Continuum theory of a moving membrane

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We derive a set of equations for the dynamics of evolving fluid membranes, such as cell membranes, in the presence of bulk fluids. We model the membrane as a surface endowed with a director field, which describes the local average orientation of the molecules on the membrane. A model for the elastic energy of a surface endowed with a director field is derived using liquid crystal theory. This elastic energy reduces to the well-known Helfrich energy in the limit when the directors are constrained to be normal to the surface. We then derive the full dynamic equations for the membrane that incorporate both the elastic and viscous effects, with and without the presence of bulk fluids. We also consider the effect of local spontaneous curvature, arising from the presence of membrane proteins. Overall, the systems of equations allow us to carry out stable, accurate, and robust numerical modeling for the dynamics of the membranes.

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I. INTRODUCTION

In this paper we develop a systematic continuum theory for the dynamics of membranes that is consistent with thermodynamics and takes into account the effect of membrane proteins, as well as the tilting of the lipid molecules away from the normal direction of the membrane. The membrane is assumed to be in the fluid phase, but with bending rigidity. Our motivation comes from the study of biomembranes, such as cell membranes.

As boundaries of living cells and organelles, membranes are crucial to life processes. Membrane consists of lipids, proteins, carbohydrates, etc. A lipid molecule has a hydrophilic head and one or two hydrophobic tails. In a water environment, lipids spontaneously form a bilayer so that the hydrophobic tails are separated from the water molecules by the hydrophilic head. Within each layer, lipids can move freely. But when a lipid molecule tries to escape from the bilayer, the aqueous environment pushes it back. It is also difficult for a lipid molecule to flip from one layer to the other because of the presence of an energy barrier [1].

The structure and properties of a membrane are very complex and refined, and might also be specially tailored to its biological functions. Despite these complexities and specialties, we will consider only some of the common features of their dynamics. Basically, we will treat a membrane as a layer of incompressible fluids, defined on a two-dimensional evolving surface with bending rigidity, and endowed with a director field which models the orientation of the lipid molecules.

During the past several decades, there has been a great deal of interest in membranes. In 1973, Helfrich [2] recognized that the lipid bilayer has the structure of a smectic liquid crystal. Based on the elastic theory of liquid crystals, he proposed the curvature elasticity model:

$$f_c = \frac{k_c}{2}(2H + C_0)^2 + kK,$$

where k_c and k are elastic constants, and H, K, and C_0 are the mean, Gaussian, and spontaneous curvature, respectively. The free energy is expressed as

$$F_H = \int_S (f_c + \mu)dS + p\int_V dV,$$

where p is the osmotic pressure, S is the surface representing the membrane, V is the volume bounded by the surface, and μ is the surface tension of the membrane. This elastic model has been proved to be very successful. A lot has been learned using the Helfrich free energy about the shapes of the cell membranes [3,4]. For example, the characteristic biconcave disklike shape can be explained using this model. Much has been done after the pioneering work of Helfrich. Evans and Skalak [5] considered the mechanics of membranes using the Helfrich energy or general elastic energy. Lomholt and Miao [7] also studied membrane mechanics from a microscopic perspective, and derived a two-dimensional model by considering the limit of full three-dimensional elastic models. Steigmann [8] considered the relationship between the Cosserat and Kirchhoff-Love theories of elastic shells. In addition, the elastic stress of the membrane has also been considered by Capovilla and Guven [6].

The dynamics of the membrane has also received attention. Oldroyd introduced surface viscosity for fluid films [9]. Scriven [10] considered Newtonian surface fluids on evolving surfaces. It was found that the dynamics and stability of an interface between two immiscible bulk fluids might be profoundly influenced by the presence of a separate surface phase located at the interface [11]. MacArthur and Berg [12] attempted to simulate the effect of cell membranes using

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some refined models which included a separate Newtonian surface phase or additional thin-film coating. Stone derived the convective-diffusion equation for surfactant transport along a deforming interface [13]. These papers did not consider explicitly the bending resistance of the membrane. However, Steigmann [14,15] considered fluid films with curvature elasticity but neglected viscous effects. Waxman [16–18] studied the kinematics and dynamics of fluids on an evolving surface with both bending resistance and viscous effects.

The dynamics of membranes in bulk fluids also attracted great interest. Seifert [19] studied the configuration of quasi-spherical vesicles in shear flow. Cai and Lubensky [20] derived the hydrodynamical equations for a fluid membrane and considered the renormalization of the compressibility and the dissipative coefficients. Pozrikidis and co-workers [21–26] followed part of the work of Waxman, but considered the membrane as a compressible shell with bending resistance. They also considered the coupling of the elastic membrane to the bulk fluid and conducted a series of important simulations on the coupled system. Miao and co-workers [27,28] considered the dynamics of a fluid membrane and the coupling between the membrane and the bulk fluids. Membrane incompressibility and other kinds of membrane entropy production processes (e.g., due to chemical reactions) were taken into account in their model.

Our motivation is as follows. We would like to follow Helfrich's lead and view membranes as a two-dimensional liquid crystal systems, but taking into account the additional effects that are important for dynamics, such as the viscous effects and the effect of the bulk fluid. Restoring the director model is important in order to model accurately small-scale effects such as defects or effects of membrane proteins. We will also derive a reduced model in the case when such small-scale variations are negligible. Our approach is closest to that of Waxman. For example, following Waxman, we will also model the effect of membrane proteins through a local spontaneous curvature. However, as we point out later, Waxman's model suffers from an inconsistency with the second law of thermodynamics, since it neglected an important elastic in-plane stress term. One by-product of our work is to correct this problem.

We take the viewpoint that the structure of cell membrane is that of a layer of smectic crystal [29]. We represent such a structure as a Cosserat surface endowed with a director field. A simple elastic energy for the director field is obtained from the Frank energy of liquid crystals. A similar treatment and elastic energy have been studied by Fournier [30,31] and applied to membrane fusion by Kozlovsky and Kozlov [32]. Fournier considered the coupling between tilt difference and dilation and the coupling between the two monolayers. As Kozlovsky and Kozlov explain, the tilt of the directors plays an important role in membrane fusion.

We study the fluid dynamics based on the elastic energy and taking into consideration the viscous effects and the effects of the bulk fluids. By applying the principle of virtual work, the torque and the elastic stress induced by the directors are determined. The bending resistance is found to be the result of a transverse stress. The dynamic equations are then obtained by using the conservation laws for the linear and angular momenta. We also consider the case when the director field is constrained to be the same as the normal vector of the surface, and derive a reduced model for this case. We also consider the effect of spontaneous curvature, which plays an important role in the shape transition of cell membranes. We make a distinction between global and local spontaneous curvature. The latter is important for many life processes, but taking it into account in previous models has been a difficulty.

Since there has been much work in the literature on the topic discussed here, we will discuss the similarities and differences of our work with existing work, after we present our model.

II. KINEMATICS OF EVOLVING SURFACES

In this section, we collect some of the mathematical background materials that we will need for describing the kinematics and dynamics of evolving surfaces. This is classic material [10,18,34,35]; but we include a brief discussion here to establish notations and terminologies.

A. Geometry of surfaces

We introduce a system of surface coordinates u^α ($\alpha = 1, 2$) at time $t=0$ to label the material points on the surface. The system of convected coordinates is obtained if we impose that all material points retain their coordinates. Let $\mathbf{R}(u^\alpha, t)$ be the position of a material point in the three-dimensional Euclidean space at time t with convected coordinates u^α. The covariant basis vectors, namely, the tangent $\mathbf{a}_\alpha$ and the unit normal vector $\mathbf{n}$, the metric tensor $a_{\alpha\beta}$, and the covariant alternating tensor $\varepsilon_{\alpha\beta}$ are defined as

$$\mathbf{a}_\alpha = \frac{\partial \mathbf{R}}{\partial u^\alpha}, \quad \mathbf{n} \cdot \mathbf{a}_\alpha = 0, \quad \mathbf{n} \cdot \mathbf{n} = 1,$$

$$a_{\alpha\beta} = \mathbf{a}_\alpha \cdot \mathbf{a}_\beta, \quad \varepsilon_{\alpha\beta} = (\mathbf{a}_\alpha \times \mathbf{a}_\beta) \cdot \mathbf{n}. \qquad (1)$$

The covariant metric tensor of the convected coordinates, along with its inverse $a^{\alpha\beta}$, is used to lower and raise the indices of vectors and tensors. For example, $b^\gamma_\beta = a^{\alpha\gamma} b_{\alpha\beta}$. $\varepsilon_{\alpha\beta}$ take the values $\varepsilon_{12} = -\varepsilon_{21} = \sqrt{a}$, $\varepsilon_{11} = \varepsilon_{22} = 0$, where $a = \det(a_{\alpha\beta})$. The surface Christoffel symbols $\Gamma^\gamma_{\alpha\beta} = \Gamma^\gamma_{\beta\alpha}$ and curvature tensor $b_{\alpha\beta} = b_{\beta\alpha}$ are given by the Gauss-Weingarten-Codazzi equations

$$\frac{\partial \mathbf{a}_\alpha}{\partial u^\beta} = \Gamma^\gamma_{\alpha\beta} \mathbf{a}_\gamma + b_{\alpha\beta} \mathbf{n},$$

$$\frac{\partial \mathbf{n}}{\partial u^\beta} = -b^\gamma_\beta \mathbf{a}_\gamma = -a^{\alpha\gamma} b_{\alpha\beta} \mathbf{a}_\gamma,$$

$$b_{\alpha\beta,\gamma} = b_{\alpha\gamma,\beta},$$

where we have used a comma followed by a lowercase Greek subscript to denote covariant derivatives based on the metric tensor $a_{\alpha\beta}$:

$$Q_{\cdots\beta\cdots,\gamma}^{\cdots\alpha\cdots} = \frac{\partial Q_{\cdots\beta\cdots}^{\cdots\alpha\cdots}}{\partial u^\gamma} + \sum Q_{\cdots\beta\cdots}^{\cdots\mu\cdots}\Gamma_{\mu\gamma}^\alpha - \sum Q_{\cdots\mu\cdots}^{\cdots\alpha\cdots}\Gamma_{\beta\gamma}^\mu. \quad (2)$$

