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Variable tilt on lipid membranes

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A continuum theory for lipid membranes is developed that accounts for mechanical interactions between lipid tilt and membrane shape. For planar membranes, a linear version of the theory is used to predict tilt variations similar to those observed in experiments and molecular dynamics simulations.

1. Introduction

Continuum models of lipid bilayers have been successfully applied to the prediction of equilibrium shapes of cell membranes and vesicles [1–3]. For the most part, these predictions have relied on the Canham–Helfrich model [4,5], in which the areal energy density of the membrane is determined by its mean and Gaussian curvatures. This model, which is based on the assumption that the lipids are everywhere normal to the membrane surface, is operative at length scales substantially exceeding membrane thickness, typically of the order of 5 nm.

There are, however, circumstances under which lipids are not aligned with the surface normal. The lipids are then said to *tilt* relative to the membrane surface; this in turn induces a change in membrane thickness, which is simply the projection of the lipid length onto the surface normal. For example, in the gel phase, lipids are uniformly tilted in a manner that depends on their packing arrangement [6]. Lipids may also exhibit tilt in the neighbourhood of an inserted protein, and manifest associated defect structures. Experimentally observed ripple phases are characterized by oscillatory thickness variations induced by spatially non-uniform tilt [7].

Models accounting for lipid tilt and attendant thickness variation have been developed by a number of workers [8–13]. While these have provided important insights into how lipid orientation and membrane shape are coupled in special cases, several open questions remain. In particular, a general description of variable

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lipid tilt coupled to changes in membrane shape is currently lacking. In this work, we develop such a model using a general framework based on a two-dimensional approximation to three-dimensional liquid crystal theory, valid to leading order in thickness for sufficiently thin films [14,15]. The main feature of this model is the relaxation of restrictions imposed in earlier theories [13,16] to permit tilt to interact mechanically with membrane shape.

The basic framework, adapted from [14], is outlined in §2. This is followed, in §3, by a variational derivation of the relevant equilibrium equations and boundary conditions coupling tilt and surface shape, with respect to any energy density of the considered class. In §4, these are further reduced for the case of constrained lipid length, and then specialized, for illustrative purposes, to a simple energy density. For the particular function adopted, it is shown that planar membranes with uniformly distributed tilt fields furnish equilibrium states. In §5, we linearize the general equations with respect to small perturbations of these simple states. Solutions to the linear system exhibit tilt fields that are either localized near boundaries or oscillatory and widespread over the interior domain. The latter are reminiscent of ripple phases. These are shown to be stable in a restricted sense under certain restrictions on the relevant moduli.

2. Theoretical framework

In [14], the two-dimensional theory of lipid membranes with variable tilt was derived systematically from the assumption that the membrane may be regarded as a thin region occupied by a liquid crystal, as suggested by Helfrich's early work on lipid bilayers [5]. The orientational degree of freedom in liquid crystals emerges as a *director* in the derived model. This is the vector field on the membrane surface that describes the lipid configurations. The basic result is that the energy of the thin film is given, to leading order in film thickness, by

$$E = \int_\omega W(\mathbf{n}, \boldsymbol{\delta}, \nabla\boldsymbol{\delta})\, \mathrm{d}a, \tag{2.1}$$

where W is the areal energy density, $\mathbf{n}$ is the unit normal to the surface ω occupied by the membrane, $\boldsymbol{\delta}$ is the director field and $\nabla\boldsymbol{\delta}$ is the gradient of the director on the surface. The latter is given explicitly by

$$\nabla\boldsymbol{\delta} = \boldsymbol{\delta}_{,\alpha} \otimes \mathbf{a}^\alpha, \tag{2.2}$$

where $\otimes$ is the standard tensor product of vectors, Greek subscripts preceded by commas are partial derivatives with respect to surface coordinates θ^α, diagonally repeated indices are summed over $\{1,2\}$, and the $\mathbf{a}^\alpha$ are vectors lying in the tangent plane to ω at the point with coordinates θ^1, θ^2. The latter are the vector duals of the natural basis vectors $\mathbf{a}_\alpha = \mathbf{r}_{,\alpha}$, where $\mathbf{r}(\theta^1, \theta^2)$ is the position field on ω. They are given by $\mathbf{a}^\alpha = a^{\alpha\beta}\mathbf{a}_\beta$, where the matrix $(a^{\alpha\beta}) = (a_{\alpha\beta})^{-1}$, in which $a_{\alpha\beta} = \mathbf{a}_\alpha \cdot \mathbf{a}_\beta$ are the metric components on the surface. Here and elsewhere we use notation that is standard in differential geometry; excellent accounts are given in the books by Sokolnikoff [17] and Kreyszig [18].

The functional dependence of the energy density on the director gradient is usually assumed to be quadratic [15,19,20], to reflect the notion that the length scale for spatial variations in the director is typically much larger than the molecular scale; here, the lipid length. The leading-order dependence on the director gradient in a thin film is then quadratic [14]; thus, we consider energies of the form

$$W = \tfrac{1}{2}\nabla\boldsymbol{\delta} \cdot \mathbf{K}[\nabla\boldsymbol{\delta}] + D(\mathbf{n}, \boldsymbol{\delta}), \tag{2.3}$$

where the fourth-order tensor $\mathbf{K}$ may depend on $\mathbf{n}$ and $\boldsymbol{\delta}$. In liquid-crystal theory, the tensor $\mathbf{K}$ is assumed to be positive-definite, to ensure that W is a convex function of the director gradient and hence that conditions associated with the existence of energy-minimizing states are satisfied [21].

This function must be such as to satisfy the requirement of Galilean invariance. In the present setting, this means that W should be invariant under replacement of $\{\mathbf{n}, \boldsymbol{\delta}, \nabla\boldsymbol{\delta}\}$ by $\{\mathbf{Q}\mathbf{n}, \mathbf{Q}\boldsymbol{\delta}, \mathbf{Q}(\nabla\boldsymbol{\delta})\mathbf{Q}^t\}$ in which $\mathbf{Q}$ is an arbitrary rotation. The structure of such functions is well

known, but the general expression is not needed here. Instead, for illustrative purposes we limit attention to the simplest case in which

$$\nabla\boldsymbol{\delta}\cdot\mathbf{K}[\nabla\boldsymbol{\delta}]=k|\nabla\boldsymbol{\delta}|^2, \tag{2.4}$$

where k is a positive constant. This expression is Galilean invariant as it stands, and so the requirement becomes $D(\mathbf{n},\boldsymbol{\delta})=D(\mathbf{Qn},\mathbf{Q}\boldsymbol{\delta})$, which is satisfied if and only if D depends on its arguments via the combinations $\mathbf{n}\cdot\boldsymbol{\delta}$ and $\boldsymbol{\delta}\cdot\boldsymbol{\delta}$. This fact suggests the orthogonal decomposition

$$\boldsymbol{\delta}=\boldsymbol{\phi}+d\mathbf{n},\quad \text{where } \boldsymbol{\phi}=(\mathbf{I}-\mathbf{n}\otimes\mathbf{n})\boldsymbol{\delta} \tag{2.5}$$

is the projection of the director onto the local tangent plane to ω. Here, $\mathbf{I}$ is the conventional tensor identity for the enveloping 3-space. The lipids of the membrane are said to be *tilted* wherever $\boldsymbol{\phi}$ is non-zero. The invariance requirement then yields the conclusion that $D(\mathbf{n},\boldsymbol{\delta})$ is determined by $\mathbf{n}\cdot\boldsymbol{\delta}$ and $\boldsymbol{\phi}\cdot\boldsymbol{\phi}$. Accordingly, we study energies of the form

$$W=\tfrac{1}{2}k|\nabla\boldsymbol{\delta}|^2+G(\xi,d),\quad \text{where } \xi=\sqrt{\boldsymbol{\phi}\cdot\boldsymbol{\phi}}. \tag{2.6}$$

We are well aware of the fact that the gradient term in this energy is too simple to furnish a complete model for tilted membranes. The general theory, which is rather complicated, is discussed in detail in Steigmann [14], where its relationship to three-dimensional liquid crystal theory is emphasized. However, the present model suffices to reveal the basic structure of the theory, and to address the specific examples considered later.

