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2002 J. Phys. A: Math. Gen. 35 6233

(http://iopscience.iop.org/0305-4470/35/30/302)

INSTITUTE OF PHYSICS PUBLISHING JOURNAL OF PHYSICS A: MATHEMATICAL AND GENERAL

J. Phys. A: Math. Gen. **35** (2002) 6233–6247 PII: S0305-4470(02)34527-X

Stresses in lipid membranes

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Received 1 March 2002, in final form 1 May 2002
Published 19 July 2002
Online at stacks.iop.org/JPhysA/35/6233

Abstract

The stresses in a closed lipid membrane described by the Helfrich Hamiltonian, quadratic in the extrinsic curvature, are identified using Noether's theorem. Three equations describe the conservation of the stress tensor: the normal projection is identified as the shape equation describing equilibrium configurations; the tangential projections are consistency conditions on the stresses which capture the fluid character of such membranes. The corresponding torque tensor is also identified. The use of the stress tensor as a basis for perturbation theory is discussed. The conservation laws are cast in terms of the forces and torques on closed curves. As an application, the first integral of the shape equation for axially symmetric configurations is derived by examining the forces which are balanced along the circles of constant latitude.

PACS numbers: 87.16.Dg, 46.70.Hg

1. Introduction

The Helfrich Hamiltonian, quadratic in the extrinsic curvature, provides a remarkably robust description of lipid membranes (see, for example, [1–6], and the comprehensive review [7]). This Hamiltonian associates an energy penalty with bending; it is invariant with respect to deformations along the membrane itself. Equilibrium configurations of the membrane will therefore satisfy a single 'shape' equation corresponding to the extrema of the Hamiltonian with respect to a deformation directed along the normal [8, 9]. This equation is geometrical. Underpinning the geometry, however, there will always be stresses within the membrane. In this paper, we will look at these stresses, as well as the corresponding torques, and examine how they are reflected in the geometry. From a mathematical point of view it might be argued that such a reformulation of an essentially geometrical problem represents a step in the wrong direction: after all, to obtain the shape equation, there is no need to know what the stresses are, much less the torques. As soon as one attempts to manipulate the membrane physically, however, one must necessarily look at the geometry as a response to external forces. We should remark that such an approach is not new in this context, dating back as it does to the early work by Evans [10]. More recently, it has also been exploited in [14] to study fluid membrane tethers with an axisymmetric geometry. Surprisingly, even in many contexts where one might have expected a geometrical approach to be indicated, by stepping back a little from the geometry in this way, a powerful and economical approach lending novel insight into the geometry itself is provided.

To construct the stress tensor we appeal to Noether's theorem: the Euclidean invariance of the Helfrich Hamiltonian implies conservation laws and corresponding conserved charges. (For an analogous treatment of elastic curves in space see [11].) In particular, translational invariance implies the proportionality of the divergence of the membrane stress tensor to any applied external forces; if the membrane is closed and the enclosed volume is fixed, this source will be the hydrostatic pressure enforcing the constraint. If the membrane is acted on by a localized external force, as is the case of micro-manipulation techniques [12, 13], this will appear as an additional distributional source on the membrane.

The recipe for the construction of the relevant conserved quantities is implicit in Noether's theorem. This is important because the corresponding Newtonian construction, while simple in principle, is *not* in practice. (See, however, [14], where the stresses and the torques are derived for axisymmetric configurations.)

The relationship between the three equations describing the conservation of the stress tensor and the (single) shape equation is very simple: the projection onto the normal of the former is the shape equation. The projection process necessarily dismantles the divergence form of these equations: the divergence of the normal stress picks up a source proportional to the local tangential stress, the 'extrinsic curvature cubed' nonlinearity in the shape equation. The fluid character of a lipid membrane is captured mathematically in the reparametrization invariance of the Hamiltonian describing it. The two tangential projections of the conservation law (or its 'Bianchi identities' in the language of gauge theory) reflect this invariance. As such, these latter two equations are satisfied even when the shape equation is not. This structure is model independent. There is thus little or no cost involved in considering a general Hamiltonian depending on the extrinsic curvature, in particular, models higher order in curvature.

It is also possible to cast the conservation of the stress tensor as a more intuitive global statement relating the total force on any closed loop lying on the surface to the action of external forces on the area enclosed by the loop. This global statement of conservation is particularly useful when the membrane possesses some spatial symmetry. The first integral of the shape equation for axially symmetric configurations of both spherical and toroidal topology is obtained as an immediate consequence when the loop coincides with a circle of constant latitude. This approach to the problem contrasts favourably with 'Hamiltonian' approaches [15, 16]. We also identify a global constraint on the tangential stress over the closed membrane, which reproduces the known scaling identity for the Helfrich Hamiltonian [7].

This paper is organized as follows. In section 2, we describe how the Hamiltonian responds to a deformation of the membrane surface. In section 3, it is shown how Noether's theorem may be applied to identify the conservation of the stress tensor as the conservation law associated with translation invariance of the two-dimensional surface. In this section, we also show how the conservation of the stress tensor can be projected to cast the shape equation in terms of derivatives of the stress tensor components. The special case of a soap bubble is used in section 4 to illustrate our approach. In section 5, we extend our considerations to the Helfrich Hamiltonian and more generally to Hamiltonians that depend on any power of the extrinsic curvature. We derive explicit expressions for the stress tensor. In section 6, we consider rotational invariance and the definition of torque. We introduce an intrinsic torque which, added to the couple due to the stress tensor, is conserved. In section 7, the global form of the conservation laws is examined; a non-trivial global relationship which involves the stress tensor itself is identified. In section 8, we comment briefly on how the stress tensor might be exploited to develop perturbation theory. In section 9, we specialize to axially symmetric configurations. We show how to obtain a relationship between the components of the stress tensor that encodes the shape equation. We conclude with some brief remarks in section 10.

