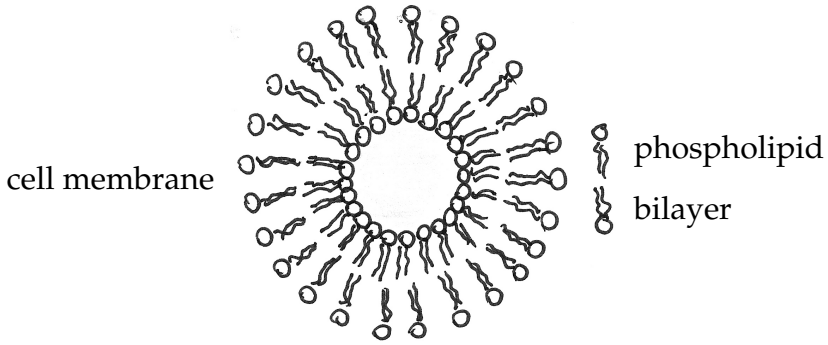

Figure 5.8: Lipid bilayer of cell membrane - characteristic arrangement of phospholipid molecules with hydrophilic polar head groups being oriented towards the aqueous phase while the hydrophobic tails are oriented towards the non-polar inside

to attain its lowest energy level. Accordingly, the nonpolar aminoacid residues of its proteins and the fatty acid chains of its phospholipids will typically be sequestered furthest away from the aqueous solvent. The ionic and polar head groups of the proteins, the lipids and the oligosaccharides, in turn, will seek to be in contact with water, see figure 5.8. Perhaps the most important lesson learned from the study of pure phospholipid bilayer membranes is that they spontaneously seal to form closed structures that separate two aqueous compartments. In the configuration of a plain sheet with ends in which the hydrophobic interior are in contact with water, bilayers are unstable. Their typical spherical architecture with no ends is the most stable state of a phospholipid bilayer.

5.2 Energy

From a structural mechanics point of view, biomembranes are characterized through their very thin structure. As you have seen, the lipid bilayer of the cell membrane has a thickness of approximately 6 nm. The typical dimensions of a cell are at least of the order of μm. Therefore, it is quite common to treat biomembranes as shell structures. In general, the notion of shells is associated with thin, curved structures that are subjected to loads that can cause in plane stretches and shear and out of plane bending. A special case of shells, a flat shell of zero curvature, would be referred to as a plate. Shells are structural elements for which one dimension, the thickness, is much smaller than their two other dimensions, the length and the width. Based on this dimensional restriction, specific kinematic assumptions can be made that significantly reduce and simplify the set of governing equations of three dimensional continua.

5.2.1 The Kirchhoff Love theory

The kinematic assumptions that seem reasonable for biomembranes are based on the classical von Kármán theory. The von Kármán theory implies that the displacements are small, while the rotations of the shell's mid surface can be moderate. Of course,

moderate is a rather vague characterization, but what is actually ment by it is rotations of up to the order of 10^o or 15^o. A detailed comparison of shell kinematics is provided by Flügge [6], see also Reddy [10] for a more recent overview. In the von Kármán theory, the displacements are assumed to satisfy the Kirchhoff hypothesis, which is essentially based on the following three assumptions.

- normals remain straight (they do not bend)
- normals remain unstretched (they keep the same length)
- normals remain normal (they remain orthogonal to the mid-surface)

The Kirchhoff hypothesis implies that the total in-plane displacements u^{tot} and v^{tot} at any point of the membrane x, y, z can be expressed as the sum of the in-plane displacements u and v at x, y and some additional displacements introduced by the rotations of the shell's mid surface $w_{,x}$ and $w_{,y}$. The latter vary linearly across the thickness direction z, as illustrated in figure **??**. According to the Kirchhoff hypothesis, the transverse displacement w^{tot} at x, y, z is constant in the thickness direction, i.e. w is only a function of the in-plane coordinates x, y.

$$\begin{aligned} u^{\text{tot}}(x,y,z) &= u(x,y) - z\, w_{,x} \\ v^{\text{tot}}(x,y,z) &= v(x,y) - z\, w_{,y} \\ w^{\text{tot}}(x,y,z) &= w(x,y) \end{aligned} \tag{5.2.1}$$

Recall the definition of the Green Lagrange E strains as introduced in chapter 2. Keep in mind that equal indices indicate normal strains and different indices indicate shear strains!

$$\begin{aligned} E_{xx} &= u_{,x} + \tfrac{1}{2}\left[u_{,x}^2 + v_{,x}^2 + w_{,x}^2 \right] \\ E_{yy} &= v_{,y} + \tfrac{1}{2}\left[u_{,y}^2 + v_{,y}^2 + w_{,y}^2 \right] \\ E_{zz} &= w_{,z} + \tfrac{1}{2}\left[u_{,z}^2 + v_{,z}^2 + w_{,z}^2 \right] \\ E_{xy} &= \tfrac{1}{2}\left[u_{,y} + v_{,x}\right] + \tfrac{1}{2}\left[u_{,x}u_{,y} + v_{,x}v_{,y} + w_{,x}w_{,y} \right] \\ E_{yz} &= \tfrac{1}{2}\left[v_{,z} + w_{,y}\right] + \tfrac{1}{2}\left[u_{,y}u_{,z} + v_{,y}v_{,z} + w_{,y}w_{,z} \right] \\ E_{zx} &= \tfrac{1}{2}\left[w_{,x} + u_{,z}\right] + \tfrac{1}{2}\left[u_{,z}u_{,x} + v_{,z}v_{,x} + w_{,z}w_{,x} \right] \end{aligned} \tag{5.2.2}$$

In the von Kármán theory, we typically assume that the deformations are small, i.e. $u_{,x}$, $u_{,y}$, $v_{,x}$, $v_{,y}$ and $w_{,z}$ are of the order $\mathcal{O}(\epsilon)$. The small strain assumption thus implies that any multiplicative combination of these terms is of the order $\mathcal{O}(\epsilon^2)$ and can thus be neglected. However, for shells, it is common to allow the rotations of the transverse normal $w_{,x}$ and $w_{,y}$ to be moderate. The wording moderate indicates that the multiplicative terms $w_{,x}^2$, $w_{,y}^2$ and $w_{,x}w_{,y}$ cannot be neglected! For small strains and moderate rotations, the kinematic equations which describe the strain displacement relations for

thin shells take the following format.

