

Brief Report

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Article

Dynamics of Membrane Tension Propagation in Eukaryotic Cells

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Abstract: The propagation of membrane tension perturbations is a potentially critical mechanism in the mechanical signal transduction across the surfaces of living cells. Tethered proteins in the cell membrane play a crucial role in the propagation of the membrane tension. Intact cell membranes in eukaryotic cells possess unique characteristics, such as transmembrane proteins bound to the underlying cortex, rendering them immobile over timescales of minutes to hours. These immobile obstacles significantly alter the dynamics of lipid flow. While existing simplified lipid flow models provide fundamental insights into membrane tension dynamics, they fall short in accounting for complex phenomena like vesicle crumpling. To address this, we propose a more sophisticated model of lipid bilayers, solving the Stokes equations in a two-dimensional framework with embedded obstacles. We employ the finite element method and the FEniCS library to solve the weak form of the Stokes equations, providing a more accurate representation of membrane behaviour under physiological conditions.

Keywords: cell membrane; Stokes equations; finite element method

Introduction

The deformability of the membrane, the outermost surface of living cells, allows cells to be dynamic, mobile and flexible. Factors that affect this deformability, such as tension on the membrane, can regulate a myriad of cellular functions, including membrane resealing, cell motility, polarization, shape maintenance, membrane area control, and endocytic vesicle trafficking [1]. Houk and coworkers showed how membrane tension regulated cell polarity in HL-60 cells [2]. Plasma membrane tension regulates many key cellular processes. It is modulated by and can modulate membrane trafficking [3]. It is widely assumed that membrane flow transmits local changes in membrane tension across the cell in milliseconds, mediating long-range signalling. Propagation of membrane tension occurs quickly in cell-attached blebs but is suppressed mainly in intact cells [4]. Fused vesicle membranes undergo actomyosin-mediated folding and retention, preventing them from incorporating into the apical surface. In addition, the diffusion of proteins and lipids between the fused vesicle and the apical surface is limited [5]. Membrane tension affects cell migration, vesicle fusion and recycling, the cell cycle, cell signalling, and mechanosensation [6–8]. However, there has been controversy over the speed and degree to which local changes in membrane tension propagate in cells [9]. In artificial lipid bilayers, changes in membrane tension propagate across a cell-sized region in milliseconds [10]. Cell migration and spreading involve the coordination of membrane trafficking, actomyosin contraction, and modifications to plasma membrane tension and area [6]. Cell membranes are not smooth, continuous surfaces. They contain immobile obstacles like transmembrane proteins anchored to the cytoskeleton. These obstacles influence the flow of lipids and proteins, creating non-uniform tension across the membrane. In this study, we solve Stokes equations with embedded obstacles, which will help to understand the model of how irregularities in the membrane affect the overall membrane tension, providing a more realistic representation of cellular behaviour.

Problem Formulation

The Stokes equations, fundamental in fluid dynamics, describe the flow of incompressible fluids. The Stokes equation is applied to describe lipid flow through a medium comprising randomly dispersed immobile obstacles [11]. These equations take the form:

$$-\Delta u + \nabla p = f \quad \text{in } \Omega,$$

$$\nabla \cdot u = 0 \quad \text{in } \Omega,$$

along with suitable boundary conditions. Here, we present a FEniCS implementation of a mixed finite element method to solve the Stokes equations in 2D. For this purpose, we need to derive the weak form of the Stokes equations.

Weak Form Derivation

To derive the weak form of the Stokes equations, we multiply the momentum equation by a test function $v \in V$ and the continuity equation by a test function $q \in Q$, then integrate over the domain Ω . Applying Green's formula, we obtain:

$$(\nabla p - \Delta u, v) = -(p, \nabla \cdot v) + (\nabla u, \nabla v) + \langle pn - \nabla u \cdot n, v \rangle_{\Gamma}.$$

We seek a finite element approximation $(u, p) \in V \times Q$ such that:

$$-(p, \nabla \cdot v) + (\nabla u, \nabla v) + (\nabla \cdot u, q) + \langle pn - \nabla u \cdot n, v \rangle_{\partial\Omega} = (f, v)$$

for all test functions $(v, q) \in V \times Q$.

