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# Undulations of a Straight Polymer Chain Embedded in a Membrane

M. Singh-Zocchi (<sup>1,\*</sup>), M.M. Kozlov (<sup>2</sup>) and W. Helfrich (<sup>1</sup>)

(<sup>1</sup>) Fachbereich Physik, Freie Universität Berlin, Arnimallee 14, 14195 Berlin, Germany

(<sup>2</sup>) Department of Physiology and Pharmacology, Sackler School of Med., Tel-Aviv University, Ramat-Aviv 69978, Israel

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**Abstract.** — We consider a sinusoidal undulation of a straight, linear polymer embedded in a flat membrane exposed to a lateral tension. We determine the shape of the membrane and compute the elastic energy associated with the undulation of the polymer. Analysing this energy at different wavelengths of the undulation, we find the criteria of stability of the straight shape of the polymer, and show them to be controlled by the difference of moduli of Gaussian curvature,  $\Delta\bar{\kappa}$ , of the polymerized and unpolymerized membrane. We also discuss formal analogies and differences between the behaviour of a polymer embedded into a membrane and a charged bilayer membrane immersed in a solution of electrolyte.

## 1. Introduction

Polymerized bilayers provide a useful model to understand the membranes of cells and sub-cellular organelles. Bilayers containing a polymerizable lipid may be partially polymerized by exposure to UV radiation [1–6]. Alternatively, polymers may be anchored to the membranes by either a covalent bonding between the polymer and the head group of the lipid molecules, or by the incorporation into the bilayer of hydrophobic side-groups attached to monomers of the polymer chain. Both cross-linked and linear polymers embedded in membranes have been obtained [2–5].

Recently [7], the conformational interaction between fluid membranes and embedded linear polymers was studied theoretically. The polymer was considered to be a continuous sequence of loosely linked monomers of fixed spacing, embedded in the same monolayer. These linked monomers were taken to differ from the neighbouring membrane molecules in their elastic parameters such as spontaneous curvature and modulus of Gaussian curvature. Owing to the local spontaneous curvature the monomers constituting the polymer can give rise to a sharp bend of the membrane along a straight chain. If a lateral tension tends to keep the bilayer flat, the sharp bend results in the formation of a ridge characterized by a ridge angle  $\psi_0$ . The polymer (and the associated ridge) is free to bend in the plane of the membrane. In the earlier

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(\*) Author for correspondence. *Present address:* 72A Blegdamsvej, 2 Th., 2100 Copenhagen, Denmark.

study [7], the effective energy of the in-plane bending of the linear polymer was considered for uniform curvature and conditions of equilibrium for straight or curved configurations of the polymer were worked out.

The goal of the present study is to analyze the energetics of lateral fluctuations of the polymer shape. This is a necessary step in understanding the statistical properties of partially polymerized membranes. We consider the straight configuration of the polymer to be an equilibrium state and investigate the energy of sinusoidal undulations.

We will characterize the undulation by the wave vector  $k$  and amplitude  $\varepsilon$ , assuming the latter to be small,  $\varepsilon \ll k^{-1}$ . The undulation energy will be calculated up to second order in  $\varepsilon$  and analyzed as a function of  $k$ . To distinguish different regimes of wave vector we make use of the fact that the lateral tension,  $\gamma_0$ , together with the bending rigidity of the membrane,  $\kappa$ , determine a length scale  $\lambda = (\kappa/\gamma_0)^{1/2}$ , which characterizes the elastic behaviour of the membrane, *i.e.* the decay length of membrane deformations. This length, referred to as the screening length, is a macroscopic quantity. It exceeds the molecular dimensions and for ordinary lipid bilayers with  $\kappa \approx 10^{-19}$  J has the value of  $\lambda \approx 300$  nm at  $\gamma_0 \approx 10^{-6}$  N/m.

Two different limiting cases will be considered: a regime of long waves where the wavelength exceeds the screening length,  $k^{-1} \gg \lambda$ ; and a regime of short waves  $k^{-1} \ll \lambda$ . We will show that in the long wavelength regime the energy of undulations is proportional to  $\varepsilon^2 k^4$  (*i.e.* to the average square of curvature), which can be interpreted as a bending energy. The corresponding effective bending rigidity of the polymer will be determined by the ridge angle  $\psi_0$  and the elastic parameters of the membrane such as the membrane bending modulus,  $\kappa$ , and the difference of the moduli of Gaussian curvature of the unpolymerized and polymerized membrane,  $\Delta\bar{\kappa} = \bar{\kappa} - \bar{\kappa}_p$ . The latter parameter will be shown to control the sign of the bending rigidity of the polymer and, thus, the stability of the straight shape.

The energy of the short wave undulations will also be found to change with  $\Delta\bar{\kappa}$ . At  $\Delta\bar{\kappa} = 0$  this energy is proportional to  $\varepsilon^2 k^2$ , which may be attributed to an effective increase of the ridge angle due to rippling of the polymer. At  $\Delta\bar{\kappa} \neq 0$ , the leading term in the energy is proportional to  $k^3$  and, depending on the value of  $\Delta\bar{\kappa}$ , can result in an instability of the straight configuration of the polymer with respect to the short wave undulations. We discuss the criteria of stability of the straight shape of the polymer with respect to the long and short wave undulations.

There is a remarkable similarity between the elastic behaviour of a polymer embedded in a membrane under lateral tension and that of a charged bilayer membrane immersed in an electrolyte. We will discuss this point at the end.

## 2. Description of the System

We consider a single polymer embedded on one side of a symmetric bilayer subjected to a lateral tension  $\gamma_0$ . The elastic properties of the unpolymerized bilayer [8] are characterized by the bending modulus,  $\kappa$ , and the modulus of Gaussian curvature,  $\bar{\kappa}$ , while the corresponding elastic moduli of polymerized membrane will be denoted by  $\kappa_p$  and  $\bar{\kappa}_p$ , respectively.

The initially straight polymer forms a ridge in the bilayer. The angle  $\psi_0$  at the top of the ridge is assumed to be constant along the polymer and not to depend on the configuration of the polymer chain. Far from the ridge, the membrane is kept flat by the lateral tension  $\gamma_0$ , the width of the ridge being of the order of the screening length  $\lambda = (\kappa/\gamma_0)^{1/2}$ .