$$\begin{aligned} \varepsilon_{xx} &= u^{\text{tot}}_{,x} + \tfrac{1}{2}\, w^{\text{tot}2}_{,x} & \varepsilon_{xy} &= \tfrac{1}{2}\left[u^{\text{tot}}_{,y} + v^{\text{tot}}_{,x}\right] + \tfrac{1}{2}\, w^{\text{tot}}_{,x} w^{\text{tot}}_{,y} \\ \varepsilon_{yy} &= v^{\text{tot}}_{,y} + \tfrac{1}{2}\, w^{\text{tot}2}_{,y} & \varepsilon_{yz} &= \tfrac{1}{2}\left[v^{\text{tot}}_{,z} + w^{\text{tot}}_{,y}\right] \\ \varepsilon_{zz} &= w^{\text{tot}}_{,z} & \varepsilon_{zx} &= \tfrac{1}{2}\left[w^{\text{tot}}_{,x} + u^{\text{tot}}_{,z}\right] \end{aligned} \tag{5.2.3}$$

By inserting the definitions of the total displacments u^{tot}, v^{tot} and w^{tot} of equation (5.2.1), we obtain the von Kármán strains

$$\begin{aligned} \varepsilon_{xx} &= u_{,x} + \tfrac{1}{2}\, w^2_{,x} - z\, w_{,xx} & \varepsilon_{xy} &= \tfrac{1}{2}\left[u_{,y} + v_{,x}\right] + w_{,x} w_{,y} - z\, w_{,xy} \\ \varepsilon_{yy} &= v_{,y} + \tfrac{1}{2}\, w^2_{,y} - z\, w_{,yy} & \varepsilon_{yz} &= 0 \\ \varepsilon_{zz} &= 0 & \varepsilon_{zx} &= 0 \end{aligned} \tag{5.2.4}$$

for the classical von Kármán shell theory. Since we required the transverse normal to be inextensible, there are no strain components in the out of plane direction, i.e. $\varepsilon_{xz} = \varepsilon_{yz} = \varepsilon_{zz} = 0$.

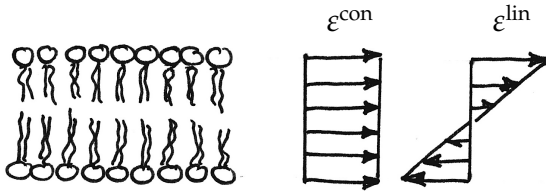

Figure 5.9: Von Kármán strains in cross section – constant terms ε^{con} related to in plain strains and linear terms ε^{lin} related to out of plane bending

By taking a closer look at the in plane strains, we realize that both the in plane normal strains ε_{xx} and ε_{yy} and the in plane shear strains ε_{xy} consist of some contributions ε^{con} which are independent of the z-coordinate and thus constant over the thickness. In addition, each in plane strain component has one contribution ε^{lin} that varies linearly over the thickness. While the former are related to the in plane deformation in the form of tension and shear, the latter are related to the out of plane deformation in the form of bending. The overall deformation of plates and shells can thus be understood as the superposition of three basic deformation modes, in plane tension and shear and out of plane bending. These three modes will be treated independently in the following subsections.

5.2.2 In plane deformation - Tension and shear

Let us first elaborate the strain contributions which are constant over the thickness. These can be related to the notions of in plane tension and shear. An infinitesimal element of the cell membrane subjected to in plane tensile forces is illustrated in figure 5.10. As we will see, these equations can be characterized through a second order differential equation. Due to its particular format it is referred to as Laplace equation. Here, it relates the second gradient of the transverse displacement w, or rather

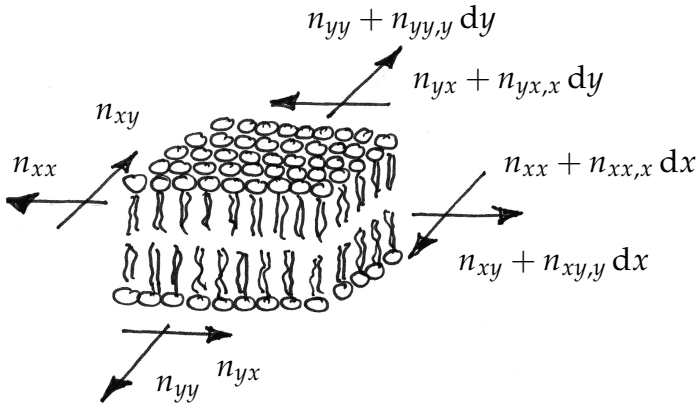

Figure 5.10: Infinitesimal element of the cell membrane with in plane tensile forces n_{xx} and n_{yy}

the curvature or inverse radius, to the transverse pressure p_z. The Laplace equation is essentially a result of the four sets of governing equations, the kinematics, the constitutive equations, the equilibrium equations and the definition of the stress resultants. To evaluate the kinematics associated with tension and shear, we take a closer look at equation (5.2.4) and extract all terms which are independent of the z-coordinate to the following constitutive equations which relate the in plane strains ε_{xx}, ε_{yy} and ε_{xy} to the displacements u, v and w.

$$\begin{aligned} \varepsilon_{xx} &= u_{,x} + \tfrac{1}{2}\, w_{,x}^2 \\ \varepsilon_{yy} &= v_{,y} + \tfrac{1}{2}\, w_{,y}^2 \\ \varepsilon_{xy} &= \tfrac{1}{2}\,[\, u_{,y} + v_{,x}\,] + w_{,x} w_{,y} \end{aligned} \tag{5.2.5}$$

Recall the constitutive equation, i.e. the stress strain relations, for a linear elastic material which we have introduced in chapter 2. Remember that similar indices denote normal stress and strain compontents whereas different indices denote shear stress and strain.

