



## Fluid vesicles in flow



David Abreu<sup>a,\*</sup>, Michael Levant<sup>b</sup>, Victor Steinberg<sup>b</sup>, Udo Seifert<sup>a</sup>

<sup>a</sup> *II. Institut für Theoretische Physik, Universität Stuttgart, 70550 Stuttgart, Germany*

<sup>b</sup> *Department of Physics of Complex Systems, Weizmann Institute of Science, Rehovot 76100, Israel*

### ARTICLE INFO

Available online 13 February 2014

#### Keywords:

Vesicle  
Viscous flow  
Bending energy  
Thermal fluctuations  
Migration  
Rheology

### ABSTRACT

We review the dynamical behavior of giant fluid vesicles in various types of external hydrodynamic flow. The interplay between stresses arising from membrane elasticity, hydrodynamic flows, and the ever present thermal fluctuations leads to a rich phenomenology. In linear flows with both rotational and elongational components, the properties of the tank-treading and tumbling motions are now well described by theoretical and numerical models. At the transition between these two regimes, strong shape deformations and amplification of thermal fluctuations generate a new regime called trembling. In this regime, the vesicle orientation oscillates quasi-periodically around the flow direction while asymmetric deformations occur. For strong enough flows, small-wavelength deformations like wrinkles are observed, similar to what happens in a suddenly reversed elongational flow. In steady elongational flow, vesicles with large excess areas deform into dumbbells at large flow rates and pearling occurs for even stronger flows. In capillary flows with parabolic flow profile, single vesicles migrate towards the center of the channel, where they adopt symmetric shapes, for two reasons. First, walls exert a hydrodynamic lift force which pushes them away. Second, shear stresses are minimal at the tip of the flow. However, symmetry is broken for vesicles with large excess areas, which flow off-center and deform asymmetrically. In suspensions, hydrodynamic interactions between vesicles add up to these two effects, making it challenging to deduce rheological properties from the dynamics of individual vesicles. Further investigations of vesicles and similar objects and their suspensions in steady or time-dependent flow will shed light on phenomena such as blood flow.

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\* Corresponding author.

E-mail addresses: [david.abreu@itp2.uni-stuttgart.de](mailto:david.abreu@itp2.uni-stuttgart.de) (D. Abreu), [michael.levant@weizmann.ac.il](mailto:michael.levant@weizmann.ac.il) (M. Levant), [victor.steinberg@weizmann.ac.il](mailto:victor.steinberg@weizmann.ac.il) (V. Steinberg), [useifert@theo2.physik.uni-stuttgart.de](mailto:useifert@theo2.physik.uni-stuttgart.de) (U. Seifert).

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## 1. Introduction

Giant unilamellar vesicles (GUVs) have become a paradigmatic soft matter system for many reasons. First, even in equilibrium they exhibit an amazing variety of shapes. At fixed area and enclosed volume, these shapes result from the minimization of the bending, or “curvature”, energy

$$\mathcal{H} = \int dA \left[ \frac{\kappa}{2} (2H - C_0)^2 + \kappa_G K \right] \quad (1)$$

written here in the form introduced by Helfrich forty years ago [1,2].  $H$  and  $K$  are the mean and Gaussian curvatures, respectively,  $\kappa$  and  $\kappa_G$  the corresponding bending energies, and  $C_0$  a spontaneous curvature reflecting bilayer asymmetry. Systematic theoretical work in the nineties in combination with experiments using video microscopy has led to a quantitative understanding of how the subtle aspects of bilayer elasticity [3–5] determine the shape diagram, as comprehensively reviewed in [6]. Second, even though biological cells have a more complex architecture, vesicles have often served as a model system for anucleate cells such as red blood cells (RBCs), whose equilibrium shapes can be predicted [7,8] by minimizing a generalized version of the energy (1). Third, and coming to the topic of this review, the behavior of vesicles in external flow field is determined by a complex interplay between membrane elasticity, hydrodynamic forces, and thermal fluctuations acting at microscopic length scales. Studying the resulting rich phenomenology is fundamental for understanding the flow dynamics of these soft objects.

