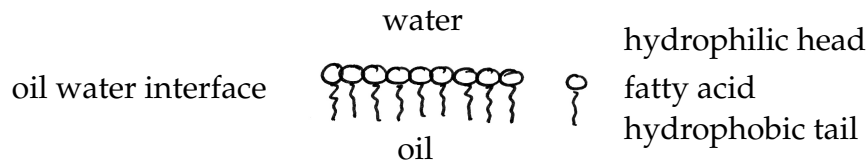


## 5.1.2 Lipid bilayers

In cell biology, the notion membrane is typically associated with the phospholipid bilayer and the proteins associated with it. In aqueous solutions, these proteins essentially display two kinds of non-covalent interactions which are referred to as hydrophobic and hydrophilic. Long polymer molecules typically tend to adopt conformations, in which non-polar residues are predominantly sequestered such that they avoid contact with water. The non-polar residues are said to be hydrophobic or water-avoiding. Polymer molecules favor conformations, in which the polar head groups are exposed to water. The polar head groups are referred to as being hydrophilic or water-loving. A typical example is the arrangement of fatty acids at an oil water interface, where the hydrophilic polar heads would typically be oriented towards the water phase while the hydrophobic tails would be oriented towards the oil phase, see figure 5.11.

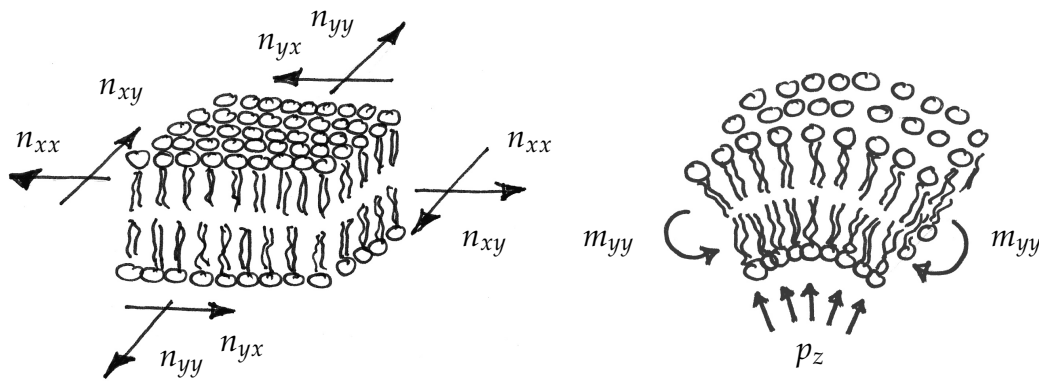


**Figure 5.11:** Oil water interface. Characteristic arrangement of fatty acid molecules with hydrophilic polar head group oriented towards the water phase and hydrophobic tail oriented towards the oil phase

From an energetic point of view, lipid bilayers show an attractive arrangement since they display both hydrophobic and hydrophilic interactions. The nonpolar fatty acid chains of the phospholipid molecules are sequestered together away from the water sandwiched between the polar head groups to maximize hydrophobic interactions. At the same time, the ionic polar head groups are in direct contact with the aqueous phase to maximize hydrophilic interactions. This dual nature of the molecules is referred to as amphiphilic.

For energetic reasons, each lipid bilayer has an inherent optimal microstructure with and optimal spacing between the lipid molecules. Any perturbation to this optimal arrangement disturbs this energetically favorable microstructure. The lipid bilayer thus exhibits an inherent resistance to deformations that cause shape changes. Typical examples are extension, for which the spacing between the head groups would increase throughout the membrane, or bending for which the head group spacing would increase on the outside while it would decrease on the inside, see figure 5.12.

