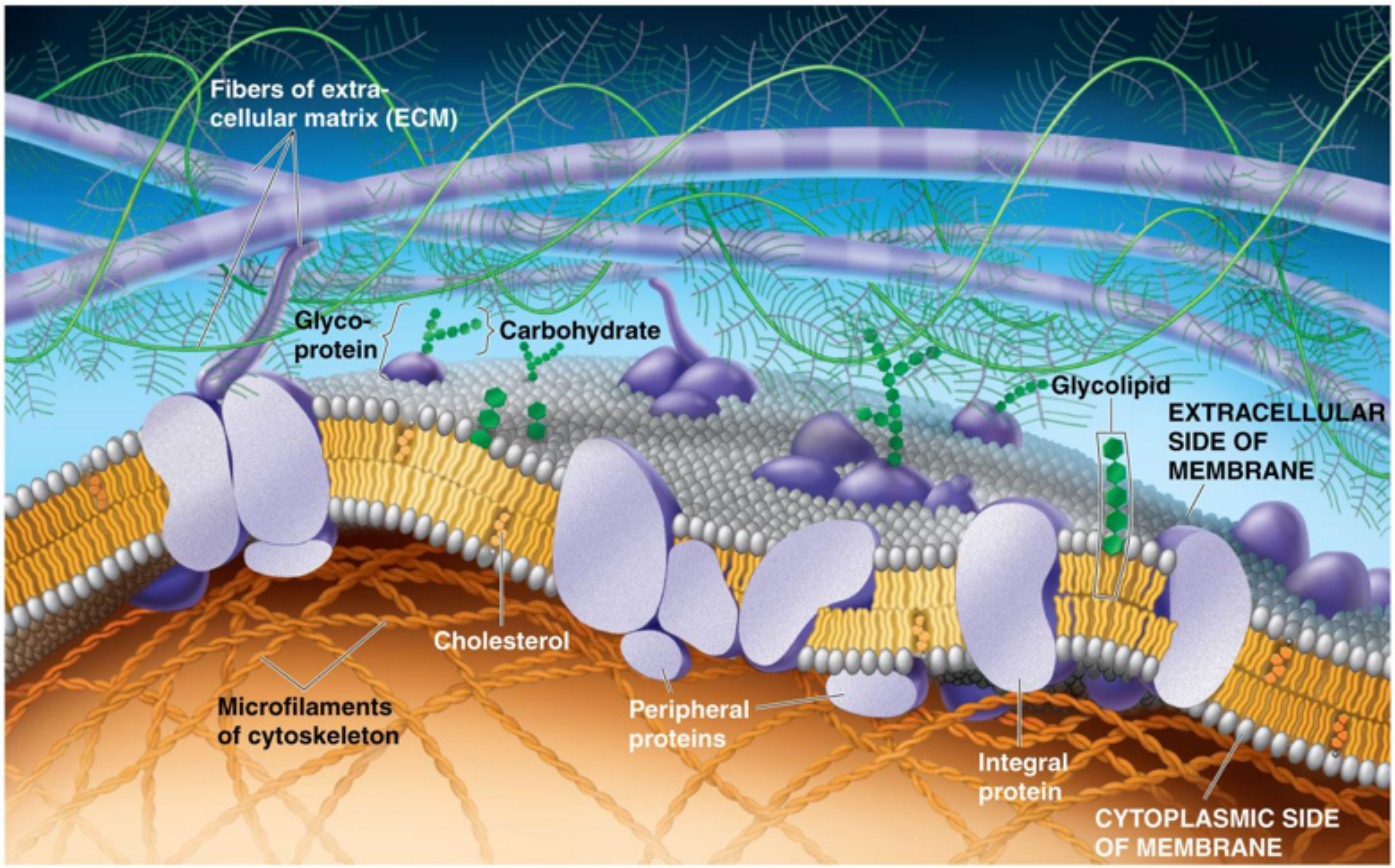
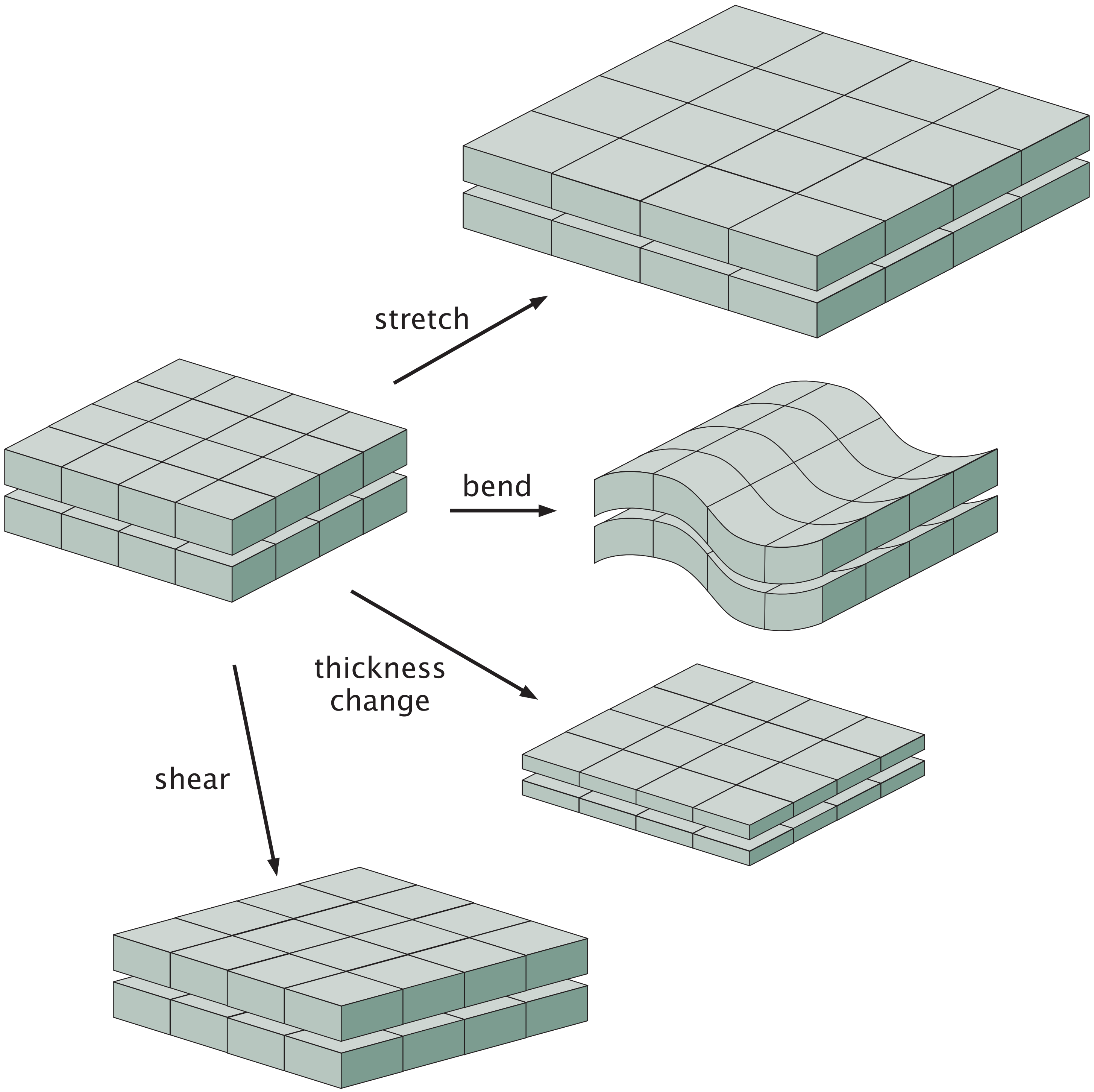
MAE 545: Lecture 15 (11/12)

Mechanics of cell membranes



Membrane deformations



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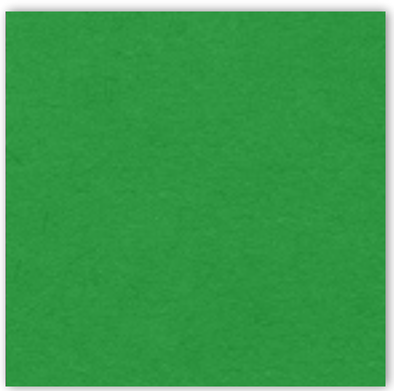
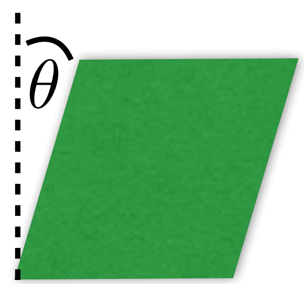
Energy cost for stretching and shearing