$$\begin{aligned} \sigma_{xx} &= \tfrac{E}{1-\nu^2}\ [\, \varepsilon_{xx} + \nu\, \varepsilon_{yy}\,] \\ \sigma_{yy} &= \tfrac{E}{1-\nu^2}\ [\, \varepsilon_{yy} + \nu\, \varepsilon_{xx}\,] \\ \sigma_{xy} &= \tfrac{E}{1+\nu}\qquad\ \varepsilon_{xy} \end{aligned} \tag{5.2.6}$$

From a material scientist's point of view, tension and shear represent completely different physical phenomena. It is not surprising though that they are related through different material constants. Sometimes the notion $G = E\,/\,[\,2\,[\,1+\nu\,]\,]$ or $\mu = E\,/\,[\,2\,[\,1+\nu\,]\,]$ is used for the material parameter relating shear stress and strain in equation $(5.2.6)_3$. In the engineering notation, the shear strains ε_{xy} are often replaced by the engineering shear strain $\gamma_{xy} = 2\varepsilon_{xy}$ and $\tau_{xy} = \sigma_{xy}$ is used for the shear strain in order to indicate that the microscopic pheneomena that cause shear are truly different from those that are related to tension and stretch.
Equation (5.2.6) gives us some information about the normal and shear stresses in a cross section. But what are the force are that act on one particular cross section of the

shell? You might all remember that stress is force divided by area, so $\sigma = N/A$. So you would probably guess that force should be stress multiplied by area, something like $N = \sigma \cdot A = \sigma \cdot b \cdot h$, where the total area A has been expressed as the product of the width b and the thickness h. Here, we are interested in forces per cross section length $n = N/b$. These would be the stresses multiplied by the thickness, $n = N/b = \sigma \cdot h$. In a somewhat more general sense, what we just did is we integrated the stresses over the thickness, $n = \int_{-h/2}^{+h/2} \sigma \, \mathrm{d}z$. You can think of this as determining the area under the sigma curve in a σ over h diagram for h running from $h = -1/2$ to $h = +1/2$. So here, since the stresses are constant over the thickness, the area of interest would simply be a rectangle. So the integral expression would just render the product of stress times thinkness, $\int_{-h/2}^{+h/2} \sigma \, \mathrm{d}z = \sigma \cdot h$. Keep in mind, however, that this is not the case for non constant stresses such as those related to bending! So here are the equations for the forces per cross section length which are sometimes also referred to as stress resultants in the structural mechanics literature.

$$\begin{aligned} n_{xx} &= \int_{-h/2}^{+h/2} \sigma_{xx} \, \mathrm{d}z = \sigma_{xx} \cdot h = \tfrac{E\,h}{[1-\nu^2]} \, [\, \varepsilon_{xx} + \nu \, \varepsilon_{yy} \,] \\ n_{yy} &= \int_{-h/2}^{+h/2} \sigma_{yy} \, \mathrm{d}z = \sigma_{yy} \cdot h = \tfrac{E\,h}{[1-\nu^2]} \, [\, \varepsilon_{yy} + \nu \, \varepsilon_{xx} \,] \\ n_{xy} &= \int_{-h/2}^{+h/2} \sigma_{xy} \, \mathrm{d}z = \sigma_{xy} \cdot h = \tfrac{E\,h}{1+\nu} \qquad \varepsilon_{xy} \end{aligned} \tag{5.2.7}$$

Here, n_{xx} and n_{yy} are the normal forces per unit length and n_{xy} is the shear force per unit length. We have implicitly assumed homogeneous material properties across the thickness, i.e. neither E nor ν are functions that vary with z. Typical examples of materials with varying properties in the z direction would be sandwiched lightweight structures or composite materials typically found in the airplane industry. For our case with homogeneous material properties, the notion extensional stiffness is usually introduced for the parameter K_N that relates the stress resultants n_{xx} and n_{yy} and strains ε_{xx} and ε_{yy}.

$$\begin{aligned} n_{xx} &= K_N \, [\, \varepsilon_{xx} + \nu \, \varepsilon_{yy} \,] \\ n_{yy} &= K_N \, [\, \varepsilon_{yy} + \nu \, \varepsilon_{xx} \,] \end{aligned} \quad \text{with} \quad K_N = \frac{E\,h}{[\,1-\nu^2\,]} \;\; \text{... extensional stiffness} \tag{5.2.8}$$

With the forces per unit length, we can now write down the three force equilibrium equations by just summing up all arrows in figure 5.10 that point in the same direction in space. Equilibrium states that the sum of these forces should always be equal to zero.

$$\begin{aligned} \textstyle\sum f_x \doteq 0: \quad & -n_{xx}\mathrm{d}y + [n_{xx} + n_{xx,x}\mathrm{d}x]\mathrm{d}y - n_{yx}\mathrm{d}x + [n_{yx} + n_{yx,x}\mathrm{d}y]\mathrm{d}x = 0 \\ \textstyle\sum f_y \doteq 0: \quad & -n_{yy}\mathrm{d}x + [n_{yy} + n_{yy,y}\mathrm{d}y]\mathrm{d}x - n_{xy}\mathrm{d}y + [n_{xy} + n_{xy,y}\mathrm{d}x]\mathrm{d}y = 0 \\ \textstyle\sum f_z \doteq 0: \quad & -n_{xx}\mathrm{d}y\, w_{,x} + [n_{xx} + n_{xx,x}\mathrm{d}x]\mathrm{d}y[w_{,x} + w_{,xx}\mathrm{d}x] \\ & -n_{xy}\mathrm{d}y\, w_{,y} + [n_{xy} + n_{yx,x}\mathrm{d}x]\mathrm{d}y[w_{,y} + w_{,yx}\mathrm{d}x] \\ & -n_{yx}\mathrm{d}x\, w_{,x} + [n_{yx} + n_{xy,y}\mathrm{d}y]\mathrm{d}x[w_{,x} + w_{,xy}\mathrm{d}y] \\ & -n_{yy}\mathrm{d}x\, w_{,y} + [n_{yy} + n_{yy,y}\mathrm{d}y]\mathrm{d}x[w_{,y} + w_{,yy}\mathrm{d}y] + p_z\,\mathrm{d}x\mathrm{d}y = 0 \end{aligned} \tag{5.2.9}$$

