BE 159: Signal Transduction and Mechanics in Morphogenesis

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14 The Young-Laplace law

In this lecture, we will derive the Young-Laplace law, a key result in interpreting the Maître, et al. paper. It is also important in many contexts in considering the mechanics of cells and tissues. It describes the relationship between surface areas of a two-dimensional sheet (like the periphery of a cell) and pressure differences across the surface. Along the way, we will consider a generic way to quantify the energetics of thin elastic shells.

14.1 Energetics of curvature of an elastic sheet

We have derived the constitutive relations for a homogeneous elastic solid, given by equation (10.20). Here, we consider a thin sheet, or shell, that is very thin along one dimension, which we will arbitrarily choose to be the z-direction. Since it is thin in one dimension, we would like to have a two-dimensional description of the object.

We can formally consider a piece of material that is very thin in z and derive an effectively two-dimensional representation of the deformations. This is done, for example, in sections 11–15 of Landau and Lifshitz *Theory of Elasticity*. Instead of taking that approach, we will take a phenomenological approach based on the **curvature** of the two-dimensional elastic sheet. Informally, this describes how curved the two-dimensional surface is. To define curvature precisely, we define the positions of the surface of a sheet with a function $h(x,y)$. Then, the **curvature tensor** is

$$C_{ij} = \partial_i \partial_j h. \tag{14.1}$$

A rank-two tensor is required to describe curvature of a two-dimensional object because the object may be curved in different ways along different axes. For example, a sphere has the same curvature everywhere, but a cylinder has finite curvature along the azimuthal direction, but infinite curvature along the axial direction.

Given the curvature tensor, we can write the deformation energy of the shell as

$$E_{\text{deform}} = \int \mathrm{d}A f(C_{ij}). \tag{14.2}$$

Here, $f(C_{ij})$ is an energy per area associate with the local curvature. We write $f(C_{ij})$ as a Taylor series in the curvature tensor to second order.

$$f(C_{ij}) \approx a_0 + a_1 C_{kk} + a_2 (C_{kk})^2 + a_3 C_{ik} C_{ik}. \tag{14.3}$$

Note that C_{kk} is the trace of the curvature tensor, which we define as $C_{kk} = 2H$, where H is called the **mean curvature**. We call it that because the **principle curvatures** (which we will call C_1 and C_2) are the eigenvalues of the curvature tensor, and the

mean of these curvatures is half the trace. That is, $H = (C_1 + C_2)/2$. (Remember, the trace is equal to the sum of the eigenvalues.)

Now, for a 2×2 tensor, $C_{ij}C_{ij} = (2H)^2 - 2K$, where $K \equiv C_1C_2$ is called the **Gaussian curvature**. So, we only two independent curvature parameters, the mean curvature and the Gaussian curvature. We can then rewrite the areal energy density as

$$f(H,K) = \gamma + \frac{\kappa}{2}(2H - C_0)^2 + \bar{\kappa}K, \tag{14.4}$$

where κ is the **bending rigidity**, $\bar{\kappa}$ is the **Gaussian rigidity**, γ is the **surface tension**, and C_0 is the **spontaneous curvature**. The relations to the original expansion coefficients are

$$a_0 = \gamma + \frac{\kappa}{2}C_0, \tag{14.5}$$

$$a_1 = \kappa C_0, \tag{14.6}$$

$$a_2 = \frac{\kappa + \bar{\kappa}}{2}, \tag{14.7}$$

$$a_3 = -\frac{\bar{\kappa}}{2}. \tag{14.8}$$

Let us pause for a moment to parse these new terms so we understand what they mean (and also how they got their names). It will help to first write the deformation energy.

$$E_{\text{deform}} = \int \mathrm{d}A f(H,K) = \int \mathrm{d}A\, \gamma + \frac{1}{2}\int \mathrm{d}A\, \kappa(2H - C_0)^2 + \int \mathrm{d}A\, \bar{\kappa}K \tag{14.9}$$