Remark. This energy subsumes a special case of the classical Canham–Helfrich energy for lipid bilayers without tilt. In that case ξ vanishes, d is a fixed constant and $W=\frac{1}{2}kd|\mathbf{b}|^2$, where $\mathbf{b}=-\nabla\mathbf{n}$ is the surface curvature. An application of the Cayley–Hamilton theorem then furnishes $W=kd(2H^2-K)$, where $H=\frac{1}{2}trace\mathbf{b}$ is the mean curvature of ω and $K=\det\mathbf{b}$ is the Gaussian curvature. In the general Canham–Helfrich theory, the energy is of the form $W=k_1H^2+k_2K$, and so the specialization of the present model yields $2k_2=-k_1$. This is not restrictive for closed membranes of prescribed genus; for, as is well known, the modulus k_2 is then irrelevant. For surfaces with boundary, k_2 is relevant if the boundary has non-vanishing geodesic curvature. However, established necessary conditions pertaining to energy minimization, while requiring $k_1>0$, do not impose any restrictions on the sign or value of k_2 [22].

3. Equilibrium equations and boundary conditions

Our strategy is to extract the equilibrium equations of the membrane and the relevant boundary conditions from the stationarity of the energy. Following common practice in the study of lipid membranes, we suppose that deformations of the surface are such as to preserve surface area; this is accommodated via a Lagrange-multiplier field. The procedure is outlined elsewhere [14]. Thus,

$$\dot{E}=P, \tag{3.1}$$

where P is the virtual power of the forces acting on the membrane and superposed dots refer to variational derivatives. Here,

$$E=\int_\omega (W+\lambda)\,\mathrm{d}a, \tag{3.2}$$

where λ is a Lagrange multiplier associated with a constraint on surface area; the associated variation is [23]

$$\dot{E}=\int_\omega\left[\dot{W}+\frac{(W+\lambda)\dot{J}}{J}\right]\mathrm{d}a, \tag{3.3}$$

where J is the surface dilation, and [24]

$$\frac{\dot{J}}{J}=\operatorname{div}\mathbf{u}=\mathbf{a}^\alpha\cdot\dot{\mathbf{a}}_\alpha, \tag{3.4}$$

where $\dot{\mathbf{a}}_\alpha = \mathbf{u}_{,\alpha}$ and $\mathbf{u} = \dot{\mathbf{r}}$ is the variation of the position field. Here and elsewhere subscripts preceded by commas refer to partial derivatives with respect to the θ^α. These variations are associated with fixed material points. The latter are identified once and for all with the fixed labels θ^α; that is, the coordinates are regarded as being convected with the material points constituting the surface. We note that in (3.3) we have not made the variation of λ explicit, because the associated Euler equation simply returns the areal incompressibility constraint ($J = 1$).

The variation of the areal energy density is

$$\dot{W} = \left(\frac{\partial W}{\partial \mathbf{a}_\alpha}\right) \cdot \dot{\mathbf{a}}_\alpha + \left(\frac{\partial W}{\partial \boldsymbol{\delta}}\right) \cdot \dot{\boldsymbol{\delta}} + \left(\frac{\partial W}{\partial \boldsymbol{\delta}_{,\alpha}}\right) \cdot \dot{\boldsymbol{\delta}}_{,\alpha}. \tag{3.5}$$

Here we have used the fact that the list $\{\mathbf{n}, \boldsymbol{\delta}, \nabla\boldsymbol{\delta}\}$—and hence W—is determined by the list $\{\mathbf{a}_\alpha, \boldsymbol{\delta}, \boldsymbol{\delta}_{,\alpha}\}$.

(a) Director variations

These are variations of $\boldsymbol{\delta}$ at fixed $\mathbf{r}$ ($\mathbf{u} = \mathbf{0}$). The relevant Euler–Lagrange equation is

$$\frac{\partial W}{\partial \boldsymbol{\delta}} - \left(\frac{\partial W}{\partial \boldsymbol{\delta}_{,\alpha}}\right)_{;\alpha} = \mathbf{0}, \tag{3.6}$$

where $(\cdot)_{;\alpha}$ is the covariant derivative; this holds in the interior of ω. The natural boundary condition is

$$\mathbf{m} = \frac{\nu_\alpha \partial W}{\partial \boldsymbol{\delta}_{,\alpha}} \tag{3.7}$$

and applies on $\partial\omega_m$, which is the complement with respect to $\partial\omega$ of the part of the boundary where $\boldsymbol{\delta}$ is assigned. Here, $\mathbf{m}$ is the director force density, $\boldsymbol{\nu} = \nu_\alpha \mathbf{a}^\alpha$ is the exterior unit normal to $\partial\omega$ in the sense of Stokes' theorem, and we have assumed the virtual power associated with director variations to be of the form

$$P_\delta = \int_{\partial\omega_m} \mathbf{m} \cdot \dot{\boldsymbol{\delta}}\, \mathrm{d}s. \tag{3.8}$$

(b) Tangential variations

In general, (3.3) must be satisfied for all $\mathbf{u}$; i.e. for all

$$\mathbf{u} = u^\alpha \mathbf{a}_\alpha + u\mathbf{n}, \tag{3.9}$$

where u^α and u, respectively, are the tangential and normal variations. We obtain the consequences of this requirement for tangential variations in the present section, and for normal variations in the next.

For tangential variations, we have

$$\dot{\mathbf{a}}_\alpha = u^\beta_{;\alpha} \mathbf{a}_\beta + u^\beta b_{\beta\alpha} \mathbf{n}, \tag{3.10}$$

where $b_{a\beta} = \mathbf{n} \cdot \mathbf{r}_{,\alpha\beta}$ are the curvature coefficients on ω. Then,

$$\frac{\dot{J}}{J} = u^\alpha_{;\alpha} \tag{3.11}$$

and

$$\frac{(W + \lambda)\dot{J}}{J} = [(W + \lambda)u^\alpha]_{;\alpha} - u^\alpha (W + \lambda)_{,\alpha}. \tag{3.12}$$

For tangential variations at fixed $\boldsymbol{\delta}$, (3.5) reduces to

$$\dot{W} = \left(\mathbf{a}_\beta \cdot \frac{\partial W}{\partial \mathbf{a}_\alpha}\right) u^\beta{}_{;\alpha} + b_{\beta\alpha}\mathbf{n} \cdot \left(\frac{\partial W}{\partial \mathbf{a}_\alpha}\right) u^\beta. \tag{3.13}$$

We conclude from (3.1) that the relevant Euler–Lagrange equations, holding in the interior of ω, are

$$(W+\lambda)_{,\beta}+\left(\mathbf{a}_\beta\cdot\frac{\partial W}{\partial\mathbf{a}_\alpha}\right)_{;\alpha}-b_{\beta\alpha}\mathbf{n}\cdot\frac{\partial W}{\partial\mathbf{a}_\alpha}=0. \tag{3.14}$$

Moreover, (3.1) and (3.13) indicate that the associated edge power is of the form

$$P_t=\int_{\partial\omega_f}f_\beta u^\beta\,\mathrm{d}a, \tag{3.15}$$

where f_β is the covariant tangential force density, and where $\partial\omega_f$ is the complement with respect to $\partial\omega$ of the part of the boundary where position is assigned. Then,

$$f_\beta=\left[(W+\lambda)\delta^\alpha_\beta+\mathbf{a}_\beta\cdot\frac{\partial W}{\partial\mathbf{a}_\alpha}\right]\nu_\alpha\quad\text{on }\partial\omega_f, \tag{3.16}$$

where δ^α_β is the Kronecker delta.

