Part IV

Strong-Coupling Theory for Membranes

Fluctuating Membranes

We investigate the violent thermal out-of-plane fluctuations of a stack of membranes between two parallel walls and calculate the pressure p that they exert upon these walls. In equilibrium with a reservoir of molecules, tension vanishes and the shape is governed by extrinsic curvature energy. The differential geometric background of this model is discussed in this chapter. The pressure law was found by Helfrich [50] and reads for N membranes

$$p_N = \frac{2N}{N+1} \alpha_N \frac{(k_B T)^2}{\kappa a^3},\tag{10.1}$$

where L=(N+1)a is the distance between the walls, and κ the bending stiffness. The universal pressure constants α_N are not calculable exactly. For a single membrane, α_1 was roughly estimated by theoretical [50] and Monte Carlo methods [85–88]. By a strong-coupling calculation [48,89], presented in Chapter 11, we find a value, which lies well within the error bounds of the latest Monte Carlo estimate [88]. In a different strong-coupling approach [49], we also calculate the pressure constants for a stack of membranes in Chapter 12. Our results are in excellent agreement with all available Monte Carlo estimates [86–88] for N=1,3,5. By an extrapolation to $N\to\infty$ we determine the pressure constant α_∞ for infinitely many membranes.

10.1 Introduction

Membranes formed by lipid bilayers are important biophysical systems occurring as boundaries of organells and vesicles. Their tension vanishes due to the lateral motion of molecules within the membrane. The flexibility of fluid membranes leads to an amazing variety of shapes of vesicles, which are large encapsulating bags with a size of up to $100\,\mu\mathrm{m}$. Changes in temperature or osmotic conditions, e.g. the concentration of ions or molecules in the membrane, induce shape transformations of vesicles. Figure 10.1 shows schematically the process of a budding transition, where the increase of temperature entails more violent membrane fluctuations, which lead to an uncoupling of a daughter vesicle, which can move independently of the mother vesicle (see Ref. [90] for microscopic photographs of a budding transition). Eventually, it can dock to another vesicle by an inverse process. Thus, shape transformations of membranes are necessary to make possible matter and energy transport between cells and organells in a complex biological system.

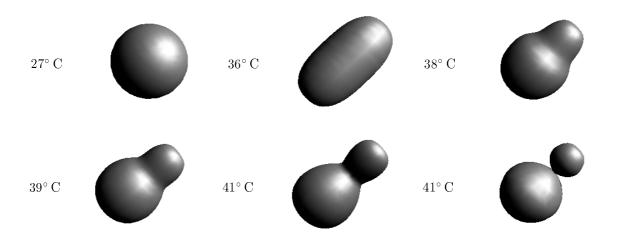


FIGURE 10.1: 3D pictures of a budding transition of a vesicle by increasing the temperature. The surfaces were modeled from microscopic photographs given in Ref. [90].

10.2 Differential Geometry for Curves and Surfaces

The geometry of the vesicle shapes can only be described locally, which means that it is necessary to apply differential geometry for modeling membranes. In what follows, we briefly review the main aspects of differential geometry.

10.2.1 Local Curvature of Curves

Topologically one-dimensional geometric objects appear in physics in different forms, for example as particle paths, polymers, strings, or vortex lines. They have in common that it is sufficient to identify each point of such an curved object by a vector in the surrounding embedding space, which depends on only one parameter. The parameter choice depends usually on the appropriate problem.

We want to describe a curve C in three-dimensional embedding space and we parameterize it with the help of the parameter s, which we choose to lie in the interval $0 \le s \le 1$. As Fig. 10.2 shows, a certain point of the curve C is given by the contravariant vector $\mathbf{r}(s) = (x^i(s)) = (x^1(s), x^2(s), x^3(s))^T$. The components of the tangent vector $\mathbf{t}(s) = (t^i(s))$ at the point $x^i(s)$ are given by the differential quotient

$$t^{i}(s) = \lim_{\Delta s \to 0} \frac{x^{i}(s + \Delta s) - x^{i}(s)}{\Delta s} = \frac{dx^{i}(s)}{ds}.$$
 (10.2)