For example, we have

$$b_{\alpha\beta,\gamma} = \frac{\partial b_{\alpha\beta}}{\partial u^\gamma} - b_{\alpha\mu}\Gamma_{\beta\gamma}^\mu - b_{\mu\beta}\Gamma_{\alpha\gamma}^\mu.$$

We may also write the Gauss-Weingarten-Codazzi equation as

$$\mathbf{a}_{\alpha,\beta} = b_{\alpha\beta}\mathbf{n}, \quad \mathbf{n}_{,\beta} = -b_\beta^\gamma\mathbf{a}_\gamma, \quad b_{\alpha\beta,\gamma} = b_{\alpha\gamma,\beta}, \quad (3)$$

which does not involve the Christoffel symbols explicitly. Note that a vector in the three-dimensional Euclidean space is not regarded as a tensor, and $\mathbf{a}_\alpha$ is regarded as a first-order tensor. The covariant derivative of a general tensor is defined by Eq. (2). The covariant derivative of a scalar or a vector is simply the partial derivative.

If $\mathbf{v}$ is a vector defined on the surface, e.g., the spatial velocity of the surface, it can be decomposed as

$$\mathbf{v} = v^\alpha\mathbf{a}_\alpha + v^{(n)}\mathbf{n}, \quad (4)$$

where $v^{(n)}$ is a scalar. The covariant (partial) derivative of $\mathbf{v}$ is given by

$$\mathbf{v}_{,\beta} = (v_{,\beta}^\alpha - v^{(n)}b_\beta^\alpha)\mathbf{a}_\alpha + (v_{,\beta}^{(n)} + v^\alpha b_{\alpha\beta})\mathbf{n}. \quad (5)$$

B. Evolution of geometrical quantities

Let $\mathbf{v}(u^\alpha, t)$ be the velocity field in the convected coordinates:

$$\mathbf{v}(u^\alpha, t) = \frac{\partial \mathbf{R}(u^\alpha, t)}{\partial t} = v^\alpha\mathbf{a}_\alpha + v^{(n)}\mathbf{n}.$$

Noting that u^α and t are independent variables, we have

$$\frac{\partial \mathbf{a}_\alpha}{\partial t} = \frac{\partial}{\partial t}\frac{\partial \mathbf{R}}{\partial u^\alpha} = \frac{\partial}{\partial u^\alpha}\frac{\partial \mathbf{R}}{\partial t} = \frac{\partial \mathbf{v}}{\partial u^\alpha}$$

$$= \mathbf{v}_{,\alpha} = (v_{,\alpha}^\mu - v^{(n)}b_\alpha^\mu)\mathbf{a}_\mu + (v_{,\alpha}^{(n)} + v^\mu b_{\alpha\mu})\mathbf{n}. \quad (6)$$

Therefore, we have

$$\frac{\partial a_{\alpha\beta}}{\partial t} = \frac{\partial \mathbf{a}_\alpha}{\partial t}\cdot\mathbf{a}_\beta + \frac{\partial \mathbf{a}_\beta}{\partial t}\cdot\mathbf{a}_\alpha = (v_{\alpha,\beta} + v_{\beta,\alpha}) - 2v^{(n)}b_{\alpha\beta},$$

$$\frac{\partial \varepsilon_{\alpha\beta}}{\partial t} = \frac{\partial \mathbf{a}_\alpha}{\partial t}\times\mathbf{a}_\beta\cdot\mathbf{n} + \mathbf{a}_\alpha\times\frac{\partial \mathbf{a}_\beta}{\partial t}\cdot\mathbf{n}$$

$$= (v_{,\alpha}^\mu - v^{(n)}b_\alpha^\mu)\varepsilon_{\mu\beta} + (v_{,\beta}^\mu - v^{(n)}b_\beta^\mu)\varepsilon_{\alpha\mu}. \quad (7)$$

Since $\mathbf{n}\cdot\mathbf{a}_\alpha = 0$, $\mathbf{n}\cdot\mathbf{n} = 1$, we have

$$\frac{\partial \mathbf{n}}{\partial t} = -(v^\mu b_\mu^\alpha + a^{\alpha\mu}v_{,\mu}^{(n)})\mathbf{a}_\alpha. \quad (8)$$

Differentiating $a^{\alpha\beta}a_{\beta\gamma} = \delta_\gamma^\alpha$ and $\varepsilon^{\alpha\beta}\varepsilon_{\beta\gamma} = -\delta_\gamma^\alpha$, we obtain

$$\frac{\partial a^{\alpha\beta}}{\partial t} = -a^{\alpha\gamma}a^{\beta\delta}(v_{\gamma,\delta} + v_{\delta,\gamma}) + 2v^{(n)}b^{\alpha\beta},$$

$$\frac{\partial \varepsilon^{\alpha\beta}}{\partial t} = -(v_{,\mu}^\beta - v^{(n)}b_\mu^\beta)\varepsilon^{\alpha\mu} - (v_{,\mu}^\alpha - v^{(n)}b_\mu^\alpha)\varepsilon^{\mu\beta}. \quad (9)$$

By differentiating the second equation of (3) with respect to time, we also obtain the time derivative of the curvature tensor:

$$\frac{\partial b_{\alpha\beta}}{\partial t} = (v^{(n)}{}_{,\alpha\beta} - v^{(n)}b_\alpha^\mu b_{\mu\beta}) + (v_{,\beta}^\mu b_{\alpha\mu} + v_{,\alpha}^\mu b_{\mu\beta}) + v^\mu b_{\alpha\beta,\mu}. \quad (10)$$

C. Accelerations and strains

Since the velocity $\mathbf{v}$ and the acceleration $\mathbf{A}$ can be decomposed as $\mathbf{v} = v^\mu\mathbf{a}_\mu + v^{(n)}\mathbf{n}$ and $\mathbf{A} = (\partial\mathbf{v}/\partial t) = A^\mu\mathbf{a}_\mu + A^{(n)}\mathbf{n}$, we have

$$A^\alpha = \frac{\partial v^\alpha}{\partial t} + v^\beta v_{,\beta}^\alpha - 2v^{(n)}v^\beta b_\beta^\alpha - a^{\alpha\beta}v^{(n)}v_{,\beta}^{(n)},$$

$$A^{(n)} = \frac{\partial v^{(n)}}{\partial t} + v^\alpha v^\beta b_{\alpha\beta} + v^\beta v_{,\beta}^{(n)}. \quad (11)$$

Strain is defined as

$$E_{\alpha\beta} = \frac{1}{2}(a_{\alpha\beta} - \mathring{a}_{\alpha\beta}), \quad (12)$$

where $\mathring{a}_{\alpha\beta}$ is the metric tensor for the strain-free state and is time independent. The rate of strain is simply the time derivative of $E_{\alpha\beta}$:

$$S_{\alpha\beta} = \frac{\partial E_{\alpha\beta}}{\partial t} = \frac{1}{2}(v_{\alpha,\beta} + v_{\beta,\alpha}) - v^{(n)}b_{\alpha\beta}. \quad (13)$$

D. Hodge decomposition

Let Ω be a smooth closed surface in the three-dimensional Euclidian space and $\mathbf{B}$ be a vector-valued function defined on the surface. We have the unique decomposition $\mathbf{B} = \mathbf{C} + \mathbf{P}$ with $C_{,\alpha}^\alpha - 2HC^{(n)} = 0$ (H is the mean curvature) and $\mathbf{P}$ takes the form $\mathbf{P} = (\Pi a^{\alpha\beta}\mathbf{a}_\alpha)_{,\beta}$. Π satisfies the equation

$$a^{\alpha\beta}\Pi_{,\alpha\beta} - 4H^2\Pi = B_{,\alpha}^\alpha - 2HB^{(n)}. \quad (14)$$

When the divergence of C^α ($C_{,\alpha}^\alpha - 2HC^{(n)}$) is a given nonzero function $c(x)$, the above decomposition also exists, and Π satisfies

$$a^{\alpha\beta}\Pi_{,\alpha\beta} - 4H^2\Pi = B_{,\alpha}^\alpha - 2HB^{(n)} - c(x).$$

If the velocity satisfies $v_{,\alpha}^\alpha - 2Hv^{(n)} = 0$, the acceleration satisfies

$$A_{,\alpha}^\alpha - 2HA^{(n)} = (v_{,\alpha}^\mu - 2v^{(n)}b_\alpha^\mu)(v_{,\mu}^\alpha - 2v^{(n)}b_\mu^\alpha) - \left(\frac{\partial\mathbf{n}}{\partial t}\right)^2,$$

where the right side is determined by the velocity. Therefore, if the velocity and the forces acting on the membrane are known, the pressure is determined by the Hodge decomposi-

tion. For numerical simulations, the Hodge decomposition is the base of the projection method.