2. Response of the Hamiltonian to surface deformations

Let us consider an embedded surface Σ in three-dimensional Euclidean space. For simplicity, we suppose that this surface is closed. The surface is described locally by three functions $\mathbf{x} = \mathbf{X}(\xi^a)$, where $\mathbf{x} = (x^1, x^2, x^3)$ are Cartesian coordinates on R^3, ξ^a, $a = 1, 2$, may be any local coordinates on the surface. We introduce two tangent vectors $\boldsymbol{e}_a$ which are defined by $\boldsymbol{e}_a = \partial \mathbf{X}/\partial \xi^a$. The surface geometry is described completely by the induced metric γ_{ab}, and the extrinsic curvature K_{ab}. The former is given by

$$\gamma_{ab} = \boldsymbol{e}_a \cdot \boldsymbol{e}_b. \tag{1}$$

We denote the covariant derivative on the surface by ∇_a which is compatible with γ_{ab}. The extrinsic curvature K_{ab} is given by

$$K_{ab} = -\boldsymbol{n} \cdot \partial_a \boldsymbol{e}_b \tag{2}$$

where $\boldsymbol{n}$ is the unit vector normal to the surface. We will indicate the trace of K_{ab} by $K = \gamma^{ab} K_{ab}$. The intrinsic and extrinsic geometries are related by the Gauss–Codazzi–Mainardi equations,

$$K^{ab} K_{ab} - K^2 - \mathcal{R} = 0 \tag{3}$$

$$\nabla_a K_{bc} - \nabla_b K_{ac} = 0 \tag{4}$$

where $\mathcal{R}$ denotes the surface scalar curvature.

Though our principal interest is in the case of a lipid membrane, we will consider any local Hamiltonian, depending on the functions $\mathbf{X}$, which is invariant under surface reparametrization; no energy penalty is associated with shearing deformations of the membrane. The surface Hamiltonian is given by

$$H_\Sigma[\mathbf{X}] = \int_\Sigma \mathrm{d}A\, h(\gamma_{ab}, K_{ab}, \nabla_a K_{bc}, \ldots) \tag{5}$$

where the scalar h is constructed locally from the geometry of the surface, and the infinitesimal area element is given by

$$\mathrm{d}A = \mathrm{d}^2\xi \sqrt{\gamma} \tag{6}$$

with $\gamma = \det \gamma_{ab}$. In particular, the Helfrich Hamiltonian is proportional to

$$H_{(2)} = \int_\Sigma \mathrm{d}A\, K^2. \tag{7}$$

If there is a spontaneous curvature C_0, K is replaced by $K - C_0$ in equation (7). If the membrane is closed there may be a contribution to the total Hamiltonian proportional to the enclosed volume V due to a constant pressure excess P. In addition, there may be global constraints imposed on the membrane geometry. For example, one or more of the area, the integrated mean curvature,

$$M = \int_\Sigma \mathrm{d}A\, K \tag{8}$$

or the enclosed volume V may be fixed. In Helfrich's original model, both A and V are fixed. In Svetina and Žekˇ's bilayer couple model, in addition to these, M gets fixed [17]. These constraints are imposed by Lagrange multipliers. We note that in the refinement of these models, known as the area difference model, the Hamiltonian is not expressible in the simple form (5): a non-local term proportional to $(M - M_0)^2$ is added to the Hamiltonian, where M_0 is some constant [18–21]. In this model, deviations in the integrated mean curvature from M_0 are penalized energetically. We will not consider this model further.

To proceed, we need to know how this Hamiltonian responds to an infinitesimal deformation of the embedding functions for the surface, $\mathbf{X}(\xi) \rightarrow \mathbf{X}(\xi) + \delta\mathbf{X}(\xi)$. We decompose $\delta\mathbf{X}$ into its parts, tangential and normal to the surface,

$$\delta\mathbf{X} = \Phi^a \boldsymbol{e}_a + \Phi \boldsymbol{n}. \tag{9}$$

As an intermediate step, we evaluate how the quantities γ_{ab} and K_{ab} respond to this deformation. The tricky bit is to do this in a way which does not depend on the particular reparametrization of the surface we choose. For the induced metric we have

$$\begin{aligned}\delta\gamma_{ab} &= \boldsymbol{e}_a \cdot \nabla_b \,\delta\mathbf{X} + \boldsymbol{e}_b \cdot \nabla_a \,\delta\mathbf{X} \\ &= 2K_{ab}\Phi + \nabla_a \Phi_b + \nabla_b \Phi_a.\end{aligned} \tag{10}$$

To obtain the second line we have used decomposition (9), together with the Gauss–Weingarten equations,

$$\nabla_a \boldsymbol{e}_b = -K_{ab}\boldsymbol{n} \tag{11}$$

$$\nabla_a \boldsymbol{n} = K_{ab}\boldsymbol{e}^b. \tag{12}$$

Similarly, for the extrinsic curvature defined by (2), we find

$$\begin{aligned}\delta K_{ab} &= -(\delta\boldsymbol{n}) \cdot \nabla_a \nabla_b \mathbf{X} - \boldsymbol{n} \cdot \nabla_a \nabla_b \delta\mathbf{X} \\ &= -\nabla_a \nabla_b \Phi + K_{ac} K^c{}_b \Phi + \Phi^c \nabla_c K_{ab} + K_{ac} \nabla_b \Phi^c + K_{bc} \nabla_a \Phi^c.\end{aligned} \tag{13}$$

Here, the first term in the first line vanishes, because of the unit vector fact: $(\delta\boldsymbol{n}) \cdot \nabla_a \nabla_b \mathbf{X} = -K_{ab}(\delta\boldsymbol{n}) \cdot \boldsymbol{n} = 0$. To obtain the third term in the second line we have used the Codazzi–Mainardi equation (4). As expected, in both equations (10), (13), the tangential deformation is the Lie derivative along the surface vector Φ^a.

