BE 159: Signal Transduction and Mechanics in Morphogenesis

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11 Applications of elasticity

In this lecture, we will look at two applications of elasticity theory. First, we will study the laser ablation experiment of the Mayer, et al. paper. Then, we will derive the Young-Laplace law, a key result in interpreting the Maître, et al. paper.

11.1 Analysis of cortical laser ablation experiments

In the Mayer, et al. paper, the authors used cortical laser ablation (COLA) to cut a line in the cortex of the *C. elegans* embryo and observe the recoil. By comparing the initial velocity of the recoil of two different experiments, they could compare the total tension present in the cortex immediately before ablation. Why is this the case?

To analyze this equation, we consider the cortex as an active *elastic* material. The cortex itself is *viscoelastic*, meaning that it exhibits both elastic (solid-like) and viscous (fluid-like) properties. On long time scale, that is for slow deformations, the cortex is viscous. This is what we have analyzed thus far when considering the flow of the cortex. Conversely, when the cortex is ablated, the response is very rapid, occurring on short time scales, and the cortex is elastic. We can write down a constitutive relation for this two-dimension active elastic material.

$$\sigma_{ij} = \frac{E}{1+\nu}\left(\varepsilon_{ij} + \frac{\nu}{1-2\nu}\,\varepsilon_{kk}\delta_{ij}\right) + \sigma_a Q_{ij}, \tag{11.1}$$

where $Q_{ij} = 1$ is $i = j = x$ or $i = j = y$ and zero otherwise. For the active term, we have taken the same approach as we did in homework 4, assuming that the filaments lie within the x-y plane and that the nematic order rapidly relaxes to its equilibrium value. Note that we have absorbed constants from Q_{ij} into σ_a, as we did in homework 4.

We will make a cut in the y-direction, which means that we are observing relaxation in the x-direction. Then, it is convenient to write the stress in the x-direction.

$$\sigma_{xx} = \frac{E}{1+\nu}\left(\frac{1-\nu}{1-2\nu}\,\varepsilon_{xx} + \frac{\nu}{1-2\nu}\left(\varepsilon_{yy}+\varepsilon_{zz}\right)\right) + \sigma_a. \tag{11.2}$$

Since we are ablating in the y-direction, the recoil of the cortex is dominantly in along the x-direction. Thus, we will take $\varepsilon_{yy}, \varepsilon_{zz} \ll \varepsilon_{xx}$, giving

$$\sigma_{xx} = \frac{E(1-\nu)}{(1+\nu)(1-2\nu)}\,\varepsilon_{xx} + \sigma_a. \tag{11.3}$$

Upon ablation, the cortex can no longer support stresses because the material has been destroyed, so $\sigma_{xx} = 0$. Thus, we take $\sigma_{xx}(t) = \sigma_{xx}^0(1-\theta(t))$, where we specify that the ablation takes place at $t = 0$. Thus, the strain prior to ablation is

$$\varepsilon^0_{xx} \equiv \varepsilon_{xx}(t < 0) = \frac{(1+\nu)(1-2\nu)}{E(1-\nu)}(\sigma^0_{xx} - \sigma_a). \tag{11.4}$$

Now that we have the stress tensor, we consider the geometry. The ablation line is at position $x = 0$. We define by x_c to be the position of the edge of the cortex at the ablation line. This moves as the cortex recoils from the ablation. For the purposes of this discussion, we will observe the right side of the ablation site. Now, $\varepsilon_{xx} = \partial_x u_x$, where u_x is the x-component of the displacement of the elements of the cortex from their equilibrium positions. If the initial extent of the cortex in the x-direction was L, and the deformation is distributed uniformly across the contracting cortex, then $\partial_x u_x \approx (x_c - L + x_0)/L$, where $\varepsilon^0_{xx} = (x_0 - L)/L$. Then, we have

$$\sigma_{xx} = \frac{E(1-\nu)}{(1+\nu)(1-2\nu)} \frac{x_c - L + x_0}{L} + \sigma_a = kx_c + kL\varepsilon^0_{xx} + \sigma_a, \tag{11.5}$$

where $k \equiv E(1-\nu)/L(1+\nu)(1-2\nu)$. We note that $kL\varepsilon^0_{xx} = \sigma^0_{xx} - \sigma_a$, so we can further simplify.

$$\sigma_{xx} = kx_c + \sigma xx^0. \tag{11.6}$$

Already we see that the active stress vanishes from the dynamics. We note that the cortex does not instantaneously achieve its new equilibrium. This is because there is dissipation due to friction with the surrounding membrane and cytoplasm. The above equation constitutes a force balance, and we need to also include the frictional force. This will be proportional to the velocity of the recoil, or $\partial_t x_c$. Thus, we get

$$\sigma_{xx} = kx_c + \sigma^0_{xx} + \zeta\partial_t x_c, \tag{11.7}$$

With this force balance, we can study the dynamics of the recoil from a COLA experiment. Upon ablation, the cortex can no longer support stresses because the material has been destroyed, so $\sigma_{xx} = 0$. Thus, we take $\sigma_{xx}(t) = \sigma^0_{xx}(1 - \theta(t))$. Then, we are left with the ODE

$$\zeta\partial_t x_c = -kx_c - \sigma^0_{xx} + \sigma^0_{xx}(1 - \theta(t)) = -kx_c - \sigma^0_{xx}\theta(t). \tag{11.8}$$