E. Reynolds transport theorem

Let Q be a function defined on the surface, and Ω be a convected subset of the surface. Then the integral of Q over the area Ω is

$$\int_\Omega Q \, dS = \int_\Omega Q \sqrt{a} \, du^1 du^2.$$

We have

$$\frac{d}{dt} \int_\Omega Q \, dS = \int_\Omega \frac{\partial}{\partial t} (Q \sqrt{a}) du^1 du^2$$

$$= \int_\Omega \left(\frac{\partial Q}{\partial t} + \frac{Q}{2a} \frac{\partial a}{\partial t} \right) \sqrt{a} \, du^1 du^2.$$

Using the fact that $a^{-1}(\partial a/\partial t) = a^{\alpha\beta}(\partial a_{\alpha\beta}/\partial t) = 2S_\alpha^\alpha$, we obtain the transport theorem

$$\frac{d}{dt} \int_\Omega Q \, dS = \int_\Omega \left(\frac{\partial Q}{\partial t} + Q S_\alpha^\alpha \right) dS. \tag{15}$$

If γ denotes the surface mass density, by applying the transport theorem, we have

$$\frac{d}{dt} \int_\Omega \gamma \, dS = \int_\Omega \left(\frac{\partial \gamma}{\partial t} + \gamma S_\alpha^\alpha \right) dS = 0.$$

Since Ω is arbitrary, we obtain

$$\frac{\partial \gamma}{\partial t} + \gamma S_\alpha^\alpha = 0. \tag{16}$$

For incompressible surface phases, this reduces to the condition

$$S_\alpha^\alpha = v^\alpha_{,\alpha} - 2Hv^{(n)} = 0. \tag{17}$$

Therefore the transport theorem for an incompressible surface fluid membrane in the convected coordinates is simply

$$\frac{d}{dt} \int_\Omega Q \, dS = \int_\Omega \frac{\partial Q}{\partial t} dS. \tag{18}$$

F. Oldroyd's theorem

Though the convected coordinate system is convenient for describing the dynamics of the membrane, it may not be suitable for analysis and numerical simulation. Let u^Γ ($\Gamma = \mathrm{I}, \mathrm{II}$) be another coordinate system, and $\mathbf{w} = \partial \mathbf{R}(u^\Gamma, t)/\partial t$. Since the normal component of $\mathbf{w}$ is independent of the coordinate system, we have

$$\mathbf{v} = \mathbf{w} + d^\alpha \mathbf{a}_\alpha = \mathbf{w} + d^\Gamma \mathbf{a}_\Gamma. \tag{19}$$

The tensors transform between the convected coordinate system and the new coordinate system at any instant of time in the usual way,
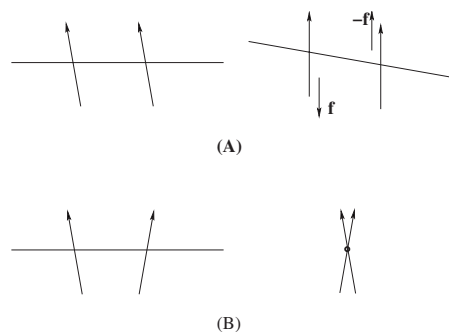

(A)

(B)

FIG. 1. (a) Deflection of directors from the normal is equivalent to slippage of the molecule along the direction of directors. Slippage causes a transverse shear stress. (b) Directors prefer to be parallel to each other. When two neighboring directors are in a splay or staggered configuration, torques are generated.

$$Q^{\cdots\Delta\cdots}_{\cdots\Gamma\cdots} = \left(\frac{\partial u^\Delta}{\partial u^\alpha} \cdots \frac{\partial u^\beta}{\partial u^\Gamma} \cdots \right) Q^{\cdots\alpha\cdots}_{\cdots\beta\cdots}. \tag{20}$$

Oldroyd's theorem [36] then defines the convected derivative of $Q^{\cdots\Delta\cdots}_{\cdots\Gamma\cdots}$

$$\frac{\delta Q^{\cdots\Delta\cdots}_{\cdots\Gamma\cdots}(u^\Lambda, t)}{\delta t} = \left(\frac{\partial u^\Delta}{\partial u^\alpha} \cdots \frac{\partial u^\beta}{\partial u^\Gamma} \cdots \right) \frac{\partial Q^{\cdots\alpha\cdots}_{\cdots\beta\cdots}(u^\mu, t)}{\partial t},$$

$$\frac{\delta Q^{\cdots\Delta\cdots}_{\cdots\Gamma\cdots}(u^\Lambda, t)}{\delta t} = \frac{\partial Q^{\cdots\Delta\cdots}_{\cdots\Gamma\cdots}(u^\Lambda, t)}{\partial t} + d^\Lambda Q^{\cdots\Delta\cdots}_{\cdots\Gamma\cdots,\Lambda} + \sum d^\Lambda_{,\Gamma} Q^{\cdots\Delta\cdots}_{\cdots\Lambda\cdots}$$

$$- \sum d^\Delta_{,\Lambda} Q^{\cdots\Lambda\cdots}_{\cdots\Gamma\cdots}. \tag{21}$$

This allows us to change between different coordinate systems.

III. ENERGETICS

We view a biomembrane as a layer of incompressible fluid of lipid molecules. We will model the membrane by a surface, together with a director field **O** defined on the surface. The director field indicates the average orientation of the lipid molecules. At this point, we will not assume that the director is normal to the surface, i.e., we allow the molecules to tilt. Normally such a tilt is very small, so later on we will consider a simplified model in which the director field is constrained to be normal to the surface.

We now consider the elastic energy for the director field **O**. Since lipids have hydrophobic tails, slippage of a molecule along the direction of the directors will cost energy. Therefore, we assume that when two directors are put together, they prefer to be parallel to each other with no slippage along the direction of directors. This is also consistent with the fact that biomembranes are single-layer smectic-A liquid crystals. If the director at a point deviates from the normal of the surface (Fig. 1), it results in slippage along the director, and stores some energy $k_2 O^\alpha O_\alpha/2$. Here k_2 is the tilt modulus. When k_2 is large, the directors are constrained to be nearly normal to the surface, and $O^\alpha O_\alpha$ must be small.

The other part of the energy comes from distortion. We start from the Frank energy density for nematic liquid crystals [29]:
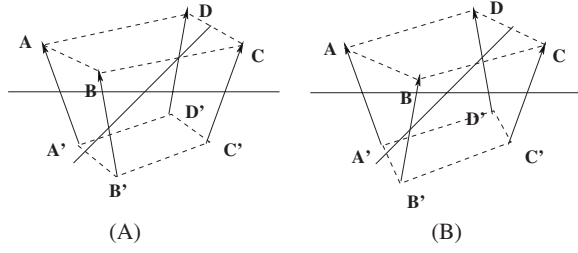
(A)　　　　　　　　　　(B)

FIG. 2. When we consider the thickness of the membrane, the change of the directors along the two coordinate curves has an effect on the density on both sides of the surface. For the second term of the free energy, (a) and (b) have the same elastic energy. The densities of the two sides in (a) are different, namely, the quadrilaterals $ABCD$ and $A'B'C'D'$ have different areas. But the densities in (b) are the same. It is natural to conclude that the energy of (a) is greater than that of (b). This is the origin of the term $\varepsilon^{\alpha\beta}(\mathbf{O}_{,\alpha} \times \mathbf{O}_{,\beta}) \cdot \mathbf{O}$.

$$E(\mathbf{O}) = \lambda_1 (\nabla \cdot \mathbf{O})^2 + \lambda_2 [\mathbf{O} \cdot (\nabla \times \mathbf{O})]^2 + \lambda_3 [\mathbf{O} \times (\nabla \times \mathbf{O})]^2.$$

Since the system under consideration has only one layer, we naturally assume that all derivatives along the normal are zero. Then the Frank energy can be expressed as

$$E(\mathbf{O}) = k_{11}(a^{\alpha\beta}\mathbf{O}_{,\alpha} \cdot \mathbf{a}_\beta)^2 + k_{22}[a^{\alpha\beta}\mathbf{O} \cdot (\mathbf{O}_{,\alpha} \times \mathbf{a}_\beta)]^2$$
$$+ k_{33}[a^{\alpha\beta}\mathbf{O} \times (\mathbf{O}_{,\alpha} \times \mathbf{a}_\beta)]^2. \quad (22)$$

For simplicity of presentation, we will make the one-constant approximation ($k_{11} = k_{22} = k_{33}$). The general case can be considered along the same lines, but the expressions of the stress and torque are much more complicated. However, since $a^{\alpha\beta}\mathbf{n}_{,\alpha} \times \mathbf{a}_\beta = 0$, when the difference between the director $\mathbf{O}$ and the normal $\mathbf{n}$ is small ($O^\alpha O_\alpha$ is small), the difference of the energy between the general case and the one-constant case is also small and can be neglected.

