partial_t \mathbf{R}$. We work with this choice in the present Letter. We present the general equations for our model in Supplemental Material [16]. We denote by ψ the "signed" concentration of a species living on or closely associated with the membrane (Fig. 1). That is, each particle of this species has

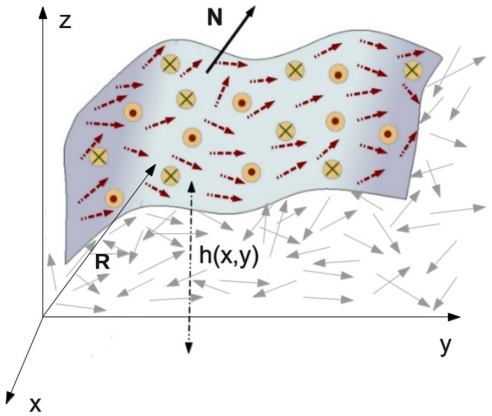

FIG. 1 (color online). Schematic diagram of a membrane in an active fluid. The membrane is depicted in Monge gauge: $\mathbf{R} = (x, y, h(x, y, t))$, where $h(x, y, t)$ is the height above points (x, y) on a reference plane. The signed species ψ is represented by circles, with dots (crosses) denoting parallel (antiparallel) alignment with respect to the outward membrane normal $\mathbf{N}$. Dashed arrows on the membrane are the in-plane polar filaments, whose concentration is c, and continuous arrows denote the bulk active orientable fluid.

a vectorial orientation, whose axis is taken to lie along the membrane normal, and is counted as + (−) for parallel (antiparallel) alignment. ψ could represent [8] actin polymerization nucleators, asymmetric membrane proteins or ion channels, or an internal state coupling to local curvature [19]. We denote by c the concentration of polar filaments restricted to the immediate vicinity of the membrane. In the cellular context, this represents tangential actin, whose presence has been persuasively argued for in recent studies on membrane composition and trafficking [20].

In the absence of flow and activity, the system relaxes to equilibrium governed by a free-energy functional $F[\mathbf{P},\mathbf{Q},\mathbf{R},\psi,c]=\int d^3r(f_b+\int_u f_m)$ with contributions f_b from the cytoplasm and f_m at the membrane. Here $\int_u \ldots \equiv \int d^2u g^{1/2}\delta(\mathbf{r}-\mathbf{R})\ldots$, with g being the determinant of the membrane metric. $f_b = (a_1/2)P^2 + (a_2/2)\mathbf{Q}:\mathbf{Q}$ controls the relaxation of the order parameter fields in the bulk. The contributions from the degrees of freedom associated with the membrane are contained in $f_m = f_c + f_R + f_{R-c} + f_{op}$. Here f_c describes the cost of concentration fluctuations of both the in-plane polar filaments and the signed species, and $f_R = (\kappa/2)(\mathrm{Tr}\mathbf{K})^2$ penalizes deformations of the membrane, where $\mathbf{K}$ is the curvature tensor [21]. $f_{R-c} = \Upsilon(c)\psi\mathrm{Tr}\mathbf{K}$ couples the signed density field and the local mean curvature RamTonPro. Lastly,

$$f_{op} = w\mathbf{Q}_u : \mathbf{NN} - \Lambda\psi p_n - w_2 p_n \mathrm{Tr}\mathbf{K} + a_c \vec{p}_t{}^2 + \alpha c \mathcal{D}_u \cdot \vec{p}_t + \kappa_p \psi \mathbf{K} : (\mathcal{D}_u \vec{p}_t) + \kappa_t \psi \vec{p}_t\, \vec{p}_t : \mathbf{K} \quad (1)$$