To describe the shape of the system we use the orthogonal coordinates  $x, y, z$ , so that the flat part of the bilayer lies in the  $x$ - $y$  plane. The shape of the membrane will be given by  $h(x, y)$  determining the deviation of the membrane from the  $x$ - $y$  plane in the  $z$ -direction and referred to as the height. The projection of the polymer shape on the  $x$ - $y$  plane will be expressed by

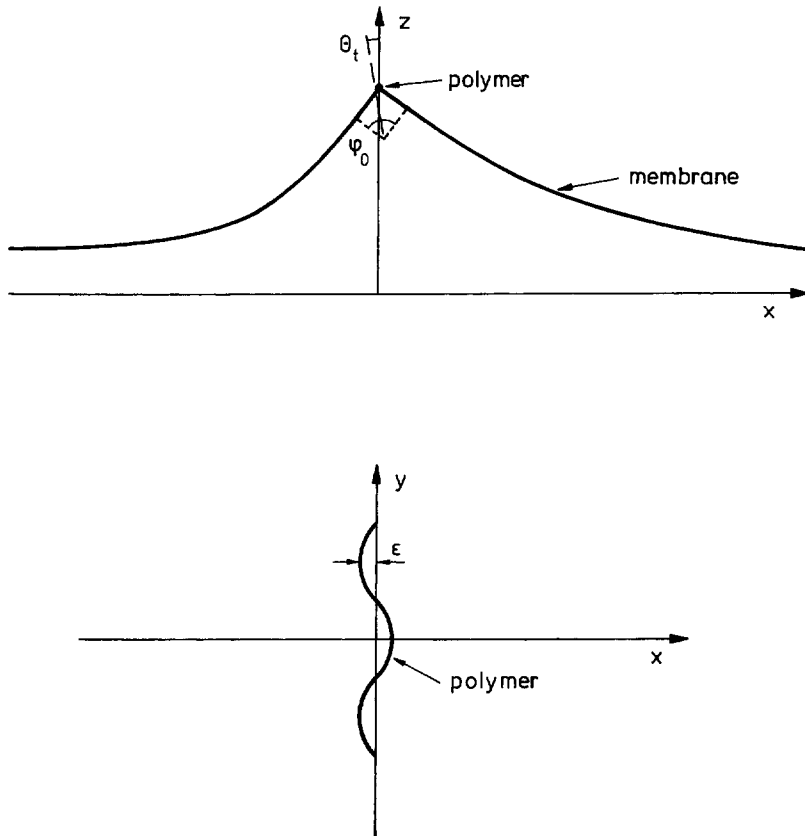


Fig. 1. — Schematic representation of the polymer-membrane system. The  $x$ - $y$  plane is the plane of the flat membrane.  $\psi_0$  is the ridge angle,  $\theta_t$  the tilt angle (the angle made by the polymer ridge with the vertical  $z$ -axis in our approximation). The polymer makes a sinusoidal undulation  $x_p(y) = \epsilon \cos(ky)$ .

$x_p(y)$ , while the height of the polymer will be denoted as  $h_p(y)$ . In its undisturbed straight conformation the polymer is in the  $y$ - $z$  plane, obeying  $x_p(y) = 0$ .

We define a lateral undulation of the polymer by its projection on the  $x$ - $y$  plane, putting

$$x_p(y) = \epsilon \cos(ky) \tag{1}$$

Note that (1) does not determine completely the shape of the undulating polymer. Indeed, at a given projection (1) the polymer can adopt different heights  $h_p(y)$ . Moreover, the top of the ridge can be tilted with respect to the  $z$ -axis. The tilt angle, illustrated in Figure 1b, will be denoted as  $\theta_t(y)$ . We will find below the functions  $h_p(y)$  and  $\theta_t(y)$  by minimizing the energy of the undulation.

### 3. Statement of the Problem

We calculate the energy of the membrane with an embedded polymer exhibiting the undulation (1) and analyse the stability of the straight conformation of the polymer. The polymer is

assumed to have no backbone elasticity, so that the energy is related to the membrane deformations only. If  $c_1$  and  $c_2$  are the two principal curvatures of the membrane surface, we may write the elastic energy per unit area of the membrane [8]

$$\gamma = \gamma_0 + \frac{1}{2}\kappa(J - J_S)^2 + \bar{\kappa}K \quad (2a)$$

where  $J = c_1 + c_2$  and  $K = c_1 c_2$  denote the total and the Gaussian curvatures of the membrane, respectively, while  $J_S$  is the spontaneous curvature vanishing in the unpolymerized bilayer but having a non-zero value at the position of the polymer. The whole energy can in principle be obtained by integration of (2a) over the whole area of the membrane, and accounting for the differences in the elastic constants  $\kappa$ ,  $\bar{\kappa}$  and  $J_S$  between the unpolymerized and polymerized parts. The spontaneous curvature at the position of the polymer creates the ridge angle  $\psi_0$  (which we assume to be independent of polymer curvature). As the area occupied by the polymer is negligible compared to the area of the unpolymerized bilayer, the integrals of the first two terms of (2a) over the polymerized area can be neglected. However, the term proportional to the Gaussian curvature  $K$  has to be taken into account because of the Gauss-Bonnet theorem. As a result, the total energy  $F$  of the system is obtained by integrating

$$\gamma = \gamma_0 + \frac{1}{2}\kappa J^2 + \Delta\bar{\kappa}K \quad (2b)$$

over the area of the bilayer except for a strip of negligible width representing the polymer, that is

$$F = \int \gamma dA \quad (3)$$

The last term in (2b) is proportional to the difference in the moduli of Gaussian curvature of the unpolymerized and the polymerized membrane,  $\Delta\bar{\kappa} = \bar{\kappa} - \bar{\kappa}_p$ , and accounts for the Gauss-Bonnet theorem.

To compute the energy (3), one has to determine the total and the Gaussian curvatures  $J$  and  $K$ , respectively, and find an expression for the element of the membrane area,  $dA$ . In other words, we have to find the shape of the membrane with undulating polymer, and then perform the integration (3) over the unpolymerized area.

#### 4. Shape of the Membrane

The goal of this section is to calculate the membrane shape described by its height  $h(x, y)$ . All the local geometrical characteristics of the membrane may be expressed in terms of the height. The total and the Gaussian curvatures are related to the height by

$$J = \frac{(1 + h_y^2)h_{xx} + (1 + h_x^2)h_{yy} - 2h_x h_y h_{xy}}{(1 + h_x^2 + h_y^2)^{3/2}}$$

and

$$K = \frac{h_{xx}h_{yy} - h_{xy}^2}{1 + h_x^2 + h_y^2}$$

respectively [9]. The element of membrane area is  $dA = \sqrt{1 + h_x^2 + h_y^2} dx dy$  and the orientation of an element of the membrane surface is determined by its normal vector  $\hat{\mathbf{n}}$ , whose  $x$ ,  $y$  and  $z$ -components are

$$\hat{\mathbf{n}} = \frac{1}{\sqrt{1 + h_x^2 + h_y^2}} [-h_x, -h_y, 1]$$

In the expressions above and everywhere below the subscripts denote differentiation with respect to the corresponding variable.

The shape equation describing the mechanical equilibrium of the membrane [10,11] involves the curvatures of the membrane surface. Therefore, starting from the shape equation we will first compute the total curvature of the membrane  $J$  and then, making use of the relationships above, we will determine all the other geometrical characteristics.