undeformed square patch

L L

patch area

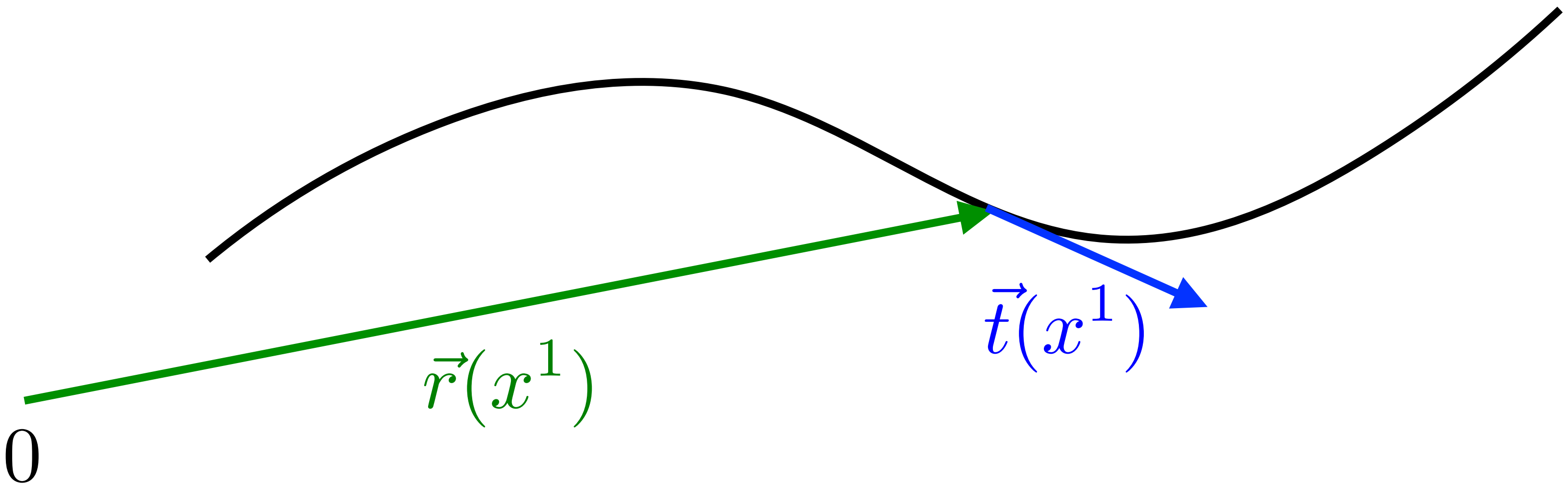
$A = L^2$

isotropic deformation	**shear deformation**	**anisotropic stretching**
 $L + \Delta L$, $L + \Delta L$	 θ, L, L	 $L(1+\lambda_2)$, $L(1+\lambda_1)$
$\frac{E}{A} = \frac{B}{2}\left(\frac{\Delta A}{A}\right)^2 \approx \frac{B}{2}\left(\frac{2\Delta L}{L}\right)^2$	$\frac{E}{A} = \frac{\mu\theta^2}{2}$	$\frac{E}{A} \approx \frac{B}{2}(\lambda_1+\lambda_2)^2 + \frac{\mu}{2}(\lambda_1-\lambda_2)^2$
bulk modulus	**shear modulus**	$\lambda_1, \lambda_2 \ll 1$
$B \sim 0.2\mathrm{N/m}$	$\mu \sim 10^{-5}\mathrm{N/m}$	
(lipid bilayer)	**(spectrin network)**	**(shearing can be interpreted as anisotropic stretching)**

Metric for measuring distances along curves

x^1 **parameter describing position along the curve**

$\vec{r}(x^1)$ **function describing shape of the curve**



$$\vec{t}(x^1) = \frac{d\vec{r}(x^1)}{dx^1}$$ **local tangent to the curve**

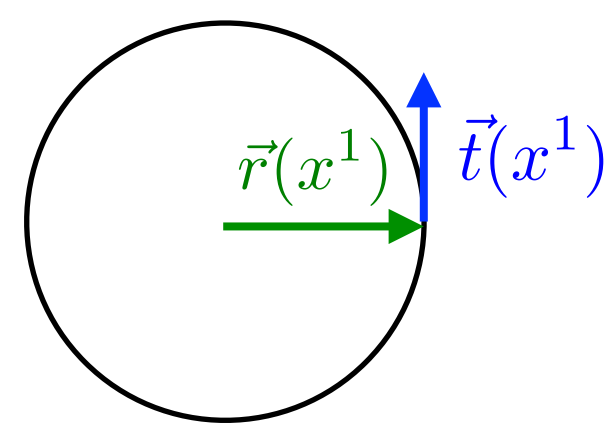
metric for measuring lengths

$$d\ell^2 = d\vec{r}^{\,2} = \vec{t}^{\,2}\left(dx^1\right)^2 = g\,\left(dx^1\right)^2$$

$$g = \vec{t}^{\,2}$$

$$d\ell = \sqrt{g}dx^1$$

Example



$$\vec{r}(x^1) = R\big(\cos(\omega x^1), \sin(\omega x^1)\big)$$

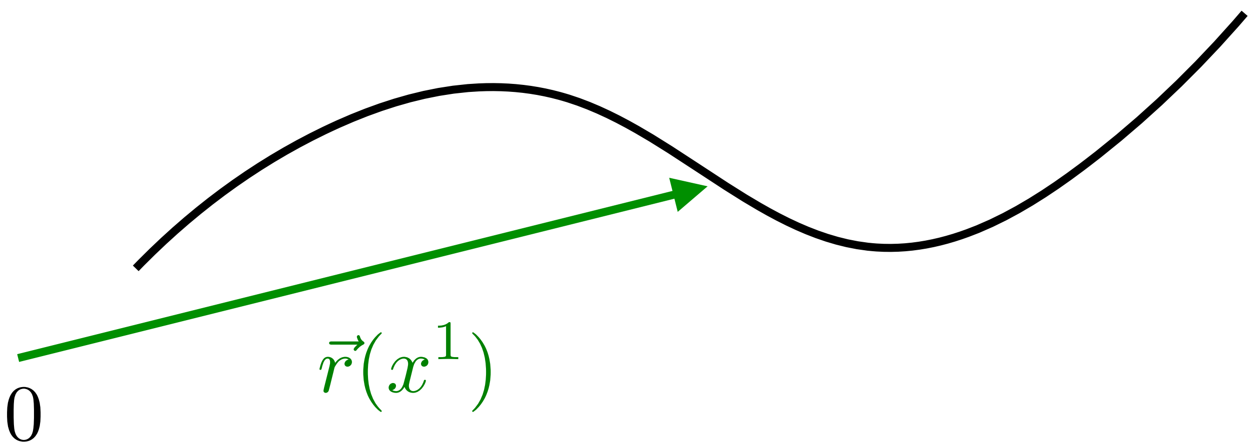
$$\vec{t}(x^1) = R\omega\big(-\sin(\omega x^1), \cos(\omega x^1)\big)$$

$$g(x^1) = R^2\omega^2$$

$$d\ell = R\omega dx^1$$

Strain for deformation of beams

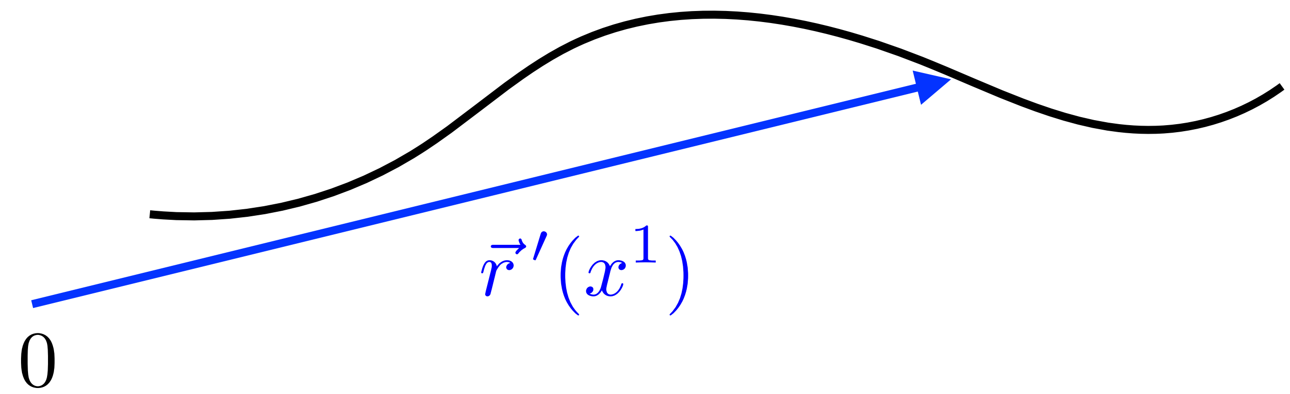
undeformed beam



$$g = \left(d\vec{r}/dx^1\right)^2$$

$$d\ell = \sqrt{g}dx^1$$

deformed beam



$$g' = \left(d\vec{r}\,'/dx^1\right)^2$$

$$d\ell' = \sqrt{g'}dx^1 = d\ell(1+\epsilon)$$

strain

$$d\ell'^2 - d\ell^2 = (2\epsilon + \epsilon^2)d\ell^2 \approx 2\epsilon\, d\ell^2$$

$$\epsilon = \frac{d\ell'^2 - d\ell^2}{2d\ell^2} = \frac{1}{2}g^{-1}\left(g' - g\right)$$

