Notes on fluctuating membranes and membrane-mediated interactions

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Contents

1 Introduction

Some nice context.

Our base model for the membrane is the Canham-Helfrich Hamiltonian [1, 2]:

$$\mathcal{E}_{\mathrm{CH}} = \int \left[\frac{\kappa}{2}(2H)^2 + \bar{\kappa}K + \sigma\right] \mathrm{d}A, \tag{1}$$

where H and K are the mean and Gaussian curvatures, κ and $\bar{\kappa}$ the bending and Gaussian rigidities, and we included a Lagrange multiplier σ to fix the (projected) membrane surface. We've left out spontaneous curvature; it could be added back in without much difficulty if needed. As per usual, we will invoke the Gauss-Bonnet theorem to integrate the Gaussian curvature term to a constant that only depends on the topology and thus can be ignored. The Lagrange multiplier σ can be interpreted as an effective surface tension (or two-dimensional pressure). For a closed membrane, we can add a term for the volume conservation, of the form

$$p \int \mathrm{d}V, \tag{2}$$

where p is the pressure difference between the inside and the outside of the membrane. For a spherical soap bubble (membrane without bending rigidity) with radius R, variation of the energy then gives the well-known Laplace pressure $p = 2\sigma/R$. A more extensive introduction of the model can be found in many review articles and textbooks, including [3] and [4].

2 Fluctuation of flat membranes

As previously calculated in e.g. [5]; this part contains a verbatim copies of parts of sections 8.2 and 8.3 of [4].

For membranes whose shape is close to one of the equilibrium shapes (a flat membrane, a sphere, or, in the presence of an external force, a cylinder), we can expand the Canham-Helfrich energy in deviations from that equilibrium shape. There are two important applications of this method: 1) The calculation of the fluctuation spectrum of the membrane at finite temperature, which will depend on the material parameters κ and σ, and allow us to determine them experimentally through fitting; and 2) The calculation of the membrane-mediated interaction potential in the weakly curved regime. To arrive at the expansion, we take the unperturbed shape as our reference, using the standard coordinates on that shape to parametrize our membrane (i.e., Cartesian coordinates x and y for the flat membrane, cylindrical coordinates z and ϕ for the tubular membrane, and spherical coordinates θ and ϕ for the spherical membrane). A point on the actual membrane is then described by a height function u that gives its displacement from the unperturbed shape. For example, for the flat membrane, we get:

$$\boldsymbol{r}(x, y) = \begin{pmatrix} x \\ y \\ u(x, y) \end{pmatrix}. \tag{3}$$

The parametrization given in equation (3) is known as the *Monge gauge*, and is in principle valid as long as there are no overhangs in the membrane (i.e. no two points that are mapped to the same reference point in the unperturbed membrane). In practice, one often assumes that both the function u and all of its relevant derivatives are small compared to the lateral size of the membrane. We note that for flat membranes, the function u is often called h in the literature.

2.1 Canham-Helfrich energy in the Monge gauge

To be concrete, we will work in this section with a flat reference frame (so using equation (3) for the membrane's parametrization); the coordinate-independent version of the equation we will arrive at holds for all three cases. We also denote derivatives of $u(x,y)$ by subscripts, so $u_x = \partial_x u(x,y)$. To calculate the appropriate expression for the Canham-Helfrich energy, we need both the mean curvature H and the area element $\mathrm{d}S$, which we readily find to be given by:

$$H = \frac{1}{2}\frac{(1+u_y^2)u_{xx} + (1+u_x^2)u_{yy} - 2u_x u_y u_{xy}}{(1+u_x^2+u_y^2)^{3/2}} \approx \frac{1}{2}(u_{xx}+u_{yy}) \tag{4}$$

$$\mathrm{d}S = \sqrt{\det(g_{ij})}\,\mathrm{d}x\,\mathrm{d}y = \sqrt{1+u_x^2+u_y^2}\,\mathrm{d}x\,\mathrm{d}y \approx (1+\frac{1}{2}(u_x^2+u_y^2))\,\mathrm{d}x\,\mathrm{d}y \tag{5}$$

retaining terms to second order in u. Note that we can also write these quantities in a coordinate-free manner as

$$H = \frac{1}{2}\boldsymbol{\nabla}_\perp^2 u,$$
$$\mathrm{d}S = (1+(\boldsymbol{\nabla}_\perp u)^2)\mathrm{d}x\,\mathrm{d}y,$$

where $\boldsymbol{\nabla}_\perp$ denotes the gradient with respect to the 'flat' coordinates x and y (or their cylindrical and spherical counterparts). We put these expressions into equation 1 for the Canham-Helfrich energy applied to a square patch of size $L \times L$, and obtain to second order in u:

$$\mathcal{E} = \frac{1}{2}\int_{L\times L}\left[\kappa(\boldsymbol{\nabla}_\perp^2 u)^2 + \sigma(\boldsymbol{\nabla}_\perp u)^2\right]\mathrm{d}x\,\mathrm{d}y, \tag{6}$$

plus a constant term σL^2 which does not influence our result.

