BE 159: Signal Transduction and Mechanics in Morphogenesis

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13 Viscoelasticity and laser ablation

13.1 Linear viscoelasticity

We have so far considered the constitutive relations for an elastic solid and a viscous fluid (including active nematic viscous fluids). The actomyosin cortex behaves both elastically and viscously. For long time scales, it can flow, like a fluid. But if the cortex is rapidly stressed, it behaves like an elastic solid. After all, it is what gives the cell its shape. Further, as described in the Mayer, et al., paper, the actomyosin cortex responds elastically when it is cut while under tension. So, it has both elastic and viscous properties. What kind of constitutive relation describes this scenario of a **viscoelastic material**?

In many cases, it is not possible to write down a constitutive relation for a viscoelastic material. Researchers instead rely on experimental characterization of the material, such as a cell and its cortex, as it experiences stress.

Nonetheless, we can write down a linear theory that will (hopefully) provide some insight and predictive power. Let us compare for a moment the constitutive relations of an elastic and a viscous active nematic material. For simplicity, we will assume an incompressible material with a Poisson ratio of zero. For convenience, we will use the **shear modulus**, μ, which you can recall from equation (10.17) is the second Lamé coefficient. It is related to the Young's modulus by $\mu = E/2(1+\nu)$. In the case of zero Poisson ratio, this is $\mu = E/2$.

$$\text{elastic: } \sigma_{ij} + \Pi\,\delta_{ij} - \beta_1(\chi - L\partial_k\partial_k)Q_{ij} - \sigma_a Q_{ij} = 2\mu\,\varepsilon_{ij}, \tag{13.1}$$

$$\text{viscous: } \sigma_{ij} + \Pi\,\delta_{ij} - \beta_1(\chi - L\partial_k\partial_k)Q_{ij} - \sigma_a Q_{ij} = 2\eta\,v_{ij}. \tag{13.2}$$

Recall that

$$\partial_t\varepsilon_{ij} = \frac{1}{2}\,\partial_t(\partial_i u_j + \partial_j u_i) = \frac{1}{2}(\partial_i\partial_t u_j + \partial_j\partial_t u_i) = \frac{1}{2}(\partial_i v_j + \partial_j v_i) = v_{ij}. \tag{13.3}$$

So, if we differentiate the constitutive relation for the elastic material with respect to time, we get

$$\partial_t\left(\sigma_{ij} + \Pi\,\delta_{ij} - \beta_1(\chi - L\partial_k\partial_k)Q_{ij} - \sigma_a Q_{ij}\right) = 2\mu\,v_{ij}, \tag{13.4}$$

which we can re-write to give

$$\tau_{\mathrm{M}}\partial_t\left(\sigma_{ij} + \Pi\,\delta_{ij} - \beta_1(\chi - L\partial_k\partial_k)Q_{ij} - \sigma_a Q_{ij}\right) = 2\eta\,v_{ij}. \tag{13.5}$$

Here, $\tau_M = \eta/\mu$ is the **Maxwell time**, which describes the time scale for relaxation of elastic stresses. We might, then interpolate between the two cases of elastic and viscous materials by adding the constitutive relations together.

$$(1 + \tau_M\partial_t)\left[\sigma_{ij} + \Pi\,\delta_{ij} - \beta_1(\chi - L\partial_k\partial_k)Q_{ij} - \sigma_a Q_{ij}\right] = 2\eta\,v_{ij}. \tag{13.6}$$

For time scales much less than τ_M, the material behaves elastically, but for time scales much longer than τ_M, the material behaves viscously. This can be seen if we nondimensionalize time by the time scale of interest, τ. Then, the dimensionless operator at the front of equation (13.6) is

$$1 + \frac{\tau_M}{\tau}\,\partial_{\tilde{t}}. \tag{13.7}$$

If $\tau \gg \tau_M$, the second term is small and we get the constitutive relation for a viscous fluid. If $\tau \ll \tau_M$, the second term dominates, and we get the constitute relation for an elastic solid.

Equation (13.6) is actually not quite correct because it is not frame invariant. To see this, let's say that we did identical experiments on this viscoelastic material, one in a laboratory, and one in a train car moving at constant velocity v_i^0. Writing the stress tensor explicitly as a function of position and time, we have, for the time derivative of the stress tensor in the second experiment using the chain rule,

$$\partial_t \sigma_{ij}(x_i + v_k^0 t, t) = \partial_t \sigma_{ij} + v_k^0 \partial_k \sigma_{ij}. \tag{13.8}$$

Since the equation in this experiment has terms not present in the experiment done in the stationary lab, the governing equations are not frame invariant, which violates Gallilean relativity. Instead, we should use the **convected corotational derivative**, which preserves frame invariance, both for linear and rotational motion. The convected corotational derivative of a second rank tensor is defined as

$$\frac{\mathrm{D}A_{ij}}{\mathrm{D}t} = \partial_t A_{ij} + v_k \partial_k A_{ij} + \omega_{ik} A_{kj} + \omega_{jk} A_{ki}. \tag{13.9}$$