The length of an infinitesimal piece of the curve is given by

$$ds^{2} = [dx^{1}(s)]^{2} + [dx^{2}(s)]^{2} + [dx^{3}(s)]^{2} = \eta_{ij}dx^{i}(s)dx^{j}(s),$$
(10.3)

where equal indices are summed over. The identity matrix $(\eta_{ij}) = \text{diag}(1,1,1)$ is used to transform covariant vectors to contravariant ones: $dx_i = \eta_{ij} dx^j$. The tangent vector $t^i(s)$ is already normalized. To show this, we perform the scalar product

$$|\mathbf{t}(s)| = \sqrt{\mathbf{t}(s) \cdot \mathbf{t}(s)} = \sqrt{t_i(s)t^i(s)} = \sqrt{\eta_{ij}t^it^j} = \sqrt{\eta_{ij}\frac{dx^i(s)}{ds}\frac{dx^j(s)}{ds}} = 1,$$
 (10.4)

where we have used relation (10.3) in the last step. Now we determine the vectors transversal to $\mathbf{t}(s)$. We know that the number of transversal vectors is D-1, where D is the dimension of the embedding space. Thus, we expect in three dimensions two independent vectors, which are orthogonal to $\mathbf{t}(s)$.

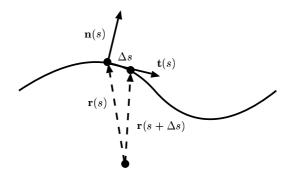


FIGURE 10.2: Curve C, parameterized by s, which we conventionally suppose to lie in the interval $0 \le s \le 1$.

One is easily determined by differentiating the scalar product $t^{i}(s)t_{i}(s) = 1$ with respect to s:

$$\frac{d}{ds}t^{i}(s)t_{i}(s) = 0 \implies \frac{dt^{i}(s)}{ds} \perp t^{i}(s). \tag{10.5}$$

The vector $dt^{i}(s)/ds$ is obviously orthogonal to $t^{i}(s)$, and we define the normal vector $\mathbf{n}(s)$ as

$$n^{i}(s) = k^{-1}(s) \frac{dt^{i}(s)}{ds} = k^{-1}(s) \frac{d^{2}x^{i}(s)}{ds^{2}}, \qquad k(s) = \left| \frac{\sqrt{\eta_{ij}dt^{i}dt^{j}}}{ds} \right|.$$
 (10.6)

The proportionality constant k(s) is called the *curvature* of the curve at the point s and the components of the curvature vector $\mathbf{k}(s)$ are given by

$$k^{i}(s) = k(s)n^{i}(s),$$
 (10.7)

thus pointing into the same direction as the normal vector. The larger its length k(s), the more curved is the curve at s. The other transversal vector is called binormal vector $\mathbf{b}(s)$ and is orthogonal to $\mathbf{n}(s)$ and $\mathbf{t}(s)$:

$$b^{i}(s) = b^{-1}(s) \frac{dn^{i}(s)}{ds}, (10.8)$$

where the length $b(s) = |dn^i(s)/ds|$ describes the strength of torsion of the curve. The more normals at neighboring points of the curve differ, the stronger is the torsion of the curve in this region.

An important quantity of a stringy object is its tension σ . This material constant is identical with the strength of the force, which acts in the opposite direction of an elongation to bring back a deformed string into its equilibrium state. In order to describe quantitatively the consequences of elongating a string with tension, we consider Fig. 10.3. The lower line represents a piece of an undeformed string. Dragging it at the position s by an amount $|\Delta \mathbf{u}(s)|$ from $\mathbf{r}(s)$ to $\mathbf{r}(s) + \Delta \mathbf{u}(s)$, where we keep the ends fixed, the overall length of this piece of string obviously increases. As we are only interested in elongations, which cause *normal* forces (which means that the force vector is parallel to the normal vector $\mathbf{n}(s)$), the displacement vector $\Delta \mathbf{u}(s)$ is parallel to the normal vector $\mathbf{n}(s)$. This ensures that the mechanical stress is the same for both legs of the triangle. It also allows us to choose one of the two rectangular triangles for the following considerations, since the ratio of the hypotenuse to the appropriate horizontal sides is identical for both. With these suppositions, we read off from Fig. 10.3:

$$\Delta s'^{2}(s) = \Delta \mathbf{u}^{2}(s)/l_{0}^{2} + \Delta s^{2}, \qquad (10.9)$$

where we have rescaled the elongation with respect to the length of the undeformed string:

$$l_0 = l_0 \int_0^1 ds. (10.10)$$

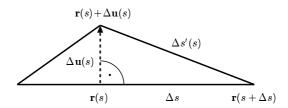


FIGURE 10.3: Change of scale $(\Delta s \to \Delta s')$ by elongating a string with tension.

Going over to infinitesimal quantities, this relation gives us the measure of the deformed string

$$ds'(s) = ds\sqrt{1 + \left[\frac{d\mathbf{u}(s)}{l_0 ds}\right]^2}.$$
 (10.11)

The length of the deformed string can thus be written as

$$l = l_0 \int_0^1 ds \sqrt{1 + \left[\frac{d\mathbf{u}(s)}{l_0 ds}\right]^2}$$
 (10.12)

in comparison to the undeformed one (10.10). Then, the energy E_{σ} of a deformed string due to its tension is equal to the mechanical work A_{σ} , which is necessary to change the length of the string from l_0 to l:

$$E_{\sigma} \equiv A_{\sigma} = \sigma(l - l_{0}) = \sigma l_{0} \left\{ \int_{0}^{1} ds \sqrt{1 + \left[\frac{d\mathbf{u}(s)}{l_{0}ds}\right]^{2}} - 1 \right\}$$

$$\approx l_{0} \frac{\sigma}{2} \int_{0}^{1} ds \left[\frac{d\mathbf{u}(s)}{l_{0}ds}\right]^{2} = l_{0} \frac{\sigma}{2} \int_{0}^{1} ds \, \eta_{ij} \frac{du^{i}(s)}{l_{0}ds} \frac{du^{j}(s)}{l_{0}ds} = \frac{\sigma}{2} \int_{0}^{l_{0}} ds \, \eta_{ij} \frac{du^{i}(s)}{ds} \frac{du^{j}(s)}{ds}, (10.13)$$

where we have performed the scaling $s \to l_0 s$ in the last step. The approximate expression (10.13) is valid in the adiabatic limit of small elongations $|\mathbf{u}(\mathbf{s})|$.

If the line-like object can be deformed without changing its overall length, such as in the case of stiff polymers, another material property becomes important: the *elasticity* or *bending rigidity* κ . The degree of elastic deformation strongly depends on the curvature k(s) at any position s. Thus, the bending or curvature energy is given by the curve integral

$$E_C = \frac{\kappa}{2} \int_0^1 ds \, k^2(s) = \frac{\kappa}{2} \int_0^1 ds \, \eta_{ij} \frac{dt^i(s)}{ds} \frac{dt^j(s)}{ds} = \frac{\kappa}{2} \int_0^1 ds \, \eta_{ij} \frac{d^2 x^i(s)}{ds^2} \frac{d^2 x^j(s)}{ds^2}, \tag{10.14}$$

where we have used the relation (10.6) between the curvature k(s) and the difference of neighboring tangential vectors $\mathbf{t}(s)$ and $\mathbf{t}(s+ds)$ per length element ds and, in the last expression, the definition (10.2) of the tangential vector.

10.2.2 Local Curvature of Surfaces

In complete analogy to line-like objects in the preceding section, we investigate now topologically twodimensional surfaces like membranes in three-dimensional embedding space. A point of a surface Smay be identified by the position vector $\mathbf{r}(u^1,u^2)=x^i(u^\mu)$ with $\mu=1,2$, where u^1 and u^2 are suitable coordinate lines and serve as a parameterization of the surface (see Fig. 10.4). We use Latin indices for components of vectors in the embedding space, while Greek indices denote components of the intrinsic coordinates of the surface. The coordinate lines u^1 , u^2 span a mesh and cover the surface completely. At the moment, the choice of these coordinates is arbitrary. Tangent vectors $\mathbf{t}_{\mu}(u^{\mu})$ point along these coordinate lines and are introduced by

$$t^{i}_{\mu}(u^{\mu}) = \frac{\partial \mathbf{r}(u^{\mu})}{\partial u^{\mu}} = \frac{\partial x^{i}(u^{\mu})}{\partial u^{\mu}}, \qquad \mu = 1, 2.$$
(10.15)

