Keywords: Bilayer membranes; Dynamics; Hydrodynamic theory; Membrane-solution systems

1. Introduction

Recently, we adopted the dynamic theory of uniaxial liquid crystals (Ericksen-Leslie's theory) to a two-dimensional thin film so as to make the theory applicable for the study of hydrodynamic behaviour of lipid bilayer membranes [1]. The membrane was considered to be isolated from spatial surroundings, which is evidently impossible to realize in experiments. In aqueous solutions lipid membranes tend to close and form vesicles, due to the spontaneous curvature, maintaining a difference of pressure between the interior and exterior liquids. Under the action of chemical or electrochemical fields, solutes of the adjacent solutions may migrate across the membrane, inducing oscillations of the membrane potential [2-4], whereas under the action of physical fields, shape or structure of the membrane may change and may keep varying for a long duration [5-8]. Such mass or momentum exchange between the membrane and its surroundings is, indeed, essential for the complex dynamic processes. The purpose of this paper is to connect in theory the film of liquid crystals with the bulk phases of normal fluids.

The theory will be extended to the membrane-solution system in the following way: one omits the thickness of the membranes, as in the foregoing paper [1], and thus is able to regard the two bulk phases as if they were in direct contact with each other. It follows that the “dividing surface” of the two liquids coincides with the “middle surface” of the membrane. In any irreversible process, on the one hand, kinematic discontinuity occurs at the “dividing surface” of the bulks, as it is expressed by the condition of compatibility (Kotchine's theorem [9]); on the other hand, instantaneous balance of mass, momentum and energy is required at the “middle surface” of the membrane, as it is presented in the context of isolated membranes [1]. It stands then to reason that a superposition of these individual laws gives the description of the desired dynamical system. It is done in the second section. A group of dynamic equations for an open (and closed) membrane system is thus established.

Here we explicitly note that the lipid crystal membrane is a two-dimensional fluid, which responds to lateral forces with the surface tension (or compressibility) and to transverse forces with the elasticity, having no elastic response to shear stretch. This is in contrast to the solid film model for red cell membranes suggested by Evans [10]. In the gel state, the lateral fluidity vanishes and the shape of the membrane varies in the bending mode (if no molecule tilting).

Recent experiments give support to the adoption of liquid crystal theory to the study of biomembranes. It was found that membrane deformations, at least those of small dimension such as shape fluctuations, are dominated by the curvature elasticity and are essentially “shear-free”. The same conclusion was obtained from the observations on both artificial lipid vesicles [11] and on erythrocytes [12]. Another argument is given by the measurements of the bending modulus ($k'_{11}$). It was reported that the bending modulus of lipid membranes is very close, in
magnitude, to that of human erythrocyte membranes: for phospholipid vesicles $k'_{11} = 1 \sim 4 \times 10^{-12}$ erg [5,13,14]† and for red blood cells $k'_{11} = 1 \sim 7 \times 10^{-12}$ erg [12,15,16]‡.

We expect that the theory presented in this paper will be extensively used in the study of dynamic processes of lipid vesicles, as well as biological cells, suspended in aqueous solutions. As a special application, one gives in section 3 the hydrostatic equations of the membrane in the field of fluid pressure and suggests to interpret the complex cell shapes by means of the analysis of stability, since biological systems are in general far from thermodynamic equilibrium.

2. Connection with liquid surroundings

The bilayer lipid membrane is considered to be adjacent to a stokesian fluid on each side. The thickness of the membrane is neglected and thus the “middle surface” of the membrane coincides with the “dividing surface” of the two fluids (see Fig. 1). The position of the two superposed geometric surfaces in an Euclidean space is given by the vector

$$r^i = r^i (\theta^1, \theta^2, t) \quad (1)$$

where $\theta^\alpha$ are curvilinear coordinates on the surface and $t$ is the time. Here and throughout the paper, block letters stand for vectors or tensors expressed in the inertial coordinates fixed in the Euclidean space and italic letters for those in the local bases (see reference [1]); Latin suffixes range over 1, 2, 3, while the Greek ones over 1, 2.

Denoting the displacement of the surface by $\zeta$, one defines the speed of the displacement movement by

$$w = \frac{\partial \zeta}{\partial t} \quad (2)$$

Both $\zeta$ and $w$ are measured in the direction normal to the surface (see the definition of the displacement movement [1]).