To simplify the above equations, we divide each by $\mathrm{d}x\mathrm{d}y$ and cancel the remaining terms with $\mathrm{d}x$ or $\mathrm{d}y$ since those are small when compared to the remaining terms. The above set of equations can then be reformulated as follows.

$$\begin{aligned} \textstyle\sum f_x \doteq 0: &\qquad n_{xx,x} + n_{xy,y} = 0 \\ \textstyle\sum f_y \doteq 0: &\qquad n_{yx,x} + n_{yy,y} = 0 \\ \textstyle\sum f_z \doteq 0: &\qquad [n_{xx}\, w_{,x} + n_{xy}\, w_{,y}]_{,x} + [n_{xy}\, w_{,x} + n_{yy}\, w_{,y}]_{,y} + p_z = 0 \end{aligned} \tag{5.2.10}$$

Another equation which has not been stated explicitly here is the balance of momentum around the z-axis $\sum m_z \doteq 0$ which immediately tells us that the shear resultants on the plane must always be in equilibrium as $n_{xy} - n_{yx} = 0$. Actually, the most relevant of the above equations is the force equilibrium in z-direction. It relates the surface pressure p_z or rather the stress on the shell's surface to its transverse or out of plane displacement w. By writing out the individual derivatives and making use of equations $(5.2.10)_1$ and $(5.2.10)_2$ we can simplify the force equilibrium in transverse direction to $[n_{xx}\, w_{,x} + n_{xy}\, w_{,y}]_{,x} + [n_{xy}\, w_{,x} + n_{yy}\, w_{,y}]_{,y} + p_z = n_{xx}\, w_{,xx} + 2\, n_{xy}\, w_{,xy} + n_{yy}\, w_{,yy} + p_z = 0$. To gain a better understanding of this equation, we will take a closer look at this expression and elborate it for two special cases, the case of planar equibiaxial tension and shear.

Equibiaxial tension

Let us assume a state for which the in plane normal stresses are the similar for both directions, i.e. $\sigma_{xx} = \sigma_{yy} = \sigma$, while the shear stress vanishes $\sigma_{xy} = 0$. Moreover, we shall assume a uniform extension such that σ takes the same values all over the membrane and is thus independent from the position in space, i.e., $\sigma \neq \sigma(x, y, z)$. In structural mechanics, this loading situation is called homogeneous equilibiaxial tension. For this special case, we have $n_{xx} = n_{yy} = n$ and $n_{xy} = 0$. Accordingly, the force equilibrium in x- and y-direction $(5.2.10)_1$ and $(5.2.10)_2$ is trivially satified. The equilibrium of forces in the transverse direction $(5.2.10)_3$ then reduces to the classical Laplace equation for membranes,

$$n\,[\,w_{,xx} + w_{,yy}\,] + p_z = 0 \tag{5.2.11}$$

which relates the pressure p_z to the second gradient of the transverse displacements w in terms of the surface tension n. Mathematicians would typically express this equation in a somewhat more compact notation through the Laplace differential operator $\Delta = \nabla^2 = \frac{\partial^2}{\partial x^2} + \frac{\partial^2}{\partial y^2}$ such that $w_{,xx} + w_{,yy} = \Delta w$.

$$p_z = -n\,\Delta w \qquad \text{with} \qquad n \;\ldots \text{ surface tension} \tag{5.2.12}$$

Recall that the negative second derivative of the transverse displacement w takes the interpretation of the curvature κ. Accordingly $-w_{,xx} = \kappa_{xx} = 1\,/\,r_y$ and $-w_{,yy} = \kappa_{yy} =$

$1 / r_x$ are the radii of curvature of the membrane about the y- and x-axis, respectively.

$$p_z = -n\,[\,w_{,xx} + w_{,yy}\,] = n\,[\,\kappa_{xx} + \kappa_{yy}\,] = n\,\left[\,\frac{1}{r_x} + \frac{1}{r_y}\,\right] \tag{5.2.13}$$

For equal radii $r_x = r_y = r$, equation (5.2.13) reduces to the classical membrane equation for spheres $p_z = -n\,\Delta w = n\,[\,1/r_x + 1/r_y\,] = 2\,n\,/\,r$ similar to the one derived for soap bubbles $\Delta p = 2\,\gamma\,/\,r$ in the motivation (5.1.3). Recall that γ was introduced as the surface tension, which is of the unit force per length. The stress resultant n, the force per cross section length, obviously has the same unit and takes a similar interpretation.

Energy minimization for the soap bubble problem Let us briefly turn back to the soap bubble problem. Although maybe a bit more cumbersome, we can, of course, derive the equilibrium equations through energy principles as well. We thus want to look for the minimum of the overall energy W with respect to all dependent quantities. Unlike in the bubble example where the kinematic unknown was just the radius r the unknowns in our formulation here are the displacements u, v and w. Similar to the soap bubble problem, the minimum of the overall energy W with respect to variations in displacements u, v and w can be expressed through the vanishing first variation δW with respect to the individual unknowns.

$$W(u,v,w) \to \min \qquad \delta W(u,v,w) = \delta W^{\text{int}} + \delta W^{\text{ext}} \doteq 0$$

The internal and external virtual work δW^{int} and δW^{ext} can then be specified as follows.