2.2 Membrane shape equation

Any function $u(x,y)$ that minimizes the energy (6) is an equilibrium shape of the membrane (around which we can expect fluctuations). For the given case, the flat membrane is the obvious solution, but it is instructive to see how we get the relevant shape equation, and which other solutions could be possible. To arrive at the equilibrium shape of a weakly bent membrane in the Monge gauge, we calculate the variation δE of the Canham-Helfrich energy (6) due to an arbitrary variation δu in the height function. Expanding

(6) to first order in δu, we obtain:

$$
\begin{aligned}
E+\delta E &= \frac{1}{2}\int \left[\kappa(\boldsymbol{\nabla}_\perp^2(u+\delta u))^2+\sigma(\boldsymbol{\nabla}_\perp(u+\delta u))^2\right]\mathrm{d}x\,\mathrm{d}y,\\
&= E+\int \left[\kappa(\boldsymbol{\nabla}_\perp^2 u)(\boldsymbol{\nabla}_\perp^2\delta u)+\sigma(\boldsymbol{\nabla}_\perp u)\cdot(\boldsymbol{\nabla}_\perp \delta u)\right]\mathrm{d}x\,\mathrm{d}y,\\
\delta E &= \int \left[\kappa(\boldsymbol{\nabla}_\perp^4 u)-\sigma(\boldsymbol{\nabla}_\perp^2 u)\right]\delta u\,\mathrm{d}x\,\mathrm{d}y, \qquad (7)
\end{aligned}
$$

where we integrated by parts in the last step, and $\boldsymbol{\nabla}_\perp^4 = \boldsymbol{\nabla}_\perp^2\boldsymbol{\nabla}_\perp^2$ is the biharmonic operator. Now if δE is to vanish for arbitrary variations δu, we get the weak-bending shape equation [6, 7]:

$$\kappa(\boldsymbol{\nabla}_\perp^4 u)-\sigma(\boldsymbol{\nabla}_\perp^2 u)=0. \qquad (8)$$

Note that equation (8) requires a set of boundary conditions to generate a solution. For a single fixed point (setting both the height and the derivative) at the origin, the system is rotationally symmetric, and reduces to the one-dimensional modified Bessel equation for the radial coordinate r; consequently, the solution can then be written as a linear combination of modified Bessel functions. If we fix the boundary at some distance away from the origin, the only allowed solution is typically the flat one.

2.3 Membrane fluctuations

To obtain the fluctuation spectrum of a patch of membrane, we expand the deviation $u(\boldsymbol{x})$ with $\boldsymbol{x}=(x,y)$ in Fourier modes:

$$u(\boldsymbol{x})=\sum_{\boldsymbol{q}} u_{\boldsymbol{q}} e^{i\boldsymbol{q}\cdot\boldsymbol{x}}, \qquad (9)$$

$$u_{\boldsymbol{q}}=\frac{1}{L^2}\int_{-L/2}^{L/2}\mathrm{d}x\int_{-L/2}^{L/2}\mathrm{d}y\,u(\boldsymbol{x})e^{-i\boldsymbol{q}\cdot\boldsymbol{x}}, \qquad (10)$$

where $\boldsymbol{q}=(q_x,q_y)=\frac{2\pi}{L}(l_x,l_y)$ with $l_x,l_y\in\mathbb{Z}$. From (9) we obtain

$$\boldsymbol{\nabla}_\perp u(\boldsymbol{x})=\sum_{\boldsymbol{q}} u_{\boldsymbol{q}}(iq_x\hat{\boldsymbol{x}}+iq_y\hat{\boldsymbol{y}})e^{i\boldsymbol{q}\cdot\boldsymbol{x}}, \qquad (11)$$

$$\boldsymbol{\nabla}_\perp^2 u(\boldsymbol{x})=-\sum_{\boldsymbol{q}} u_{\boldsymbol{q}}(\boldsymbol{q}\cdot\boldsymbol{q})e^{i\boldsymbol{q}\cdot\boldsymbol{x}}. \qquad (12)$$

The squares of equations (11) and (12) both appear in equation (6), which relates a real displacement to a real energy. However, the Fourier modes $u_{\boldsymbol{q}}$ can in general be complex, so in order to arrive at a real number, to take the square we multiply with the complex conjugate. We then find:

$$
\begin{aligned}
\int_{L\times L}(\boldsymbol{\nabla}_\perp u(\boldsymbol{x}))^2\mathrm{d}\boldsymbol{x} &= \int_{L\times L}\sum_{\boldsymbol{q},\boldsymbol{q}'} u_{\boldsymbol{q}}u_{\boldsymbol{q}'}^*(q_x\hat{\boldsymbol{x}}+q_y\hat{\boldsymbol{y}})(q_x'\hat{\boldsymbol{x}}+q_y'\hat{\boldsymbol{y}})e^{i\boldsymbol{q}\cdot\boldsymbol{x}}e^{-i\boldsymbol{q}'\cdot\boldsymbol{x}}\mathrm{d}\boldsymbol{x}\\
&= L^2\sum_{\boldsymbol{q}} u_{\boldsymbol{q}}u_{\boldsymbol{q}}^*(\boldsymbol{q}\cdot\boldsymbol{q}), \qquad (13)
\end{aligned}
$$

$$\int_{L\times L}\boldsymbol{\nabla}_\perp^2 u(\boldsymbol{x})^2\mathrm{d}\boldsymbol{x}=L^2\sum_{\boldsymbol{q}} u_{\boldsymbol{q}}u_{\boldsymbol{q}}^*(\boldsymbol{q}\cdot\boldsymbol{q})^2, \qquad (14)$$

where we used that

$$\frac{1}{L^2}\int_{L\times L} e^{-i\boldsymbol{q}\cdot\boldsymbol{x}} e^{i\boldsymbol{q}'\cdot\boldsymbol{x}} \mathrm{d}\boldsymbol{x} = \delta_{\boldsymbol{q}\boldsymbol{q}'}. \tag{15}$$