2.1 Mass balance

† The data cited here are for egg lecithin. For pure phospholipid membranes, it was found that $k'_{11} = 4 \sim 5 \times 10^{-13}$ erg [17,18]. Adding cholesterol to the pure lipid membranes may elevate the magnitude to one order higher. For example, the modulus of dimyristoylphosphatidycholine containing 50 mol% cholesterol has the value $k'_{11} = 4 \times 10^{-12}$ erg [19]. This composition equals to that of erythrocyte membranes which contains 50 mol% phospholipids and 50 mol% cholesterol.

‡ The data cited here correspond to the exciting wave length comparable to the cell dimension (10 $\mu m$). It was also reported that to short wave length excitation (0.1 $\sim$ 0.3 $\mu m$), the bending modulus of red cell membranes is $1 \sim 2 \times 10^{-13}$ erg [20,21]. For a discussion about the discrepancy refer to [12].
In the absence of exchange with the surroundings, the membrane has a constant total mass. The mass conservation principle for an arbitrary area $S$ is written
\[ \frac{d}{dt} \int_S \gamma \, ds = 0 \] (3)
where $\gamma$ is the surface density of mass.

When the membrane is permeable to certain solutes but not to the solvent, the total mass balance is given by
\[ \frac{d}{dt} \int_S \gamma \, ds = - \sum_k \int_S \left[ j_{k(n)} \right] \, ds \] (4)
where $j_k$ is the current density of the $kth$ considered species crossing the membrane. The subscript $(n)$ denotes the normal component of vectors. The square brackets stand for the discontinuities. For an arbitrary physical quantity $\phi$ the jump at the surface is defined as
\[ [\phi] = \phi_{\text{conv}} - \phi_{\text{conc}} \]
with the subscript $\text{conc}$ for the concave side and $\text{conv}$ for the convex side of the surface.

When osmosis of the adjacent solutions occur, the instantaneous mass change is additionally furnished by the absorption flux over the area. So one has
\[ \frac{d}{dt} \int_S \gamma \, ds = - \sum_k \int_S \left[ j_{k(n)} \right] \, ds - \int_S \left[ \rho \left( u_{(n)} - w \right) \right] \, ds \] (5)
where $\rho$ is the mass density and $u$ the velocity of the bulk fluids.

However, the Reynolds transport theorem for two-dimensional fluids asserts that [22]
\[ \frac{d}{dt} \int_S \phi \, ds = \int_S \left[ \dot{\phi} + \phi \left( \frac{\dot{a}}{2a} + v^\alpha \gamma_{\alpha} \right) \right] \, ds \] (6)
where, $\phi$ is any scalar function of position and time, $a$ the determinant of the metric tensor of the curvilinear coordinate system and $v$ the velocity of the fluids. The top dot stands for the convected derivative and the comma for the covariant derivative.

† In this paper, $u$ denotes the velocity of the surrounding fluids, whereas $v$ denotes that of the membrane. In the local bases, the velocity of the membrane (without thickness) is expressed as
\[ v = v^\alpha e_\alpha + w e_3 \]
with $e_3 = n$, $n$ being the normal unit vector.
derivative along the surface. Summation convention is followed here and throughout the paper. Besides, the dilation of the area element is related to the displacement movement by [9]

\[
\frac{\dot{a}}{2a} = -2Hw
\]  

(7)

\(H\) being the mean curvature of the surface. So Eqs.(3-5) may be written in the differential form

\[
\dot{\gamma} + \gamma \left( v^{\alpha}_{,\alpha} - 2Hw \right) = 0
\]

(for closed membrane system)  

(8)

\[
\dot{\gamma} + \gamma \left( v^{\alpha}_{,\alpha} - 2Hw \right) = -\sum_k \left[ j_{k(n)} \right]
\]

(for solute permeation process)  

(9)

\[
\dot{\gamma} + \gamma \left( v^{\alpha}_{,\alpha} - 2Hw \right) = -\sum_k \left[ j_{k(n)} \right] - \left[ \rho \left( u_{(n)} - w \right) \right]
\]

(for solution osmosis process)  

(10)

Here we have omitted the lateral diffusion of the particles moving across the membrane.