(c) Normal variations

In this case, $\mathbf{u}=u\mathbf{n}$ and

$$\dot{\mathbf{a}}_\alpha=u_{,\alpha}\mathbf{n}-ub_{\alpha\beta}\mathbf{a}^\beta, \tag{3.17}$$

yielding

$$\frac{\dot J}{J}=-2Hu, \tag{3.18}$$

where $H=\frac{1}{2}b_{\alpha\beta}a^{\alpha\beta}$ is the mean curvature of ω. Then,

$$\frac{(W+\lambda)\dot J}{J}=-2H(W+\lambda)u \tag{3.19}$$

in place of (3.12), whereas

$$\left(\frac{\partial W}{\partial\mathbf{a}_\alpha}\right)\cdot\dot{\mathbf{a}}_\alpha=\left(\mathbf{n}\cdot\frac{\partial W}{\partial\mathbf{a}_\alpha}\right)u_{,\alpha}-ub_{\alpha\beta}\mathbf{a}^\beta\cdot\frac{\partial W}{\partial\mathbf{a}_\alpha}. \tag{3.20}$$

The relevant Euler–Lagrange equation, holding in the interior of ω, is

$$2H(W+\lambda)+\left(\mathbf{n}\cdot\frac{\partial W}{\partial\mathbf{a}_\alpha}\right)_{;\alpha}+b_{\alpha\beta}\mathbf{a}^\beta\cdot\frac{\partial W}{\partial\mathbf{a}_\alpha}+p=0, \tag{3.21}$$

where p is the net lateral pressure on the membrane in the direction of $\mathbf{n}$, and the associated boundary condition is

$$f=\nu_\alpha\mathbf{n}\cdot\frac{\partial W}{\partial\mathbf{a}_\alpha}\quad\text{on }\partial\omega_f, \tag{3.22}$$

where f is the transverse shear force density on the boundary. Here, we have assumed that the part of the power associated with normal variations has the form

$$P_n=\int_{\partial\omega_f}fu\,\mathrm{d}s+\int_\omega pu\,\mathrm{d}a. \tag{3.23}$$

The net power from all sources is

$$P=P_\delta+P_t+P_n. \tag{3.24}$$

(d) Specialization

The foregoing equilibrium equations and boundary conditions apply to all energies that are determined by the list $\{\mathbf{a}_\alpha,\boldsymbol{\delta},\boldsymbol{\delta}_{,\alpha}\}$. We specialize them to the particular energy defined by (2.6).

To proceed we write $|\nabla\boldsymbol{\delta}|^2 = a^{\alpha\beta}\boldsymbol{\delta}_{,\alpha}\cdot\boldsymbol{\delta}_{,\beta}$ and derive

$$\dot{W} = ka^{\beta\alpha}\boldsymbol{\delta}_{,\beta}\cdot\dot{\boldsymbol{\delta}}_{,\alpha} + \tfrac{1}{2}k\dot{a}^{\alpha\beta}\boldsymbol{\delta}_{,\alpha}\cdot\boldsymbol{\delta}_{,\beta} + G_\xi\dot{\xi} + G_d\dot{d}. \tag{3.25}$$

For example,

$$\dot{d} = \mathbf{n}\cdot\dot{\boldsymbol{\delta}} + \boldsymbol{\delta}\cdot\dot{\mathbf{n}}, \tag{3.26}$$

in which $\dot{\mathbf{n}}$ is determined by $\dot{\mathbf{a}}_\alpha$, as demonstrated below. Accordingly, the relevant contribution to $\partial W/\partial\boldsymbol{\delta}$ is $G_d\mathbf{n}$. In the same way,

$$\xi\dot{\xi} = \boldsymbol{\phi}\cdot\dot{\boldsymbol{\phi}}, \quad \text{with } \dot{\boldsymbol{\phi}} = (\mathbf{I}-\mathbf{n}\otimes\mathbf{n})\dot{\boldsymbol{\delta}} - (\mathbf{n}\otimes\mathbf{n})^{\cdot}\boldsymbol{\delta}, \tag{3.27}$$

where

$$(\mathbf{n}\otimes\mathbf{n})^{\cdot}\boldsymbol{\delta} = d\dot{\mathbf{n}} + (\boldsymbol{\delta}\cdot\dot{\mathbf{n}})\mathbf{n}. \tag{3.28}$$

Thus,

$$\xi\dot{\xi} = \boldsymbol{\phi}\cdot\dot{\boldsymbol{\delta}} - d\boldsymbol{\phi}\cdot\dot{\mathbf{n}}, \tag{3.29}$$

and the relevant contribution to $\partial W/\partial\boldsymbol{\delta}$ is $\xi^{-1}G_\xi\boldsymbol{\phi}$. Altogether,

$$\frac{\partial W}{\partial\boldsymbol{\delta}} = \xi^{-1}G_\xi\boldsymbol{\phi} + G_d\mathbf{n}. \tag{3.30}$$

The computation of $\partial W/\partial\boldsymbol{\delta}_{,\alpha}$ proceeds easily from (3.5) and (3.25); thus,

$$\frac{\partial W}{\partial\boldsymbol{\delta}_{,\alpha}} = ka^{\beta\alpha}\boldsymbol{\delta}_{,\beta}. \tag{3.31}$$

This yields

$$\left(\frac{\partial W}{\partial\boldsymbol{\delta}_{,\alpha}}\right)_{;\alpha} = ka^{\beta\alpha}\boldsymbol{\delta}_{;\beta\alpha}, \tag{3.32}$$

where

$$\boldsymbol{\delta}_{;\beta\alpha} = \boldsymbol{\delta}_{,\beta\alpha} - \Gamma^\lambda_{\beta\alpha}\boldsymbol{\delta}_{,\lambda} \tag{3.33}$$

in which $\Gamma^\lambda_{\beta\alpha}$ are the Christoffel symbols on ω [17].

The computation of $\partial W/\partial\mathbf{a}_\alpha$ involves variations $\dot{\mathbf{a}}_\alpha$ at fixed $\boldsymbol{\delta}$ and $\boldsymbol{\delta}_{,\alpha}$. A contribution arises from the second term in (3.25). To obtain it, we differentiate $a^{\alpha\gamma}a_{\gamma\beta} = \delta^\alpha_\beta$, obtaining

$$\dot{a}^{\alpha\beta} = -a^{\alpha\gamma}a^{\beta\lambda}\dot{a}_{\gamma\lambda}, \quad \text{where } \dot{a}_{\gamma\lambda} = \mathbf{a}_\gamma\cdot\mathbf{u}_{,\lambda} + \mathbf{a}_\lambda\cdot\mathbf{u}_{,\gamma}. \tag{3.34}$$

For example, tangential variations yield

$$\dot{a}^{\alpha\beta} = -a^{\beta\lambda}u^\alpha_{;\lambda} - a^{\alpha\lambda}u^\beta_{;\lambda}, \tag{3.35}$$

and it follows that

$$\tfrac{1}{2}\dot{a}^{\alpha\beta}\boldsymbol{\delta}_{,\alpha}\cdot\boldsymbol{\delta}_{,\beta} = -\boldsymbol{\delta}_{,\beta}\cdot\boldsymbol{\delta}_{,\lambda}a^{\lambda\alpha}u^\beta_{;\alpha}. \tag{3.36}$$

We also have (see equation (A 5) in appendix A)

$$\dot{\mathbf{n}} = -\mathbf{a}^\beta b_{\alpha\beta}u^\alpha. \tag{3.37}$$

Therefore,

$$\dot{d} = \boldsymbol{\delta}\cdot\dot{\mathbf{n}} = -\phi^\beta b_{\alpha\beta}u^\alpha \quad \text{and} \quad \xi\dot{\xi} = -d\boldsymbol{\phi}\cdot\dot{\mathbf{n}} = d\phi^\beta b_{\alpha\beta u^\alpha}. \tag{3.38}$$

Comparison with (3.13) furnishes

$$\mathbf{a}_\beta\cdot\frac{\partial W}{\partial\mathbf{a}_\alpha} = -k\boldsymbol{\delta}_{,\beta}\cdot\boldsymbol{\delta}_{,\lambda}a^{\lambda\alpha} \quad \text{and} \quad b_{\beta\alpha}\mathbf{n}\cdot\frac{\partial W}{\partial\mathbf{a}_\alpha} = (d\xi^{-1}G_\xi - G_d)\phi^\alpha b_{\beta\alpha}. \tag{3.39}$$

