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A MATHEMATICAL EXAMINATION OF SQUEEZING AND STRETCHING OF SPHERICAL VESICLES

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Abstract. The geometry of a few simple models closely related to the Cole's and Yoneda's experiments are studied in some detail. Their principal differences are through the boundary conditions at the points where the membranes detach themselves from the compressing planes. Mathematically this affect the equilibrium configurations as in all these cases the mean curvature suffers a discontinuity while this is not so for the tangent vector. A new parametrization of the Delaunay's nodoids is derived.

1. Introduction

The mechanism maintaining the distinctive biconcave shape of the red blood cell has been a subject of considerable curiosity since its discovery more than two century ago. Actually, the shape of red blood cells and other closed biological membranes (vesicles) is closely related to the formation of lipid bilayer vesicles in aqueous medium. The interface, i.e., the lipid membrane is treated as a thin elastic shell and possesses four modes of deformation – dilatation, bending, shearing and torsion. From the geometrical viewpoint the bending and torsion are related to variations of the two principal curvatures of the interface.

Quantitatively, the elastic properties of the open lipid membranes and vesicles are described by the free energy which itself depends on the principal curvatures of the surfaces that represent them. By taking the first order variation of the free energy one derives a highly nonlinear equation which describes the possible equilibrium shapes [12]. The difficulties which one encounters in any serious attempt to solve this equation suggests that all kind of information providing more deep understanding of the observed highly nonlinear behaviour of vesicles is without any doubt of a definite value.

The curvature dependence of the interfacial tension has been investigated for the fist time by Young and Laplace in their study of the Euler-Lagrange variational problem connected with the minimization of the following functional

$$\Delta p \int \mathrm{d}V + \sigma \int \mathrm{d}\mathcal{A}. \tag{1}$$

Here, Δp is the pressure difference across the interface, V is the volume, σ is the surface tension and $\mathcal{A}$ is the area of the vesicle. The solution of the above mentioned variational problem leads to constant mean curvature surfaces described by the Laplace–Young equation

$$\Delta p = \sigma(\frac{1}{R_1} + \frac{1}{R_2}) = 2\sigma H \tag{2}$$

in which R_1 and R_2 are the two principal radii of curvature at the given point and $H = \frac{1}{2}\left(\frac{1}{R_1} + \frac{1}{R_2}\right)$ is the so-called mean (meaning average) curvature there. Modern expositions of the classical differential geometry along relevant variational issues can be found in [6] and [7].

The equation (2) which accounts the equilibrium between the surface pressure and surface tension has been used by Cole [2] in his experiments in order to find the latter. In this experiment the vesicles (sea-urchin eggs) have been compressed with known forces between two parallel plates and the surface tension was calculated by the degree of their flattening.

Later on a similar experiment was performed by Yoneda [11] who had adopted however another defining equation for σ.

As is common in scientific investigation the advances are sought on both theoretical and experimental fronts, and "exact solutions" are confined to the cases of simplest geometries. The present work is not an exception of the above trend and in what follows we will consider in some detail three different geometrical models which are relevant to the appropriate experiments. They have been chosen here because as we will see they lead to relatively simple mathematical expressions which real merit is their analytical form.

2. Cole's Model

It seems appropriate to remind here the essential points of Cole's method of calculations. He have compressed a spherical egg of initial radius a between two parallel plates with a fixed force F. The surface tension is evaluated by the measurement of flattening (the half-thickness h), the radius r of the contact area A and the equatorial radius R (see Fig. 1).