Once we know how the geometry changes under a surface deformation, we are in a position to vary any Hamiltonian of the form (5). However, we can exploit reparametrization invariance to simplify matters. The infinitesimal change in the Hamiltonian can always be decomposed into its tangential and normal parts,

$$\delta H = \delta_\parallel H + \delta_\perp H. \tag{14}$$

Away from the boundaries, the tangential deformation can be identified with a reparametrization of Σ since $\delta_\parallel H$ is a boundary term. It is simple to show why this is so: we have that $\delta_\parallel f = \Phi^a \partial_a f$ for any scalar function $f(\xi)$ defined on Σ; in addition, under a tangential deformation, the induced metric on Σ tranforms as a Lie derivative, as given by the tangential part of (10). Thus we have

$$\delta_\parallel \sqrt{\gamma} = \partial_a(\sqrt{\gamma}\,\Phi^a). \tag{15}$$

The identification of a conservation law will require us to isolate a divergence in the variation of the Hamiltonian. Thus, let us consider the behaviour of the Hamiltonian H_{Σ_0} when it is restricted to some connected domain Σ_0 with a boundary $\mathcal{C}$. In the case of a surface with spherical topology, we will suppose without loss of generality that Σ_0 is also simply connected so that $\mathcal{C}$ is a contractable closed curve. For toroidal or higher genus surfaces, one might also be interested in regions which are not simply connected with a non-contractable, disconnected boundary. For notational simplicity, we will proceed as though $\mathcal{C}$ is also connected. For an arbitrary deformation of Σ_0 we have

$$\delta H_{\Sigma_0} = \int_{\Sigma_0} \mathrm{d}^2\xi \{(\delta\sqrt{\gamma})h + \sqrt{\gamma}(\delta h)\}. \tag{16}$$

A tangential deformation of the surface thus always results in a pure divergence,

$$\delta_\| H_{\Sigma_0} = \int_{\Sigma_0} \mathrm{d}^2\xi\, \partial_a(\sqrt{\gamma} h \Phi^a) = \int_{\mathcal{C}} \mathrm{d}s\, h l_a \Phi^a \tag{17}$$

where we have used Stokes theorem in the second equality, s is the arclength along the boundary curve $\mathcal{C}$, induced by its embedding in Σ_0, say $\xi^a = Y^a(s)$, and l^a is the unit normal on $\mathcal{C}$ pointing out of Σ_0.

A reparametrization of Σ_0 can only move its boundary. Thus, if there is no boundary, $\delta_{||} H_\Sigma = 0$. If we are interested in a stiff membrane, so that no local change in the area is permitted, then Φ_a itself must respond to Φ to maintain the constraint, $\delta\sqrt{\gamma} = 0$. Then, as follows from equation (10), $\nabla_a \Phi^a + K\Phi = 0$. Clearly this implies no constraint for a Euclidean motion. For general deformations, we only require that the tangential deformation results in a divergence. Thus none of our conclusions is modified. The enclosed volume also clearly does not change under a surface reparametrization.

Whereas the tangential variation of the Hamiltonian is simple, the normal variation is, in general, non-trivial. However, the latter can always be cast in the form

$$\delta_\perp H_{\Sigma_0} = \int_{\Sigma_0} \mathrm{d}A \{\mathcal{E}(h)\Phi + \nabla_a S^a[\Phi]\} \tag{18}$$

i.e. as a bulk part plus a pure divergence. Here $\mathcal{E}(h)$ is the Euler–Lagrange derivative of h with respect to surface deformations, projected onto the normal $\boldsymbol{n}$ to the surface; S^a is a linear differential operator on the surface which operates on the normal deformation Φ as follows:

$$S^a[\Phi] = S^a_{(0)}\Phi + S^{ab}_{(1)}\nabla_b\Phi + \cdots. \tag{19}$$

To construct $S^a[\Phi]$, integration by parts is used to collect all surface gradients and higher derivatives of Φ in a pure divergence. Such terms will show up in the normal deformation of K_{ab} and its derivatives.

Summing the two independent variations we have

$$\delta H_{\Sigma_0} = \int_{\Sigma_0} \mathrm{d}A [\mathcal{E}(h)\Phi + \nabla_a Q^a] \tag{20}$$

where the Noether charge is

$$Q^a = S^a[\Phi] + h\,\Phi^a. \tag{21}$$

Note that Q^a is not unique; clearly $Q^a \to Q^a + \epsilon^{ab}\nabla_b f$, for some scalar density f, with ϵ^{ab} the surface Levi-Civita density, will leave equation (20) unchanged.

The variational principle restricted to normal deformations determines the equilibria. Suppose that the enclosed volume is fixed at some value V_0. The total Hamiltonian

$$H = H_\Sigma - P(V - V_0) \tag{22}$$

is then stationary with respect to normal deformations of Σ when the Euler–Lagrange equation

$$\mathcal{E}(h) = P \tag{23}$$

is satisfied. This is the 'shape' equation determining the equilibria of the membrane. We have used the fact that the interior volume varies as

$$\delta_\perp V = \int_\Sigma \mathrm{d}A\,\Phi. \tag{24}$$

3. Stresses in the membrane

To this point, we have considered arbitrary deformations of the functions $\mathbf{X}$. We now ask what occurs if we subject the membrane to a translation or a rotation. Let us then consider an infinitesimal Euclidean motion, $\delta\mathbf{X} = \mathbf{a} + \mathbf{b} \times \mathbf{X}$, where $\mathbf{a}$ is an infinitesimal constant translation and $\mathbf{b}$ represents an infinitesimal rotation. Let us focus on translations. Rotations will be considered in section 6.

If we decompose $\delta\mathbf{X}$ according to equation (9), then for an infinitesimal spatial translation, $\delta\mathbf{X} = \mathbf{a}$, we have $\Phi = \mathbf{a} \cdot \boldsymbol{n}$, and $\Phi_a = \mathbf{a} \cdot \boldsymbol{e}_a$. Substituting into equation (20), the variation of the Hamiltonian associated with this translation can be cast in the form

$$\delta H_{\Sigma_0} = \mathbf{a} \cdot \int_{\Sigma_0} \mathrm{d}A[\mathcal{E}(h)\boldsymbol{n} - \nabla_a \boldsymbol{f}^a]. \tag{25}$$

The surface vector $\boldsymbol{f}^a$ is given by

$$\boldsymbol{f}^a = -\boldsymbol{S}^a[\boldsymbol{n}] - h\boldsymbol{e}^a \tag{26}$$

where $\boldsymbol{S}^a[\boldsymbol{n}]$ is defined by

$$S^a[\Phi] = \mathbf{a} \cdot \boldsymbol{S}^a[\boldsymbol{n}]. \tag{27}$$

The quantity $\boldsymbol{f}^a$ describes the non-vanishing components of the stress tensor as appropriate for a two-dimensional system: it is both a spatial vector and a surface vector. The ambiguity in the Noether charge Q^a translates into an ambiguity in the stress $\boldsymbol{f}^a \to \boldsymbol{f}^a + \epsilon^{ab}\nabla_b \boldsymbol{W}$, for some arbitrary vector density $\boldsymbol{W}$.