is the free-energy associated with orientational order at the membrane: $\mathbf{P}_u(\vec{u}) = \mathbf{P}(\mathbf{r}=\mathbf{R}(\vec{u}))$ and $\mathbf{Q}_u(\vec{u}) = \mathbf{Q}(\mathbf{r}=\mathbf{R}(\vec{u}))$, parametrized by $\vec{u}$. $\mathcal{D}_u$ is the covariant derivative on the membrane [14], and $\mathbf{N}(\vec{u})$ is the membrane normal. We decompose $\mathbf{P}_u$ into its normal component $p_n = \mathbf{P}_u \cdot \mathbf{N}$ and the tangent plane vector $\vec{p}_t = \mathbf{e}^u \cdot \mathbf{P}_u$, where the projector $\mathbf{e}^u \equiv (\mathbf{e}^1(\vec{u}), \mathbf{e}^2(\vec{u})) = (\partial_{u_1}\mathbf{R}, \partial_{u_2}\mathbf{R})$. The local polarity ψ of the membrane favors one direction of $\mathbf{P}$ through Λ, while w, depending on its sign, softly anchors the filaments parallel or perpendicular to the membrane [22]. w_2, κ_p, and κ_t couple orientation to curvature [23], and a_c controls the orientational free energy of membrane-associated tangential polar filaments (hereafter, "horizontal filaments"). The coefficient α governs local spontaneous splay in response to polar filament concentration [24,25].

In the presence of active processes, the membrane, treated as a permeable fluid film [21], has a local velocity

$$\mathbf{V}_m = [\mathbf{V} + v_0\mathbf{P} + \zeta\nabla\cdot(\mathbf{PP})]|_{\mathbf{r}=\mathbf{R}} - \mu_p g^{-1/2}\frac{\delta F}{\delta \mathbf{R}}, \quad (2)$$

where $\mathbf{V}$ is the three-dimensional hydrodynamic velocity. The second and third terms in square brackets in (2), forbidden in a passive system, arise as follows [6]: Free energy is dissipated at a rate $\mathcal{R}\Delta\mu$, where $\mathcal{R}$ is the reaction rate and $\Delta\mu$ the chemical potential difference between the fuel (e.g., ATP) and its reaction products. Let us treat $\mathbf{V}_m$ and $\mathcal{R}$ as fluxes [26,27], with corresponding forces $\delta F/\delta\mathbf{R}$ and $\Delta\mu$. To first order in gradients, $\mathbf{P}$ and $\nabla\cdot(\mathbf{PP})$, measuring local polarity, contribute terms of the form $\zeta_1\mathbf{P}\cdot\delta F/\delta\mathbf{R}$ and $\zeta_2\nabla\cdot(\mathbf{PP})\cdot\delta F/\delta\mathbf{R}$ to $\mathcal{R}$, where the independent kinetic coefficients ζ_1 and ζ_2 vanish for an impermeable membrane, as does μ_p. The symmetry of dissipative Onsager coefficients then implies terms $\zeta_1\Delta\mu\mathbf{P} \equiv v_0\mathbf{P}$ and $\zeta_2\Delta\mu\nabla\cdot(\mathbf{PP}) \equiv \zeta\nabla\cdot(\mathbf{PP})$ in the $\mathbf{V}_m$ equation. In the cellular context, v_0 is the scale of the drift speed of the membrane arising from filament polymerization [28].

The signed density field ψ has a dynamics given by

$$\mathcal{D}_t\psi = -\mathcal{D}_u\cdot\vec{J} - k_2\psi + k_1, \quad (3)$$

where $\mathcal{D}_t$ is the covariant time derivative, and k_1, k_2 are rates of association and dissociation with the membrane. The current

$$\vec{J} = \vec{J}_0 \equiv -\psi\mathbf{e}^u\cdot\partial_t\mathbf{R} - D\left[\psi\mathcal{D}_u\left(g^{-1/2}\frac{\delta F}{\delta\psi}\right)\right] \quad (4)$$

contains drift and diffusion; the diffusivity D can include active contributions.