Of these h and R can be measured with enough high accuracy, but this is not the case with r particularly when the contact angle is very close to $180°$. The other two parameters which enter into the model are the inner radius ρ of the torus like

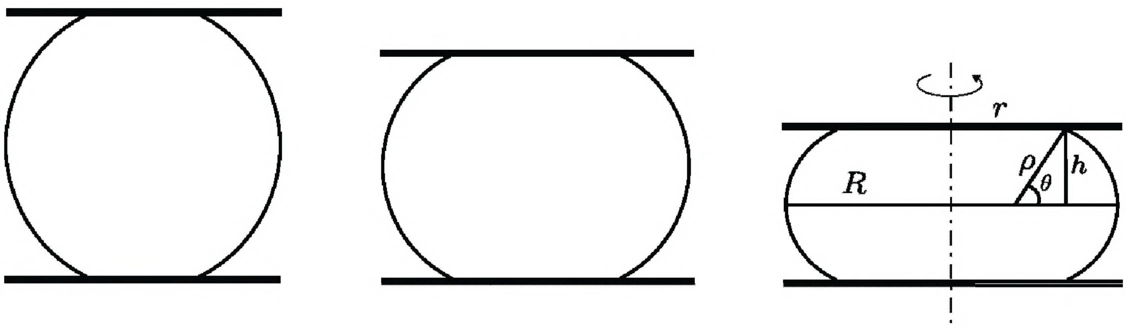

Figure 1: Geometry of Cole's experiment. The shown profiles are obtained using the linear approximations $R(m) = 1.64a - 0.68ma$, $\rho(m) = 1.12ma$ and different values of the deformational parameter $m \in (0, 1]$.

outer part of the membrane and the contact angle θ. Relying again to geometry one can easily find that the above parameters are given by the expressions

$$\rho = \frac{h^2 + (R-r)^2}{2(R-r)}, \qquad \theta = \arcsin\frac{h}{\rho}. \tag{3}$$

The profile curve of the torus like part of the egg is parameterized explicitly by the formulas

$$x = R - \rho + \rho\cos u, \quad z = \rho\sin u, \qquad u \in \left[-\arcsin\frac{h}{\rho}, \arcsin\frac{h}{\rho}\right]$$

and this is enough for finding the volume, respectively the surface area in the form

$$V = 2\pi\left[h(R^2 + 2\rho^2 - 2R\rho + (R-\rho)\sqrt{\rho^2 - h^2} + \rho^2(R-\rho)\theta - \frac{h^3}{3}\right] \tag{4}$$

$$S = 4\pi\rho[(R-\rho)\theta + h] + 2\pi r^2. \tag{5}$$

By photographically obtained values for R, ρ and h the first two are plotted against the third and after that analytically fitted by explicit functions of $h \equiv z$. The remaining parameter r can be found by solving equation (3) with respect to this variable and this gives

$$r(z) = R - \rho - \sqrt{\rho^2 - z^2}.$$

Having $\rho(z)$, $R(z)$ and $r(z)$ one can put back them into (4) and to check practical constancy of the volume $V = (4/3)\pi a^3$. Besides, one can found the values of $1/R + 1/\rho$ for the points at equator and using

$$P = F/A = \sigma(1/R + 1/\rho) \tag{6}$$

to determine the surface tension σ which was the main purpose of Cole [2] and all considerations above.

3. An Intermediate Model

The real merit of the lateral compression is its technical simplicity which is of great advantage for studying long-term changes of the cell as a whole. However, the photomicrographs taken from one direction alone are not enough to describe the three dimensional shape of the compressed membrane. Actually, the main problem is with the contact area. The adhesion in two dimensions has been explored by

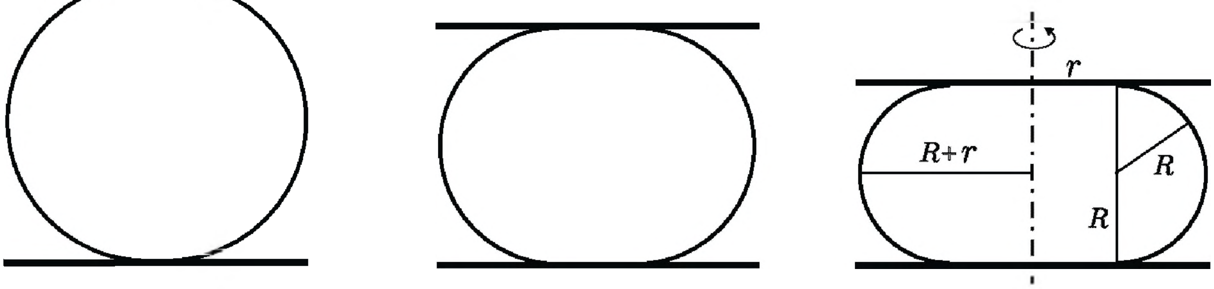

Figure 2: Geometry of the intermediate model.

