

Endocytosis analysis

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August 23, 2024

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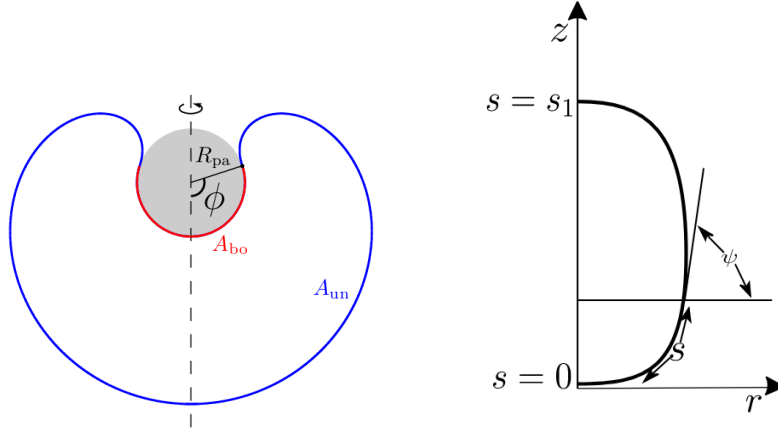
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1 Introduction

Note: This part follows closely what has been done by the supplementary material of [1] The code is adapted from [5] and from supplementary materials of [2].

We are studying the interaction between a spherical membrane and a spherical particle. They interact with each other through an adhesive interaction. The spherical particle does not have any other properties. The membrane instead is modeled as an elastic surface following the Helfrich theory of elasticity. It has a bending modulus k and a surface tension Σ .

The system equilibrium state is the result of the interplay between two competing phenomena: the first one is the particle wrapping that decreases the free energy and the second one is the increase of energy due to the bending of the membrane surface.



(a) image taken from supplementary material of [1]

The total free energy of the system will be composed by two contribution representing the bound and unbound segment:

$$E = E_{bo} + E_{un}$$

The bound segment of the membrane will follow the particle contour but the unbound segment does not have a trivial shape.

E_{bo} has an adhesive and a bending energy contribution: [1]

$$E_{bo} = (-2\pi|W|R_{pa}^2 + 4\pi k(1+mR_{pa})^2)(1-\cos\phi) = (-2\pi|W|R_{pa}^2 + 4\pi k)(1-\cos\phi)$$

where ϕ is the wrapping angle and we are considering a vesicle bilayer with zero spontaneous curvature, ie $m = 0$.

In order to find the shape of the unbound segment that minimizes E_{un} , for a fixed value of contact angle ϕ , and satisfies the constraints on the total membrane area $A - A_{bo}$ and enclosed volume $V + V_{bo}$ of the vesicle, we must minimize the shape functional

$$F = E_{un} + \Sigma(A - A_{bo}) - \Delta P(V + V_{bo}) = \int_{A_{un}} dA 2kH^2 + \Sigma(A - A_{bo})$$

where $\int_{A_{un}} dA 2kH^2$ is the Helfrich energy integral.

In our simulations we dont have any control or constraint on the vesicle volume, we dont pay a cost to change the vesicle volume then we put the volume term equal to zero.

Assuming that the vesicle shape will be axis-symmetric around z-axis It is possible to rewrite F in terms of $s, \psi(s), x(s)$:

$$F = \int_{s_0}^{s^*} L(s, \psi(s), x(s)) ds$$

The mean curvature H is given by

$$H = \frac{1}{2}(C_1 + C_2)$$

From figure 2 follows that:

$$C_1 = \frac{1}{R_1} = \frac{\sin\psi}{x(s)}$$

C_2 is given by the definition of curvature: the rate at which ψ changes with respect to the arc length s , which gives:

$$C_2 = \frac{d\psi}{ds}$$

C_1 defines the curvature straight into (or out of) the paper, and C_2 defines the curvature in the direction of s .