The Stokesian hydrodynamic velocity field $\mathbf{V}(\mathbf{r}) = \int_{\mathbf{r}'}\mathbf{H}(\mathbf{r}-\mathbf{r}')\cdot\mathcal{F}(\mathbf{r}')$, where $\mathbf{H}(\mathbf{r}')$ is the Oseen tensor [29]. The force density $\mathcal{F}(\mathbf{r},t) = \nabla\cdot\boldsymbol{\sigma}^{\mathbf{Q}} + \int_u \delta F/\delta\mathbf{R}$, where the order parameter stress [30] $\boldsymbol{\sigma}^{\mathbf{Q}}$ has an active contribution of the form $\zeta_Q\mathbf{Q}$ [31,32].

The order parameters have standard equations of motion [6] $\dot{\mathbf{P}} = -\Gamma_p\delta F/\delta\mathbf{P}$ and $\dot{\mathbf{Q}} = \lambda_0\mathbf{S} - \Gamma_Q\delta F/\delta\mathbf{Q}$, where $\mathbf{S}$ is the symmetrized velocity gradient tensor.

The local dynamics of the membrane on scales that are small compared to the whole cell can be understood in the Monge gauge (Fig. 1), $\mathbf{R} = (\mathbf{x}, h(\mathbf{x},t))$, $g = 1 + (\nabla_\perp h)^2$, and $\mathbf{N} = g^{-1/2}(-\nabla_\perp h, 1)$, where $h(\mathbf{x})$ is the height of the membrane above a point $\mathbf{x}$ on the reference plane. We first concentrate on the coupled dynamics of h and ψ in an isotropic bulk phase with negligible c. On long time scales the order parameters relax to values governed by their coupling to the membrane which, to lowest order in gradients, are

$$\mathbf{P}_u = \psi\frac{\Lambda}{a_1}\mathbf{N}, \quad (5a)$$

$$\mathbf{Q}_u = \frac{\Gamma_Q\lambda_0}{a_2}\mathbf{S}|_{\mathbf{r}=\mathbf{R}} - \frac{w}{a_2}(\mathbf{NN} - \mathbf{I}/3). \quad (5b)$$

Using these expressions for $\mathbf{P}$ and $\mathbf{Q}$ in Eqs. (2), (3) and (4) leads to the coupled equations

$$\partial_t h = g^{1/2}\left[\tilde{v}\psi - \mu_p\frac{\delta F}{\delta h}\right] - \int_{\mathbf{q}} e^{i\mathbf{q}_\perp\cdot\mathbf{x}}\frac{1}{4\tilde{\eta}q_\perp}\left(\gamma_{act}q_\perp^2 h_{\mathbf{q}} + \frac{\delta F}{\delta h}\right), \quad (6a)$$

$$\partial_t \psi = \tilde{v}\nabla_\perp \cdot (g^{-1/2}\psi^2 \nabla_\perp h) + D\nabla_\perp \cdot \left[\psi \nabla_\perp \left(g^{-1/2}\frac{\delta F}{\delta \psi}\right)\right] - k_2 \psi + k_1, \quad (6b)$$

in which the active stress contributes a tension $\gamma_{\rm act} = -\zeta_Q w/a_2$ (see Ref. [22] for a one-dimensional analogue) and, as in Ref. [33], a modified viscosity $\tilde{\eta} = \eta + (-\lambda_0 a_2 + \zeta_Q)\Gamma_Q \lambda_0/a_2$. We have not included the effects of the active term with the coefficient ζ defined in Eq. (2). The lowest order term it contributes to the height equation is $\nabla_\perp^2 h$, i.e., an active nonhydrodynamic tension. Its more crucial consequences are examined later in this Letter. Note that the active modification of the hydrodynamic tension is missing in Ref. [10], where the force dipoles are taken to be situated at the reference rather than the actual location of the membrane. Local polarity leads to the propulsion of the membrane at a rate $\psi\tilde{v} = \psi v_0 \Lambda/a_1$. F in Eqs. (6a) and (6b) is the original free-energy functional, with $\mathbf{P}$ and $\mathbf{Q}$ eliminated in favor of ψ and h via Eqs. (5a) and (5b), respectively. The first term on the right-hand side in Eq. (6b) arises kinematically, due to the change of density of an in-membrane species resulting from a change in the conformation of the fluid film [21]. Setting k_1 and k_2 to zero to specialize to the case of a zero mean conserved species, Eqs. (6a) and (6b) take precisely the form presented [9] on general grounds for an active membrane [34]. This establishes one of our main results: A membrane in an active fluid is an active membrane, propelled by polar activity—polymerization, in the context of actomyosin—with a tension from contractility. Equations (2)–(6), with suitable boundary conditions, can be applied to cell membranes or reconstituted systems.