We will assume the principal curvatures of the membrane to be small compared to the inverse screening length,  $|c_1|, |c_2| \ll \sqrt{\gamma_0/\kappa}$ . Then the shape equation may be written in the approximate form

$$\nabla^2 J(x, y) = \frac{\gamma_0}{\kappa} J \tag{4}$$

where  $\nabla^2$  is the two-dimensional Laplacian in the  $x$ - $y$  plane. In (4) we retained only the contributions linear in the total curvature  $J$  and neglected the terms of higher order in  $J$  and those proportional to the Gaussian curvature  $K$ . It will be seen below that the total curvature resulting from (4) is of the order of magnitude of  $J \approx \psi_0 \sqrt{\gamma_0/\kappa}$ . Therefore, our approximation of small curvatures is equivalent to considering small ridge angles,  $\psi_0 \ll 1$ , and neglecting in (4) all the terms of higher than linear order in  $\psi_0$ .

There is an additional simplification used in (4). In the exact shape equation the two-dimensional Laplacian refers to the plane tangent to the membrane rather than to the  $x$ - $y$  plane. However, the unit normal vector to the membrane,  $\hat{n}$ , is parallel to the  $z$ -axis up to corrections of the order of  $\psi_0^2$ . Therefore, in linear approximation in  $\psi_0$  the operator  $\nabla^2$  in (4) as well as all the differential operators below will be taken in the  $x$ - $y$  plane. Moreover, in the approximations of the first non-vanishing order in  $\psi_0$  the exact expressions above relating the curvatures and the height will be replaced by  $J = h_{xx} + h_{yy}$  and  $K = h_{xx}h_{yy} - h_{xy}^2$ .

A first boundary condition for solutions of (4) is derived from the requirement that there are no normal forces acting on the ridge. In other words, we are looking for the shape of the system whose energy is minimized with respect to deviations of the polymer in the normal direction ( $z$ -axis). The normal force  $f_n$  determined per unit length of the polymer consists of two contributions. The first contribution is expressed through the two-dimensional derivative of the bending moment across the surface [8, 11, 12]. If the coordinate  $m$  denotes the direction perpendicular to the polymer projected in the  $x$ - $y$  plane then this force on the two sides of the ridge may be expressed as  $\kappa \frac{\partial J_L}{\partial m}$  and  $-\kappa \frac{\partial J_R}{\partial m}$ . Here and in the following the subscripts L and R refer to the membrane on the left- and right-hand sides of the ridge, respectively. The second contribution to the normal force is determined by the  $z$ -component of the lateral tension  $\gamma_0$ , which in our approximation of small  $\psi_0$  is  $\gamma_0 \cdot \chi$ , where  $\chi = \partial h / \partial m$  is the gradient angle of the membrane (Fig. 1). Taking into account that the gradient angle is positive on the left and negative on the right, the total normal forces on the two sides may be expressed as  $f_{nL} = \kappa \frac{\partial J_L}{\partial m} - \gamma_0 \chi_L$  and  $f_{nR} = -\kappa \frac{\partial J_R}{\partial m} + \gamma_0 \chi_R$ . The resulting boundary condition of zero total normal force on the polymer is:

$$\kappa \left( \frac{\partial J_L}{\partial m} - \frac{\partial J_R}{\partial m} \right) = \gamma_0 (\chi_L - \chi_R) \tag{5a}$$

where all values are taken at the polymer (1).

Another boundary condition relates the gradient angles at top of the ridge to the ridge angle,  $\psi_0$ , and the tilt angle,  $\theta_t$ , by the following equations:

$$\chi_L(x = x_p, y) - \chi_R(x = x_p, y) = \psi_0 \tag{6a}$$

and

$$\chi_L(x = x_p, y) + \chi_R(x = x_p, y) = 2\theta_t. \tag{6b}$$

To discuss the approximations involved in (6) we need to know the expression for the shape of the membrane. Therefore, we will return to this question in the Discussion.

Notice that owing to (6a), the equilibrium condition at the ridge, (5a), may be rewritten as

$$\kappa \left( \frac{\partial J_L}{\partial m} - \frac{\partial J_R}{\partial m} \right) = \gamma_0 \psi_0 \quad (5b)$$

Next, the heights of the membrane at the left- and right-hand sides should match at the top of the ridge,

$$h_L(x_p, y) = h_R(x_p, y) = h_p(y). \quad (7)$$

A fourth boundary conditions derives from the requirement that far from the polymer the membrane remains flat and lies in the  $x$ - $y$  plane:

$$h, h_x, h_y \text{ and } J \rightarrow 0, \text{ as } x \rightarrow \pm\infty \quad (8)$$

We shall first solve the differential equation (4) subject to the boundary condition (5b), for the total curvature,  $J$ . Then we will solve for the height  $h$ , related to  $J$  in our approximation by the equation

$$\nabla^2 h = J \quad (9)$$

In calculating  $h(x, y)$  we will take into account the remaining boundary conditions.

In solving the boundary value problem for the total curvature  $J(x, y)$ , defined by (4), (5b) and (8), we make use of smallness of the amplitude  $\varepsilon$  of polymer undulations and seek a perturbative solution based on an expansion in  $\varepsilon$ :

$$J(x, y) = J^{(0)}(x) + J^{(1)}(x, y)\varepsilon + J^{(2)}(x, y)\varepsilon^2 + \dots \text{ etc.}$$

The detailed calculation is presented in Appendix A. Solving order by order up to second order, we obtain for the curvature of the membrane on the right- and left-hand sides of the ridge

$$J_{L,R}(x, y) = \frac{\psi_0}{2} q e^{\pm qx} \mp \varepsilon \alpha e^{\pm p_1 x} \cos(ky) + \varepsilon^2 \left\{ \frac{\exp(\pm qx)}{2} \left[ \alpha q + \frac{\psi_0}{2} \frac{q}{2} (k^2 - q^2) \right] + \frac{\cos(2ky) \exp(\pm p_2 x)}{2p_2} \left( \alpha (p_1^2 + k^2) - \frac{\psi_0}{2} \frac{p_1^2 q^2}{2} \right) \right\} \quad (10)$$

where  $q = \frac{1}{\lambda} = \sqrt{\frac{\gamma_0}{\kappa}}$ ,  $p_1^2 = k^2 + q^2$ ,  $p_2^2 = 4k^2 + q^2$ ,

To solve (9) we take the sum of the particular solution  $h_{ps}$  of (9), accounting for (10), and of the general solution  $h_{ms}$  of the equation  $\nabla^2 h = 0$ , the latter describing the shapes with zero total curvature (minimal surfaces), *i.e.*, we have  $h = h_{ps} + h_{ms}$ .

The minimal surface solution has the form  $h_{ms}^{L,R} = \sum_{n=1}^{\infty} a_n^{L,R} e^{\pm n k x} \cos(nky)$ .