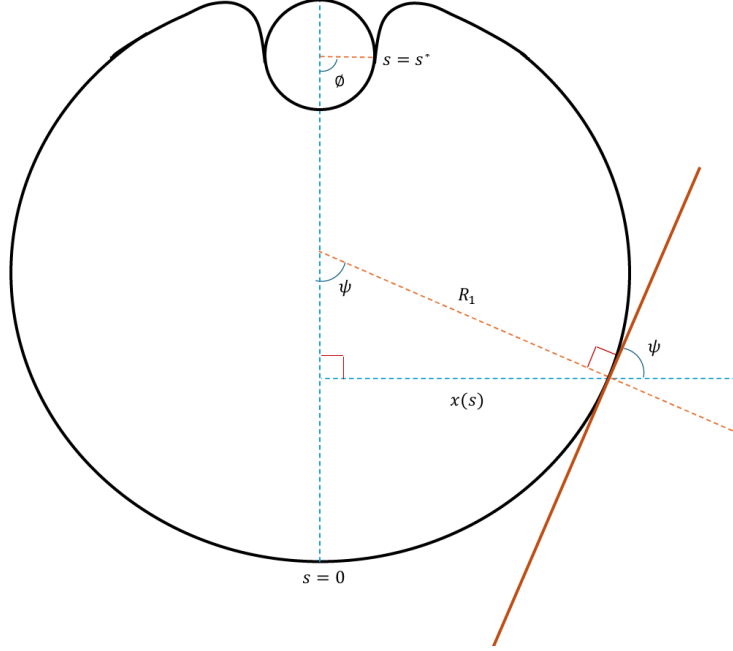


Figure 2: Visualization of the curvature

These two curvatures together give the mean curvature:

$$H^2 = \frac{1}{4} \left(\frac{d\psi}{ds} + \frac{\sin \psi}{x(s)} \right)^2$$

Now we will parameterize F in terms of $s, \psi(s), x(s)$

$$F = \int_{A_{un}} dA \, 2kH^2 + \Sigma A_{un} = \int_{s_0}^{s^*} L(s, \psi(s), x(s)) \, ds$$

For this step we need to rewrite an integral in terms of dA to an integral in terms of s . To do this we use the following formula:

$$dA = 2\pi x ds$$

applying this formula to F gives:

$$F = \int_{A_{un}} dA \, 2kH^2 + \Sigma A_{un} = \int_{s_0}^{s^*} 2\pi x ds \, 2kH^2 + \Sigma \int_{s_0}^{s^*} 2\pi x ds$$

Now we will add the two integrals together and fill in H:

$$F = 2\pi k \int_{s_0}^{s^*} \frac{x}{2} \left(\dot{\psi} + \frac{\sin \psi}{x} \right)^2 + \frac{\Sigma}{k} x ds$$

To make sure the relation between x and ψ is satisfied, the Lagrange multiplier $\gamma(s)$ is added to the integral.

$$F = 2\pi k \int_{s_0}^{s^*} \frac{x}{2} \left(\dot{\psi} + \frac{\sin \psi}{x} \right)^2 + \frac{\Sigma}{k} x + \gamma \frac{\dot{x} - \cos \psi}{2\pi k} ds$$

$$L(s, \psi, \dot{\psi}, x, \dot{x}, \gamma) = \frac{x}{2} \left(\dot{\psi} + \frac{\sin \psi}{x} \right)^2 + \frac{\Sigma}{k} x + \gamma \frac{\dot{x} - \cos \psi}{2\pi k}$$

$\gamma(s)$ is a Lagrange multiplier function that ensure the relation between x and ψ is satisfied.

We aim to minimize the functional F using a variational approach, where $\delta F = 0$. Here, δF represents the variation with respect to the shape of the vesicle. Upon minimizing this functional, we obtain a system of differential equations that characterizes the shape of the vesicle.

This process is analogous to the method used in classical mechanics for minimizing the action functional with respect to a trajectory.

Euler-Lagrange equations: The solution of the minimization of functional F is given by the Euler-Lagrange equations.

In general, given a functional I :

$$I = \int_{x_a}^{x_b} L(x, f_1(x), f_2(x), \dots, \dot{f}_1(x), \dot{f}_2(x), \dots)$$

where $\dot{f}_i(x) = \frac{df_i}{dx}$ the Euler-Lagrange equations are:

$$\frac{d}{dx} \left[\frac{\partial L}{\partial \dot{f}_i} \right] - \frac{\partial L}{\partial f_i} = 0$$