Here,

$$(v, w) = \int_{\Omega} v \cdot w \, dx, \quad \langle v, w \rangle_{\partial\Omega} = \int_{\partial\Omega} v \cdot w \, ds.$$

Boundary Conditions

We divide the boundary into $\partial\Omega = \Gamma_D \cup \Gamma_N$, with the boundary conditions:

$$u = g_D \quad \text{on } \Gamma_D,$$

$$pn - \nabla u \cdot n = g_N \quad \text{on } \Gamma_N.$$

For $x \in \Gamma_D$, the test function v vanishes. With $g_N = 0$, the boundary term is zero, simplifying the residual form:

$$r(u, p; v, q) = -(p, \nabla \cdot v) + (\nabla u, \nabla v) + (\nabla \cdot u, q) - (f, v).$$

Finite Element Approximation

We use inf-sup stable Taylor-Hood approximation spaces for the finite element method. To implement the velocity boundary conditions, a penalty formulation is employed with a penalty parameter $\gamma = C/h$, where $C > 0$ is a constant and h is the local mesh size. A "do nothing" stress-free boundary condition is applied at the outflow boundary.

FEniCS Implementation

The FEniCS implementation involves defining the mesh, function spaces, boundary conditions, and the variational problem. The solution is computed and saved as PVD files, which can be visualized using ParaView. The velocity and pressure fields are also plotted using FEniCS plotting functions.

Results

Initial simulations in a rectangular domain with circular obstacles demonstrate smooth and continuous velocity fields. The pressure distribution aligns well with theoretical predictions. See Figures 2 and 3. Figures 6–8 are captured using ParaView software. Code is accessible via GitHub in [12].

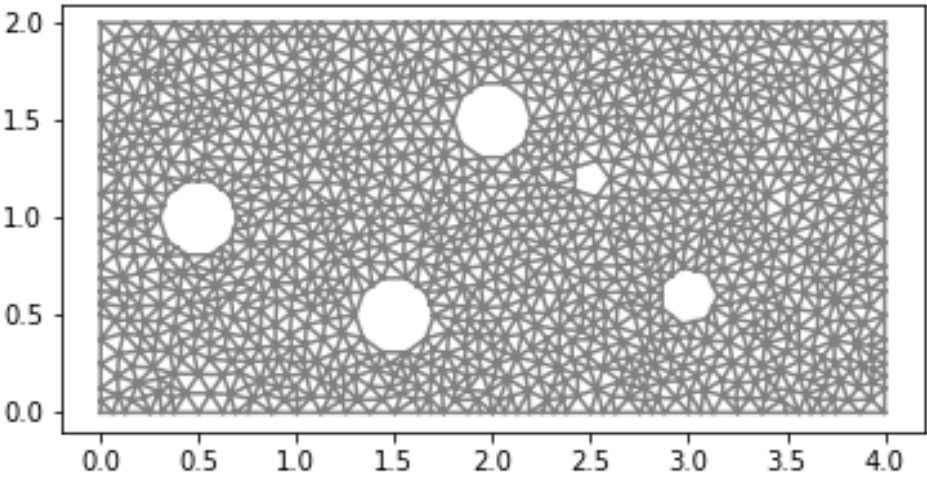


Figure 1. Mesh.

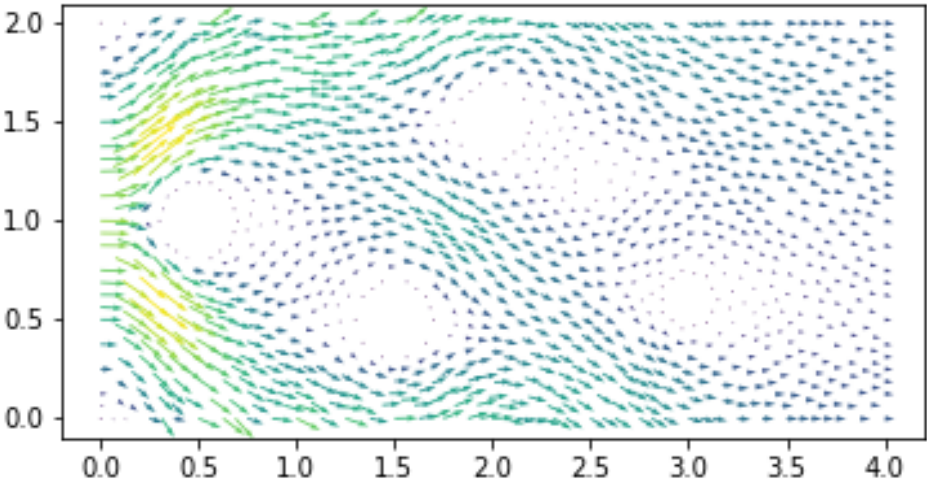


Figure 2. Velocity.