2.2 General form of balance equations

Suppose first that no exchange of the physical quantity \(\phi\) occurs between the membrane and the bulk phases. Let \(\phi = \gamma \tilde{\phi}^s\). One may write then the instantaneous balance in the form

\[
\frac{d}{dt} \int_S \gamma \tilde{\phi}^s \, ds = \int_S \int Q \, ds - \oint_L J^\alpha \, dl_\alpha
\]

(11)

where \(L\) is the periphery of the area \(S\), \(Q\) the production of \(\phi\) per unit time per unit area and \(J\) the current density of \(\phi\) along the surface. Making use of theorem (6), as well as the Stokes theorem, and taking account of (7), one obtains

\[
\gamma \dot{\tilde{\phi}}^s + \tilde{\phi}^s \left[ \dot{\gamma} + \gamma \left( v^{\alpha}_{,\alpha} - 2Hw \right) \right] = Q - J^\alpha_{,\alpha}
\]

(12)

Imagine next that the two bulk phases are in direct contact with each other without the presence of the membrane between them. The condition of compatibility at the dividing surface is given as (Kotchine’s theorem [9])

\[
\left[ \rho \tilde{\phi}^v (u_{(n)} - w) \right] + \left[ j_{(n)} \right] = 0
\]

(13)

where \(\rho \tilde{\phi}^v = \phi\) and \(j\) is the influx of \(\phi\) from the volumes to the surface.

Then we consider the membrane being in contact with the surroundings. Evidently, in this case the accumulation brought by the flux from the volumes makes a
part of the total amount of \( \phi \) pertinent to the membrane. As the middle surface of the membrane and the dividing surface of the two bulks are coincident, one obtains naturally the desired balance equation by summing Eqs.(12) and (13)

\[
\gamma \dot{\phi}^s + \dot{\phi}^s \left[ \dot{\gamma} + \gamma (v^{\alpha, \alpha} - 2Hw) \right] = Q - J^{\alpha, \alpha} - \left[ j_{(n)} \right] - \left[ \rho \dot{\phi}^v (u_{(n)} - w) \right]
\]

(14)

In particular, put \( \bar{\phi}^s = \bar{\phi}^v = 1 \), then Eq.(14) will be reduced to Eq.(10), if the source of substances is null and the lateral diffusion of components is negligible.

Inserting (8), (9) and (10) respectively into Eq.(14) gives the balance equations of \( \phi \), for the closed membrane system

\[
\gamma \dot{\phi}^s = Q - J^{\alpha, \alpha} - \left[ j_{(n)} \right] - \left[ \rho \dot{\phi}^v (u_{(n)} - w) \right]
\]

(15)

for the solute permeation process

\[
\gamma \dot{\phi}^s = Q - J^{\alpha, \alpha} - \left[ j_{(n)} \right] - \left[ \rho \dot{\phi}^v (u_{(n)} - w) \right] + \bar{\phi}^s \sum_k \left[ j_{k(n)} \right]
\]

(16)

and for the solution osmosis process

\[
\gamma \dot{\phi}^s = Q - J^{\alpha, \alpha} - \left[ j_{(n)} \right] - \left[ \rho \dot{\phi}^v (u_{(n)} - w) \right] + \bar{\phi}^s \sum_k \left[ j_{k(n)} \right] + \bar{\phi}^s \left[ \rho (u_{(n)} - w) \right]
\]

(17)

In the following, one considers only the closed membrane system.

2.3 Momentum exchange

With regard to the momentum exchange, the physical quantity \( \bar{\phi} \) is interpreted as the velocities

\[
\bar{\phi}^s = v^{\alpha, t^i} + wn^i
\]

\[
\bar{\phi}^v = u^i
\]

(18)

where \( n \) is the unit normal vector to the surface and \( t \) is the 3 \( \times \) 2 hybrid tensor having the components

\[
t^i_{\alpha} = \frac{\partial x^i}{\partial \theta^\alpha}
\]

(19)

\( x^i \) being the inertial coordinates. The net influx \( \left[ j_{(n)} \right] \) is interpreted as the resultant of the forces that the bulk phases exert on the surface

\[
\left[ j_{(n)} \right] = [\rho] \hat{\mathbf{g}}_{(n)} n^i - [p] n^i + 2 \left[ \mu \epsilon^{ij} \right] n_j
\]

(20)

where \( \rho \) equals to the mass density \( \rho \) multiplied by a unit length, \( \hat{\mathbf{g}} \) is the gravitational acceleration, \( p \) the thermodynamic pressure, \( \epsilon^{ij} \) the rate of strain tensor and
\( \mu_v \) the viscosity coefficient of the bulk fluids. The source of \( \phi \) is interpreted as the gravitational attraction to the membrane

\[
Q = \gamma \hat{g}^i
\]  