As a reminder, $\omega_{ij} = (\partial_i v_j - \partial_j v_i)/2$ is the antisymmetric part of the velocity gradient tensor. The convected corotational derivative is like the material derivative in that it sets the frame as the co-moving, corotational frame. So, for an active nematic viscoelastic fluid, which is solid-like at short time scales and viscous-like at long time scales, a linear viscoelastic model gives a constitutive relation of

$$\left(1 + \tau_M \frac{D}{Dt}\right)\left[\sigma_{ij} + \Pi\,\delta_{ij} - \beta_1(\chi - L\partial_k\partial_k)Q_{ij} - \sigma_a Q_{ij}\right] = 2\eta\, v_{ij}. \tag{13.10}$$

We will make use of this in interpreting the laser ablation experiments in the Mayer, et al. paper.

13.2 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 address this question, we consider the cortex as an active nematic *elastic* material. In the elastic limit, we use the constitutive relation (13.1),

$$\sigma_{ij} = -\Pi\,\delta_{ij} + \beta_1(\chi - L\partial_k\partial_k)Q_{ij} + \sigma_a Q_{ij} + 2\mu\,\varepsilon_{ij}. \tag{13.11}$$

We assume that the nematic order is constant in space, so $\partial_k\partial_k Q_{ij} = 0$.

We assume the ablation line is along the y-direction so that the response is primarily along the x-direction. It is convenient, then, to write the xx-component of the constitutive relation.

$$\sigma_{xx} = -\Pi + (\beta_1\chi + \sigma_a)Q_{xx} + 2\mu\,\varepsilon_{xx}. \tag{13.12}$$

Note that in assuming the Poisson ratio is zero, motions in the y and z directions do not enter into the dynamics. If we had a nonzero Poisson ratio, we could still neglect these dynamics since $\varepsilon_{yy}, \varepsilon_{zz} \ll \varepsilon_{xx}$ because the recoil is primarily in the x-direction.

Now 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 deformation is distributed uniformly across the contracting cortex, the strain is $\varepsilon_{xx} = \partial_x u_x \approx (x_c - x_0)/(\ell - x_c)$. Here, the numerator is the displacement of the cortex from its equilibrium position x_0, and the denominator is the total length of the cortex. We have introduced ℓ as the total extent of the embryo. Prior to ablation, $x_c = 0$, so the initial strain is $\varepsilon^0_{xx} = -x_0/\ell$. For the stress, we have

$$\sigma_{xx} = -\Pi + (\beta_1\chi + \sigma_a)Q_{xx} + \frac{2\mu}{\ell - x_c}(x_c - x_0). \tag{13.13}$$

As the cortex initial retracts from the ablation, $\ell \gg x_c$, so the stress can be approximated as

$$\sigma_{xx} = -\Pi + (\beta_1\chi + \sigma_a)Q_{xx} + \frac{2\mu}{\ell}(x_c - x_0) = kx_c + \sigma^0_{xx}, \tag{13.14}$$

where we have defined a spring constant

$$k = 2\mu/\ell \tag{13.15}$$

and

$$\sigma^0_{xx} = -\Pi + (\beta_1\chi + \sigma_a)Q_{xx} - 2\mu\varepsilon^0_{xx} \tag{13.16}$$

as the stress present in the cortex immediately prior to ablation. Already we see that the active stress is not distinguishable in the dynamics, so we will not be able to ascertain it in an ablation experiment.

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

$$\sigma_{xx} = kx_c + \sigma^0_{xx} + \zeta\,\partial_t x_c, \tag{13.17}$$

where ζ is the friction coefficient. 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 $\sigma_{xx}(t) = \sigma^0_{xx}(1 - \theta(t))$, where $\theta(t)$ is a unit step function. Then, we are left with the ODE

$$\zeta\,\partial_t x_c = -kx_c - \sigma^0_{xx} + \sigma^0_{xx}(1 - \theta(t)) = -kx_c - \sigma^0_{xx}\theta(t). \tag{13.18}$$

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

$$\zeta\,\partial_t x_c = -kx_c - \sigma^0_{xx}. \tag{13.19}$$

This first order linear differential equation is solved to give

$$x_c(t) = c\,\mathrm{e}^{-kt/\zeta} - \frac{\sigma^0_{xx}}{k} \tag{13.20}$$

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

$$x_c(t) = \frac{\sigma^0_{xx}}{k}(1 - \mathrm{e}^{-kt/\zeta}). \tag{13.21}$$

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

$$v(t) = \partial_t x_c = \frac{\sigma^0_{xx}}{\zeta}\,\mathrm{e}^{-kt/\zeta}. \tag{13.22}$$

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 assess the value of σ^0_{xx} because we do not know what ζ is. And, as mentioned before, we also cannot tell how much of the total stress is due to active stress. However, we can compare experiments to see the *relative* magnitudes of the total 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. We note, though, that this result is only valid for times shortly after the ablation, because the cortex is viscoelastic, so it loses its elastic character at longer times. Furthermore, the *C. elegans* cortex has a wound-healing response at longer times as well.