Neglecting some divergence terms, since a biomembrane has no boundary, we have the elastic energy density

$$E(\mathbf{O}) = k|\nabla \mathbf{O}|^2 = ka^{\alpha\beta}\mathbf{O}_{,\alpha} \cdot \mathbf{O}_{,\beta}.$$

Therefore the simplest form of the elastic energy density is given by

$$E_{el} = \frac{k_2}{2}O^\alpha O_\alpha + \frac{k_1 + \varepsilon_1}{2}a^{\alpha\beta}\mathbf{O}_{,\alpha} \cdot \mathbf{O}_{,\beta}$$
$$+ \frac{k_1 - \varepsilon_1}{2}\varepsilon^{\alpha\beta}(\mathbf{O}_{,\alpha} \times \mathbf{O}_{,\beta}) \cdot \mathbf{O}, \quad (23)$$

where k_1, k_2, and ε_1 are positive elastic moduli and $k_1 \geq \varepsilon_1$ (see Fig. 2). The last term $\varepsilon^{\alpha\beta}(\mathbf{O}_{,\alpha} \times \mathbf{O}_{,\beta}) \cdot \mathbf{O}$ does not actually cause any torque or any stress [but will cause torque and stress when we consider the spontaneous curvature; see the energy estimate in Appendix A]. This term reduces to the Gaussian curvature when $\mathbf{O} = \mathbf{n}$, and the integral of this term over any closed surface is a constant, which is the Euler characteristic of the surface. Thus it plays a role only when the topology of the membrane changes. Note that this elastic energy density E_{el} reduces to the Helfrich energy density $C^{\alpha\beta\gamma\delta}b_{\alpha\beta}b_{\gamma\delta}$ when $\mathbf{O} = \mathbf{n}$. A similar form to the first two terms was also introduced by Kozlovsky and Kozlov [32].

Their elastic energy also reduces to Helfrich's elastic energy when $\mathbf{O} = \mathbf{n}$. Fournier also considered directors with tilt energy. His free energy does not reduce to Helfrich's energy and plays the role of an addition to Helfrich's free energy [30,31].

IV. DYNAMIC LAWS OF MOTION

Now we derive the dynamic equation of an incompressible fluid membrane. If the net force exerted on Ω is denoted by $\mathbf{F}$, we have

$$\frac{d}{dt}\int_\Omega \gamma\mathbf{v}\, dS = \mathbf{F}. \quad (24)$$

The net force may be decomposed into external forces on Ω and traction acting on the boundary $\partial\Omega$. The external force $\mathbf{f}$ consists of the body forces as well as normal and shear stresses exerted on the surface by the neighboring bulk fluids. To understand the contribution to the internal forces acting on the boundary curve, we decompose the total surface stress into two parts: one part induced by the material points, and another part induced by the directors. Naturally, the first part should be an in-plane one. The other part should contain the transverse shear stress. Therefore, the total in-plane stress $T^{\alpha\beta}m_\alpha \mathbf{a}_\beta$ over an in-plane curve, where $\mathbf{m} = m^\alpha \mathbf{a}_\alpha$ is the in-plane unit normal vector of the curve, can be written as

$$T^{\alpha\beta} = T_0^{\alpha\beta} + T_1^{\alpha\beta}, \quad (25)$$

where $T_0^{\alpha\beta}$ is the part induced by the material points themselves, and $T_1^{\alpha\beta}$ is the in-plane stress induced by the directors. $T_0^{\alpha\beta}$ has the same form as that of a two-dimensional bulk fluid:

$$T_0^{\alpha\beta} = -\Pi a^{\alpha\beta} + J^{\alpha\beta}, \quad (26)$$

where Π is the net surface pressure, and $J^{\alpha\beta}$ is a symmetric tensor reflecting the dynamic component of surface stress. For a pure lipid bilayer, $J^{\alpha\beta}$ is accurately modeled by the Newtonian relation [10]

$$J^{\alpha\beta} = C^{\alpha\beta\gamma\delta}S_{\gamma\delta}. \quad (27)$$

For isotropic fluids, the fourth-order tensor $C^{\alpha\beta\gamma\delta}$ has only two independent parameters:

$$C^{\alpha\beta\gamma\delta} = (k_0 - \varepsilon_0)a^{\alpha\beta}a^{\gamma\delta} + \varepsilon_0(a^{\alpha\gamma}a^{\beta\delta} + a^{\alpha\delta}a^{\gamma\beta}).$$

Here k_0 and ε_0 are the dilation and shear viscosity. Since we are considering an incompressible fluid, $J^{\alpha\beta}$ reduces to

$$J^{\alpha\beta} = 2\varepsilon_0 S^{\alpha\beta}. \quad (28)$$

Cell membranes are also endowed with a cytoskeleton and a cell cortex. The cytoskeleton or the cell cortex will deform along with the membrane, and the relaxation process will cause stress on the membrane. As a result, the membrane exhibits some levels of viscoelastic response. We use the well-known Oldroyd-B model to describe this viscoelastic response:

$$J^{\alpha\beta} = 2\varepsilon_0 S^{\alpha\beta} + \Sigma^{\alpha\beta},$$

$$\lambda \frac{\partial \Sigma^{\alpha\beta}}{\partial t} + \Sigma^{\alpha\beta} = 2\mu S^{\alpha\beta}, \tag{29}$$

where λ is the characteristic time for the deformed cytoskeleton and cell cortex to relax to its steady state, and μ is the polymeric viscosity. In Waxman's model [18], the convected derivative is replaced by the corotational derivative. Since the cytoskeleton and cell cortex are affected by the strain, the corotational derivative is not suitable.

The other part of the stress is induced by the directors. By applying the principle of virtual work, we can obtain the expressions for the stresses and torques on the directors (see Appendix A).

On one hand, when the director at a point is deflected from the normal, a transverse shear stress $k_2 O^{(n)} O^{\alpha} m_{\alpha} \mathbf{n}$ will result on the boundary. This transverse shear stress is the origin of bending resistance. On the other hand, the difference between the two neighboring directors will induce a torque

$$[(k_1 + \varepsilon_1) a^{\alpha\beta} \mathbf{O} \times \mathbf{O}_{,\alpha} - (k_1 - \varepsilon_1) \varepsilon^{\alpha\beta} \mathbf{O}_{,\alpha}] m_\beta$$

on the boundary. We notice that the strain can also affect the elastic energy. This suggests that there should be an in-plane stress $T_1^{\alpha\beta}$ which acts on the material points. The expression of $T_1^{\alpha\beta}$ is obtained from the principle of virtual work:

$$T_1^{\alpha\beta} = (k_1 + \varepsilon_1) a^{\alpha\gamma} a^{\beta\delta} \mathbf{O}_{,\gamma} \cdot \mathbf{O}_{,\delta}. \tag{30}$$

Conservation of momentum gives:

$$\frac{\partial}{\partial t} \int_\Omega \gamma \mathbf{v} \, dS = \int_\Omega \gamma \mathbf{A} \, dS$$

$$= \int_\Omega \mathbf{f} \, dS + \oint_\Omega (T^{\alpha\beta} \mathbf{a}_\beta + k_2 O^{(n)} O^{\alpha} \mathbf{n}) m_\alpha dl.$$

Applying Green's theorem to the boundary integral, and noting that Ω is arbitrary, we obtain

$$\gamma A^{\alpha} = f^{\alpha} + T^{\beta\alpha}{}_{,\beta} - k_2 O^{(n)} O^{\beta} b^{\alpha}_{\beta},$$

$$\gamma A^{(n)} = f^{(n)} + T^{\alpha\beta} b_{\alpha\beta} + k_2 (O^{(n)} O^{\alpha})_{,\alpha}. \tag{31}$$

Let $\mathbf{L}$ be the external couple (e.g., an electric and magnetic couple or the couple that comes from the bulk fluid) acting on the director (thus $\mathbf{O} \cdot \mathbf{L} = 0$). The total net torque on the area Ω is

$$\tau = \int_\Omega (\mathbf{L} + \mathbf{R} \times \mathbf{f}) dS + \oint_\Omega (T^{\alpha\beta} \mathbf{R} \times \mathbf{a}_\beta + k_2 O^{(n)} O^{\alpha} \mathbf{R} \times \mathbf{n})$$

$$\times m_\alpha dl + \oint_\Omega (k_1 + \varepsilon_1) a^{\alpha\beta} \mathbf{O} \times \mathbf{O}_{,\alpha} m_\beta dl$$

$$- \oint_\Omega (k_1 - \varepsilon_1) \varepsilon^{\alpha\beta} \mathbf{O}_{,\alpha} m_\beta dl. \tag{32}$$

Applying the conservation of angular momentum, we have

$$\frac{\partial}{\partial t} \int_\Omega \left(\gamma \mathbf{R} \times \mathbf{v} + \gamma\varphi \mathbf{O} \times \frac{\partial \mathbf{O}}{\partial t} \right) dS = \tau, \tag{33}$$

where $\gamma\varphi$ is the moment of inertia about an axis lying in the surface. Using Green's theorem, and noting that

$$\varepsilon^{\alpha\beta} \mathbf{O}_{,\alpha\beta} = 0,$$

$$O^{\alpha} \mathbf{a}_\alpha \times (\mathbf{O} - O^{(n)} \mathbf{n}) = O^{\alpha} \mathbf{a}_\alpha \times (O^{\beta} \mathbf{a}_\beta) = 0,$$

we obtain

$$\gamma\varphi \mathbf{O} \times \frac{\partial^2 \mathbf{O}}{\partial t^2} = \mathbf{L} - k_2 O^{\alpha} \mathbf{O} \times \mathbf{a}_\alpha + (k_1 + \varepsilon_1) a^{\alpha\beta} \mathbf{O} \times \mathbf{O}_{,\alpha\beta}. \tag{34}$$