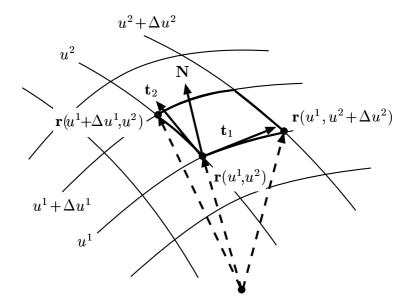


FIGURE 10.4: Surface S, which is parameterized by intrinsic coordinates u^1 and u^2 .

The surface normal vector $\mathbf{N}(u^{\mu})$ is then given by the cross product of the tangent vectors:

$$\mathbf{N}(u^{\mu}) = \frac{\mathbf{t}_1(u^{\mu}) \times \mathbf{t}_2(u^{\mu})}{|\mathbf{t}_1(u^{\mu}) \times \mathbf{t}_2(u^{\mu})|},\tag{10.16}$$

or, written in components,

$$N^{i}(u^{\mu}) = \frac{\varepsilon_{ijk}t_{1}^{j}t_{2}^{k}}{\sqrt{\varepsilon_{ijk}t_{1}^{j}t_{2}^{k}\varepsilon^{ilm}t_{1,l}t_{2,m}}},$$
(10.17)

where ε_{ijk} is the totally antisymmetric tensor

$$\varepsilon_{ijk} = \begin{cases} +1 & \{ijk\} = \{123\} \text{ or cyclic,} \\ -1 & \{ijk\} = \{213\} \text{ or cyclic,} \\ 0 & \text{else.} \end{cases}$$
 (10.18)

An infinitesimal square length element on the surface is obviously introduced by

$$ds^{2} = [dx^{1}(u^{1}, u^{2})]^{2} + [dx^{2}(u^{1}, u^{2})]^{2} + [dx^{3}(u^{1}, u^{2})]^{2} = dx_{i}(u^{\mu})dx^{i}(u^{\mu}).$$
(10.19)

Substituting the total differentials by

$$dx^{i}(u^{\mu}) = \frac{\partial x^{i}(u^{\mu})}{\partial u^{\mu}} du^{\mu} = t^{i}_{\mu} du^{\mu}, \tag{10.20}$$

Eq. (10.19) can be rewritten as the first fundamental form

$$ds^2 = g_{\mu\nu} du^{\mu} du^{\nu}, \tag{10.21}$$

with the metric

$$g_{\mu\nu} = t^{i}_{\mu} t_{i,\nu} = \frac{\partial x^{i}}{\partial u^{\mu}} \frac{\partial x_{i}}{\partial u^{\nu}} = \begin{pmatrix} \left(\frac{\partial \mathbf{r}}{\partial u^{1}}\right)^{2} & \frac{\partial \mathbf{r}}{\partial u^{1}} \cdot \frac{\partial \mathbf{r}}{\partial u^{2}} \\ \frac{\partial \mathbf{r}}{\partial u^{1}} \cdot \frac{\partial \mathbf{r}}{\partial u^{2}} & \left(\frac{\partial \mathbf{r}}{\partial u^{2}}\right)^{2} \end{pmatrix}_{\mu\nu} . \tag{10.22}$$

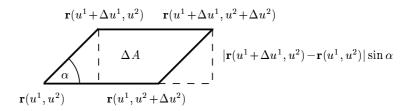


Figure 10.5: Planar projection of a surface element.

The metric is a symmetric tensor, which uniquely characterizes the shape of the surface. It is diagonal, if the tangent vectors are perpendicular to each other, which happens to be for orthogonal coordinates.

