



Interface-mediated interactions

*from ground state calculations to
fluctuation-induced effects*

KITP Workshop on Fluctuation-Induced Interactions, 11/17/08

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Motivation

The four pictures can be found in Fig. 1 of the reference below.

- a) plasma membrane
- b) endoplasmic reticulum (green)
- c) Golgi complex (red/yellow) & endoplasmic reticulum
- d) vesicular membrane carriers

M. M. Kozlov, Nature **447**, 387 (2007).





Motivation

The picture can be found in the reference below (Fig. 7a).

E. Gottwein et al, J. Virol. **77**, 9474 (2003).





Questions: How can these structures be explained?
What forces shape the membranes of the biological cell?





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- Direct specific interactions
- Electromagnetic interactions
- Interface-mediated interactions

between particles (proteins) embedded in the lipid membrane.





What are interface-mediated interactions? (1)

Example:

Interaction of two needles floating on water

For the movie see <http://www.geomnat.com>

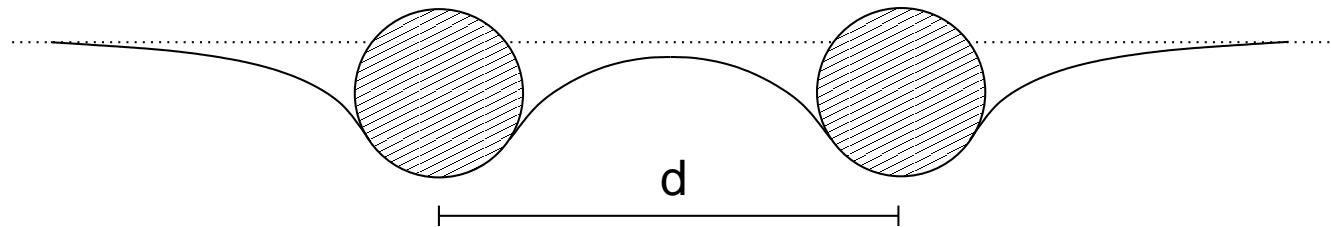
W. A. Gifford, L. E. Scriven, *Chem. Eng. Sci.* **26**, 287 (1971).

D. Vella, L. Mahadevan, *Am. J. Phys.* **73**, 817 (2005).



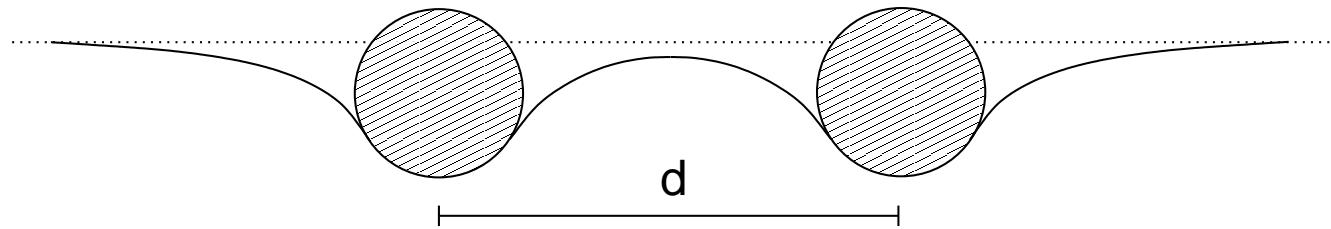


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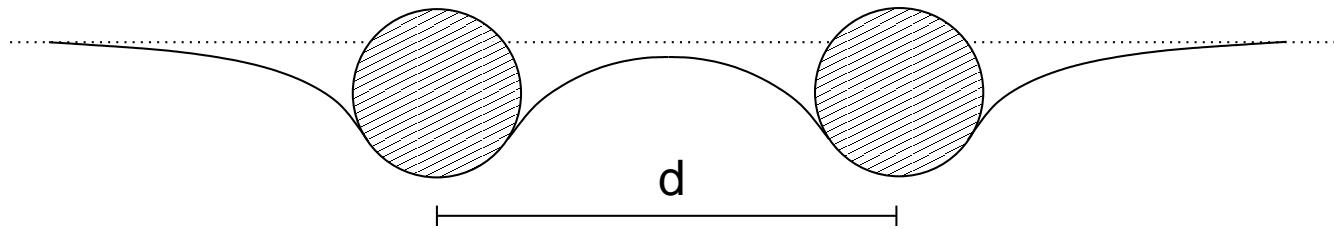


$$E(d)$$





What are interface-mediated interactions? (2)

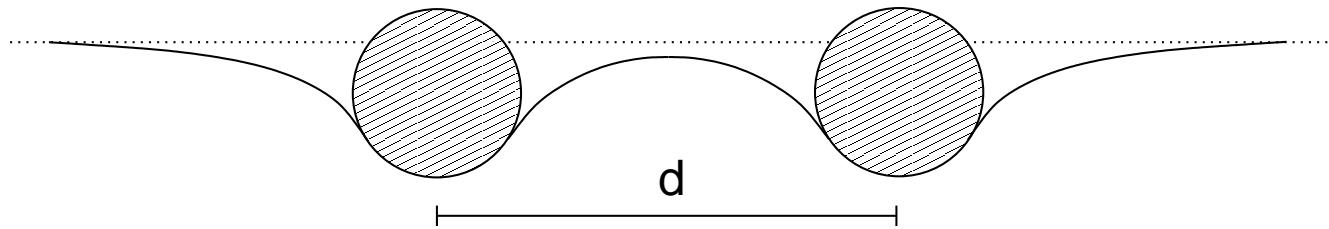


$$E(d) \Rightarrow F(d) = -\frac{\partial E}{\partial d}$$





What are interface-mediated interactions? (2)



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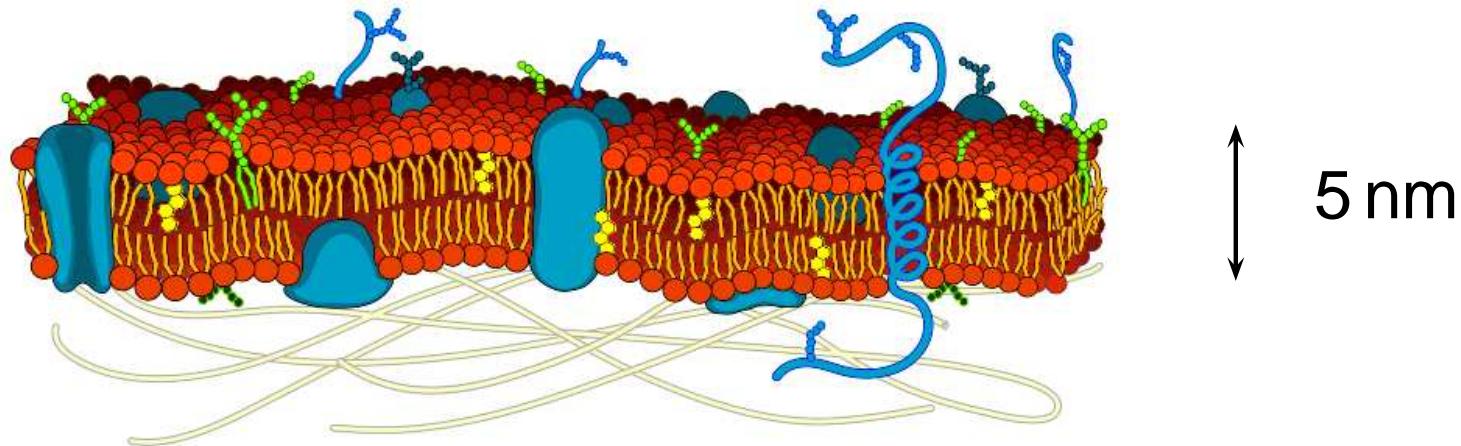
⇒ Traditional approach:

- Determine the energy of the system for every possible particle configuration.
- Derive with respect to the appropriate particle coordinate to get the force.





