BE/APh 161: Physical Biology of the Cell, Winter 2014
Homework #7
Due at the start of lecture, 1PM, March 12, 2014.

Problem 7.1 (Antenna model for microtubule length control, 25 pts)**.**
Do problem 15.7 of *PBoC2*.

Problem 7.2 (Power input for cytoplasmic streaming, 10 pts)**.**
Cytoplasmic streaming in *Drosophila* oocytes is driven by kinesin motors. Figure 1 shows a quantification of cytoplasmic streaming velocities. From this figure, estimate the number of kinesin motors driving streaming. *Hint:* Use rules of thumb for kinesin's velocity and force to estimate the power each motor can transmit to the cytoplasm. Then estimate the power dissipated by viscous losses in the streaming cytoplasm. Assume that the cytoplasm is a fluid with viscosity approximately 200× that of water.

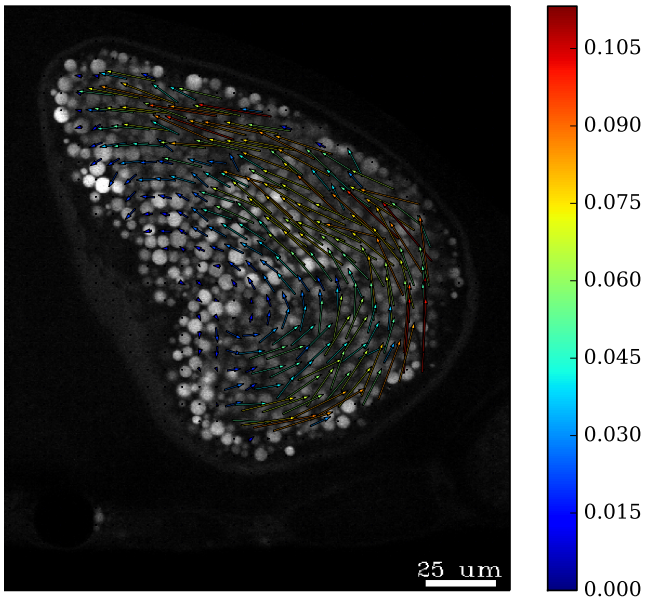

Figure 1: Quantification of cytoplasmic flow velocities in a streaming *Drosophila* oocyte as measured using particle image velocimetry. Autofluorescent granules in a thin focal slice in the center of the oocyte was imaged using a fluorescent confocal microscope. The arrows indicate the local flow velocity. They are color-coded according to speed. The units on the colorbar are µm/s. Scale bar, 25 µm.

Problem 7.3 (Measurement of cortical tension by laser ablation, 15 pts)**.**
The acto-myosin cortex is a thin meshwork of actin filaments lying just below the cell membrane. The actin filaments are crosslinked by myosin motors, creating an active gel. Laser ablation has been employed as a valuable technique to measure stresses in the cortex. In these experiments, a portion of the cortex is ablated, meaning it is completely destroyed. The cortex then recoils due to the stresses that were present immediately before ablation. To be concrete: at times $t < 0$, the cortex is intact and under tension with active stress σ_a. At time $t = 0$, a piece of the cortex is instantly ablated and the cortex recoils.

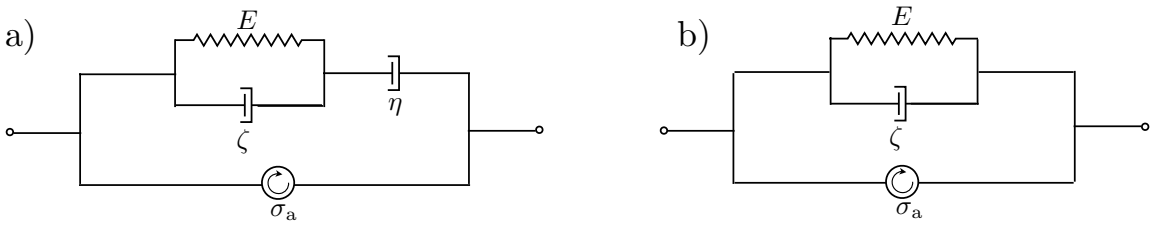

Figure 2: a) Schematic of an active Jeffreys fluid. b) Schematic of an active Kelvin-Voigt solid at short time scales.