As the explicit calculation shows, the determinant of the metric is obtained by the square absolute value of the cross product of the tangent vectors

$$g \equiv \det g_{\mu\nu} = |\mathbf{t}_1 \times \mathbf{t}_2|^2 = \varepsilon_{ijk} t_1^i t_2^j \varepsilon^{ilm} t_{1,l} t_{2,m}. \tag{10.23}$$

In Fig. 10.4, we have highlighted a surface element and we calculate its area as follows. For an infinitesimal small surface element, which is enclosed by the coordinates (u^1, u^2) , $(u^1 + du^1, u^2)$, $(u^1, u^2 + du^2)$, and $(u^1 + du^1, u^2 + du^2)$, the surface element and its planar projection are identical and we have to calculate the area of a parallelogram as shown in Fig. 10.5. Since the area of a parallelogram is identical to that of a rectangle with one shortened side, we obtain

$$dA = \left| \mathbf{r}(u^{1}, u^{2} + du^{2}) - \mathbf{r}(u^{1}, u^{2}) \right| \left| \mathbf{r}(u^{1} + du^{1}, u^{2}) - \mathbf{r}(u^{1}, u^{2}) \right| \sin \alpha = \left| \frac{\partial \mathbf{r}}{\partial u^{1}} \right| du^{1} \left| \frac{\partial \mathbf{r}}{\partial u^{2}} \right| du^{2} \sin \alpha$$

$$= \left| \frac{\partial \mathbf{r}}{\partial u^{1}} \times \frac{\partial \mathbf{r}}{\partial u^{2}} \right| du^{1} du^{2} = \left| \mathbf{t}_{1} \times \mathbf{t}_{2} \right| du^{1} du^{2} = \sqrt{g} du^{1} du^{2}, \tag{10.24}$$

where we have used relation (10.23) in the last step. The overall area of the surface S is thus given by the parameter integral

$$A_S = \int_S dA = \int du^1 du^2 \sqrt{g}.$$
 (10.25)

In the following we investigate the local curvature of a surface. For the one-dimensional curve, we have defined the curvature k as the proportionality constant between the normal vector $\mathbf{n}(s)$ at a position s and the derivative with respect to s of the tangent vector $\mathbf{t}(s)$ in Eq. (10.6). A surface possesses an infinite number of tangent vectors, since the two independent ones (10.15), which point along the coordinate lines u^1 and u^2 span a tangential plane, in which all possible tangential vectors at the point $\mathbf{r}(u^1, u^2)$ reside. Thus there are infinitely many curves on the surface, which touch the point $\mathbf{r}(u^1, u^2)$ and have different curvatures in this point. Thus we need a new definition for what we want to call the curvature of a surface. Let $\mathbf{r}(s)$ be a point of a curve C with curvature k(s) on the surface S, where the same point is parameterized by $\mathbf{r}(u^1, u^2)$. Then, $\mathbf{n}(s) = d^2\mathbf{r}(s)/kds^2$ denotes the normal vector of the curve and $\mathbf{N}(u^1, u^2)$ the surface normal at this point. We define the normal curvature k_n at this point by

$$k_n \equiv N_i \frac{d^2 x^i}{ds^2} = k_n^i N_i = k N_i n^i = k \cos \Theta, \qquad (10.26)$$

where we have used the definition (10.7) for the curvature vector. The angle between \mathbf{n} and \mathbf{N} at a certain point is denoted by Θ .

If we consider the surface coordinates as functions of the curve parameter, $u^{\mu} = u^{\mu}(s)$, we rewrite the tangent and the normal vector of the curve at s as

$$t^{i}(u^{\mu}(s)) = \frac{dx^{i}(u^{\mu}(s))}{ds} = \frac{\partial x^{i}}{\partial u^{\mu}} \frac{du^{\mu}}{ds},$$

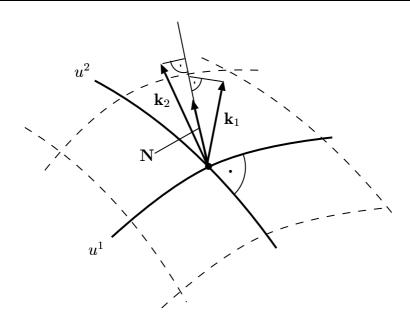


Figure 10.6: Definition of main curvature lines.