1. Surface model

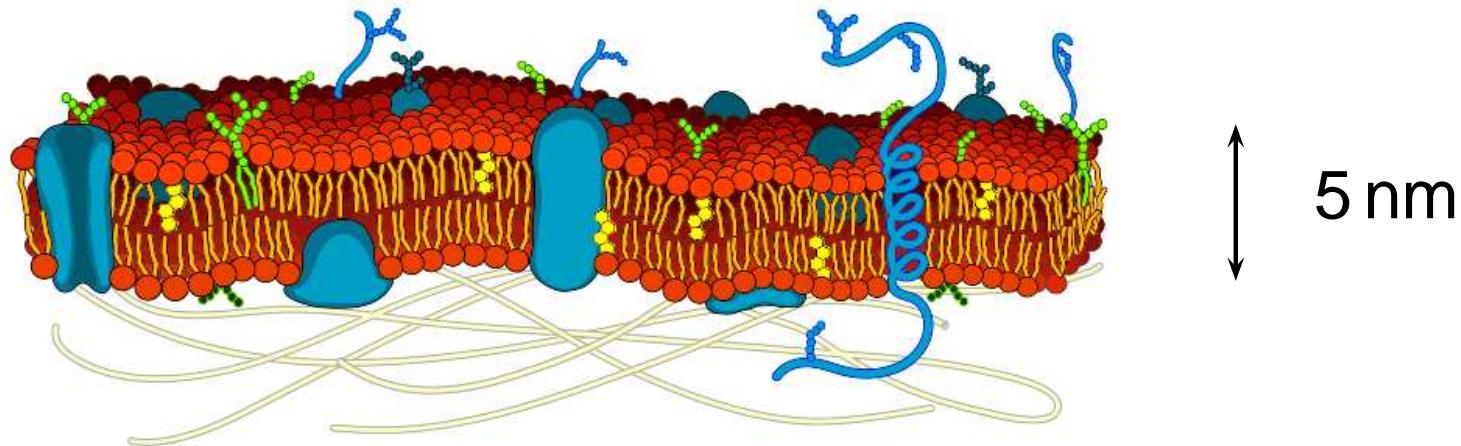


from <http://www.wikipedia.org>





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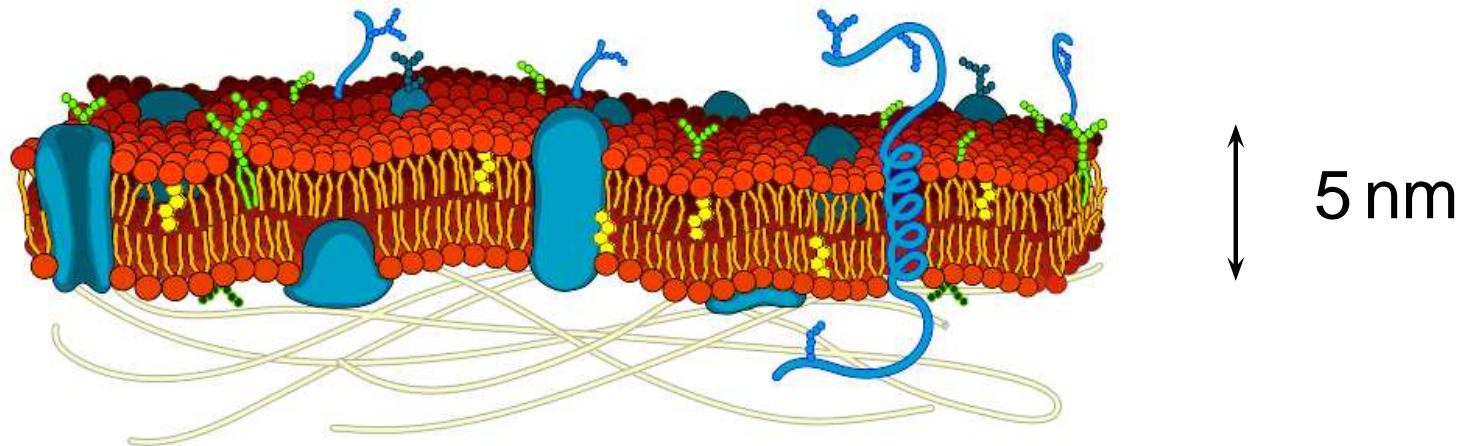
from <http://www.wikipedia.org>

- Biological membranes consist of a lipid double layer (red-orange) in which other particles such as proteins (blue) are embedded.





1. Surface model



from <http://www.wikipedia.org>

- Biological membranes consist of a lipid double layer (red-orange) in which other particles such as proteins (blue) are embedded.
- Under physiological conditions the molecules can diffuse relatively easily in the membrane plane.





1. Surface model

- Use a continuum description and model the bio-membrane/interface as a two-dimensional surface.





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$$H = \int_{\Sigma} dA \mathcal{H} .$$





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- Its energy is given as a surface integral over a scalar density \mathcal{H} :

$$H = \int_{\Sigma} dA \mathcal{H} .$$

- Easiest example: constant energy per area (surface tension σ) governs the behaviour of the surface

$$\mathcal{H}_{\text{soap film}} = \sigma .$$





Surface model

- Fluid lipid membrane:

$$\mathcal{H}_{\text{biomembrane}} = \sigma + \frac{1}{2} \kappa K^2 + \bar{\kappa} K_{\mathbf{G}}$$

Helfrich (1973)





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Helfrich (1973)

surface
tension





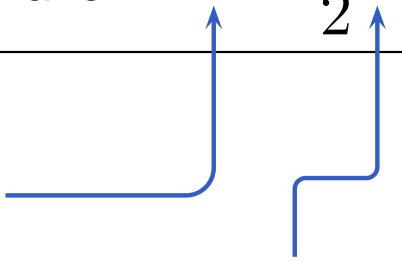
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Helfrich (1973)

surface tension bending rigidity





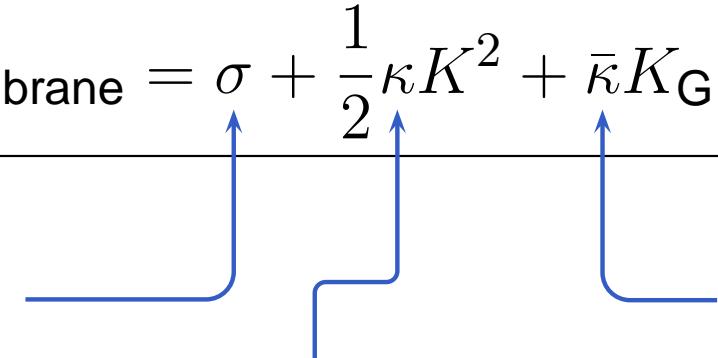
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saddle-splay
modulus





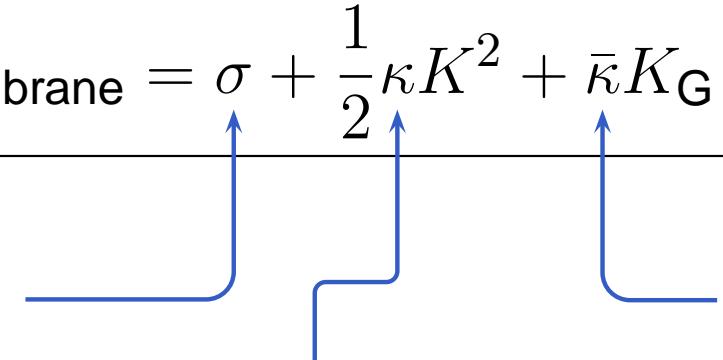
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- In general: $\mathcal{H} = \mathcal{H}(K, K_G, \nabla K)$.





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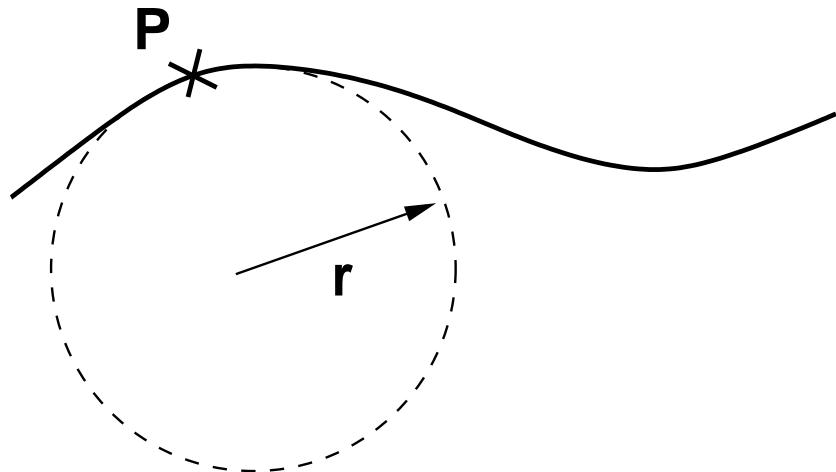
- In general: $\mathcal{H} = \mathcal{H}(K, K_G, \nabla K)$.
- How are the curvatures K and K_G defined?