Finally, the complete system of equations for the dynamics of an evolving membrane is as follows:

$$\gamma A^{\alpha} = f^{\alpha} + T^{\beta\alpha}{}_{,\beta} - k_2 O^{(n)} O^{\beta} b^{\alpha}_{\beta},$$

$$\gamma A^{(n)} = f^{(n)} + T^{\alpha\beta} b_{\alpha\beta} + k_2 (O^{(n)} O^{\alpha})_{,\alpha},$$

$$\gamma\varphi \mathbf{O} \times \frac{\partial^2 \mathbf{O}}{\partial t^2} = \mathbf{L} - k_2 O^{\alpha} \mathbf{O} \times \mathbf{a}_\alpha + (k_1 + \varepsilon_1) a^{\alpha\beta} \mathbf{O} \times \mathbf{O}_{,\alpha\beta}, \tag{35}$$

where the constitutive relation for the Newtonian fluid is

$$T^{\alpha\beta} = -\Pi a^{\alpha\beta} + 2\varepsilon_0 S^{\alpha\beta} + (k_1 + \varepsilon_1) a^{\alpha\gamma} a^{\beta\delta} \mathbf{O}_{,\gamma} \cdot \mathbf{O}_{,\delta}, \tag{36}$$

and for viscoelastic fluids,

$$T^{\alpha\beta} = -\Pi a^{\alpha\beta} + 2\varepsilon_0 S^{\alpha\beta} + \Sigma^{\alpha\beta} + (k_1 + \varepsilon_1) a^{\alpha\gamma} a^{\beta\delta} \mathbf{O}_{,\gamma} \cdot \mathbf{O}_{,\delta},$$

$$\lambda \frac{\partial \Sigma^{\alpha\beta}}{\partial t} + \Sigma^{\alpha\beta} = 2\mu S^{\alpha\beta}. \tag{37}$$

This system of equations has the following energy dissipation relation (neglecting the external force and coupling):

$$\frac{d}{dt} \int \left(\frac{\gamma}{2} |\mathbf{v}|^2 + \frac{\gamma\varphi}{2} \left| \mathbf{O} \times \frac{\partial \mathbf{O}}{\partial t} \right|^2 + E_{el} \right) dS = -2\varepsilon_0 \int S^{\alpha\beta} S_{\alpha\beta} dS \tag{38}$$

for the Newtonian case or

$$\frac{d}{dt} \int \left(\frac{\gamma}{2} |\mathbf{v}|^2 + \frac{\gamma\varphi}{2} \left| \mathbf{O} \times \frac{\partial \mathbf{O}}{\partial t} \right|^2 + E_{el} + \frac{1}{2} \Sigma^{\alpha}_{\alpha} \right) dS$$

$$= -\int \left(2\varepsilon_0 S^{\alpha\beta} S_{\alpha\beta} + \frac{1}{2\lambda} \Sigma^{\alpha}_{\alpha} \right) dS \tag{39}$$

for the viscoelastic case. This is proven in Appendix A.

When a director rotates, the speeds of its two ends are different from the speed of the bulk fluid. The bulk fluid will causes an additional friction force on the director. This frictional force is typically much larger than the inertial force. Therefore the director equation may be simplified to

$$\eta \mathbf{O} \times \frac{\partial \mathbf{O}}{\partial t} = \mathbf{L} - k_2 O^\alpha \mathbf{O} \times \mathbf{a}_\alpha + (k_1 + \varepsilon_1) a^{\alpha\beta} \mathbf{O} \times \mathbf{O}_{,\alpha\beta}. \tag{40}$$

The energy dissipation relation changes to

$$\frac{d}{dt} \int \left(\frac{\gamma}{2} |\mathbf{v}|^2 + E_{el} \right) dS$$

$$= -2\varepsilon_0 \int C^{\alpha\beta\gamma\delta} S_{\alpha\beta} S_{\gamma\delta} dS - \eta \int \left| \mathbf{O} \times \frac{\partial \mathbf{O}}{\partial t} \right|^2 dS. \tag{41}$$

If we define vorticity by $\zeta = \varepsilon^{\alpha\beta} v_{\beta,\alpha}$, we have the vorticity equation

$$\frac{\partial}{\partial t} \left(\frac{\zeta}{\gamma} \right) = \frac{1}{\gamma} \varepsilon^{\alpha\beta} A_{\beta,\alpha}. \tag{42}$$

V. SPONTANEOUS CURVATURE

Spontaneous curvature is important for the shape of a membrane [2–4]. The origin of spontaneous curvature might be very complex. Some factors that influence the spontaneous curvature include the binding of proteins, such as the clathrin coat protein, to a monolayer; one monolayer might have more lipids than the other; or the two monolayers might have different fractions of some particular lipids. We will take these effects into account, by replacing $\mathbf{O}_{,\alpha}$ in the elastic energy density by $\mathbf{O}_{,\alpha} + \mathbf{b}_\alpha$:

$$E_{el} = \frac{k_2}{2} O^\alpha O_\alpha + \mu_1 a^{\alpha\beta} (\mathbf{O}_{,\alpha} + \mathbf{b}_\alpha) \cdot (\mathbf{O}_{,\beta} + \mathbf{b}_\beta)$$

$$+ \frac{k_1 - \varepsilon_1}{2} \varepsilon^{\alpha\beta} [(\mathbf{O}_{,\alpha} + \mathbf{b}_\alpha) \times (\mathbf{O}_{,\beta} + \mathbf{b}_\beta)] \cdot \mathbf{O}, \tag{43}$$

where $\mu_1 = (k_1 + \varepsilon_1)/2$, $\mu_2 = (k_1 - \varepsilon_1)/2$, and $\mathbf{b}_\alpha$ satisfies the equations

$$\mathbf{O} \times \left(\frac{\partial \mathbf{b}_\alpha}{\partial t} - S_\alpha^\pi \mathbf{b}_\pi - \frac{\zeta}{2} \mathbf{O} \times \mathbf{b}_\alpha \right) = 0 \quad \text{and} \quad \mathbf{O} \cdot \mathbf{b}_\alpha = 0. \tag{44}$$

The term $-S_\alpha^\pi \mathbf{b}_\pi$ comes from the influence of the strain. The term $-(\zeta/2)\mathbf{O} \times \mathbf{b}_\alpha$ comes from the assumption that $\mathbf{b}_\alpha$ rotates along the director $\mathbf{O}$ with the angular speed $\zeta/2$. This rotation induces some angular momentum along the director. When there is no strain and no vorticity, $\mathbf{b}_\alpha$ rotates along with $\mathbf{O}$. When $\mathbf{O}$ is constrained to be the normal $\mathbf{n}$, $\mathbf{a}_\alpha$ is a solution of this equation (see Appendix B).

As a result, the dynamic equations of the surface fluids change to

$$\gamma A^\alpha = f^\alpha + T^{\beta\alpha}_{,\beta} - k_2 O^{(n)} O^\beta b^\alpha_\beta,$$

$$\gamma A^{(n)} = f^{(n)} + T^{\alpha\beta} b_{\alpha\beta} + k_2 (O^{(n)} O^\alpha)_{,\alpha},$$

$$\gamma \varphi \mathbf{O} \times \frac{\partial^2 \mathbf{O}}{\partial t^2} = \mathbf{L} - k_2 O^\alpha \mathbf{O} \times \mathbf{a}_\alpha + 2\mu_1 a^{\alpha\beta} \mathbf{O} \times (\mathbf{O}_{,\alpha} + \mathbf{b}_\alpha)_{,\beta}$$

$$+ 2\mu_2 \varepsilon^{\alpha\beta} \mathbf{O} \times (\mathbf{O} \times \mathbf{b}_{\alpha,\beta}), \tag{45}$$

where the in-plane stress tensor is also modified:

$$T^{\alpha\beta} = -\Pi a^{\alpha\beta} + 2\varepsilon_0 S^{\alpha\beta} + [\mu_1 (a^{\alpha\gamma} a^{\beta\delta} + a^{\alpha\delta} a^{\beta\gamma})$$

$$- 2\mu_2 \varepsilon^{\alpha\beta} \varepsilon^{\gamma\delta}] \cdot (\mathbf{O}_{,\gamma} + \mathbf{b}_\gamma) \cdot \mathbf{O}_{,\delta} + [\mu_2 (\varepsilon^{\alpha\gamma} a^{\beta\delta} + \varepsilon^{\beta\gamma} a^{\alpha\delta})$$

$$+ 2\mu_1 \varepsilon^{\alpha\beta} a^{\gamma\delta}] \cdot (\mathbf{O}_{,\gamma} + \mathbf{b}_\gamma) \times \mathbf{O}_{,\delta} \cdot \mathbf{O}. \tag{46}$$

The energy dissipation relation is now

$$\frac{d}{dt} \int \left(\frac{\gamma}{2} |\mathbf{v}|^2 + \frac{\gamma\varphi}{2} \left| \mathbf{O} \times \frac{\partial \mathbf{O}}{\partial t} \right|^2 + E_{el} \right) dS$$

$$= -2\varepsilon_0 \int S^{\alpha\beta} S_{\alpha\beta} dS. \tag{47}$$

VI. THE LIMIT AS $k_2 \to \infty$

In reality, cell membranes are often considered to be in the smectic-A phase, i.e., $\mathbf{O} = \mathbf{n}$. In this section, we will derive the dynamic equations in that case.