$$\begin{aligned}
\delta W^{\text{int}} &= \int_A \int_{-h/2}^{+h/2} \sigma_{xx}\,\delta\varepsilon_{xx} + 2\sigma_{xy}\,\delta\varepsilon_{xy} + \sigma_{yy}\,\delta\varepsilon_{yy} \qquad \mathrm{d}A \\
&= \int_A \qquad\qquad n_{xx}\,\delta\varepsilon^{\text{con}}_{xx} + 2n_{xy}\,\delta\varepsilon^{\text{con}}_{xy} + n_{yy}\,\delta\varepsilon^{\text{con}}_{yy} \;\mathrm{d}z\,\mathrm{d}A \\
\delta W^{\text{ext}} &= \int_A \qquad\qquad p\,\delta w \qquad\qquad\qquad\qquad\qquad \mathrm{d}A
\end{aligned}$$

Energy considerations can sometimes be very illustrative. They immediately provide information about the so called energy conjugate pairs. For example, from the above expression, you can easily see that the shear stresses σ_{xy} are energetically conjugate to the shear strains ε_{xy} or that the normal stress resultants n_{xx} are conjugate to the corresponding strains $\varepsilon^{\text{con}}_{xx}$ which are constant over the thickness. The entire set of equilibrium equations (5.2.10) can be extracted from the energy formulation by making use of the kinematic equations and expressing the strains through the displacements. Then we would perform an integration by parts and sort all contributions with respect to δu, δv and δw. Each related term would then represent one of the equilibrium equations stated in equation (5.2.10). In this context, the equilibrium equations would be referred to as the Euler-Lagrange equations.

Surface strain

To this point, we have only looked into changes of geometry in each direction independently. Sometimes it is interesting to know the response of a two-dimensional element, say in terms of the membrane area A. What is the relation between the applied pressure and the change of an area element of the shell mid-surface? Let us first define a measure for this change in area. By increasing the pressure p_z, or rather by blowing up the soap bubble in section 5.1.2, a small square shell element of initial area $A = L^2$ will increase its area to $a = l^2 = [1+\varepsilon]^2 L^2$. Accordingly, the dimensionless change is defined as the ratio between the deformed and the initial area, $\Delta A = a \,/\, A$. Similar to the one dimensional strain $\Delta L/L = [\, l - L \,]/L = \varepsilon$ which is nothing but the length change ΔL scaled by the original length L, we could thus introduce a two dimensional area strain as the area change ΔA scaled by the original area A.

$$\frac{\Delta A}{A} = \frac{a - A}{A} = \frac{[1+\varepsilon]^2 L^2 - L^2}{L^2} = 2\,\varepsilon + \varepsilon^2 \approx 2\,\varepsilon \tag{5.2.14}$$

Here, we have made use of the assumption of small strains and therefore neglected the quadratic term $\mathcal{O}(\varepsilon^2)$. In the case of equibiaxial tension with $n_{xx} = n_{yy} = n$, the in plane force equilibrium $(5.2.7)_1$, and similarly $(5.2.7)_2$, can obviously be further simplified. With the help of $\varepsilon_{xx} = \varepsilon_{yy} = \varepsilon$ with $\varepsilon = [\Delta A \,/\, A] \,/\, 2$, equation $(5.2.7)_1$ can then be rewritten in the following form.

$$n = \frac{E\,h}{1-\nu^2}\,[\,\varepsilon_{xx} + \nu\,\varepsilon_{yy}\,] = \frac{E\,h}{1-\nu^2}\,[1+\nu]\,\varepsilon = \frac{E\,h}{2\,[\,1-\nu\,]}\,\frac{\Delta A}{A} \tag{5.2.15}$$

The proportionality factor of Young's modulus E devided by $[1-\nu]$ scaled by the thickness h is often referred to as area expansion modulus $K_A = [E\,h] \,/\, 2\,[\,1-\nu\,]$. It relates the membrane forces n and the area strain $\Delta A \,/\, A$.

$$n = K_A\,\frac{\Delta A}{A} \quad \text{with} \quad K_A = \frac{E\,h}{2\,[\,1-\nu\,]} \;\; \text{... area expansion modulus} \tag{5.2.16}$$

You can easily check that it has the dimensions of force per length similar to the stress resultant n. Typical values of the area expansion modulus for lipid bilayers are in the range of $K_A = 0.1 - 1.0$ N/m. The cell membrane of red blood cells, for example, has an area expansion modulus of approximately $K_A = 0.45$ N/m. This value is incredibly huge as compared to the other moduli which indicates that cell membranes can be treated as nearly incompressible. The large resistance to area change can be attributed to the changes in energy associated with exposing the hydrophobic core of the lipid bilayer to water as the spacing between the individual molecules is increased.

Shear

Until now, we have assumed that the in plane normal stresses are the similar for both directions and that the shear term vanishes. A typical loading scenario that would

involve shear though is the application of tension in one direction, say σ_{xx} such that the membrane stretches in x direction while it contracts under smaller tension σ_{yy} in the y direction. Although we only apply normal stresses of different magnitude and we do not apply shear stress in the original coordinate system where $\sigma_{xy} = 0$, surfaces oriented under an angle of 45^o exhibit pure shear stress which is of the magnitude $\sigma_{xy} = [\,\sigma_{xx} - \sigma_{yy}\,] \,/\, 2$. Biological membranes, in particular the lipid bilayer that forms the cell membrane, hardly display any resistance to shear. In that sense, they behave like fluids and are therefore often treated as a two-dimensional liquids. You can simply check the lack of shear resistance by putting a flat plate on the surface of water. The force you need to apply to move the plate around is relatively small as compared to, for instance, the force you would need in order to press it down. This characteristic behavior is reflected through a relatively small shear modulus $G = E \,/\, [\,2\,[1+\nu]]$ and a relatively large bulk or rather volume expansion modulus $K = E \,/\, [\,3\,[1-2\nu]]$. From the constitutive equation introduced in chapter 2, we can extract the stress strain relation for the shear component $\sigma_{xy} = E \,/\, [\,1+\nu\,]\,\varepsilon_{xy} = 2\,G\,\varepsilon_{xy}$. It introduces the following constitutive relation between the shear stress resultant $n_{xy} = \sigma_{xy}\,h$ and the shear strain ε_{xy}.

$$n_{xy} = K_S\,\varepsilon_{xy} \quad \text{with} \quad K_S = 2\,G\,h = \frac{E\,h}{1+\nu} \;\; \text{... membrane shear stiffness} \tag{5.2.17}$$

Here, we have introduced the membrane shear stiffness $K_S = 2\,G\,h = [\,E\,h\,] \,/\, [\,1+\nu,\,]$, which has the unit force per length. The cell membrane of a red blood cell would have a typical value of $K_S = 6 - 9 \cdot 10^{-6}$ N/m. This value is extremely small, especically when compared to the area expansion modulus of red blood cell membranes $K_A = 0.45$ N/m. This indicates that the effect of shear can usually be neglected under static loading. However, it might play a significant role under dynamic loading conditions: Fluids typically display a significant strain rate sensitivity, an effect which is referred to as viscosity.