Definition of K and K_G

Curvature in one dimension:



$$k = \frac{1}{r}$$

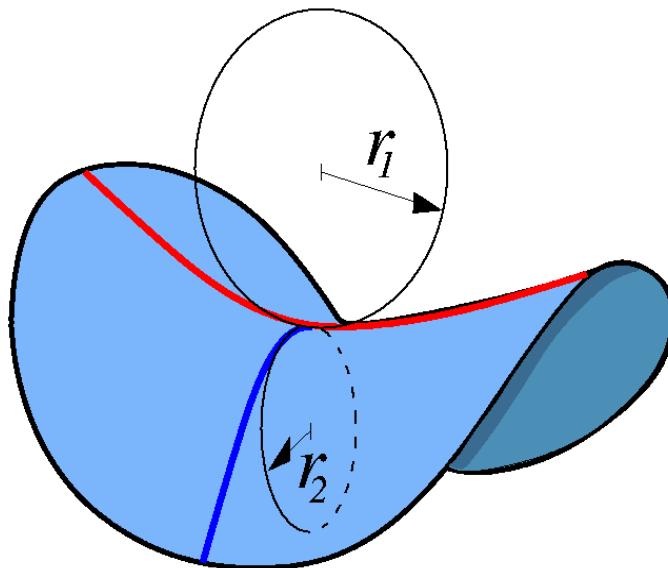




Definition of K and K_G

In two dimensions:

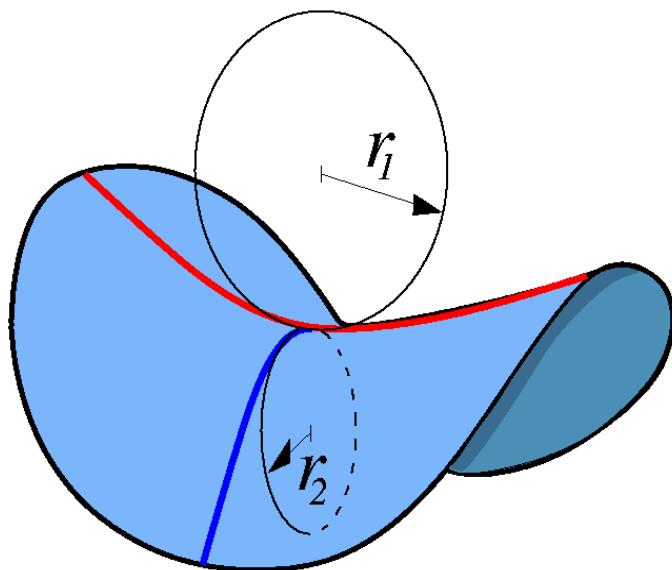
$$H = \int dA \left(\sigma + \frac{1}{2} \kappa K^2 + \bar{\kappa} K_G \right)$$





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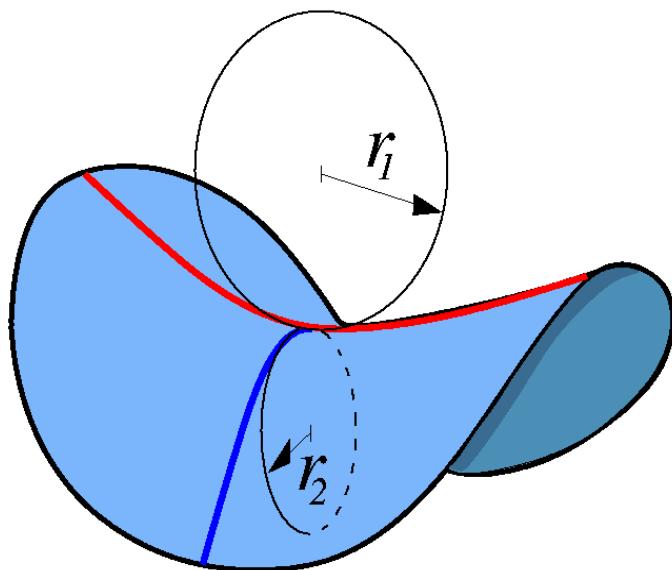
$$K = \frac{1}{r_1} + \frac{1}{r_2} \propto \text{mean curvature}$$





Definition of K and K_G

In two dimensions:



$$H = \int dA \left(\sigma + \frac{1}{2} \kappa K^2 + \bar{\kappa} K_G \right)$$

$$K = \frac{1}{r_1} + \frac{1}{r_2}$$

$$K_G = \frac{1}{r_1} \cdot \frac{1}{r_2}$$

Gaussian curvature

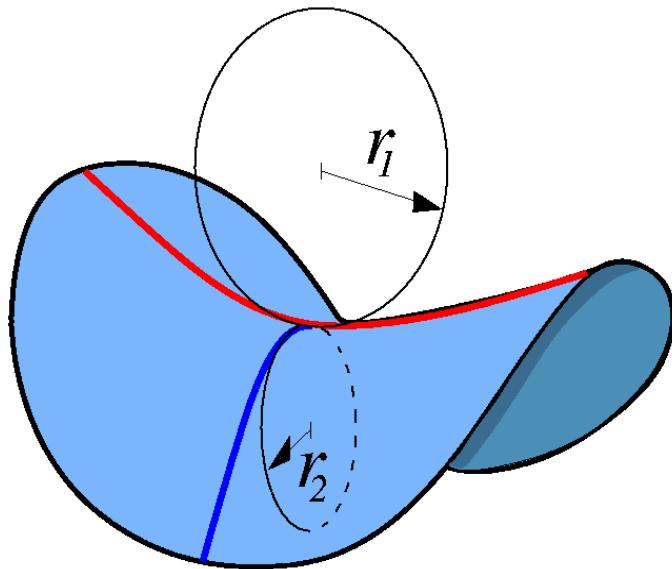




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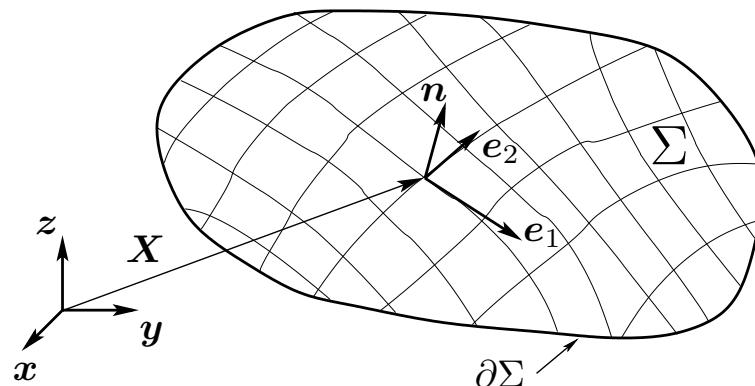
- How can the shape of the surface be determined?





Differential geometry

- Consider 2D surface Σ , which is described locally by its position $X(\xi^1, \xi^2) \in \mathbb{R}^3$, where the ξ^a are a suitable set of local coordinates on the surface.

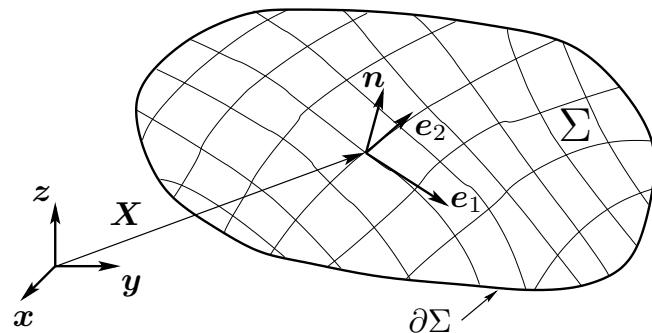




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- Basis:

$$e_a = \frac{\partial X}{\partial \xi^a}; \quad n = \frac{e_1 \times e_2}{|e_1 \times e_2|}.$$



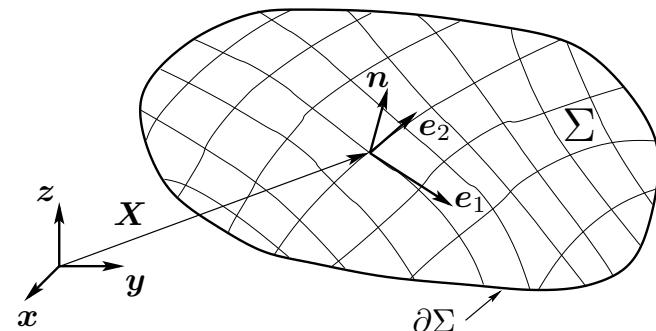


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- metric and extrinsic curvature tensor ($a, b \in \{1, 2\}$):

$$g_{ab} = e_a \cdot e_b; \quad K_{ab} = e_a \cdot \frac{\partial n}{\partial \xi^b} = e_a \cdot \nabla_b n.$$

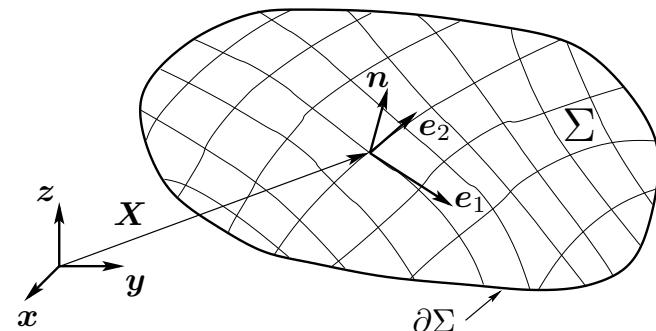




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$$g_{ab} = e_a \cdot e_b; \quad K_{ab} = e_a \cdot \frac{\partial n}{\partial \xi^b} = e_a \cdot \nabla_b n.$$

- Note that: $K = K_{ab}g^{ab}$ and $K_G = \frac{1}{2}(K^2 - K_{ab}K^{ab})$.