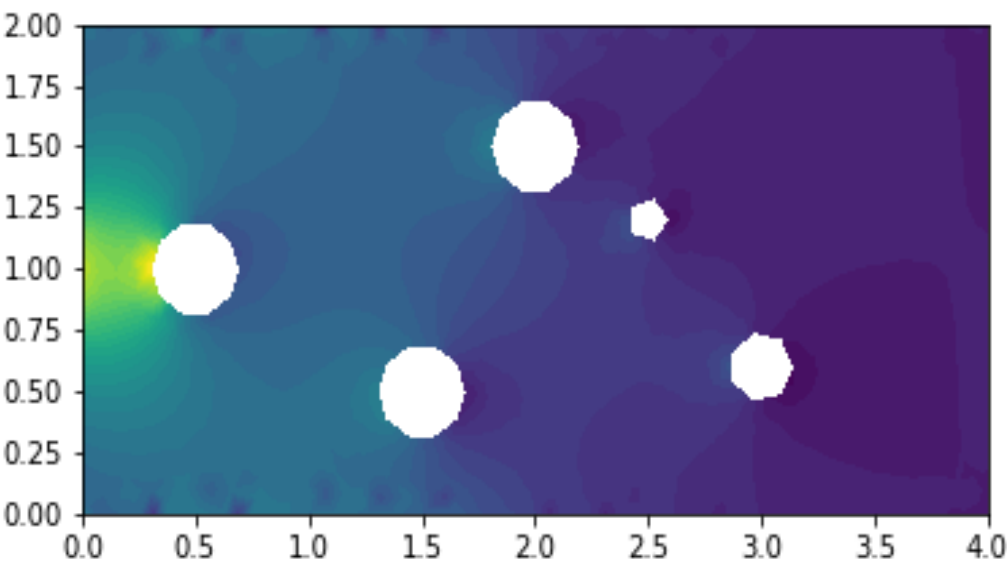


Figure 3. Pressure.

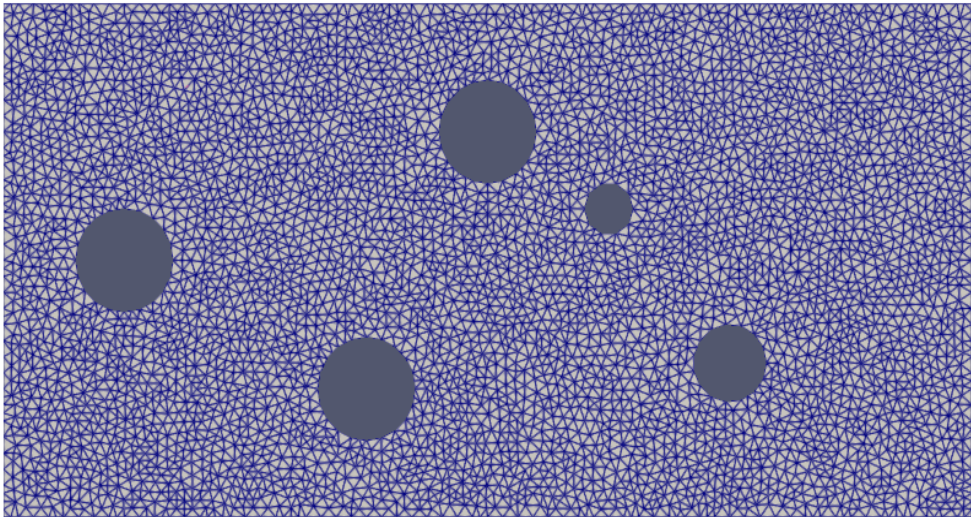


Figure 4. Mesh.

