The Many Faces of Membrane Tension for Biomembranes and Vesicles

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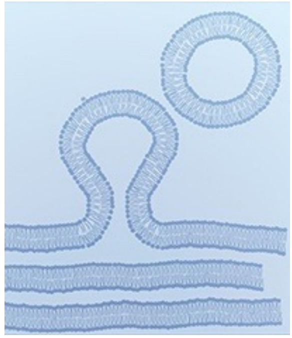
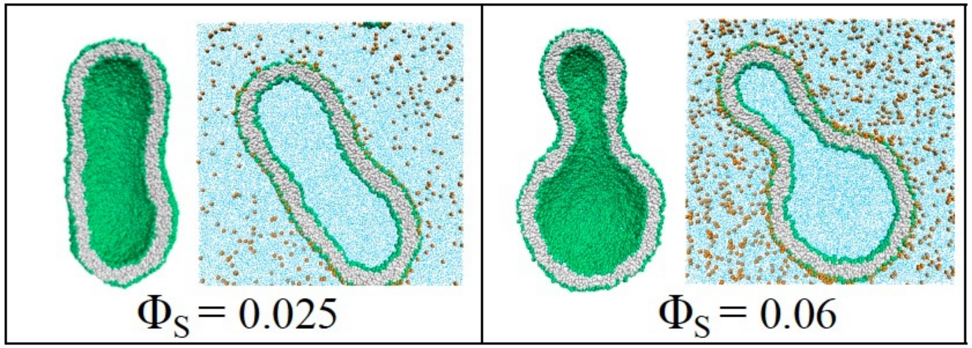
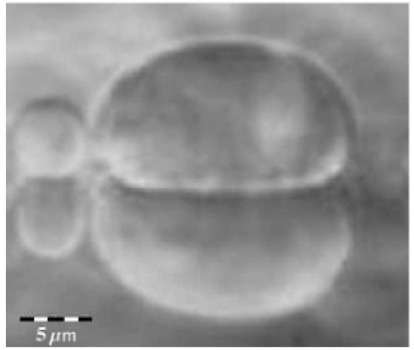
Ubiquity of Membrane Tension

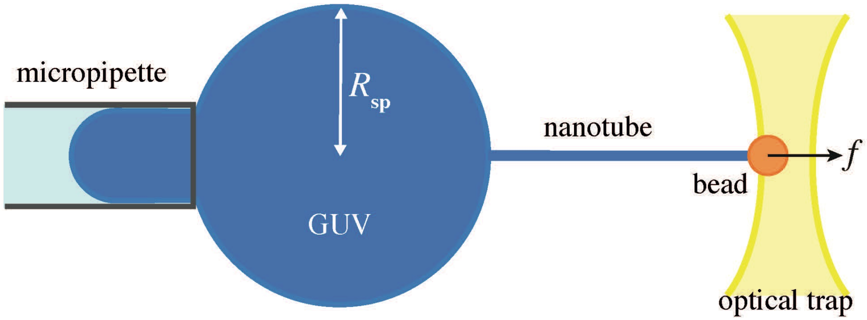
- Vesicle preparation
- Osmotic in/deflation
- Adhesion

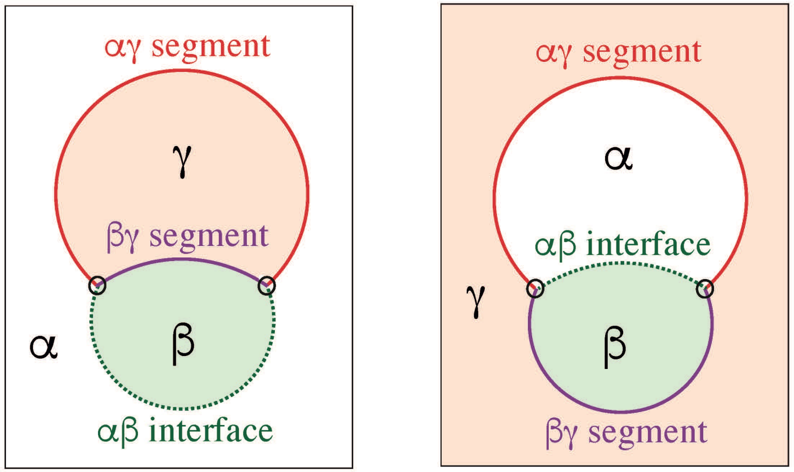






- Micropipette aspiration
- Condensate droplets





Membrane Tension ⇔ Membrane Area

- Common feature in all examples:

  Membrane subject to external forces or constraints that affect the membrane‘s surface area

- Difficulty:

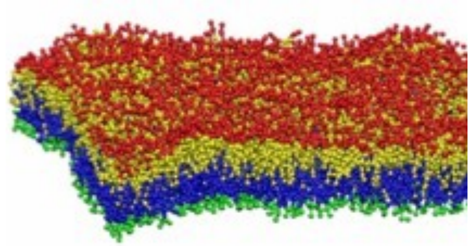
  Area changes are necessarily small because the membrane ruptures for area changes of a few percent