Shape equation

Consider ground state in equilibrium





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- An analytical solution only exists for special cases (e.g. for a translationally invariant membrane)

M. M. M., M. Deserno, J. Guven, *Phys. Rev. E* **76**, 011921 (2007).





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- This nonlinear partial differential equation has to be solved to determine the membrane shape.
- An analytical solution only exists for special cases (e.g. for a translationally invariant membrane)
- It is not trivial to solve the shape equation with all given boundary conditions.





Previous work (*incomplete list*)

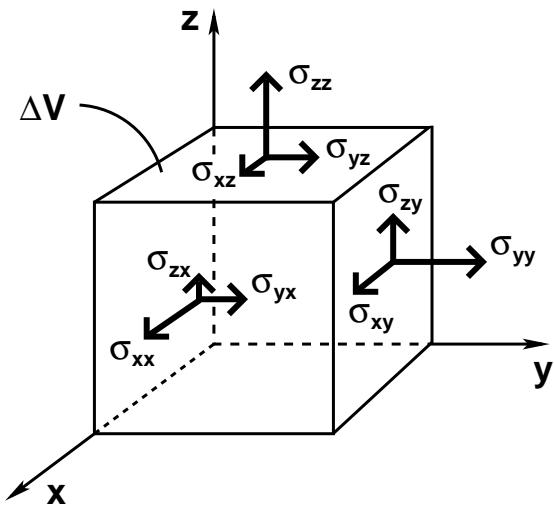
- M. Goulian, R. Bruinsma, and P. Pincus, *Europhys. Lett.* **22**, 145 (1993).
- P. A. Kralchevsky, V. N. Paunov, N. D. Denkov, K. Nagayama, *J. Chem. Soc. Faraday Trans.* **91**, 3415 (1995).
- T. R. Weikl, M. M. Kozlov, and W. Helfrich, *Phys. Rev. E* **57**, 6988 (1998).
- K. S. Kim, J. Neu, and G. Oster, *Biophys. J.* **75**, 2274 (1998).
- P. G. Dommersnes, J.-B. Fournier, and P. Galatola, *Europhys. Lett.* **42**, 233 (1998).
- V. I. Marchenko and C. Misbah, *Eur. Phys. J. E* **8**, 477 (2002).
- P. Biscari, F. Bisi, and R. Rosso, *J. Math. Biol.* **45**, 37 (2002).
- P. Biscari and F. Bisi, *Eur. Phys. J. E* **7**, 381 (2002).
- T. R. Weikl, *Eur. Phys. J. E* **12**, 265 (2003).
- A. Dominguez, M. Oettel, and S. Dietrich, *J. Chem. Phys.* **128** 114904 (2008).





2. Stress and torque tensor

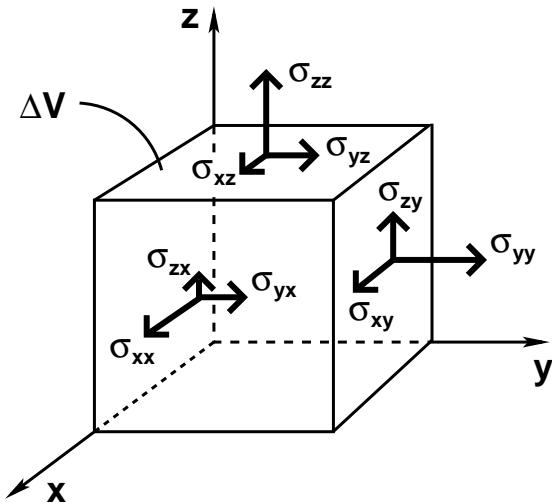
Stress tensor in 3D bodies





2. Stress and torque tensor

Stress tensor in 3D bodies



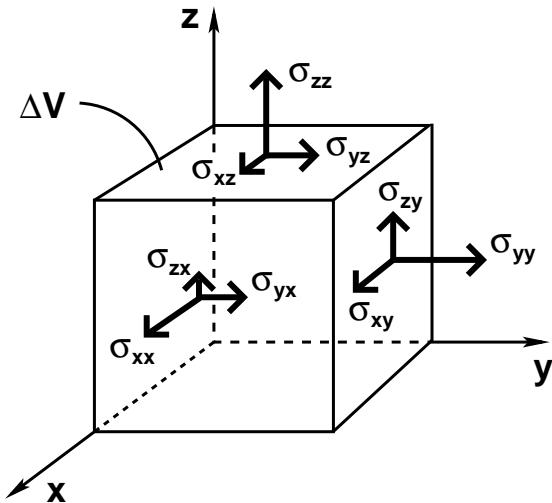
Stress tensor σ is a 3×3 matrix; e.g. component σ_{xy} : x -component of the force on the unit area perpendicular to the y -axis.





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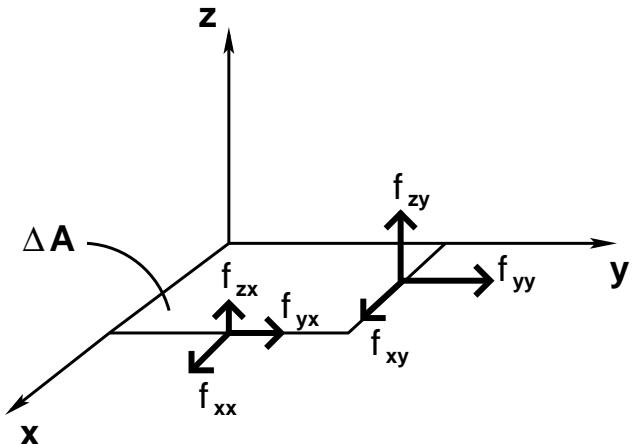
Total force on ΔV :

$$\mathbf{F}_{\text{ext}} = \oint_{\Sigma} \boldsymbol{\sigma} \cdot d\mathbf{A} = \int_{\Delta V} \nabla \boldsymbol{\sigma} \cdot dV$$



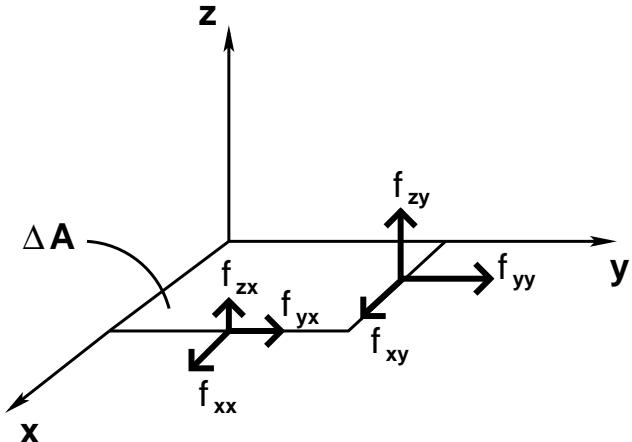


Stresses in surfaces





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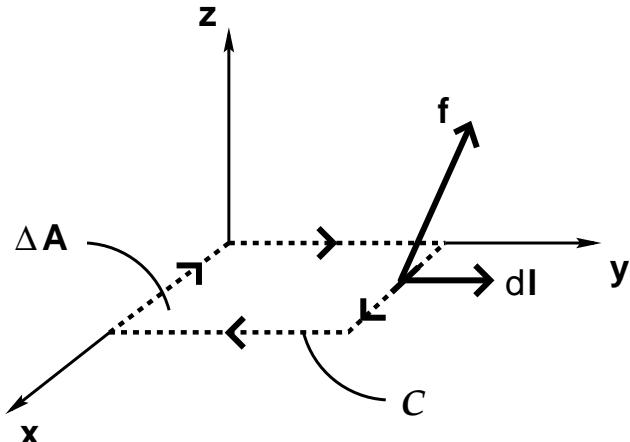


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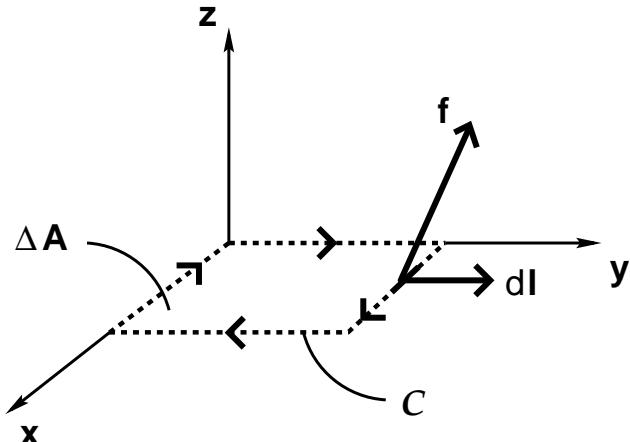
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Membrane is non-planar \Rightarrow differential geometry!