(21)

The surface flux \( J \) is interpreted as the surface force inherent in the membrane

\[
J^\alpha = -T^{\alpha\beta} t_\beta^i - T^{\alpha3} n_i
\]  

(22)

where \( T \) is the stress tensor of the membrane. With these interpretations, Eq.(15) reads

\[
\gamma \frac{d}{dt} \left( v^\alpha t_\alpha^i + w n_i \right) = \gamma \hat{g}^i + (T^{\alpha\beta} t_\beta^i + T^{\alpha3} n_i) , \alpha - [\hat{g}] \hat{g}^j n_j^i + [p] n^i - 2 \left[ \mu_v e^{ij} \right] n_j
\]  

(23)

In writing (23) we have supposed the continuity of velocity at the surface

\[
u(n) = w
\]  

(24)

Making use of the kinematic formulae [23,24]

\[
\dot{t}_\alpha^i = (w n^i) , \alpha + t_{\alpha, \beta} v^\beta
\]  

(25)

and

\[
\dot{n}^i = \partial_t n^i + n_{, \beta} v^\beta + w \left\{ i \atop j \ k \right\} n^j n^k
\]

\[
= - a^{\alpha\beta} t_\alpha^i (w n^i) , \beta n_j + n_{, \beta} n^i v^\beta
\]

\[
= - t_\alpha^i (a^{\alpha\beta} \partial_\beta w + b_{\beta}^\alpha v^\beta)
\]  

(26)

where \( a_{\alpha\beta} \) and \( b_{\alpha\beta} \) are respectively the first and the second magnitude of the surface, \( \left\{ i \atop j \ k \right\} \) is the second kind of Christoffel symbol, one rewrites the first term on the left side of (23) as

\[
\gamma \frac{d}{dt} \left( v^\alpha t_\alpha^i + w n_i \right) = \gamma (\dot{v}^\alpha - 2 b_{\beta}^\alpha v^\beta w - a^{\alpha\beta} w \partial_\beta w) t_\alpha^i + 
\]

\[
+ \gamma \left( \dot{w} + v^\alpha \partial_\alpha w + b_{\alpha\beta} v^\alpha v^\beta \right) n_i
\]  

(27)

Additionally, one expands the second term on the right side of (23) in the form (see Appendix)

\[
(T^{\alpha\beta} t_\beta^i + T^{\alpha3} n_i) , \alpha
\]

\[
= \left( T^{\alpha\beta} , \alpha(\tau) - b_{\alpha}^\beta T^{\alpha3} \right) t_\beta^i + \left( T^{\alpha3} , \alpha(\tau) + b_{\alpha\beta} T^{\alpha\beta} \right) n_i
\]  