- **Surface tension**, γ: Imagine we increased the area of the sheet by some amount. The deformation energy due to the surface tension term grows proportionally to the increased area. If we have two immersed liquids, increasing the interfacial area results in greater interfacial energy because of surface tension. The name, then, comes from a tension that results from increasing surface area. This term describes the energetics of **stretching** deformations.
- **Bending rigidity**, κ: The bending rigidity multiplies the mean curvature. So, the more sharply curved the sheet is, the greater the deformation energy. The terms involving the mean curvature and the Gaussian curvature describe **bending** deformations.
- **Spontaneous curvature**, C_0: Some elastic sheets are *inherently* curved. A cell membrane that has asymmetric lipid layers is an example. For a symmetric sheet, $C_0 = 0$, but it can be nonzero for inherently curved sheets.

- **Gaussian rigidity**, $\bar{\kappa}$: This multiplies the Gaussian curvature, hence the name. We will discuss this momentarily when we talk about Gauss's Theorema Egregium and the Gauss-Bonnet Theorem.

While we will not derive it here, Gauss's Theorema Egregium states that the Gaussian curvature K is invariant under isometric transformation. In other words, the Gaussian curvature K does not change for any deformation that does not stretch the sheet. Furthermore, the Gauss-Bonnet theorem says that $\int \mathrm{d}A\, K = 2\pi\chi(S)$, where $\chi(S)$ is the Euler-Poincaré characteristic, $\chi(S) = 2(1-g)$, where g is the genus of the surface. The genus is the number of handles, or donut holes in the surface. A torus has $g = 1$; a sphere has $g = 0$. These two theorems together guarantee that provided we do not stretch or introduce holes into the surface, the quantity $\int \mathrm{d}A\, \bar{\kappa} K$ is constant, provided $\bar{\kappa}$ is constant.

14.2 Young-Laplace Law for a sphere

Consider now a sheet that is restricted to being spherical. For a sphere or radius R, the two principle curvatures are $C_1 = C_2 = 1/R$. We will assume that γ, κ, and $\bar{\kappa}$ are all constants. We further assume the material has no intrinsic curvature. In this case, the energy of deformation is

$$E_{\text{deform}} = 4\pi R^2 \left(\gamma + \frac{\kappa}{R^2} + \frac{\bar{\kappa}}{R^2} \right) = 4\pi R^2 \gamma + 4\pi(\kappa + \bar{\kappa}). \tag{14.10}$$

The differential energy of deformation is then

$$\mathrm{d}E_{\text{deform}} = 8\pi R \gamma \,\mathrm{d}R. \tag{14.11}$$

The differential free energy of the shell, including now pV contributions is

$$\begin{aligned} \mathrm{d}F &= \mathrm{d}E_{\text{deform}} - p\,\mathrm{d}V \\ &= 8\pi R\gamma\,\mathrm{d}R - \frac{4}{3}\pi p\,\mathrm{d}R^3 \\ &= 8\pi R\gamma\,\mathrm{d}R - 4\pi R^2 p\,\mathrm{d}R \\ &= 4\pi R(2\gamma - Rp)\mathrm{d}R. \end{aligned} \tag{14.12}$$

As evident from the form of the total differential, the free energy is minimal when $2\gamma = Rp$, or $p = 2\gamma/R$. Now, this p is really a pressure *difference* between the interior and exterior of the spherical shell. So, we have

$$p_{\text{in}} - p_{\text{out}} = \frac{2\gamma}{R}. \tag{14.13}$$

This result is commonly known as the **Young-Laplace Law**. But beware! This result that holds for a sphere, where we included both stretching and bending energy, is not general. Let us consider another example from the physics of tissues that shows where we can run into trouble.