Stress and torque tensor of a membrane

stress tensor

$$\mathbf{f}^a = \left[\kappa(K^{ab} - \frac{1}{2}Kg^{ab}) K - \sigma g^{ab} \right] \mathbf{e}_b - \kappa(\nabla^a K) \mathbf{n} .$$

$a, b \in \{1, 2\}$

R. Capovilla, J. Guven, *J. Phys. A* **35**, 6233 (2002); J. Guven, *J. Phys. A* **37**, L313 (2004).





Stress and torque tensor of a membrane

stress tensor

tangent vectors

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Stress and torque tensor of a membrane

stress tensor tangent vectors normal vector

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extrinsic curvature

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Stress and torque tensor of a membrane

$$\text{stress tensor} \quad \text{tangent vectors} \quad \text{normal vector}$$
$$f^a = \left[\kappa(K^{ab} - \frac{1}{2}Kg^{ab}) K - \sigma g^{ab} \right] e_b - \kappa(\nabla^a K) n .$$

extrinsic curvature metric covariant derivative

The diagram illustrates the components of the stress tensor f^a . It shows three main parts: the extrinsic curvature term $\kappa(K^{ab} - \frac{1}{2}Kg^{ab}) K$, the metric term $-\sigma g^{ab}$, and the covariant derivative term $\kappa(\nabla^a K) n$. Blue arrows point from the labels 'stress tensor', 'tangent vectors', and 'normal vector' to their respective components in the equation. Brackets group the extrinsic curvature term, the metric term, and the covariant derivative term.

R. Capovilla, J. Guven, *J. Phys. A* **35**, 6233 (2002); J. Guven, *J. Phys. A* **37**, L313 (2004).





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stress tensor tangent vectors normal vector

extrinsic curvature metric covariant derivative

torque tensor

$$\boxed{\boldsymbol{m}^a = \boldsymbol{X} \times \boldsymbol{f}^a + [(\kappa + \bar{\kappa})Kg^{ab} - \bar{\kappa}K^{ab}] (\boldsymbol{e}_b \times \boldsymbol{n})}.$$

M. M. Müller, M. Deserno, J. Guven, *Phys. Rev. E* **76**, 011921 (2007).

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Stress and torque tensor of a membrane

$$\boxed{\begin{aligned} \text{stress tensor} & \qquad \text{tangent vectors} \qquad \text{normal vector} \\ f^a &= \left[\kappa(K^{ab} - \frac{1}{2}Kg^{ab})K - \sigma g^{ab} \right] e_b - \kappa(\nabla^a K)n . \\ \text{extrinsic curvature} & \qquad \text{metric} \qquad \text{covariant derivative} \\ \text{torque tensor} & \qquad \text{position vector} \\ m^a &= X \times f^a + [(\kappa + \bar{\kappa})Kg^{ab} - \bar{\kappa}K^{ab}] (e_b \times n) . \end{aligned}}$$

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Don't worry about details!!





Stress and torque tensor of a membrane

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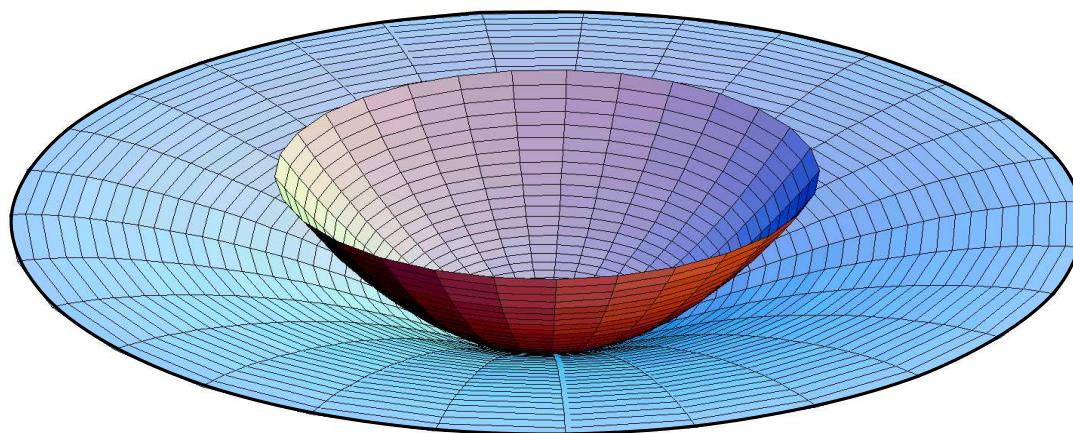
Remember: If the *surface geometry* is known, the *stresses* and *torques* are known and consequently the external force as well!!



3. Interface-mediated interactions



Example: AFM tip indenting a membrane



S. Steltenkamp *et al.*, *Biophys. J.* **91**, 217 (2006);

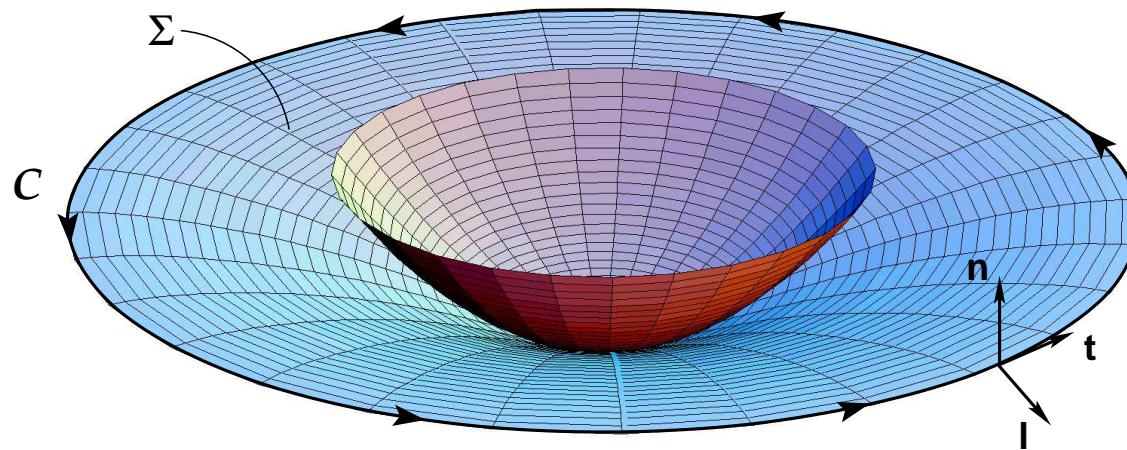
D. Norouzi, M. M. M., M. Deserno, *Phys. Rev. E* **74**, 061914 (2006).



3. Interface-mediated interactions



Example: AFM tip indenting a membrane



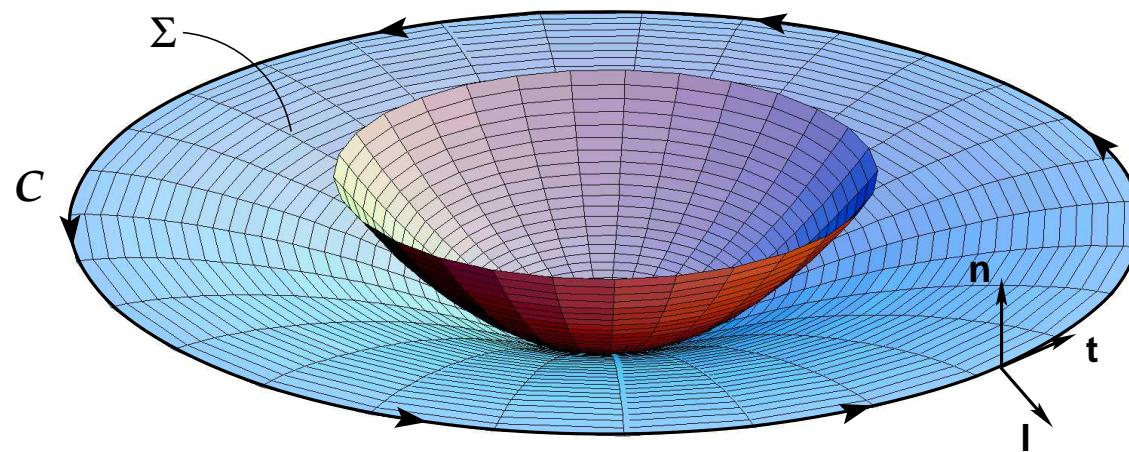
Force F_{ext} exerted by the tip on the membrane patch:

$$F_{\text{ext}} = \int_{\Sigma} dA \nabla_a f^a = \oint_C ds l_a f^a , \quad \text{where } l = l_a e^a .$$