In (43), the term $k_2 O^\alpha O_\alpha / 2$ can be viewed as the relaxation of the constraint that $\mathbf{O} = \mathbf{n}$. To obtain a model for which $\mathbf{O} = \mathbf{n}$, we consider the limit as $k_2 \to \infty$. We show in Appendix B that in this case, the equation for $\mathbf{b}_\alpha$ has the solution $\mathbf{b}_\alpha = B^\gamma_\alpha \mathbf{a}_\gamma$, where

$$\frac{D_s B_{\alpha\beta}}{Dt} = \frac{\partial B_{\alpha\beta}}{\partial t} - B^\mu_\alpha S_{\mu\beta} - B^\mu_\beta S_{\alpha\mu} = 0. \tag{48}$$

Using this, we obtain

$$\lim_{k_2 \to \infty} T_1^{\alpha\beta} = M^{\alpha\mu} b^\beta_\mu,$$

$$M^{\alpha\beta} = C^{\alpha\beta\gamma\delta} (B_{\alpha\beta} - b_{\alpha\beta}). \tag{49}$$

Since the directors oscillate with a large frequency when k_2 is large, the transverse shear stress $k_2 O^{(n)} O^\alpha$ also changes fast, and the average effect is determined by the equilibrium position. The equilibrium position is determined by minimizing the total elastic energy $\int E_{el} dS$. Expanding the elastic energy to first order in $\|\mathbf{O} - \mathbf{n}\|$ [but keeping the term $(k_2/2) O^\alpha O_\alpha$ since k_2 is large], we have

$$\frac{k_2}{2} O^\alpha O_\alpha + \mu_1 a^{\alpha\beta} (\mathbf{O}_{,\alpha} + \mathbf{b}_\alpha) \cdot (\mathbf{O}_{,\beta} + \mathbf{b}_\beta) + \mu_2 \varepsilon^{\alpha\beta} ((\mathbf{O}_{,\alpha} + \mathbf{b}_\alpha)$$

$$\times (\mathbf{O}_{,\beta} + \mathbf{b}_\beta)) \cdot \mathbf{O} = C^{\alpha\beta\gamma\delta} K_{\alpha\beta} K_{\gamma\delta}$$

$$+ (a \ divergence \ term) + o(\|\mathbf{O} - \mathbf{n}\|) + \frac{k_2}{2} O^\alpha O_\alpha$$

$$- 2\mu_1 a^{\alpha\beta} O^\gamma K_{\gamma\beta,\alpha} - 2\mu_2 \varepsilon^{\alpha\beta} \varepsilon_{\gamma\delta} O^\gamma K^\delta_{\beta,\alpha}.$$

The terms in the last line are the leading order terms, which determine the leading order corrections to the preferred configuration of the director. Therefore, the average effect of the transverse shear stress is:

$$\lim_{k_2 \to \infty} k_2 \overline{O^{(n)} O^\alpha} = 2\mu_2 (K^{\alpha\beta} + \varepsilon^{\beta\gamma} \varepsilon^{\alpha\delta} K_{\delta\gamma})_{,\beta} + 2\varepsilon_1 K^{\alpha\beta}_{,\beta} = M^{\alpha\beta}_{,\beta}.$$

$$(50)$$

Hence, we obtain the dynamic equation in this limit:

$$\gamma A^\alpha = f^\alpha + T^{\beta\alpha}_{,\beta} - q^\beta b^\alpha_\beta,$$

$$\gamma A^{(n)} = f^{(n)} + T^{\alpha\beta} b_{\alpha\beta} + q^\alpha_{,\alpha}, \qquad (51)$$

where the transverse shear stress q^α and the in-plane stress $T^{\alpha\beta}$ are given by

$$T^{\alpha\beta} = -\Pi a^{\alpha\beta} + J^{\alpha\beta} + M^{\alpha\mu} b^\beta_\mu,$$

$$q^\alpha = (M^{\alpha\beta})_{,\beta}. \qquad (52)$$

We call this the *reduced model*.

In the case when the spontaneous curvature is caused by the difference in the number of lipids in the two monolayers, we may simply let $B_{\alpha\beta} = B a_{\alpha\beta}$, which corresponds to a global spontaneous curvature. The spontaneous curvature may also be caused by some local but intrinsic properties of the membrane. For example, the binding of the clathrin and adaptin proteins to the membrane [1] is important for endocytosis and exocytosis. The membrane tends to bend locally as a result of the binding of these proteins. The sizes of these regions are small compared to the size of membrane, and the use of continuum mechanics may be called into question. But, formally at least, we can use $B_{\alpha\beta} = B(u^1, u^2) a_{\alpha\beta}$ [where $B(u^1, u^2)$ is a local function and independent of the time] as the spontaneous curvature. We call this the local spontaneous curvature. This is also a solution of Eq. (48) (see Appendix B). For such $B_{\alpha\beta}$, the in-plane stress $M^{\alpha\mu} b^\beta_\mu$ is symmetric, and

$$(M^{\alpha\mu} b^\beta_\mu)_{,\beta} - q^\beta b^\alpha_\beta = -4k_1 H a^{\alpha\beta} B_{,\beta} - a^{\alpha\mu}(\mu_2 H^2 + \varepsilon_1 b^{\alpha\beta} b_{\alpha\beta}$$
$$- 4k_1 H B)_{,\mu}.$$

Therefore, absorbing the gradient term into the pressure Π, we obtain

$$\gamma A^\alpha = f^\alpha + (-\Pi a^{\alpha\beta} + J^{\alpha\beta})_{,\beta} - 4k_1 H a^{\alpha\beta} B_{,\beta},$$

$$\gamma A^{(n)} = f^{(n)} - 2H\Pi + J^{\alpha\beta} b_{\alpha\beta} + 2k_1 (a^{\alpha\beta} B_{,\alpha\beta} - 2KB)$$
$$- 4\mu_1 [a^{\alpha\beta} H_{,\alpha\beta} + 2H(H^2 - K)]. \qquad (53)$$

This result is consistent with the results in [7,19,20].

It is easy to see that the following energy dissipation relation holds for the model (51) and (52):

$$\frac{1}{2} \frac{d}{dt} \int (\gamma |\mathbf{v}|^2 + C^{\alpha\beta\gamma\delta} K_{\alpha\beta} K_{\gamma\delta}) dS = -2\varepsilon_0 \int S^{\alpha\beta} S_{\alpha\beta} dS. \qquad (54)$$

Moreover, the elastic energy density

$$E_{el} = C^{\alpha\beta\gamma\delta}(B_{\alpha\beta} - b_{\alpha\beta})(B_{\gamma\delta} - b_{\gamma\delta}) = C^{\alpha\beta\gamma\delta} K_{\alpha\beta} K_{\gamma\delta} \quad (55)$$

is simply the Helfrich energy density. Equations (51) and (52) can also be obtained using the principle of virtual work.

Next we consider some special cases of this model. For a flat membrane (without normal velocity), the curvature tensor is zero. Accordingly Eqs. (51) become

$$\gamma A^\alpha = (f^\alpha + \gamma G^\alpha) + (-\Pi a^{\alpha\beta} + J^{\alpha\beta})_{,\beta}, \qquad (56)$$

which is the Lagrangian form of the Navier-Stokes equations. Using Oldroyd's theorem, we can write Eq. (56) in the Eulerian coordinate system

$$\mathbf{A} = \left(\frac{\partial \mathbf{v}}{\partial t} + \mathbf{v} \cdot \nabla \mathbf{v} - \mathbf{v} \cdot \nabla \mathbf{v}\right) + \mathbf{v} \cdot \nabla \mathbf{v} = \frac{\partial \mathbf{v}}{\partial t} + \mathbf{v} \cdot \nabla \mathbf{v}.$$

In fixed coordinates, (56) becomes

$$\gamma \left(\frac{\partial \mathbf{v}}{\partial t} + \mathbf{v} \cdot \nabla \mathbf{v}\right) = \mathbf{f} - \nabla \Pi + \varepsilon_0 \Delta \mathbf{v}$$

for Newtonian fluids. This is the Eulerian form of the Navier-Stokes Equations.

For a membrane with cylindrical symmetry, we can describe its dynamics by the motion of its transversal. If we use the arc length parameter as the coordinate at $t = 0$, the convected coordinate for the transversal is still the arc length parameter for the deformed configuration because of the incompressibility. Therefore, Eqs. (53) simplifies to

$$\gamma A^1 = f^1 - \partial_s \Pi - 4k_1 H \partial_s B,$$

$$\gamma A^{(n)} = f^{(n)} - 2H\Pi + 2k_1 \partial_s^2 B - 4\mu_1 (\partial_s^2 H + 2H^3), \quad (57)$$

where ∂_s and ∂_s^2 are the first- and second-order derivatives along the transverse. In fact, these are the equations of an incompressible string with bending resistance.

