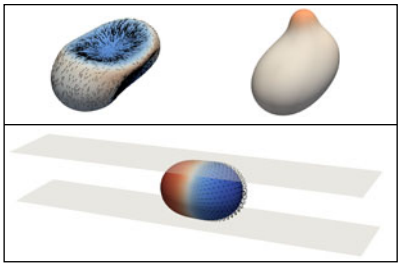
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Fluid deformable surfaces



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Lipid membranes are examples of fluid deformable surfaces, which can be viewed as two-dimensional viscous fluids with bending elasticity. With this solid–fluid duality any shape change contributes to tangential flow and *vice versa* any tangential flow on a curved surface induces shape deformations. This tight coupling between shape and flow makes curvature a natural element of the governing equations. The modelling and numerical tools outlined in Torres-Sánchez *et al.* (*J. Fluid Mech.*, vol. 872, 2019, pp. 218–271) open a new field of study by enabling the exploration of the role of curvature in this context.

Key words: membranes, interfacial flows, morphological instability

1. Introduction

Fluid deformable surfaces are ubiquitous interfaces in biology, playing an essential role in processes from the subcellular to the tissue scale. For instance, lipid membranes are fluidic thin sheets that define the boundaries of cells and compartmentalize them. From a mechanical point of view, lipid membranes are soft materials exhibiting a solid–fluid duality: while they store elastic energy when stretched or bent, like solid shells, they cannot do so under in-plane shear, a situation under which they flow as two-dimensional, viscous fluids. These two features, out-of-plane elasticity and interfacial viscosity, have often been examined separately. Mechanical equilibrium can essentially be understood with the classical bending model of Helfrich (1973) and the modelling of the hydrodynamics of fluid films goes back to Scriven (1960). Based on Onsager's variational formalism Torres-Sánchez, Millán & Arroyo (2019*a*) derive a first approximation to the dynamics of lipid membranes by combining bending and surface hydrodynamics. Omitting inertial effects, the derived equations correspond to the force and torque balance equations and the constitutive

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laws postulated in Salbreux & Jülicher (2017) as well as the thin-film limit of the corresponding bulk model equations in Nitschke, Reuther & Voigt (2019). The major contribution of Torres-Sánchez *et al.* (2019*a*) is not only a systematic and transparent way to derive the governing equations in the fully nonlinear regime, but also a computational framework for these equations which goes beyond previously studied axisymmetric settings (Arroyo & DeSimone 2009). Thus, the tight coupling between tangent flows and shape changes in the presence of curvature can for the first time be explored in its full beauty. Any shape change contributes to strains and so must be accompanied by a tangent flow and *vice versa*, tangential flows on curved surfaces induce shape deformations. This coupling makes curvature a natural element of the governing equations of fluid deformable surfaces. This pioneering exploration of the role of curvature is made possible with the modelling and numerical tools outlined in Torres-Sánchez *et al.* (2019*a*).

2. Overview

Besides their excellent overview of the subject, Torres-Sánchez *et al.* (2019*a*) make three main contributions: they use Onsager's variational formalism to derive equations in a thermodynamically consistent way, they apply an arbitrary Lagrangian–Eulerian (ALE) formulation for their numerical solution and they consider various applications, with models and simulations which surpass previous approaches.

It is a challenging task to derive governing equations which couple shape evolution and surface flow in a thermodynamically consistent way. In contrast to scalar quantities, where the transport theorem provides all the necessary tools to transport them on an evolving surface, such tools do not exist for vector quantities, like the tangential velocity field. A componentwise interpretation, a concept we are used to in flat space, does not make sense on a curved surface. There are various options to mathematically define a directional derivative on an evolving surface, each with a different physical meaning, either more appropriate for solids or for fluids. The derivation of the equations using variational methods requires, e.g. to vary the underlying energy with respect to shape changes, while considering the surface quantity, here the tangential velocity, as an independent variable. The definition of the directional derivative is key to this approach and needs to be considered carefully given the solid–fluid duality of lipid membranes. Although Torres-Sanchez *et al.* also have to deal with this issue, they consider a more abstract setting, a nonlinear Onsager formalism; see Doi (2011), Mielke (2012) and Arroyo *et al.* (2018). This provides a unified variational framework for the dissipative dynamics of soft matter systems, where the dynamics minimizes a Rayleighian functional and results from the interplay between energetic driving forces, dissipative drag forces and external forces, each of them deriving from potentials that are the sum of individual contributions for each physical mechanism. This formalism is ideally suited for complex multiphysics problems, because new components can simply be added term by term to the energy and dissipation potentials together with their interaction. Also constraints can be added in a natural way using Lagrange multipliers. As long as inertial effects can be neglected, the nonlinear Onsager formalism is certainly the most systematic and transparent way to derive such nonlinearly coupled systems of equations.