When we now substitute our expressions (13) and (14) back into the Canham-Helfrich energy, we obtain an expression that is quadratic in each Fourier mode $u_{\boldsymbol{q}}$:

$$E = \frac{1}{2}L^2 \sum_{\boldsymbol{q}} \left[\kappa(\boldsymbol{q}\cdot\boldsymbol{q})^2 + \sigma(\boldsymbol{q}\cdot\boldsymbol{q})\right] u_{\boldsymbol{q}} u_{\boldsymbol{q}}^*. \tag{16}$$

In equation (16) we have expanded the Canham-Helfrich energy in Fourier modes, with one mode per $(2\pi/L)^2$ in $\boldsymbol{q}$-space. The equipartition theorem tells us that each quadratic mode in the energy contributes $\frac{1}{2}k_{\mathrm{B}}T$ to the thermal energy of a system. If we equate the energy of each of the modes with that thermal energy, we find for the thermal average of a mode

$$\left\langle |u_q|^2 \right\rangle = \left\langle u_{\boldsymbol{q}} u_{\boldsymbol{q}}^* \right\rangle = \frac{1}{L^2}\frac{k_{\mathrm{B}}T}{\kappa q^4 + \sigma q^2}, \tag{17}$$

where q is the length of $\boldsymbol{q}$.

3 Fluctuations of spherical membranes

3.1 A spherical version of the Monge gauge

Expansions in this part follow [8].

We can do much the same as in section 2 for fluctuations around a spherical membrane. Our 'Monge gauge' description of the membrane in spherical coordinates (ρ, θ, ϕ) (with the origin at the center of the vesicle) can be written as a simple expansion of the distance between the membrane and the origin (i.e. the 'local radius'):

$$r(\theta, \phi) = R\left[1 + u(\theta, \phi)\right], \tag{18}$$

where R is the radius of the sphere describing the membrane in the absence of fluctuations. Rather than expanding in Fourier modes, it now makes sense to expand in their spherical counterpart, the spherical harmonics $Y_l^m(\theta, \phi)$ (see appendix). As is well known, the $l = 0$ mode represents uniform growing/shrinking of the vesicle, and the three modes with $l = 1$ represent translations (in the three cardinal directions if we use real spherical harmonics); we will of course ignore these translation modes when talking about fluctuations.

We can express the volume, area, and energy of the vesicle in terms of the 'fluctuation function' u. We first define

$$V_0 = \frac{4}{3}\pi R^3, \qquad S_0 = 4\pi R^2(1+s),$$

so s is any access area (compared to a sphere) present in the membrane. We can then calculate the actual volume and area to second order in u:

$$V[u] = \frac{1}{3}R^3 \int (1+u)^3 \,\mathrm{d}\Omega \approx R^3 \int \left(\frac{1}{3} + u + u^2\right) \mathrm{d}\Omega, \tag{19a}$$

$$S[u] = R^2 \int \left[(1+u)^2 + \frac{1}{2}\left(\boldsymbol{\nabla}_{\perp} u\right)^2\right] \mathrm{d}\Omega, \tag{19b}$$

where $\mathrm{d}\Omega = \sin\theta \mathrm{d}\theta \mathrm{d}\phi$ is the solid angle, the integrals are over the whole surface ($0 \leq \theta \leq \pi$, $0 \leq \phi \leq 2\pi$), and $(\boldsymbol{\nabla}_\perp u)^2$ as defined in equation (24a).

The calculation of the bending energy is now more work, but remains straightforward. As intermediate steps, we find for the mean curvature, twice the square of the mean curvature and for the square root of the metric, to second order in u:

$$H = \frac{1}{R}\left[1 - \frac{1}{2}\left(2u + \boldsymbol{\nabla}_\perp^2 u\right) + u\left(u + \boldsymbol{\nabla}_\perp^2 u\right)\right], \tag{20}$$

$$(2H)^2 = \frac{4}{R^2}\left[1 - \left(2u + \boldsymbol{\nabla}_\perp^2 u\right) + \left(2u^2 + 2u\boldsymbol{\nabla}_\perp^2 u + \frac{1}{4}\left(2u + \boldsymbol{\nabla}_\perp^2 u\right)^2\right)\right], \tag{21}$$

$$\sqrt{\det(\boldsymbol{g})} = \left[1 + 2u + u^2 + \frac{1}{2}\left(\boldsymbol{\nabla}_\perp u\right)^2\right] R^2 \sin\theta, \tag{22}$$

where we grouped terms in the first line for easier reading of the order. The product of these two terms (retaining only terms to quadratic order in u) gives us the bending energy of the sphere as a functional of u:

$$\mathcal{E}_{\text{bending}}^{\text{sphere}}[u] = \frac{\kappa}{2}\int \left[4 - 4\boldsymbol{\nabla}_\perp^2 u + 4u\boldsymbol{\nabla}_\perp^2 u + \left(\boldsymbol{\nabla}_\perp^2 u\right)^2 + 2\left(\boldsymbol{\nabla}_\perp u\right)^2\right] \mathrm{d}\Omega, \tag{23}$$

where, in spherical coordinates (with subscripts on u denoting partial derivatives):

$$\left(\boldsymbol{\nabla}_\perp u\right)^2 = u_\theta^2 + \frac{1}{\sin^2\theta} u_\phi^2, \tag{24a}$$

$$\boldsymbol{\nabla}_\perp^2 u = u_{\theta\theta} + \frac{\cos\theta}{\sin\theta} u_\theta + \frac{1}{\sin^2\theta} u_{\phi\phi}. \tag{24b}$$