If the ablation happens at time $t = 0$, then for $t < 0$, we have $\partial_t x_c = 0$. This is consistent with $x_c(t = 0) = 0$. For $t > 0$, we have

$$\zeta\partial_t x_c = -kx_c - \sigma^0_{xx}. \tag{11.9}$$

This first order linear differential equation is easily solved to give

$$x_c(t) = c\mathrm{e}^{-kt/\zeta} - \frac{\sigma^0_{xx}}{k} \tag{11.10}$$

where c is a constant of integration. We match to the initial condition that $x_c = 0$ to get that $c = \sigma^0_{xx}/k$. Thus, we have

$$x_c(t) = \frac{\sigma^0_{xx}}{k}(1 - \mathrm{e}^{-kt/\zeta}). \tag{11.11}$$

The outward velocity of the bleeding edge of the ablation is then

$$v(t) = \partial_t x_c = \frac{\sigma^0_{xx}}{\zeta}\,\mathrm{e}^{-kt/\zeta}. \tag{11.12}$$

So, the initial outward velocity is σ^0_{xx}/ζ, which is proportional to the total x-directional stress that was present in the cortex immediately prior to ablation. We cannot access the value of σ^0_{xx} because we do not know what ζ is. However, we can compare experiments to see the *relative* magnitudes of the stress present in the cortex. Further, if ζ is the same across experiments, which we would expect it to be, the decay of the outward velocity is proportional to the stiffness (the Young's modulus) of the cortex.

11.2 The Young-Laplace Law

As we move on to study the Maître, et al. paper, we derive an important result, the **Young-Laplace law**. It describes the relationship between surface areas of a two-dimensional sheet (like the periphery of a cell) and pressure differences across the surface. We will first consider a simple version of the law and then derive a more general one.

11.2.1 Young-Laplace law for a sphere

Consider a small piece of an elastic sheet of area a_0. Now, let us stretch the sheet such that the area is a. Then, the *areal strain* is $\varepsilon_a = (a - a_0)/a_0$. If we write the stretching energy as a function of the areal strain, we get

$$E_{\text{stretch}} = \int \mathrm{d}A\, f(\varepsilon_a). \tag{11.13}$$

We write $f(\varepsilon_a)$ as a Taylor series about $\varepsilon_a = 0$, we get

$$E_{\text{stretch}} = \frac{1}{2}\int \mathrm{d}A\, K_a\, \varepsilon_a^2, \tag{11.14}$$

where we have taken the unstretched energy to be zero and have neglected terms higher than second order. The parameter K_a is the areal stretch modulus, and has units of energy per area.

Now, we define the **surface tension**, γ, as the energy it takes to expand a differential element of the sheet by a differential area. That is,

$$\gamma = \frac{\partial E_{\text{stretch}}}{\partial A}. \tag{11.15}$$

For a small differential element of area a,

$$E_{\text{stretch}} = \frac{1}{2}\int \mathrm{d}A\, K_a\, \varepsilon_a^2, \approx \frac{K_a}{2}\, a_0\, \varepsilon_a^2 = \frac{K_a}{2}\, \frac{(a-a_0)^2}{a_0}. \tag{11.16}$$

so the surface tension is

$$\gamma = \frac{\partial E_{\text{stretch}}}{\partial a} = K_a\, \frac{(a-a_0)}{a_0} = K_a\, \varepsilon_a. \tag{11.17}$$

So, we can write the stretching energy as

$$E_{\text{stretch}} = \int \mathrm{dA}\, \gamma. \tag{11.18}$$

For a sphere, this is

$$E_{\text{stretch}} = 4\pi R^2 \gamma. \tag{11.19}$$

Now, consider the free energy of such a vesicle, making sure to consider also pV contributions.

$$F = E_{\text{stretch}} - pV = E_{\text{stretch}} - (p_{\text{in}} - p_{\text{out}})V = 4\pi R^2\gamma + \frac{4}{3}\pi R^3(p_{\text{out}} - p_{\text{in}}). \tag{11.20}$$

To find the equilibrium radius, we differentiate and set the derivative to zero.

$$\frac{\partial F}{\partial R} = 8\pi R\gamma - 4\pi R^2(p_{\text{in}} - p_{\text{out}}) = 0. \tag{11.21}$$