At this point, to use the boundary condition (6b), we must specify the functional form of the tilt angle  $\theta_t(y)$ . Since the tilt of the ridge is a consequence of the undulation of the polymer (1) we may conclude from symmetry considerations that the tilt angle changes along the polymer with the same wave vector as the undulation. We may express it as  $\theta_t = (\varepsilon \theta_1 + \varepsilon^2 \theta_2) \cos(ky)$ . We will find from our treatment below, that the second order term,  $\theta_2$  vanishes.

Again, expressing  $h$  as a perturbative expansion in  $\varepsilon$ , and solving by the same procedure as in the case of curvature  $J$  by making use of the boundary conditions (6a), (6b), (7) and (8), we may determine all the unknown parameters  $a_n$ 's and  $\alpha$  (see Appendix). We find that  $\theta_2$  vanishes and that

$$\alpha = -q^2 \left( \frac{\psi_0}{2} \frac{q - k}{k - p_1} - \frac{\theta_1}{k - p_1} \right)$$

We obtain for the shape of the membrane the following expression:

$$\begin{aligned}
 h^{L,R}(x, y) = & \frac{\psi_0}{2q} e^{\pm qx} \pm \frac{\varepsilon \cos(ky)}{k - p_1} \left[ \left( \frac{\psi_0}{2} (q - k) - \theta_1 \right) e^{\pm p_1 x} + \left( \frac{\psi_0}{2} (p_1 - q) + \theta_1 \right) e^{\pm kx} \right] \\
 & + \frac{\varepsilon^2}{2q} \left[ \frac{\frac{\psi_0}{2} (p_1^2 k - k^2 p_1 - q^3) + q^2 \theta_1}{k - p_1} - \frac{\psi_0 q^2}{2} \frac{q^2}{2} \right] e^{\pm qx} \\
 & + \varepsilon^2 \cos(2ky) \left\{ \frac{e^{\pm p_2 x}}{2p_2} \left[ \frac{\psi_0}{2} \left( \frac{-q^2}{2} + \frac{k - q}{k - p_1} p_1^2 \right) + \theta_1 \frac{p_1^2}{k - p_1} \right] \right. \\
 & \left. - \frac{k e^{\pm 2kx}}{4} \left[ \frac{\psi_0}{2} \frac{k - q}{k - p_1} + \frac{\theta_1}{k - p_1} \right] \right\} \tag{11}
 \end{aligned}$$

In the zeroth order in  $\varepsilon$  the height shows no dependence on  $y$ , since in this approximation the undulation of the polymer is completely neglected and the membrane shape is that of a straight ridge. In the first order in  $\varepsilon$  we obtain a modulation of the membrane height proportional to the undulation  $\varepsilon \cos(ky)$ . This contribution does not change the average value of the membrane height. In the second order we obtain another contribution to  $h(x, y)$  independent of  $y$  and therefore changing the average height; in addition, we find a contribution proportional to the second harmonic  $\cos(2ky)$ . The character of the dependence of the height on  $y$  in all orders can be understood by symmetry considerations taking into account that  $h(x, y)$  must remain unchanged if we replace  $\varepsilon$  by  $-\varepsilon$  and  $ky$  by  $(ky + \pi)$ .

**5. Energy of Undulation and Stability of Straight Shape of Polymer**

We compute the energy in (3), neglecting the contributions of the order higher than  $\varepsilon^2$ . The energy per unit length of the polymer may be expressed as:

$$f = \frac{F}{L_p} = \frac{2}{\sqrt{1 + \left(\frac{dy_p}{dx}\right)^2}} \left( \frac{\kappa}{2} \int_{\varepsilon \cos kx}^{\infty} J^2 dy + \frac{\gamma_0}{2} \int_{\varepsilon \cos kx}^{\infty} (h_x^2 + h_y^2) dy + \Delta \bar{\kappa} \int_{\varepsilon \cos kx}^{\infty} K dy \right)$$

where  $L_p$  is the length of the polymer whose element is given by  $dL_p = \sqrt{1 + \left(\frac{dy_p}{dx}\right)^2} dx$ .

Making use of (9) and (11), and averaging over a wavelength we obtain in our approximation

$$f = \sqrt{\gamma_0 \kappa} \left\{ \left( \frac{\psi_0}{2} \right)^2 (1 + a\varepsilon^2) + \theta_1^2 b\varepsilon^2 + \frac{\psi_0}{2} \theta_1 \varepsilon^2 c \right\} + \Delta \bar{\kappa} \varepsilon^2 k^2 \frac{\psi_0}{2} \theta_1 \tag{12}$$

where

$$\begin{aligned}
 a &= \frac{k^2}{a} - \frac{q^2}{2} + \frac{kq(q - p_1) - q^2(q - k)}{2(k - p_1)}, \\
 b &= \frac{-q}{2(k - p_1)},
 \end{aligned}$$

and

$$c = q \frac{q - p_1}{k - p_1}.$$

To determine an equilibrium shape of the membrane at the given undulation of the polymer, (1), we have to minimize the energy, (12), with respect to the tilt angle  $\theta_1$ . As a result we obtain:

$$\theta_1^{eq} = -\frac{\psi_0}{2} \left( \frac{c}{2b} + \frac{\Delta \bar{\kappa}}{\sqrt{\gamma_0 \kappa}} \frac{k^2}{2b} \right) = \frac{\psi_0}{2} \left[ q - p_1 + \frac{\Delta \bar{\kappa}}{\sqrt{\gamma_0 \kappa}} \frac{k^2(k - p_1)}{q} \right] \tag{13}$$



Making use of (12) and (13) we arrive at

$$f^{\text{eq}} = \sqrt{\gamma_0 \kappa} \left( \frac{\psi_0}{2} \right)^2 \left\{ 1 + \frac{\varepsilon^2}{2} \left( p_1^2 - p_1 q - \frac{k^2}{2} + \frac{k^4(k - p_1)}{q} \frac{(\Delta \bar{\kappa})^2}{\gamma_0 \kappa} + \frac{2\Delta \bar{\kappa} k^2(q - p_1)}{\sqrt{\gamma_0 \kappa}} \right) \right\} \quad (14)$$

The energy (14) consists of two contributions: the first does not depend on the amplitude of undulation,  $\varepsilon$ , and gives the energy of the straight polymer; the second is proportional to  $\varepsilon^2$  and represents the energy associated with the undulation,  $f_{\text{und}}$ .