3. Interface-mediated interactions

Example: AFM tip indenting a membrane



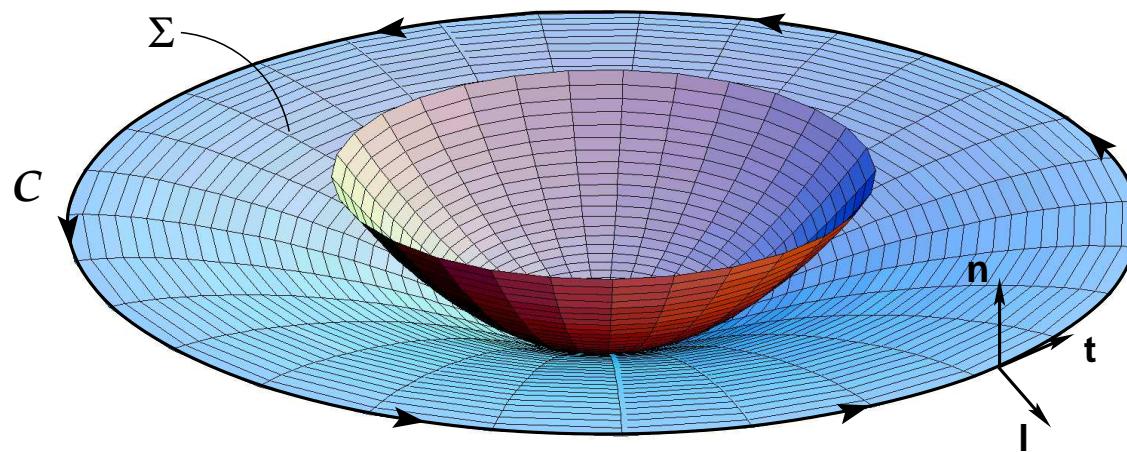
Insertion yields:

$$F_{\text{ext}} = 2\pi R_{\text{pore}} \cdot \kappa \frac{\partial K}{\partial \rho} \Big|_{\rho=R_{\text{pore}}} .$$



3. Interface-mediated interactions

Example: AFM tip indenting a membrane



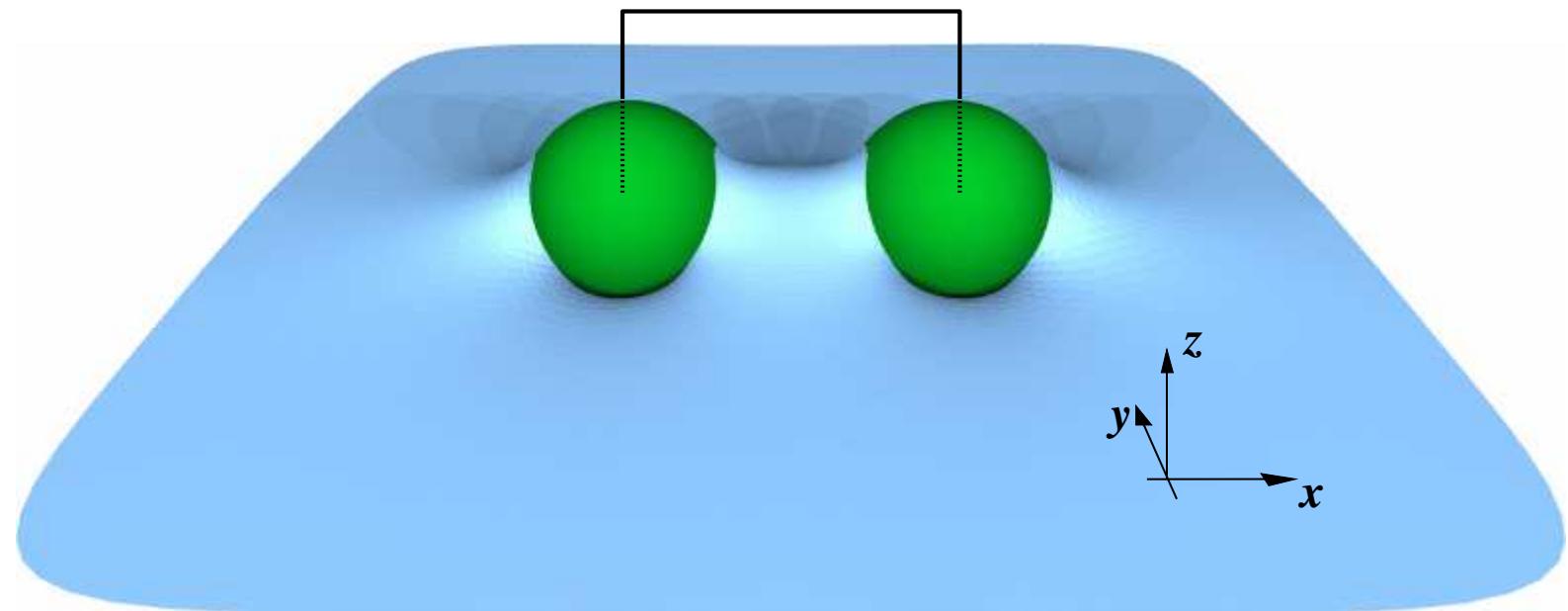
Torque M_{ext} exerted on the membrane patch:

$$M_{\text{ext}} = \int_{\Sigma} dA \nabla_a \mathbf{m}^a = \oint_C ds l_a \mathbf{m}^a .$$