$$n^{i}(u^{\mu}(s)) = k^{-1} \frac{d^{2}x^{i}(u^{\mu}(s))}{ds^{2}} = k^{-1} \left(\frac{\partial^{2}x^{i}}{\partial u^{\mu}\partial u^{\nu}} \frac{du^{\mu}}{ds} \frac{du^{\nu}}{ds} + \frac{\partial x^{i}}{\partial u^{\mu}} \frac{d^{2}u^{\mu}}{ds^{2}} \right). \tag{10.27}$$

Multiplying the second relation by N_i and acknowledging that the second term vanishes due to $\mathbf{N}(u^{\mu}) \perp \partial x^i(u^{\mu})/\partial u^{\mu} = \mathbf{t}_{\mu}(u^{\mu})$, we obtain

$$N_i \frac{d^2 x^i}{ds^2} \equiv k_n = h_{\mu\nu} \frac{du^{\mu}}{ds} \frac{du^{\nu}}{ds},$$
 (10.28)

where we have introduced the curvature tensor

$$h_{\mu\nu} = N_i \frac{\partial^2 x^i}{\partial u^\mu \partial u^\nu} = N_i \frac{\partial}{\partial u^\mu} t^i_\nu. \tag{10.29}$$

Now we differentiate the relation $N_i t^i_{\mu} = 0$ with respect to u^{ν} , yielding

$$N_{i} \frac{\partial^{2} x^{i}}{\partial u^{\mu} \partial u^{\nu}} \equiv h_{\mu\nu} = -\frac{\partial x^{i}}{\partial u^{\mu}} \frac{\partial N_{i}}{\partial u^{\nu}} = -\frac{dx^{i}}{du^{\mu}} \frac{dN_{i}}{du^{\nu}}, \tag{10.30}$$

where we could use total differentials since $du^{\mu}/du^{\nu} = \delta^{\mu}_{\nu}$. Expression (10.30) exhibits the second fundamental form [91,92]

$$-dx^i dN_i = h_{\mu\nu} du^\mu du^\nu. \tag{10.31}$$

Writing the right equation of (10.28) as $k_n ds^2 = h_{\mu\nu} du^{\mu} du^{\nu}$ and substituting ds^2 by the first fundamental form (10.21), we obtain the important expression

$$k_n = \frac{h_{\mu\nu} du^{\mu} du^{\nu}}{g_{\kappa\rho} du^{\kappa} du^{\rho}},\tag{10.32}$$

which relates the normal curvature with the metric and the curvature tensor of the surface. As stated above, there is an infinite number of curves touching a certain point (u^1, u^2) of the surface and having a curvature vector \mathbf{k} at this point. In order to find a measure for the curvature of the surface in this point, we determine the curves with maximum and minimum curvature. This is done by extremizing

the relation (10.32). Introducing abbreviations $l^{\mu} = du^{\mu}$ and $\alpha_{\mu\nu} = h_{\mu\nu} - k_n g_{\mu\nu} (=0)$, Eq. (10.32) can be written as

$$a_{\mu\nu}l^{\mu}l^{\nu} = 0. {(10.33)}$$

Differentiating this equation with respect to l^{κ} yields

$$\alpha_{\mu\kappa}l^{\mu} = 0, \tag{10.34}$$

where we have utilized the symmetry of $\alpha_{\mu\nu}$. Re-expanding the abbreviations, multiplying by $g^{\nu\kappa}$, and substituting $g_{\mu}^{\nu}du^{\mu}=du^{\nu}$ leads to

$$h_{\mu}{}^{\nu}du^{\mu} - k_n du^{\nu} = 0. {(10.35)}$$

This is a set of two equations ($\nu = 1, 2$), which constitutes an eigenvalue equation:

$$\begin{pmatrix} h_1^1 & h_2^1 \\ h_1^2 & h_2^2 \end{pmatrix} \begin{pmatrix} du^1 \\ du^2 \end{pmatrix} = k_n \begin{pmatrix} du^1 \\ du^2 \end{pmatrix}. \tag{10.36}$$