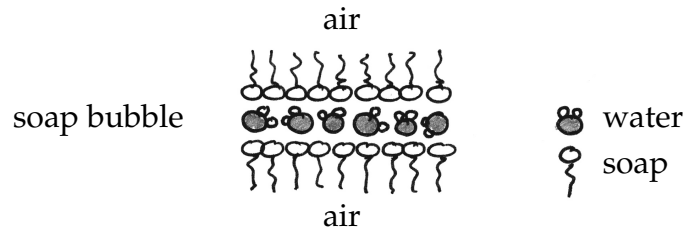
One of the key issues of this chapter is the identification of characteristic macroscopic parameters that display the nature of these intermolecular effects in a phenomenological way and account for the resistance of the cell membrane to extension, shear and bending. To this end, we will first look at a lipid bilayer structure that everybody can easily reproduce and elaborate at home, the structure of soap bubbles. When having understood how soap bubbles behave and how they can be described by mathematical equations, we will turn to elaborating the structural behavior of the cell membrane which is slightly more complicated but obey a similar set of equations from a mathematical point of view.



**Figure 5.12:** Infinitesimal element of the cell membrane subject to tension causing in plane deformation and shear (left) and bending causing out of plane deformation (right)

### 5.1.3 Soap bubbles

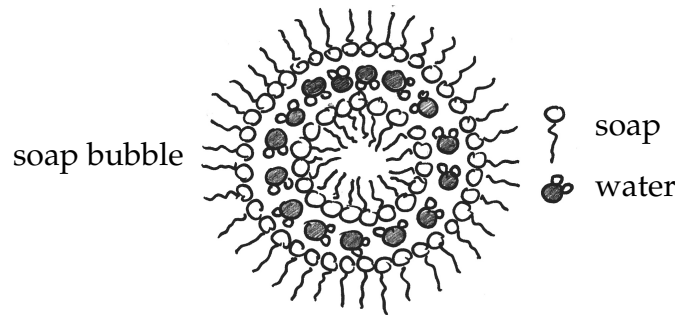
Soap bubbles are fascinating structures that display many similar features as the cell membrane. They can be used as model system to illustrate the qualitative behavior of a lipid bilayer. Soap bubbles are an excellent example of a self-assembled system. Their surface consists of a thin layer of water trapped between two layers of surfactant, typically soap. The surfactant possesses hydrophilic heads attracted to the thin water layer. Its hydrophobic tails form the inner and outer surface of the bubble as sketched figure 5.13. When being disturbed, the bubble pops.



**Figure 5.13:** Lipid bilayer of soap bubbles - characteristic arrangement of soap molecules with a thin water layer being sandwiched between the hydrophilic polar head groups while the hydrophobic tails are oriented to the non-polar air

The spherical shape of a soap bubble nicely displays the principle of energy minimization. Surface tension causes the bubble to form a sphere because this shape, as proposed by Archimedes and proven rigorously by Schwarz in 1884, is the minimal surface enclosing a fixed given volume. The spherical shape can be visibly distorted by additional external forces, you can easily test this by blowing against the bubble surface. If a bubble is subject to an environment without any additional external forces acting on it, however, it should always remain nearly spherical as displayed in figure 5.14.

An interesting question to ask about soap bubbles is what is the radius  $r$  of a soap bubble that is blown up at a pressure  $\Delta p$ ? Here  $\Delta p = p^{\text{int}} - p^{\text{out}}$  would be the pressure difference between the inside and outside of the bubble. To answer this question, we consider spherical soap bubble with initial radius  $r$ , that has a surface of  $A = 4\pi r^2$  and a volume of  $V = \frac{4}{3}\pi r^3$ . The inflation of the surface induces an internal energy



**Figure 5.14:** Lipid bilayer of soap bubbles - characteristic arrangement of soap molecules with a thin water layer being sandwiched between the hydrophilic polar head groups while the hydrophobic tails are oriented to the non-polar air

$W^{\text{int}}$  which is assumed to be proportional to the increase in membrane surface  $A$ . In the simplest case,  $W^{\text{int}} = \gamma A$  where, for now,  $\gamma$  is introduced as a mere proportionality constant. Its unit is obviously force per length and its physical interpretation will be discussed later. The external work  $W^{\text{ext}}$  is equal to the pressure difference  $\Delta p$  acting on the enclosed volume  $V$ , such that  $W^{\text{ext}} = \Delta p V$ . The total energy  $W$  of the bubble thus consists of the internal energy  $W^{\text{int}}$  and the external energy  $W^{\text{ext}}$ .

$$W(r) = W^{\text{int}} - W^{\text{ext}} \quad \text{with} \quad \begin{aligned} W^{\text{int}} &= \gamma A = \gamma 4 \pi r^2 \\ W^{\text{ext}} &= \Delta p V = \Delta p \frac{4}{3} \pi r^3 \end{aligned} \quad (5.1.9)$$

The minimum of the overall energy  $W$  with varying bubble radius  $r$  is obviously equivalent to the vanishing first variation  $\delta W$  with respect to  $r$ .