Energy cost for stretching/compressing

$$E = \int \left(\sqrt{g}dx^1\right)\ \frac{1}{2}k\epsilon^2$$

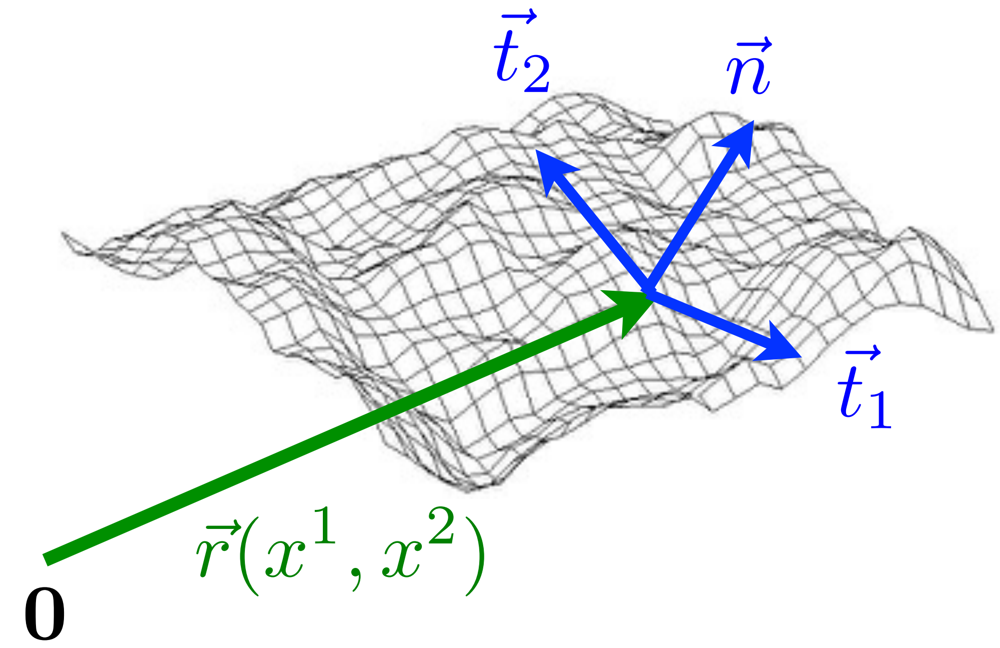
Metric tensor for measuring distances on surfaces

x^1, x^2 **parameters describing position along the surface**

$\vec{r}(x^1, x^2)$ **function describing shape of the surface**

$$\vec{t}_i = \frac{\partial \vec{r}}{\partial x^i}$$ **local tangent vectors to the surface**

$$\vec{n} = \frac{\vec{t}_1 \times \vec{t}_2}{|\vec{t}_1 \times \vec{t}_2|}$$ **unit normal vector of the surface**



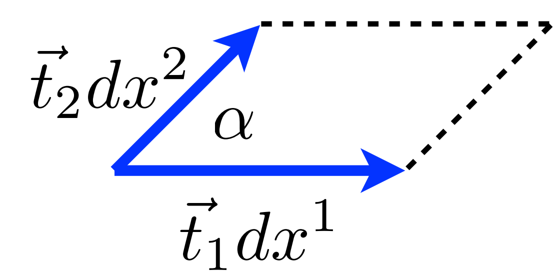
metric tensor for measuring lengths

$$d\ell^2 = d\vec{r}^{\,2} = \sum_{i,j} \vec{t}_i \cdot \vec{t}_j dx^i dx^j = \sum_{i,j} g_{ij} dx^i dx^j$$

$$g_{ij} = \vec{t}_i \cdot \vec{t}_j = \begin{pmatrix} \vec{t}_1 \cdot \vec{t}_1, & \vec{t}_1 \cdot \vec{t}_2 \\ \vec{t}_2 \cdot \vec{t}_1 & \vec{t}_2 \cdot \vec{t}_2 \end{pmatrix}$$

$$g = \det(g_{ij}) = |\vec{t}_1 \times \vec{t}_2|^2$$

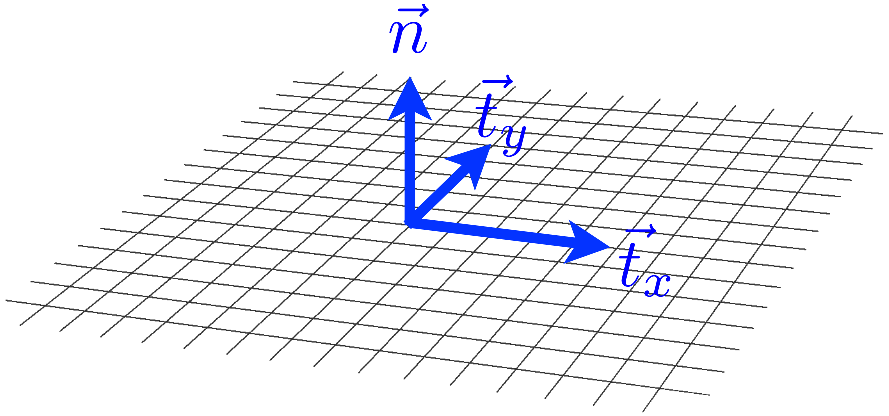
area element



$$dA = |\vec{t}_1||\vec{t}_2| \sin\alpha dx^1 dx^2$$

$$dA = \sqrt{g}\, dx^1 dx^2$$

Examples



$$\vec{r}(x,y) = (x,y,0)$$

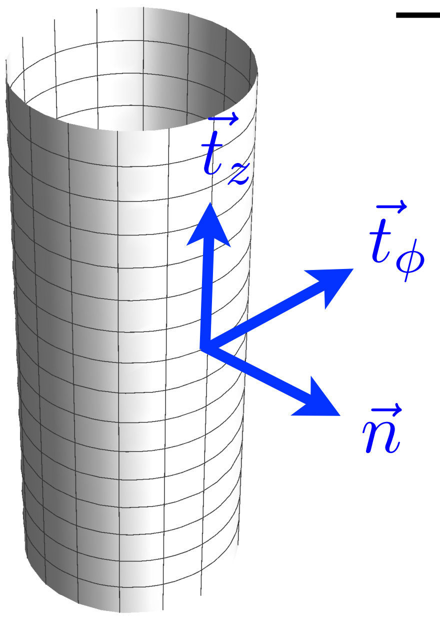
$$\vec{t}_x = \frac{\partial \vec{r}}{\partial x} = (1,0,0)$$

$$\vec{t}_y = \frac{\partial \vec{r}}{\partial y} = (0,1,0)$$

$$\vec{n} = \frac{\vec{t}_x \times \vec{t}_y}{|\vec{t}_x \times \vec{t}_y|} = (0,0,1)$$

$$g_{ij} = \vec{t}_i \cdot \vec{t}_j = \begin{pmatrix} 1, & 0 \\ 0, & 1 \end{pmatrix}$$

$$dA = dxdy$$



$$\vec{r}(\phi,z) = (R\cos\phi, R\sin\phi, z)$$

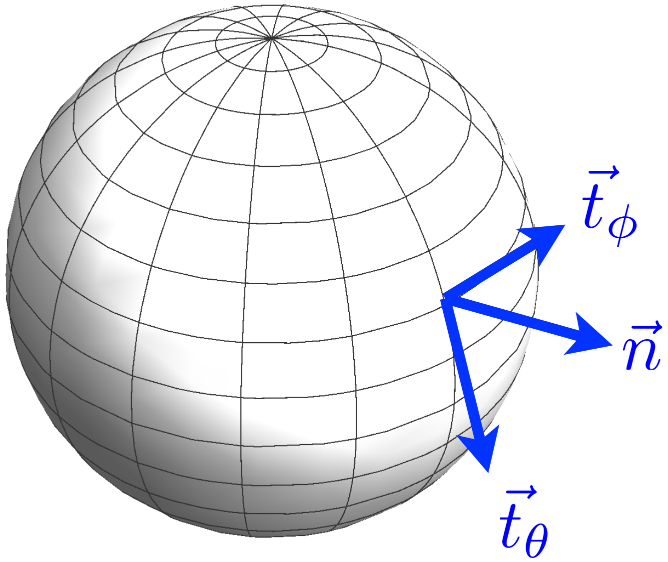
$$\vec{t}_\phi = \frac{\partial \vec{r}}{\partial \phi} = R(-\sin\phi, \cos\phi, 0)$$

$$\vec{t}_z = \frac{\partial \vec{r}}{\partial z} = (0,0,1)$$

$$\vec{n} = \frac{\vec{t}_\phi \times \vec{t}_z}{|\vec{t}_\phi \times \vec{t}_z|} = (\cos\phi, \sin\phi, 0)$$

$$g_{ij} = \vec{t}_i \cdot \vec{t}_j = \begin{pmatrix} R^2, & 0 \\ 0, & 1 \end{pmatrix}$$

$$dA = R\,d\phi dz$$



$$\vec{r}(\theta,\phi) = R(\sin\theta\cos\phi, \sin\theta\sin\phi, \cos\theta)$$

$$\vec{t}_\theta = \frac{\partial \vec{r}}{\partial \theta} = R(\cos\theta\cos\phi, \cos\theta\sin\phi, -\sin\theta)$$

$$\vec{t}_\phi = \frac{\partial \vec{r}}{\partial \phi} = R\sin\theta(-\sin\phi, \cos\phi, 0)$$