The fluid mosiac model What does a low shear stiffness mean for a cell? We have seen that different biological membranes have different functions depending on the proteins associated with their membrane. The low shear resistance indicates that membrane proteins and lipids can easily diffuse laterally or sideways throughout the membrane, giving it its characteristic appearance of a fluid rather than a solid. This property was first recognized by Singer and Nicolson in 1972 who coined the notion of the fluid mosaic model [11]. The fluid mosaic model of lipid bilayer membranes is a two-dimensional fluid, or liquid crystal, in which the hydrophobic integral components such as lipids and membrane proteins are constrained within the plane of the membrane, but are free to diffuse laterally. From a mechanics point of view, biomembranes can thus be understood as fluids as they bear very little resistance to shear.

5.2.3 Transverse deformation - Bending

In the previous subsection, we have elaborated the contributions to the strains which are constant over the thickness and could be related to in plane tension and shear. Let us now examine the contributions which vary linearly over the thickness. These contributions are related to the transverse displacement w or rather its second derivative. From a structural mechanics point of view they introduce a phenomenon which is referred to as bending, as illustrated in figure 5.11.

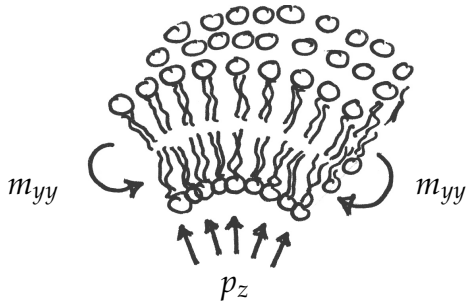

Figure 5.11: Infinitesimal element of the cell membrane with pressure p_z and bending moment m_{yy}

In this section, we derive the classical Kirchhoff plate equation, a fourth order differential equation that essentially governs the transverse displacement or rather out of plane deflection w in response to a given pressure p_z acting in the out-of-plane direction z. The plate equation is a result of four sets of governing equations, the kinematics, the constitutive equations, the definition of the stres resultants and the equilibrium equations which are illustrated in detail in the sequel. Similar to the previous subsection, we begin by taking a look at equation (5.2.4). This time, we extract all non constant terms that involve the z-coordinate. The resulting kinematic equations relate the in in plane normal strains ε_{xx} and ε_{yy} and the in plane shear strain ε_{xy} to the second derivatives of the membrane deflection $w_{,xx}$, $w_{,yy}$ and $w_{,xy}$.

$$\begin{aligned} \varepsilon_{xx} &= -w_{,xx}\ z = \kappa_{xx}\ z \\ \varepsilon_{yy} &= -w_{,yy}\ z = \kappa_{yy}\ z \\ \varepsilon_{xy} &= -w_{,xy}\ z = \kappa_{xy}\ z \end{aligned} \tag{5.2.18}$$

Recall that, from a kinematical point of view, the second derivatives of the deflection represent the curvatures $-w_{,xx} = \kappa_{xx}$, $-w_{,yy} = \kappa_{yy}$ and $-w_{,xy} = \kappa_{xy}$. From chapter 2, we can extract the relevant constitutive equations, i.e. the equations relating stress and strain. In particular they relate the in plane normal stresses σ_{xx} and σ_{yy} and the in plane shear stress σ_{xy} to the corresponding strains ε or curvatures κ

$$\begin{aligned} \sigma_{xx} &= \tfrac{E}{1-\nu^2}\ [\,\varepsilon_{xx} + \nu\,\varepsilon_{yy}\,] = \tfrac{E}{1-\nu^2}\ [\,\kappa_{xx} + \nu\,\kappa_{yy}\,]\ z \\ \sigma_{yy} &= \tfrac{E}{1-\nu^2}\ [\,\varepsilon_{yy} + \nu\,\varepsilon_{xx}\,] = \tfrac{E}{1-\nu^2}\ [\,\kappa_{yy} + \nu\,\kappa_{xx}\,]\ z \\ \sigma_{xy} &= \tfrac{E}{1+\nu}\ \varepsilon_{xy} = \tfrac{E}{1+\nu}\ \kappa_{xy}\ z \end{aligned} \tag{5.2.19}$$

Similar to the previous section, we could rewrite the last equation of this set as $\sigma_{xy} = G\,\varepsilon_{xy}$ where $G = \frac{E}{2\,[1+\nu\,]}$ is the shear modulus. Equation (5.2.19) tells us something about the stresses in a particular cross section. Stresses, however, cannot be directly used to evaluate equilibrium. To state the equilibrium equations, we therefore derive the stress resultants m_{xx}, m_{yy} and m_{xy} in terms of corresponding stresses integrated over the surface thickness h. These resultants are the moments per cross section length which unlike the forces introduced in the previous section are not continuous across the cross section. Therefore, as indicated before, we really have to evaluate them through an integration across the thickness.

$$\begin{aligned} m_{xx} &= \int_{-h/2}^{+h/2} \sigma_{xx}\, z\, \mathrm{d}z = \frac{E\,h^3}{12\,[1-\nu^2]}\,[\,\kappa_{xx} + \nu\,\kappa_{yy}\,] \\ m_{yy} &= \int_{-h/2}^{+h/2} \sigma_{yy}\, z\, \mathrm{d}z = \frac{E\,h^3}{12\,[1-\nu^2]}\,[\,\kappa_{yy} + \nu\,\kappa_{xx}\,] \\ m_{xy} &= \int_{-h/2}^{+h/2} \sigma_{xy}\, z\, \mathrm{d}z = \frac{E\,h^3}{12\,[1+\nu]}\,\kappa_{xy} \end{aligned} \tag{5.2.20}$$