The terms proportional to $\tilde{v}$ in Eq. (6) constitute an excitatory-inhibitory pair which, we now show, leads to sustained spontaneous oscillations in a regime of parameter space. We work in one dimension, retaining only the smallest wave number and only one nonlinear term: $\nabla_\perp \cdot (\psi^2 \nabla_\perp h)$ in Eq. (6b). The resulting coupled ODEs [16], upon rescaling and defining new constants, describe a generalized Van der Pol oscillator with linear damping and cubic nonlinearities:

$$\ddot{\phi} + \phi + s_1\dot{\phi} + s_2\phi^2\dot{\phi} + s_3\phi(\dot{\phi})^2 + s_4\phi^3 = 0, \quad (7)$$

which has been shown [35] to have a limit cycle if $\mathrm{sgn}(s_1 s_2) = -1$. We provide further details regarding the mode truncation and present a representative phase portrait in Ref. [16].

Note that wavelike dispersion relations, as in Refs. [7,36], are distinct from the experimentally observed membrane waves [2,3], which are not a response to an external perturbation but are self-generated, in a manner consistent with our findings from the truncated model. Moreover, the wave speed in our theory is set solely by the normal drift speed, not by free-energy couplings.

Our analysis of Eq. (6) suggests an explanation for the experimentally observed waves [2,3] on the lamellipodium [37] of a crawling or spreading cell, whose leading edge should be viewed as an actively moving one-dimensional membrane. We expect similar waves on the surface of self-propelled drops [38], e.g., in parameter regimes corresponding to the instability discussed in Ref. [9], which arises here if $\tilde{v}\Upsilon > 0$. In the case we present here and in Supplemental Material [16], actin polymerization, not contractility, is the proximate cause of the membrane waves [3]. Note that even without permeability, a local normal velocity at the membrane, proportional to $|q_\perp|\psi_{\mathbf{q}}$, which can be shown to arise from an active contractile stress, can generate spontaneous waves with dispersion $\omega^2 \sim q^3$ [10,16].

Now we examine another case of importance to cell biology, in which a distinct population of filaments, lying in the vicinity of the membrane and disposed parallel to it, are present at sufficient concentration for their dynamics to be slow and therefore relevant on the time scale of interest to this work. This is motivated by experimental studies [20] of the nanoclustering of cell-surface molecules, whose anomalous statistical properties are naturally accounted for as arising from active transport mediated by a new class of "horizontal actin filaments." We study the effect of such tangential active orientable filaments on membrane fluctuations and make predictions that can be tested in future experiments. For this, we introduce a separate dynamical equation for the polar order parameter $\mathbf{P}_u$ at the membrane [21]:

$$\mathcal{D}_t \mathbf{P}_u - (\mathbf{e}^u \cdot \partial_t \mathbf{R}) \cdot \mathcal{D}_u \mathbf{P}_u + v_p \vec{p}_t \cdot \mathcal{D}_u \mathbf{P}_u = -g^{-1/2}\Gamma_p \delta F/\delta \mathbf{P}_u, \quad (8)$$

where v_p is the self-propulsion velocity [39]. In the following treatment, for simplicity, we replace hydrodynamic damping by local friction with respect to a fixed background medium. We assume the horizontal filaments are close to an ordering transition but take the normal component p_n to relax rapidly. To the lowest order in gradients, Eq. (5a) implies $p_n = (\Lambda/a_1)\psi$. The equation for the tangential component is