The total variation δF is:

$$\delta F = \int_{s_1}^{s_2} \left[\left(\frac{d}{ds} \left[\frac{\partial L}{\partial \dot{\psi}} \right] - \frac{\partial L}{\partial \psi} \right) \delta \psi + \left(\frac{d}{ds} \left[\frac{\partial L}{\partial \dot{x}} \right] - \frac{\partial L}{\partial x} \right) \delta x \right] ds$$

The two Euler-Lagrange terms in equation must vanish separately at equilibrium, leading to the following differential equations:

$$\frac{d}{ds} \left[\frac{\partial L}{\partial \dot{\psi}} \right] - \frac{\partial L}{\partial \psi} = 0$$

Substituting will lead to

$$\ddot{\psi} = \frac{\sin \psi \cos \psi}{x^2} - \gamma \frac{\sin \psi}{2\pi k x} - \frac{\dot{x} \dot{\psi}}{x}$$

Similarly, for the second term:

$$\frac{d}{ds} \left[\frac{\partial L}{\partial \dot{x}} \right] - \frac{\partial L}{\partial x} = 0$$

Substituting here gives:

$$\dot{\gamma} = 2\pi \Sigma + k\pi \dot{\psi}^2 - \frac{k\pi \sin(\psi)^2}{x^2}$$

We can rewrite in first order terms substituting $\dot{\psi} = u$:

$$\begin{cases} \frac{d\psi}{ds} = u \\ \frac{du}{ds} = \left[-\frac{u}{x} \cos \psi + \frac{\cos(\psi) \sin(\psi)}{x^2} + \frac{\gamma \sin \psi}{2\pi k x} \right] \\ \frac{d\gamma}{ds} = \left[\pi k \left(u^2 - \frac{\sin^2 \psi}{x^2} \right) + 2\pi \Sigma \right] \end{cases} \quad (1)$$

Hamiltonian function:

$$H = -L + \dot{\psi} \frac{\partial L}{\partial \dot{\psi}} + \dot{x} \frac{\partial L}{\partial \dot{x}} = \frac{1}{2} u^2 x + \gamma \frac{\cos \psi}{2k\pi} - \frac{x \Sigma}{k} - \frac{\sin \psi^2}{x}$$

H is conserved because $\frac{\partial L}{\partial s} = 0$. It also leads to the boundary condition for $\gamma(s)$ see eqs 3.7 from [6].

1.1 Physical quantity of the system

The following ones are the physical quantities or the constitutive relations involved in our system of interest:

- R_{pa} particle radius
- $|W|$ adhesive energy density for area unit
- R_{ve} radius of vesicle
- k bending rigidity

We can describe the system using two adimensional quantity:

$$r_{pa} = \frac{R_{pa}}{R_{ve}}$$

$$w = \frac{|W|R_{pa}^2}{k}$$

2 Shape ODE system

The following is the set of differential equation needed to describe the equilibrium shape of a membrane that interacts with an external particle. This system of equation is:

- ordinary because the independent variable is always \bar{s} .
- First order because all the derivatives are first derivative
- Non linear because of non linear terms like squares or trigonometric functions.
- it is a system because the dependent variables are coupled.

$$\begin{cases} \frac{d\psi}{ds} = u \\ \frac{du}{ds} = \left[-\frac{u}{x} \cos \psi + \frac{\cos(\psi) \sin(\psi)}{x^2} + \frac{\gamma \sin \psi}{2\pi k x} \right] \\ \frac{d\gamma}{ds} = \left[\pi k \left(u^2 - \frac{\sin^2 \psi}{x^2} \right) + 2\pi \Sigma \right] \\ \frac{dx}{ds} = \cos \psi \end{cases} \quad (2)$$

2.1 Non-dimensionalization step

$$R_{ve} = \sqrt{\frac{A}{4\pi}}$$

Given R_{ve} as length scale, k as basic energy scale and s^\star as the bound arc length we can rewrite our equation in a unitless form:

The dash symbols are the unitless quantities. **write in a better way, maybe in a table**

$$\bar{\psi} = \psi$$

$$\bar{u} = uR_{ve}$$

$$\bar{x} = \frac{x}{R_{ve}}$$

$$\bar{\gamma} = \gamma R_{ve}$$

$$\bar{\Sigma} = \Sigma \frac{R_{ve}^2}{k}$$

$$\bar{A} = \frac{A}{4\pi R_{ve}^2}$$

$$\bar{V} = \frac{3V}{4\pi R_{ve}^3}$$

$$\bar{s} = \frac{s}{s^\star}$$

$$s^\star = \frac{s^\star}{s^\star} = 1$$

$$\Omega = \frac{s^\star}{R_{ve}}$$

Substitute in the system we get:

$$\begin{cases} \frac{d\bar{\psi}}{d\bar{s}} = \Omega \bar{u} \\ \frac{d\bar{u}}{d\bar{s}} = \Omega \left[-\frac{\bar{u}}{\bar{x}} \cos \bar{\psi} + \frac{\cos(\bar{\psi}) \sin(\bar{\psi})}{\bar{x}^2} + \frac{\bar{\gamma} \sin \bar{\psi}}{2\pi k \bar{x}} \right] \\ \frac{d\bar{\gamma}}{d\bar{s}} = \Omega \left[\pi k (\bar{u}^2 - \frac{\sin^2 \bar{\psi}}{\bar{x}^2}) + 2\pi \bar{\Sigma} k \right] \\ \frac{d\bar{x}}{d\bar{s}} = \Omega \cos \bar{\psi} \end{cases} \quad (3)$$

2.2 Initial conditions and parameters

We ended up with 5 ODEs, we have five boundary conditions at the South Pole ($s = 0$):

$$\psi(s = 0) = 0, u(s = 0) = u_0, \gamma(s = 0) = 0$$

$$x(s = 0) = 0$$

Explanation of BCs: We also have 3 boundary conditions at the North Pole $s = s^*$:

$$\bar{\psi}(s^*) = \bar{\psi}^* = \pi + \phi$$

$$\bar{x}(s^*) = \bar{x}^* = \frac{R_{pa}}{R_{ve}} \sin \phi = r_{pa} \sin \phi$$

$$\bar{u}(s^*) = \bar{u}^* = \frac{R_{ve}}{R_{pa}} = \frac{1}{r_{pa}}$$

Oss: We dont have an equation for the volume because in simulation we are not constraining it and there is no energy cost in changing vesicle internal volume.

Then, we have 3 unknown parameters:

$$\Sigma, s^*, u_0$$

We can use some informed guesses to put some bounds on these parameters.

- u_0 should be positive

- Ω should be equal to π in the unperturbed (no particle) case.
- Σ not too big

Boundary values of $\gamma(s)$ Hamiltonian $H(s = 0) = 0$ and substituting the value for ψ, x I obtain $\gamma(s = 0) \cos(\psi(s = 0)) = 0$ and then $\gamma(s = 0) = 0$. Assuming that H is conserved because it is an energy, $H(s = s^*) = 0$:

$$\gamma^* = -2\pi R_{pa} \Sigma \tan \phi$$

3 Numerical protocol

- assuming that the constitutive relations of the system r_{pa} and w are given and we know its values.
- you will choose a value for ϕ the wrapping angle and you will know the A_{bo} **it would be cool to have the phi as optimal parameter from minimization of the total free energy instead of setting his value manually**
- now you have everything to calculate the bound free energy E_{bo}
- shooting method for the unbound shape:
 - you will start with choosing random free parameters Σ , s^* and u_0
 - you will numerically integrate the ODE system knowing the initial conditions for ψ, u, γ, x
 - after the integration you calculate the residual function R as the error between the boundary conditions and the solution (obtained integrate the ODEs) at $s = s^*$:

$$R = (\psi(s^*) - \bar{\psi}^*)^2 + (u(s^*) - \bar{u}^*)^2 + (x(s^*) - \bar{x}^*)^2$$

We have three unknown free parameters so you will need three residuals to have a well defined problem.(3 residual equation, 3 unknowns). Minimize this error function corresponds to find the best parameters that match the solution with the boundary conditions. To minimize this function a variety of algorithm are possible, we will use least squares method.

- calculate the total free energy of the system
- establish if the total free energy is a minimum/stable state for the chosen combination of constitutive relations and contact angle ϕ .

Oss: the values obtained for the free parameters changes when you change the angle ϕ . in the same way the free parameters changed in the Felix paper when he changed m and ν .

3.1 Least squares method

4 Expansion at the South pole

At $s = 0$ $x(s)$ goes to zero and it appears as denominator and it leads to divergences causing numerical instability. An easy way to solve this is to regularize the functions at the "South pole" when $s = 0$. Regularization means Taylor expansion of all functions around $s = 0$.

