BE 159: Signal Transduction and Mechanics in Morphogenesis

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Winter, 2017

10 Continuum mechanics II: conservation of momentum

10.1 Conservation of linear momentum

Recall the general conservation law,

$$\partial_t \xi = -\partial_i j_i. \tag{10.1}$$

Let's take $\xi = \rho v_i$, the linear momemtum density. The total linear momentum of a volume element is $\int \mathrm{d}V \rho v_i$, so taking $\xi = \rho v_i$ means that we are describing a conservation law for linear momentum. In this case, $\partial_t(\rho v_i)$ is a rank one tensor, so the flux must be a rank two tensor. We will denote this flux as Σ_{ij}, the **total momentum flux tensor**. It is the flux of momentum density coming out of a volume element. The statement of conservation of linear momentum, called the equation of motion, is

$$\partial_t \rho v_i = -\partial_j \Sigma_{ij}. \tag{10.2}$$

Now, we can split the total momentum flux tensor into two pieces. First, we have the momentum flux due to material flowing in and out of the volume element. This is $\rho v_i v_j$. The second part of the total momentum flux is all the other stuff, which we will denote by σ_{ij}. This object, σ_{ij}, is called the **stress tensor**.

$$\Sigma_{ij} = \rho v_i v_j + \sigma_{ij}. \tag{10.3}$$

Therefore, we have

$$\partial_t \rho v_i = -\partial_j \rho v_i v_j - \partial_j \sigma_{ij}. \tag{10.4}$$

Now, we will apply the chain rule to terms on both sides of this equation.

$$\rho \partial_t v_i + v_i \partial_t \rho = -\rho v_j \partial_j v_i - v_i \partial_j \rho v_j - \partial_j \sigma_{ij}. \tag{10.5}$$

Rearranging, we get

$$\rho (\partial_t + v_j \partial_j) v_i = -v_i [\partial_t \rho + \partial_j \rho v_j] - \partial_j \sigma_{ij}. \tag{10.6}$$

The parenthetical term on the left hand side is the material derivative. The bracketed term is zero by conservation of mass, cf. equation (9.20). Thus, we arrive at our statement of conservation of linear momentum.

$$\frac{\mathrm{d}v_i}{\mathrm{d}t} = -\partial_j \sigma_{ij}. \tag{10.7}$$

10.2 Physical interpretation of the stress tensor

The stress tensor describes forces resulting from relative motion of a material. It has units of force per area, or momentum flux. To see this, note that momentum has dimension of ML/T. A flux introduces dimension of $1/L^2T$. Putting it together, the stress has units of M/LT^2, or force per area.

To understand how it describes forces due to relative motion consider for example the case where part of the material moves left and another part moves right, we have a stretching motion. The material pulls in resistance to this motion. The component of the stress tensor describing resistance to this mode of relative motion is σ_{xx}.

10.3 Constitutive relations

This is all fine and good, but can we write a mathematical expression for σ_{ij} so that we can put it to use? An expression for the stress tensor is called a **constitutive relation**. A constitutive relation relates physical quantities in a material-specific way. We already saw a constitutive relation in the last lecture, Fick's first law, which relates diffusive flux to a concentration gradient, $j_i^k = -M^k D^k \partial_i c^k$.

We stated Fick's first law without proof, and in general, the derivations constitutive relations are often nontrivial. We will explore constitutive relations in the this and the next lecture and explore their meanings.

10.4 Constitutive relation for a homogeneous elastic solid

We first consider a homogeneous elastic solid. The stress tensor is given in terms in the **strain** tensor, which we will first characterize.

10.4.1 Elastic strain tensor

We define by x_i the position of a piece of the solid in space. We then deform the solid such that that same piece is now at position x_i'. We define the **displacement**, $u_i = x_i' - x_i$. If an object changes shape, then the displacement varies across the solid. If u_i is constant across the solid, the solid is not being deformed; rather, it is being translated in the direction of u_i. However, if u_i varies in space, we do have a deformation. So, the quantity $\partial_i u_j$ reflects local deformations in the solid.