As usual, the eigenvalues k_n are obtained from the vanishing determinant

$$\begin{vmatrix} h_1^1 - k_n & h_2^1 \\ h_1^2 & h_2^2 - k_n \end{vmatrix} = 0. ag{10.37}$$

Solving the quadratic equation $({h_1}^1 - k_n)({h_2}^2 - k_n) - {h_1}^2 {h_2}^1 = 0$ yields the two eigenvalues

$$k_{1,2} = \frac{1}{2} h_{\mu}^{\ \mu} \pm \sqrt{\frac{1}{4} (h_{\mu}^{\ \mu})^2 - \det h_{\mu}^{\ \nu}}.$$
 (10.38)

Defining the Gaussian curvature

$$K = k_1 k_2 = \det h_{\mu}{}^{\nu} \tag{10.39}$$

and the mean curvature

$$H = \frac{1}{2}(k_1 + k_2) = \frac{1}{2}h_{\mu}{}^{\mu} = \frac{1}{2}\operatorname{Tr}h_{\mu}{}^{\nu}, \tag{10.40}$$

Eq. (10.38) can be expressed by

$$k_{1,2} = H \pm \sqrt{H^2 - K}. ag{10.41}$$

These solutions are called *main curvatures* of the surface. The corresponding curves with curvature vectors $\mathbf{k}_{1,2}$ satisfying $k_{1,2} = \mathbf{k}_{1,2} \cdot \mathbf{N}_{1,2}$ at the point (u^1, u^2) are denoted as *main curvature lines* on the surface. Their tangent vectors $\mathbf{t}_{1,2}$ are orthogonal to another. Thus the eigenvectors of h_{μ}^{ν} form a local orthonormal coordinate system at this point of the surface as shown in Fig. 10.6.

Following Helfrich [93], the definitions of mean and Gaussian curvature are used to write the bending energy as an expansion in the curvature. The lowest-order contribution is then given by

$$E_C = \int_S dA \left(2\kappa H^2 + \kappa_G K \right), \tag{10.42}$$

which is quadratic in the main curvatures k_1 and k_2 . The elastic constants κ and κ_G are denoted as bending rigidity and Gaussian bending rigidity, respectively, and have the dimension energy. The second term in the parentheses in Eq. (10.42) is the topological invariant $4\pi\kappa_G(1-G)$ as follows from the global Gauss-Bonnet theorem [91]. The number G counts the handles of the surface and is called the *genus* of the surface. Since we assume the surface topology to be fixed, this constant energy

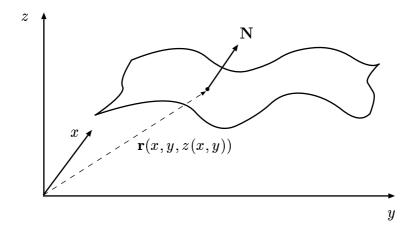


FIGURE 10.7: Out-of-plane deformations of an almost planar surface are described with the Monge representation, where Cartesian coordinates are used. The coordinates x and y span the parameter space, and only z = z(x, y) depends on the parameterization.

contribution can be omitted, leaving us with an curvature energy, which only depends on the mean curvature. Thus, Eq. (10.42) is written as

$$E_C = \frac{\kappa}{2} \int d^2 u \, \sqrt{g} (h_\mu^{\ \mu})^2. \tag{10.43}$$

This is the classical curvature model for bilayer membranes and is valid for curvature radii much larger than the membrane thickness (4nm) [94]. The membrane equilibrium shape is then determined by minimizing the curvature energy.

A frequently used special parameterization of an almost planar surface is the *Monge representation*. As shown in Fig. 10.7, it is characterized by the following choice of parameters:

$$x(u^1, u^2) = u^1, \quad y(u^1, u^2) = u^2, \quad z(u^1, u^2) = z(x, y).$$
 (10.44)

In this simple case, only deformations orthogonal to the xy-plane can be described. Although this is a strong restriction for the investigation of the influence of thermal fluctuations, which have no preferred direction upon a membrane, we will use an even more simplified form of this representation throughout the subsequent calculations. In Monge representation, the tangent vectors pointing into the direction of the x and y unit vectors read

$$\mathbf{t}_1 = (1, 0, \partial_x z)^T, \qquad \mathbf{t}_2 = (0, 1, \partial_y z)^T.$$
 (10.45)