14.3 Squishing a balled-up tissue

In a classic experiment in the early 1990s, Foty and coworkers took living tissues from 5-6 day old chick embryos, dissociated the tissues in solution, and then allowed them to reaggregate. The now-spherical tissue was placed between parallel plates to which the tissue does not adhere and squished by applying force F to the top plate while the bottom plate is fixed. The authors then observed the shape of the tissue, as shown in Fig. 14. From the shape of the tissue, they could extract the quantities R_1, R_2, and R_3. The goal from the experiment is to extract the interfacial tension, γ, between the tissue and the surroundings. The approach is to derive a similar Young-Laplace law relating the pressure to the radii R_1, R_2, and R_3, knowing that we can measure the pressure by a force balance on the plates,

$$p = \frac{F}{\text{area in contact with top plate}} = \frac{F}{\pi R_3^2}. \tag{14.14}$$

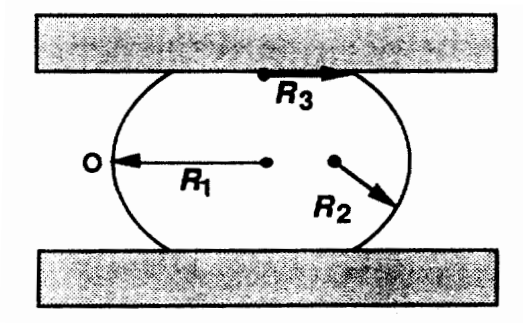

Figure 14: Sketch of the tissue compression experiment. Taken from Foty, et al., *Phys. Rev. Lett.*, **72**, 2298–2301, 1994.

If we go about it as before, we define two areas, A_1, which is in contact with the solvent and has interfacial tension γ_1, and A_2, which is in contact with the plates and has interfacial tension γ_2. The radius of curvature on the region in contact with the plates is infinite, so the curvature is zero, so this region does not enter into the terms involving mean and Gaussian curvature. In the region in contact with solvent, there are two orthogonal axes of curvature with respective radii of curvature R_1 and R_2. Then, we have

$$E_{\text{deform}} = \gamma_1 A_1 + \gamma_2 A_2 + \frac{\kappa}{2} A_1 \left(\frac{1}{R_1} + \frac{1}{R_2} \right)^2 + \frac{\bar{\kappa} A_1}{R_1 R_2}. \tag{14.15}$$

We have neglected the apparent discontinuity in the curvature along the ring where the tissue is in contact with both a plate and the solvent. When we evaluated E_{deform} for a sphere, the radius of curvature in the terms relating to bending energy all canceled. This is not the case here, so the parameters κ and $\bar{\kappa}$ appear in the equilibrium expressions and are unknown. To make matters worse, after doing some geometry and calculations involving solids of rotation, the we get

$$A_1 = 2\pi R_2^2 \left(2\sin\frac{\theta}{2} + \left(\frac{R_1}{R_2} - 1 \right) \theta \right), \tag{14.16}$$

$$A_2 = 2\pi R_3^2, \tag{14.17}$$

$$\begin{aligned} V = {} & \frac{\pi R_2^3}{6} \left(21\sin\frac{\theta}{2} - 6(\theta - \sin\theta) + \sin\frac{3\theta}{2} \right) \\ & + \pi R_1 R_2^2 \left(\theta - \sin\theta - 4\sin\frac{\theta}{2} \right) + 2\pi R_1^2 R_2 \sin\frac{\theta}{2} \\ & + 2\pi R_2 R_3^2 \sin\frac{\theta}{2}, \end{aligned} \tag{14.18}$$

where

$$\theta = 2\cos^{-1}\left(1 - \frac{R_1 - R_3}{R_2} \right). \tag{14.19}$$

This is clearly a mess, and minimizing the free energy, $F = E_{\text{deform}} - pV$ would be very difficult.

14.4 Generalized Young-Laplace

I now clarify what people mean when they refer to a Young-Laplace law. When deriving a Young-Laplace law, the *bending energy is neglected*. This greatly simplifies calculations, and is often justified, especially in tissues and biological membranes, since stretching energy is usually far greater than bending energy. Even if we neglect the bending energy, though, considering the whole geometry of the sheet and taking the thermodynamic approach we have been doing is very cumbersome. Instead, we will take a thermodynamic approach in which we consider only a small piece of a sheet.