Because there is a screening length  $\lambda$  in our problem, it is interesting to examine the behaviour at wavelengths longer and shorter than  $\lambda$ . For wavelengths longer than  $\lambda$  ( $k \ll q$ ), the energy of undulations can be approximated as:

$$f_{\text{und}} = \sqrt{\gamma_0 \kappa} \left( \frac{\psi_0}{2} \right)^2 \varepsilon^2 k^4 \left\{ \frac{1}{8q^2} - \frac{1}{q^2} \left( \left( \frac{\Delta \bar{\kappa}}{\kappa} \right)^2 + \frac{\Delta \bar{\kappa}}{\kappa} \right) \right\} \quad (15)$$

The energy (15) is proportional to the fourth power of the wave vector,  $k^4$ . Therefore, it can be viewed as an elastic energy of the polymer characterized by an effective bending elasticity

$$\mu = 2 \left( \frac{\psi_0}{2} \right)^2 \left( \frac{\kappa^3}{\gamma_0} \right)^{1/2} \left( \frac{1}{8} - \left( \frac{\Delta \bar{\kappa}}{\kappa} \right)^2 - \frac{\Delta \bar{\kappa}}{\kappa} \right) \quad (16)$$

This result is in agreement with the results of [7], where it was shown that in a straight configuration a polymer embedded in a membrane acquires an additional rigidity given by (16). So long as  $\mu$  is positive, the straight configuration remains stable under long wavelength fluctuations. However, this condition holds only as long as  $\Delta \bar{\kappa}/\kappa$  falls within the range:

$$-\frac{\sqrt{3/2+1}}{2} \leq \frac{\Delta \bar{\kappa}}{\kappa} \leq \frac{\sqrt{3/2-1}}{2} \quad (17)$$

In the special case when  $\Delta \bar{\kappa} = 0$ , the effective rigidity of the polymer is simply

$$\mu_{\Delta \bar{\kappa}=0} = \frac{\kappa}{4} \sqrt{\frac{\kappa}{\gamma_0}} \left( \frac{\psi_0}{2} \right)^2$$

In the limiting case of small wavelengths,  $k \gg q$ , the dependence of the undulation energy on wave vector is controlled again by  $\Delta \bar{\kappa}$ . At  $\Delta \bar{\kappa} = 0$ , the undulation energy is approximately equal to

$$f_{\text{und}} = \sqrt{\gamma_0 \kappa} \left( \frac{\psi_0}{2} \right)^2 \frac{\varepsilon^2 k^2}{4} \quad (18)$$

The  $k^2$  term dominates the short wavelength behaviour in this case. The increase in energy due to short wavelength ripples may be attributed to an increase of the effective ridge angle by the ripples. For  $\Delta \bar{\kappa} \neq 0$  the leading term for the undulation energy is proportional to the third power of the wave vector being,

$$f_{\text{und}} = -\sqrt{\gamma_0 \kappa} \left( \frac{\psi_0}{2} \right)^2 \frac{|k^3| \varepsilon^2}{q} \left[ \frac{1}{4} \left( \frac{\Delta \bar{\kappa}}{\kappa} \right)^2 + \frac{\Delta \bar{\kappa}}{\kappa} \right] \quad (19)$$

This contribution to the undulation energy may be seen to arise from a coupling of the curvature of the polymer chain to the tilt angle contributed by the Gaussian term. Expression (19) yields

a criterion of stability of the straight conformation of the polymer with respect to the short wave undulations. The straight conformation is stable as long as the undulation energy (19) remains positive, *i.e.*, the parameter  $\Delta\bar{\kappa}/\kappa$  satisfies

$$-4 < \frac{\Delta\bar{\kappa}}{\kappa} < 0 \quad (20)$$

Comparing the ranges (17) and (20) we find the straight configuration of the polymer to be stable under deformations of all wavelengths so long as  $\frac{\Delta\bar{\kappa}}{\kappa}$  falls within the range  $-\frac{\sqrt{3/2+1}}{2} \leq \frac{\Delta\bar{\kappa}}{\kappa} \leq 0$ . This means that, when it is stable with respect to the short wave undulations, the straight conformation of the polymer is also stable with respect to the long wave ones. However, if the value of the control parameter lies in the range  $-4 \leq \frac{\Delta\bar{\kappa}}{\kappa} \leq -\frac{\sqrt{3/2+1}}{2}$  the straight conformation becomes unstable under the long wave undulations but still remains stable with respect to the short wave and if it lies in the range  $0 \leq \frac{\Delta\bar{\kappa}}{\kappa} \leq \frac{\sqrt{3/2-1}}{2}$ , the straight polymer is stable under the long wave undulations but not the short wave ones. In the range  $\frac{\Delta\bar{\kappa}}{\kappa} < -4$  and  $\frac{\Delta\bar{\kappa}}{\kappa} > \frac{\sqrt{3/2-1}}{2}$  the straight conformation is unstable under the undulations of all wavelengths.

## 6. Discussion

We analysed the shape and the energy of a membrane embedding an undulating polymer. The results provided us with criteria of stability of the straight polymer with respect to the undulations of short and long wavelengths, the parameter controlling the stability being the difference of the moduli of Gaussian curvature of polymerized and unpolymerized membrane,  $\Delta\bar{\kappa}$ .

There are two independent small parameters in our problem: the ridge angle  $\psi_0 \ll 1$  and the amplitude of undulation of the polymer  $\varepsilon \ll k^{-1}$ . In our description we look for approximate solutions for the shape of the membrane retaining contributions up to the linear order in  $\psi_0$  and quadratic order in  $\varepsilon$ . We discussed already the simplifications of the shape equation (4) resulting from the smallness of  $\psi_0$ . However, an important approximation using the smallness of the amplitude  $\varepsilon$  still remains to be discussed. It played a role in the equation for the boundary condition of the fixed ridge angle (6a). In the exact approach the ridge angle is constant along the polymer line and is equal to the angle between the normal vectors to the membrane on the left and right hand sides of the polymer,  $\hat{\mathbf{n}}_L \cdot \hat{\mathbf{n}}_R$ . The exact form of the boundary condition is given by  $\hat{\mathbf{n}}_L \cdot \hat{\mathbf{n}}_R = \cos \psi_0$ . It can be readily seen that if the height of the ridge changes (*i.e.* if the polymer is "sloping"), this exact condition differs from (6a). The latter boundary condition is expressed in terms of the gradient angles  $\chi$  and is therefore approximate. To check the validity of this approximation we write down the variation of the height of the ridge as obtained by substituting (13) in (11)

$$h_p(y) = \frac{\psi_0}{2q_D} + \varepsilon^2 \frac{\psi_0}{2} \left[ \frac{q}{2} + \frac{k^2}{2q} - \frac{p_1}{2} + \frac{\Delta\bar{\kappa}}{\sqrt{\gamma_0\kappa}} \left( \frac{k^2}{2} + \frac{k^2(k-p_1)}{2q} \right) \right. \\ \left. + \left( \frac{2k^2+q^2}{4p_2} - \frac{k}{4} + \frac{q}{4} - \frac{p_1}{2} + \frac{\Delta\bar{\kappa}}{\sqrt{\gamma_0\kappa}} \frac{(2k^2p_1^2+k^3p_2-2k^2p_1p_2)}{4qp_2} \right) \cos(2ky) \right] \quad (21)$$

Variation of the height of the ridge in the vertical direction is a way for the membrane-polymer system to relax when the polymer ridge makes sinusoidal undulations in the plane of the membrane. Notice that these variations occur only in the second order of  $\varepsilon$  and that the

energy remains unchanged to this order when the undulating height is replaced by the average height.