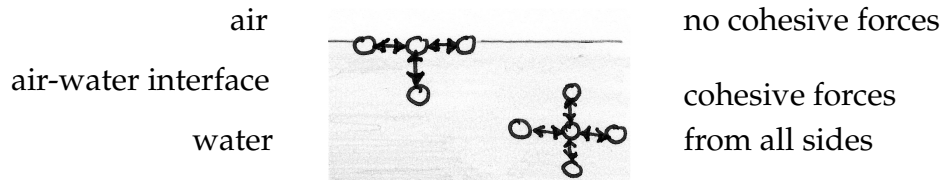
$$W(r) \rightarrow \min \quad \delta W(r) \doteq 0 \quad \text{with} \quad \begin{aligned} \delta W^{\text{int}} &= \gamma 8 \pi r \\ \delta W^{\text{ext}} &= \Delta p 4 \pi r^2 \end{aligned} \quad (5.1.10)$$

Evaluating the above equation  $\gamma 8 \pi r - \Delta p 4 \pi r^2 \doteq 0$  we obtain the following simple relation between the pressure difference  $\Delta p$  and the bubble radius  $r$

$$\Delta p = 2 \gamma \frac{1}{r} \quad (5.1.11)$$

which has been developed independently by Young and Laplace more than 200 years ago [25,44]. In the literature, equation (5.1.11) is referred to as the Young-Laplace equation. The historical controversy about its development is documented by Müller & Strehlow [32]. We will see later how this equation for spherical membranes such as soap bubbles can be derived in a more rigorous form.

The cohesive forces between liquid molecules are responsible for the phenomenon which is referred to as surface tension. Cohesive forces between molecules are shared between all neighboring molecules. Unlike molecules in the bulk of the liquid, molecules close to the surface are surrounded by neighboring molecules from only one side. These molecules on the surface thus exhibit stronger attractive forces upon their nearest neighbors than do those on the inside. This enhancement of intermolecular attractive forces close to the surface is called surface tension, see figure 5.18.



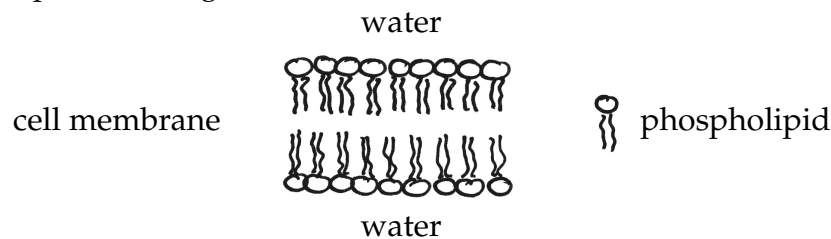
**Figure 5.15:** Air water interface - molecular interpretation of surface tension

More than a century ago, an illustrative set of experiments on surface tension was carried out by Boys [6]. You can easily visualize the effect of surface tension by carefully laying down a paper clip on a surface of water. Although the density of the paper clip should be higher than that of water and you would expect it to sink down, it actually floats on top of the water surface due to surface tension.

**Surface tension** Surface tension is typically measured in force per length related to the units dynes per cm. Since  $1 \text{ dyne} = 10 \text{ mN}$ ,  $1 \text{ dyne/cm} = 1 \text{ mN/m}$ . Alternatively, especially in thermodynamics, the notion surface energy is used instead. Surface energy is measured in ergs per length squared, where one erg, the force of one dyne exerted for a distance of one cm is equal to gram centimeter squared per second squared  $\text{g cm}^2/\text{s}^2$  or, equivalently,  $10^{-7}$  joules. The surface tension of water at room temperature is  $\gamma^{\text{water}} = 72 \text{ dynes/cm}$ , ethanol has a lower surface tension of  $\gamma^{\text{ethanol}} = 22 \text{ dynes/cm}$  and mercury has a surface tension as large as  $\gamma^{\text{mercury}} = 465 \text{ dynes/cm}$ .

