Measuring bending elasticity of lipid bilayers

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The bending elastic energy per unit membrane area, F_c, is (Helfrich [1973]):

$$F_c = \frac{k_c}{2}(c_1 + c_2 - c_0)^2 + \bar{k}_c c_1 c_2$$

where: k_c and $\bar{k}_c$ are the elastic modules for cylindrical and saddle bending; c_1 and c_2 are the principal curvatures at the given point; c_0 is the membrane's spontaneous curvature. For symmetric membranes $c_0 = 0$.

In polar coordinates a quasi-spherical vesicle could be described by the equation:

$$r(\theta, \varphi, t) = R[1 + u(\theta, \varphi, t)]$$

where: R is the mean vesicle radius; $u(\theta, \varphi, t)$ is the deviation from the spherical shape as a function of the polar angles θ, φ and the time t. For small deformations $|u(\theta, \varphi, t)| \ll 1$. By definition, its mean over the time is zero:

$$\langle u(\theta, \varphi, t) \rangle = 0$$

If $\vec{r}(\theta, \varphi)$ is the radius-vector of a point on the quasi-spherical vesicle, parametrized by the polar angles θ and φ, then the vectors $\vec{r}_\theta = \frac{\partial \vec{r}}{\partial \theta}$, $\vec{r}_\varphi = \frac{\partial \vec{r}}{\partial \varphi}$, are tangential to the vesicle membrane and could be used for a local coordinate system with a metric tensor, $g^{\alpha\beta}(\theta, \varphi)$:

$$g^{\alpha\beta}(\theta, \varphi) = \begin{pmatrix} \vec{r}_\theta . \vec{r}_\theta & \vec{r}_\theta . \vec{r}_\varphi \\ \vec{r}_\varphi . \vec{r}_\theta & \vec{r}_\varphi . \vec{r}_\varphi \end{pmatrix}$$

and its inverse, $g_{\alpha\beta}(\theta, \varphi)$:

$$g_{\alpha\beta}(\theta, \varphi) = \frac{1}{\det g^{\alpha\beta}} \begin{pmatrix} \vec{r}_\varphi . \vec{r}_\varphi & -\vec{r}_\varphi . \vec{r}_\theta \\ -\vec{r}_\theta . \vec{r}_\varphi & \vec{r}_\theta . \vec{r}_\theta \end{pmatrix}$$

so, $g^{\alpha\gamma} g_{\gamma\beta} = \delta^{\alpha .}_{.\beta}$ (implicit summation over γ is assumed).

The unit vector normal to the membrane, $\vec{n}(\theta,\varphi)$, is:

$$\vec{n}(\theta,\varphi) = \frac{\vec{r}_\theta \times \vec{r}_\varphi}{|\vec{r}_\theta \times \vec{r}_\varphi|}, \qquad \vec{n}.\vec{n} = 1$$

Its derivatives $\vec{n}_\theta = \dfrac{\partial \vec{n}}{\partial \theta}$, $\vec{n}_\varphi = \dfrac{\partial \vec{n}}{\partial \varphi}$, $(\vec{n}.\vec{n}_\theta = \vec{n}.\vec{n}_\varphi = 0)$ are tangential to the membrane, and therefore are linear combination of $\vec{r}_\theta$ and $\vec{r}_\varphi$. The matrix of the coefficients is the curvature tensor, $C^{\alpha\beta}(\theta,\varphi)$, of the quasi-spherical vesicle surface:

$$C^{\alpha\beta}(\theta,\varphi) = \begin{pmatrix} \vec{n}_\theta.\vec{r}_\theta & \vec{n}_\theta.\vec{r}_\varphi \\ \vec{n}_\varphi.\vec{r}_\theta & \vec{n}_\varphi.\vec{r}_\varphi \end{pmatrix}$$

Of practical interest is the tensor $C^{\alpha\cdot}_{\cdot\beta}(\theta,\varphi)$ derived from $C^{\alpha\beta}(\theta,\varphi)$ by lowering an index using $g_{\alpha\beta}$, $C^{\alpha\cdot}_{\cdot\beta} = C^{\alpha\gamma}g_{\gamma\beta}$ (implicit summation over γ is assumed):

Its trace is the mean curvature $c_1 + c_2$:

$$C^{\gamma\cdot}_{\cdot\gamma} = c_1 + c_2$$

and its determinant is the Gaussian curvature $c_1 c_2$:

$$\det C^{\alpha\cdot}_{\cdot\beta} = c_1 c_2$$

Integrating the bending elastic energy per unit area, F_c, over the area of the membrane, the vesicle curvature energy is obtained.

Due to the spherical symmetry it is convenient to express the deviations from the spherical shape, $u(\theta, \varphi, t)$, in series of spherical harmonics, $Y_n^m(\theta, \varphi)$ with amplitudes $U_n^m(t)$:

$$u(\theta, \varphi, t) = \sum_{n=0}^{\infty} \sum_{m=-n}^{n} U_n^m(t) Y_n^m(\theta, \varphi)$$

Milner & Safran [1987] have shown that the bending elastic energy, $\mathcal{F}_c$, of a quasi-spherical vesicle at constant vesicle volume and membrane area is:

$$\mathcal{F}_c = \frac{k_c}{2} \sum_n \sum_m (n-1)(n+2)[\bar{\sigma} + n(n+1)] |U_n^m(t)|^2$$

where $\bar{\sigma}$ is dimensionless parameter connected to the conservation of membrane area.

$$\mathcal{F}_c = \frac{1}{2}\sum_n \sum_m k_c(n-1)(n+2)[\bar{\sigma} + n(n+1)]|U_n^m(t)|^2$$

The vesicle energy, $\mathcal{F}_c$, is a sum of harmonic oscillators with elastic constants $k_c(n-1)(n+2)[\bar{\sigma} + n(n+1)]$ and amplitudes $U_n^m(t)$. According to the equipartition theorem the mean energy of each oscillator is $\frac{k_B T}{2}$, where k_B is Boltzmann's constant and T is the absolute temperature. Comparing both expressions Milner & Safran [1987] obtained:

$$\langle |U_n^m(t)|^2 \rangle = \frac{k_B T}{k_c} \frac{1}{(n-1)(n+2)[\bar{\sigma} + n(n+1)]}$$

Thus the membrane bending modulus, k_c, could be calculated by measuring the mean squared amplitude of spherical harmonics, $\langle|U_n^m(t)|^2\rangle$:

$$\frac{k_B T}{k_c} = (n-1)(n+2)[\bar{\sigma} + n(n+1)]\langle|U_n^m(t)|^2\rangle$$

The unknown parameter $\bar{\sigma}$ must be so selected that the right-hand side is independent on the deformation mode number, n.

References:

1. W. Helfrich [1973]: Elastic properties of lipid bilayers: theory and possible experiments, Z. Naturforsch. **28c**, 693–703.
2. S.T. Milner, S.A. Safran [1987]: Dynamical fluctuations of droplet microemulsions and vesicles, Phys. Rev. A **36**, 4371–4379.