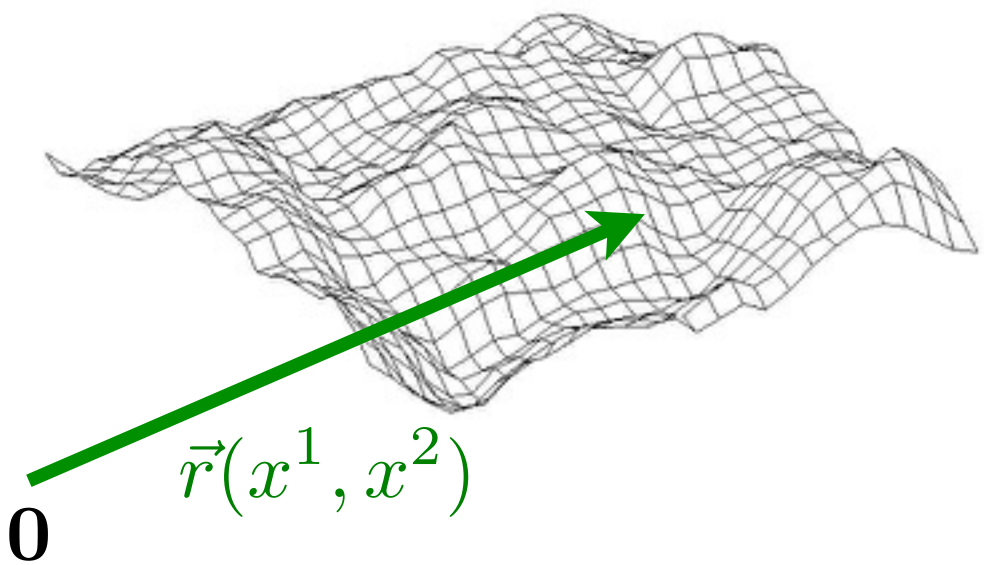
$$\vec{n} = \frac{\vec{t}_\theta \times \vec{t}_\phi}{|\vec{t}_\theta \times \vec{t}_\phi|} = (\sin\theta\cos\phi, \sin\theta\sin\phi, \cos\theta)$$

$$g_{ij} = \vec{t}_i \cdot \vec{t}_j = \begin{pmatrix} R^2, & 0 \\ 0, & R^2\sin^2\theta \end{pmatrix}$$

$$dA = R^2 \sin\theta\, d\theta d\phi$$

Strain tensor for deformation of membranes

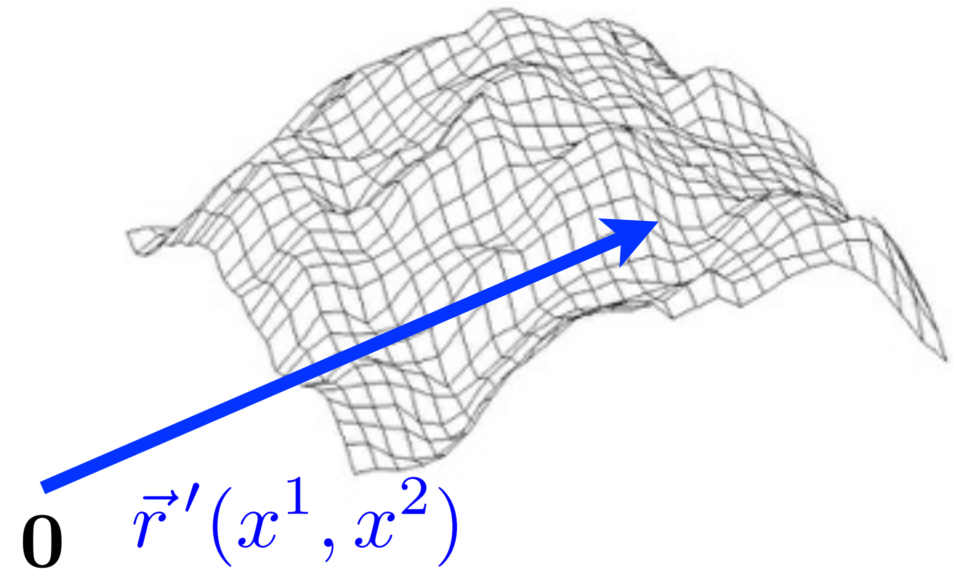
undeformed membrane



$$g_{ij} = \frac{\partial \vec{r}}{\partial x^i} \cdot \frac{\partial \vec{r}}{\partial x^j}$$

$$d\ell^2 = \sum_{i,j} g_{ij} dx^i dx^j$$

deformed membrane



$$g'_{ij} = \frac{\partial \vec{r}\,'}{\partial x^i} \cdot \frac{\partial \vec{r}\,'}{\partial x^j}$$

$$d\ell'^2 = \sum_{i,j} g'_{ij} dx^i dx^j$$

strain tensor

$$u_{ij} = \frac{1}{2} \sum_k (g^{-1})_{ik} \left(g'_{kj} - g_{kj} \right)$$

inverse metric tensor

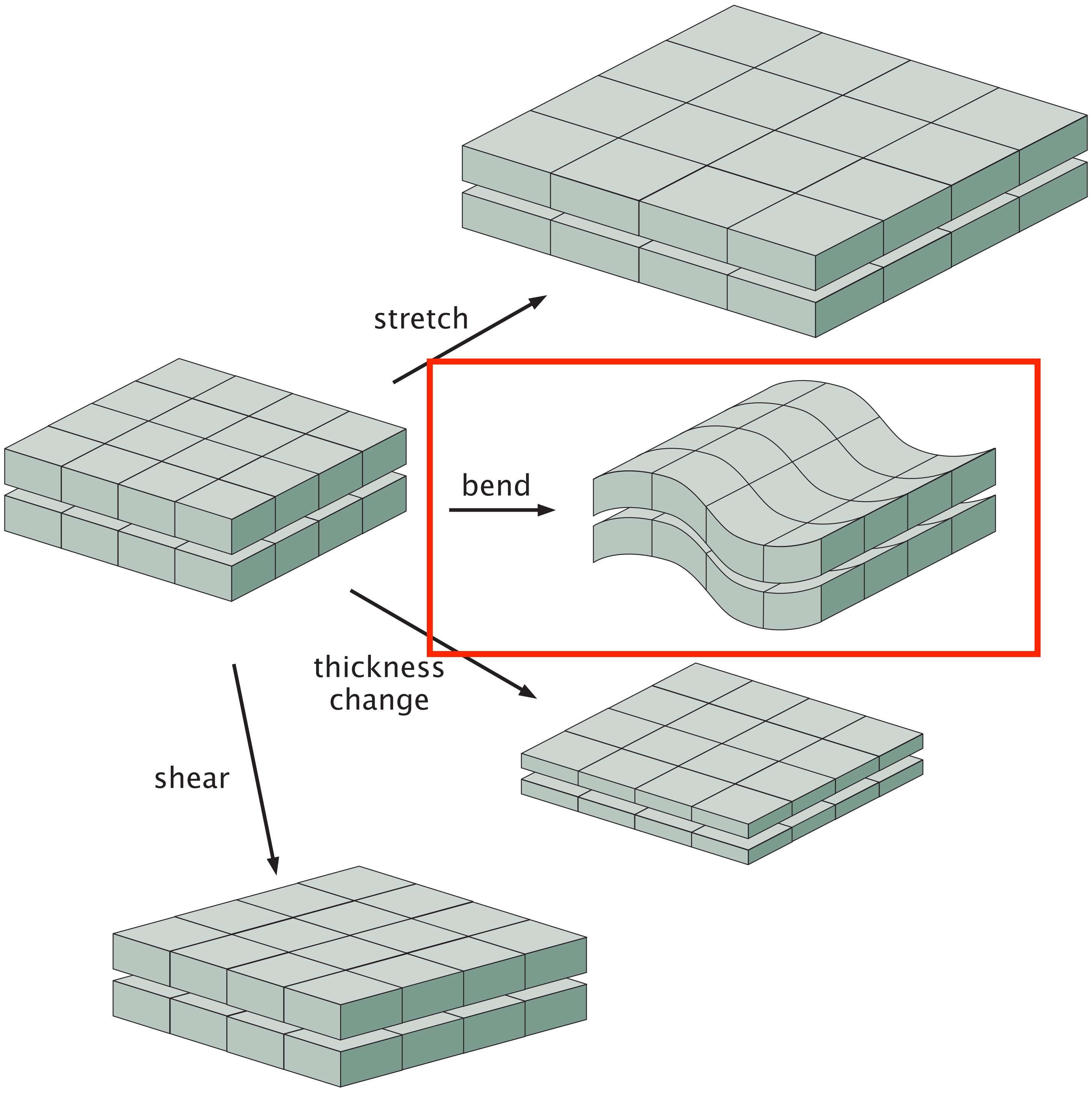
$$\sum_k (g^{-1})_{ik} g_{kj} = \sum_k g_{ik} (g^{-1})_{kj} = \delta_{ij}$$

Energy cost for stretching/compressing

$$E = \int \sqrt{g}\, dx^1 dx^2 \, \frac{1}{2} \left[(B - \mu) (\sum_i u_{ii})^2 + 2\mu \sum_{i,j} u_{ij}^2 \right]$$