- Tension for three biomimetic model membranes:

  Planar lipid bilayers, unilamellar nanovesicles, and giant unilamellar vesicles (GUVs)

Planar Lipid Bilayers

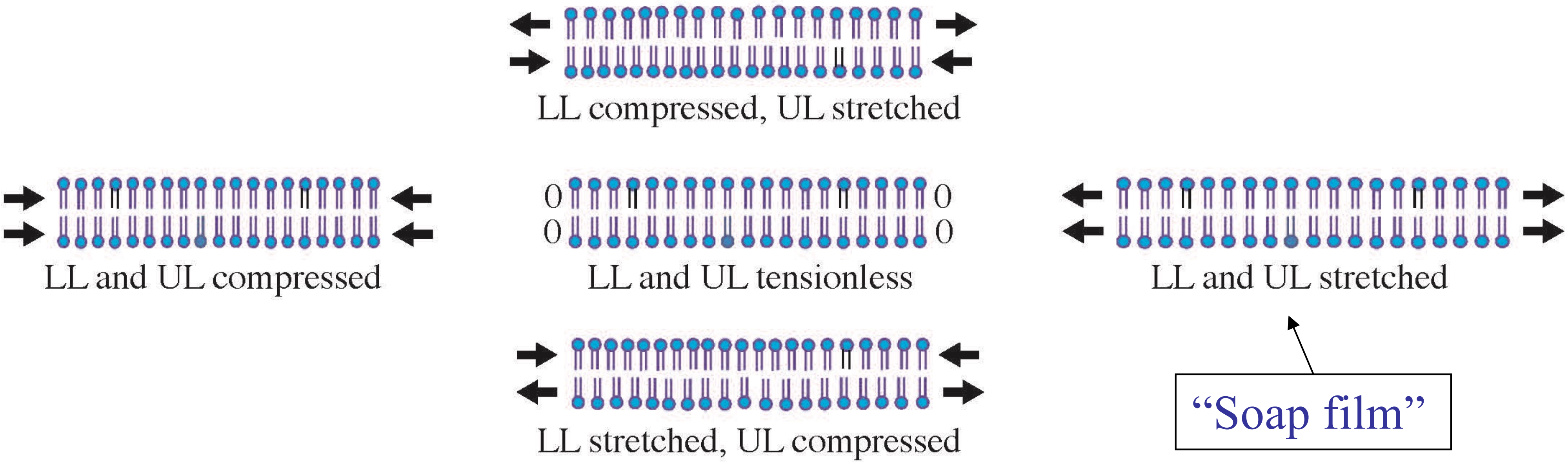
Rozycki and Lipowsky, *J. Chem. Phys*, 2015 = Ref 6
Lipowsky et al, *Biomolecules*, 2023 = Ref 1



- Upper leaflet with N_{ul} lipids and leaflet tension Σ_{ul}
- Lower leaflet with N_{ll} lipids and leaflet tension Σ_{ll}
- Bilayer tension $\Sigma_{bil} = \Sigma_{ul} + \Sigma_{ll}$
- Each leaflet can be compressed, tensionless, or stretched ⇔
  Each leaflet tension can be negative, zero, or positive
- Reference state with tensionless leaflets, $\Sigma_{ul} = \Sigma_{ll} = 0$
- Tensionless leaflets imply tensionless bilayer.
  In contrast, a tensionless bilayer does not imply tensionless leaflets but only opposite leaflet tensions, $\Sigma_{ll} = - \Sigma_{ul}$

Leaflet Tensions of Bilayers

- Elastic states of lower leaflet (LL) and upper leaflet (UL):

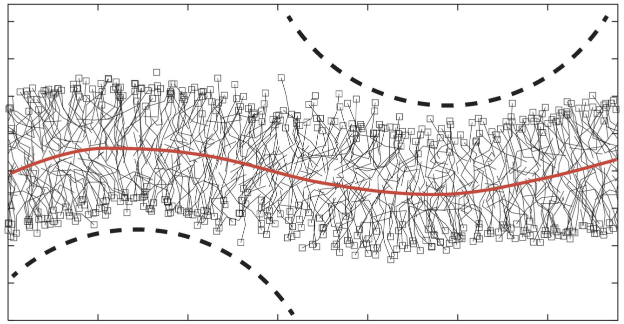


- Analogous elastic states for two leaflets of nanovesicles
- Main difference: Reference state more difficult to find

Fluctuation Tension

Goetz et al, *Phys Rev Lett*, 1999
= Ref 14

- Excess area stored in shape fluctuations
- Membrane with bending rigidity κ
- Bending modes with wavenumber *q*
- Fluctuation spectrum



$$S(q) = \frac{k_B T}{\Sigma_{fl} q^2 + \kappa q^4}$$

Fluctuation tension Σ_{fl}

- Bilayer tension $\Sigma_{bil} = 0$ implies fluct tension $\Sigma_{fl} = 0$
- Latest simulation study provides evidence for $\Sigma_{fl} = \Sigma_{bil}$

Shiba et al, *Soft Matter*, 2016 = Ref 29

Giant Unilamellar Vesicles (GUVs)

- Spontaneous curvature model Helfrich, *Z. Naturforsch.* 1973 = ESI Ref 1
- Applies to membranes with cholesterol !