Seifert [9], while Rosso and Virga [8] have modelled it by considering the one-dimensional vesicle contour specified by the symmetry. The latter approach is based on great achievement due to Seifert and Lipowsky [10] who have shown that the vesicles suffer a discontinuity in their principal curvatures (and therefore mean as well) on the contour along which they detach themselves from the wall.

We will not discuss further these developments here but let us mention that the important for the biology haptotaxis migration which is induced by the adhesion gradient can be described by the same one-dimensional considerations (see [1] for more details).

Instead, we will introduce a model of deformation of the cell which is intermediate between that ones of Cole and Yoneda (to be discussed in the next section). The radius of the contact area is again r but in the new case R denotes the internal radius of the torus like outer part. After some computation one can deduce from Fig. 2 the following formula for the volume

$$V = 2\pi r^2 R + \pi^2 r R^2 + \frac{4}{3}\pi R^3 \tag{7}$$

of the deformed sphere. As the contents of the cell is considered to be incompressible and the volume of the sphere with radius a is

$$V = \frac{4}{3}\pi a^2 \tag{8}$$

one can find immediately from (7) and (8) the relation

$$r = \frac{-\pi R + \sqrt{\pi^2 R^2 + 32(a^3 - R^3)/3R}}{4}. \tag{9}$$

It turns out convenient to introduce the deformational parameter m via the formula

$$R = ma, \qquad m \in (0, 1] \tag{10}$$

so that

$$r_m = r(m) = \frac{-\pi ma + \sqrt{\pi^2 m^2 a^2 + 32a^2(1 - m^3)/3m}}{4}. \tag{11}$$

The respective formulas for the surface area are

$$S = 2\pi(r^2 + \pi r R + 2R^2) \tag{12}$$

and

$$S(m) = 2\pi(r_m^2 + \pi m a r_m + 2m^2 a^2). \tag{13}$$

4. Yoneda's Approach

In order to bypass the ambiguity in the measurement of the radius r of the contact disk Yoneda [11] have proposed another method for calculation of the surface tension. It is based on the following arguments. Let us assume that the egg is compressed to the thickness z under the external force F. If under the slightly increasing force the egg is compressed further by $-\mathrm{d}z$, the work required for this additional compression is $-F\mathrm{d}z$ is assumed to be expended entirely for stretching the cortex neglecting any other effects (bending, etc.). If $\mathrm{d}S$ is the stretching of the surface produced by the compression $-\mathrm{d}z$, this work is just the surface force σ (supposing that it is uniform on the entire surface) multiplied by $\mathrm{d}S$, i.e.,

$$-F\mathrm{d}z = \sigma \mathrm{d}S \qquad \text{or} \qquad F = -\sigma\frac{\mathrm{d}S}{\mathrm{d}z}. \tag{14}$$

If F is plotted against $-\frac{\mathrm{d}S}{\mathrm{d}z}$, the last equation implies that σ is given as the slope of the line through the origin and this is confirmed experimentally [11].

5. Constant Mean Curvature Surfaces

Looking at (2) it is clear that the surface tension will be constant provided we deal with surfaces of constant mean curvature H. The profile curve of the only relevant for our considerations axially-symmetric surface which is referred as *nodoid* and belongs to the Delaunay class [3] (for the modern presentation see [5]) is depicted in Fig. 3. Actually there one sees just one segment of it as it is periodic along the symmetry axis but one easily recognizes that the distance from the curve to this axis has one local minimum ρ and one local maximum R in each period. Notice also that here ρ has a different meaning from the one introduced earlier.