While tangential deformations do not participate in the variational derivation of the shape equation, we see that they do contribute in a simple but essential way to the construction of the stress tensor.

Suppose that H_{Σ_0} is invariant under translations, $\delta H_{\Sigma_0} = 0$. Because Σ_0 is arbitrary in equation (25), the integrand vanishes pointwise so that

$$\nabla_a \boldsymbol{f}^a = \mathcal{E}(h)\boldsymbol{n}. \tag{28}$$

If, in addition, the Euler–Lagrange equation for H as given by equation (22) is satisfied, then $\mathcal{E}(h) = P$ in equation (28).

Let us examine equation (28) a little more closely. We note that there are three conservation laws, whereas there is only one shape equation. To resolve this discrepancy, we decompose the space vector $\boldsymbol{f}^a$ into its tangential and normal parts,

$$\boldsymbol{f}^a = f^{ab}\boldsymbol{e}_b + f^a \boldsymbol{n}. \tag{29}$$

Note that, in general, the surface tensor f^{ab} need not be symmetric in its indices. The surface covariant divergence of $\boldsymbol{f}^a$ gives

$$\nabla_a \boldsymbol{f}^a = \left(\nabla_a f^{ab} + K^b{}_a f^a\right)\boldsymbol{e}_b + (\nabla_a f^a - K_{ab} f^{ab})\boldsymbol{n} \tag{30}$$

where we have made use of the Gauss–Weingarten equations for the surface Σ (equations (11), (12)). The surface projections of equation (28) are therefore given by

$$\nabla_a f^a - K_{ab} f^{ab} = \mathcal{E}(h) \tag{31}$$

$$\nabla_a f^{ab} + K^b{}_a f^a = 0. \tag{32}$$

The first equation expresses the Euler–Lagrange derivative $\mathcal{E}(h)$ in terms of f^{ab} and f^a. Using $\mathcal{E} = P$, the shape equation takes the remarkably simple universal form

$$\nabla_a f^a - K_{ab} f^{ab} = P. \tag{33}$$

Note that only the symmetric part of f^{ab} contributes.

The conservation of the stress tensor along the tangents to the membrane (32) is independent of $\mathcal{E}$. They provide consistency conditions on the components of the stress tensor, telling us how the tangential stress must respond to a given normal stress whether or not the shape equation holds. One can think of these equations as the Bianchi identities associated with surface reparametrizations. It is also clear that they hold separately for each term contributing to H.

Our treatment so far has been entirely general: the only properties of the Hamiltonian we have used are its reparametrization and translational invariance. We will now evaluate the Euler–Lagrange derivative and the stress tensor for specific models.

4. Soap bubbles

In order to illustrate the ideas that have been developed in the previous sections, we consider first the case of a surface dominated by surface tension, e.g. a soap bubble. The Hamiltonian is simply proportional to the area

$$H = \mu \int_\Sigma \mathrm{d}A \tag{34}$$

where the constant μ is the surface tension. This is the simplest Hamiltonian one can write down for a surface; it depends only on the intrinsic geometry of the surface. The normal deformation of this Hamiltonian is given by

$$\delta_\perp H = \mu \int_\Sigma \mathrm{d}A\, K \Phi \tag{35}$$

where we have used the familiar expression relating the Lie derivative along the normals of the area element of Σ to its mean extrinsic curvature $K = \gamma^{ab} K_{ab}$, as follows from equation (10),

$$\delta_\perp \, \mathrm{d}A = K \mathrm{d}A. \tag{36}$$

The tangential deformation of this Hamiltonian is simply given by equation (17), with $h = \mu$.

In this geometrical language, the shape equation is given by

$$\mu K = P. \tag{37}$$

The surfaces that extremize the Hamiltonian have constant mean extrinsic curvature. This is a second-order hyperbolic partial differential equation for the embedding functions, $\mathbf{X}(\xi)$. To bring the Euler–Lagrange equations into a more conventional form, using the Gauss–Weingarten equations (11), we have that $K = -\boldsymbol{n} \cdot \Delta \mathbf{X}$, where Δ is the surface Laplacian. The tangential projections of $\Delta \mathbf{X}$ vanish identically. We can now peel this expression and its tangential counterpart to recover,

$$\mu \Delta \mathbf{X} = -P \boldsymbol{n}. \tag{38}$$

In this model, there is no surface term arising from the normal variation, so that the quantity introduced in equation (18) vanishes identically, $S^a[\Phi] = 0$, and only the tangential variation contributes to the Noether charge. This feature is unique to this Hamiltonian. The invariance of the area Hamiltonian under Euclidean motions gives the stress

$$\boldsymbol{f}^a = -\mu \boldsymbol{e}^a \tag{39}$$

which is not only tangential but also isotropic, $f^{ab} = -\mu \gamma^{ab}$.

5. The Helfrich Hamiltonian

Let us now consider the problem of extremizing the bending energy of a surface given by equation (7) subject to constraints on V, A (and possibly M). To implement the constraints on the area and the integrated mean curvature, we construct the constrained Hamiltonian

$$H = \alpha H_{(2)} + \beta(M - M_0) + \mu(A - A_0). \tag{40}$$

This is a sum of the terms of the form

$$H_{(n)} = \int \mathrm{d}A\, K^n. \tag{41}$$

One could consider a Hamiltonian with a more general dependence on the K_{ab}, or on its derivatives. However, at quadratic order, a term proportional to $K_{ab}K^{ab}$ is locally equivalent to K^2. This is because the Gauss–Codazzi equation (3) relates the difference $K^2 - K_{ab}K^{ab}$ to the surface scalar curvature $\mathcal{R}$, and the Hamiltonian constructed from $\mathcal{R}$ is a topological invariant, as follows from the Gauss–Bonnet theorem.