In this problem, we will use the linear viscoelastic model for the cell cortex presented in class in which the cortex is represented as a Jeffreys fluid in series with a dashpot, all in parallel with an active stress (Figure 2a).

a) Show that for the short time scales associated with ablation, the cortex may be described as an active Kelvin-Voigt solid, as in Figure 2b.

b) Show that the recoil velocity is an exponentially decaying function of time,

$$v(t) = v_0 \mathrm{e}^{-t/\tau}. \tag{7.1}$$

Show that the initial recoil velocity v_0 is proportional to the total stress present in the cortex immediately before ablation. Show that τ is inversely proportional to the Young's modulus of the cortex.

c) Explain why ablation experiments alone cannot give numerical values of cortical properties such as the Young's modulus or total stress, but only proportionalities. I.e., we can only find the ratio of total stress from two different ablation experiments, but not the difference.

Problem 7.4 (The cell cortex and optical cell stretching, 25 pts)**.**
We briefly discussed optical cell stretchers in lecture. Optical cell stretchers work by taking advantage of the difference in index of refraction between a cell and the surrounding solution to trap a free cell in two counter-propagating laser beams. The power of the laser is then increased to exert stress and elongate the trapped cell. The induced stress is proportional to the laser power. The constant of proportionality, F_G is dependent on geometry and cannot be ascertained. The deformation (strain) is measured by taking images with a light microscope. The process is illustrated in Figure 3. In this way, the mechanical properties of an entire cell can be measured.

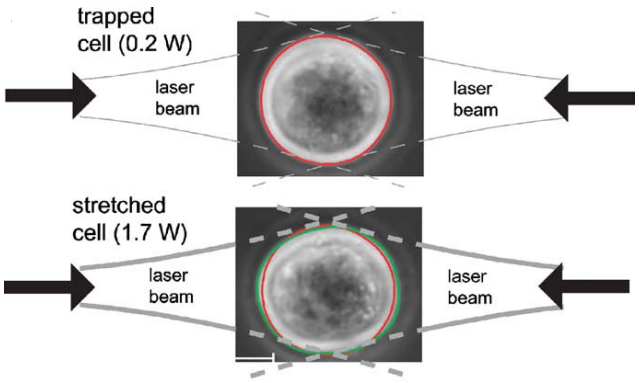

Figure 3: Schematic of an optical stretcher. The cell stretches along the axis parallel to the laser beams. The strain is given by the fractional change of the diameter of the cell along the stretching axis. Figure take from Wottawah, et al., *Acta Biomaterialia*, **1**, 263–271, 2005.

This technique was used to assess the mechanical properties of two mammalian cell types, 3T3 and SVT2 (which have reduced actin), in Wottawah, et al., *PRL*, **94**, 098103, 2005. In this work, the authors performed a stress step experiment in which a constant stress σ_0 was applied at $t = 0$, as in lecture. The stress was set back to zero at time $t = t_1$. The authors can obtain the creep compliance from this measurement.

a) Derive an expression for the strain in the stress step experiment if we model the cell as an active Jeffreys fluid as in Figure 2a. The stress step can be described mathematically as $\sigma(t) = F_G\sigma_0\theta(t)\theta(t_1 - t)$, where $\theta(t)$ is the Heaviside step function. Assume the active stress is constant, given by σ_a.

b) The authors perform curve fits of the expression you derived in part (a) to get values for the parameters of the cell. Explain why they cannot independently measure E, η, and ζ, but only products thereof. Can a constant active stress be detected in this experiment?

c) The authors then use the curve fit parameters to compute the storage and loss moduli (E' and E'') of the cell. Derive expressions for the storage and loss moduli from the fit parameters. (*Note*: These reported storage and loss moduli are dependent on choosing a model for the viscoelastic behavior of the cell. This is not ideal, but is apparently a necessity due to experimental constraints.)