Rearranging gives the Young-Laplace Law,

$$p_{\text{in}} - p_{\text{out}} = \frac{2\gamma}{R} \tag{11.22}$$

11.2.2 Energetics of curvature of an elastic sheet

In addition to stretching a sheet, we may also bend it. We can describe the bending using the **curvature** of a sheet. We define the positions of the surface of a sheet with a function $h(x,y)$. Then, analogously to how bending of a filament is a function of the curvature of the filament, the bending energy of a sheet is a function of the **curvature tensor**,

$$C_{ij} = \partial_i \partial_j h. \tag{11.23}$$

We can write the total bending energy of a sheet as

$$E = \int \mathrm{d}A f(C_{ij}). \tag{11.24}$$

We write $f(C_{ij})$ as a Taylor series in the curvature tensor to second order.

$$f(C_{ij}) \approx a_0 + a_1 C_{kk} + a_2 (C_{kk})^2 + a_3 C_{ik} C_{ik}. \tag{11.25}$$

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. For a 2×2 tensor, $C_{ij}C_{ij} = (2H)^2 - 2K$, where $K = C_1 C_2$. This is called the **Gaussian curvature**. So, we only have two independent parameters, the mean curvature and the Gaussian curvature. We can re-write this as

$$f(H, K) = \gamma + \frac{\kappa}{2}(2H - C_0)^2 + \bar{\kappa} K, \tag{11.26}$$

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

$$a_0 = \gamma + \frac{\kappa}{2} C_0, \tag{11.27}$$

$$a_1 = \kappa C_0, \tag{11.28}$$

$$a_2 = \frac{\kappa + \bar{\kappa}}{2}, \tag{11.29}$$

$$a_3 = -\frac{\bar{\kappa}}{2}. \tag{11.30}$$

While we will not derive it here, Gauss's Theorema Egregium states that K is invariant under isometric transformation. 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 holds in the surface. A torus has $g = 1$; a sphere has $g = 0$. These two theorems together guarantee that provided we do not introduce holes into the surface, the quantity $\int \mathrm{d}A\, \bar{\kappa} K$ is constant, provided $\bar{\kappa}$ is constant. Thus, the energy of the surface is

$$E = \text{constant} + \int \mathrm{d}A\, \gamma + \int \mathrm{d}A\, \frac{\kappa}{2}(2H - C_0)^2. \tag{11.31}$$

The first term is the stretching energy we have already derived and the second term is the bending energy.

11.2.3 Generalized Young-Laplace

The simple treatment we used in section 11.2.1 to derive the Young-Laplace law for a sphere may be generalized. Specifically, for a sphere, we found that the stretching term in the above expression for energy is

$$E_{\text{stretch}} = \int \mathrm{d}A\, \gamma = 4\pi R^2 \gamma\,, \tag{11.32}$$

where γ is constant on the sphere. To compute the energy for a more general geometry, we need to consider the differential areal element, $\mathrm{d}A$. Determining $\mathrm{d}A$ requires some techniques of differential geometry, which we we not go into here, except to say that the differential areal element depends on the local curvature C_{ij} and an object known as the metric tensor. Instead of delving into differential geometry (which is a beautiful and fascinating field of mathematics), we will instead attempt to work out the dependence of the total stretching energy on the curvature by doing a local force balance.

Imagine we have a small piece of a sheet. At a point on the 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 (11.23). Let the arc that lies along direction 1 be of length $\mathrm{d}s_1$ and that along direction 2 be of length $\mathrm{d}s_2$. Then, the areal element is $\mathrm{d}A = \mathrm{d}s_1\,\mathrm{d}s_2$. The force in the direction normal to the surface is $\gamma\,\mathrm{d}s_2\,\sin\theta_1$, which for a small θ_1 (which is the case for a differential element) is approximately $\gamma\,\mathrm{d}s_2\,\theta_1$. But, $\theta_1 C_1 = \mathrm{d}s_1$, as given by the formula for arc length. Thus, the force acting normal to the surface due to curvature in the 1-direction is $\gamma\,\mathrm{d}s_1\mathrm{d}s_2/C_1$. Similarly, for the 2-direction, we have a force of $\gamma\,\mathrm{d}s_1\mathrm{d}s_2/C_2$. So, we have a total normal force due to surface tension of $\gamma\,\mathrm{d}s_1\mathrm{d}s_2/(C_1 + C_2) = 2H\mathrm{d}s_1\,\mathrm{d}s_2$. This force is balanced by the pressure force, which is $(p_{\text{in}} - p_{\text{out}})\mathrm{d}A = (p_{\text{in}} - p_{\text{out}})\mathrm{d}s_1\,\mathrm{d}s_2$. Thus, we have

$$p_{\text{in}} - p_{\text{out}} = 2H\gamma\,, \tag{11.33}$$

our generalized Young-Laplace law. Recall that for a sphere, $H = 1/R$, so we recover the expression we derived before.