Steinkühler et al, *Nature Commun*, 2020 = Ref 40
Bhatia et al, *Soft Matter*, 2020 = Ref 41

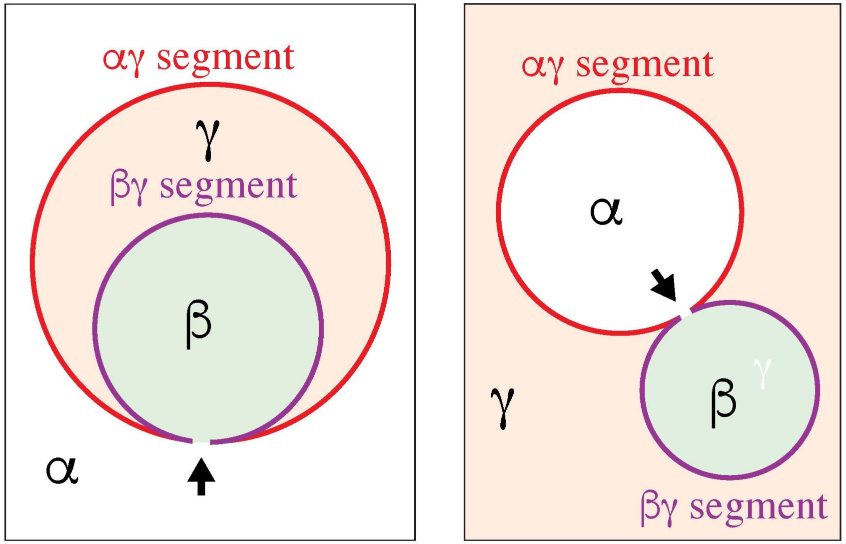
- Local shape equation $\Delta P = 2\, \Sigma_{tot}\, M + \ldots$
- Total membrane tension $\Sigma_{tot} = \Sigma + 2\kappa m^2$
- Mechanical membrane tension Σ
  and curvature-elastic tension $2\kappa m^2$
- Both tensions have observable consequences

Vesicles and Condensate Droplets

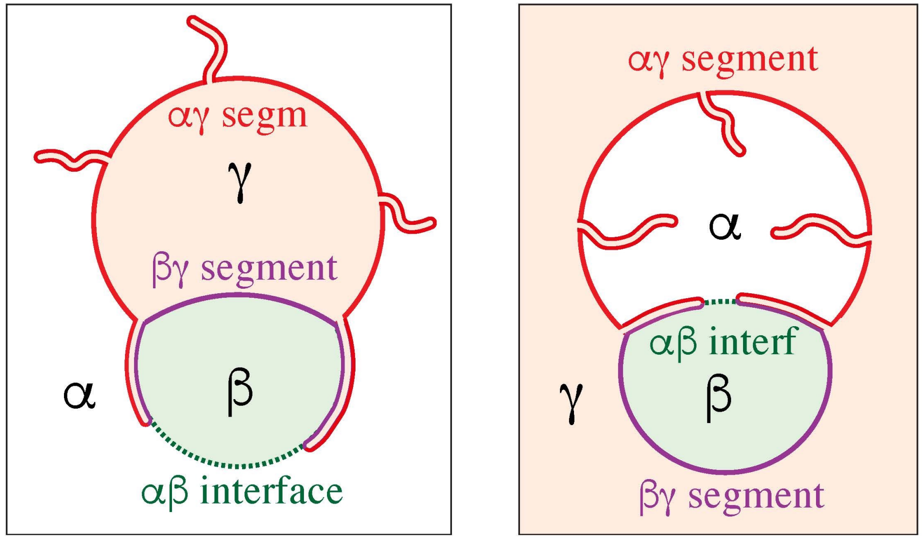
- Cond droplets enclosed by liquid-liquid interface between two liquid phases α and β, third liquid phase γ
- Interface between α and β has interfacial tension $\Sigma_{\alpha\beta}$

Lipowsky, JPC B, 2018 = Ref 69

- Complete engulfment:



- Membrane nanotubes:



- Interfacial tension large compared to curv-elastic tensions
- Interfacial tension small compared to curv-elastic tensions

Membrane Tension $\neq$ Interfacial Tension

- In the literature, frequent analogies between mechanical membrane tension Σ and interfacial tension Σ_{int} but

Fundamentally different properties of Σ and Σ_{int} :

- Positive interfacial tension $\Sigma_{int} > 0$ in contrast to Σ
- Mech membrane tension Σ depends on vesicle size and shape in contrast to interfacial tension Σ_{int}
- Different scaling properties of shape fluctuations
- Mechanical and thermodynamic (Gibbs) route to Σ_{int} but

No meaningful thermodynamic (Gibbs) route to Σ !

- For $\Sigma \leq 0$, crumpled states for sufficiently large membranes
- For $\Sigma > 0$, pore formation for sufficiently large membranes