If we neglect bending energy, the differential free energy is

$$\mathrm{d}F = -p\,\mathrm{d}V + \gamma\,\mathrm{d}A. \tag{14.20}$$

Consider a tiny piece of an undeformed sheet with area $\mathrm{d}A$. It is then deformed with a displacement along the normal to the surface of δh. Now, at a point on the

deformed surface, we define two orthogonal directions, 1 and 2. These orthogonal directions can be the directions of principle curvature, i.e., the eigenvectors of the local curvature tensor C_{ij}. The eigenvectors can be made to be orthonormal, since the curvature tensor is real and symmetric, cf. equation (14.1). (This is a general property of real symmetric matrices.) Let the arc that lies along direction 1 of the undeformed sheet be of length $\mathrm{d}s_1$ and that along direction 2 be of length $\mathrm{d}s_2$. Then, the areal element is

$$\mathrm{d}A_{\text{unstretch}} = \mathrm{d}s_1\,\mathrm{d}s_2. \tag{14.21}$$

Now, upon deformation, the differential volume is $\mathrm{d}s_1\,\mathrm{d}s_2\;\delta h$. Thus,

$$-p\,\mathrm{d}V = -p\;\delta h\,\mathrm{d}s_1\,\mathrm{d}s_2. \tag{14.22}$$

Now, due to curving upon deformation, the sheet must stretch, so the differential distances along the principle curvatures experience a differential change. If we consider the 1-direction, the differential change in the length element is $\mathrm{d}s_1\,\delta h/R_1$, where R_1 is the first principle radius of curvature. Similarly, $\mathrm{d}s_2$ is increased to $\mathrm{d}s_2(1+\delta h/R_2)$. Thus, the areal element is now

$$\begin{aligned}\mathrm{d}A_{\text{stretch}} &= \mathrm{d}s_1\left(1+\frac{\delta h}{R_1}\right)\mathrm{d}s_2\left(1+\frac{\delta h}{R_2}\right)\\ &\approx \mathrm{d}s_1\,\mathrm{d}s_2\left(1+\frac{\delta h}{R_1}+\frac{\delta h}{R_2}\right),\end{aligned} \tag{14.23}$$

where in the approximation we have neglected terms of second order in the displacement δh. Thus, the total change in area due to curvature is

$$\mathrm{d}A = \mathrm{d}A_{\text{stretch}} - \mathrm{d}A_{\text{unstretch}} = \mathrm{d}s_1\,\mathrm{d}s_2\;\delta h\left(\frac{1}{R_1}+\frac{1}{R_2}\right). \tag{14.24}$$

We now have a total differential free energy of

$$\mathrm{d}F = \left(-p+\gamma\left(\frac{1}{R_1}+\frac{1}{R_2}\right)\right)\delta h\,\mathrm{d}s_1\,\mathrm{d}s_2. \tag{14.25}$$

The free energy is therefore minimal when

$$p = \gamma\left(\frac{1}{R_1}+\frac{1}{R_2}\right). \tag{14.26}$$

Again, noting that this pressure is really the difference in pressure on either side of the sheet and recalling that the mean curvature is

$$H = \frac{1}{2}\left(\frac{1}{R_1}+\frac{1}{R_2}\right), \tag{14.27}$$

we arrive at a generalized Young-Laplace law,

$$p_{\text{in}} - p_{\text{out}} = 2\gamma H. \tag{14.28}$$

Remember in this derivation that no bending energy was considered; only stretching energy.

14.5 Squishing tissue again

Now that we have the generalized Young-Laplace law, let's re-evaluate the squished tissue problem. The Young-Laplace law must hold at all points on the surface, so we can arbitrarily choose point O in Fig. 14. The mean curvature here is $H = (R_1^{-1} + R_2^{-1})/2$. So, we have

$$p_{\text{in}} - p_{\text{out}} = \gamma_1 \left(\frac{1}{R_1} + \frac{1}{R_2} \right). \tag{14.29}$$

We know the pressure in terms of the applied force from equation (14.14), so we have

$$\frac{F}{\pi R_3^3} = \gamma_1 \left(\frac{1}{R_1} + \frac{1}{R_2} \right), \tag{14.30}$$

which allows us to write the interfacial tension between the tissue and the media in terms of known quantities as

$$\gamma_1 = \frac{F}{\pi R_3^3} \left(\frac{1}{R_1} + \frac{1}{R_2} \right)^{-1}. \tag{14.31}$$