As always, the tangential variation of the Hamiltonian is straightforward (see equation (17)). We note that the normal variation of $H_{(n)}$ is given by

$$\delta_\perp H_{(n)} = \int_\Sigma \mathrm{d}A\{K^{n+1}\Phi + nK^{n-1}(\delta_\perp K)\} \tag{42}$$

where we have used equation (36) in the first term. Using equations (10) and (13) for the normal variation of the induced metric and the extrinsic curvature, respectively, we find

$$\delta_\perp K = -\Delta\Phi - K_{ab}K^{ab}\Phi. \tag{43}$$

Inserting this expression into equation (42), and performing two integrations by parts to collect the derivatives of Φ in a divergence, we obtain

$$\delta_\perp H_{(n)} = \int_{\Sigma_0} \mathrm{d}A\{-n\Delta K^{n-1} + K^{n-1}(K^2 - nK_{ab}K^{ab})\}\Phi \\ - n\int_{\Sigma_0} \mathrm{d}A\nabla_a\{K^{n-1}\nabla^a\Phi - \nabla^a K^{n-1}\Phi\}. \tag{44}$$

We immediately identify the Euler–Lagrange derivative as

$$\mathcal{E}(H_{(n)}) = -n\Delta K^{n-1} + K^{n-1}(K^2 - nK_{ab}K^{ab}). \tag{45}$$

Generically, the Euler–Lagrange equation $\mathcal{E} = 0$ is of second order in derivatives of K_{ab}, so it is of fourth order in derivatives of the embedding functions $\mathbf{X}$. In the exceptional case $n = 1$, note that $\mathcal{E} = \mathcal{R}$ follows from equation (3) which is of second order in derivatives of $\mathbf{X}$.

The shape equation for the model described by equation (40) takes the form

$$-2\alpha\Delta K + \alpha K(K^2 - 2K_{ab}K^{ab}) + \beta\mathcal{R} + \mu K = P. \tag{46}$$

If the membrane possesses a boundary, appropriate boundary conditions in the variational principle are identified by examining the divergence appearing in equation (44). There $\Phi = 0$, which kills both the second term appearing in the divergence as well as the contribution from the derivative of Φ along $\mathcal{C}$ to the term proportional to $\nabla_a\Phi$. The normal derivative $l^a\nabla_a\Phi$ remains. Thus we must set $l^a\nabla_a\Phi = 0$ on $\mathcal{C}$.

We identify the operator $S^a[\Phi]$ introduced in equation (18) which corresponds to $H_{(n)}$ as the 'Wronskian':

$$S^a_{(n)}[\Phi] = -n(K^{n-1}\nabla^a\Phi - \Phi\nabla^a K^{n-1}). \tag{47}$$

In particular, if Φ corresponds to a background translation, we have

$$S^a_{(n)} = \mathbf{a}\cdot\boldsymbol{S}^a_{(n)}[\boldsymbol{n}] = -n\mathbf{a}\cdot[K^{n-1}K^{ab}\boldsymbol{e}_b - \nabla^a K^{n-1}\boldsymbol{n}] \tag{48}$$

where we exploit the Gauss–Weingarten equation (12) to simplify the first term. We thus have, from equation (26), the general expression for contribution to the stress tensor coming from $H_{(n)}$,

$$\boldsymbol{f}^a_{(n)} = (nK^{n-1}K^{ab} - K^n\gamma^{ab})\boldsymbol{e}_b - n\nabla^a K^{n-1}\boldsymbol{n}. \tag{49}$$

Unlike the soap Hamiltonian proportional to the area, the stress tensor $\boldsymbol{f}^a_{(n)}$ does possess a component normal to the surface. If $n = 1$, however, note that $f^a_{(1)} = 0$—the corresponding stress is tangential. If $\nabla_a K = 0$ at any point, the normal stress vanishes there. Note that the antisymmmetric part of f^{ab} vanishes identically for the geometrical Hamiltonians we consider.

The Hamiltonian $H_{(2)}$ is invariant under scale transformations. It is easy to see that this is equivalent to

$$f^{ab}_{(2)}\gamma_{ab} = 0. \tag{50}$$

For the complete Helfrich Hamiltonian (40), the stress takes the form

$$\boldsymbol{f}^a = [\alpha K(2K^{ab} - K\gamma^{ab}) + \beta(K^{ab} - K\gamma^{ab}) - \mu\gamma^{ab}]\boldsymbol{e}_b - 2\alpha\nabla^a K\boldsymbol{n}. \tag{51}$$

This is the principal result of this paper. In general, the tangential stress f^{ab} is neither homogeneous nor isotropic. Indeed, it may vanish in places. We note, in particular, that whereas the parameter μ is the thermodynamic tension, determining the response of the energy to a change in the membrane area, it is not the mechanical surface tension.

6. Rotations and torque

Let us now consider an infinitesimal rotation $\delta\mathbf{X} = \mathbf{b}\times\mathbf{X}$. We have $\Phi = \mathbf{b}\cdot\mathbf{X}\times\boldsymbol{n}$ and $\Phi_a = \mathbf{b}\cdot\mathbf{X}\times\boldsymbol{e}_a$, and variation (20) of the Hamiltonian associated with a rotation reduces to

$$\delta H_{\Sigma_0} = \mathbf{b}\cdot\int_\Sigma \mathrm{d}A[\mathcal{E}(h)\mathbf{X}\times\boldsymbol{n} - \nabla_a\boldsymbol{m}^a] \tag{52}$$

where the surface vector $\boldsymbol{m}^a$ is given by

$$\boldsymbol{m}^a = -\boldsymbol{S}^a[\mathbf{X}\times\boldsymbol{n}] - h\mathbf{X}\times\boldsymbol{e}^a. \tag{53}$$