The full energy functional now contains contributions from curvature, surface, and volume, and reads

$$\begin{aligned}\mathcal{E}[u] = \kappa \int \Bigg[& 2 - 2\boldsymbol{\nabla}_\perp^2 u + 2u\boldsymbol{\nabla}_\perp^2 u + \frac{1}{2}\left(\boldsymbol{\nabla}_\perp^2 u\right)^2 + \left(\boldsymbol{\nabla}_\perp u\right)^2 \\ & + \bar{\sigma}\left(1 + 2u + u^2 + \frac{1}{2}\left(\boldsymbol{\nabla}_\perp u\right)^2\right) - \bar{p}\left(\frac{1}{3} + u + u^2\right)\Bigg] \mathrm{d}\Omega,\end{aligned} \tag{25}$$

where we introduced dimensionless versions of the surface tension and the pressure:

$$\bar{\sigma} = \frac{\sigma R^2}{\kappa}, \qquad \bar{p} = \frac{p R^3}{\kappa}. \tag{26}$$

Note that in equation (25), we have added the constraint to keep the volume constant; we have also dropped irrelevant constant terms.

3.2 Membrane shape equation

To find the shape equation of a membrane with a spherical reference state, we proceed as before, and introduce a variation δu to the equilibrium shape u_0 (where we add the subscript 0 to distinguish the equilibrium shape from the general deformation u). As before, we calculate the variation of the energy to first order in δu:

$$\begin{aligned}
\mathcal{E}+\delta\mathcal{E} = \kappa \int \Big[& 2 - 2\,\boldsymbol{\nabla}_\perp^2(u+\delta u) + 2(u+\delta u)\boldsymbol{\nabla}_\perp^2(u+\delta u) \\
& + \frac{1}{2}\left(\boldsymbol{\nabla}_\perp^2(u+\delta u)\right)^2 + \left(\boldsymbol{\nabla}_\perp(u+\delta u)\right)^2 \\
& + \bar{\sigma}\left(1 + 2(u+\delta u) + (u+\delta u)^2 + (\boldsymbol{\nabla}_\perp(u+\delta u))^2\right) \\
& - \bar{p}\left(\frac{1}{3} + (u+\delta u) + (u+\delta u)^2\right)\Big]\,\mathrm{d}\Omega \\
= \mathcal{E} + \kappa \int \Big[& -2\,\boldsymbol{\nabla}_\perp^2(\delta u) + 2\,u\,\boldsymbol{\nabla}_\perp^2(\delta u) + 2\,\delta u\,\boldsymbol{\nabla}_\perp^2 u + \left(\boldsymbol{\nabla}_\perp^2 u\right)\left(\boldsymbol{\nabla}_\perp^2 \delta u\right) \\
& + 2\,(\boldsymbol{\nabla}_\perp u)\cdot(\boldsymbol{\nabla}_\perp \delta u) \\
& + \bar{\sigma}\left(2\,\delta u + 2\,u\,\delta u + (\boldsymbol{\nabla}_\perp u)\cdot(\boldsymbol{\nabla}_\perp \delta u)\right) - \bar{p}\,(\delta u + 2\,u\,\delta u)\Big]\,\mathrm{d}\Omega. \qquad (27)
\end{aligned}$$

Integrating by parts, we find for the variation of the energy:

$$\begin{aligned}
\delta\mathcal{E} = & -2\kappa \int \boldsymbol{\nabla}_\perp^2(\delta u)\,\mathrm{d}\Omega \\
& + \kappa \int \Big[\left(4\,\boldsymbol{\nabla}_\perp^2 u + \boldsymbol{\nabla}_\perp^2\left(\boldsymbol{\nabla}_\perp^2 u\right) - 2\,\boldsymbol{\nabla}_\perp^2 u\right)\delta u \\
& \qquad + \bar{\sigma}\left(2\delta u + 2u\delta u - (\boldsymbol{\nabla}_\perp^2 u)\delta u\right) - \bar{p}\,(\delta u + 2u\delta u)\Big]\,\mathrm{d}\Omega, \\
= & \;\kappa \int \left[2\,\boldsymbol{\nabla}_\perp^2 u + \boldsymbol{\nabla}_\perp^2\left(\boldsymbol{\nabla}_\perp^2 u\right) + 2\bar{\sigma}(1+u) - \bar{\sigma}(\boldsymbol{\nabla}_\perp^2 u) - \bar{p}(1+2u)\right]\delta u\,\mathrm{d}\Omega. \qquad (28)
\end{aligned}$$