(28)
with
\[
T_{\alpha}(\alpha) = \partial_\alpha T^{\alpha} + \frac{1}{2a} T^{\alpha} \partial_\alpha a + \left\{ \begin{array}{c} \beta \\ \sigma \end{array}, \alpha \right\} T^{\alpha}
\]
\[
T^{\alpha3}(\alpha) = \partial_\alpha T^{\alpha3} + \frac{1}{2a} T^{\alpha3} \partial_\alpha a
\]
where the subscript (\(\alpha\)) is used to denote the tangential component of vectors or tensors. Then, by using (27) and (28), one splits Eq.(23) into the tangential part
\[
\gamma \left( \dot{v}^\alpha - 2b^\alpha v^\beta w - a^\alpha w \partial_\beta w \right)
\]
\[
= \gamma \dot{g}_{i,j}^i j^\beta a^\beta + b^\alpha T^{\beta3} - 2 [\mu_e e_{ij}] n_i t_j a^\beta
\]
and the normal part
\[
\gamma \left( w + v^\alpha \partial_\alpha w + b_{\alpha\beta} v^\alpha v^\beta \right)
\]
\[
= \gamma \dot{g} n^i + T^{\beta3} - b_{\alpha\beta} T^{\alpha3} - [\partial] \dot{g} n^i + [p] - 2 [\mu_e e_{ij}] n_i n_j
\]
The rate of strain tensor for the stokesian fluids is given, as well known, by
\[
e_{ij} = \frac{1}{2} (u_{i,j} + u_{j,i})
\]
The stress tensor of the membranes without any chiral structure has the components
\[1\]
\[
T^{\alpha\beta} = - \sigma a^{\alpha\beta} + (k'_1 - 2Hk_{11}) b^{\alpha\beta} + (k'_2 + k'_{24}) K \alpha^{\alpha\beta} - (\mu - \eta) 2H w a^{\alpha\beta} - \eta \left\{ 2w b^{\alpha\beta} - \frac{1}{2} E^{\alpha\beta\lambda\mu} (v_{\lambda,\mu} + v_{\mu,\lambda}) \right\}
\]
\[
T^{\alpha3} = - \frac{\alpha_3}{2} b^{\alpha} v^\beta
\]
where, the \(k'_i\)'s and the \(k'_{ij}\)'s are the elastic moduli, \(\mu\) and \(\eta\) the dilatation viscosity and the shear viscosity, respectively, \(\sigma\) is the surface tension, \(\alpha_3\) the viscosity relevant to the intrinsic rotation of the molecules, \(K\) the gaussian curvature, \(\varepsilon^{\alpha\beta}\) the two-parametric permutation tensor having the components \(\varepsilon^{11} = \varepsilon^{22} = 0, \varepsilon^{12} = \varepsilon^{21} = 1/\sqrt{a}\), \(E^{\alpha\lambda\mu\nu}\) the fourth-order transversely isotropic tensor defined as \(E^{\alpha\lambda\mu\nu} = a^{\alpha\lambda} a^{\beta\mu} + a^{\alpha\mu} a^{\beta\lambda} - a^{\alpha\beta} a^{\lambda\mu}\). Inserting relations (32) and (33) into Eqs.(30) and (31), one obtains finally the explicit form of the equation of motion for the internal flow within the membrane
\[
\gamma \left( \dot{v}^\alpha - 2b^\alpha v^\beta w - a^\alpha w \partial_\beta w \right)
\]
\[
= \gamma \dot{g}_{i,j}^i j^\beta a^\beta - a^\beta a \partial_\beta \sigma + k'_1 a^\beta a \partial_\beta (2H) - k'_1 (b^\alpha + 2Ha^\alpha) \partial_\beta (2H) + (k'_2 + k'_{24}) a^\beta a \partial_\beta K - (\mu + \eta) a^\beta a \partial_\beta (2H) w - ((\mu - \eta) 2H w a^\alpha + 2\eta b^\alpha) \partial_\beta w + \eta E^{\alpha\lambda\mu\nu} (v_{\lambda,\mu} + v_{\mu,\lambda}) + \frac{\alpha_3}{2} (2Hb^\alpha v^\beta - K v^\alpha) - [\mu_v (u_{i,j} + u_{j,i})] n_i t_j a^\beta
\]
and that for the displacement movement of the membrane
\( \gamma \left( \dot{w} + v^\alpha \partial_\alpha w + b_{\alpha\beta} v^\alpha v^\beta \right) \)
\( = \gamma \hat{g}_j n^j - 2H\sigma + (k'_1 - 2Hk'_{11}) (4H^2 - 2K) + (k'_{22} + k'_{24}) 2HK - \)
\( - 4 \left\{ (\mu + \eta) H^2 - \eta K \right\} w + \eta (b^\lambda\mu - Ha^{\lambda\mu}) (v_{\lambda,\mu} + v_{\mu,\lambda}) - \)
\( - \frac{\alpha_3}{2} \left\{ b_\alpha^\beta v^\sigma,\beta + v^\beta \partial_\beta (2H) \right\} - [\rho] \hat{g}_j n^j + [p] - \)
\( - [\mu v (u_{i,j} + u_{j,i})] n^i n^j \) \hfill (35)

### 2.4 Energy exchange

With regard to the energy exchange, one might interpret the physical quantity \( \bar{\phi} \) in (15) as the energy of unit mass, the surface flux \( J \) as the sum of the current density of heat and work, and so on, to get the balance equation. But here we use the results obtained before to make the discussion brief.