Under normal variations, we have (see equation (A 6) in appendix A)

$$\dot{\mathbf{n}} = -\nabla u = -\mathbf{a}^\alpha u_{,\alpha}. \tag{3.40}$$

Then,

$$\dot{d} = \boldsymbol{\delta}\cdot\dot{\mathbf{n}} = -\phi^\alpha u_{,\alpha} \quad \text{and} \quad \xi\dot{\xi} = -d\boldsymbol{\phi}\cdot\dot{\mathbf{n}} = d\phi^\alpha u_{,\alpha}. \tag{3.41}$$

Further, from (3.34),

$$\dot{a}^{\alpha\beta} = 2ub^{\alpha\beta}. \tag{3.42}$$

Comparison with (3.13) then yields

$$b_{\alpha\beta}\mathbf{a}^{\beta} \cdot \frac{\partial W}{\partial \mathbf{a}_{\alpha}} = -kb^{\alpha\beta}\boldsymbol{\delta}_{,\alpha} \cdot \boldsymbol{\delta}_{,\beta}, \tag{3.43}$$

which is consistent with $(3.39)_1$, and

$$\mathbf{n} \cdot \frac{\partial W}{\partial \mathbf{a}_{\alpha}} = (d\xi^{-1}G_{\xi} - G_d)\phi^{\alpha}, \tag{3.44}$$

which is consistent with $(3.39)_2$.

(e) Summary

Substitution of the foregoing results in the general equations (3.6), (3.14) and (3.21) delivers the final differential equations for the model thus far:

$$ka^{\beta\alpha}\boldsymbol{\delta}_{;\beta\alpha} = \xi^{-1}G_{\xi}\boldsymbol{\phi} + G_d\mathbf{n}, \tag{3.45}$$

$$(W+\lambda)_{,\beta} = ka^{\lambda\alpha}(\boldsymbol{\delta}_{,\beta} \cdot \boldsymbol{\delta}_{,\lambda})_{;\alpha} + (d\xi^{-1}G_{\xi} - G_d)\phi^{\alpha}b_{\beta\alpha} \tag{3.46}$$

and

$$2H(W+\lambda) + [(\mathrm{d}\xi^{-1}G_{\xi} - G_d)\phi^{\alpha}]_{;\alpha} - kb^{\alpha\beta}\boldsymbol{\delta}_{,\alpha} \cdot \boldsymbol{\delta}_{,\beta} + p = 0. \tag{3.47}$$

The natural boundary conditions are (3.7), (3.16) and (3.22), which reduce to

$$\mathbf{m} = k\nu^{\alpha}\boldsymbol{\delta}_{,\alpha}, \quad f_{\beta} = (W+\lambda)\nu_{\beta} - k\boldsymbol{\delta}_{,\beta} \cdot \boldsymbol{\delta}_{,\alpha}\boldsymbol{\nu}^{\alpha} \quad \text{and} \quad f = (\mathrm{d}\xi^{-1}G_{\xi} - G_d)\nu_{\alpha}\phi^{\alpha}. \tag{3.48}$$

4. Constrained distension

Most treatments of lipid systems presume lipid length to be fixed and independent of membrane deformation. In the present framework based on descent from three-dimensional liquid crystal theory, this is consistent with the widespread assumption that the directors associated with liquid crystal orientation are also fixed in length [15,20,25]. In this section, we consider the adjustments to the foregoing model required to accommodate this condition.

The constraint on lipid length is

$$|\boldsymbol{\delta}| = t, \tag{4.1}$$

where t is a fixed constant. Thus, from (2.5) and $\xi = |\boldsymbol{\phi}|$,

$$\boldsymbol{\delta} = \boldsymbol{\phi} + d\mathbf{n}, \quad \text{where } \xi = \sqrt{t^2 - d^2}. \tag{4.2}$$

Accordingly, the areal energy density is given by (2.6), in which

$$G(\xi, d) = F(d), \quad \text{where } F(d) = G(\sqrt{t^2 - d^2}, d). \tag{4.3}$$

Of course the energy density W also depends on $\nabla\boldsymbol{\delta}$. Because it is defined pointwise, and because $\boldsymbol{\delta}$ and $\nabla\boldsymbol{\delta}$ may be specified independently at a point on ω, it is necessary to account for the constraint on $\nabla\boldsymbol{\delta}$ induced by (4.1) when deriving the equilibrium equations from stationarity of the energy. This further constraint may be expressed in the form

$$\boldsymbol{\delta} \cdot \boldsymbol{\delta}_{,\alpha} = 0. \tag{4.4}$$

It is easily verified that (4.1) and (4.4) are automatically satisfied by (4.2). However, it is convenient to adopt an extended variational formulation in which the constraints are relaxed. In this formulation, we do not impose (4.2), but instead consider the auxiliary energy

$$E^* = \int_{\omega} (W+\lambda)\,\mathrm{d}a + \int_{\Omega} \left[\bar{\mu}^{\alpha}\boldsymbol{\delta} \cdot \boldsymbol{\delta}_{,\alpha} + \frac{1}{2}\bar{\mu}(\boldsymbol{\delta} \cdot \boldsymbol{\delta} - t^2)\right] \mathrm{d}A, \tag{4.5}$$

where W is given by (2.6) with ξ and d regarded as being independent; where $\bar{\mu}^{\alpha}$ and $\bar{\mu}$ are Lagrange-multiplier fields; and where Ω is a fixed reference surface, with $da = JdA$. This

expression reduces to the actual energy when the constraints (4.1) and (4.4) are operative and is well defined when they are not; it therefore furnishes an extension of the actual energy from configurations that satisfy the constraint to arbitrary configurations. Stationarity with respect to the multipliers simply returns the constraints as the relevant Euler–Lagrange equations. Moreover, stationarity of E^* with respect to unconstrained variations implies stationarity with respect to constrained variations in particular, and hence stationarity of the actual energy. We use this observation to derive equilibrium equations for the actual constrained system. This has already been exploited in §3 in connection with the constraint of areal incompressibility. We note that while the replacement of E by E^* is permissible for the purpose of extracting stationarity (i.e. equilibrium) conditions, it may not be used to extract further necessary conditions for energy *minimizers* in the absence of external power. This follows simply from relaxation of constraints, yielding: $\inf E^* \leq \inf E$.

Proceeding, we have

$$\dot{E}^* = P, \tag{4.6}$$

where

$$\dot{E}^* = \int_\omega \left[\dot{W} + \frac{(W+\lambda)\dot{J}}{J} + \mu^\alpha(\boldsymbol{\delta}\cdot\boldsymbol{\delta}_{,\alpha} + \boldsymbol{\delta}\cdot\dot{\boldsymbol{\delta}}_{,\alpha}) + \mu\boldsymbol{\delta}\cdot\dot{\boldsymbol{\delta}} \right] \mathrm{d}a, \tag{4.7}$$

where $\mu^\alpha = J^{-1}\bar{\mu}^\alpha$, $\mu = J^{-1}\bar{\mu}$, and it is understood, having suppressed the variations of the multipliers, that all terms in this expression are to be evaluated, *post facto*, at states satisfying (4.1) and (4.4).

The procedure for deriving equilibrium equations is exactly as in §3, and now yields

$$\frac{\partial W}{\partial \boldsymbol{\delta}} + \mu\boldsymbol{\delta} - \left(\frac{\partial W}{\partial \boldsymbol{\delta}_{,\alpha}}\right)_{;\alpha} - \mu^\alpha_{;\alpha}\boldsymbol{\delta} = \mathbf{0}, \tag{4.8}$$

in place of (3.6), together with

$$\mathbf{m} = \nu_\alpha \left(\frac{\partial W}{\partial \boldsymbol{\delta}_{,\alpha}} + \mu^\alpha \boldsymbol{\delta} \right), \tag{4.9}$$

in place of (3.7). All remaining equations and boundary conditions in §3 are unaffected.