The linear term in the energy (with the Laplacian of u) gave us the Laplacian of δu; writing out the terms, we find that (after one integration by parts) the terms over θ cancel; the remaining term with the second derivative to ϕ is identically zero for any δu that satisfies the periodicity of ϕ. For a minimum energy shape, the variation of the energy must also vanish, so we obtain for the shape equation:

$$\mathcal{L}[u] \equiv \boldsymbol{\nabla}_\perp^2\left(\boldsymbol{\nabla}_\perp^2 u\right) + (2-\bar{\sigma})\boldsymbol{\nabla}_\perp^2 u + 2(\bar{\sigma}-\bar{p})u = \bar{p} - 2\bar{\sigma}. \qquad (29)$$

For the sphere, $\mathcal{L}[u] = 0$, and we retrieve the expression for the Laplace pressure, $p = 2\sigma/R$. To get the fluctuation spectrum, it is useful to expand our functions u in eigenfunctions of the operator $\mathcal{L}$. As it happens, these are just the spherical harmonics, the 'Fourier modes' on the sphere, defined as (see appendix):

$$Y_n^m(\theta,\phi) = (-1)^m\sqrt{\frac{2n+1}{4\pi}\frac{(n-m)!}{(n+m)!}}P_n^m(\cos\theta)e^{im\phi}, \qquad (30)$$

where the $P_n^m(x)$ are the associated Legendre polynomials. We could also introduce real versions (also eigenfunctions) of the spherical harmonics simply by combining the $\pm m$ versions (giving us sines and cosines). The eigenvalues λ_n of the spherical harmonics as eigenfunctions of our operator $\mathcal{L}$ depend only on the value of n, and are given by (as can be checked easily from the defining equation (51) of the spherical harmonics):

$$\lambda_n = n^2(n+1)^2 - n(n+1)(2-\bar{\sigma}) + 2(\bar{\sigma}-\bar{p}). \qquad (31)$$

3.3 Membrane fluctuations

To find the fluctuation spectrum around a spherical membrane, we expand the 'height' function $u(\theta, \phi)$ in spherical harmonics, i.e., we write

$$u(\theta, \phi) = \sum_{n,m} u_{nm} Y_n^m(\theta, \phi), \tag{32}$$

where the spherical harmonics can be either the real or the complex functions (it won't matter if we focus only on the equatorial plane). We already know what the surface Laplacian does with the spherical harmonics, but we also need the square of the gradient, which we can find using the orthonormality of the spherical harmonics:

$$(\nabla_\perp Y_n^m)^2 = \langle \nabla_\perp Y_n^m \,|\, \nabla_\perp Y_n^m \rangle = -\left\langle Y_n^m \,\middle|\, \nabla_\perp^2 Y_n^m \right\rangle = n(n+1) \langle Y_n^m \,|\, Y_n^m \rangle = n(n+1). \tag{33}$$

For the vesicle volume and surface area we then obtain (where $u_0 = u_{00}$ is the amplitude of the zeroth-order volume-changing mode):

$$V[u] = \frac{4}{3} R^3 (1 + u_0)^3 + R^3 \sum_{n>0} |u_{nm}|^2 , \tag{34a}$$

$$S[u] = 4\pi R^2 (1 + u_0)^2 + R^2 \sum_{n>0} |u_{nm}|^2 \left(1 + \frac{1}{2} n(n+1)\right), \tag{34b}$$

while for the bending energy we get

$$\mathcal{E}_{\text{bending}}[u] = 8\pi\kappa + \frac{\kappa}{2} \sum_{n,m} n(n+2)(n+1)(n-1) |u_{nm}|^2 . \tag{34c}$$

4 Interactions on flat membranes

Dommersnes and Fournier [9] solved the problem of the interaction of N point-like inclusions on flat membranes by imposing constraints on the three second derivatives of the height function at the position of every inclusion. Their results apply to tension-free membranes, but can be extended relatively easily to membranes with tension [4]. The result for two particles reproduces the known result. It can also be extended to tubular membranes [10]. Extending it to spherical membranes has proved difficult however, due to the intrinsic curvature of the sphere. Therefore, we'll take a different approach here: rather than setting the second derivatives of the height function u, we set the mean curvature at the inclusion points; the result should be the same as that of Dommersnes and Fournier (extended to membranes with tension) in the case that the imposed derivatives are isotropic. Note that we can still put different values of the mean curvature for different inclusions.

Our starting point is the Canham-Helfrich energy in the Monge gauge, to second order in the height function u, equation (6). To this energy we add constraints on the mean curvature at specific points $\boldsymbol{x} = \boldsymbol{x}_\alpha$ (where $\boldsymbol{x} = (x, y)$). These constraints only go up to linear order in u, due to the presence of the Dirac delta function that localizes the point. For N inclusions, we then have

$$\mathcal{E} = \frac{1}{2}\kappa \int \left[(\boldsymbol{\nabla}_\perp^2 u)^2 + k^2 (\boldsymbol{\nabla}_\perp u)^2 - \sum_\alpha \Lambda_\alpha \left((\boldsymbol{\nabla}_\perp^2 u) - 2H_\alpha \right) \delta_\perp (\boldsymbol{x} - \boldsymbol{x}_\alpha) \right] \mathrm{d}x \, \mathrm{d}y, \tag{35}$$