The quantity $\boldsymbol{m}^a$ is identified as the torque about the origin acting on Σ. Invariance of H_{Σ_0} under rotation then implies, using $\mathcal{E} = P$,

$$\nabla_a\boldsymbol{m}^a = P\mathbf{X}\times\boldsymbol{n}. \tag{54}$$

We isolate the contribution due to the couple of $\boldsymbol{f}^a$ about the origin

$$\boldsymbol{m}^a = \mathbf{X}\times\boldsymbol{f}^a + \mathbf{s}^a \tag{55}$$

where

$$\mathbf{s}^a = \mathbf{X}\times\boldsymbol{S}^a[\boldsymbol{n}] - \boldsymbol{S}^a[\mathbf{X}\times\boldsymbol{n}]. \tag{56}$$

Neither $\boldsymbol{s}^a$ nor the couple due to $\boldsymbol{f}^a$ alone is conserved. An immediate consequence of equations (28), (54), (55) is the relation

$$\nabla_a\mathbf{s}^a = \boldsymbol{f}^a\times\boldsymbol{e}_a. \tag{57}$$

We emphasize that this relation between $\mathbf{s}^a$ and $\boldsymbol{f}^a$ does not depend on the shape equation (23); it holds for each term contributing to H. Note that $\mathbf{s}^a$ does not involve derivatives in K_{ab} other than those already contained in $\boldsymbol{f}^a$.

We can also expand $\mathbf{s}^a$ analogously to equation (29) with tangential and normal projections, $\mathbf{s}^a = s^{ab}\boldsymbol{e}_b + s^a\boldsymbol{n}$. We have

$$\nabla_a s^a - K_{ab}s^{ab} = \sqrt{\gamma}\epsilon_{ba}f^{ab} \tag{58}$$

$$\nabla_a s^{ab} + K^b{}_a s^a = \sqrt{\gamma}\epsilon_{ac} f^a \gamma^{cb} \tag{59}$$

where we have used $\epsilon_{ab} = \epsilon_{\mu\nu\alpha}\, e_a^\mu\, e_b^\nu\, n^\alpha/\sqrt{\gamma}$, and $\epsilon_{\mu\nu\alpha}$ is the Levi-Civita density. The antisymmetric part of f^{ab}, if present, would contribute to equation (58). For models that depend on polynomials of the extrinsic curvature, the symmetric part of s^{ab} vanishes, and there is no torque about the normal, $s^a = 0$.

In particular, for the soap bubble the torque is simply that due to the couple of $\boldsymbol{f}^a$. The intrinsic torque associated with $H_{(n)}$, however, is generally non-vanishing,

$$\mathbf{s}^a_{(n)} = nK^{n-1}\boldsymbol{e}^a \times \boldsymbol{n}. \tag{60}$$

Thus for the Helfrich Hamiltonian $\mathbf{s}^a$ is given by

$$\mathbf{s}^a = (2\alpha K + \beta)\boldsymbol{e}^a \times \boldsymbol{n}. \tag{61}$$

7. Global conservation

Applying the divergence theorem to equation (28) with $\mathcal{E} = P$ provides the global statement

$$\boldsymbol{F}(\mathcal{C}) = \int_{\mathcal{C}} \mathrm{d}s\, l_a\, \boldsymbol{f}^a = P \int_{\Sigma_0} \mathrm{d}A\, \boldsymbol{n}. \tag{62}$$

Recall that l^a denotes the unit normal on $\mathcal{C}$ pointing out of Σ_0. The total force exerted on the area element Σ_0 by the enclosed pressure P is balanced by the internal forces exerted on the boundary curves $\mathcal{C}$. If $P = 0$, $\boldsymbol{F}(\mathcal{C})$ vanishes. For spherical topology, or for a contractible loop $\mathcal{C}$ on a higher genus surface this is also true for the individual closed $\mathcal{C}$. On a non-contractible loop, however, we have instead that $\boldsymbol{F}(\mathcal{C})$ is a non-vanishing constant vector. For a surface with the topology of a torus, there are two distinct constant vectors corresponding to the two topologically distinct non-contractible circuits. Note that the modulus of this vector can be identified with the Casimir of the Euclidean group associated with translations. For a surface of genus g, there are $g + 1$ distinct values.

The corresponding global statement for the total torque acting on any closed loop $\mathcal{C}$

$$\boldsymbol{M}(\mathcal{C}) := \int_{\mathcal{C}} \mathrm{d}s\, l_a \boldsymbol{m}^a = P \int_{\Sigma} \mathrm{d}A\, \mathbf{X} \times \boldsymbol{n} \tag{63}$$

follows from equation (54).

The total force $\boldsymbol{F}$ on a loop $\mathcal{C}$ on a soap film is given by

$$\boldsymbol{F}(\mathcal{C}) = -\mu \int_{\mathcal{C}} \mathrm{d}s\, \mathbf{l} \tag{64}$$

where $\mathbf{l} = l^a \boldsymbol{e}_a$ is the unit normal pointing out of the surface at a given point on $\mathcal{C}$ treated as a space vector. The corresponding torque acting on a loop $\mathcal{C}$ due to the enclosed membrane, $\boldsymbol{M}(\mathcal{C})$, is given by

$$\boldsymbol{M}(\mathcal{C}) = -\mu \int_{\mathcal{C}} \mathrm{d}s\, \mathbf{X} \times \mathbf{l}. \tag{65}$$

The conservation law, equation (28) has non-trivial consequences which imply global constraints on the tangential projections f^{ab}. Let us dot equation (28) with $\mathbf{X}$. We have

$$\mathbf{X} \cdot \nabla_a \boldsymbol{f}^a = \nabla_a(\mathbf{X} \cdot \boldsymbol{f}^a) - \boldsymbol{e}_a \cdot \boldsymbol{f}^a = -P\mathbf{X} \cdot \boldsymbol{n}. \tag{66}$$

We note that $\boldsymbol{e}_a \cdot \boldsymbol{f}_b = f_{ab}$. We integrate over Σ to obtain the global constraint on the trace of f^{ab},

$$\int_{\Sigma} \mathrm{d}A\, f^a{}_a = -3P\, V. \tag{67}$$

We have used the representation

$$V = \frac{1}{3}\int_{\Sigma} \mathrm{d}A\, \mathbf{X}\cdot \boldsymbol{n} \tag{68}$$

for the enclosed volume. In addition to equation (67), there is the global constraint

$$\int \mathrm{d}A\, K_{ab} f^{ab} = PA \tag{69}$$

obtained directly by integrating projection (32) over the surface.