Unlike in the previous section, where the stress resultants had the charcter of forces per length we have now introduced resultants which are of the unit force times length per length which is characteristic for distributed moments. By assuming a uniform thickness and homogeneous material properties across the thickness, we can introduce the membrane bending stiffness $K_B = \int_{-h/2}^{+h/2} \frac{E}{1-\nu^2}\, z^2\, \mathrm{d}z = \frac{E\,h^3}{12\,[1-\nu^2\,]}$. The equilibrium equations for bending which can be motivated from figure 5.11 consist of the force equilibrium in z-direction and the equilibrium of momentum around the x- and y-axis.

$$\begin{aligned} \textstyle\sum f_x \doteq 0: \quad & -n_{xx}\mathrm{d}y + [n_{xx} + n_{xx,x}\mathrm{d}x]\mathrm{d}y - n_{yx}\mathrm{d}x + [n_{yx} + n_{yx,x}\mathrm{d}y]\mathrm{d}x = 0 \\ \textstyle\sum f_y \doteq 0: \quad & -n_{yy}\mathrm{d}x + [n_{yy} + n_{yy,y}\mathrm{d}y]\mathrm{d}x - n_{xy}\mathrm{d}y + [n_{xy} + n_{xy,y}\mathrm{d}x]\mathrm{d}y = 0 \\ \textstyle\sum f_z \doteq 0: \quad & -n_{xx}\mathrm{d}y\, w_{,x} + [n_{xx} + n_{xx,x}\mathrm{d}x]\mathrm{d}y[w_{,x} + w_{,xx}\mathrm{d}x] \\ & -n_{xy}\mathrm{d}y\, w_{,y} + [n_{xy} + n_{yx,x}\mathrm{d}x]\mathrm{d}y[w_{,y} + w_{,yx}\mathrm{d}x] \\ & -n_{yx}\mathrm{d}x\, w_{,x} + [n_{yx} + n_{xy,y}\mathrm{d}y]\mathrm{d}x[w_{,x} + w_{,xy}\mathrm{d}y] \\ & -n_{yy}\mathrm{d}x\, w_{,y} + [n_{yy} + n_{yy,y}\mathrm{d}y]\mathrm{d}x[w_{,y} + w_{,yy}\mathrm{d}y] + p_z\,\mathrm{d}x\mathrm{d}y = 0 \end{aligned} \tag{5.2.21}$$

Just like for the in plane deformation equilibrium, we divide each equation by $\mathrm{d}x\mathrm{d}y$ and cancel the remaining terms with $\mathrm{d}x$ or $\mathrm{d}y$ which are small when compared to the remaining terms. The remaining terms then yield the following simplified set of equations.

$$\begin{aligned} \textstyle\sum f_z &\doteq 0 \qquad q_{x,x} + q_{y,y} + p_z = 0 \\ \textstyle\sum m_y &\doteq 0 \qquad m_{xx,x} + m_{yx,y} - q_x = 0 \\ \textstyle\sum m_x &\doteq 0 \qquad m_{yy,y} + m_{xy,x} - q_y = 0 \end{aligned} \tag{5.2.22}$$

With the use of the x-derivative of the balance of momentum $(5.2.22)_2$ $q_{,xx} = m_{xx,xx} + m_{yx,yx}$, the y-derivative of the balance of momentum $(5.2.22)_3$ $q_{,yy} = m_{yy,yy} + m_{xy,xy}$ and the fact that $m_{xy,xy} = m_{yx,yx}$, we can rewrite the balance of forces in thickness direction

$(5.2.22)_1$. The equilibrium equations (5.2.22) can thus be summarized in just one simple equation.

$$m_{xx,xx} + 2\,m_{xy,xy} + m_{yy,yy} + p_z = 0 \tag{5.2.23}$$

The above equation can be reformulated by inserting the definition of the stress resultants, by making use of the constitutive equations and the kinematic assuptions to finally yield the classical fourth order differential equation for thin plates, the Kirchhoff plate equation.

$$p_z = K_B\,[\,w_{,xxxx} + 2\,w_{,xxyy} + w_{,yyyy}\,] \tag{5.2.24}$$

It relates the pressure p_z to the fourth gradient of the transverse displacements w in terms of the bending stiffness K_B. Mathematicians would rewrite the plate equation in compact notation in terms of the Laplace differential operator $\Delta = \nabla^2 = \frac{\partial^2}{\partial x^2} + \frac{\partial^2}{\partial y^2}$.

$$p_z = K_B\,\Delta^2 w \quad \text{with} \quad K_B = \frac{E\,h^3}{12\,[1-\nu^2]} \;\; \text{... membrane bending stiffness} \tag{5.2.25}$$

Typical values for the membrane bending stiffness K_B are in the order of 10^{-19} Nm for lipid bilayers such as the cell membrane of the red blood cell. This is a really low value as compared to the area expansion modulus K_A. It is even low when compared to the membrane shear modulus K_S! This indicates that the effect of bending is of minor order in biomembranes. This is not surprising though since membrane structures are, by their very definition, structures that try to achieve an optimal stiffness to weight ratio by carrying loads exclusively through in plane normal forces and avoiding out of plane bending as much as possible!