A simple estimation based on (21) shows that the correction to (6a) related to the change of height is of order  $\varepsilon^4$  and, therefore, can be neglected in the approximation used.

It is, finally, useful to discuss the formal similarities and differences between undulations of a polymer embedded in a membrane and those of a charged membrane immersed in an electrolyte [13].

A charged membrane with a constant surface charge density  $\sigma_0$  and immersed in an electrolyte (of Debye length,  $\chi^{-1} = \sqrt{\frac{\varepsilon k_B T}{8\pi\rho_0 q^2}}$  <sup>(1)</sup>) is characterized by a potential that satisfies in a linear approximation the Debye-Hückel equation [14]:

$$\nabla^2\psi = \chi^2\psi \quad (22)$$

This equation is similar to equation (4) for total curvature of the membrane. Since the effect of the electric charge is not felt far from the membrane, we have the following boundary condition for the potential, which is similar to the boundary condition (8) for the curvature

$$\psi, \psi_z \rightarrow 0, \text{ for } z \rightarrow \pm\infty \quad (23)$$

(we have taken the charged membrane to coincide with the  $x$ - $y$  plane).

In addition, if  $\hat{\mathbf{n}}$  is the normal to the membrane in the positive  $z$  direction, the potential has a normal derivative discontinuity at any point on the membrane:

$$\left(\frac{\partial\psi_+}{\partial\hat{\mathbf{n}}}\right)_S - \left(\frac{\partial\psi_-}{\partial\hat{\mathbf{n}}}\right)_S = -\frac{4\pi\sigma_0}{\varepsilon} \quad (24)$$

This condition seems analogous to the condition (5b) expressing the balance of forces on the polymer. We may conclude that there is a formal analogy between the total curvature,  $J$ , and the electric potential,  $\psi$ , the screening length,  $\lambda = \sqrt{\kappa/\gamma_0}$ , and the Debye length,  $\chi^{-1}$ , the ridge angle,  $\psi_0$ , and the surface charge density,  $\sigma_0$ . In an insulated membrane, the total surface charge density  $\sigma_0$  remains constant; however the distribution of charges on the two sides is not be the same. The normal derivative of the potential at any point on the membrane determines the surface charge density at that point. The difference of the normal derivative of the potential on the two sides (excess charge) seems analogous to the tilt angle  $\theta_t$  in our problem.

However, the problem of the embedded polymer is richer than that of the charged membrane, as there are no electrostatic analogies for the Gaussian curvature,  $K$ , and the modulus of Gaussian curvature,  $\bar{\kappa}$ . Therefore, the instability of the polymer shape produced by  $\Delta\bar{\kappa}$ , does not come into play in the case of charged membrane.

## Appendix A

### Determination of Curvature

We determine the curvature by solving the boundary value problem comprising of equation (4) and the boundary conditions (5b) and (8). We assume a Fourier series expansion as a solution for  $J$

$$J_{L,R}(x, y) = \sum_{n=0}^{\infty} (a_n^{L,R}(x)\cos(nky) + b_n^{L,R}(x)\sin(nky))$$

---

<sup>(1)</sup> here  $k_B$  is the Boltzmann constant,  $\varepsilon$  is the dielectric constant of the electrolyte,  $\rho_0$  is the bulk charge density of the electrolyte, and  $q$  is the charge of each ion.

However, since the shape of the undulating polymer (1) is given by an even function of  $y$ , we may assume that  $J$  also is even in  $y$ , *i.e.*

$$J_{L,R}(x, y) = \sum_{n=0}^{\infty} a_n^{L,R}(x) \cos(nky) \tag{A.1}$$

Inserting in (4) subject to the boundary condition (8), we may further find the form of the functions  $a_n(x)$ . The result is

$$J_{L,R}(x, y) = \sum_{n=0}^{\infty} A_n^{L,R} \cos(nky) \exp(\pm p_n x) \tag{A.2}$$

where  $p_n^2 = q^2 + n^2 k^2$ , and the  $A_n$ 's are unknown constants which will be determined from the boundary condition (5b).

The derivatives of curvature (A.2) entering the boundary condition (5b) may be written as follows

$$\begin{aligned} \frac{dJ_{L,R}}{dm} &= \sum_{n=0}^{\infty} \pm p_n A_n^{L,R} \cos(nky) \frac{\exp(\pm p_n x)}{\sqrt{1 + \varepsilon^2 k^2 \sin^2(ky)}} \\ &\quad - \sum_{n=0}^{\infty} nk A_n^{L,R} \sin(nky) \frac{\varepsilon k \sin(ky) \exp(\pm p_n x)}{\sqrt{1 + \varepsilon^2 k^2 \sin^2(ky)}} \end{aligned} \tag{A.3}$$

Here use has been made of the fact that the projection of the normal to the polymer on the  $x$ - $y$  plane is

$$\hat{m} = (1, \varepsilon k \sin ky) \frac{1}{\sqrt{1 + \varepsilon^2 k^2 \sin^2 ky}}$$

and that

$$\frac{dJ}{dm} = \frac{dJ}{dx} \frac{1}{\sqrt{1 + \varepsilon^2 k^2 \sin^2(ky)}} + \frac{dJ}{dy} \frac{\varepsilon k \sin(ky)}{\sqrt{1 + \varepsilon^2 k^2 \sin^2(ky)}}$$

We may further make a perturbative expansion of  $J$  (valid for the case of small amplitudes of polymer undulation) and solve the problem described above order by order up to second order in  $\varepsilon$ . Therefore, if we write

$$J(x, y) = J^{(0)}(x) + \varepsilon J^{(1)}(x) + \varepsilon^2 J^{(2)}(x) + \dots \tag{A.4}$$

we must also consider a corresponding expansion of the coefficients  $A_n$ 's as defined in (A.2)

$$A_n = A_n^{(0)} + \varepsilon A_n^{(1)} + \varepsilon^2 A_n^{(2)} + \dots \tag{A.5}$$

In the zeroth order  $J = J^{(0)}(x)$ , and is not a function of  $y$ , so that the only coefficient in (A.3) which is different from zero is  $A^{(0)}$

We may thus write

$$J_{L,R}^{(0)} = A_0^{L,R(0)} \exp(\pm qx)$$

The constants  $A_0^{L,R(0)}$  are determined from the boundary condition (5b) whose form in the zeroth order in  $\varepsilon$  gives  $A_0^{L(0)} + A_0^{R(0)} = q\psi_0$ .

