Mechanics of cell membranes
Cell membranes

Eukaryotic cells

- Plasma membrane
- Rough endoplasmic reticulum
- Nuclear envelope
- Nuclear pore complex
- Secretory complex
- Ribosome

E. Coli

- Inner membrane
- Outer membrane
- Cell wall
- Lipopolysaccharide

Figure 11.2: Key examples of membranes in biological systems. Eukaryotic cells, such as this fibroblast, are rife with many specialized membranes. The plasma membrane is a single phospholipid bilayer riddled with membrane proteins. The rough endoplasmic reticulum, also a single bilayer, is the site of synthesis of membrane-bound and secreted proteins. The ribosomes synthesizing these proteins are intimately associated with a transport apparatus in the endoplasmic reticulum membrane. The nuclear envelope consists of two phospholipid bilayers with a thin space between them. This nuclear envelope is perforated by nuclear pores that permit transport of materials from the cytoplasm to the nucleus and back. Bacterial cells rarely have internal membranous organelles, but may have very complex external membranes. For *E. coli*, these cells consist of two bilayers—an inner membrane and an outer membrane—separated by a rigid cell wall. The outer leaflet of the outer membrane is largely composed of an unusual molecule called lipopolysaccharide, rather than of phospholipids.

The starting point for thinking about membrane organization is that its shape is dictated by the physical properties of the two layers of phospholipids that make up the lipid bilayer. This lipid bilayer is two lipid molecules thick, riddled with a dazzling array of membrane proteins. Figure 11.4 shows several generations of models for cell membrane structure. The fluid mosaic model of Singer and Nicolson (1972) envisioned a lipid bilayer as a two-dimensional fluid in which embedded membrane proteins were able to easily move laterally in the plane of the membrane, but could not move out of the plane. Later versions of this model acknowledged the fact that there is a great deal of structural heterogeneity within the lipid layer. For example, membranes containing multiple types of lipids that tend to mix nonideally can have a complex organization in which structurally compatible lipids assemble into microdomains. Along similar lines, membrane proteins can generate local order in the lipids that surround them and lipid domains can strongly influence protein organization. In living cells, the membrane does not exist in isolated two-dimensional splendor—long branched chains of carbohydrates protrude into the third dimension and structural elements within the cell such as the cytoskeleton interact extensively with membrane components to shape the membrane surface.
Cell membrane

- Lipids

- Microfilaments of cytoskeleton

- Cholesterol

- Peripheral proteins

- Integral protein

- Glycosylation proteins

- Carbohydrate

- Fibers of extracellular matrix (ECM)

- Glycolipid

- EXTRACELLULAR SIDE OF MEMBRANE

- CYTOPLASMIC SIDE OF MEMBRANE

- 5nm
Lipid membrane behaves like fluid

Lipid molecules and proteins can move around! Flipping of lipid molecules between the layer is unlikely.
Membrane attached spectrin network provides solid-like behavior

Spectrin network provides structural stability for cells

Alberts et al., Molecular Biology of the Cell
Lipid membrane

In water solution lipid molecules spontaneously aggregate to prevent undesirable interactions between water and hydrophobic tails.
Flat lipid bilayers vs lipid vesicles

Flat bilayer

- Energy cost on the edge between lipid tails and water molecules:
  \[ E \propto L \]

Vesicle

- Bending energy cost:
  \[ E \propto \text{const} \]

Large vesicles have lower energy cost than flat bilayers!
Shape of lipid molecules can induce spontaneous curvature of structures

bilayer

micelle

H-II phase

inverted micelle

R. Phillips et al., Physical Biology of the Cell
Membrane proteins can induce spontaneous curvature

binding of rigid curved proteins

interactions between coat proteins bend the membrane

insertions of protein parts between lipid molecules on one side of the layer

Membrane deformations

Membrane Stretching Geometry Can Be Described by a Simple Area Function

The top image in Figure 11.13 illustrates the first class of deformations we will consider, namely, when the area of the patch of membrane is increased by an amount $\Delta a$. Just as the parameter $\Delta L$ was introduced in Section 5.4.1 (p. 216) to characterize the homogeneous stretching of a beam, the parameter $\Delta a$ will provide a simple way to characterize the change in the area of a membrane. To be explicit about the fact that the amount of stretch could in principle vary at different points on the membrane, we introduce a function $\Delta a(x, y)$ that tells us how the area of the patch of membrane at position $(x, y)$ is changed upon deformation.

Membrane Bending Geometry Can Be Described by a Simple Height Function, $h(x, y)$

To consider bending deformations, we treat surfaces as shown in Figure 11.14. We lay down an $x$–$y$ grid on the reference plane and we
Energy cost for stretching and shearing

**undeformed square patch**

\[ A = L^2 \]

**isotropic deformation**

\[ E \approx \frac{B}{2} \left( \frac{\Delta A}{A} \right)^2 \approx \frac{B}{2} \left( \frac{2\Delta L}{L} \right)^2 \]

**bulk modulus**

\[ B \sim 0.2\text{N/m} \]

(lipid bilayer)

**shear deformation**

\[ E = \frac{\mu \theta^2}{2} \]

**shear modulus**

\[ \mu \sim 10^{-5}\text{N/m} \]

(spectrin network)

**anisotropic stretching**

\[ E \approx \frac{B}{2} \left( \lambda_1 + \lambda_2 \right)^2 + \frac{\mu}{2} \left( \lambda_1 - \lambda_2 \right)^2 \]

\[ \lambda_1, \lambda_2 \ll 1 \]

(shearing can be interpreted as anisotropic stretching)