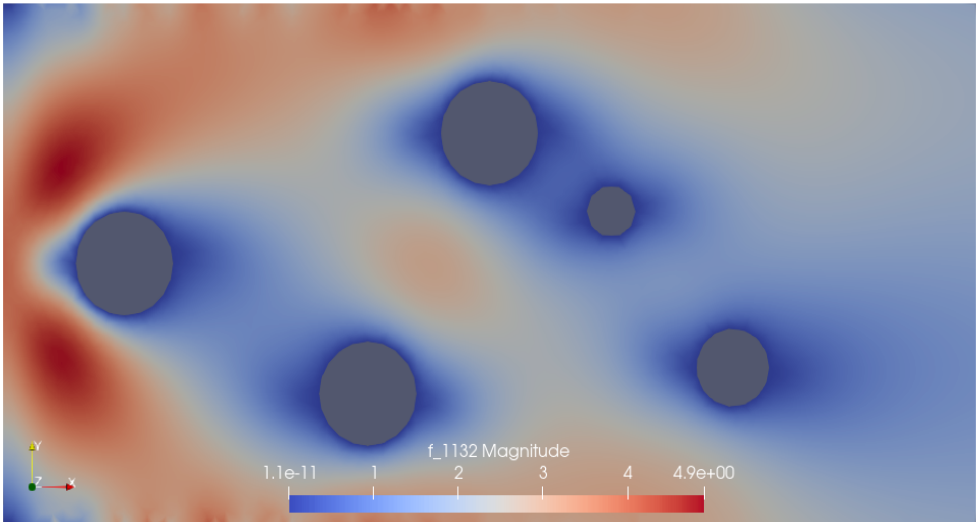


Figure 5. Velocity.

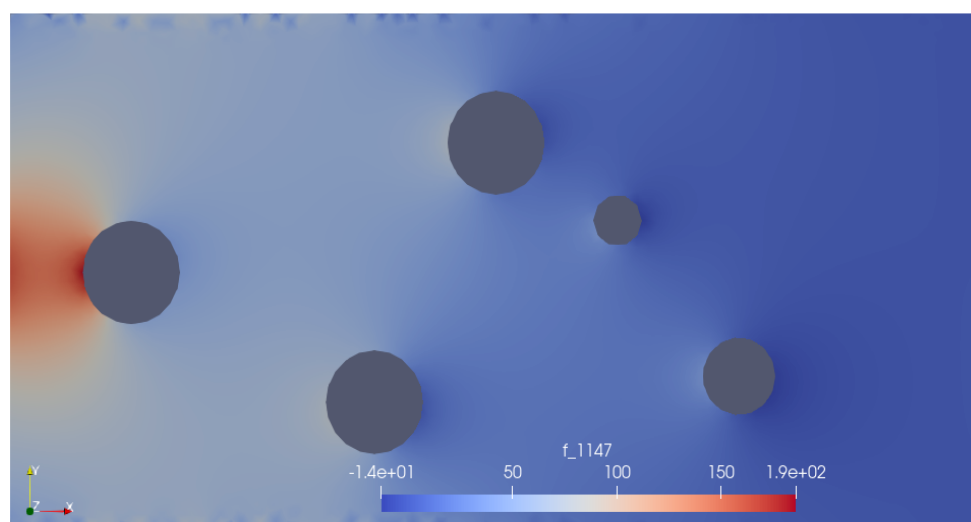


Figure 6. Pressure.

Conclusions and Way Forward

In this study, we have successfully solved the Stokes equations in a 2D framework with embedded obstacles, applying no-slip and periodic boundary conditions. This approach will be helpful to simulate the complex flow dynamics and membrane tension distribution in a simplified model of the cellular membrane environment. The results of our simulations will provide valuable insights to study further how obstacles, such as tethered proteins, can influence the behaviour of lipid flow and membrane tension propagation. Pressure drop boundary conditions will be implied to test whether the flow is Darcy. The paper [11] will help implement the pressure boundary conditions. It is reasonable to consider the code written in [13] to move the circular solids with the fluid velocity and to calculate the density of the circular obstacles in the fluid. To understand the code [13], one has to understand the Arbitrary Lagrangian Eulerian (ALE) formulation.

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