First you need to expand $x(s), \psi(s), u(s), \gamma(s)$ and substitute the expansion in each equation (both sides) of the system. Then equating the coefficient of the polynomials you can get the series coefficient.

$$u(s) = u(0) + u_1 s + \frac{u_2}{2} s^2 + \frac{u_3}{6} s^3 + \frac{u_4}{24} s^4 + O(s^4)$$

$$\cos(\psi(s)) = 1 - \frac{\psi(s)^2}{2} + \frac{\psi(s)^4}{24} = 1 - \frac{1}{2} U_0^2 s^2 + \frac{U_0 \psi_2}{2} s^3 + \left(\frac{\psi_2^2}{8} + \frac{U_0 \psi_3}{6} \right) s^4 + O(s^4);$$

Considering the simplest (and not trivial) equation from our system $\frac{dx}{ds} = \cos \psi$ and performing this substitution we'll get the coefficients for x expansion:

$$x_1 = 1, \quad x_2 = 0, \quad x_3 = -u_0^2, \quad x_4 = 0$$

$$x(s) = s - \frac{s^3 u_0^2}{6};$$

The another equations from the system are quite challenging to deal on pen and paper and for that we have used a Mathematica script to perform the expansion. The final values for the coefficient are:

$$x_1 = 1, \ x_2 = 0, \ x_3 = -u_0^2, \ x_4 = 0$$

$$\begin{aligned} \psi_1 &= u_0, \ \psi_2 = 0, \ \psi_4 = 0 \\ \psi_3 &= \frac{3\gamma_1 u_0 - 4\pi k u_0^3}{2\pi k} = \frac{6\pi \Sigma u_0 - 4\pi k u_0^3}{2\pi k} \end{aligned}$$

$$\begin{aligned} \gamma_1 &= 2\pi \Sigma, \ \gamma_2 = 0 \\ \gamma_3 &= \frac{4}{3} k \pi \psi_3 u_0 = 4\pi (\Sigma u_0 - \frac{2}{3} k u_0^3), \ \gamma_4 = 0 \end{aligned}$$

$$A_1 = 0, \ A_2 = 2\pi, \ A_3 = 0, \ A_4 = -2\pi u_0^2$$

Then if you want to reconstruct the series:

$$x(s) = x_1 s + \frac{x_2}{2} s^2 + \frac{x_3}{6} s^3 + \frac{x_4}{24} s^4 = s - \frac{u_0^2}{6} s^3$$

$$\gamma(s) = 2\pi \Sigma s + \frac{2}{9} k \pi \psi_3 u_0 s^3 = 2\pi \Sigma s + \frac{1}{9} u_0 (6\pi u_0 \Sigma - 4k u_0^3) s^3$$

$$\psi(s) = u_0 s + \frac{3\Sigma u_0 - 2k u_0^3}{6k} s^3$$

$$\begin{aligned} u(s) &= u(0) + u_1 s + \frac{u_2 s^2}{2} + \frac{u_3 s^3}{6} + \frac{u_4 s^4}{24} = u_0 + \psi_2 s + \frac{\psi_3 s^2}{2} + \frac{\psi_4 s^3}{6} + \frac{\psi_5 s^4}{24} \\ &= u_0 + \frac{3\Sigma u_0 - 2k u_0^3}{2k} s^2 \end{aligned}$$

This expansions still need to be non-dimensionalized.

4.1 Non-dimensionalization of the expansion

The dash symbols are the unitless quantities and we applied the same transformations previously used.

$$\bar{x}_1 = \Omega, \quad \bar{x}_3 = -\Omega^3 \bar{u}_0^2$$

$$\bar{\psi}_1 = \Omega \bar{u}_0$$

$$\bar{\psi}_3 = (3\bar{\Sigma}\bar{u}_0 - 2\bar{u}_0^3)\Omega^3$$

$$\bar{u}_0 = \bar{u}_0$$

$$\bar{u}_1 = \frac{\Omega^2}{2}(3\bar{u}_0\bar{\Sigma} - 2\bar{u}_0^3)$$

$$\gamma_1 = 2\pi\bar{\Sigma}k\Omega$$

$$\gamma_3 = \frac{4}{3}\pi k\bar{u}_0\Omega^3(3\bar{\Sigma}\bar{u}_0 - 2\bar{u}_0^3)$$

$$\bar{V}_4 = \frac{9}{2}\bar{u}_0\Omega^4$$

$$\bar{A}_2 = \frac{1}{2}\Omega^2, \quad \bar{A}_4 = -\frac{1}{2}\bar{u}_0^2\Omega^4$$

5 Expansion at North Pole

Our problem is different from [5] because we are not integrating from Southpole $s = 0$ to the Northpole where we have again divergence caused from the radius $x(s = 1) = 0$.