where $k = \sqrt{\sigma/\kappa}$ is the reciprocal of a characteristic length scale, the sum runs over all inclusions, H_α is the imposed mean curvature, and Λ_α the Lagrange multiplier that fixes the imposed constraint. If we now perform the same variational calculation as in section 2.2, we obtain for the variation in the energy

$$\delta E = \kappa \int \left[(\boldsymbol{\nabla}_\perp^4 u) - k^2 (\boldsymbol{\nabla}_\perp^2 u) - \sum_\alpha \Lambda_\alpha \left(\boldsymbol{\nabla}_\perp^2 \delta_\perp (\boldsymbol{x} - \boldsymbol{x}_\alpha) \right) \right] \delta u \, \mathrm{d}x \, \mathrm{d}y, \tag{36}$$

and thus our shape equation becomes

$$(\boldsymbol{\nabla}_\perp^4 u) - k^2 (\boldsymbol{\nabla}_\perp^2 u) = \sum_\alpha \Lambda_\alpha \left(\boldsymbol{\nabla}_\perp^2 \delta_\perp (\boldsymbol{x} - \boldsymbol{x}_\alpha) \right). \tag{37}$$

The equation of Dommersnes and Fournier [9] is similar, and they proceed by writing down the Green's function of the linear operator on the left-hand side. For the case where the tension is nonzero, that Green's function is given by

$$G(\boldsymbol{x}) = -\frac{1}{2\pi k^2} \left[K_0(kr) + \log(kr) \right], \tag{38}$$

where $r = |\boldsymbol{x}|$, K_0 is the zeroth modified Bessel function of the second kind, and log represents the natural logarithm. We take a different approach here that we can more easily extend to the spherical case. We write both u and $\delta_\perp$ in terms of Fourier modes (see section 2.3 for the expansion of u); for the Dirac delta function we get the simple expansion

$$\delta_\perp(\boldsymbol{x}) = \sum_{\boldsymbol{q}} e^{-i\boldsymbol{q}\cdot\boldsymbol{x}_\alpha} e^{i\boldsymbol{q}\cdot\boldsymbol{x}}. \tag{39}$$

As the Fourier components are all orthogonal, equation (37) must be satisfied for each component, i.e., for each wave vector $\boldsymbol{q}$, which gives us the simple relation

$$\left(q^4 + k^2 q^2 \right) u_{\boldsymbol{q}} = -\sum_\alpha \Lambda_\alpha q^2 e^{-i\boldsymbol{q}\cdot\boldsymbol{x}_\alpha} \tag{40}$$

Equation (40) still contains the unknown Lagrange multipliers Λ_α. We can find them by calculating the mean curvature from the shape u and equating it to the imposed mean curvature at each point $\boldsymbol{x}_\alpha$, which gives us exactly N equations for the N unknowns:

$$\begin{aligned} 2H_\alpha = 2\, H|_{\boldsymbol{x}=\boldsymbol{x}_\alpha} &= \left(\boldsymbol{\nabla}_\perp^2 u \right)\big|_{\boldsymbol{x}=\boldsymbol{x}_\alpha} \\ &= \sum_{\boldsymbol{q}} \frac{q^2}{q^4 + k^2 q^2} \sum_\beta \Lambda_\beta q^2 e^{-i\boldsymbol{q}\cdot\boldsymbol{x}_\beta} e^{i\boldsymbol{q}\cdot\boldsymbol{x}_\alpha} \\ &= \sum_\beta \Lambda_\beta \sum_{\boldsymbol{q}} \frac{e^{-i\boldsymbol{q}\cdot\left(\boldsymbol{x}_\beta - \boldsymbol{x}_\alpha\right)}}{1 + k^2/q^2} = \sum_\beta M_{\alpha\beta} \Lambda_\beta \end{aligned} \tag{41}$$

Formally the problem is now solved. We can invert equation (41) to find the Lagrange multipliers $\Lambda_\beta = 2\sum_\alpha M_{\alpha\beta}^{-1} H_\alpha$, which we substitute in (40) to get the amplitudes $u_{\boldsymbol{q}}$ for the modes, and eventually the solution $u(\boldsymbol{x})$. We'll need to regularize the diagonal elements of the matrix M by introducing a finite-wavenumber cutoff in the sum over $\boldsymbol{q}$, and evaluating the elements of M (or u) in closed form is not easy, but we can approximate the actual solution numerically relatively easily by introducing a general cutoff and evaluating our sums explicitly. [TO DO but we move to spheres first.]

5 Interaction on spherical membranes

In contrast to flat membranes, no closed-form solution for the interaction between particles on a spherical membrane is known. However, we can easily generalize the Fourier method approach from section 4 to spheres, and give a similar formal solution. The main difference is that the Fourier modes are now the spherical harmonics $Y_n^m(\theta,\phi)$ and our Dirac delta function in the angular coordinates carries a $1/(R^2\sin(\theta))$ prefactor, i.e.

$$\delta_\perp(\theta-\theta_0,\phi-\phi_0)=\frac{\delta(\theta-\theta_0)\delta(\phi-\phi_0)}{R^2\sin(\theta)} \tag{42}$$

such that

$$R^2\int\delta_\perp(\theta-\theta_0,\phi-\phi_0)\,\mathrm{d}\Omega=\int_0^\pi\delta(\theta-\theta_0)\,\mathrm{d}\theta\int_0^{2\pi}\delta(\phi-\phi_0)\,\mathrm{d}\phi=1. \tag{43}$$