### 5.1.4 Cell membranes

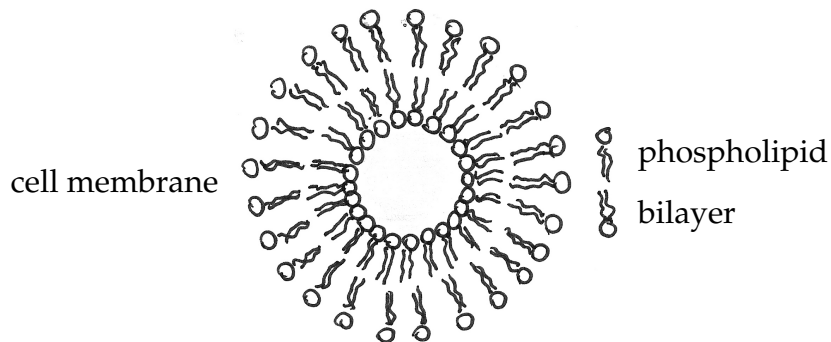
The most intriguing of all biomembranes is the cell membrane, a semipermeable phospholipid bilayer common to all living cells. This lipid bilayer which is approximately 6-7 nm thick consists of a variety of different biopolymers the most common of which are proteins, lipids and oligosaccharides.



**Figure 5.16:** Lipid bilayer of the 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

The term lipid specifies a category of water-insoluble, energy rich macromolecules, typical of fats, waxes, and oils. Throughout the phospholipid bilayer, we find aggregates of globular proteins which are irregularly dispersed and free to move within the layer giving the membrane a fluid-like appearance. On the inside, the lipid bilayer serves as attachment for the cytoskeleton which is primarily responsible to control the

cell shape, see figure 5.16. On the outside, the cell membrane plays an important role in attaching to the extracellular matrix. Specific proteins embedded in the cell membrane can act as molecular signals and to allow for cell to cell interaction. In fungi, bacteria and plants, the cell membrane is further surrounded by the cell wall. In an aqueous



**Figure 5.17:** 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

environment, the intact cell membrane seeks 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 5.17. 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  $\mu\text{m}$ . 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 [17, 22, 36, 41].

### 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  $10^\circ$  or  $15^\circ$ . A detailed comparison of shell kinematics is provided by Flügge [15], see also Reddy [39] 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  $u^{\text{tot}}$  and  $v^{\text{tot}}$  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  $w^{\text{tot}}$  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!

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

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

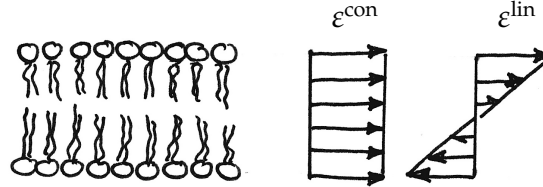
normal  $w_{,x}$  and  $w_{,y}$  to be moderate. The wording moderate indicates that the multiplicative terms  $w_{,x}^2$ ,  $w_{,y}^2$  and  $w_{,x}w_{,y}$  cannot be neglected! For small strains and moderate rotations, the kinematic equations which describe the strain displacement relations for thin shells take the following format.

$$\begin{aligned}
 \varepsilon_{xx} &= u_{,x}^{\text{tot}} + \frac{1}{2} w_{,x}^{\text{tot}2} & \varepsilon_{xy} &= \frac{1}{2} [u_{,y}^{\text{tot}} + v_{,x}^{\text{tot}}] + \frac{1}{2} w_{,x}^{\text{tot}} w_{,y}^{\text{tot}} \\
 \varepsilon_{yy} &= v_{,y}^{\text{tot}} + \frac{1}{2} w_{,y}^{\text{tot}2} & \varepsilon_{yz} &= \frac{1}{2} [v_{,z}^{\text{tot}} + w_{,y}^{\text{tot}}] + \frac{1}{2} w_{,y}^{\text{tot}} w_{,z}^{\text{tot}} \\
 \varepsilon_{zz} &= w_{,z}^{\text{tot}} & \varepsilon_{zx} &= \frac{1}{2} [w_{,x}^{\text{tot}} + u_{,z}^{\text{tot}}] + \frac{1}{2} w_{,z}^{\text{tot}} w_{,x}^{\text{tot}}
 \end{aligned} \tag{5.2.3}$$