To investigate the magnitude of deformations, we consider the differential squared distance between neighboring points in the solid.

$$\mathrm{d}\ell^2 = \mathrm{d}x_i\,\mathrm{d}x_i. \tag{10.8}$$

If we have a deformation, this distance changes by

$$d\ell'^2 = dx'_i \, dx'_i. \tag{10.9}$$

To get an experession for dx'_i, we can use the chain rule.

$$d(x'_i - x_i) = du_i = (\partial_j u_i) dx_j, \tag{10.10}$$

which gives

$$dx'_i = dx_i + (\partial_j u_i) dx_j. \tag{10.11}$$

Then, we have

$$\begin{aligned} d\ell'^2 &= (dx_i + (\partial_j u_i) dx_j)\,(dx_i + (\partial_k u_i) dx_k) \\ &= dx_i \, dx_i + (\partial_j u_i) dx_j \, dx_i + (\partial_k u_i) dx_k \, dx_i + (\partial_j u_i)(\partial_k u_i) dx_j \, dx_k \\ &= d\ell^2 + [\partial_i u_j + \partial_j u_i + (\partial_i u_k)(\partial_j u_k)] \, dx_i \, dx_j, \end{aligned} \tag{10.12}$$

where in the last line we have renamed indices to collect terms multiplying $dx_i \, dx_j$. We can write this down as

$$d\ell'^2 - d\ell^2 = 2\,\varepsilon_{ij} \, dx_i \, dx_j, \tag{10.13}$$

where we have defined the **strain tensor** as

$$\varepsilon_{ij} = \frac{1}{2}\left(\partial_i u_j + \partial_j u_i + (\partial_i u_k)(\partial_j u_k)\right). \tag{10.14}$$

The last term in the strain tensor is small for small displacements, so we have, to linear order in $\partial_i u_i$,

$$\varepsilon_{ij} \approx \frac{1}{2}(\partial_i u_j + \partial_j u_i). \tag{10.15}$$

10.4.2 Elastic stress tensor

We have established that the strain describes deformations of the solid. We can derive a relationship between the stress tensor, which describes the forces necessary to achieve the deformations, using thermodynamic arguments. Instead, we will just start with Hooke's law, which is valid for small deformations. As Hooke said, "*ut tensio sic vis*," or the force is proportional to extension. Because the stress tensor is a rank 2 tensor, as is the strain tensor, to write a linear relationship between the two, most generally, we need a rank 4 tensor.

$$\sigma_{ij} = C_{ijkl} \, \varepsilon_{kl}. \tag{10.16}$$

There are $3^4 = 81$ entries in the tensor C_{ijkl}. This looks really intimidating, but by symmetry arguments, we can show that the entries are not all independent. For example, because the strain tensor ε_{ij} is symmetric, $\varepsilon_{ij} = \varepsilon_{ji}$. The stress tensor must also show this symmetry, so therefore so must C_{ijkl}. This implies that $C_{ijkl} = C_{jikl} = C_{ijlk}$. We will not go through all of the symmetry arguments here, but in the end, we find that there are only two independent parameters. Generally, it can be shown that a linear relationship between two rank 2 symmetric tensors that remains invariant under change of coordinates has the form

$$\sigma_{ij} = \lambda\, \varepsilon_{kk} \delta_{ij} + 2\mu\, \varepsilon_{ij}, \tag{10.17}$$

where the constants λ and μ are called the **Lamé coefficients**. This gives us our constitutive relation for an elastic solid.