For the particular energy considered here (cf. (2.6)), equations (4.8) and (4.9) reduce to

$$k a^{\beta\alpha}\boldsymbol{\delta}_{;\beta\alpha} + \mu^\alpha_{;\alpha}\boldsymbol{\delta} = (\xi^{-1}G_\xi + \mu)\boldsymbol{\phi} + (G_d + \mu d)\mathbf{n} \tag{4.10}$$

and

$$\mathbf{m} = k\nu^\alpha \boldsymbol{\delta}_{,\alpha} + \nu_\alpha \mu^\alpha \boldsymbol{\delta}. \tag{4.11}$$

To effect a further reduction, we recall that all terms in these equations are associated with stationary states, and hence with states that satisfy (4.2) in particular. To exploit this, we invoke (4.3) for a one-parameter family of such states, parametrized by a variable u, say. Differentiating with respect to u yields

$$F'(d)\dot{d} = G_\xi \dot{\xi} + G_d \dot{d}. \tag{4.12}$$

Here the vector $(\dot{\xi}, \dot{d})$ is not arbitrary; rather, it is tangential to the curve $(\xi(d), d)$ defined by $(4.2)_2$. Thus, $(\dot{\xi}, \dot{d}) = (-d\xi^{-1}, 1)$, where we have adopted the parameter $u = d$ without sacrificing generality. Any vector orthogonal to this is representable in the form $a(1, d\xi^{-1})$, where a is a real number. It follows that (4.12) is unaffected if the vector (G_ξ, G_d), in which $G(\xi, d)$ is an arbitrary extension of $F(d)$ from the constraint curve, is replaced by $(G_\xi, G_d) + a(1, d\xi^{-1})$, yielding

$$(G_\xi + a)\xi'(d) + G_d + ad\xi^{-1} - F'(d) = 0, \tag{4.13}$$

where $a \in \mathbb{R}$ is arbitrary. In effect, a is a Lagrange multiplier. Because the extension $G(\xi, d)$ is arbitrary, we may choose it such that $G_\xi + a = 0$ without restricting a, which then remains at our

disposal. Identifying the latter with $\xi\mu$ and invoking $(4.2)_2$, we reduce the right-hand side of (4.10) to

$$(\xi^{-1}G_\xi + \mu)\boldsymbol{\phi} + (G_d + \mu d)\mathbf{n} = F'(d)\mathbf{n}. \tag{4.14}$$

We thus reach the final system of differential equations (cf. (3.45)–(3.48)), consisting of

$$ka^{\beta\alpha}\boldsymbol{\delta}_{,\beta\alpha} + \psi\boldsymbol{\delta} = F'(d)\mathbf{n}, \quad \text{where } \psi = \mu^\alpha_{,\alpha}, \tag{4.15}$$

together with

$$(W+\lambda)_{,\beta} = ka^{\lambda\alpha}(\boldsymbol{\delta}_{,\beta}\cdot\boldsymbol{\delta}_{,\lambda})_{;\alpha} - F'(d)\phi^\alpha b_{\beta\alpha} \tag{4.16}$$

and

$$2H(W+\lambda) - [F'(d)\phi^\alpha]_{;\alpha} - kb^{\alpha\beta}\boldsymbol{\delta}_{,\alpha}\cdot\boldsymbol{\delta}_{,\beta} + p = 0, \tag{4.17}$$

in which $d = \boldsymbol{\delta}\cdot\mathbf{n}$ and $\phi^\alpha = \boldsymbol{\delta}\cdot\mathbf{a}^\alpha$. These are subject to the constraint

$$a_{\alpha\beta}\phi^\alpha\phi^\beta = t^2 - d^2. \tag{4.18}$$

The system is closed by appending the two constraints contained in (4.4), and the natural boundary conditions are

$$\mathbf{m} = k\nu^\alpha\boldsymbol{\delta}_{,\alpha} + \nu_\alpha\mu^\alpha\boldsymbol{\delta}, \quad f_\beta = (W+\lambda)\nu_\beta - k\boldsymbol{\delta}_{,\beta}\cdot\boldsymbol{\delta}_{,\alpha}\nu^\alpha \quad \text{and} \quad f = -F'(d)\nu_\alpha\phi^\alpha. \tag{4.19}$$

We remark that precisely the same system is derived on identifying the extended energy with $F(d)$ and using the auxiliary energy functional

$$E^{**} = \int_\omega (W + \lambda + \mu^\alpha\boldsymbol{\delta}\cdot\boldsymbol{\delta}_{,\alpha})\,\mathrm{d}a \tag{4.20}$$

in place of (4.5). In this case, d is subject only to the restriction $d^2 < t^2$ and does not carry a Lagrange multiplier.

Equations (4.15)–(4.17) comprise a nonlinear system coupling the director field and membrane shape. Nevertheless, it is possible to identify some simple solutions. To this end, we specialize the theory further by normalizing the areal energy density such that it vanishes when $\boldsymbol{\delta}(\theta^\alpha)$ is a constant vector, $\boldsymbol{\delta}_0$ say, with $|\boldsymbol{\delta}_0| = t$, and when d is fixed at a value d_0, say, with $0 < d_0^2 \le t^2$; then, $F(d_0) = 0$. At this state, the equilibrium equations reduce to

$$\psi\boldsymbol{\delta}_0 = F'(d_0)\mathbf{n}, \quad \lambda_{,\beta} = -F'(d_0)\phi^\alpha b_{\beta\alpha} \quad \text{and} \quad 2H\lambda - [F'(d_0)\phi^\alpha]_{;\alpha} + p = 0, \tag{4.21}$$

where

$$\boldsymbol{\phi} = \boldsymbol{\delta}_0 - d_0\mathbf{n}. \tag{4.22}$$

The first equation yields $\psi\boldsymbol{\delta}_0\cdot\mathbf{n} = F'(d_0)$ and hence $\psi = d_0^{-1}F'(d_0)$, a constant. Further, because $d_0 = \mathbf{n}\cdot\boldsymbol{\delta}_0$ is constant, we have $\nabla d_0 = \mathbf{0}$, and thus $(\nabla\mathbf{n})^t\boldsymbol{\delta}_0 = \mathbf{0}$, which is equivalent to

$$\mathbf{b}\boldsymbol{\phi} = \mathbf{0}, \tag{4.23}$$

where $\mathbf{b}$ is the curvature tensor. Then, it follows from $(4.21)_2$ that $\lambda = \text{const}$. Combining these results with $\phi^\alpha = \mathbf{a}^\alpha\cdot\boldsymbol{\delta}_0$ and the Gauss equation $\mathbf{a}^\alpha_{,\alpha} = 2H\mathbf{n}$, we find that $(4.21)_3$ reduces to the classical capillarity equation

$$2H\lambda_0 + p = 0, \tag{4.24}$$

where $\lambda_0 = \lambda - d_0\psi$ plays the role of the surface tension, except that here its sign is unrestricted. The only remaining restrictions are those implied by (4.23). There are two possibilities: (i) the tilt vanishes ($\boldsymbol{\phi} = \mathbf{0}$), which requires that $d_0 = t$ and $\boldsymbol{\delta}_0 = t\mathbf{n}$; then $\mathbf{n}$ is constant, the surface is a plane and $(4.21)_3$ requires that $p = 0$; (ii) the tilt is non-vanishing ($\boldsymbol{\phi} \neq \mathbf{0}$) and the Gaussian curvature $K(= \det\mathbf{b})$ vanishes. The surface is then either plane or developable onto a plane, with the pressure again vanishing and the tilt $\boldsymbol{\phi}$ being uniform in the former case. These solutions remain valid when $F'(d_0) = 0$, which we assume henceforth, the only effect of this being that ψ then vanishes.

Naturally, these solutions pertain to the assumed form of the gradient term in the areal energy density. Alternative solutions exhibiting tilt, including the so-called ribbon phases, have been derived using different forms [26,27].