The Canham-Helfrich energy with constraints on the mean curvature now reads

$$\begin{aligned}\mathcal{E}[u]=\kappa\int\Bigg[&2-2\boldsymbol{\nabla}_\perp^2u+2u\boldsymbol{\nabla}_\perp^2u+\frac{1}{2}\left(\boldsymbol{\nabla}_\perp^2u\right)^2+\left(\boldsymbol{\nabla}_\perp u\right)^2\\&+\bar{\sigma}\left(1+2u+u^2+\frac{1}{2}\left(\boldsymbol{\nabla}_\perp u\right)^2\right)-\bar{p}\left(\frac{1}{3}+u+u^2\right)\\&-\sum_\alpha\Lambda_\alpha\left(1-\frac{1}{2}(2u+\boldsymbol{\nabla}_\perp^2u)-\bar{H}_\alpha\right)\delta_\perp\left(\theta-\theta_\alpha,\phi-\phi_\alpha\right)\Bigg]\,\mathrm{d}\Omega,\end{aligned} \tag{44}$$

where Λ_α now carries dimension of area and $\bar{H}_\alpha=RH_\alpha$ is the non-dimensionalized imposed mean curvature. For the variation of the energy we obtain

$$\delta\mathcal{E}=2\kappa\int\left[\mathcal{L}[u]+(2\bar{\sigma}-\bar{p})+\sum_\alpha\Lambda_\alpha\left(1+\frac{1}{2}\boldsymbol{\nabla}_\perp^2\right)\delta_\perp\left(\theta-\theta_\alpha,\phi-\phi_\alpha\right)\right]\delta u\,\mathrm{d}\Omega, \tag{45}$$

so our shape equation now reads

$$\mathcal{L}[u]+(2\bar{\sigma}-\bar{p})=-\sum_\alpha\Lambda_\alpha\left(1+\frac{1}{2}\boldsymbol{\nabla}_\perp^2\right)\delta_\perp\left(\theta-\theta_\alpha,\phi-\phi_\alpha\right). \tag{46}$$

We now expand both u and $\delta_\perp$ in spherical harmonics. For u we have equation (32), while for $\delta_\perp$ we obtain

$$\delta_\perp\left(\theta-\theta_\alpha,\phi-\phi_\alpha\right)=\sum_{n,m}Y_n^{m*}(\theta_\alpha,\phi_\alpha)Y_n^m(\theta,\phi). \tag{47}$$

Substituting the expansions in equation (46), we obtain (writing the constant term as a multiple of the zeroth spherical harmonic mode):

$$\sum_{n,m}\lambda_nu_{nm}Y_n^m(\theta,\phi)+(2\bar{\sigma}-\bar{p})\sqrt{4\pi}Y_0^0=\sum_\alpha\Lambda_\alpha\sum_{n,m}\frac{1}{2}(n+2)(n-1)Y_n^{m*}(\theta_\alpha,\phi_\alpha)Y_n^m(\theta,\phi). \tag{48}$$

For the amplitudes of the modes we thus get

$$u_{00} = \frac{-1}{2(\bar{\sigma} - \bar{p})} \left[(2\bar{\sigma} - \bar{p}) + \frac{1}{\sqrt{4\pi}} \sum_\alpha \Lambda_\alpha \right], \tag{49a}$$

$$u_{nm} = \sum_\alpha \Lambda_\alpha \frac{(n+2)(n-1)}{2\lambda_n} Y_n^{m*}(\theta_\alpha, \phi_\alpha), \tag{49b}$$

where equation (49b) is valid for $n > 0$. Unsurprisingly, for $n = 1$ we find $u_{nm} = 0$, as these modes correspond to global translations. To find the Lagrange multipliers Λ_α, we substitute the found solution in our constraints, which gives

$$\begin{aligned} \bar{H}_\alpha &= \bar{H}[u]\big|_{\theta=\theta_\alpha, \phi=\phi_\alpha} \\ &= 1 - \frac{2\bar{\sigma} - \bar{p}}{2(\bar{\sigma} - \bar{p})} + \frac{1}{4} \sum_{n,m} \frac{(n+2)^2(n-1)^2}{\lambda_n} \sum_\beta \Lambda_\beta Y_n^{m*}(\theta_\beta, \phi_\beta) Y_n^m(\theta_\alpha, \phi_\alpha) \\ &= \frac{-\bar{p}}{2(\bar{\sigma} - \bar{p})} + \sum_\beta M_{\alpha\beta} \Lambda_\beta. \end{aligned} \tag{50}$$

We have again formally solved the problem, but still have quite some work to do to get an actual picture. In particular, we need to regularize the diagonal elements of the matrix M by terminating the sum of the spherical harmonics at some maximum value of n, after which we have a range of sums to evaluate.

5.1 Two particle interactions on the sphere

If we have only two particles, it makes sense to put one at a convenient coordinate position, either on the 'north pole' ($\theta = 0$) or on the 'equator' ($\theta = \pi/2$, $\phi = 0$), and have the other particle either keep $\phi = 0$ or $\theta = \pi/2$ fixed. We put particle 1 at the north pole, which means that $Y_n^m(\theta_1, \phi_1)$ equals 0 if $m \neq 0$.