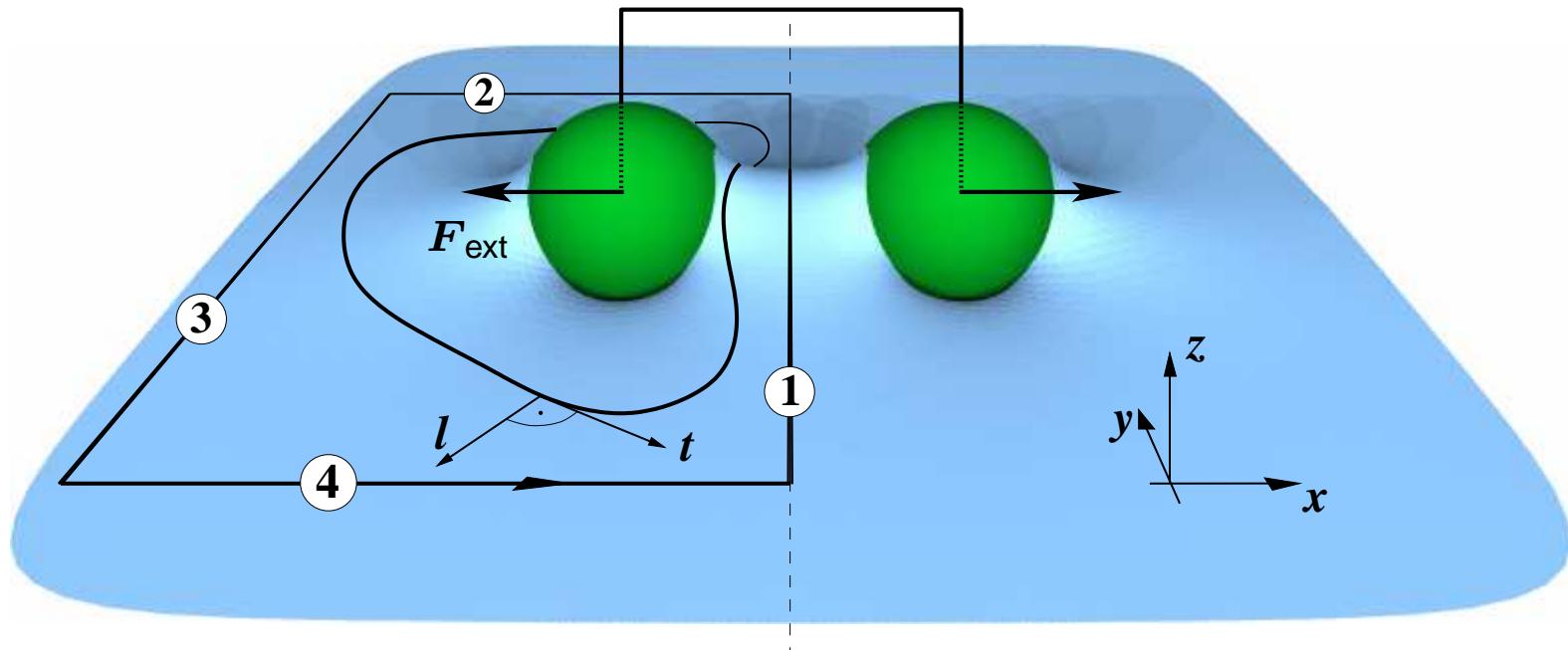




Membrane-mediated interactions



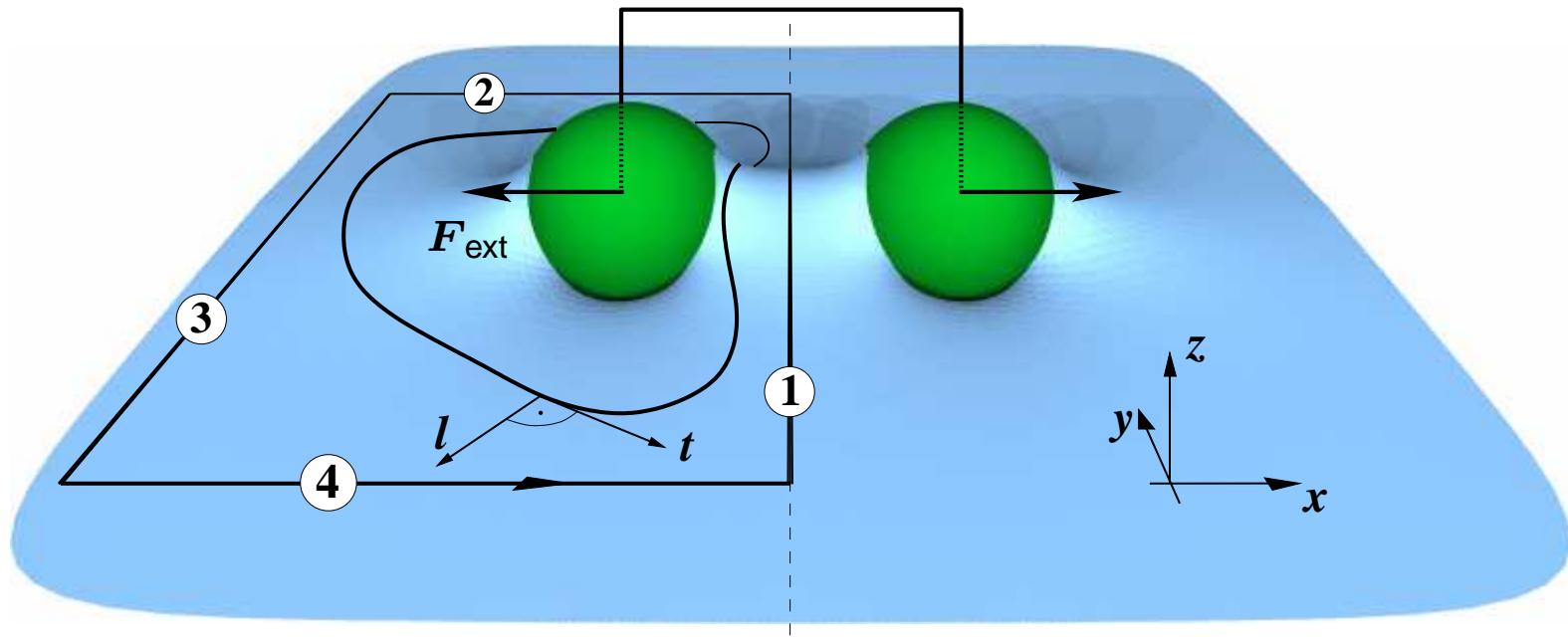
Membrane-mediated interactions



$$\mathbf{F} = -\mathbf{F}_{\text{ext}} = - \left(\int_{①} + \int_{③} \right) \mathrm{d}s \ l_a \mathbf{f}^a$$

M. M. M., M. Deserno, J. Guven, *EPL* **69**, 482 (2005); *PRE* **72**, 061407 (2005).

Membrane-mediated interactions



$$\mathbf{F}_{\text{sym}} = \left[\sigma \Delta L - \frac{1}{2} \kappa \int_{①} \mathrm{d}s \left(K_{\perp}^2 - K_{\parallel}^2 \right) \right] \mathbf{x}$$

M. M. M., M. Deserno, J. Guven, *EPL* **69**, 482 (2005); *PRE* **72**, 061407 (2005).



Symmetric situation

$$\boldsymbol{F}_{\text{sym}} = \left[\sigma \Delta L - \frac{1}{2} \kappa \int_{\textcircled{1}} \mathrm{d}s \left(K_{\perp}^2 - K_{\parallel}^2 \right) \right] \boldsymbol{x}$$





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length difference
between ① and ③





Symmetric situation

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length difference
between ① and ③ curvatures
at ①





Symmetric situation

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length difference
between ① and ③

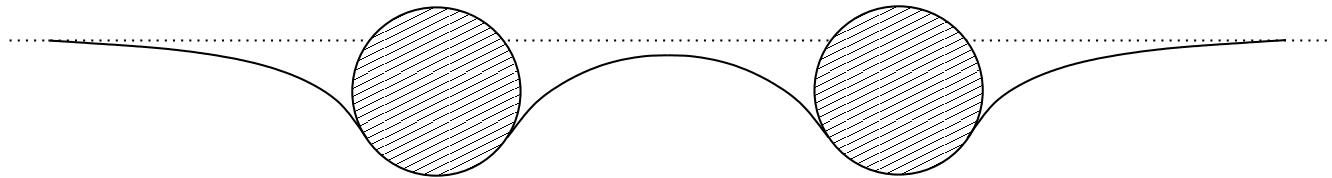
curvatures
at ①

force is
horizontal





Special case: two parallel cylinders

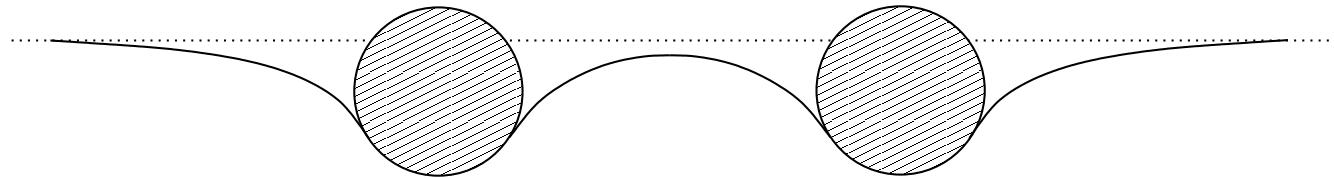


T. R. Weikl, *EPJE* **12**, 265 (2003).





Special case: two parallel cylinders



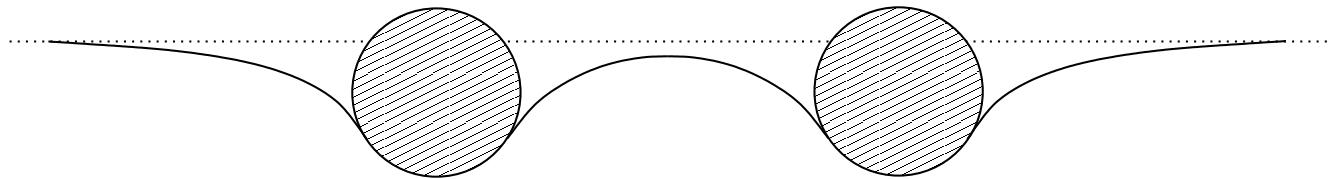
$$\mathbf{F}_{\text{sym}} = \left[\sigma \Delta L - \frac{1}{2} \kappa \int_{①} \mathrm{d}s \left(K_{\perp}^2 - K_{\parallel}^2 \right) \right] \mathbf{x}$$

M. M. M., M. Deserno, J. Guven, *EPL* **69**, 482 (2005); *PRE* **72**, 061407 (2005).





Special case: two parallel cylinders



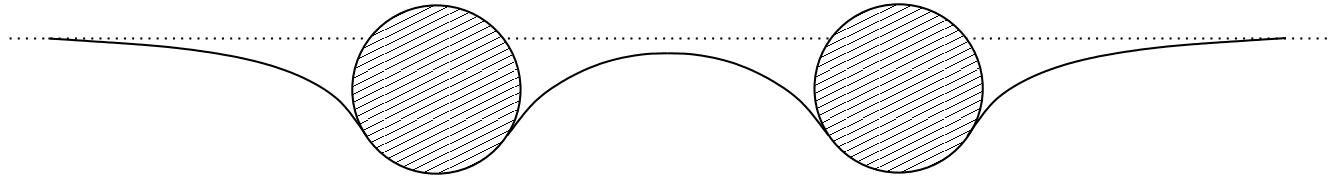
$$\mathbf{F}_{\text{sym}} = \left[\sigma \Delta L - \frac{1}{2} \kappa \int_{①} \mathrm{d}s \left(K_{\perp}^2 - K_{\parallel}^2 \right) \right] \mathbf{x}$$

- ① and ③ are straight lines $\Rightarrow \Delta L = 0$.





