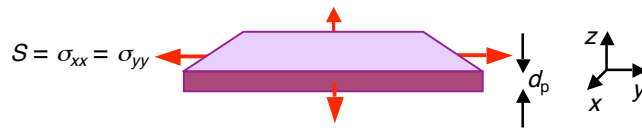


PHYS 4xx Mem 2 - Compression and bending resistance

In the next few lectures, we investigate the mechanical properties of membranes, incorporating the effects of thermal fluctuations. We start with the elastic parameters for compression and bending.

Compression resistance in 2D: K_A

Naïve approach: View the bilayer as a homogeneous rigid sheet. To find its area, apply a tensile stress S to a square plate of thickness d_p :



From Eq. (6.19) of Mechanics of the Cell, the elements of the strain tensor for an isotropic material in three dimensions are:

$$u_{ij} = \delta_{ij} \text{tr} \sigma / 9K_V + (\sigma_{ij} - \delta_{ij} \text{tr} \sigma / 3) / 2\mu,$$

where K_V and μ are the volume compression and shear moduli in three dimensions.

Here, $\sigma_{xx} = \sigma_{yy} = S$, so the in-plane elements are

$$u_{xx} = u_{yy} = S (2 / 9K_V + 1 / 6\mu).$$

The (two-dimensional) tension τ is related to the three-dimensional stress S through $\tau = Sd_p$ which gives rise to a relative change in area $u_{xx} + u_{yy}$ according to $\tau = K_A(u_{xx} + u_{yy})$:

$$\begin{aligned} Sd_p = \tau &= K_A(u_{xx} + u_{yy}) \\ &= K_A 2 \cdot (2 / 9K_V + 1 / 6\mu) \end{aligned}$$

or

$$K_A = d_p K_V / (4/9 + K_V / 3\mu).$$

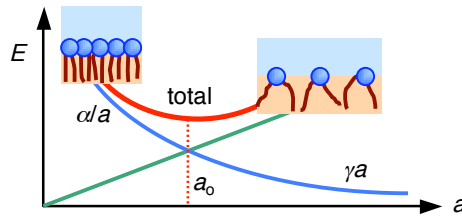
Surface tension approach: consider only the interface energy (water/amphiphile with oily interior).

At low density, the energy penalty per molecule for exposing the amphiphile's hydrocarbon chains is equal to γa , where a is the mean interface area occupied by an amphiphile and γ is the surface tension of the water+amphiphile interface.

At high density, the molecules are crowded together, and their repulsive energy rises with density as a power of $1/a$.

The simplest dependence of the interface energy per molecule on a is then

$$E = \alpha / a + \gamma a.$$



E has a minimum at the equilibrium value of a , namely a_0 .

$$0 = dE/da = d(\alpha/a + \gamma a) / da$$

$$= -\alpha/a^2 + \gamma$$

Hence

$$a_0 = \sqrt{(\alpha/\gamma)},$$

permitting E to be written as

$$E = 2\gamma a_0 + (\gamma/a_0) \cdot (a - a_0)^2.$$

For $a \sim a_0$, E changes by $(\gamma/a_0) \cdot (a - a_0)^2$ relative to E at $a = a_0$, giving an elastic energy density of $\gamma [(a - a_0)/a_0]^2$ when divided by the area per molecule a_0 .

Now, the deformation energy density also can be written as $(K_A/2) \cdot (u_{xx} + u_{yy})^2$, where $u_{xx} + u_{yy}$ equals the relative change in area, $(a - a_0)/a_0$. [from $tru = \Delta A / A$]

Comparing these expressions for the deformation energy density yields:

$$K_A = 2\gamma$$

monolayer

$$K_A = 4\gamma,$$

bilayer

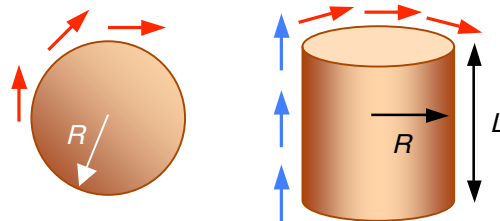
where the difference between the monolayer and bilayer arises because there are two interfaces to the latter.

Experimentally, $\gamma \sim 0.02 - 0.05 \text{ J/m}^2$ for the water+amphiphile interface. The surface tension approach predicts that $K_A \sim 0.08 - 0.2 \text{ J/m}^2$, independent of bilayer thickness.