As is commonly done, is is convenient to write the Lamé coefficients in a different form. We define

$$\lambda = \frac{E\nu}{(1+\nu)(1-2\nu)}, \tag{10.18}$$

$$\mu = \frac{E}{2(1+\nu)}, \tag{10.19}$$

where E is called the Young's modulus and ν is the Poisson ratio. The resulting expression for the stress tensor is

$$\sigma_{ij} = \frac{E}{1+\nu}\left(\varepsilon_{ij} + \frac{\nu}{1-2\nu}\,\varepsilon_{kk}\delta_{ij}\right), \tag{10.20}$$

The second law of thermodynamics dictates that $E \geq 0$ and $-1 \leq \nu \leq 1/2$ (which we will not derive here). Thus, the stress associated with an elastic deformation is of order $E\varepsilon$.

10.4.3 Equation of motion for an elastic solid

Now that we have our constitutive relation, we can write the equation of motion from the statement of conservation of linear momentum. The local velocity, v_i, is related to the displacement as $v_i = \partial_t u_i$. Thus, we can write

$$\rho\,\frac{\mathrm{d}v_i}{\mathrm{d}t} = \rho\,\left(\partial_t^2 u_i + (\partial_t u_j)\partial_j\partial_t u_i\right) = -\partial_j\sigma_{ij}, \tag{10.21}$$

where the t's denote time derivatives and are not summed over. Evidently, this is a wave equation in the displacement. The dynamics describe elastic waves through the solid. We know these waves as sound. The dynamics are usually very fast compared to biological time scales of interest, so we usually neglect the left hand side of the equation of motion. Typically with elastic solids, we will study only statics, as governed by the constitutive relation itself, in this case, equation (10.20).

10.5 Constitutive relation for an isotropic viscous fluid

If we look at the expression for the elastic stress, we see that it scales like the displacement, $\sigma \sim E\varepsilon$. For a fluid, we would not expect this to be the case. If we displace a fluid and then let it rest, we do not have to exert any more force to maintain the displacement. Instead, we expect that the stress we need to exert on a fluid to move it will be related to the *rate* at which we make deformations,

$$\partial_t \partial_i u_j = \partial_i \partial_t u_j = \partial_i v_j, \tag{10.22}$$

where $v_j = \partial_t u_j$ is the velocity at which the material is moving. In other words, if we want to move a fluid more rapidly, it will require more force than to move it slowly. The actual magnitude of the displacement will not matter; only the rate at which we make displacements. The velocity gradient tensor can be written as

$$\partial_i v_j = \frac{1}{2}(\partial_i v_j + \partial_j v_i) + \frac{1}{2}(\partial_i v_j - \partial_j v_i) = \frac{1}{2}(v_{ij} + \omega_{ij}). \tag{10.23}$$

Here, we have defined

$$v_{ij} \equiv \frac{1}{2}(\partial_i v_j + \partial_j v_i) \tag{10.24}$$

as the symmetric part of the velocity gradient tensor and

$$\omega_{ij} \equiv \frac{1}{2}(\partial_i v_j - \partial_j v_i) \tag{10.25}$$

as the antisymmetric part. Due to the symmetry of an isotropic fluid and conservation of angular momentum (which we will not formally consider here), the stress tensor must be symmetric, which means that ω_{ij} does not contribute to it.

We might also expect the stress to include the hydrostatic pressure, p. After all, pumps move fluids around by exerting pressure on them. So, we additionally have a $-p\,\delta_{ij}$ term in the stress tensor. For an isotropic viscous fluid, then, we have

$$\sigma_{ij} = -p\,\delta_{ij} + C_{ijkl} v_{kl}. \tag{10.26}$$

Again, we use the fact that a linear relationship between two rank 2 symmetric tensors that remains invariant under change of coordinates can be written with Lamé coefficients.

$$\sigma_{ij} = -p\,\delta_{ij} + \lambda\, v_{kk}\,\delta_{ij} + 2\mu\, v_{ij}. \tag{10.27}$$

We will define η and η_v such that $\mu = \eta$ and $\lambda = (\eta_v - 2\eta)/3$. Then, we have

$$\sigma_{ij} = -p\,\delta_{ij} + 2\eta\left(v_{ij} - \frac{v_{kk}}{3}\,\delta_{ij}\right) + \frac{\eta_v}{3}\, v_{kk}\,\delta_{ij}. \tag{10.28}$$