Special case: two parallel cylinders



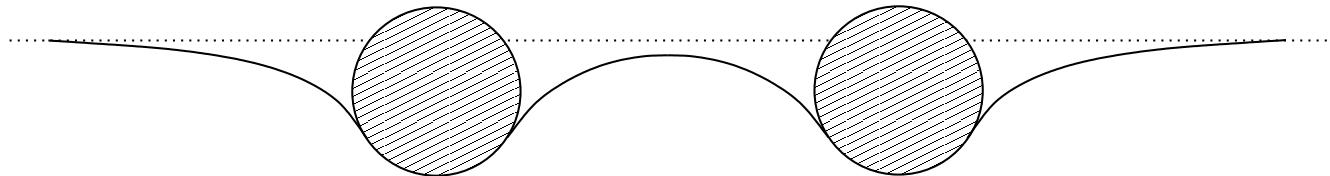
$$\mathbf{F}_{\text{sym}} = \left[\sigma \cancel{\Delta L} - \frac{1}{2} \kappa \int_{①} \mathrm{d}s \left(K_{\perp}^2 - \cancel{K_{\parallel}^2} \right) \right] \mathbf{x}$$

- ① and ③ are straight lines $\Rightarrow \Delta L = 0$.
- tangential curvature at ① is zero.





Special case: two parallel cylinders



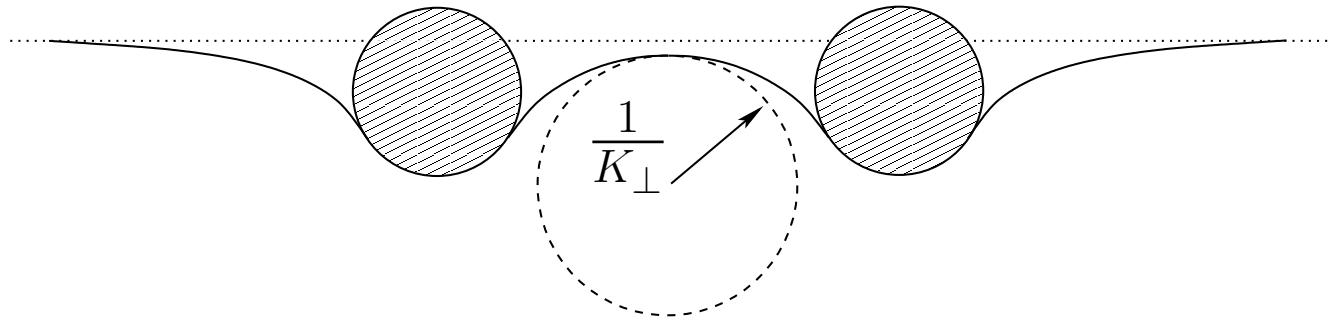
$$\mathbf{F}_{\text{sym}} = \left[\sigma \cancel{\Delta L} - \frac{1}{2} \kappa \int_{①} \mathrm{d}s \left(K_{\perp}^2 - \cancel{K_{\parallel}^2} \right) \right] \mathbf{x}$$

- ① and ③ are straight lines $\Rightarrow \Delta L = 0$.
- tangential curvature at ① is zero.
- K_{\perp} is constant at ① .





Special case: two parallel cylinders

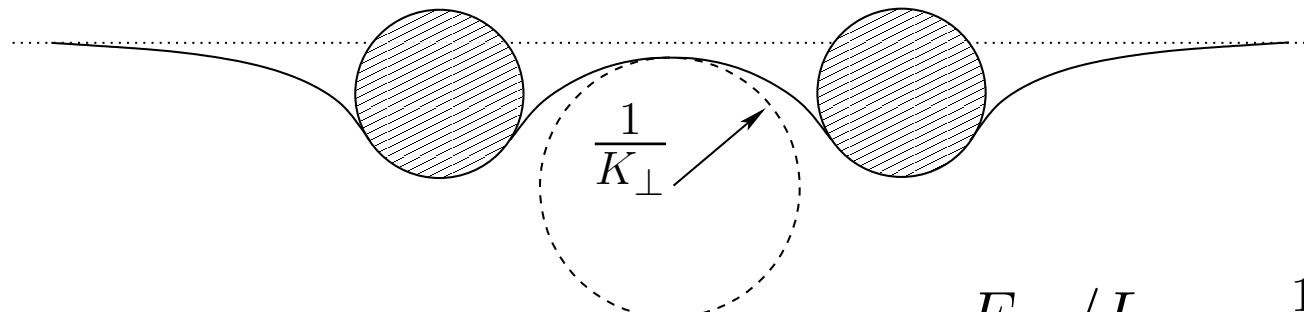


$$\Rightarrow F_{\text{sym,cyl}}/L = -\frac{1}{2}\kappa K_{\perp}^2$$

- The force is *always repulsive* in this case.
- The curvature at the midpoint determines the strength of the interaction.

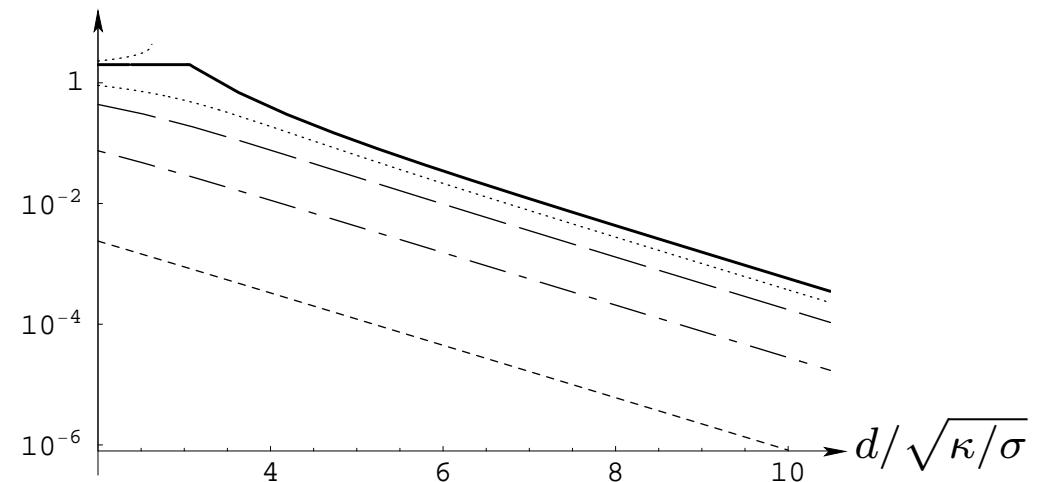
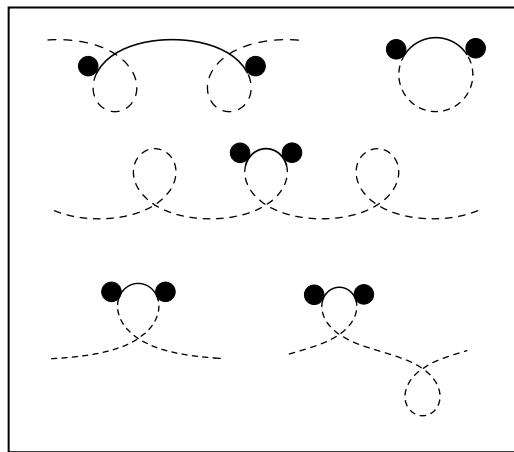


Special case: two parallel cylinders



$$F_{\text{cyl}}/L = -\frac{1}{2}\kappa K_{\perp}^2$$

$$|F_{\text{cyl}}|/\sigma L$$



M. M. M., M. Deserno, J. Guven, *Phys. Rev. E* **76**, 011921 (2007).





Is this the whole picture?





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- I have neglected membrane fluctuations so far.





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Is this the whole picture? → No!

- I have neglected membrane fluctuations so far.
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- Multibody forces are relevant. To determine them, however, is not trivial.

⇒ Run a simulation!





Simulation

The movie of the simulation is included in the supplementary material of the reference B. Reynwar et al below.

*The picture can be found in
E. Gottwein et al, J. Virol. 77, 9474
(2003), Fig. 7a.*

- I. Cooke, K. Kremer, M. Deserno, *Phys. Rev. E* **72**, 011506 (2005).
- B. J. Reynwar, G. Illya, V. A. Harmandaris, M. M. M., K. Kremer, M. Deserno *Nature* **447**, 461 (2007).





4. Conclusions

- Interface-mediated interactions are one possible candidate for explaining the evolution of membrane shapes in the biological cell.
- A combination of analytical methods, numerical calculations and simulations has to be applied to understand them.
- In continuum theory, the stress tensor can be used to determine analytically exact expressions for the force between the particles.





4. Conclusions

- Simulations indicate that cooperative behavior of many proteins (multi-body interactions) leads to aggregation and vesiculation.
- What about fluctuation-induced effects?





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CENTRE NATIONAL
DE LA RECHERCHE
SCIENTIFIQUE

Many thanks for your attention!

