Tutorial 3: Membrane-filament interactions

Physics of Complex Systems M2 – Biophysics

1 Membrane fluctuations

Here we consider a membrane whose average position is within the $z = 0$ plane. Let $u(\mathbf{r})$ be the vertical fluctuation of the membrane at a point with horizontal coordinates $\mathbf{r} = (x, y)$. The membrane does not have a spontaneous curvature, but is endowed with a bending modulus κ and a tension γ.

1.1 Write the Helfrich Hamiltonian $\mathcal{H}$ describing the energy of the membrane as the sum of a curvature energy and a tension energy. You may start by writing is as a surface integral involving the membrane's total curvature. Assuming a small membrane deformation, write $\mathcal{H}$ as an integral over the coordinates x, y that only involves κ, γ and the spatial derivatives of $u(\mathbf{r})$. Finally, express $\mathcal{H}$ in Fourier space, that is as a function of $\tilde{u}(\mathbf{q})$, la transformée de Fourier de $u(\mathbf{r})$. We will define the Fourier transform through:

$$u(\mathbf{r}) = \int \tilde{u}(\mathbf{q}) e^{i\mathbf{q}.\mathbf{r}} \frac{\mathrm{d}^2\mathbf{q}}{(2\pi)^2}, \quad \tilde{u}(\mathbf{q}) = \int u(\mathbf{r}) e^{-i\mathbf{q}.\mathbf{r}} \mathrm{d}^2\mathbf{r}. \tag{1}$$

1.2 Compute the mean square displacement in Fourier space $\langle \tilde{u}(\mathbf{q})\tilde{u}(\mathbf{q}')\rangle$. Deduce that the real-space mean-square displacement of the membrane fluctuations is $\delta^2 = \langle u(\mathbf{r})^2\rangle = \frac{kT}{4\pi\gamma} \ln \frac{q_{\min}^2 + q_c^2}{q_{\min}^2}$, where $q_{\min}$ is a small-wavevector cutoff that you will specify as a function of the system size, and q_c is to be expressed as a function of the parameters of the problem.

1.3 How does the mean square displacement δ^2 depend on the system size if the membrane tension is large? How about the $\gamma \to 0$ limit? Can you cite and experiment allowing to measure this amplitude?

2 Membrane going through a fixed point

2.1 We impose a fixed displacement $u(\mathbf{0}) = a$ on the membrane at the origin of coordinates $\mathbf{r} = \mathbf{0}$. Thus the membrane always goes through the point $(x = 0, y = 0, z = a)$. Explain why the partition function reads

$$Z_p = \int \mathcal{D}u[.] \delta(u(\mathbf{0}) - a) e^{-\mathcal{H}/kT}$$

where δ is a Dirac distribution. The symbol $\mathcal{D}u[.]$ indicates a sum over all possible states of the membrane, and thus over all possible fluctuations $u(\mathbf{r})$. In practice, this boils down to summing over all Fourier components $\tilde{u}(\mathbf{q})$. By replacing the Dirac delta by its Fourier transform $\delta(x) = \int_{-\infty}^{+\infty} e^{i\lambda x} \mathrm{d}\lambda/(2\pi)$, write hte partition function as

$$Z_p = \int_{-\infty}^{+\infty} \frac{\mathrm{d}\lambda}{2\pi} \int \mathcal{D}\tilde{u}[.] \exp\left[\int \frac{\mathrm{d}^2\mathbf{q}}{(2\pi)^2} \left(-|\tilde{u}|^2 \frac{\kappa q^4 + \gamma q^2}{2kT} + i\lambda\tilde{u}\right)\right] e^{-i\lambda a}$$

Compute the Gaussian integrals over $\tilde{u}$ by going to discrete q modes and by pretending that $\tilde{u}$ is real. We recall that $\int_{-\infty}^{+\infty} e^{-\alpha x^2} \mathrm{d}x = \sqrt{\pi/\alpha}$. Deduce that

$$\begin{aligned} Z_p &= Z_0 \int_{-\infty}^{+\infty} \frac{\mathrm{d}\lambda}{2\pi} e^{-\frac{\lambda^2\delta^2}{2} - i\lambda a} \\ &= Z_0' \exp\left(-\frac{a^2}{2\delta^2}\right) \end{aligned}$$

where Z_0 and Z_0' are constants which we will not seek to determine.

