

# Dynamic fluctuations of vesicles with nontrivial topology

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The role of conformal degeneracy of the Helfrich energy for shape fluctuations of vesicles is discussed. For a vesicle with a nontrivial topology (genus  $g > 1$ ) there exists a two-parametric set of transformations of the shape which does not influence the Helfrich energy, surface, and volume of the vesicle.<sup>4</sup> It is shown that the region  $\mathcal{L}$  of the phase space corresponding to the transformations is finite. Higher-order corrections to the Helfrich energy which breaks the degeneracy are small in comparison with the temperature  $T$ . It leads to the equipartition over the region  $\mathcal{L}$ . The characteristic time of the shape fluctuations of a vesicle is on the order of  $\eta R^3/T$ , where  $T$  is the temperature,  $\eta$  is the viscosity of the liquid surrounding the vesicle, and  $R$  is its size. © 1995 American Institute of Physics.

Vesicles (closed structures constructed from membranes which are bilayer films) with a nontrivial topology (genus  $g > 1$ ) have recently been observed experimentally.<sup>1</sup> The characteristic feature of such vesicles is the existence of strong shape fluctuations, which are much larger than conventional bending fluctuations. To explain this behavior, the authors of Ref. 2 have analyzed the consequences of a conformal degeneracy of the bending energy. They have used numerical simulation for a discretized version of the bending energy for the so-called Lawson's surfaces with  $g=2$ . Their numerical results show that a certain region exists in the phase space in which the volume and the area of the vesicles are held constant. This property alone leads to strong shape fluctuations of Lawson's vesicles. Here we are going to investigate the general physical consequences of this conformal degeneracy of vesicles with  $g \geq 2$ .

The incompressibility of the bilayer and of the liquid contained in a vesicle imposes two constraints on the fluctuations of the vesicle shape. These constraints are the area  $S$  and the volume  $V$  conservation laws. The fluctuations within the constraints are governed by the Helfrich (bending) energy of a bilayer<sup>3</sup>

$$F = \frac{\kappa}{2} \int dS \left( \frac{1}{R_1} + \frac{1}{R_2} \right)^2, \quad (1)$$

where  $R_1$  and  $R_2$  are the local curvature radii of the film. The combination in the brackets is the double mean curvature. In general, the term with the Gaussian curvature  $(R_1 R_2)^{-1}$  should be added to (1), but the integral of the Gaussian curvature over the surface is proportional to its genus. The term therefore is not influenced by fluctuations which do not change the topology of the vesicle. We will consider only such fluctuations and therefore will not take the term with the Gaussian curvature into account.

The Helfrich energy (1) is conformally invariant.<sup>4</sup> This means that any element of the conformal group transforms a vesicle shape into a new one with the same energy (1). The total symmetry group of the Helfrich energy (1) contains translations, rotations, reflections, and dilations. It is clear that a deviation of the vesicle shape from the ground state which is associated with a transformation of the group and which is consistent with the two constraints,  $V=\text{const}$  and  $S=\text{const}$ , is very soft, because in the main approximation it does not change the thermodynamic potential of the vesicle. We will call such fluctuations conformal fluctuations.

Any transformation  $\mathbf{r} \rightarrow \mathbf{r}'$  from the group can be represented as a combination of a conformal transformation with the center at the origin

$$\frac{\mathbf{r}'}{r'^2} = \frac{\mathbf{r}}{r^2} + \mathbf{a}, \quad (2)$$

of a dilation  $\mathbf{r}' = \lambda \mathbf{r}$  and of a translation, a reflection and a rotation. Clearly, translations, rotations, and reflections do not change the shape of the vesicle. Thus, we generally have a four-parametric set of nontrivial transformations of the vesicle shape which do not influence the energy (1). These parameters can be viewed as three components of a vector  $\mathbf{a}$  determined by (2) and one scaling parameter  $\lambda$  describing a dilation. At first sight, it seems that we can always satisfy two constraints  $S=\text{const}$  and  $V=\text{const}$  and retain two free parameters for conformal fluctuations. However, this statement is not true for spheres and Clifford tori (tori with the ratio of the principal radii  $1/\sqrt{2}$ ) which provide a minimum of (1) with  $g=0$  and  $g=1$ , respectively.

A dilation or a conformal transformation of a sphere produces a sphere again. Therefore, a four-parametric set of transformations in this case reduces to a one-parametric set which is described by the radius of the sphere. The constraint  $V=\text{const}$  determines the radius of this sphere unambiguously. For a Clifford torus the dilation gives a Clifford torus again. Any conformal transformation (2) can be represented as the result of two transformations with the vectors  $\mathbf{a}_{\parallel}$  parallel to the axis of the torus and  $\mathbf{a}_{\perp}$  perpendicular to it, since the conformal group is an Abelian group. The conformal transformation of a Clifford torus with  $\mathbf{a}_{\parallel}$  produces a Clifford torus again. Thus, a four-parametric set of transformations in this case reduces to a two-parametric set which is described by the size of the Clifford torus and by the absolute value of  $\mathbf{a}_{\perp}$ . Both parameters are fixed by the constraints  $V=\text{const}$  and  $S=\text{const}$ . Thus, in the cases  $g=0$  and  $g=1$  the minimum of (1) with two constraints,  $S=\text{const}$  and  $V=\text{const}$ , fixes the shape of the vesicle unambiguously. This is the consequence of the high symmetry of the spheres and Clifford tori. For vesicles with  $g \geq 2$  a two-parametric set of conformal transformations exists. It describes the conformal fluctuations introduced above. For Lawson's surfaces with  $g=2$  this set was determined numerically in Ref. 2.

