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Research Paper

Fractional hereditariness of lipid membranes: Instabilities and linearized evolution

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ABSTRACT

In this work lipid ordering phase changes arising in planar membrane bilayers is investigated both accounting for elasticity alone and for effective viscoelastic response of such assemblies. The mechanical response of such membranes is studied by minimizing the Gibbs free energy which penalizes perturbations of the changes of areal stretch and their gradients only (Deseri and Zurlo, 2013). As material instabilities arise whenever areal stretches characterizing homogeneous configurations lie inside the spinodal zone of the free energy density, bifurcations from such configurations are shown to occur as oscillatory perturbations of the in-plane displacement. Experimental observations (Espinosa et al., 2011) show a power-law in-plane viscous behavior of lipid structures allowing for an effective viscoelastic behavior of lipid membranes, which falls in the framework of Fractional Hereditariness. A suitable generalization of the variational principle invoked for the elasticity is applied in this case, and the corresponding Euler–Lagrange equation is found together with a set of boundary and initial conditions. Separation of variables allows for showing how Fractional Hereditariness owes bifurcated modes with a larger number of spatial oscillations than the corresponding elastic analog. Indeed, the available range of areal stresses for material instabilities is found to increase with respect to the purely elastic case. Nevertheless, the time evolution of the perturbations solving

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the Euler–Lagrange equation above exhibits time-decay and the large number of spatial oscillation slowly relaxes, thereby keeping the features of a long-tail type time-response.

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1. Introduction

Lipid bilayers are known to be building blocks of almost all types of biological membranes, as they surround the cells of almost of all living organisms. In the last decade, the growing availability of advanced microscopy and imaging techniques has determined a blooming of interest in the study of biological membranes, often revealing spectacular examples of intricate patterns at micro and nano scales (see, e.g., Baumgart et al., 2003).

The intimate presence of lipids in the cell membrane strongly influences its multiphysics and, hence, its mechanical behavior. Of course this is highly dependent on a rich list of parameters such as the configuration assumed by the lipids, the chemical composition, temperature of their watery environment and applied osmotic pressure (Bermúdez et al., 2004; Das et al., 2008; Iglic, 2012; Sackmann, 1995; Hu et al., 2012; Norouzi and Müller, 2006; Agrawal and Steigmann, 2008, 2009; Walani et al., 2015; Baumgart et al., 2005).

In particular, these amazing structures are capable to sustain bending moments and normal stress, due to their special constitutive nature, showing ordering–disordering phenomena which allow changes in the shape for responding to the external solicitations. The pioneering works on modeling the bending behavior of biological membranes can be traced back to Canham (1970) and Helfrich (1973). These models rely upon the assumptions of (i) “in-plane fluidity” and (ii) elasticity of the membrane, hence in-plane shear stress cannot arise.

Other studies on the equilibrium shapes of biomembranes include the influence of presence of embedded proteins (Canham, 1970; Jenkins, 1977; Agrawal and Steigmann, 2009; Biscari and Bisi, 2002).

The ordering–disordering phenomena have been extensively investigated (Akimov and Kuzmin, 2004; Chen et al., 2001; Falkovitz et al., 1982; Goldstein and Leibler, 1989; Iglic, 2012; Jahnig, 1981; Owicki et al., 1978; Owicki and McConnell, 1979) in order to understand their influence on the mechanical behavior of the biological membranes. This leads to the formation of buds (Lipowsky, 1992), but this transition can be also related to the molecules structure (Komura et al., 2004; Pan et al., 2009; Rawicz et al., 2000).

The energetics governing the thermo-chemo-mechanical behavior of this structure was recently derived (Deseri et al., 2008; Deseri and Zurlo, 2013; Agrawal and Steigmann, 2009; Maleki et al., 2013) for a better understanding of the mechanics of the biological membranes and a powerful tool for predicting their response whenever specific conditions occur.

The main feature of this approach is that the energetics of the membrane can be described through one single ingredient: the in-plane membrane stretching elasticity. This allows for describing the response with respect to local area changes

on the membrane mid-surface. The principle of the minimum of energy allows for characterizing the governing equation of the mechanical response of the membrane. This approach allows for determining the profile and the boundary layer of the disordering–ordering phenomena, i.e. the change from a thicker domain (ordered phase) to a thinner one (disordered phase), and their associated rigidities.

The main feature of the energy derived in Deseri and Owen (2010) is the presence of two turning points in the local stress governing the biological membrane behavior (see Fig. 2(a)). They are placed in a region characterized by material instabilities, i.e. in a spinodal zone. Henceforth, whenever the external conditions are such that the areal stretch, i.e. the reciprocal of the thinning, is enclosed in this region, the response may produce a rapid change of the geometry, i.e. material instabilities can occur. In this work, we show that this occurrence is exhibited even when the in-plane viscosity of the lipid membrane is accounted for. In this regard, the experimental observations of lipid viscous behavior showed that the loss and storage moduli are well described by power law functions (Espinosa et al., 2011). This observation suggests that the viscoelastic behavior of the biological membrane is properly described in the framework of the Fractional Hereditariness. Indeed, upon introducing an enriched kinematics accounting for in-plane shears and the exhibited in-plane power-law viscosity in a parallel contribution, a dimension reduction procedure analog to one shown in Deseri et al. (2008) and Deseri and Zurlo (2013) will be used for studying the fractional viscoelastic behavior mentioned above.

The onset of bifurcated configurations possibly arising from homogeneous configurations characterized by an areal stretch lying in the spinodal region is studied in Section 2. Here we minimize the total elastic (Gibbs free) energy to determine the bifurcated modes and the relationships between the number of nucleated spatial waves with the critical values of the areal stretches.

The influence of the effective viscoelasticity on the material instabilities exhibited by the membrane is studied in Section 3.

The problem is formulated by seeking for the values of the areal stretches for which unknown time evolving bifurcated configurations could occur. To this aim, in full analogy with the elastic case, a variational principle is employed. Here, the Gibbs free energy density is taken from Deseri et al. (2014), where a rheological model yields the Staverman–Schartz free energy (Del Piero and Deseri, 1996, 1997; Deseri et al., 2006; Deseri and Golden, 2007) as the one for power-law materials.

As in the elastic case, the viscoelastic free energy has a local and a nonlocal part. There, the power at which stress and hyperstress (which performs work against changes of the displacement gradient $u_{,x}$, see (Deseri and Zurlo, 2013) for

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