5. Linearization

(a) Linearization of the equilibrium equations

Having shown that plane surfaces with uniform tilt yield equilibria under zero pressure, we proceed to linearize the theory about such states for the purpose of deriving a tractable system for the description of variable tilt. We continue the use of the superposed dot notation; here, for the purpose of identifying small departures of various functions from equilibrium values satisfying the nonlinear equations. The latter values are called *base states*. Thus, if f is a base state, then we linearize the equations satisfied by the perturbation $f+\dot{f}$, assuming that $\dot{f}$ and its gradients are sufficiently small—after suitable non-dimensionalization—to justify the suppression of all nonlinear terms.

For example, the linearization of (4.15) is

$$k[\dot{a}^{\beta\alpha}\boldsymbol{\delta}_{;\beta\alpha}+a^{\beta\alpha}(\boldsymbol{\delta}_{;\beta\alpha})^{\cdot}]+\dot{\psi}\boldsymbol{\delta}+\psi\dot{\boldsymbol{\delta}}=F'(d)\dot{\mathbf{n}}+F''(d)\dot{d}\mathbf{n}, \tag{5.1}$$

where (cf. (3.33))

$$(\boldsymbol{\delta}_{;\beta\alpha})^{\cdot}=\dot{\boldsymbol{\delta}}_{,\beta\alpha}-\dot{\Gamma}^{\lambda}_{\beta\alpha}\boldsymbol{\delta}_{,\lambda}-\Gamma^{\lambda}_{\beta\alpha}\dot{\boldsymbol{\delta}}_{,\lambda}.$$

Adopting the base states $\boldsymbol{\delta}=\boldsymbol{\delta}_0$ and $\psi=0$ associated with $F'(d_0)=0$ yields the simplifications

$$(\boldsymbol{\delta}_{;\beta\alpha})^{\cdot}=\dot{\boldsymbol{\delta}}_{,\beta\alpha}-\Gamma^{\lambda}_{\beta\alpha}\dot{\boldsymbol{\delta}}_{,\lambda}=\dot{\boldsymbol{\delta}}_{;\beta\alpha} \tag{5.2}$$

and

$$k\Delta\dot{\boldsymbol{\delta}}+\dot{\psi}\boldsymbol{\delta}_0=F''(d_0)\dot{d}\mathbf{n}, \tag{5.3}$$

where $\Delta(\cdot)=a^{\beta\alpha}(\cdot)_{;\beta\alpha}$ is the Laplacian operator on the plane.

Proceeding in the same way, we find the linearization of (4.16) to be

$$\begin{aligned}(\dot{W}+\dot{\lambda})_{,\beta}=k\{&\dot{a}^{\lambda\alpha}(\boldsymbol{\delta}_{,\beta}\cdot\boldsymbol{\delta}_{,\lambda})_{;\alpha}+a^{\lambda\alpha}[(\boldsymbol{\delta}_{,\beta}\cdot\boldsymbol{\delta}_{,\lambda})_{;\alpha}]^{\cdot}\}\\&-F'(d)(\dot{\phi}^{\alpha}b_{\beta\alpha}+\phi^{\alpha}\dot{b}_{\beta\alpha})-F''(d)\dot{d}\phi^{\alpha}b_{\beta\alpha},\end{aligned} \tag{5.4}$$

where

$$\dot{W}=ka^{\beta\alpha}\boldsymbol{\delta}_{,\beta}\cdot\dot{\boldsymbol{\delta}}_{,\alpha}+\tfrac{1}{2}k\dot{a}^{\alpha\beta}\boldsymbol{\delta}_{,\alpha}\cdot\boldsymbol{\delta}_{,\beta}+F'(d)\dot{d}. \tag{5.5}$$

Assuming the same base state yields $\dot{W}=0$, and if the base surface is a plane, (5.4) reduces to $\dot{\lambda}_{,\beta}=ka^{\lambda\alpha}(\boldsymbol{\delta}_{,\beta}\cdot\boldsymbol{\delta}_{,\lambda})^{\cdot}_{;\alpha}$, where $(\boldsymbol{\delta}_{,\beta}\cdot\boldsymbol{\delta}_{,\lambda})^{\cdot}=\boldsymbol{\delta}_{0,\beta}\cdot\dot{\boldsymbol{\delta}}_{,\lambda}+\dot{\boldsymbol{\delta}}_{,\beta}\cdot\boldsymbol{\delta}_{0,\lambda}$. This vanishes, yielding the substantial simplification

$$\nabla\dot{\lambda}=0. \tag{5.6}$$

Accordingly, $\dot{\lambda}=\text{const}$.

Finally, the linearization of (4.17) is

$$\begin{aligned}&2[\dot{H}(W+\lambda)+H(\dot{W}+\dot{\lambda})]-F''(d)\phi^{\alpha}\dot{d}_{,\alpha}-F'(d)(\phi^{\alpha}_{;\alpha})^{\cdot}\\&-k\dot{b}^{\alpha\beta}\boldsymbol{\delta}_{,\alpha}\cdot\boldsymbol{\delta}_{,\beta}-kb^{\alpha\beta}(\boldsymbol{\delta}_{,\alpha}\cdot\boldsymbol{\delta}_{,\beta})^{\cdot}+\dot{p}=0.\end{aligned} \tag{5.7}$$

Once again we specialize to the same base state on a planar surface, obtaining

$$2\dot{H}\lambda+\dot{p}=F''(d_0)\boldsymbol{\phi}_0\cdot\nabla\dot{d}, \tag{5.8}$$

where $\boldsymbol{\phi}_0=\boldsymbol{\delta}_0-d_0\mathbf{n}$, with $\mathbf{n}$ constant, is the base tilt vector. Here $\dot{H}$ is the linearized mean curvature, which can be represented in terms of the Laplacian of the small transverse deflection of the membrane (see [23]).

To close this system, we append the linearizations of the constraint equations (4.1) and (4.4); namely, $\boldsymbol{\delta}\cdot\dot{\boldsymbol{\delta}}=0$ and $\boldsymbol{\delta}_{,\alpha}\cdot\dot{\boldsymbol{\delta}}+\boldsymbol{\delta}\cdot\dot{\boldsymbol{\delta}}_{,\alpha}=0$. When applied to the aforementioned base state, these reduce to $\boldsymbol{\delta}_0\cdot\dot{\boldsymbol{\delta}}=0$ and $(\boldsymbol{\delta}_0\cdot\dot{\boldsymbol{\delta}})_{,\alpha}=0$, respectively, the second of these being redundant. With

$\dot{\boldsymbol{\delta}} = \dot{\boldsymbol{\phi}} + \dot{d}\mathbf{n} + d\dot{\mathbf{n}}$ and $(\boldsymbol{\phi}\cdot\mathbf{n})^{\cdot}$ vanishing identically, we arrive at the constraint

$$\boldsymbol{\phi}_0\cdot\dot{\boldsymbol{\phi}} + d_0\dot{d} = 0, \tag{5.9}$$

which implies that $\dot{d}$ can be non-zero only if the base-state tilt $\boldsymbol{\phi}_0$ is non-zero.