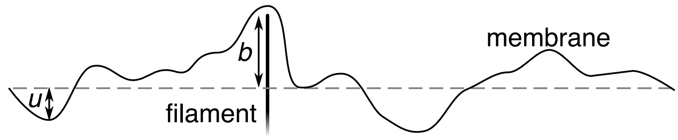

Figure 1: Illustration of the problem studied in Sec. 3.

2.2 Can you assign a physical meaning to Z_0'? What is the membrane's free energy under the constraint that we impose on it?

2.3 What force $f(a)$ must we impose on the membrane to impose a deformation of magnitude a at the location $\mathbf{r} = \mathbf{0}$?

3 Interaction entre un filament et la membrane

We now study the interaction between the membrane and a filament—a microtubule for instance. The experiment is schematized in Fig. 1. The filament has a fixed length and is maintained at a constant position so that its tip is at an altitude b above the average plane of the membrane. The filament cannot go through the membrane.

3.1 Explain why the filament exerts a force on the membrane.

3.2 Show that if the filament is fixed, the membrane's partition function is $Z_f = \int_b^{+\infty} Z_p(a)\,\mathrm{d}a$. Compute the free energy of the membrane and the force exerted on the filament. We will introduce the function $\mathrm{erfc}(x) = \frac{2}{\sqrt{\pi}} \int_x^{+\infty} e^{-y^2} \mathrm{d}y$ which is such that $\mathrm{erfc}(0) = 1$ and that for large x we have $\mathrm{erfc(x)} \sim \frac{1}{\sqrt{\pi} x} e^{-x^2}$.

3.3 Compute an order of magnitude for the force at $b = 0$ if the tension is $\gamma = 5.10^{-5}$ N.m^{-1} and the bending modulus $\kappa = 20 k_B T$. We will assume that the membrane has a lateral size $L = 5\,\mu$m.

3.4 The filament is now a biological polymer regarded as fixed at its lower extremity. This filament grows through monomer addition at its upper tip. What are the three possible outcomes of such an experiment? Discuss the conditions under which each of them is observed. You are welcome to draw inspiration from the treatment of Ref. [1]; see also Fig. 2. We recall that when a rigid filament of length l is compressed, it buckles provided that the force is larger than the critical force $f_c = k_B T \ell_p \pi^2 / l^2$, where ℓ_p is its persistence length.

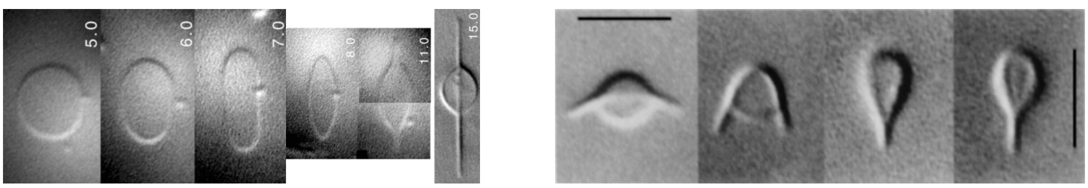

Figure 2: (left) A phospholipid vesicle deformed by 1 to 3 vertical microtubules. (right) Spontaneous buckling of microtubules inside a ϕ-shaped vesicle. In the final image, the microtubules are bent completely and continue to grow with both ends sheathed in a single membrane sleeve. Scale bar: 5 μm [2].

References

[1] D R Daniels, D Marenduzzo, and M S Turner. Stall, spiculate, or run away: The fate of fibers growing towards fluctuating membranes. *Phys. Rev. Lett.*, 97:098101, September 2006.

[2] Deborah Kuchnir Fygenson, John F. Marko, and Albert Libchaber. Mechanics of microtubule-based membrane extension. *Phys. Rev. Lett.*, 79(22):4497–4500, December 1997.