Since, in the zeroth order we expect the profile of the membrane to be symmetric on the two sides of the ridge, we have  $A_0^{L(0)} = A_0^{R(0)} = \frac{q\psi_0}{2}$  and

$$J_{L,R}^{(0)} = \frac{q\psi_0}{2} \exp(\pm qx) \quad (\text{A.6})$$

Moving next to the first order, we have

$$J_{L,R}^{(1)}(x, y) = \sum_{n=0}^{\infty} A_n^{L,R(1)} \cos(nky) \exp(\pm p_n x)$$

In this order (5b) may be written as  $\frac{dJ_L^{(1)}}{dm} = \frac{dJ_R^{(1)}}{dm}$ . Again using (A.3) at  $x = x_p = \varepsilon \cos(ky)$ , we have

$$A_0^{L(0)} q^2 \cos(ky) + \sum A_n^{L(1)} p_n \cos(nky) = A_0^{R(0)} q^2 \cos(ky) - \sum A_n^{R(1)} p_n \cos(nky)$$

This gives us  $A_n^{L(1)} = -A_n^{R(1)}$ .

Solving finally in the second order, we assume solutions of the form

$$J_{L,R}^{(2)}(x, y) = \sum_{n=0}^{\infty} A_n^{L,R(2)} \cos(nky) \exp(\pm p_n x)$$

The boundary condition (5b) is expressed as  $\frac{dJ_L^{(2)}}{dm} = \frac{dJ_R^{(2)}}{dm}$

Substituting  $x = x_p = \varepsilon \cos(ky)$  in (A.3) we obtain in this order

$$\begin{aligned} & -qA_0^{L(0)} \frac{k^2}{2} \sin^2(ky) + qA_0^{L(0)} \frac{q^2}{2} \cos^2(ky) - \sum A_n^{L(1)} p_n^2 \cos(ky) \cos(nky) + \sum A_n^{L(2)} p_n \cos(nky) \\ & + k^2 \sin(ky) \sum n A_n^{L(1)} \sin(nky) = qA_0^{R(0)} \frac{k^2}{2} \sin^2(ky) - qA_0^{R(0)} \frac{q^2}{2} \cos^2(ky) \\ & + \sum A_n^{R(1)} p_n^2 \cos(ky) \cos(nky) - \sum A_n^{R(2)} p_n \cos(nky) - k^2 \sin(ky) \sum n A_n^{R(1)} \sin(nky) \end{aligned}$$

We may first deduce from this expression that  $A_1^{L(1)} = -A_1^{R(1)} \equiv -\alpha$ , while all  $A_n^{(1)}$ 's with  $n \neq 1$  vanish, so that we may write

$$J_{L,R}^{(1)}(x, y) = \mp \alpha \cos ky \exp(\mp p_1 x). \quad (\text{A.7})$$

Here  $\alpha$  is an undetermined parameter which will be identified on solving the problem for  $h$ .

The only second order coefficients that do not vanish are those of  $n = 0$  and 2, with  $A_n^{L(2)} = A_n^{R(2)} \equiv A_n^{(2)}$  and

$$A_0^{L(2)} + A_0^{R(2)} \equiv 2A_0^{(2)} = \alpha q + \frac{\psi_0 q}{2} (k^2 - q^2)$$

and

$$A_2^{L(2)} + A_2^{R(2)} \equiv 2A_2^{(2)} = \alpha \frac{p_1^2 + k^2}{p_2} - \frac{\psi_0 p_1^2 q^2}{2 p_2}$$

We may thus write

$$\begin{aligned} J_{L,R}^{(2)}(x, y) &= \frac{1}{2} \left[ \alpha q + \frac{\psi_0 q}{2} (k^2 - q^2) \right] \exp(\pm qx) + \frac{1}{2} \\ &\quad \left[ \alpha \frac{p_1^2 + k^2}{p_2} - \frac{\psi_0 p_1^2 q^2}{2 p_2} \right] \exp(\pm p_2 x) \cos(2ky) \end{aligned} \quad (\text{A.8})$$

**Appendix B**

**Determination of Height**

The height is given by the following 2nd order inhomogeneous differential equation

$$h_{xx} + h_{yy} = J$$

As mentioned in the main text, solutions to such an equation are of two kinds: the particular solution,  $h_{ps}$  which may be derived directly from integrating (10), and the general solution of the homogeneous equation  $\nabla^2 h = 0$ . We shall call this the minimal surface solution,  $h_{ms}$ , as it corresponds to vanishing total curvature  $J = 0$ . Again, by a similar reasoning as for  $J$ , we assume the following forms for the two kinds of solutions:

$$h_{ms}^{L,R} = \sum_{n=1}^{\infty} c_n^{L,R} e^{\pm nky} \cos(nkx) \quad \text{and} \quad h_{ps}^{L,R} = \sum_{n=0}^{\infty} d_n^{L,R} e^{\pm p_n x} \cos(nky)$$

The height functions must also satisfy boundary conditions (6a), (6b) and (7). In particular, we shall make use of (7), (10) and the following combination of the equations (6a) and (6b):

$$\chi_L^2 = (h_L)_x^2 + (h_L)_y^2 = \left( \frac{\psi_0}{2} + \theta_t \right)^2 \tag{B.1a}$$

and

$$\chi_R^2 = (h_R)_x^2 + (h_R)_y^2 = \left( \frac{\psi_0}{2} - \theta_t \right)^2 \tag{B.1b}$$

with the derivatives taken at the polymer. As mentioned in the Discussion, there is an approximation of the order  $\varepsilon^4$  involved when we express the boundary conditions (6) in terms of the gradient angles...

As in the case of determination of  $J$ , in order to determine the above coefficients  $c_n^{L,R}$  and  $d_n^{L,R}$  for all orders (upto 2nd order in  $\varepsilon$ ), we expand the height function in powers of  $\varepsilon$

$$h(x, y) = h^{(0)}(y) + \varepsilon h^{(1)}(x, y) + \varepsilon^2 h^{(2)}(x, y) + \dots \tag{B.2}$$

for both right and left hand sides and we introduce a corresponding expansion of the coefficients

$$c_n = c_n^{(0)} + \varepsilon c_n^{(1)} + \varepsilon^2 c_n^{(2)} + \dots \quad \text{and} \quad d_n = d_n^{(0)} + \varepsilon d_n^{(1)} + \varepsilon^2 d_n^{(2)} + \dots$$

We further express the boundary condition (7) as

$$h_L(x_p, y) = h_R(x_p, y) = h_p(y) = h_p^{(0)} + \varepsilon h_p^{(1)} + \varepsilon^2 h_p^{(2)} + \dots \tag{B.3}$$