The derived set of equations contains surface-vector-valued partial differential equations (PDE), e.g. the surface Stokes equation with the tangential velocity field as an unknown. Again, tools used for scalar quantities cannot be applied to each component, as would be appropriate in flat space, and new numerical methods are

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required. Torres-Sánchez *et al.* (2019*a*) circumvent this problem by considering a vorticity–streamfunction approach, which transforms the problem into a set of scalar-valued PDEs for which various numerical approaches have been developed; see Dziuk & Elliott (2013) for an overview. As also mentioned in Torres-Sánchez *et al.* (2019*a*), this restricts applicability to simply connected surfaces, as otherwise the tangential velocity field contains, in addition to irrotational and solenoidal components, non-trivial harmonic vector fields that cannot be represented by the vorticity, see Nitschke, Reuther & Voigt (2017) for an example. For general surfaces a direct approach using velocity and pressure as unknowns is required. One idea to deal with tangential velocity fields is to consider non-tangential fields on the surface and impose tangentiality through constraints; see Fries (2018), Reuther & Voigt (2018) for a finite element realization for surface Navier–Stokes equations. The concept is extended to general surface vector and tensor fields in Nestler, Nitschke & Voigt (2019). Another approach to solve surface vector- and tensor-valued PDEs is considered in Torres-Sánchez, Santos-Olivan & Arroyo (2019*b*), which is based on a local Monge parameterization and does not required any additional degrees of freedom in the normal direction. Numerical analysis results needed for both approaches, and moreover a comparison in terms of stability, computational cost and implementational effort, do not yet exist. However, all these approaches, including that for scalar-valued PDEs, require a surface mesh that evolves in time. As for bulk problems on evolving domains, it proves computationally efficient to consider a mesh velocity which is different from the interpolated material velocity, as the additional freedom can be used to obtain beneficial mesh properties; see, e.g. Elliott & Styles (2012) and Elliott & Venkataraman (2014). The ALE formulation in Torres-Sánchez *et al.* (2019*a*) is related to these approaches, and leads to similar conclusions.

With a view to applications, the model of lipid membranes as a viscous fluid with bending elasticity is extended to the Seifert–Langer model (Seifert & Langer 1993), which accounts for the bilayer structure of the membrane by including stretching elasticity and lipid density on each layer. The ALE approach is well suited for this model, as it allows resolution of the density of both layers on the same mesh. A third model considers a viscous layer which is driven by active tension and an additional cortical density. The numerical examples considered show the relaxation dynamics from shape or density perturbations and in the last example, migration as a result of self-polarization. In all cases the solid–fluid duality of the system and the role of curvature in the coupling of shape changes and surface flow are highlighted, and the applicability of the ALE approach to solve the derived models is demonstrated.

3. Future

Torres-Sánchez *et al.* (2019*a*) outline the modelling and numerical tools to study fluid deformable surfaces and explore the role of curvature in the interaction between shape changes and flow properties. The same framework could be used to consider the interaction with chemistry, where a notable example is curving proteins, which can diffuse and absorb/dissorb. Such interaction is involved in the morphogenesis of organelle; see, e.g. Shibata *et al.* (2009) and Le Roux *et al.* (2019). Although these couplings have so far only been explored in passive systems, the most promising applications are found in active systems, where the tools outlined provide opportunities to study the dynamics of self-organized active surfaces. Modelling the cellular cortex or epithelia sheets with these tools paves the way towards an exploration of the regulatory role of curvature in morphogenetic processes. While first steps in this

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direction have already been considered for axisymmetric settings (Mietke, Jülicher & Sbalzarini 2019), primarily applicable to the fruit fly Drosophila, developmental processes in other organisms deviate from axisymmetric shapes at early times and require more general tools. Besides these new applications for fluid mechanics, new challenges can also be found in the numerical analysis of the proposed and related algorithms (Sahu *et al.* 2018; Nestler *et al.* 2019), and benchmark problems for fluid deformable surfaces would be valuable to further develop the field.

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