For a soap bubble, the integrability condition (67) gives

$$2\mu A = 3PV. \tag{70}$$

This also follows as a consequence of stationarity of extremal configurations with respect to scaling. We have

$$\mu A[\lambda\mathbf{X}] - PV[\lambda\mathbf{X}] = \lambda^2 \mu A[\mathbf{X}] - \lambda^3 PV[\mathbf{X}] \tag{71}$$

which is extremized, with $\lambda = 1$, when equation (70) is satisfied.

For the Helfrich Hamiltonian, the integrability condition (67) gives the well-known scaling identity (see [7], equation (3.10))

$$\beta M + 2\mu A = 3PV. \tag{72}$$

Note that the scale invariant $H_{(2)}$ does not contribute.

8. Perturbations

As an application of the conservation law (28) let us examine briefly perturbations about equilibrium. We will evaluate $\delta\mathcal{E}$ using our knowledge of the stress tensor and compare our result with that obtained using a 'direct' approach [9]. In particular, the tangential perturbation is simply $\delta_\parallel \mathcal{E}(h) = \Phi^a \partial_a \mathcal{E}(h)$. For the normal variation, it is convenient to consider the linearization of (28):

$$\delta_\perp \nabla_a \boldsymbol{f}^a = (\delta_\perp \mathcal{E}(h))\boldsymbol{n} + \mathcal{E}(h)\delta_\perp \boldsymbol{n}. \tag{73}$$

To express this equation in a more useful form we can use $\delta_\perp \boldsymbol{n} = -(\nabla_a \Phi)\boldsymbol{e}^a$, together with

$$\delta_\perp \nabla_a\, \boldsymbol{f}^a = \nabla_a\, \delta_\perp\, \boldsymbol{f}^a - [\nabla_a(K\Phi)]\, \boldsymbol{f}^a \tag{74}$$

where we have used for the normal deformation of the connection, $\delta_\perp \Gamma^b{}_{ab} = \nabla_a(K\Phi)$. Now, taking projections of equation (73), we obtain the 'linearized Bianchi identity'

$$[\nabla_a \delta_\perp \boldsymbol{f}^a]\cdot \boldsymbol{e}_b - f_b{}^a \nabla_a(K\Phi) = -(\nabla_a \Phi)\mathcal{E}(h) \tag{75}$$

and

$$[\nabla_a \delta_\perp \boldsymbol{f}^a]\cdot \boldsymbol{n} - f^a \nabla_a(K\Phi) = \delta_\perp \mathcal{E}(h). \tag{76}$$

The task of computing the linearization of the Euler–Lagrange derivative is reduced by one order: one needs only to compute the linearization of the stress tensor.

Let us introduce the quantities

$$p_a = \mathbf{X}\cdot \boldsymbol{e}_a \qquad q = \mathbf{X}\cdot \boldsymbol{n}. \tag{77}$$

Note that $p_a = \nabla_a \mathbf{X}^2/2$ is a gradient. The Gauss–Weingarten equations can be cast in the alternative form

$$\nabla_a p_b = -K_{ab} q + \gamma_{ab} \tag{78}$$

$$\nabla_a q = K_{ab} p^b. \tag{79}$$

Consider an infinitesimal dilatation under which $\delta\mathbf{X} = \lambda\mathbf{X}$. Then q represents the normal component. As such, we would expect $\delta\mathcal{E}[q] = inhom$, where $\delta\mathcal{E}$ is the linearized Euler–Lagrange derivative and by 'inhom' we mean the terms which correspond to infinitesimal changes in the parameters of the model. We note that under an infinitesimal rotation (three parameters), $\epsilon \approx \epsilon^{ab}\mathbf{b} \times \boldsymbol{e}_a p_b$ satisfies $\delta\mathcal{E} = 0$. Together with the (three-parameter) infinitesimal translation $\epsilon = \mathbf{a} \cdot \boldsymbol{n}$ they exhaust the zero modes of $\delta\mathcal{E} = 0$. A membrane with translation symmetry along the z-axis defines a unique loop on the orthogonal x–y plane. The infinitesimal deformation of this loop induced by a rotation about this axis has $\epsilon \approx p$, where $p = \mathbf{X} \cdot \boldsymbol{t}$ and $\boldsymbol{t}$ is the tangent vector to loop. Thus, in this case, both projections of $\mathbf{X}$ satisfy the linearized equation. The consequences in the planar reduction of the Helfrich problem are discussed in detail in [22].

9. Symmetries

The approach we have developed is particularly appropriate when the membrane geometry possesses some degree of spatial symmetry. In particular, let us consider a membrane which is axially symmetric. Then we can exploit the integrated form of the conservation law given by equation (62), and balancing forces on a circle of constant latitude we obtain a relation between the appropriate components of the stress tensor and the external pressure. When we specialize our considerations to the Helfrich Hamiltonian (40), this relation reduces to the well-known first integral of the Helfrich shape equation for axially symmetric configurations (see, e.g., [15, 23, 16]).

We choose the standard axially symmetric chart on R^3: ρ, z, φ. As coordinates on the surface we choose the arc-length along the meridians, l, as well as φ. The embedding of this geometry in R^3 can then be expressed as

$$\rho = R(l) \qquad z = Z(l). \tag{80}$$

The line element induced on the surface is

$$\mathrm{d}s^2 = \mathrm{d}l^2 + R(l)^2\,\mathrm{d}\varphi^2. \tag{81}$$

The relation

$$R'^2 + Z'^2 = 1 \tag{82}$$

defines l, where the prime denotes a derivative with respect to arc-length l. A basis of tangent vectors for the surface adapted to this coordinate system is then given by

$$\boldsymbol{e}_l = (R', Z', 0) \qquad \boldsymbol{e}_\varphi = (0, 0, 1) \tag{83}$$

and the outward pointing normal is

$$\boldsymbol{n} = (-Z', R', 0). \tag{84}$$

Let us consider a configuration with spherical topology. We choose the loop $\mathcal{C}$ to coincide with a circle of fixed latitude, $z =$ constant. The vectors $l^a = (1, 0)$, and $\epsilon^a = (0, R^{-1})$ denote the unit normal and tangent vectors, respectively, to this circle on the surface. We note that $\mathbf{l} = \boldsymbol{e}_a l^a = \boldsymbol{e}_l$.