(b) Example

A particularly tractable system that isolates tilt emerges if the membrane remains flat in the course of the perturbation. Then, $\dot{\mathbf{n}} = \mathbf{0}$, $\dot{H} = 0$ and, imposing $\dot{p} = 0$, we find that (5.8) simplifies to

$$F''(d_0)\boldsymbol{\phi}_0\cdot\nabla\dot{d} = 0, \tag{5.10}$$

which combines with (5.3) to yield a system for $\dot{\boldsymbol{\delta}}$ and $\dot{\psi}$. Using

$$\dot{\boldsymbol{\delta}} = \dot{\boldsymbol{\phi}} + \dot{d}\mathbf{n}, \quad \text{with } \mathbf{n}\cdot\dot{\boldsymbol{\phi}} = 0 \tag{5.11}$$

in this case, the latter is seen to be equivalent to the system

$$k\Delta\dot{\boldsymbol{\phi}} + \dot{\psi}\boldsymbol{\phi}_0 = \mathbf{0}, \quad k\Delta\dot{d} + \dot{\psi}d_0 = F''(d_0)\dot{d}. \tag{5.12}$$

To treat this system, we first project $(5.12)_1$ onto $\boldsymbol{\phi}_0$. Combining the resulting equation with (5.9), we reach

$$\dot{\psi} = k\left(\frac{d_0}{|\boldsymbol{\phi}_0|^2}\right)\Delta\dot{d}, \tag{5.13}$$

which is substituted into $(5.12)_2$ to obtain the Helmholtz equation

$$\Delta\dot{d} = \kappa\dot{d}, \quad \text{with } \kappa = k^{-1}F''(d_0)\cos^2\gamma_0, \tag{5.14}$$

where γ_0 is the base-state tilt angle defined by $\tan\gamma_0 = d_0/|\boldsymbol{\phi}_0|$. Invoking (5.10) and assuming that $F''(d_0) \neq 0$, we conclude that $\dot{d}$ has no directional derivative along $\boldsymbol{\phi}_0$. Let x, y be Cartesian coordinates on the plane with the x-axis directed along $\boldsymbol{\phi}_0$; then, $\dot{d}$ is a function of y alone, and (5.14) reduces to the simple ordinary differential equation $\dot{d}''(y) = \kappa\dot{d}(y)$. We solve this on a rectangular strip bounded by the lines $y = \pm l$.

To illustrate, we impose $\dot{d}(\pm l) = D$ with $|D|/d_0 \ll 1$, finding that

$$\dot{d}(y) = D\left[\frac{\exp(\sqrt{\kappa}l) - \exp(-\sqrt{\kappa}l)}{\exp(2\sqrt{\kappa}l) - \exp(-2\sqrt{\kappa}l)}\right][\exp(\sqrt{\kappa}y) - \exp(-\sqrt{\kappa}y)], \quad \text{if } \kappa > 0 \tag{5.15}$$

or

$$\dot{d}(y) = D\frac{\cos(\sqrt{|\kappa|}y)}{\cos(\sqrt{|\kappa|}l)} \quad \text{if } \kappa < 0, \tag{5.16}$$

these corresponding, respectively, to positive and negative values of $F''(d_0)$. In the first alternative, the tilt perturbation is localized in boundary layers near the edges $y = \pm l$; in the second, this field is oscillatory and permeates the entire strip. Both modes have been simulated using coarse-grained molecular dynamics [28–30]. The oscillatory mode corresponds to *ripple phases* that have been detected experimentally [31]. Evidently, these emerge when $F(d)$ possesses a local maximum at d_0. Intuitively, we might therefore expect such phases to be unstable. However, as we show in the next section, the positive-definite gradient term in the energy regularizes the problem, conferring stability in a sense to be described.

It remains only to project $(5.12)_1$ onto the direction $\mathbf{j} = \mathbf{n}\times\mathbf{i}$ perpendicular to $\boldsymbol{\phi}_0$, where $\mathbf{i} = |\boldsymbol{\phi}_0|^{-1}\boldsymbol{\phi}_0$. This yields

$$\Delta\varphi = 0, \tag{5.17}$$

where $\varphi = \mathbf{j}\cdot\dot{\boldsymbol{\phi}}$. Accordingly,

$$\dot{\boldsymbol{\phi}} = \varphi\mathbf{j} - \dot{d}\tan\gamma_0\mathbf{i}, \tag{5.18}$$

where $\varphi(x, y)$ is a harmonic function subject to Dirichlet data or to suitable boundary conditions which may be deduced from the appropriate linearizations of $(3.48)_{1-3}$.

(c) Conditional stability

We have seen that $\dot{W}$, evaluated at the base state, vanishes. Accordingly, because W also vanishes there, the energy density attending small perturbations of the base state is given to leading order by the base-state values of $\frac{1}{2}\ddot{W}$, where, in general (cf. (5.5)),

$$\begin{aligned}\ddot{W} = {} & ka^{\beta\alpha}\dot{\boldsymbol{\delta}}_{,\beta}\cdot\dot{\boldsymbol{\delta}}_{,\alpha} + ka^{\beta\alpha}\boldsymbol{\delta}_{,\beta}\cdot\ddot{\boldsymbol{\delta}}_{,\alpha} + k\dot{a}^{\beta\alpha}\boldsymbol{\delta}_{,\beta}\cdot\dot{\boldsymbol{\delta}}_{,\alpha} \\ & + \tfrac{1}{2}k\ddot{a}^{\alpha\beta}\boldsymbol{\delta}_{,\alpha}\cdot\boldsymbol{\delta}_{,\beta} + k\dot{a}^{\alpha\beta}\boldsymbol{\delta}_{,\alpha}\cdot\dot{\boldsymbol{\delta}}_{,\beta} + F'(d)\ddot{d} + F''(d)\dot{d}^2. \end{aligned} \tag{5.19}$$

Here we use superposed double dots to denote further perturbations of a base-state function, f say, approximating the perturbed function by $f + \dot{f} + \frac{1}{2}\ddot{f}$. Imposing $F'(d_0) = 0$, the base-state value is thus given simply by

$$\ddot{W} = k|\nabla\dot{\boldsymbol{\delta}}|^2 + F''(d_0)\dot{d}^2, \quad \text{where } \nabla\dot{\boldsymbol{\delta}} = \dot{\boldsymbol{\delta}}_{,\alpha}\otimes\mathbf{a}^\alpha. \tag{5.20}$$

In the previous section, we considered a class of problems for which the membrane shape remains unperturbed; i.e. those for which $\dot{\mathbf{n}}$ vanishes. In this case, (5.11) is applicable and yields

$$\nabla\dot{\boldsymbol{\delta}} = \nabla\dot{\boldsymbol{\phi}} + \mathbf{n}\otimes\nabla\dot{d}, \tag{5.21}$$

implying that $|\nabla\dot{\boldsymbol{\delta}}|^2 = |\nabla\dot{\boldsymbol{\phi}}|^2 + |\nabla\dot{d}|^2$. The energy density in such a state is thus given by

$$U(\dot{\boldsymbol{\delta}}) = k(|\nabla\dot{\boldsymbol{\phi}}|^2 + |\nabla\dot{d}|^2) + F''(d_0)\dot{d}^2, \quad \text{with } \mathbf{n}\cdot\dot{\boldsymbol{\phi}} = 0 \quad \text{and} \quad \dot{d} = \mathbf{n}\cdot\dot{\boldsymbol{\delta}}. \tag{5.22}$$

Consider another perturbation of the base state, superposed on $\dot{\boldsymbol{\delta}}$, that leaves the shape unperturbed. We denote this by $\dot{\boldsymbol{\delta}} + \boldsymbol{\delta}^*$, where, as in (5.11),

$$\boldsymbol{\delta}^* = \boldsymbol{\phi}^* + d^*\mathbf{n}, \quad \text{with } \mathbf{n}\cdot\boldsymbol{\phi}^* = 0 \quad \text{and} \quad d^* = \mathbf{n}\cdot\boldsymbol{\delta}^*. \tag{5.23}$$

This associated energy density is

$$U(\dot{\boldsymbol{\delta}} + \boldsymbol{\delta}^*) = U(\dot{\boldsymbol{\delta}}) + U(\boldsymbol{\delta}^*) + 2[k\nabla\boldsymbol{\delta}^*\cdot\nabla\dot{\boldsymbol{\delta}} + F''(d_0)d^*\dot{d}]. \tag{5.24}$$

Because $\dot{\boldsymbol{\delta}} + \boldsymbol{\delta}^*$ is a small perturbation, it satisfies the (linearized) constraint $\boldsymbol{\delta}_0\cdot(\dot{\boldsymbol{\delta}} + \boldsymbol{\delta}^*) = 0$ with $\boldsymbol{\delta}_0\cdot\dot{\boldsymbol{\delta}} = 0$; thus, $\boldsymbol{\delta}_0\cdot\boldsymbol{\delta}^* = 0$.