We can expect completely different consequences whether the region  $\mathcal{L}$  of conformal deformations in the two-dimensional parameter space is finite or not. Let us assume for a moment that this region  $\mathcal{L}$  is infinite. This means, for example, that there exists a combination of a dilation and a transformation (2) which conserves  $S$  and  $V$  with an unrestricted value of  $\mathbf{a}$ . We can represent this combination as

$$\frac{\mathbf{r}'}{r'^2} = \frac{1}{\lambda} \left( \frac{\mathbf{r}}{r^2} + \mathbf{a} \right). \quad (3)$$

For a large  $|\mathbf{a}|$  Eq. (3) reduces to

$$r'_i - \frac{a_i}{a^2} = \frac{\lambda}{a^2} \left( \delta_{ik} - 2 \frac{a_i a_k}{a^2} \right) \frac{r_k}{r^2}. \quad (4)$$

This expression is the principal term of the expansion of (3) in the limit  $a \gg r^{-1}$ . The transformation (4) is the product of the translation [the second term on the left side of Eq. (4)], of the dilation (the first factor on the right side of the equation), of the reflection of the coordinate along the vector  $\mathbf{a}$  (the combination in the brackets), and of the inversion with the center at the origin (the third factor on the right side of the equation). Since the reflection retains  $V$  and  $S$ , we have only one free parameter in (4), namely,  $\lambda/a^2$ , and it is impossible to satisfy both constraints.  $V = \text{const}$  and  $S = \text{const}$ . Therefore, our assumption leads to a contradiction which proves that the region  $\mathcal{L}$  should be finite. This is reasonable from the physical point of view, since it is hard to imagine a strong deformation of the vesicle shape that would conserve  $V, S$ , and the energy (1).

The conformal degeneracy of the bending energy is broken by higher-order terms:

$$F_a = \gamma \int dS (\nabla_{\perp} (R_1^{-1} + R_2^{-1}))^2 + \dots, \quad (5)$$

where  $\nabla_{\perp}$  is the gradient along the film. We have written in (5) explicitly only one term. Other contributions, denoted in (5) by dots, have structures similar to one of the terms and can be evaluated identically. The coefficient  $\gamma$  is estimated to be

$$\gamma \sim \kappa a_m^2,$$

where  $a_m$  is the typical molecular scale. The characteristic scale of the conformal fluctuations is on the order of the size  $R$  of the vesicle, and therefore for conformal fluctuations the energy (5) is

$$F_a \sim \kappa \left( \frac{a_m}{R} \right)^2.$$

Usually, the modulus  $\kappa$  is larger than the temperature  $T$ , but it does not exceed it significantly (as a rule, it is on the order of  $T \approx \kappa/10$ ), and  $a_m \ll R$ . Thus, the energy  $F_a$  is much lower than the temperature. This means that the conformal fluctuations are not sensitive to  $F_a$ .

The conformal fluctuations are therefore governed only by a thermal noise, which leads to the equipartition of the allowed region  $\mathcal{L}$  in the phase space. Using the equipartition, we can estimate the mean-square amplitude of the shape fluctuations related to the conformal mode

$$\langle (\Delta R)^2 \rangle \sim R^2. \quad (6)$$

We emphasize that the crucial factor for this conclusion is the existence of a finite region  $\mathcal{L}$  in the phase space, in which the conformal transformations take place. Expression (6)

shows that the amplitude of the conformal fluctuations is much larger than one of the conventional bending fluctuations, which are weak due to the small value of  $T/\kappa$ .

To investigate the dynamic behavior of the conformal fluctuations, we should analyze the hydrodynamic motion of the liquid near the vesicle. There exist specific degrees of freedom associated with the variations of the shape of the vesicle, including those associated with the conformal fluctuations. The latter are the softest. To describe their dynamic behavior, we can use an adiabatic approximation. The rigorous procedure to investigate dynamic fluctuations is described elsewhere<sup>5</sup> (see also Ref. 6, in which the bending fluctuations of membranes are discussed). However, qualitative results concerning conformal fluctuations can be deduced without using this cumbersome technique. Since the bending energy in the region  $\mathcal{L}$  is negligible, we deal with the passive motion or with the advection of the vesicle shape in the region  $\mathcal{L}$ . Properties of the motion are determined by the competition of the thermal noise and the viscous forces, which means that the characteristic time  $t$  of the conformal fluctuations is

$$t \sim \eta R^3 / T. \quad (7)$$

To derive this estimate, we recall that, according to (6), the characteristic amplitude of the conformal fluctuations is on the order of  $R$ . The dynamics of the fluctuations can be called the conformal diffusion, since estimate (7) for  $t$  is the conventional Einstein diffusion time (see, e.g., Ref. 7).

In summary, we have shown that fluctuations of the shape of a vesicle with  $g \geq 2$  are associated with the conformal degeneracy of the Helfrich energy. These fluctuations can be thought of as the diffusion along the finite region  $\mathcal{L}$  in the phase space. This diffusion is characterized by Eqs. (6) and (7).

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