We now examine the integrated form of the conservation law given by equation (62). We decompose the components of the stress tensor, f^{ab} and f^a, with respect to the surface basis $\{l^a, \epsilon^a\}$ as

$$f^{ab} = f_{\perp\perp} l^a l^b + f_{\parallel\,\parallel}(\gamma^{ab} - l^a l^b) \tag{85}$$

$$f^a = f_\perp l^a + f_\parallel \epsilon^a \tag{86}$$

where all four coefficients are independent of the angle φ. The potential off-diagonal term in f^{ab} is zero by axial symmetry. The term that appears on the l.h.s. of equation (62) is

$$l_a \boldsymbol{f}^a = f_{\perp\perp}\mathbf{l} + f_\perp \boldsymbol{n} \tag{87}$$

so that integrating around the loop, and using $\mathrm{d}s = R(l)\,\mathrm{d}\varphi$, we have

$$\int \mathrm{d}s\, l_a \boldsymbol{f}^a = 2\pi R(f_{\perp\perp}\langle\mathbf{l}\rangle + f_\perp\langle\boldsymbol{n}\rangle) \tag{88}$$

where $\langle\cdot\rangle$ denotes an average over φ. All but the z-components vanish. We have

$$\langle\mathbf{l}\rangle = (0, Z'', 0) \qquad \langle\boldsymbol{n}\rangle = (0, R', 0). \tag{89}$$

For the r.h.s. of equation (62), this gives

$$2\pi P \int \mathrm{d}l\, R\langle\boldsymbol{n}\rangle = \pi R^2 P(0, 1, 0). \tag{90}$$

Therefore equation (62) reduces to the relation

$$f_{\perp\perp}Z' + f_\perp R' = \frac{RP}{2}. \tag{91}$$

We emphasize that this expression does not depend on the details of the model, but only on the assumption of axial symmetry and the choice of the particular loop.

We define now the angle Θ by $\sin\Theta = Z'$, $\cos\Theta = R'$. Then

$$\tan\Theta = \frac{\mathrm{d}Z}{\mathrm{d}R}. \tag{92}$$

When we decompose the extrinsic curvature as in equation (85), we find

$$K_{\perp\perp} = \Theta' \qquad K_{\|\,\|} = \frac{\sin\Theta}{R} \tag{93}$$

and for the mean extrinsic curvature,

$$K = \Theta' + \frac{\sin\Theta}{R}. \tag{94}$$

For a soap bubble, the relevant components of the stress tensor are, from equation (39),

$$f_{\perp\perp} = -\mu \qquad f_\perp = 0 \tag{95}$$

so that relation (91) reduces to

$$\sin\Theta = -R/R_0 \tag{96}$$

where $R_0 = 2\mu/P$. The unique solution which is regular at the poles is a circle of radius R_0.

Let us now consider a membrane described by the Helfrich Hamiltonian (40). As follows from equation (49) for $\boldsymbol{f}^a_{(n)}$ we have

$$f^{\perp\perp}_{(2)} = K(2K_{\perp\perp} - K) = \left(\Theta' + \frac{\sin\Theta}{R}\right)\left(\Theta' - \frac{\sin\Theta}{R}\right)$$
$$f^{\perp}_{(2)} = -2K' = -2\left(\Theta' + \frac{\sin\Theta}{R}\right)'$$
$$f^{\perp\perp}_{(1)} = K_{\perp\perp} - K = -\sin\Theta/R$$
$$f^{\perp}_{(1)} = 0.$$

Therefore, using these expressions, together with those in (95), relation (91) gives

$$-2\alpha\cos\Theta\left(\Theta'+\frac{\sin\Theta}{R}\right)'+\alpha\left(\Theta'+\frac{\sin\Theta}{R}\right)\left(\Theta'-\frac{\sin\Theta}{R}\right)\sin\Theta \\ -\beta\frac{\sin^2\Theta}{R}-\mu\sin\Theta=\frac{PR}{2}. \qquad (97)$$

This coincides with the first integral for the axisymmetric shape equation obtained in [15], and which is studied, e.g., in [24]. Our approach should be useful in providing an interpretation for an additional constant of integration C that appears in these works.

Had we taken another loop, for example, the closed loop running along the meridan ($\rho = 0$), we would find that we did not obtain such a useful integral identity.

10. Remarks

In this paper, we have exploited a combination of variational principles, and conservation laws to examine the physics of two-dimensional surfaces which are described, at a mesoscopic level, by an effective Hamiltonian which depends locally on the surface geometry. In the case of the Helfrich Hamiltonian, using this approach, we have derived both the stress tensor and the torque, associated with translational and rotational invariance, respectively. The shape equation, which determines equilibrium configurations, is now identified as one element of a conservation law.

The shift in focus onto the stresses in the membrane provides both an intuitive description of equilibria and a useful calculational tool. We demonstrated this in the context of axially symmetric configurations. Using the integrated form of the conservation law for the stress tensor, the first integral of the shape equation associated with this symmetry was obtained in a surprisingly economical way.

We have explored various applications of this framework: a membrane with an exposed free boundary in [25]; and the adhesion of a membrane onto a substrate in [26]. While both problems have been addressed previously in the axisymmetric context, the boundary conditions associated with the geometry make them very awkward to handle when this symmetry is relaxed. We show how our framework is well suited not only for identifying these boundary conditions in this case, but also for providing a physical interpretation for them. In a forthcoming paper, we will examine in detail how to approach perturbation theory in the same framework.

Acknowledgments

We thank C Chryssomalakos for useful comments. RC is partially supported by CONACyT under grant 32187-E. JG is partially supported by CONACyT under grant 32307-E and DGAPA at UNAM under grant IN119799. We thank an anonymous referee for bringing Evans's early work to our attention.

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