In our problem we will integrate from $s = 0$ to the contact point between particle and vesicle. this contact point is not that close to the z-axis (rotational simmetry axis) such that $x(s^*) \neq 0$ and not leading to any divergence.

It should be enough to just check after having set the constitutive relation if $x(s^*)$ is big enough to not lead to divergences. Felix sets this threshold at 0.035.

For $\phi \leq 20^\circ$ or $\phi \geq 165^\circ$: in this case it is needed to expand the north pole as done in the south pole case.

6 Non-dimensionalization of E_{bo} and E_{un}

$$\bar{E}_{bo} = (-2\pi\bar{W}r_{pa}^2 + 4\pi)(1 - \cos \phi)$$

$$\bar{E}_{un} =$$

6.1 Doubts and Questions

- Assess the stability of the solution: from different initial guess you can get slightly different solutions.
- Compare the Energy with the unperturbed spherical vesicle $E = 8\pi k$ (maybe 4 ?)

See the code at: Github repository

7 More on Shooting method

The following two are two complex examples solved using shooting method. First for the tallest column [4] and second for optimal javelin shape [3]. Found these two papers from here <https://mathoverflow.net/questions/21257/what-is-state-of-the-art-for-the-shooting-method>

7.1 Stability of the procedure

Unfortunately, we have noticed that the final value of the free parameters is affected but their initial guesses.

This is related to the fact that we have used Least squares method, a local optimization algorithm and we are not exploring all the parameters space. So we get stuck in a local minima.

TODO list

- understand concepts of stable manifold, fixed points etc
- another possibility is that our description of the system is not correct
- insted of shooting till the north pole, we can try to match the BCs in the middle of the path.

7.2 Least squares method

check <https://www2.imm.dtu.dk/pubdb/edoc/imm3215.pdf> for nice intro

A Jacobian Matrix

This ODE system now is written in the standard form:

$$\frac{d}{ds}\mathbf{Y} = \mathbf{f}(\mathbf{Y})$$

where

$$\mathbf{Y} = (\bar{\psi}, \bar{u}, \bar{\gamma}, \bar{x}, \bar{A}, \bar{V})$$

and

$$\mathbf{f} : \mathbb{R}^6 \rightarrow \mathbb{R}^6$$

The Jacobian is needed for the algorithm used by Felix but in principle with Runge-Kutta methods is not needed because it is calculated by finite difference method.

Oss: Now the following quantities are not dashed but they are already in their adimensional form, so consider for example $\psi(s)$ as $\bar{\psi}(\bar{s})$.

However:

$$\mathbf{J} = \begin{bmatrix} \frac{\partial f_1}{\partial \mathbf{Y}} \\ \frac{\partial f_2}{\partial \mathbf{Y}} \\ \vdots \\ \frac{\partial f_n}{\partial \mathbf{Y}} \end{bmatrix} = \begin{bmatrix} \frac{\partial f_1}{\partial \psi} & \frac{\partial f_1}{\partial u} & \frac{\partial f_1}{\partial \gamma} & \dots & \dots \\ \frac{\partial f_2}{\partial \psi} & \frac{\partial f_2}{\partial u} & \frac{\partial f_2}{\partial \gamma} & & \\ \vdots & \vdots & & & \\ \frac{\partial f_n}{\partial \psi} & \frac{\partial f_n}{\partial u} & \frac{\partial f_n}{\partial \gamma} & \dots & \dots \end{bmatrix}$$

$$\mathbf{J} = \begin{bmatrix} 0 & a_{12} & 0 & 0 & 0 & 0 \\ a_{21} & a_{22} & a_{23} & a_{24} & 0 & 0 \\ a_{31} & a_{32} & 0 & a_{34} & 0 & 0 \\ a_{41} & 0 & 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & a_{54} & 0 & 0 \\ a_{61} & 0 & 0 & a_{64} & 0 & 0 \end{bmatrix}$$