$$g = \det(g_{ij})$$

Membrane deformations



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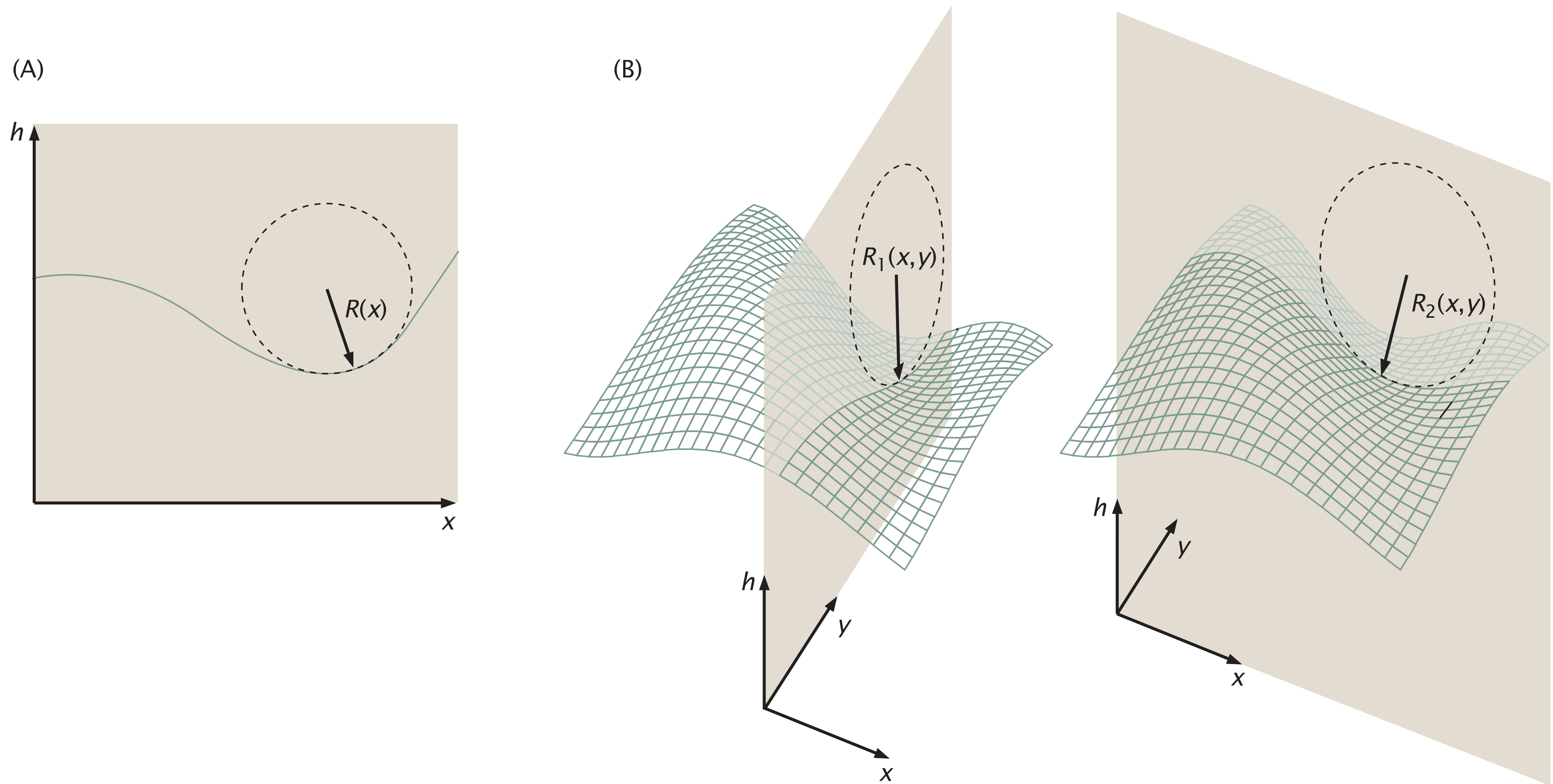
Curvature of surfaces

curvature for space curves

curvature for surfaces depends on the orientation



maximal and minimal curvatures are called principal curvatures and they appear in orthogonal directions

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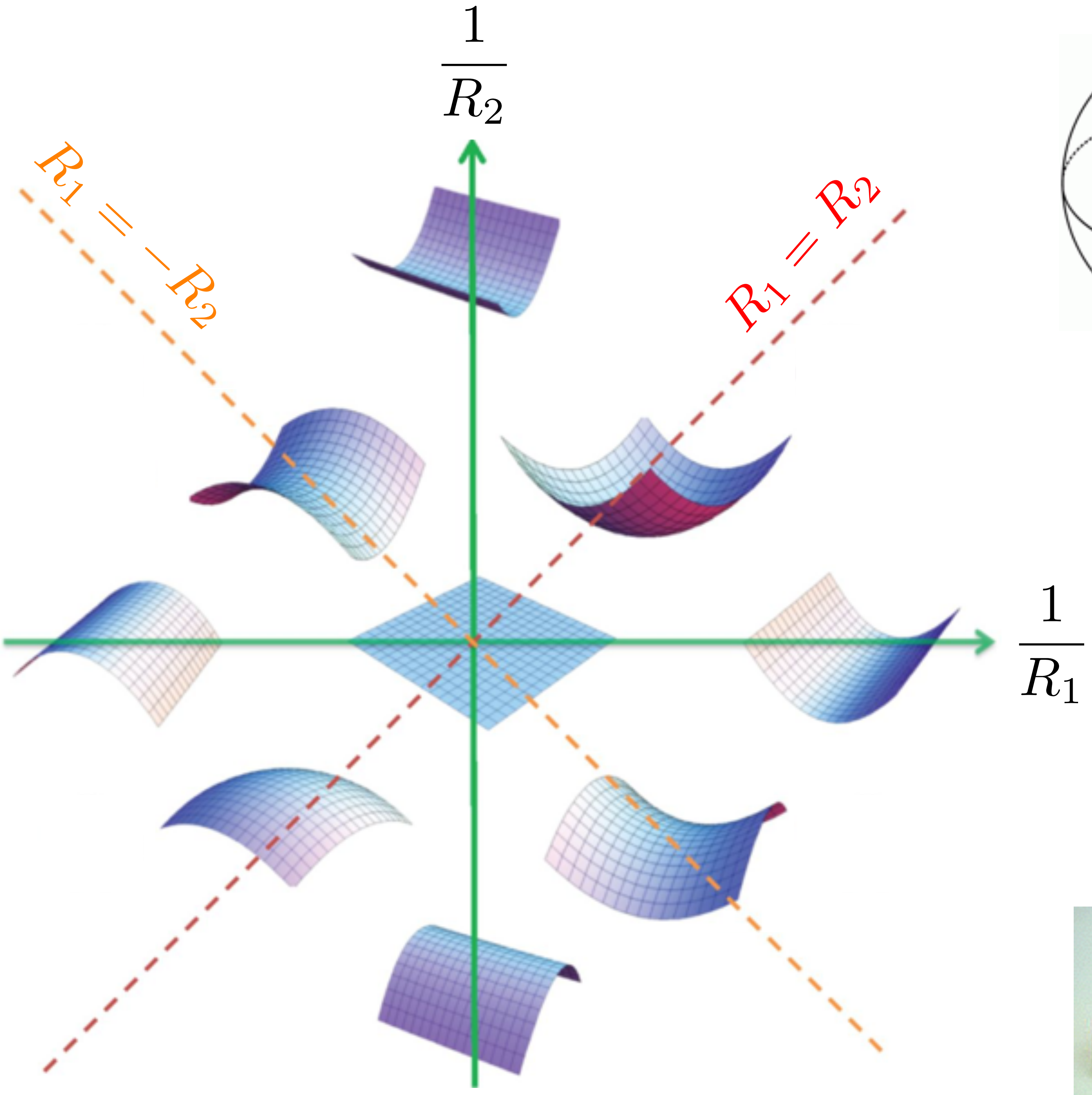
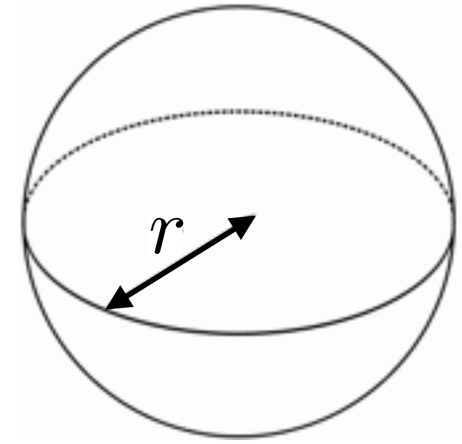
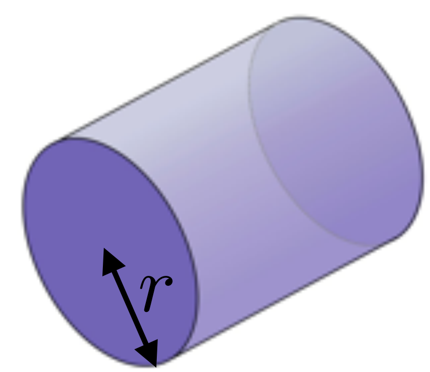
Surfaces of various principal curvatures



