

Reply to “Comment on ‘Theory for the bending anisotropy of lipid membranes and tubule formation’”

C. -M. Chen

Physics Department, National Taiwan Normal University, Taipei, Taiwan, Republic of China

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We answer questions raised in the preceding Comment by Fournier and Peliti [Phys. Rev. E **63**, 013901 (2001)] that relate to the size distribution of lipid vesicles. In particular, we point out several theoretical and experimental papers that are consistent with the model postulated in our previous paper [Phys. Rev. E **59**, 6192 (1999)].

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The preceding Comment by Fournier and Peliti [1] points out that our proposed mechanism for the bending anisotropy of lipid bilayers upon cooling in Ref. [2] can be relevant for the stability of tubules for asymmetric bilayers. For symmetric bilayers, they discuss the case in which the unlocking of the monolayer nematic directors breaks the bilayer symmetry and leads to stable tubules [3]. Their model predicts a transition from flat membranes to tubes upon cooling, which has not been observed experimentally so far.

Based on experimental observations, we intend to build a model that predicts the transition from vesicles to tubes in a dilute solution. For a dilute phase of bilayer vesicles, Ref. [4] shows that the free energy of a single vesicle increases logarithmically with vesicle size due to finite-size contribution to the fluctuation free energy. Therefore the size distribution of vesicles peaks sharply at the cutoff size (or the minimal size $l \sim \kappa/\tau$ set by the bending rigidity κ and the line tension τ). The distribution of vesicles of size $r \gg l$ is predicted to be $\rho_v(r) \propto r^{-7/3} \exp[-(r/r_\mu)^2]$, where $r_\mu \propto \rho_t^{3/5}$ and ρ_t is the total number density of lipids [4]. In fact, the asymmetric size distribution predicted in Ref. [4] is qualitatively similar to the size distribution of vesicles observed in various experiments, for example, the Weibull distribution, with a high

peak at the minimal size and a sharp decrease with vesicular size [5–7]. Thus it is sensible to introduce a spontaneous curvature term associated with the edge tension that does not contradict experimental observations.

In Ref. [2], we have postulated a model in which the edge effect has been introduced by replacing the edge energy of a corresponding flat bilayer with the integral

$$C = \frac{\tau}{2} \oint_{\Sigma} d\sigma (c_1 + c_2), \quad (1)$$

where Σ represents the vesicle surface and c_1 and c_2 are its local principal curvatures. This substitution is valid for both spherical vesicles and open tubules, provided that the radius of tubules is half of that of the spheres. The above argument for substitution is self-consistent in our model [2]. As mentioned by Fournier and Peliti, we note that the integral in Eq. (1) is not independent of the vesicular shape; however, this should not invalidate our results since we only focus on the phase transition between the two ground states (open tubules and spherical vesicles), not the general shape transformation that occurs upon cooling. Nevertheless, we agree that a rigorous derivation of our model in Ref. [2] is desired and it is under our investigation.

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 [7] The Weibull probability distribution is given by $\rho(r) = (\delta/\eta)[(r-r_0)/\eta]^{\delta-1} \exp[-(r-r_0)/\eta]^{\delta}$, where r is the vesicle diameter. The physical meaning of the three-parameter (r_0, η, δ) has been assigned as the following: r_0 is the minimum vesicle diameter, η is related to the efficiency of the lipid membrane fragmentation process, and δ represents the dimensionality of the vesicle formation process [6].