One has already the energy balance equation of an isolated membrane [1]

\( \gamma C_l \dot{\Theta} = Q^h - J_{h,\alpha}^\alpha + T^\beta\alpha v_{\alpha,\beta} + T^\beta\beta \partial_\beta w \) \hfill (36)

with the constitutive relation of heat flux

\( J^h = -\kappa_\perp \partial_j \Theta e^j - \kappa_\parallel \partial_j \Theta n^j e^3 \) \hfill (37)

where, \( C_l \) is the heat capacity per unit mass of the membrane medium in the static state, \( \Theta \) the temperature, \( Q^h \) the heat source, \( \kappa \) the heat conductivity with the subscripts \( \perp \) or \( \parallel \) indicating the conduction direction perpendicular or parallel to the normal vector and \( e^k \) are the reciprocal local bases. While the membrane is in contact with the bulk fluids, energy current flows from the volume phases to the surface in the form of heat and work

\( - [j_{(n)}] = [k_v \Theta, k] n^k - w \left\{ [\rho] \hat{g}_{(n)} - [p] + 2 [\mu_v e_{ij}] n^i n^j \right\} \) \hfill (38)

where \( k_v \) is the heat conductivity of the volume phases. By summing (36) and (38), one obtains the energy balance equation

\( \gamma C_l \dot{\Theta} = Q^h + \kappa_\perp \left( \partial_j \Theta \right), k (g^{kj} - n^k n^j) - \kappa_a 2H (n^i \partial_j \Theta) + \)
\( + \left( -\sigma a^{\alpha\beta} + (k'_{1} - 2Hk'_{11}) b^{\alpha\beta} + \right) \)
\( + (k'_{22} + k'_{24}) K a^{\alpha\beta} - (\mu - \eta) 2Ha^{\alpha\beta} w - \)
\( -\eta \left\{ 2wb^{\alpha\beta} - \frac{1}{2} E^{\alpha\beta\lambda\mu} (v_{\lambda,\mu} + v_{\mu,\lambda}) \right\} v_{\alpha,\beta} - \)
\( - \frac{\alpha_3}{2} b_\alpha^\beta v^\alpha \partial_\beta w + [k_v \partial_k \Theta] n^k - \)
\( - w \left\{ [\rho] \hat{g}_j n^j - [p] + [\mu_v (u_{i,j} + u_{j,i})] n^i n^j \right\} \) \hfill (39)
where \( \kappa_a = \kappa || - \kappa_\perp \). In writing (39), one took relations (33) and (38) into account.

3. Hydrostatic equilibrium

Let \( v^\alpha = w = u^i = 0 \), Eqs.(34) and (35) give

\[
\gamma \hat{g} \cdot \nabla_s \sigma + k'_1 \nabla_s (2H) + (k'_{22} + k'_{24}) \nabla_s K + k''_{11} \{(\nabla_s n) \cdot \nabla_s (2H) - 2H \nabla_s (2H)\} = 0
\]

(40)

and

\[
\gamma \hat{g}_{(n)} - 2H \sigma + k'_1 (4H^2 - 2K) + (k'_{22} + k'_{24}) 2HK - k''_{11} 2H (4H^2 - 2K) - [\varrho] \hat{g}_{(n)} + [p] = 0
\]

(41)

where the differential operator is defined by

\[
\nabla_s = e^\beta \frac{\partial}{\partial \vartheta^\beta}
\]

(42)

For a non-spherical vesicle, the pressure difference between the interior and the exterior may be estimated to be of the order of \( 1 \sim 10 \text{ dyn} \cdot \text{cm}^{-2} \) [25], whereas the gravitational attraction \( \gamma \hat{g} \) is approximately \( 5 \times 10^{-4} \text{ dyn} \cdot \text{cm}^{-2} \). So the later is negligible as an external force. On the other hand, theoretical analyses and experiments show that the saddle-shape conformation, given by the term of \( k'_{22} + k'_{24} \), can not be observed in lipid-water systems except when the water content is extremely low [26]. Therefore Eqs.(40) and (41) can be simplified to

\[
\nabla_s \sigma - k'_1 \nabla_s (2H) - k''_{11} \{(\nabla_s n) \cdot \nabla_s (2H) - 2H \nabla_s (2H)\} = 0
\]

(40')

and

\[
2H \sigma - k'_1 (4H^2 - 2K) + k''_{11} 2H (4H^2 - 2K) + [\varrho] \hat{g}_{(n)} - [p] = 0
\]

(41')