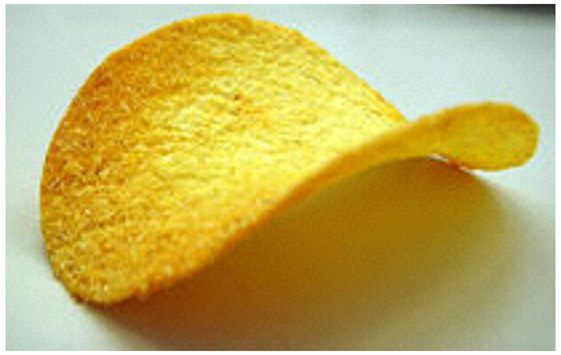


$$\frac{1}{R_1} = \frac{1}{R_2} = \frac{1}{r}$$



$$\frac{1}{R_1} = \frac{1}{r}$$

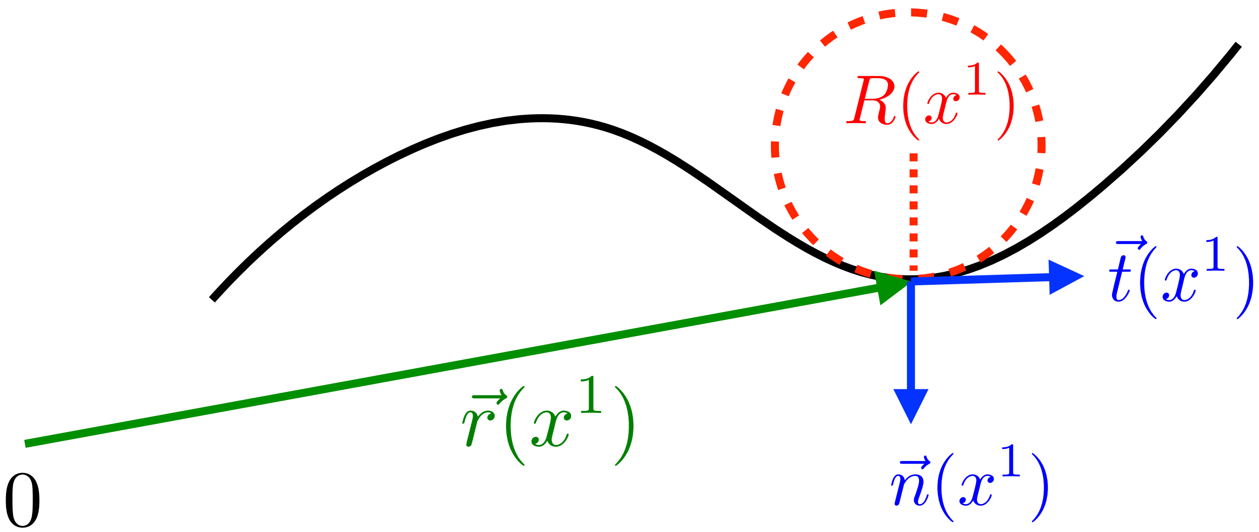
$$\frac{1}{R_2} = 0$$



$$\frac{1}{R_1} > 0$$

$$\frac{1}{R_2} < 0$$

Curvature of curves



x^1 **parameter describing position along the curve**

$\vec{r}(x^1)$ **function describing shape of the curve**

$$\vec{t}(x^1) = \frac{d\vec{r}(x^1)}{dx^1}$$ **local tangent to the curve**

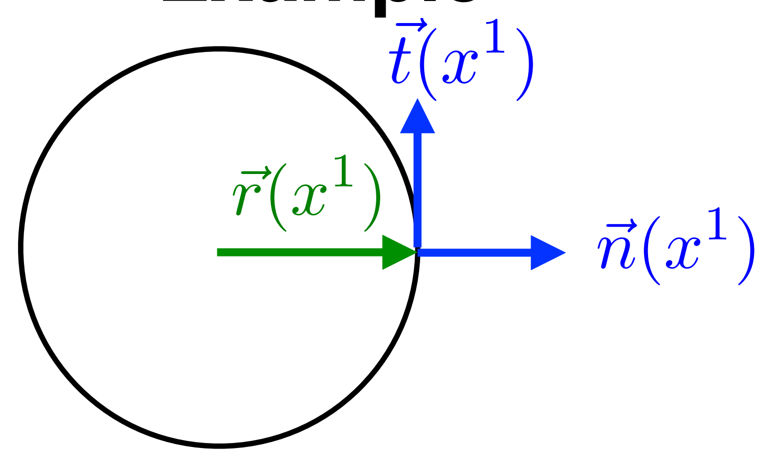
$\vec{n}(x^1)$ **local unit normal vector to the curve**

$g = \vec{t}^{\,2}$ **metric for measuring lengths**

curvature of curve

$$\frac{1}{R} = K = \frac{1}{g}\left(\vec{n}\cdot\frac{d^2\vec{r}}{d(x^1)^2}\right)$$

Example



$$\vec{r}(x^1) = R\big(\cos(\omega x^1), \sin(\omega x^1)\big)$$

$$\vec{n}(x^1) = \big(\cos(\omega x^1), \sin(\omega x^1)\big)$$

$$g(x^1) = R^2\omega^2$$

$$K = -\frac{1}{R}$$

Curvature tensor for surfaces

x^1, x^2 parameters describing position along the surface

$\vec{r}(x^1, x^2)$ function describing shape of the surface

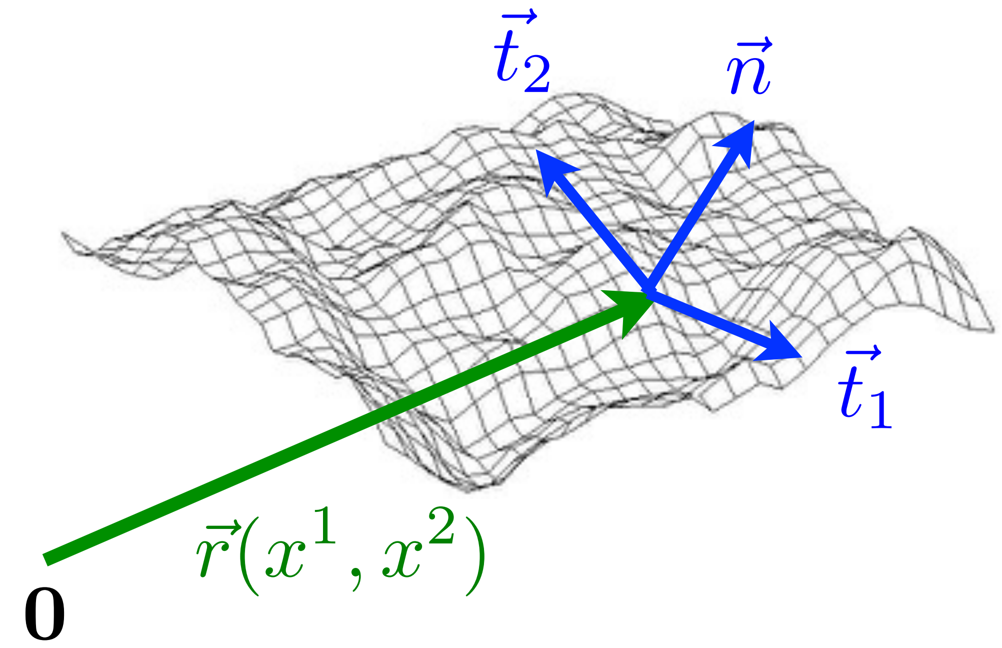
$\vec{t}_i = \dfrac{\partial \vec{r}}{\partial x^i}$ local tangent vectors to the surface

$\vec{n} = \dfrac{\vec{t}_1 \times \vec{t}_2}{|\vec{t}_1 \times \vec{t}_2|}$ unit normal vector of the surface

$g_{ij} = \vec{t}_i \cdot \vec{t}_j$ metric tensor for measuring lengths

curvature tensor for surfaces

$$K_{ij} = \sum_k \left(g^{-1}\right)_{ik} \left(\vec{n} \cdot \frac{\partial^2 \vec{r}}{\partial x^k \partial x^j}\right)$$



principal curvatures correspond to the eigenvalues of curvature tensor

$$\frac{1}{R_1}, \frac{1}{R_2}$$

mean curvature

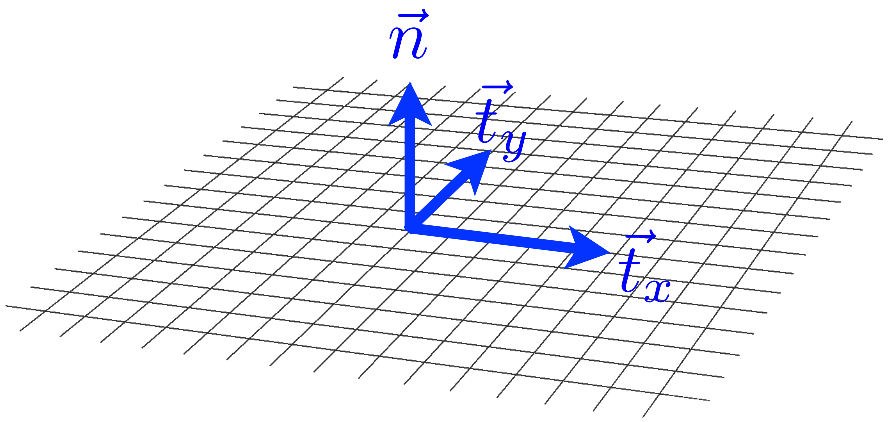
$$\frac{1}{2}\left(\frac{1}{R_1} + \frac{1}{R_2}\right) = \frac{1}{2}\sum_i K_{ii} = \frac{1}{2}\mathrm{tr}(K_{ij})$$

Gaussian curvature

$$\frac{1}{R_1 R_2} = \det(K_{ij})$$

Examples

$$K_{ij} = \sum_k (g^{-1})_{ik} \left(\vec{n} \cdot \frac{\partial^2 \vec{r}}{\partial x^k \partial x^j} \right)$$



$$\vec{r}(x,y) = (x,y,0)$$

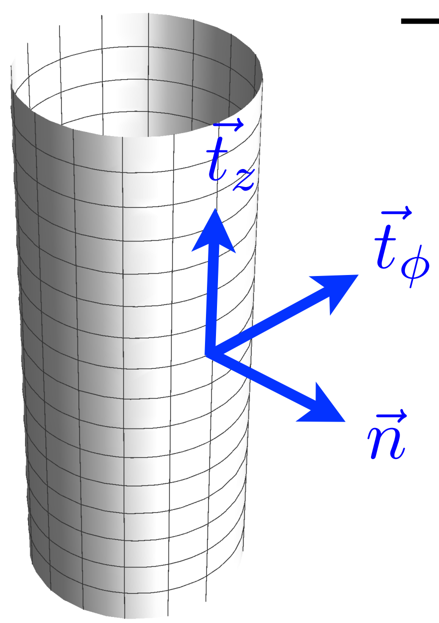
$$\vec{t}_x = \frac{\partial \vec{r}}{\partial x} = (1,0,0)$$

$$\vec{t}_y = \frac{\partial \vec{r}}{\partial y} = (0,1,0)$$

$$\vec{n} = \frac{\vec{t}_x \times \vec{t}_y}{|\vec{t}_x \times \vec{t}_y|} = (0,0,1)$$

$$g_{ij} = \vec{t}_i \cdot \vec{t}_j = \begin{pmatrix} 1, & 0 \\ 0, & 1 \end{pmatrix}$$