$$\mathcal{D}_t \vec{p}_t - \mathbf{e}^u \cdot [(\mathbf{e}^u \cdot \partial_t \mathbf{R}) \cdot \mathcal{D}_u \mathbf{P}_u] + v_p \mathbf{e}^u \cdot (\vec{p}_t \cdot \mathcal{D}_u \mathbf{P}_u) = -\frac{1}{\sqrt{g}}\Gamma_p \mathbf{e}^u \cdot \frac{\delta F}{\delta \mathbf{P}_u} + (\mathcal{D}_t \mathbf{e}^u) \cdot \mathbf{P}_u, \quad (9)$$

Conservation of horizontal filaments implies

$$\mathcal{D}_t c = -\mathcal{D}_u \cdot (c\vec{v}_c) + D_c \mathcal{D}_u \cdot \left[c\mathcal{D}_u \left(g^{-1/2}\frac{\delta F}{\delta c}\right)\right], \quad (10a)$$

$$\vec{v}_c = -\mathbf{e}^u \cdot \partial_t \mathbf{R} + v_1 \vec{p}_t. \quad (10b)$$

The membrane conformation is given by Eq. (2), while the current of ψ in Eq. (3) is modified to $\vec{J} = \vec{J}_0 + v_\psi \vec{p}_t$. v_1 and v_ψ are active polar velocity parameters, independent of each other and of v_p in Eq. (8).

Equations (2), (3), (9), and (10) are a formally complete description of the dynamics of a membrane endowed with in-plane polar orientational order and signed species coupled to active "horizontal" and "vertical" filaments. A complete exploration of the range of behaviors of this system requires a numerical study. We limit ourselves here to a linear stability analysis about the isotropic and in-plane ordered states in a steadily moving membrane which is flat on average. This is the regime in which dynamics of ψ is fast and relaxes to a steady state value $\psi_0 = k_1/k_2$, Eq. (3). As $k_2^{-1} \sim 0.1$–1s [40] our assumption is justified if we are looking at the dynamics on time scales greater than 1s. We rescale our equations so that $\psi_0 = 1$.

The coupled equations of the height field h, the in-plane component of the polar order parameter $\mathbf{p}$ and concentration c, to leading order in gradients, are

$$\partial_t h = \tilde{v}(c) + \frac{\zeta}{a_1}\nabla_\perp \cdot [\Lambda(c)\mathbf{p}] + \mu_p[\Sigma\nabla_\perp^2 h - \kappa\nabla_\perp^4 h + \nabla_\perp^2 \Upsilon(c) - \kappa_p \nabla_\perp^2 \nabla_\perp \cdot \mathbf{p} - \kappa_t \nabla_\perp \nabla_\perp : \mathbf{pp}], \tag{11a}$$

$$\partial_t \mathbf{p} = -v_p \mathbf{p}\cdot\nabla_\perp \mathbf{p} + \frac{\tilde{v}(c)v_0}{a_1}\nabla_\perp \Lambda(c) + \Gamma_p[-\tilde{A}\mathbf{p} + \kappa_p \nabla_\perp \nabla_\perp^2 h + \alpha \nabla_\perp c - \kappa_t \mathbf{p}\cdot\nabla_\perp\nabla_\perp h] + D_p\nabla_\perp^2 \mathbf{p}, \tag{11b}$$

$$\partial_t c = \nabla_\perp \cdot [c(v_1 \mathbf{p} + \tilde{v}(c)\nabla_\perp h)] + D_c \nabla_\perp^2 c, \tag{11c}$$