The quantity η is called the **viscosity**, or shear viscosity, and η_v is called the bulk viscosity. It is clear that η_v determines the contribution of isotropic compression to the stress. For am incompressible fluid, the continuity equation (9.23) gives that $v_{kk} = \partial_k v_k = 0$, so the stress tensor is

$$\sigma_{ij} = -p\,\delta_{ij} + 2\eta\, v_{ij} = -p\,\delta_{ij} + \eta\,(\partial_i v_j + \partial_j v_i). \tag{10.29}$$

10.6 Equation of motion for an incompressible isotropic viscous fluid

Now that we have the constitutive relation, we can write down the equation of motion for an incompressible isotropic viscous fluid. This is the statement of conservation of linear momentum.

$$\frac{\mathrm{d}v_i}{\mathrm{d}t} = -\partial_j \sigma_{ij} = \partial_i p - \eta\, \partial_j \partial_j v_i, \tag{10.30}$$

This equation, together with the continuity equation, $\partial_i v_i = 0$, are known as the **Navier-Stokes equations**. We can nondimensionalize this equation, choosing $x = \ell \tilde{x}$, $t = \tau \tilde{t}$, $v_i = U \tilde{v}_i$, and $p = \tilde{p} \eta\, U/\ell$. Here, ℓ and τ are respectively length and time scales of interest, and U is the characteristic velocity. The resulting equation is

$$\frac{\rho\, \ell^2}{\eta \tau}\, \partial_t \tilde{v}_i + \frac{\rho U \ell}{\eta}\, \tilde{v}_j \partial_j \tilde{v}_j = \partial_i \tilde{p} - \partial_j \partial_j \tilde{v}_i, \tag{10.31}$$

where the derivatives are now over dimensionless variables. We can collect the constants to define dimensionless parameters, the **Reynolds number**, $\mathrm{Re} = \rho U \ell / \eta$, and the **Strouhal number**, $\mathrm{Sr} = (\ell / U)/\tau$.

$$\mathrm{Re}\, (\mathrm{Sr}\, \partial_t + \partial_j \tilde{v}_j)\, \tilde{v}_i = \partial_i \tilde{p} - \partial_j \partial_j \tilde{v}_i. \tag{10.32}$$

The Reynolds number is the ratio of the inertial energy, $\rho U^2 \ell^3$, to the energy loss due to viscous dissipation, $\eta U \ell^2$. The Strouhal number is the ratio of the advective time scale, ℓ/U to any other pertinent time scale of interest, τ. If $\mathrm{Re} \ll 1$ and $\mathrm{Re}\,\mathrm{Sr} \ll 1$, then the left hand side of the equation of motion is negligible compared to each term in the right hand side. In cell and developmental biology, this is generally the case. To satisfy us that this is indeed the case, we can estimate the Reynolds number for processes in a developing embryo. The density of our material is close to that of water, or 10^3 kg/m^3. The smallest viscosity is that of water, which is about 10^{-3} kg-m/s. The longest length scale we generally consider in early embryos is about 1 mm = 10^{-3} m. The fastest speeds could conceivably be that of the fastest motor proteins, about 100 µm/s = 10^{-4} µm/s. Putting this together gives a Reynolds number of $\mathrm{Re} = 0.1$. We have intentionally overestimated this, since most fluid-like embryonic movements more more slowly, over shorter distances, and with much higher viscosity. So, we are generally justified in neglecting the left hand side of the equation of motion, and we have

$$\partial_j \sigma_{ij} = 0. \tag{10.33}$$

We will talk in more depth about dynamics of isotropic incompressible viscous fluids at low Reynolds number when we study the He, at al. paper toward the end of the course. In the next lecture, we will look at complex fluid (those that are not isotropic, such as an actin cortex, which is comprised of filaments) and *active*, meaning that the material can consume energy (for example via ATP hydrolysis by motor proteins).