BE 159: Signal Transduction and Mechanics in Morphogenesis

Justin Bois

Caltech

Winter, 2018

11 Viscous flows in development

In the He, et al. paper, we will study viscous flows in the context of apical constriction in ventral furrow formation in *Drosophila* development. He and coworkers do not consider the contracting material, but rather the passive components beneath. These can be modeled as a viscous fluid.

11.1 Dynamical equations of Stokes flow

An isotropic viscous fluid has a stress tensor given by

$$\sigma_{ij} = -p\,\delta_{ij} + 2\eta\, v_{ij} = -p\,\delta_{ij} + \eta\,(\partial_i v_j + \partial_j v_i). \tag{11.1}$$

The equation of motion, as we have seen before is

$$\rho\,\frac{\mathrm{d}v_i}{\mathrm{d}t} = \partial_j\,\sigma_{ij}, \tag{11.2}$$

where $\mathrm{d}/\mathrm{d}t$ denotes the material derivative we have seen in previous lectures. As we have seen before, in most developmental contexts, the Reynolds number is very small, so the lefthand side of the equation of motion is effectively zero. The resulting equation of motion is then

$$\partial_j\,\sigma_{ij} = -\partial_i p + \eta\,\partial_j\partial_j v_i = 0. \tag{11.3}$$

We have used the continuity equation, $\partial_i v_i = 0$ in writing this, and have made the assumption that the viscosity η is constant. Flow described by these equations is called **Stokes flow**, named after George Stokes, who was a pioneer in the study of low Reynolds number fluid dynamics.

11.2 Qualitative features of Stokes flow

Now that we have the equations governing Stokes flow, we can make some very powerful qualitative statements about Stokes flow.

1. The Stokes equations are linear. Therefore, for a given set of boundary conditions, the velocity field is unique. This is not true for flows with $\mathrm{Re} > 0$.
2. There is no time present in the Stokes equations, except possibly for time-dependent boundary conditions. This means that the flow field is set *instantaneously* by the boundary conditions. Knowledge of the flow at any other time is unnecessary.

3. Because the Stokes equations are linear, the dynamics are **reversible**. This means that if v_i is a solution of the Stokes equations, then so is $-v_i$ if the sign of the pressure field is also flipped.

$$-\partial_i(-p) + \eta\,\partial_j\partial_j(-v_i) = \partial_i p - \eta\,\partial_j\partial_j v_i = 0 = -\left(-\partial_i p + \eta\,\partial_j\partial_j v_i\right). \tag{11.4}$$

This also means that the dynamics are reversible in time. That is, if the time-dependent boundary conditions were run in reverse, the fluid dynamics would be exactly reversed as well.

4. Hydrodynamic forces are long-ranged. To see this, consider an object moving through a fluid. The fluid around the object moves, and as a result, momentum is carried through the fluid. The momentum flux is given by the stress tensor. So,

$$\text{momentum flux} \equiv j_{\text{mom}} \sim \partial_j v_i \sim \partial_r v, \tag{11.5}$$

where r is the radial distance from the translating object. We will assume a power law dependence of the momentum flux on r,

$$j_{\text{mom}} \sim r^{-\alpha-1}. \tag{11.6}$$

The total momentum flux through any spherical shell of radius R must be the same as any other spherical shell. The total momentum flux through a spherical shell scales like $j_{\text{mom}}R^2 \sim R^{-\alpha+1}$. For this to be the same for all shells, we must have $\alpha = 1$. Thus,

$$\partial_r v \sim r^{-2}, \tag{11.7}$$

such that $v \sim r^{-1}$. So, the velocity field decays away like $1/r$, in contrast to high Reynolds number where it decays away like $1/r^3$. In two dimensions, the decay is even slower, $v \sim \ln r$. So, hydrodynamic forces are felt over large distances.

11.3 Green's functions for Stokes flow

Consider a point force F_i in a fluid. In this case, the governing equations are

$$-\partial_i p + \eta\,\partial_j\partial_j v_i = -F_i\,\delta(x_i), \tag{11.8}$$

$$\partial_i v_i = 0. \tag{11.9}$$

The velocity and pressure fields that solve these equations are known as the **Green's functions**. We could solve for the Green's functions, but it is perhaps easier to "invent" the solution and then verify that it works. The result is

$$v_i = \frac{1}{8\pi\eta} F_j G_{ij}, \tag{11.10}$$

$$p = \frac{1}{8\pi\eta} F_i P_i, \tag{11.11}$$

where

$$G_{ij} = \frac{\delta_{ij}}{r} + \frac{x_i x_j}{r^3}, \tag{11.12}$$

$$P_i = 2\eta \frac{x_i}{r^3} + P_i^\infty, \tag{11.13}$$

where $r = \sqrt{x_i x_i}$ and $F_i P_i^\infty$ is the pressure very far away from the point source. From this expression, we see the $1/r$ dependence of the velocity field. Here, G_{ij} is known as the **Oseen tensor**, after the Swedish physicist Carl Wilhelm Oseen. The quantity v_i, as defined above, which is the Green's function for the Stokes equations, is called a **Stokeslet**. The stress field from the point source is $F_k \Sigma_{ijk}$, where

$$\Sigma_{ijk} = -\frac{3}{4\pi} \frac{x_i x_j x_k}{r^5}. \tag{11.14}$$

In two dimensions, velocity field is instead

$$v_i = \frac{1}{4\pi\eta} F_j G_{ij}, \tag{11.15}$$

$$G_{ij} = \ln r \delta_{ij} - \frac{x_i x_j}{r^2}, \tag{11.16}$$

so the decay of the velocity field is even slower than in three dimensions.

11.4 Solutions of Stokes equations using Green's functions

He, et al. solved the Stokes equations by choosing a distribution and strength of point forces such that the fluid flow velocity matched that what was measured at he apical surface. In other words, the apical surface is contracting and constitutes a moving boundary. The boundary conditions were approximated by placing points sources that gave the right result at the boundary. Because the solution to the Stokes equations is unique, this give the correct fluid flow. Note, however, that this crude method does not give the correct stresses. Getting those requires more careful methods like boundary integral methods, which are beyond the scope of our discussion here.