VII. COUPLING TO THE BULK FLUIDS FOR THE REDUCED MODEL

Membranes are often immersed in a bulk fluid, which will also be modeled as an incompressible fluid. The Navier-Stokes equation for the bulk fluid in the Eulerian coordinate system is

$$\rho \left(\frac{\partial \mathbf{U}}{\partial t} + \mathbf{U} \cdot \nabla \mathbf{U}\right) = -\nabla P + \nabla \cdot \tau,$$

$$\nabla \cdot \mathbf{U} = 0, \qquad (58)$$

where ρ is the density of the bulk fluid, $\mathbf{U}$ is the velocity, P is the pressure, and τ is the stress. Without loss of generality, we assume that the stress τ satisfies the Newtonian relation

$$\tau = 2\nu D = \nu [\nabla \mathbf{U} + (\nabla \mathbf{U})^T], \qquad (59)$$

where ν is the viscosity coefficient.

When we consider a membrane in a bulk fluid, the inertia of the membrane becomes unimportant since the membrane is very thin. If we apply the no-slip condition, the velocity of the membrane is simply that of the bulk fluid at the same position. The effect of the membrane is to produce some extra stress. As a result, the bulk stress jumps across the membrane

$$[PI - \tau] \cdot \mathbf{n} = (T^{\alpha\beta} \mathbf{a}_\alpha)_{,\beta} + (q^\alpha \mathbf{n})_{,\alpha}. \qquad (60)$$

This jump of stress acts on the membrane and balances the membrane stress. Since the incompressibility condition of a

membrane in an incompressible bulk fluid is $\mathbf{n} \cdot D \cdot \mathbf{n} = 0$, we can decompose the stress into

$$2\nu_0[D] \cdot \mathbf{n} = (q^\beta b_\beta^\alpha - T_{,\beta}^{\alpha\beta})\mathbf{a}_\alpha,$$

$$[P] = T^{\alpha\beta}b_{\alpha\beta} + q_{,\alpha}^\alpha, \tag{61}$$

where ν_0 is the viscosity coefficient between the membrane and the surrounding bulk fluid. This condition is different from that of Pozrikidis [26] due to the presence of the additional stress term. At steady state, the condition becomes

$$\Pi_{,\beta} = -4k_1 H B_{,\beta},$$

$$[P] = -2\Pi H + 2k_1(a^{\alpha\beta}B_{,\alpha\beta} - 2KB)$$
$$-4\mu_1[a^{\alpha\beta}H_{,\alpha\beta} + 2H(H^2 - K)]. \tag{62}$$

Therefore H and B must satisfy the relation $\lambda_1 H_{,\beta} + \lambda_2 B_{,\beta} = 0$ at the steady state. If B is a constant, the pressure is also a constant, and the equation becomes

$$[P] = -2\Pi H - 4k_1 KB - 4\mu_1[a^{\alpha\beta}H_{,\alpha\beta} + 2H(H^2 - K)]. \tag{63}$$

For $B = 0$ and $\Pi = 0$, we get the Euler-Lagrange equation for the Willmore problem. The no-slip condition also indicates that $[-\boldsymbol{\nabla}P + \boldsymbol{\nabla} \cdot \tau] \cdot \mathbf{n} = 0$, or

$$[\boldsymbol{\nabla}P \cdot \mathbf{n}] = [\boldsymbol{\nabla} \cdot \tau \cdot \mathbf{n}] = [\nu\Delta\mathbf{U} \cdot \mathbf{n}]. \tag{64}$$

The energy dissipation relation of the coupled system (viscous case) is

$$\frac{d}{dt}\left(\int \rho|\mathbf{U}|^2 dV + \int_S E_{el} ds\right)$$
$$= -\nu \int |\boldsymbol{\nabla}\mathbf{U}|^2 dV - \frac{\nu\varepsilon_0}{\nu_0}\int_S C^{\alpha\beta\gamma\delta}S_{\alpha\beta}S_{\gamma\delta}ds. \tag{65}$$

VIII. COMPARISON WITH EXISTING WORK AND CONCLUSIONS

There are three main components in the models we presented above: the director model, the reduced model, and the model for local spontaneous curvature, which accounts for the effect of membrane proteins. Most existing literature deals with the reduced model without discussing the effect of local spontaneous curvature. In itself the reduced model also consists of four parts: the elastic part, the viscous part, the viscoelastic response, and the coupling with the bulk fluid. From this viewpoint, the work of Miao *et al.* is closest to ours: If we neglect the viscoelastic response, our model reduces to that of Miao *et al.* [27,28]. However, taking into account local spontaneous curvature does not seem to be trivial in their model. Other existing models in general contain less components. Waxman's model [18] lacked the important elastic in-plane stress term. The model of Capovilla and Guven [6] and the model of Steigmann [8,14,15] contain the elastic stress term which are the same as ours, but neglects the viscous contributions. In the models of Evans and

Skalak [5], Capovilla and Guven [6], and Lomholt and Miao [7], the mechanics of the membrane with bending energy was considered, but not the dynamics. Since these models focus on the equilibrium states of the membrane, the viscous effects are not considered in this papers. In Seifert's work, the effects of the bulk fluid is considered and the membrane viscous effects is neglected. In the work of Cai and Lubensky [20], the in-plane viscous effects are considered but the effects of the bulk fluid are neglected.

Our reduced model is quite similar in appearance to that of Waxman, except for an additional in-plane stress term. This is particularly noticeable when local spontaneous curvature is taken into account. But, contrary to Waxman's model, our equations satisfy the natural energy dissipation relation, as a result of this additional stress term. Such an oversight may go back to some earlier papers on elastic shells [33]. As pointed out by Steigmann [8], in Naghdi's [33] treatment of this subject, the Kirchhoff-Love theory is not derived from the Cosserat theory but instead considered separately on the basis of distinct balance and invariance postulates. Since this stress is an elastic stress, it appears in the models which are derived from the free energy [6,8,14,27,28]. When the spontaneous curvature is a constant, this stress can be absorbed by the in-plane pressure, and the resulting equations are consistent with the models [5,7,19,20]. Including this elastic term is important, not only for consistency with thermodynamics, but also for carrying out stable and robust numerical simulations for the fluid dynamics of the membrane, which was our original motivation for this project.

APPENDIX A: ENERGY DISSIPATION RELATION

Consider

$$\gamma A^\alpha = T^{\beta\alpha}_{,\beta} - k_2 O^{(n)}Ob_\beta^\alpha,$$

$$\gamma A^{(n)} = T^{\alpha\beta}b_{\alpha\beta} + k_2(O^{(n)}O^\alpha)_{,\alpha},$$

$$\gamma\varphi\mathbf{O} \times \frac{\partial^2\mathbf{O}}{\partial t^2} = -k_2 O^\alpha\mathbf{O} \times \mathbf{a}_\alpha + 2\mu_1 a^{\alpha\beta}\mathbf{O} \times (\mathbf{O}_{,\alpha} + \mathbf{b}_\alpha)_{,\beta}$$
$$+ 2\mu_2\varepsilon^{\alpha\beta}\mathbf{O} \times (\mathbf{O} \times \mathbf{b}_{\alpha,\beta}).$$

For the left-hand side, we have the next equations:

$$\int \gamma(A^\alpha v_\alpha + A^{(n)}v^{(n)})dS = \frac{1}{2}\frac{\partial}{\partial t}\int \gamma|\mathbf{v}|^2 dS$$

and

$$\int \gamma\varphi\left(\mathbf{O}\times\frac{\partial\mathbf{O}}{\partial t}\right)\cdot\left(\mathbf{O}\times\frac{\partial^2\mathbf{O}}{\partial t^2}\right)dS$$

$$=\frac{1}{2}\frac{\partial}{\partial t}\int \gamma\varphi\left|\mathbf{O}\times\frac{\partial\mathbf{O}}{\partial t}\right|^2 dS.$$

For the right-hand side, we have

$$\int (T^{\beta\alpha}{}_{,\beta}v_\alpha + T^{\alpha\beta}b_{\alpha\beta}v^{(n)})dS$$

$$=\int (-T^{\beta\alpha}v_{\alpha,\beta} + T^{\alpha\beta}b_{\alpha\beta}v^{(n)})dS$$

$$=\int (\Pi S^a_{,\alpha} - 2\varepsilon_0 S^{\alpha\beta}S_{\alpha\beta})dS + \int T_1^{\beta\alpha}(-v_{\alpha,\beta} + b_{\alpha\beta}v^{(n)})dS$$

$$=-2\varepsilon_0\int S^{\alpha\beta}S_{\alpha\beta}dS + \int T_1^{\beta\alpha}(-v_{\alpha,\beta} + b_{\alpha\beta}v^{(n)})dS,$$

$$\int [(-O^{(n)}O^\beta b_\beta^\alpha)v_\alpha + (O^{(n)}O^\alpha)_{,\alpha}v^{(n)}]dS$$

$$-\int\left(\mathbf{O}\frac{\partial\mathbf{O}}{\partial t}\right)\cdot O^\alpha\mathbf{O}\times\mathbf{a}_\alpha dS$$

$$=-\int (v_\mu b_\alpha^\mu + v^{(n)}_{,\alpha})O^{(n)}O^\alpha dS - \int\frac{\partial\mathbf{O}}{\partial t}\cdot O^\alpha\mathbf{a}_\alpha dS$$