$$K_{ij} = \begin{pmatrix} 0, & 0 \\ 0, & 0 \end{pmatrix}$$



$$\vec{r}(\phi,z) = (R\cos\phi, R\sin\phi, z)$$

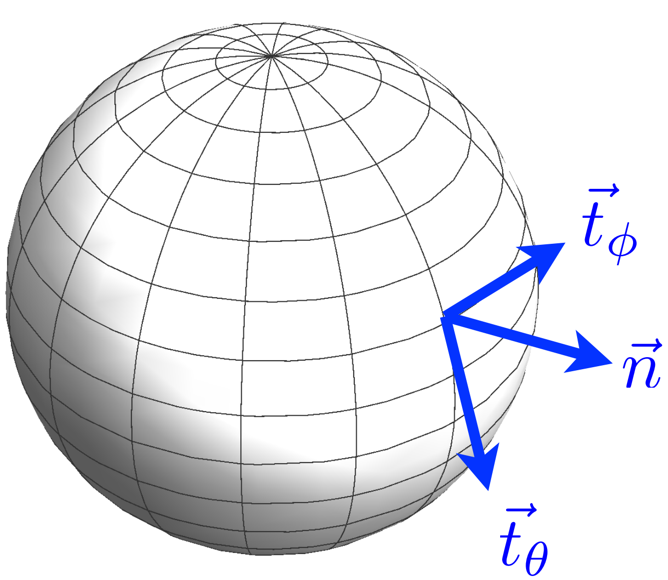
$$\vec{t}_\phi = \frac{\partial \vec{r}}{\partial \phi} = R(-\sin\phi, \cos\phi, 0)$$

$$\vec{t}_z = \frac{\partial \vec{r}}{\partial z} = (0,0,1)$$

$$\vec{n} = \frac{\vec{t}_\phi \times \vec{t}_z}{|\vec{t}_\phi \times \vec{t}_z|} = (\cos\phi, \sin\phi, 0)$$

$$g_{ij} = \vec{t}_i \cdot \vec{t}_j = \begin{pmatrix} R^2, & 0 \\ 0, & 1 \end{pmatrix}$$

$$K_{ij} = \begin{pmatrix} -\frac{1}{R}, & 0 \\ 0, & 0 \end{pmatrix}$$



$$\vec{r}(\theta,\phi) = R(\sin\theta\cos\phi, \sin\theta\sin\phi, \cos\theta)$$

$$\vec{t}_\theta = \frac{\partial \vec{r}}{\partial \theta} = R(\cos\theta\cos\phi, \cos\theta\sin\phi, -\sin\theta)$$

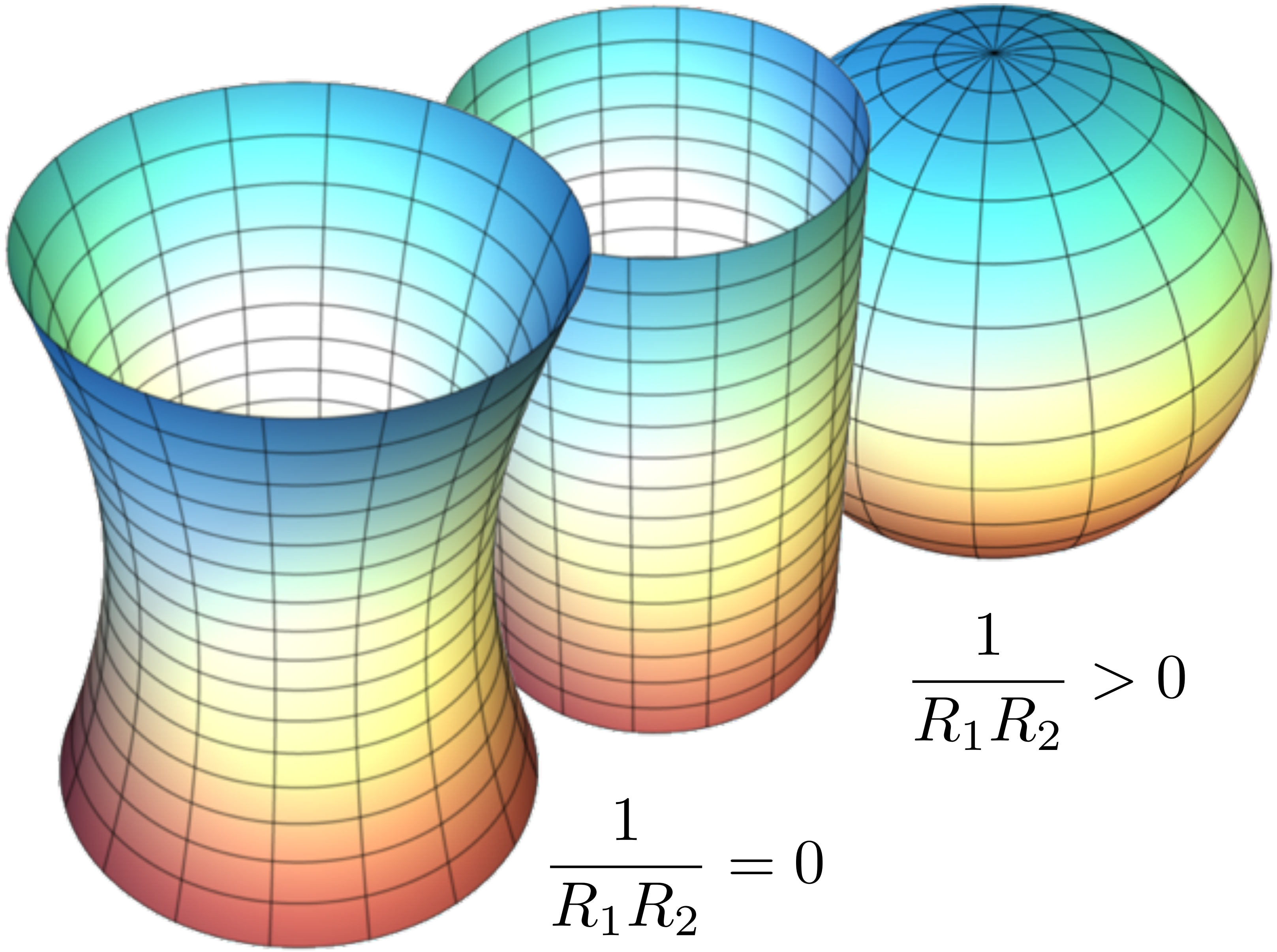
$$\vec{t}_\phi = \frac{\partial \vec{r}}{\partial \phi} = R\sin\theta(-\sin\phi, \cos\phi, 0)$$

$$\vec{n} = \frac{\vec{t}_\theta \times \vec{t}_\phi}{|\vec{t}_\theta \times \vec{t}_\phi|} = (\sin\theta\cos\phi, \sin\theta\sin\phi, \cos\theta)$$

$$g_{ij} = \vec{t}_i \cdot \vec{t}_j = \begin{pmatrix} R^2, & 0 \\ 0, & R^2\sin^2\theta \end{pmatrix}$$

$$K_{ij} = \begin{pmatrix} -\frac{1}{R}, & 0 \\ 0, & -\frac{1}{R} \end{pmatrix}$$

Examples for Gaussian curvature



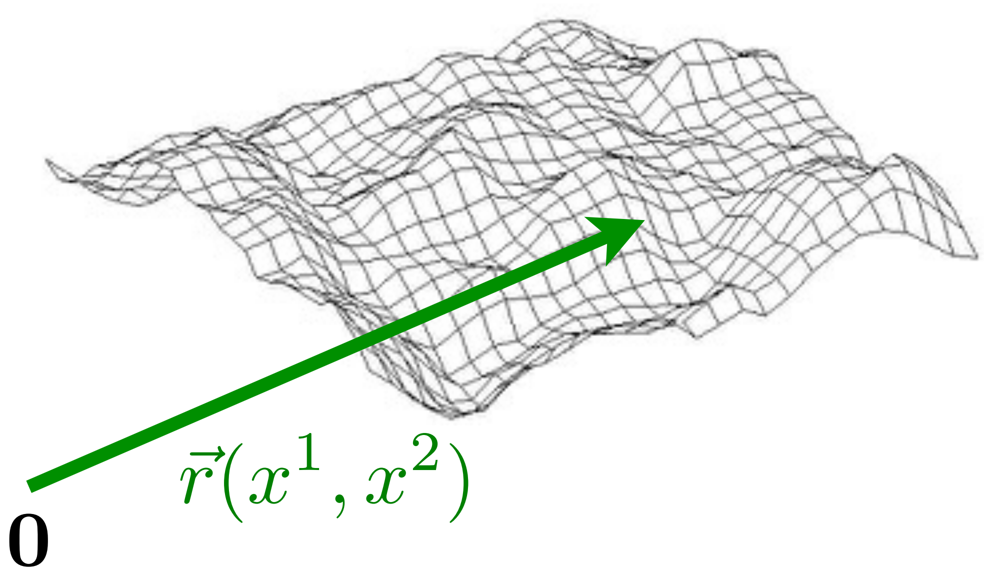
$$\frac{1}{R_1 R_2} > 0$$

$$\frac{1}{R_1 R_2} = 0$$

$$\frac{1}{R_1 R_2} < 0$$

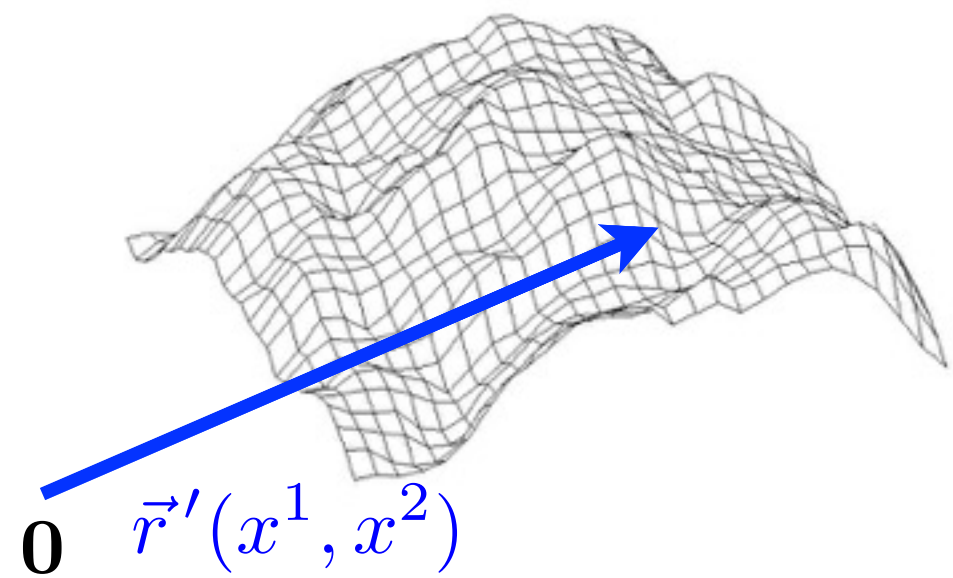
Bending energy for deformation of membranes