The solution $\dot{\boldsymbol{\delta}}$ obtained in the previous section, holding in the strip $y\in[-l, l]$, is deemed conditionally stable if it minimizes the energy with respect to arbitrary shape-preserving perturbations $\boldsymbol{\delta}^*$ satisfying the constraint $\boldsymbol{\delta}_0\cdot\boldsymbol{\delta}^* = 0$ that are compactly supported in a region ω_c contained within the strip. In particular, such $\boldsymbol{\delta}^*$ vanish on $\partial\omega_c$ and in the part of the strip exterior to ω_c. The energy difference is thus given by

$$E_{\mathrm{lin}}[\dot{\boldsymbol{\delta}} + \boldsymbol{\delta}^*] - E_{\mathrm{lin}}[\dot{\boldsymbol{\delta}}] = 2\int_{\omega_c}[k\nabla\boldsymbol{\delta}^*\cdot\nabla\dot{\boldsymbol{\delta}} + F''(d_0)d^*\dot{d}]\,\mathrm{d}a + E_{\mathrm{lin}}[\boldsymbol{\delta}^*], \tag{5.25}$$

where

$$E_{\mathrm{lin}}[\boldsymbol{\delta}^*] = \int_{\omega_c} U(\boldsymbol{\delta}^*)\,\mathrm{d}a \tag{5.26}$$

and where, in general, $\frac{1}{2}E_{\mathrm{lin}}[\cdot]$ is the energy appropriate to the linearized theory; i.e. the leading-order approximation to the actual membrane energy E for small perturbations of the base state (cf. (2.1)).

To reduce this, we use Gauss's theorem in the integral in (5.25) and invoke $\boldsymbol{\delta}^* = \mathbf{0}$ on $\partial\omega_c$, obtaining

$$\int_{\omega_c} [k\nabla\boldsymbol{\delta}^* \cdot \nabla\dot{\boldsymbol{\delta}} + F''(d_0)d^*\dot{d}]\,\mathrm{d}a = \int_{\omega_c} [F''(d_0)d^*\dot{d} - k\boldsymbol{\delta}^* \cdot \Delta\dot{\boldsymbol{\delta}}]\,\mathrm{d}a. \tag{5.27}$$

Substituting $\Delta\dot{\boldsymbol{\delta}}$ from (5.3) and using $\mathbf{n} \cdot \boldsymbol{\delta}^* = d^*$, together with the constraint $\boldsymbol{\delta}_0 \cdot \boldsymbol{\delta}^* = 0$, we conclude that $k\boldsymbol{\delta}^* \cdot \Delta\dot{\boldsymbol{\delta}} = F''(d_0)d^*\dot{d}$ and hence that the integral vanishes; thus,

$$E_{\mathrm{lin}}[\dot{\boldsymbol{\delta}} + \boldsymbol{\delta}^*] - E_{\mathrm{lin}}[\dot{\boldsymbol{\delta}}] = k\int_{\omega_c} (|\nabla\boldsymbol{\phi}^*|^2 + |\nabla d^*|^2)\,\mathrm{d}a + F''(d_0)\int_{\omega_c} (d^*)^2\,\mathrm{d}a. \tag{5.28}$$

The energy difference is always non-negative if $F''(d_0) > 0$, and vanishes if and only if both d^* and $\nabla\boldsymbol{\phi}^*$ vanish together; the restriction $\boldsymbol{\delta}^* = \mathbf{0}$ on $\partial\omega_c$ then requires that $\boldsymbol{\phi}^*$ vanish, and hence that $\boldsymbol{\delta}^* = \mathbf{0}$ in ω_c. It follows that $E_{\mathrm{lin}}[\dot{\boldsymbol{\delta}} + \boldsymbol{\delta}^*] > E_{\mathrm{lin}}[\dot{\boldsymbol{\delta}}]$ for all non-zero admissible $\boldsymbol{\delta}^*$, and hence, according to the linearized theory, that the solution $\dot{\boldsymbol{\delta}}$ is conditionally stable in the sense described; that is, stable against perturbations that leave membrane shape unaltered. We do not know if it is stable in the sense of minimizing energy with respect to perturbations that also alter membrane shape.

The case $F''(d_0) < 0$ is different. In this case, we invoke the Poincaré inequality for null Dirichlet data [32], which ensures the existence of a positive constant C, depending only on ω_c, such that

$$\int_{\omega_c} |\nabla d^*|^2\,\mathrm{d}a \geq C\int_{\omega_c} (d^*)^2\,\mathrm{d}a. \tag{5.29}$$

This furnishes

$$E_{\mathrm{lin}}[\dot{\boldsymbol{\delta}} + \boldsymbol{\delta}^*] - E_{\mathrm{lin}}[\dot{\boldsymbol{\delta}}] \geq k\int_{\omega_c} |\nabla\boldsymbol{\phi}^*|^2\,\mathrm{d}a + \left(k - \frac{|F''(d_0)|}{C}\right)\int_{\omega_c} |\nabla d^*|^2\,\mathrm{d}a. \tag{5.30}$$

Thus, if

$$k > \frac{|F''(d_0)|}{C}, \tag{5.31}$$

then we conclude, as before, that $E_{\mathrm{lin}}[\dot{\boldsymbol{\delta}} + \boldsymbol{\delta}^*] > E_{\mathrm{lin}}[\dot{\boldsymbol{\delta}}]$ for all non-zero admissible $\boldsymbol{\delta}^*$; and hence that the solution $\dot{\boldsymbol{\delta}}$ is again conditionally stable. Accordingly, ripple phases, which are observed as persistent features in experiments [31], are predicted to be conditionally stable in the present theory if the modulus k is sufficiently large. The lower bound is problem specific, however, as it depends on ω_c via the constant C.

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Appendix A

In Steigmann [14], it is shown that the variation of $\mathbf{n}$ induced by any arbitrary variation $\mathbf{u} = \dot{\mathbf{r}}$ is

$$\dot{\mathbf{n}} = \varepsilon^{\beta\alpha}\mathbf{a}_\beta \times \dot{\mathbf{a}}_\alpha - \left(\frac{\dot{J}}{J}\right)\mathbf{n}, \tag{A 1}$$

where $\varepsilon^{\beta\alpha}$ is the contravariant permutation tensor.

Under tangential variations $\mathbf{u} = u^\alpha\mathbf{a}_\alpha$, we have $\dot{J}/J = u^\alpha_{,\alpha}$. Using the identities

$$\mathbf{a}_\beta \times \mathbf{a}_\lambda = \varepsilon_{\beta\lambda}\mathbf{n}, \tag{A 2}$$

where $\varepsilon_{\beta\lambda}$ is the covariant permutation tensor, together with $\varepsilon^{\beta\alpha}\varepsilon_{\beta\lambda} = \delta^\beta_\lambda$ (the Kronecker delta), we derive

$$\dot{\mathbf{n}} = \varepsilon^{\beta\alpha}b_{\lambda\alpha}u^\lambda\mathbf{a}_\beta \times \mathbf{n}. \tag{A 3}$$

Combining this with

$$\mathbf{n} \times \mathbf{a}_\beta = \varepsilon_{\beta\gamma}\mathbf{a}^\gamma, \tag{A 4}$$

we finally obtain

$$\dot{\mathbf{n}} = -b_{\lambda\alpha} u^{\lambda} \mathbf{a}^{\alpha}. \tag{A 5}$$

For normal variations $\mathbf{u} = u\mathbf{n}$, we have $\dot{J}/J = -2Hu$. The foregoing procedure now delivers

$$\dot{\mathbf{n}} = \varepsilon^{\beta\alpha} \mathbf{a}_{\beta} \times (u_{,\alpha} \mathbf{n} - u b^{\lambda}_{\alpha} \mathbf{a}_{\lambda}) + 2Hu\mathbf{n} = -\mathbf{a}^{\alpha} u_{,\alpha} = -\nabla u. \tag{A 6}$$

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