Energy minimization Again, we can write derive the equilibrium equations through an energy principle. To this end, we would minimize the overall energy with respect to the transvere displacement w, or, equivalently, evaluate its vanishing first variation δW with respect to w.

$$W(w) \rightarrow \min \qquad \delta W(w) = \delta W^{\text{int}} + \delta W^{\text{ext}} \doteq 0$$

The internal and external energy expression could then be expressed as follows.

$$\begin{aligned}
\delta W^{\text{int}} &= \int_A \int_{-h/2}^{+h/2} \sigma_{xx}\,\delta\varepsilon_{xx} + 2\sigma_{xy}\,\delta\varepsilon_{xy} + \sigma_{yy}\,\delta\varepsilon_{yy} \;\; \mathrm{d}z\,\mathrm{d}A \\
&= \int_A \qquad m_{xx}\,\delta\kappa_{xx} + 2m_{xy}\,\delta\kappa_{xy} + m_{yy}\,\delta\kappa_{yy} \qquad \mathrm{d}A \\
\delta W^{\text{ext}} &= \int_A \qquad\qquad p\,\delta w \qquad\qquad\qquad\qquad\quad \mathrm{d}A
\end{aligned}$$

We can immediately see that the stress resultants m are energetically conjugate to the curvature κ. Again, by carrying out an intergration by parts, energy minimization would yield the equilibrium equations (5.2.22) which in that context, would be referred to as the Euler-Lagrange equations.

In plane vs transverse deformation - Tension vs bending

For the sake of clarity, we have treated the load cases of tension and bending as individual phenomena so far. Of course, in reality, both usually occur simultaneously, however, most of the times one really dominates the other. An overall description that captures both phenomena and is thus representative for biomembranes in general summarizes both transverse force equilibrium equations $(5.2.10)_3$ and $(5.2.22)_1$ or rather equations (5.2.11) and (5.2.24) in one single equation.

$$n\,[\,w_{,xx} + w_{,yy}\,] - K_B\,[\,w_{,xxxx} + 2\,w_{,xxyy} + w_{,yyyy}\,] + p_z = 0 \tag{5.2.26}$$

The ratio between the two constants n and K_B would then immediately tell us which of the two phenomena is dominant. Let w be the transverse displacement and λ be a characteristic length over which these transverse displacements may vary. The membrane term would thus scale with $n\,w\,/\,\lambda^2$ while the bending term scales with $K_B\,w\,/\,\lambda^4$. The ratio of these scaling factors $K_B\,/\,[n\,\lambda^2]$ could give us an indication of whether tension or bending is relevant under the given conditons.

$$\begin{aligned} \tfrac{K_B}{n\,\lambda^2} &\ll 1 \qquad \text{tension dominated} \\ \tfrac{K_B}{n\,\lambda^2} &\gg 1 \qquad \text{bending dominated} \end{aligned} \tag{5.2.27}$$

A typical value for cells at $K_B = 10^{-18}\text{Nm}$, $n = 5 \cdot 10^5\text{N/m}$ and $\lambda = 1\mu\text{m}$ would be $\frac{K_B}{n\,\lambda^2} = 0.02$ which would indicate that in biological cells, membrane effects are typically dominant over bending.

5.3 Summary

5.4 Problems

Problem 5.1 - Visualization of surface tension

We have seen that surface tension is important to give the cell membrane its spherial shape. A way to visualize surface tension is to float a paper clip on the surface of water. Think of other ways to illustrate surface tension!
If you fill a glass with water, you will be able to add water above the rim of the glass because of surface tension! Small insects such as the water strider can walk on water because their weight is not enough to penetrate the surface.

Problem 5.2 - Platonic solids

Look up the number of sides and the surface to volume ratio for the five platonic solids. Show that the surface to volume ratio decreases with increasing number of sides. Compare your results against the surface to volume ratio of a sphere with infinely many sides.

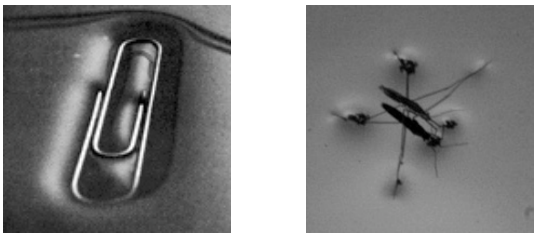

Figure 5.12: Visualization of surface tension: A paper clip floating on the surface of water and a water strider walking on water

solid	no of sides	volume	surface
tetrahedron	4	1 cubic inch	7.21 square inches
cube	6	1 cubic inch	6.00 square inches
octahedron	8	1 cubic inch	5.72 square inches
dodecahedron	12	1 cubic inch	5.32 square inches
icosahedron	20	1 cubic inch	5.15 square inches
sphere	∞	1 cubic inch	4.84 square inches

Table 5.1: Surface to volume ratio of platonic solids

Problem 5.3 - Von Kármán strains

In the text, we have described the derivation of the von Kármán strains

$$\begin{aligned} \varepsilon_{xx} &= u_{,x} + \tfrac{1}{2}\, w_{,x}^2 - z\, w_{,xx} & \qquad \varepsilon_{xy} &= \tfrac{1}{2}\,[u_{,y} + v_{,x}] + w_{,x} w_{,y} - z\, w_{,xy} \\ \varepsilon_{yy} &= v_{,y} + \tfrac{1}{2}\, w_{,y}^2 - z\, w_{,yy} & \qquad \varepsilon_{yz} &= 0 \\ \varepsilon_{zz} &= 0 & \qquad \varepsilon_{zx} &= 0 \end{aligned}$$

in words. Verify these equations by following what is described in the text in going from the nonlinear Green Lagrange strains E to the small strains ε by neglecting higher order terms. Make sure you understand which terms can be neglected and why! Then, insert the definitions of the total displacments u^{tot}, v^{tot} and w^{tot} to end up with the Kármán strains.

Problem 5.4 - Membrane equation

You have seen that the force equilibrium in transverse direction $n_{xx}\, w_{,xx} + 2\, n_{xy}\, w_{,xy} + n_{yy}\, w_{,yy} + p_z = 0$ is really important. In the text we have described how this simplified form can be obtained from the more general format $[n_{xx}\, w_{,x} + n_{xy}\, w_{,y}]_{,x} + [n_{xy}\, w_{,x} + n_{yy}\, w_{,y}]_{,y} + p_z = 0$ by making use of equations $(5.2.10)_1$ and $(5.2.10)_2$. Verify that the two expressions above are identical!