undeformed membrane



$$K_{ij} = \sum_k \left(g^{-1}\right)_{ik} \left(\vec{n} \cdot \frac{\partial^2 \vec{r}}{\partial x^k \partial x^j} \right)$$

deformed membrane



$$K'_{ij} = \sum_k \left(g'^{-1}\right)_{ik} \left(\vec{n}' \cdot \frac{\partial^2 \vec{r}\,'}{\partial x^k \partial x^j} \right)$$

bending strain tensor

$$b_{ij} = K'_{ij} - K_{ij}$$

(local measure of deviation from preferred curvature)

Energy cost of bending

$$E = \int \sqrt{g}\, dx^1 dx^2 \left[\frac{1}{2} \kappa \,\mathrm{tr}(b_{ij})^2 + \kappa_G \det(b_{ij}) \right]$$

Bending energy

$$E = \int dA \left[\frac{\kappa}{2} \left(\frac{1}{R_1} + \frac{1}{R_2} - C_0 \right)^2 + \frac{\kappa_G}{R_1 R_2} \right]$$

Helfrich free energy

bending rigidity $\kappa \sim 20 k_B T$

mean curvature $H = \frac{1}{2} \left(\frac{1}{R_1} + \frac{1}{R_2} \right)$

Gaussian bending rigidity $\kappa_G \sim -0.8\kappa$

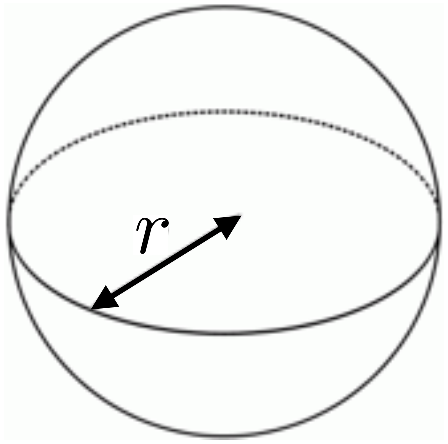
Gaussian curvature $G = \frac{1}{R_1 R_2}$

spontaneous curvature C_0

Example: bending energy for a sphere

$$\frac{1}{R_1} = \frac{1}{R_2} = \frac{1}{r}$$

$$C_0 = 0$$



$$E = 4\pi \left(2\kappa + \kappa_G \right) \sim 300 k_B T$$

bending energy is independent of the sphere radius!

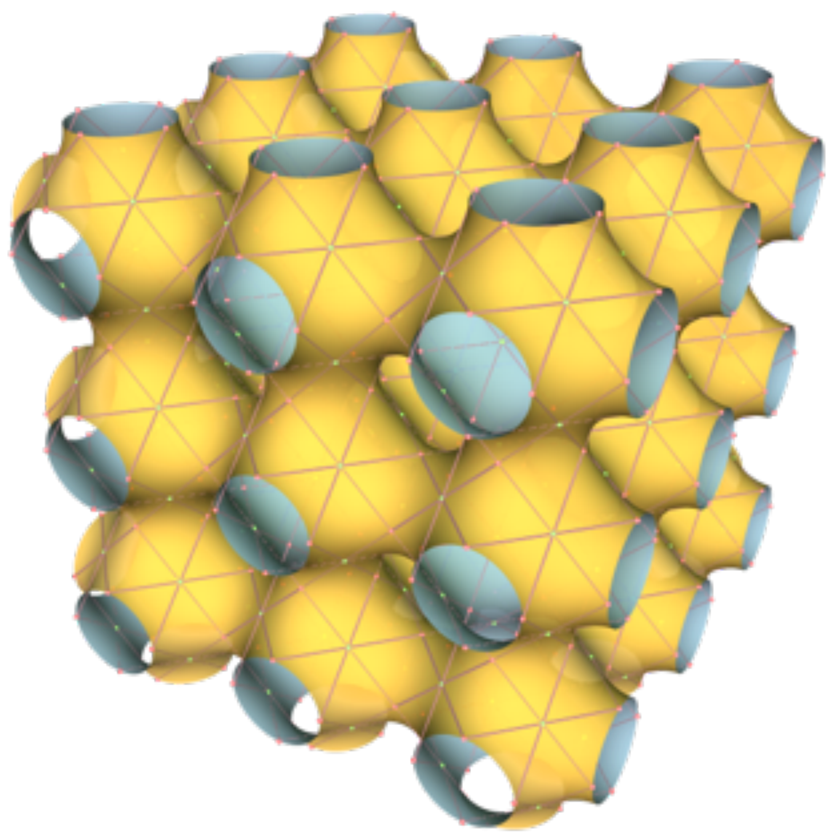
Bending energy

$$E = \int dA \left[\frac{\kappa}{2} \left(\frac{1}{R_1} + \frac{1}{R_2} - C_0 \right)^2 + \frac{\kappa_G}{R_1 R_2} \right]$$

Gaussian bending rigidity κ_G has to be negative for stability of membranes

Schwarz minimal surface

Such surfaces would be preferred for positive Gaussian bending rigidity, when C_0=0.



$$\frac{1}{R_1} + \frac{1}{R_2} = 0$$

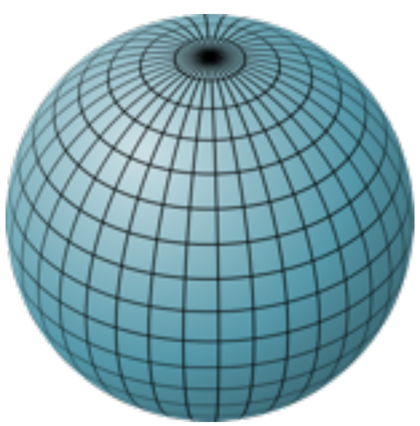
$$\frac{1}{R_1 R_2} < 0$$

Gauss-Bonet theorem

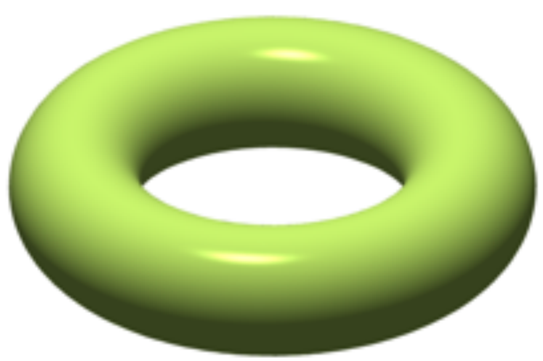
For closed surfaces the integral over Gaussian curvature only depends on the surface topology!

$$\int \frac{dA}{R_1 R_2} = 4\pi\,(1-g)$$

$g = 0$

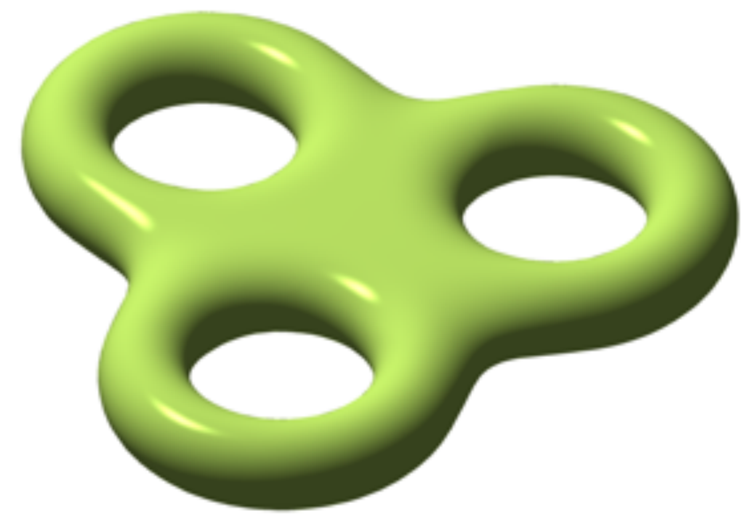


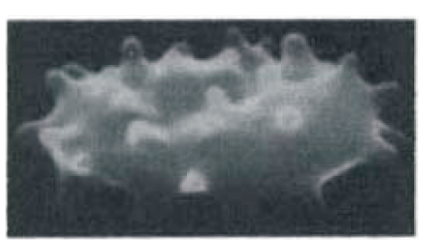
$g = 1$



$g = 2$

$g = 3$





It is hard to experimentally measure the Gaussian bending rigidity for cells, because cell deformations don't change the topology!