Lipid membranes:
- Main component of the life cell, made of phospholipids
- In a planar form or highly curved shapes such as:
  - Quasi spherical shapes (e.g. lysosomes and peroxisomes)
  - Tubular shapes (e.g. Mitochondria, cell connection tubes)
  - Complexes (e.g. Golgi apparatus)
- Actively dynamic during cell functions, also at thermodynamic equilibrium states, i.e. lipid membranes are fluctuating at thermal bath

Mechanical properties:
- Extendible surfaces
- In-plane fluidity
- Bending flexibility
- Interlayer slippage

Thermal undulations of a planar membrane

Motivation

Lipid membranes in eukaryotic cells have been observed in highly curved geometries in some organelles such as lysosomes and peroxisomes, which are relatively spherical, or mitochondria and endoplasmic reticulum (ER) which form tubular networks. In general, cellular membrane shapes are actively dynamic during cell processes such as fusion, fission, bud and tube growth, but also under steady state conditions. We determine the relaxation dynamics and the shape fluctuations of quasi-spherical vesicles at equilibrium or non-equilibrium thermodynamics. Extending the classical continuum formulations, we include the membrane viscosity in addition to the interlayer slippage and the friction due to the bulk fluid viscosity. We show that depending on the size of the vesicle, even for small deviations, the membrane viscosity can significantly change the dynamical time scales of the thermally excited vesicles (eigenvalues of the spherical modes), and the characterizing length scales. We introduce a length scale in which the in-plane lipid flow becomes observable using high resolution optical measurements. We conclude that the membrane viscosity plays a nontrivial role in dynamics and shape fluctuations of highly curved organelles. Finally, we discuss the limitations of the linearized theory in estimation of the dynamics of the excited vesicles by comparison of the results with ones calculated by a fully nonlinear simulation.

Spherical Harmonics

Approximation for physical and geometrical variables, for quasi spherical vesicles:

\[ x(t, \varphi, \theta) = \sum_{n=0}^{\infty} \sum_{m=-n}^{n} x_{nm}(t) Y_{nm}(\varphi, \theta), \]

Main advantages:
- In contrast with planar configuration, membrane viscosity appears in the linearized equations.
- A few shape functions are enough to explain the excitation/relaxation dynamics

Continuum model

Surface lipid flow:
Newtonian 2D-compressible Stokes flow

Surrounding flow:
Newtonian 3D-incompressible Stokes flow

\[ W^{\text{mem}}[\mathbf{v}^{\pm}, \rho_{\pm}] = \frac{1}{2} \int_{\Omega} \left( 2 \mu_{s} \mathbf{d} : \mathbf{d} + \lambda_{s} (\mathbf{tr} \mathbf{d})^{2} \right) \pm dS, \]

Membrane dissipation

\[ W^{\text{bulk}}[\mathbf{v}^{\pm}, \rho_{\pm}] = -\frac{1}{2} \int_{\Omega} \rho \mathbf{v}^{\pm} \cdot \mathbf{v}^{\pm} dS, \]

Surrounding fluid dissipation

\[ W^{\text{slip}}[\mathbf{v}^{\pm}] = b_{m} \int_{\Omega} \left| \mathbf{v}^{+} - \mathbf{v}^{-} \right|^{2} dS, \]

Interlayer slippage

\[ \Pi[\mathbf{x}(\mathbf{r}), \rho] = \int_{\Omega} \frac{K_{\perp}}{2} \left( \frac{\mathbf{p}^{+} - 1}{\rho^{+}} - \frac{\mathbf{p}^{-} - 1}{\rho^{-}} \right)^{2} dS + \int_{\Omega} \frac{K_{\parallel}}{2} (H - C_{0})^{2} dS, \]

Extensional elastic energy

\[ W^{\text{tot}} \rightarrow \Pi \]

Minimization of the Lagrangian form

Dynamical frequencies and the response amplitudes
- Membrane viscosity plays a significant role
- These effects disappear for larger vesicles