In lowest order ( $\varepsilon^0$ ), since the solutions do not show any  $y$  dependence, the  $h_{ms}$  solutions of zeroth order do not contribute and we have

$$h^{L,R(0)} = d_0^{L,R} e^{\pm qx}$$

satisfying the boundary conditions for both right-hand and left-hand sides, and

$$h^{L(0)}(x = 0) = h^{R(0)}(x = 0) = h_p^{(0)}$$

We get

$$h^{L,R(0)}(x) = \frac{\psi_0}{2q} e^{\pm qx} \tag{B.4}$$

The zeroth order contribution to the height of the ridge is

$$h_p^{(0)} = \frac{\psi_0}{2q}. \tag{B.5}$$

Let us next consider solutions of first order, namely

$$h^{L(1),R} = \sum_{n=0}^{\infty} d_n^{L,R(1)} e^{\pm p_n x} \cos(nky) + \sum_{n=1}^{\infty} c_n^{L,R(1)} e^{\pm nkx} \cos(nky).$$

The function  $h^{(1)}$  satisfies the following boundary conditions representing (B.1a), (B.1b) and (B.3), respectively:

$$\begin{aligned} (d_0^{L(0)})^2 q^3 \cos(ky) + d_0^{L(0)} q \sum p_n d_n^{L(1)} \cos(nky) + d_0^{L(0)} q \sum nk c_n^{L(1)} \cos(nky) &= \frac{\psi_0}{2} \theta_1 \cos(ky) \\ -(d_0^{R(0)})^2 q^3 \cos(ky) + d_0^{R(0)} q \sum p_n d_n^{R(1)} \cos(nky) + d_0^{R(0)} q \sum nk c_n^{R(1)} \cos(nky) &= -\frac{\psi_0}{2} \theta_1 \cos(ky) \\ \sum (c_n^{L(1)} + d_n^{L(1)}) \cos(nky) + q d_0^{L(0)} \cos(ky) &= \sum (c_n^{R(1)} + d_n^{R(1)}) \cos(nky) - q d_0^{R(0)} \cos(ky) \\ &= h_p^{(1)} \end{aligned}$$

It is straightforward to get the following expressions for  $h^{(1)}$ .

$$\begin{aligned} h^{(1)L} &= \left( \frac{\psi_0}{2} (q - k) - \theta_1 \right) \frac{e^{p_1 x} \cos(ky)}{k - p_1} + \left( \frac{\psi_0}{2} (p_1 - q) + \theta_1 \right) \frac{e^{kx} \cos(ky)}{k - p_1} \quad \text{and} \\ h^{(1)R} &= - \left( \frac{\psi_0}{2} (q - k) - \theta_1 \right) \frac{e^{-p_1 x} \cos(ky)}{k - p_1} - \left( \frac{\psi_0}{2} (p_1 - q) + \theta_1 \right) \frac{e^{-kx} \cos(ky)}{k - p_1} \end{aligned} \tag{B.6}$$

First order contribution to the height of the ridge:

$$h_p^{(1)} = 0 \tag{B.7}$$

Equations of second order in  $\epsilon$  may be written as:

$$h^{L(2),R} = \sum_{n=0}^{\infty} d_n^{L,R(2)} e^{\pm p_n x} \cos(nky) + \sum_{n=1}^{\infty} c_n^{L,R(2)} e^{\pm nkx} \cos(nky)$$

The coefficients in this equation are obtained from the boundary conditions (B.1a) and (B.1b), expressed as

$$\begin{aligned} &\cos^2(ky) \left( \left( q^2 d_0^{L,R(0)} \right)^2 + q^4 \left( d_0^{L,R(0)} \right)^2 \right) \\ &+ 2\cos^2(ky) \left( q^2 d_0^{L,R(0)} \left( c_1^{L,R(1)} k + d_1^{L,R(1)} p_1 \right) + q d_0^{L,R(0)} \left( c_1^{L,R(1)} k^2 + d_1^{L,R(1)} p_1^2 \right) \right) \\ &+ \left( c_1^{L,R(1)} k + d_1^{L,R(1)} p_1 \right)^2 + k^2 \sin^2(ky) \left( c_1^{L,R(1)} + d_1^{L,R(1)} \right)^2 \\ &+ 2q \cos(ky) d_0^{L,R(0)} \sum \left[ nk c_n^{L,R(2)} + p_n d_n^{L,R(2)} \right] \\ &= \theta_1^2 \cos^2(ky) \pm 2 \frac{\psi_0}{2} \theta_2 \cos(ky) \end{aligned}$$

and from the boundary condition (B.5)

$$\begin{aligned} & \sum \left( c_n^{L(2)} + d_n^{L(2)} \right) \cos(ky) + \cos^2(ky) \left( c_1^{L(1)} k + d_1^{L(1)} p_1 \right) + \frac{\cos^2(ky)}{2} q^2 d_0^{L(0)} \\ & = \sum \left( c_n^{R(2)} + d_n^{R(2)} \right) \cos(ky) + \cos^2(ky) \left( c_1^{R(1)} k + d_1^{R(1)} p_1 \right) + \frac{\cos^2(ky)}{2} q^2 d_0^{R(0)} = h_p^{(2)} \end{aligned}$$

Straightforward calculations lead to:

$$\begin{aligned} h^{L,R(2)} &= -\frac{1}{2q} \left[ \frac{\psi_0}{2} \left( \frac{q^2}{2} + \frac{k^2 p_1 + q^3 - p_1^2 k}{k - p_1} \right) - \theta_1 \frac{q^2}{k - p_1} \right] e^{\pm qx} \\ &+ \cos(2ky) \left\{ \frac{e^{\pm p_2 x}}{2p_2} \left[ \frac{\psi_0}{2} \left( \frac{-q^2}{2} + \frac{k - q}{k - p_1} p_1^2 \right) + \theta_1 \frac{p_1^2}{k - p_1} \right] - \frac{ke^{\pm 2kx}}{4} \left[ \frac{\psi_0}{2} \frac{k - q}{k - p_1} + \frac{\theta_1}{k - p_1} \right] \right\} \end{aligned} \quad (\text{B.8})$$

and  $\theta_2 = 0$ .

For the second order contribution to the height of the ridge, we get

$$\begin{aligned} h_p^{(2)}(y) &= -\frac{1}{2q} \left[ \frac{\psi_0}{2} \left( \frac{p_1^2 + q^2}{2} + \frac{k^2 p_1 + q^3 - p_1^2 k}{k - p_1} \right) - \theta_1 \left( q + \frac{q^2}{k - p_1} \right) \right] \\ &+ \cos(2ky) \left[ -\frac{1}{4p_2} \left\{ \frac{\psi_0}{2} \left( q^2 - k^2 + 2 \frac{k^2 p_1 + q^3 - p_1^2 k}{k - p_1} \right) - \theta_1 \frac{2q^2}{k - p_1} \right\} + \frac{\theta_1}{2} - \frac{\psi_0 q}{2 \cdot 4} \right] \end{aligned} \quad (\text{B.9})$$

Collecting the contributions of different orders, we arrive at the shape of the membrane (11).

Taking the Laplacian of (11), we find  $\alpha = -q^2 \left( \frac{\psi_0}{2} \frac{q-k}{k-p_1} - \frac{\theta_1}{k-p_1} \right)$ . This gives us a complete solution for  $J$ .

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