Equations (40’) and (41’) serve as the conditions of mechanical equilibrium for the membrane-fluid system in the directions tangential and normal to the surface, respectively. Eq.(41’) gives explicitly the dependence of the elasticity of the membrane on the discontinuity of the pressure field. It is worth while to note that these conditions are different from those of thermodynamic equilibrium [25,27,28]. For the latter requires further the minimality of the free energy stored in the whole elastic surface. When the elasticity vanishes and the buoyancy is negligible, Eq.(41’) is reduced to the well known Laplace law

\[
2H \sigma = [p]
\]

(43)

4. Concluding remarks

Eqs.(15), (16) and (17) are given as the general form of balance equations for membrane-solution systems. Specifically, Eq.(15) is for the process without mass
exchange between the membrane and the liquid surroundings, Eq.(16) for the process of solute permeation and Eq.(17) for the solvent osmosis across the membrane. Particular uses of Eq.(15) yield the equations of motion (34) and (35), respectively for the internal molecular flow inside the membrane and the displacement of the membrane configuration, as well as the balance equation of energy Eq.(39). The conditions for the membrane in hydrostatic equilibrium with the adjacent fluids are given as a special application of Eqs.(34) and (35).

Acknowledgement

This work is supported by the National Foundation for Natural Sciences and by the Foundation of the Ministry of Education of China.

Appendix. Derivation of Eq.(28)

Recalling the covariant differentiation [22]

$$t^i_{\alpha\beta} = \frac{\partial t^i_{\alpha}}{\partial \theta^\beta} + \left\{ \begin{array}{l} j \\ k \end{array} \right\} t^i_{\alpha} t^k_{\beta} - \left\{ \begin{array}{l} \gamma \\ \alpha \beta \end{array} \right\} t^i_{\gamma}$$

one writes the first term of (28) as

$$\begin{align*}
(T^{\alpha\beta} t^i_{\beta})_{,\alpha} &= \partial_\alpha (T^{\alpha\beta} t^i_{\beta}) + \left\{ \begin{array}{l} \alpha \\ \alpha \mu \end{array} \right\} T^{\mu\beta} t^i_{\beta} + \left\{ \begin{array}{l} i \\ j \\ k \end{array} \right\} t^i_{\alpha} t^k_{\beta} T^{\alpha\beta} \\
&= t^i_{\beta} \left( \partial_\alpha T^{\alpha\beta} + \right. \\
&+ T^{\alpha\beta} \left( \partial_\alpha t^i_{\beta} + \left\{ \begin{array}{l} i \\ j \\ k \end{array} \right\} t^i_{\alpha} t^k_{\beta} - \left\{ \begin{array}{l} \mu \\ \alpha \beta \end{array} \right\} t^i_{\mu} \right) \\
&= t^i_{\beta} T^{\alpha\beta}_{,\alpha(\tau)} + T^{\alpha\beta} t^i_{\beta,\alpha} \\
&= t^i_{\beta} T^{\alpha\beta}_{,\alpha(\tau)} + T^{\alpha\beta} b_{\alpha\beta} n^i
\end{align*}$$

and the second term as

$$\begin{align*}
(T^{\alpha3} n^i)_{,\alpha} &= \partial_\alpha (T^{\alpha3} n^i) + \left\{ \begin{array}{l} \alpha \\ \alpha \mu \end{array} \right\} T^{\alpha3} n^i + \left\{ \begin{array}{l} i \\ j \end{array} \right\} t^k_{\alpha} T^{\alpha3} n^i \\
&= n^i \left( \partial_\alpha T^{\alpha3} + \right. \\
&+ T^{\alpha3} \left( \partial_\alpha n^i + \left\{ \begin{array}{l} i \\ j \end{array} \right\} t^k_{\alpha} n^j \right) \\
&= n^i T^{\alpha3}_{,\alpha(\tau)} + T^{\alpha3} b_{\alpha\beta} t^i_{\beta} \\
&= n^i T^{\alpha3}_{,\alpha(\tau)} - T^{\alpha3} b_{\alpha\beta} n^i
\end{align*}$$

Hence one obtains

$$\begin{align*}
(T^{\alpha\beta} t^i_{\beta} + T^{\alpha3} n^i)_{,\alpha} &= (T^{\alpha\beta}_{,\alpha(\tau)} - T^{\alpha3} b_{\alpha\beta}) t^i_{\beta} + (T^{\alpha3}_{,\alpha(\tau)} + T^{\alpha3} b_{\beta\alpha}) n^i
\end{align*}$$
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Figure captions

Fig.1 Illustration of the middle surface of the membrane and the dividing surface of the two bulk phases.