The cross product of these tangent vectors yields the surface normal vector

$$\mathbf{N} = \frac{1}{\sqrt{1 + (\partial_x z)^2 + (\partial_y z)^2}} (-\partial_x z, -\partial_y z, 1)^T,$$
(10.46)

which we have normalized according to Eq. (10.16). The covariant and contravariant metrics are given by

$$g_{\mu\nu} = \begin{pmatrix} 1 + (\partial_x z)^2 & \partial_x z \partial_y z \\ \partial_x z \partial_y z & 1 + (\partial_y z)^2 \end{pmatrix}_{\mu\nu}, \quad g^{\mu\nu} = \frac{1}{g} \begin{pmatrix} 1 + (\partial_y z)^2 & -\partial_x z \partial_y z \\ -\partial_x z \partial_y z & 1 + (\partial_x z)^2 \end{pmatrix}^{\mu\nu}, \tag{10.47}$$

where g is the determinant of the covariant metric

$$g = \det g_{\mu\nu} = 1 + (\partial_x z)^2 + (\partial_y z)^2.$$
 (10.48)

For the curvature tensor we obtain

$$h_{\mu\nu} = \frac{1}{\sqrt{g}} \begin{pmatrix} \partial_x^2 z & \partial_x \partial_y z \\ \partial_x \partial_y z & \partial_y^2 z \end{pmatrix}_{\mu\nu}, \tag{10.49}$$

or in the form we need it for calculating the mean and the Gaussian curvature:

$$h_{\mu}{}^{\nu} = g^{\rho\nu}h_{\mu\rho} = \frac{1}{g^{3/2}} \left(\begin{bmatrix} 1 + (\partial_{y}z)^{2} \end{bmatrix} \partial_{x}^{2}z - \partial_{x}z\partial_{y}z\partial_{x}\partial_{y}z & \left[1 + (\partial_{y}z)^{2} \right] \partial_{x}\partial_{y}z - \partial_{x}z\partial_{y}z\partial_{y}^{2}z \\ \left[1 + (\partial_{x}z)^{2} \right] \partial_{x}\partial_{y}z - \partial_{x}z\partial_{y}z\partial_{x}^{2}z & \left[1 + (\partial_{x}z)^{2} \right] \partial_{y}^{2}z - \partial_{x}z\partial_{y}z\partial_{x}\partial_{y}z \end{pmatrix}_{\mu}^{\nu}.$$

$$(10.50)$$

The mean curvature (10.40) of a Monge parameterized surface in the point (x, y, z(x, y)) is half the trace of the tensor (10.50). Thus it is given by

$$H = \frac{1}{2} \frac{1}{\left[1 + (\partial_x z)^2 + (\partial_y z)^2\right]^{3/2}} \left\{ \left[1 + (\partial_x z)^2\right] \partial_y^2 z + \left[1 + (\partial_y z)^2\right] \partial_x^2 z - 2\partial_x z \partial_y z \partial_x \partial_y z \right\}$$
(10.51)

$$\approx \frac{1}{2} \Delta z \left[1 + \mathcal{O}\left((\nabla z)^2\right)\right],$$
(10.52)

where Δ is the Laplace operator $\partial_x^2 + \partial_y^2$ and ∇ the gradient (∂_x, ∂_y) in two dimensions. The Gaussian curvature (10.39) is obtained from the determinant of $h_{\mu}^{\ \nu}$:

$$K = \frac{1}{[1 + (\partial_x z)^2 + (\partial_y z)^2]^2} \left[\partial_x^2 z \partial_y^2 z - (\partial_x \partial_y z)^2 \right].$$
 (10.53)

The simplest form of the curvature energy (10.43) for a membrane, which can be parameterized with the Monge representation is given by the expression

$$E_C = \frac{\kappa}{2} \int dx dy \left[\Delta z(x, y) \right]^2, \tag{10.54}$$

which we will use in the sequel to describe thermal fluctuations of membranes between walls.