where $\nabla_\perp^2 \Upsilon(c)$ arises from the free-energy contribution f_{R-c}. Σ in Eq. (11a) is an active tension [9], arising, for example, via an interplay of the active polymerization and the polar anchoring modeled by the free-energy cost $-\int_u w_2 p_n \mathrm{Tr}\mathbf{K}$ in Eq. (1). This coupling generates a term of the form $\nabla_\perp^2 h$ in the p_n equation and, therefore, because of propulsion, an effective tension in the h equation. Equation (11b) was obtained by projecting (9) onto the reference horizontal, with $\tilde{A} = (a_c + a_1)$. The term with coefficient D_p arises from the Frank elasticity of the polar filaments. Note the absence of a term proportional to $\nabla_\perp h$ in Eq. (11b), a consequence of three-dimensional rotation invariance [11]. The propulsive velocity $\tilde{v}$ in Eq. (11) is taken to depend only on c, as ψ has been set to a constant value. We turn next to some original instability mechanisms emerging from Eq. (11).

First consider the case of large positive $\tilde{A}$. $\mathbf{p}$ is then deep in the isotropic phase and can thus be eliminated in favor of h and c on time scales that are long compared to its finite relaxation time. The resulting equations are then those of Ref. [9], with a modified diffusivity $D_c \to D_c + \alpha v_1/\tilde{A}$. The complete problem, including the dynamics of $\mathbf{p}$, is characterized by two eigenmodes with relaxation rates $\sim q^0$ and two of order $\sim q^2$, unaffected to leading order in q by the coupling $\nabla_\perp \nabla_\perp^2 h$ in the $\mathbf{p}$ equation. A large enough negative α leads to an instability with aggregation of c and modulation of h. This picture is borne out by a linear stability analysis in which the dynamics of $\mathbf{p}$ is retained [16], revealing an eigenvalue of order q^2 that changes sign for sufficiently large negative αv_1. The projection of the corresponding eigenvector onto h grows with increasing $\tilde{v}$. The underlying process involves the focusing of $\mathbf{p}$ and hence the concentration, leading, through the $\tilde{v}(c)$ term in Eq. (11a), to growth of the height field. Whether the focusing of $\mathbf{p}$ takes the form of asters or walls, leading, respectively, to height modulations in the form of tubules or ridges, requires a numerical calculation. If both $\tilde{A}$ and α are negative, an extrapolation of the results of Ref. [25] would suggest the formation of ordered modulations of h.

In flocking models [41], just past the onset of the ordered phase of $\mathbf{p}$, the coupled dynamics of c and $\mathbf{p}$ gives rise, through the c dependence of $\tilde{A}$, to a state with traveling bands of concentration [42]. In the present context where the dynamics takes place on a membrane, this should be accompanied, through $\tilde{v}(c)$ in Eq. (11a), by a one-dimensional fore-aft asymmetric modulation of the membrane height.

The coupled dynamics of $\mathbf{p}$ and h with c fixed shows a distinct class of modes and instabilities deep in the regime where $\mathbf{p}$ is ordered. For $v_p = 0$ there is a traveling instability with a relaxation rate of transverse fluctuations $\sim q_y q_x^{1/2}$, if the ordering direction is taken along x. As v_p is increased, this crosses over to $\sim q_y^2$ [16]. Note that, despite the similarity of form with the mode structure of Ref. [43], the detailed mechanisms are different.

To summarize, we have shown that the equations of motion for an active membrane [9] emerge from the dynamics of an ordinary fluid membrane coupled to a medium with active, motile filaments. We find that the resulting equations display spontaneous sustained oscillations driven by the active motion of the membrane normal to itself, which are the natural explanation of membrane waves [2,3]. In addition, when polar "horizontal filaments" [20] are included, the coupled dynamics of their concentration and orientation and the membrane height leads to instabilities towards one- or two-dimensional modulations, as well as traveling undulations. Deep in the orientationally ordered phase of the filaments, we find propagating instabilities with singularly anisotropic dependence on the wave vector. Ongoing numerical studies of the long-time dynamics emerging from these instabilities find a varied range of behaviors, including stable tubules and spatiotemporal chaos [44]. Meanwhile, we look forward to tests of our predictions in actomyosin extracts with ATP and actin nucleators in contact with model lipid membranes.

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