$$a_{12} = \frac{df_\psi}{du} = \Omega$$

$$a_{21} = \frac{df_u}{d\psi} = \Omega \left(\frac{u}{x} \sin \psi + \frac{1}{x^2} \cos^2 \psi - \frac{1}{x^2} \sin^2 \psi \frac{\gamma}{2\pi k x} \cos \psi \right)$$

$$a_{22} = \frac{df_u}{du} = -\frac{\Omega}{x} \cos \psi$$

$$a_{23} = \frac{df_u}{d\gamma} = \Omega \frac{\sin \psi}{2\pi k x}$$

$$a_{24} = \frac{df_u}{dx} = \Omega \left(\frac{u}{x^2} \cos \psi - 2 \frac{\cos \psi \sin \psi}{x^3} - \frac{\gamma \sin \psi}{2\pi k x^2} \right)$$

$$a_{31} = \frac{df_\gamma}{d\psi} = \Omega \left(-\pi k \frac{\cos \psi}{x^2} \right)$$

$$a_{32} = \frac{df_\gamma}{du} = \Omega \pi k 2u$$

$$a_{34} = \frac{df_\gamma}{dx} = 2\Omega \pi k \sin \psi \frac{1}{x^3}$$

$$a_{41} = \frac{df_x}{d\psi} = -\Omega \sin \psi$$

$$a_{54} = \frac{df_A}{dx} = \Omega$$

$$a_{61} = \frac{df_V}{d\psi} = \Omega \frac{3}{4} x^2 \cos \psi$$

$$a_{64} = \frac{df_V}{dx} = \frac{3}{2} \Omega x \sin \psi$$

References

- [1] Jaime Agudo-Canalejo and Reinhard Lipowsky. “Critical Particle Sizes for the Engulfment of Nanoparticles by Membranes and Vesicles with Bilayer Asymmetry”. In: *ACS Nano* 9.4 (Apr. 28, 2015), pp. 3704–3720. ISSN: 1936-0851, 1936-086X. DOI: 10.1021/acsnano.5b01285. URL: <https://pubs.acs.org/doi/10.1021/acsnano.5b01285> (visited on 05/02/2024).
- [2] Simon Christ et al. “Active Shape Oscillations of Giant Vesicles with Cyclic Closure and Opening of Membrane Necks”. In: *Soft Matter* 17.2 (2021), pp. 319–330. ISSN: 1744-683X, 1744-6848. DOI: 10.1039/D0SM00790K. URL: <http://xlink.rsc.org/?DOI=D0SM00790K> (visited on 06/15/2023).
- [3] Yossi Farjoun and John C. Neu. *The Optimal Shape of a Javelin*. Nov. 5, 2007. arXiv: 0711.0734 [math-ph]. URL: <http://arxiv.org/abs/0711.0734> (visited on 06/21/2024). Pre-published.
- [4] Yossi Farjoun and John C. Neu. *The Tallest Column – A Dynamical System Approach Using a Similarity Solution*. Jan. 21, 2008. arXiv: 0711.0730 [math-ph]. URL: <http://arxiv.org/abs/0711.0730> (visited on 06/21/2024). Pre-published.
- [5] Felix Frey and Timon Idema. “Membrane Area Gain and Loss during Cytokinesis”. In: *Physical Review E* 106.2 (Aug. 2, 2022), p. 024401. ISSN: 2470-0045, 2470-0053. DOI: 10.1103/PhysRevE.106.024401. URL: <https://link.aps.org/doi/10.1103/PhysRevE.106.024401> (visited on 08/25/2023).
- [6] Udo Seifert, Karin Berndl, and Reinhard Lipowsky. “Shape Transformations of Vesicles: Phase Diagram for Spontaneous- Curvature and Bilayer-Coupling Models”. In: *Physical Review A* 44.2 (July 1, 1991), pp. 1182–1202. ISSN: 1050-2947, 1094-1622. DOI: 10.1103/PhysRevA.44.1182. URL: <https://link.aps.org/doi/10.1103/PhysRevA.44.1182> (visited on 04/30/2024).