$$=\int O^{(n)}\frac{\partial\mathbf{n}}{\partial t}\cdot O^\alpha\mathbf{a}_\alpha dS - \frac{1}{2}\frac{\partial}{\partial t}\int (O^\beta\mathbf{a}_\beta)^2 dS$$

$$-\int\frac{\partial(O^{(n)}\mathbf{n})}{\partial t}\cdot O^\alpha\mathbf{a}_\alpha dS = -\frac{1}{2}\frac{\partial}{\partial t}\int O^\alpha O_\alpha dS,$$

$$\int\left(\mathbf{O}\times\frac{\partial\mathbf{O}}{\partial t}\right)\cdot a^{\alpha\beta}\mathbf{O}\times(\mathbf{O}_{,\alpha}+\mathbf{b}_\alpha)_{,\beta}dS$$

$$=\int\frac{\partial\mathbf{O}}{\partial t}\cdot a^{\alpha\beta}(\mathbf{O}_{,\alpha}+\mathbf{b}_\alpha)_{,\beta}dS$$

$$=-\int\frac{\partial\mathbf{O}_{,\beta}}{\partial t}\cdot a^{\alpha\beta}(\mathbf{O}_{,\alpha}+\mathbf{b}_\alpha)dS$$

$$=-\frac{1}{2}\frac{\partial}{\partial t}\int [a^{\alpha\beta}(\mathbf{O}_{,\alpha}+\mathbf{b}_\alpha)\cdot(\mathbf{O}_{,\beta}+\mathbf{b}_\beta)]dS$$

$$+\int (\mathbf{O}_{,\alpha}+\mathbf{b}_\alpha)\cdot\mathbf{O}_{,\beta}S^{\alpha\beta}dS$$

$$-\frac{1}{2}\int \zeta a^{\alpha\beta}\mathbf{O}\cdot[(\mathbf{O}_{,\alpha}+\mathbf{b}_\alpha)\times\mathbf{O}_{,\beta}]dS,$$

and

$$\int\left(\mathbf{O}\times\frac{\partial\mathbf{O}}{\partial t}\right)\cdot\varepsilon^{\alpha\beta}[\mathbf{O}\times(\mathbf{O}\times\mathbf{b}_{\alpha,\beta})]dS$$

$$=\int\frac{\partial\mathbf{O}}{\partial t}\cdot[\varepsilon^{\alpha\beta}\mathbf{O}\times(\mathbf{O}_{,\alpha}+\mathbf{b}_\alpha)_{,\beta}]dS$$

$$=-\int\frac{\partial\mathbf{O}_{,\beta}}{\partial t}\cdot[\varepsilon^{\alpha\beta}\mathbf{O}\times(\mathbf{O}_{,\alpha}+\mathbf{b}_\alpha)]dS$$

$$=-\frac{1}{2}\frac{\partial}{\partial t}\int [\varepsilon^{\alpha\beta}(\mathbf{O}_{,\alpha}+\mathbf{b}_\alpha)\times(\mathbf{O}_{,\beta}+\mathbf{b}_\beta)\cdot\mathbf{O}]dS$$

$$-\int (\varepsilon^{\gamma\beta}a^{\alpha\delta}+\varepsilon^{\gamma\alpha}a^{\beta\delta})(\mathbf{O}_{,\gamma}+\mathbf{b}_\gamma)\times\mathbf{b}_\delta\cdot\mathbf{O}S_{\alpha\beta}dS$$

$$+\frac{1}{2}\int \zeta\varepsilon^{\alpha\beta}(\mathbf{O}_{,\alpha}+\mathbf{b}_\alpha)\cdot\mathbf{b}_\beta dS.$$

Note that $\zeta=\varepsilon^{\alpha\beta}v_{\beta,\alpha}=\varepsilon^{\alpha\beta}(v_{\beta,\alpha}-v^{(n)}b_{\alpha\beta})$; we then obtain

$$(k_1+\varepsilon_1)\int\left(\mathbf{O}\times\frac{\partial\mathbf{O}}{\partial t}\right)\cdot[a^{\alpha\beta}\mathbf{O}\times(\mathbf{O}_{,\alpha}+\mathbf{b}_\alpha)]_{,\beta}dS$$

$$-(k_1-\varepsilon_1)\int\left(\mathbf{O}\times\frac{\partial\mathbf{O}}{\partial t}\right)\cdot[\varepsilon^{\alpha\beta}(\mathbf{O}_{,\alpha}+\mathbf{b}_\alpha)]_{,\beta}dS$$

$$=-\frac{\partial}{\partial t}\int E_{el}dS - \int T_1^{\beta\alpha}(-v_{\alpha,\beta}+b_{\alpha\beta}v^{(n)})dS.$$

Finally, we get

$$\frac{\partial}{\partial t}\int\left(\frac{\gamma}{2}|\mathbf{v}|^2 + \frac{\gamma\varphi}{2}\left|\mathbf{O}\times\frac{\partial\mathbf{O}}{\partial t}\right|^2 + E_{el}\right)dS = -2\varepsilon_0\int S^{\alpha\beta}S_{\alpha\beta}dS.$$

APPENDIX B: EQUATIONS FOR THE COROTATIONAL DERIVATIVE

The corotational derivative is defined as

$$\frac{D_s B_{\alpha\beta}}{Dt} = \frac{\partial B_{\alpha\beta}}{\partial t} - B_\alpha^\mu S_{\mu\beta} - B_\beta^\mu S_{\alpha\mu},$$

$$\frac{D_s B_\beta^\alpha}{Dt} = \frac{\partial B_\beta^\alpha}{\partial t} - B^{\alpha\mu}S_{\mu\beta} + S^{\alpha\mu}B_{\mu\beta},$$

$$\frac{D_s B^{\alpha\beta}}{Dt} = \frac{\partial B^{\alpha\beta}}{\partial t} + B^{\alpha\mu}S_\mu^\beta + S^{\alpha\mu}B_\mu^\beta.$$

By simple calculations, we find

$$\frac{D_s a^{\alpha\beta}}{Dt} = 0, \quad \frac{D_s a_{\alpha\beta}}{Dt} = 0,$$

$$\frac{D_s C^{\alpha\beta\gamma\delta}B_{\gamma\delta}}{Dt} = C^{\alpha\beta\gamma\delta}\frac{D_s B_{\gamma\delta}}{Dt},$$

$$\frac{\partial(C^{\alpha\beta\gamma\delta}B_{\alpha\beta}B_{\gamma\delta})}{\partial t} = B_{\alpha\beta}\frac{D_s C^{\alpha\beta\gamma\delta}B_{\gamma\delta}}{Dt}.$$

For $\mathbf{b}_\alpha$, if we define

$$\frac{D_\lambda \mathbf{b}_\alpha}{Dt} = \frac{\partial \mathbf{b}_\alpha}{\partial t} - S_\alpha^\beta \mathbf{b}_\beta - \frac{\zeta}{2} \mathbf{O} \times \mathbf{b}_\alpha,$$

then we have

$$\mathbf{O} \times \frac{D_\lambda B_\alpha^\beta \mathbf{b}_\beta}{Dt} = \mathbf{O} \times \left(\frac{\partial B_\alpha^\beta \mathbf{b}_\beta}{\partial t} - S_\alpha^\beta B_\beta^\gamma \mathbf{b}_\gamma - \frac{\zeta}{2} \mathbf{O} \times B_\alpha^\beta \mathbf{b}_\beta \right)$$

$$= \mathbf{O} \times \left(\frac{\partial B_\alpha^\beta}{\partial t} \mathbf{b}_\beta + B_\alpha^\beta \frac{\partial \mathbf{b}_\beta}{\partial t} \right.$$

$$\left. - S_\alpha^\beta B_\beta^\gamma \mathbf{b}_\gamma - \frac{\zeta}{2} \mathbf{O} \times B_\alpha^\beta \mathbf{b}_\beta \right)$$

$$= \mathbf{O} \times \left(\frac{\partial B_\alpha^\beta}{\partial t} \mathbf{b}_\beta + B_\alpha^\beta S_\beta^\gamma \mathbf{b}_\gamma \right.$$

$$\left. - S_\alpha^\beta B_\beta^\gamma \mathbf{b}_\gamma \right) + B_\alpha^\beta \mathbf{O} \times \frac{D_\lambda \mathbf{b}_\beta}{Dt}$$

$$= \mathbf{O} \times \left(\frac{D_s B_\alpha^\beta}{Dt} \mathbf{b}_\beta + B_\alpha^\beta \frac{D_\lambda \mathbf{b}_\beta}{Dt} \right).$$

When $\mathbf{O} = \mathbf{n}$, we have

$$\mathbf{n} \times \left(\frac{\partial \mathbf{a}_\alpha}{\partial t} - S_\alpha^\pi \mathbf{a}_\pi - \frac{\zeta}{2} \mathbf{n} \times \mathbf{a}_\alpha \right) = 0 \quad \text{and} \quad \mathbf{n} \cdot \mathbf{a}_\alpha = 0.$$

Therefore

$$\mathbf{n} \times \frac{D_\lambda B_\alpha^\beta \mathbf{a}_\beta}{Dt} = \frac{D_s B_\alpha^\beta}{Dt} \mathbf{n} \times \mathbf{a}_\beta = 0.$$

Hence, we obtain

$$\frac{D_s B_{\alpha\beta}}{Dt} = 0.$$

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