Membrane	T (C)	Apparent K_A (J/m ²)	Reference
diAPC	21	0.183±0.008	Rawicz <i>et al.</i> , 2000
diGDG	23	0.160±0.007	Evans and Rawicz, 1990
diMPC	21	0.150±0.014	Rawicz <i>et al.</i> , 2000
diOPC	21	0.237±0.016	Rawicz <i>et al.</i> , 2000
SDPC	30	0.12	Koenig <i>et al.</i> , 1997
SOPC	15	0.19±0.02	Needham and Nunn, 1990
red cell plasma membrane (stiffened by cholesterol)		0.45	Evans and Waugh, 1977

Membrane bending rigidity κ_b

Bending resistance is proportional to the curvature of the membrane, much like the bending resistance of a polymer. As in polymers, the curvature C is also written as the reciprocal of the radius of curvature: $C = 1/R$. Unlike polymers, the curvature depends on the path along the membrane's surface:



There are two principle curvatures, denoted as C_1 and C_2 . The cylinder is described by two inequivalent curvatures: $C_1 \equiv 1/R_1 = 1/R$ and $C_2 \equiv 1/R_2 = 0$.

The simplest form for the energy density of deformation \mathcal{F} involves the squared mean curvature $(C_1/2 + C_2/2)^2 = (1/R_1 + 1/R_2)^2/4$ and the Gaussian curvature $C_1 C_2 = 1/R_1 R_2$, where R_1 and R_2 are the two radii of curvature:

$$\mathcal{F} = (\kappa_b/2) \cdot (1/R_1 + 1/R_2)^2 + \kappa_G/(R_1 R_2),$$

where the material-specific parameters κ_b and κ_G are the bending rigidity and the Gaussian bending rigidity, respectively. For the two shells above, the bending energy compared to a flat surface is

$$E = 4\pi(2\kappa_b + \kappa_G)$$

sphere

$$E = \pi\kappa_b L/R,$$

cylinder

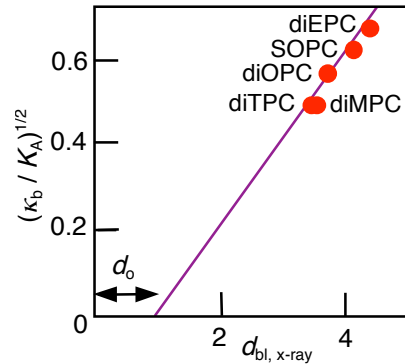
Membrane	κ_b ($\times 10^{-19}$ J)	κ_b ($k_B T$)	Reference
diAPC	0.44±0.05	11	Evans and Rawicz, 1990
diGDG	0.44±0.03	11	Evans and Rawicz, 1990
diMPC	1.30±0.08	33	Méléard <i>et al.</i> , 1997
diMPE	0.7±0.1	18	Mutz and Helfrich, 1990
diOPC	0.85±0.10	21	Rawicz <i>et al.</i> , 2000
SOPC	0.90±0.06	23	Evans and Rawicz, 1990
red cell membrane	1.4-4.3	35-108	Peterson <i>et al.</i> , 1992

The bending of a bilayer involves a compression of one surface and an extension of the other, the magnitude of the strain being governed by the area compression modulus K_A .

Various models for the deformation (e.g., solid material, independent leaflets, polymer brushes...) can be summarized by

$$\kappa_b = K_A d_{bl}^2 / \alpha, \quad (\text{KB.1})$$

where the numerical constant $\alpha = 12, 24$ or 48 . If K_A is independent of d_{bl} for the bilayers of interest then this equation predicts $\kappa_b \propto d_{bl}^2$; a rigid plate, however, obeys $K_A \propto d_{bl}$, which leads to $\kappa_b \propto d_{bl}^3$. Eq. (KB.1) is supported by the data:



Ratio of bilayer bending rigidity κ_b to area compression modulus K_A as a function of bilayer thickness $d_{bl, X-ray}$ as determined by X-ray scattering; the straight line is Eq. (KB.1) with $\alpha = 24$ and offset $d_0 = 1$ nm (after Rawicz *et al.*, 2000). Abbreviations: diEPC = dierucoyl-PC, SOPC = stearyl-oleoyl-PC, diOPC = dioleoyl-PC, diMPC = dimyristoyl-PC, and diTPC = ditridecanoyl-PC, where PC = phosphatidylcholine.