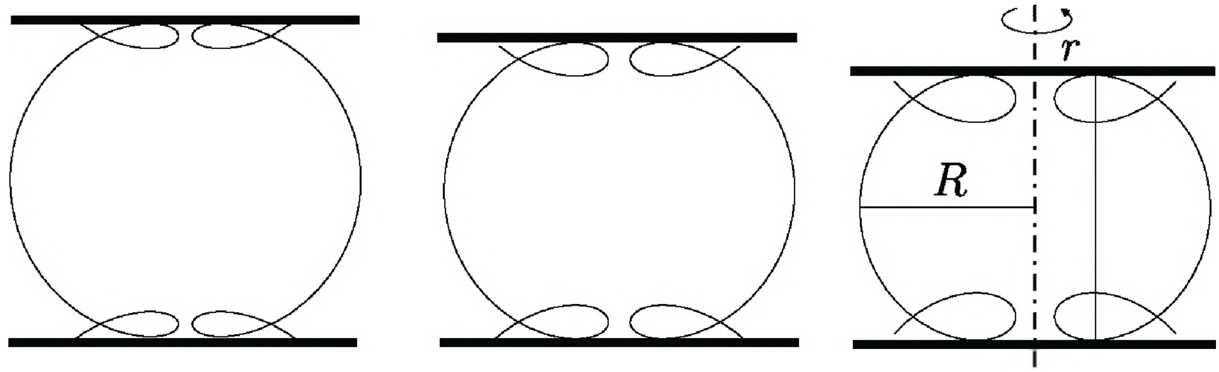

Figure 3: Nodoid's geometry.

As a byproduct of the considerations in the present work we will derive a parametrization of the nodoids which is quite useful for our main purpose.

To do this we will start with the well known fact that the parallels and meridians on the rotational surfaces are curvature lines. If $\theta(x)$ is the angle made by the surface normal $\mathbf{n}$ with the symmetry axis, we can express the principal curvatures $k_p(x)$ and $k_m(x)$ as follows

$$k_p(x) = \frac{\sin\theta(x)}{x}, \qquad k_m(x) = \cos\theta(x)\frac{\mathrm{d}\theta(x)}{\mathrm{d}x}. \tag{15}$$

By differentiating $k_p(x)$ and taking into account the expression for $k_m(x)$ one can eliminate $\theta(x)$ and obtain a simple differential equation which expresses the assumption of rotational symmetry

$$\frac{\mathrm{d}k_p(x)}{\mathrm{d}x} = \frac{k_m(x) - k_p(x)}{x}. \tag{16}$$

Being in the class of constant mean curvature surfaces we have as well

$$H := \frac{k_m(x) + k_p(x)}{2} = \mathrm{h} = \text{const}. \tag{17}$$

Elimination of $k_m(x)$ from Equations (16) and (17) yields

$$\frac{\mathrm{d}k_p(x)}{\mathrm{d}x} = \frac{2(\mathbb{h} - k_p(x))}{x}. \tag{18}$$

This equation can be easily integrated and gives

$$k_p(x) = \mathbb{h} + \mathbb{b}/x^2 \tag{19}$$

where $\mathbb{b}$ is the integration constant that will be determined below. Before that we have to mention that the contour $z(x)$ can be recovered by the geometrical relation

$$\frac{\mathrm{d}z(x)}{\mathrm{d}x} = \tan\theta(x) \tag{20}$$

and the first expression in (15) which reads

$$\sin\theta(x) = xk_p(x). \tag{21}$$

Combined (20) and (21) give us

$$z(x) = z(\rho) + \int_\rho^x \frac{\xi k_p(\xi)}{\sqrt{1 - \xi^2 k_p^2(\xi)}}\,\mathrm{d}\xi. \tag{22}$$