The physical properties of the membrane play a key role in this dynamics. The lipid bilayer with a thickness of approximately 5 nm is very small compared to the GUV radius ( $\sim 10 \mu\text{m}$ ). This bilayer is often in a liquid phase at room temperature [9] making the vesicle very deformable. Bending deformations involve much lower energies than stretching and shearing ones which can be neglected [6]. The bending rigidity  $\kappa$  is typically between  $10^{-20}$  and  $2 \times 10^{-19}$  J (approximately  $2\text{--}50k_B T$  at room temperature, although lipids widely used in dynamical experiments have a much narrower range of  $25\text{--}50k_B T$ ) [6,9–11]. The membrane viscosity is about  $10^{-8}$  to  $10^{-9}$  Pa s [9,10,12–15]. Typically, the membrane can be considered incompressible since the number of lipids in it is constant and the stretching energy is very large [16]. Therefore, the total membrane area is constant. Moreover, the membrane is permeable to water but impermeable to many other molecules. For a vesicle in equilibrium, any influx of water creates an osmotic pressure which is relaxed by an outflux of the same magnitude [1]. In experiment, one tries to keep a zero net osmotic pressure. Even if a small net flow still exists, volume changes occur on a time-scale of several hours, which is much longer than the typical experimental time-scale of about 10 to 15 minutes. We can thus consider the vesicle volume to be constant as well. These few properties are sufficient to characterize the forces that will counteract the external forcing.

We first review the general theoretical, numerical, and experimental methods used to address this problem. Then, we consider the case of planar linear flow, for which vesicle dynamics has been thoroughly studied in recent years. Afterwards, we describe the effect of walls and capillary flows on single vesicles. Moving further up the scale from micro to macro, we discuss hydrodynamic interactions and the rheology of vesicle suspensions. Finally, we present related questions on the non-equilibrium dynamics of vesicles and similar objects.

## 2. Methods

We present the theoretical tools for describing the dynamics of vesicles under hydrodynamic flows, then the techniques used in direct numerical simulations, and finally the experimental setups.

### 2.1. Theoretical modeling

The membrane is modeled as a two-dimensional sheet of incompressible fluid [17]. It encloses an internal liquid of viscosity  $\eta_i$  and is suspended in an outer liquid of viscosity  $\eta_o$ , defining the viscosity contrast  $\lambda \equiv \eta_i/\eta_o$ . The volume  $V$  and the surface area  $A$  are constant but the vesicle is not necessarily spherical. We thus define the effective radius  $R_0 \equiv (3V/4\pi)^{1/3}$ , which is the radius of a sphere of the same volume. Relatively to this sphere, the vesicle has an excess area  $\Delta \equiv A/R_0^2 - 4\pi \geq 0$ .<sup>1</sup> Ignoring for simplicity the energy due to Gaussian curvature (constant for spherical geometry) and spontaneous curvature, the bending energy of the membrane is given by [1,18]

$$\mathcal{H}_\kappa = \int dA \frac{\kappa}{2} [(2H)^2 + \sigma], \quad (2)$$

where  $\sigma$  is the surface tension, a Lagrange multiplier that ensures local and global area conservation. Unlike for droplets,  $\sigma$  is here a dynamical variable, analogous to pressure for three-dimensional fluids, which adjusts itself to compensate the external stresses. It can therefore take negative values as explained further below. This vesicle is subject to an external flow. Due to the vesicle dimensions, the Reynolds number  $Re$  is small – for a vesicle of radius  $10 \mu\text{m}$  suspended in water (viscosity of  $10^{-3}$  Pa s) and subject to a shear flow with rate  $1 \text{ s}^{-1}$ ,  $Re \sim 10^{-4}$  – and the flow is described by the Stokes equations

$$\nabla \mathbf{v} = 0 \quad \nabla p = \eta \nabla^2 \mathbf{v}, \quad (3)$$

where  $\mathbf{v}$  is the flow velocity,  $p$  the pressure, and  $\eta$  the viscosity. These equations have to be solved for the inner and outer fluids. The velocities and stresses are then matched at the membrane with no-slip boundary conditions and under the constraints of membrane incompressibility and impermeability.

Analytical models need further assumptions to derive equations of motion for the vesicle. One strategy consists in describing the dynamics effectively with only a few degrees of freedom [19–25]. These models are based on the Keller–Skalak (KS) model [19], which assumes vesicles of fixed ellipsoidal shape with fluid membrane. Their dynamics in shear flow is then described by only two variables: the inclination angle  $\theta$  of the long axis of the vesicle relative to the flow direction, and the angle  $\phi$  describing the displacement of a membrane element, see Fig. 3. Another strategy relies on looking at quasi-spherical vesicles, i.e., vesicles with small excess area  $\Delta \ll 1$  [16,26–32]. The radius of such vesicles

$$r(\theta, \phi) \equiv R_0 \left( 1 + \sum_{l,m} u_{lm} \mathcal{Y}_{lm} \right) \quad (4)$$

<sup>1</sup> Some authors define an effective radius over the area as  $R_0' \equiv \sqrt{A/4\pi}$  and a reduced volume  $\tau \equiv V/(4\pi R_0'^3/3) \leq 1$ . The excess area is then given by  $\Delta = 4\pi(\tau^{-2/3} - 1)$ .

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