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

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

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.  $\varepsilon_{xz} = \varepsilon_{yz} = \varepsilon_{zz} = 0$ .

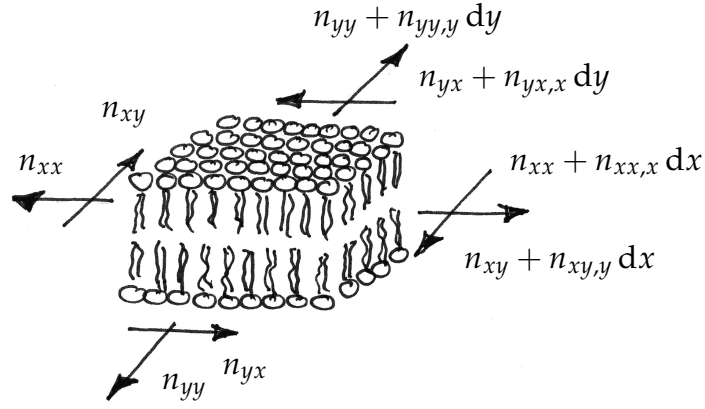


**Figure 5.18:** Von Kármán strains in cross section – constant terms  $\varepsilon^{\text{con}}$  related to in plane strains and linear terms  $\varepsilon^{\text{lin}}$  related to out of plane bending

By taking a closer look at the in plane strains, we realize that both the in plane normal strains  $\varepsilon_{xx}$  and  $\varepsilon_{yy}$  and the in plane shear strains  $\varepsilon_{xy}$  consist of some contributions  $\varepsilon^{\text{con}}$  which are independent of the  $z$ -coordinate and thus constant over the thickness. In addition, each in plane strain component has one contribution  $\varepsilon^{\text{lin}}$  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



**Figure 5.19:** Infinitesimal element of the cell membrane with in plane tensile forces  $n_{xx}$  and  $n_{yy}$

element of the cell membrane subjected to in plane tensile forces is illustrated in figure 5.19. 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 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  $\varepsilon_{xx}$ ,  $\varepsilon_{yy}$  and  $\varepsilon_{xy}$  to the displacements  $u$ ,  $v$  and  $w$ .

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

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 components whereas different indices denote shear stress and strain.

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

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)<sub>3</sub>. In the engineering notation, the shear strains  $\varepsilon_{xy}$  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 phenomena 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,  $n = \int_{-h/2}^{+h/2} \sigma dz$ . You can think of this as determining the area under the sigma curve in a  $\sigma$  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 thickness,  $\int_{-h/2}^{+h/2} \sigma dz = \sigma \cdot h$ . 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.

$$\begin{aligned} n_{xx} &= \int_{-h/2}^{+h/2} \sigma_{xx} dz = \sigma_{xx} \cdot h = \frac{Eh}{[1-\nu^2]} [\varepsilon_{xx} + \nu \varepsilon_{yy}] \\ n_{yy} &= \int_{-h/2}^{+h/2} \sigma_{yy} dz = \sigma_{yy} \cdot h = \frac{Eh}{[1-\nu^2]} [\varepsilon_{yy} + \nu \varepsilon_{xx}] \\ n_{xy} &= \int_{-h/2}^{+h/2} \sigma_{xy} dz = \sigma_{xy} \cdot h = \frac{Eh}{1+\nu} \varepsilon_{xy} \end{aligned} \quad (5.2.7)$$

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  $\nu$  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  $\varepsilon_{xx}$  and  $\varepsilon_{yy}$ .

$$\begin{aligned} n_{xx} &= K_N [\varepsilon_{xx} + \nu \varepsilon_{yy}] \\ n_{yy} &= K_N [\varepsilon_{yy} + \nu \varepsilon_{xx}] \end{aligned} \quad \text{with} \quad K_N = \frac{Eh}{[1-\nu^2]} \dots \text{extensional stiffness} \quad (5.2.8)$$

With the forces per unit length, we can now write down the three force equilibrium equations by just summing up all arrows in figure 5.19 that point in the same direction in space. Equilibrium states that the sum of these forces should always be equal to

zero.