Now we switch to determination of the integration constants $\mathbb{h}$ and $\mathbb{b}$ which are necessary for the evaluation of the above integral. A genuine geometry of the model infer that at $x = r$ we obviously have $\theta(r) \equiv 0$, while for $x = R$, $\theta(R) = \pi/2$ and therefore

$$r\mathbb{h} + \frac{\mathbb{b}}{r} = 0, \qquad R\mathbb{h} + \frac{\mathbb{b}}{R} = 1 \tag{23}$$

Solving the system (23) one gets

$$\mathbb{h} = \frac{R}{R^2 - r^2}, \qquad \mathbb{b} = -\frac{Rr^2}{R^2 - r^2}. \tag{24}$$

Some additional analysis leads to the conclusion that ρ is determined uniquely by r and R and that the precise relationship among these parameters is

$$r^2 = \rho R \tag{25}$$

which, when replaced in (24) produces

$$\mathbb{h} = \frac{1}{R - \rho}, \qquad \mathbb{b} = -\frac{R\rho}{R - \rho}. \tag{26}$$

Because of the above it turns convenient to switch in (20) again to the parameters ρ and R as in this situation we have to evaluate the integral

$$\int_\rho^z \frac{(\xi^2 - R\rho)\,\mathrm{d}\xi}{\sqrt{(R^2 - \xi^2)(\xi^2 - \rho^2)}} \tag{27}$$

which gives the contour

$$x(u) = R\,\mathrm{dn}(u, k), \qquad z(u) = R(E(u, k) - \varepsilon^2 F(u, k)) \tag{28}$$

where,

$$k^2 = 1 - \varepsilon^4, \quad \varepsilon = \rho/R, \quad u \in \left[-\arcsin\frac{1}{\sqrt{1+\varepsilon^2}}, \arcsin\frac{1}{\sqrt{1+\varepsilon^2}}\right]. \tag{29}$$

Here $\mathrm{dn}(u, k)$ is one of the three elliptic functions introduced by Jacobi while $F(u, k)$ and $E(u, k)$ denote the incomplete **elliptic integrals** of the first and second kind, and k is the so called **elliptic module**. The complete elliptic integrals $F(\pi/2, k)$ and $E(\pi/2, k)$ of the first and second kind will be denoted respectively by $K(k)$ and $E(k)$. For a straightforward exposition and properties of the elliptic functions and integrals see [4].

The parametrization of the corresponding surface of revolution (the **nodoid**) is respectively,

$$\begin{aligned} x[u, v] &= R\,\mathrm{dn}(u, k)\cos v, \qquad y[u, v] = R\,\mathrm{dn}(u, k)\sin v \\ z[u, v] &= R(E(u, k) - \varepsilon^2 F(u, k)), \quad u \in (-\infty, \infty), \quad v \in [0, 2\pi). \end{aligned} \tag{30}$$

The analytical form of the slice of the egg given by the above formulas can be used again along the fact that during the compression the volume is conserved and in this way the relationship between geometrical parameters to be obtained. The realization of this strategy gives

$$R = a\left[\left(\left(1 - \frac{3\varepsilon^2}{2} + \varepsilon^4\right)(1 - \varepsilon^2 + E(k)) + \varepsilon^2\left(1 - \varepsilon^2 - \frac{\varepsilon^2 K(k)}{2}\right)\right)/2\right]^{-\frac{1}{3}} \tag{31}$$

and this means that measuring R one can find ε and therefore by (29) and (28) the actual profile of the compressed egg. The formula for the surface area is also available so that one can perform the analysis according Yoneda's approach. The great advantage of the 'intermidate' and nodoid models is that all computations are of analytical form. The respective details will be presented elsewhere.

Conclussions

Lipid membranes are described remarkably well by a Hamiltonian of purely geometrical origin. While the variational approach captures the geometrical nature of the boundary conditions, the physical interpretation of these conditions is still not quite clear. Most straightforward, one would like to interpret them in terms of the balance of the forces and momenta acting at the edge. However, in the axially-symmetric case adopted here we have demonstrated how very simple geometrical arguments may be exploited to derive membrane geometry and respective continuous deformations.

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