A Spherical harmonics

The spherical harmonics are the eigenfunctions of the angular part of the Laplacian in spherical coordinates, for eigenvalue $-n(n+1)$, i.e., the spherical harmonics Y_n^m satisfy

$$\boldsymbol{\nabla}_\perp^2 Y_n^m = -n(n+1)Y_n^m, \tag{51}$$

or, writing out the Laplacian on the sphere

$$\frac{\partial^2 Y_n^m}{\partial\theta^2} + \cot(\theta)\frac{\partial Y_n^m}{\partial\theta} + \frac{1}{\sin^2(\theta)}\frac{\partial^2 Y_n^m}{\partial\phi^2} = -n(n+1)Y_n^m(\theta,\phi). \tag{52}$$

Multiplying through by $\sin^2(\theta)$, we see that we can write the Laplacian as the sum of two differential operators:

$$\sin(\theta)\frac{\partial}{\partial\theta}\left(\sin(\theta)\frac{\partial Y_n^m}{\partial\theta}\right) + \frac{\partial^2 Y_n^m}{\partial\phi^2} = -n(n+1)\sin^2(\theta)Y_n^m(\theta,\phi). \tag{53}$$

Partial differential equations in which the differential operator can be written as the sum of operators on single variables can always be separated. Writing $Y_n^m(\theta,\phi) = \Theta(\theta)\Phi(\phi)$, we find

$$\frac{\sin(\theta)}{\Theta(\theta)}\frac{\partial}{\partial\theta}\left(\sin(\theta)\frac{\partial Y_n^m}{\partial\theta}\right) + n(n+1)\sin^2(\theta)\Theta(\theta) = -\frac{1}{\Phi(\phi)}\frac{\partial^2\Phi}{\partial\phi^2} = m^2, \tag{54}$$

where we write the constant as m^2 for later convenience. The equation for Φ is easy, as it is simply that of the harmonic oscillator in classical mechanics, with solutions of the form

$$\Phi(\phi) = e^{im\phi}. \tag{55}$$

Invoking the fact that the azimuthal angle ϕ is periodic, the values of m are restricted to integers ($m \in \mathbb{Z}$). For the Θ equation we need a bit more work. First, we re-write it as an ode, then make the variable substitution $x = \cos(\theta)$ (such that $\mathrm{d}/\mathrm{d}\theta = -\sin(\theta)\mathrm{d}/\mathrm{d}x$):

$$\begin{aligned} \sin(\theta)\frac{\mathrm{d}}{\mathrm{d}\theta}\left(\sin(\theta)\frac{\mathrm{d}\Theta}{\mathrm{d}\theta}\right) + \left[n(n+1)\sin^2(\theta) - m^2\right]\Theta = 0 \\ \left(1-x^2\right)^2\frac{\mathrm{d}^2P(x)}{\mathrm{d}x^2} - 2x(1-x^2)\frac{\mathrm{d}P}{\mathrm{d}x} + \left[n(n+1)\left(1-x^2\right) - m^2\right]P(x) = 0, \end{aligned}$$

where we introduced the notation $P(x)$ to distinguish between the θ and x-dependent functions. We will first consider the case where $m = 0$; for x between (but not equal to) ±1 the equation then simplifies to the Legendre differential equation

$$\left(1-x^2\right)\frac{\mathrm{d}^2P(x)}{\mathrm{d}x^2} - 2x\frac{\mathrm{d}P}{\mathrm{d}x} + n(n+1)P(x) = 0. \tag{56}$$

We now substitute a series solution for $P(x)$:

$$\begin{aligned}
P(x) &= \sum_{k=0}^{\infty} a_k x^k, \\
xP'(x) &= \sum_{k=0}^{\infty} k a_k x^k, \\
(1-x^2)P''(x) &= \sum_{k=0}^{\infty} k(k-1)a_k \left(x^{k-2} - x^k\right) = \sum_{k=0}^{\infty} \left[(k+2)(k+1)a_{k+2} - k(k-1)a_k\right] x^k, \\
0 &= \sum_{k=0}^{\infty} \left[(k+2)(k+1)a_{k+2} - \left(k(k-1) + 2k - n(n+1)\right) a_k\right] x^k.
\end{aligned}$$

By orthogonality of the polynomials on the interval $[-1,1]$, if the sum equals zero, so must each of its terms, which gives us a reciprocal relation between the coefficients

$$a_{k+2} = \frac{k(k+1) - n(n+1)}{(k+2)(k+1)} a_k. \tag{57}$$

The Legendre polynomials are the solutions for which the series terminates at $k = n$, combined with initial choices $P_0(x) = 1$ and $P_1(x) = x$. With these choices, they satisfy Rodrigues' formula

$$P_n(x) = \frac{1}{2^n n!} \frac{\mathrm{d}^n}{\mathrm{d}x^n} \left(x^2 - 1\right)^n. \tag{58}$$

The Legendre polynomials are orthogonal but not normalized on $[-1,1]$:

$$\int_{-1}^{1} P_m(x) P_n(x) \,\mathrm{d}x = \frac{2}{2n+1} \delta_{mn}. \tag{59}$$

They are complete; for any piecewise continuous function $f(x)$ we have

$$f(x) = \sum_{k=0}^{\infty} a_k P_k(x), \qquad a_k = \frac{2k+1}{2} \int_{-1}^{1} f(x) P_k(x) \,\mathrm{d}x \tag{60}$$

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