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

To simplify the above equations, we divide each by  $dx dy$  and cancel the remaining terms with  $dx$  or  $dy$  since those are small when compared to the remaining terms. The above set of equations can then be reformulated as follows.

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

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)<sub>1</sub> and (5.2.10)<sub>2</sub> 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 elaborate 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  $\sigma$  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 equibiaxial 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)<sub>1</sub> and (5.2.10)<sub>2</sub> is trivially satisfied. The equilibrium of forces in the transverse direction (5.2.10)<sub>3</sub> then reduces to the classical Laplace equation for membranes,

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

**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  $\delta W$  with respect to the individual unknowns.

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

The internal and external virtual work  $\delta W^{\text{int}}$  and  $\delta W^{\text{ext}}$  can then be specified as follows.

$$\begin{aligned} \delta W^{\text{int}} &= \int_A \int_{-h/2}^{+h/2} \sigma_{xx} \delta \varepsilon_{xx} + 2\sigma_{xy} \delta \varepsilon_{xy} + \sigma_{yy} \delta \varepsilon_{yy} \quad dA \\ &= \int_A n_{xx} \delta \varepsilon_{xx}^{\text{con}} + 2n_{xy} \delta \varepsilon_{xy}^{\text{con}} + n_{yy} \delta \varepsilon_{yy}^{\text{con}} \quad dz dA \\ \delta W^{\text{ext}} &= \int_A p \delta w \quad dA \end{aligned}$$

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  $\sigma_{xy}$  are energetically conjugate to the shear strains  $\varepsilon_{xy}$  or that the normal stress resultants  $n_{xx}$  are conjugate to the corresponding strains  $\varepsilon_{xx}^{\text{con}}$  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  $\delta u$ ,  $\delta v$  and  $\delta w$ . 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.

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  $w_{,xx} + w_{,yy} = \Delta w$ .

$$p_z = -n \Delta w \quad \text{with} \quad n \dots \text{surface tension} \quad (5.2.12)$$

Recall that the negative second derivative of the transverse displacement  $w$  takes the interpretation of the curvature  $\kappa$ . 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.

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

For equal radii  $r_x = r_y = r$ , equation (5.2.13) reduces to the classical membrane equation for spheres  $p_z = -n \Delta w = n [1/r_x + 1/r_y] = 2n/r$  similar to the one derived for soap bubbles  $\Delta p = 2\gamma/r$  in the motivation (5.1.11). Recall that  $\gamma$  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.

## 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 5.1.3, 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  $\Delta L$  scaled by the original length  $L$ , we could thus introduce a two dimensional area strain as the area change  $\Delta A$  scaled by the original area  $A$ .

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

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)<sub>1</sub>, and similarly (5.2.7)<sub>2</sub>, can obviously be further simplified. With the help of  $\varepsilon_{xx} = \varepsilon_{yy} = \varepsilon$  with  $\varepsilon = [\Delta A / A] / 2$ , equation (5.2.7)<sub>1</sub> can then be rewritten in the following form.

$$n = \frac{Eh}{1 - \nu^2} [\varepsilon_{xx} + \nu \varepsilon_{yy}] = \frac{Eh}{1 - \nu^2} [1 + \nu] \varepsilon = \frac{Eh}{2[1 - \nu]} \frac{\Delta A}{A} \quad (5.2.15)$$

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

$$n = K_A \frac{\Delta A}{A} \quad \text{with} \quad K_A = \frac{Eh}{2[1 - \nu]} \quad \dots \text{ area expansion modulus} \quad (5.2.16)$$

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.