Critical Fluctuations of Tense Fluid Membrane Tubules

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We show that, contrary to planar membranes under tension, tense membrane tubules exhibit important critical fluctuations originating from unidimensional Goldstone modes. The latter yield unexpected behavior, such as correlations extending over the whole tube length and the increase of the fluctuating area over the projected area with increasing tension.

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It is widely known that fluid lipid bilayer membranes form planar or vesicular structures \([1,2]\); however, they form also tubular structures. Membrane nanotubes (or tethers) are ubiquitous in vivo, e.g., in the endoplasmic reticulum \([3,4]\). They are also actively studied in physics, e.g., in relation with molecular motors \([5]\), or as means to connect vesicles used as microreactors \([6]\). The physics of long tubular membranes being rather simple, theoretical investigations have examined either the formation mechanism of membrane tubes \([7,8]\), or the shapes of membranes deviating from a cylinder \([9]\). Since membrane tubes are subject to a strong (pulling) tension \(\sigma\), one should think that the fluctuations around the tubular shape are largely suppressed (see, e.g., Ref. \([8]\)) \(^1\). This is indeed the case for planar membranes \([10]\), due to the presence of a correlation length \(\sim \sigma^{-1/2}\); critical behaviors in membranes are rather observed in fluid tensionless \([11,12]\) or polymerized membranes \([13,14]\). In this Letter, we show on the contrary that tense membrane tubes exhibit important fluctuations of critical character. This behavior originates from the existence of effectively unidimensional Goldstone modes. In particular, we show that the relative excess area increases with membrane tension (while the total area decreases), and that the fluctuations are correlated over the whole length of the tube, implying, e.g., distance-independent Casimir forces.

Let us consider a tubular membrane, submitted to a tension \(\sigma\), that fluctuates around a cylindrical shape of length \(L\) and radius \(R\). We model the membrane as an ideal surface, parametrized, in a Cartesian frame, by

\[
\mathbf{r}(\phi, \zeta) = \left( \begin{array}{c} x \\ y \\ z \end{array} \right) = R \left( \begin{array}{c} [1 + u(\phi, \zeta)] \cos \phi \\ [1 + u(\phi, \zeta)] \sin \phi \\ \zeta \end{array} \right),
\]

where \(0 \leq \phi \leq 2\pi\) and \(0 \leq \zeta \leq L/R\) are dimensionless cylindrical coordinates. The function \(u(\phi, \zeta)\) is the relative deformation field in the cylindrical normal gauge \([2]\). For the distortion free energy, we take the Canham-Helfrich Hamiltonian \([15,16]\):

\[
F = \int dS \left( \frac{1}{2} \kappa H^2 + \sigma \right).
\]

where \(\kappa\) is the bending rigidity, \(\sigma\) the tension, \(H\) the sum of the two principal curvatures of the membrane, and \(dS\) the surface area element. Differential geometry yields \(dS = |\partial_\phi \mathbf{r} \times \partial_\zeta \mathbf{r}| d\phi d\zeta\) and \(H = (2bB - cA - aC)/(AC - B^2)\), where \(A = (\partial_\phi \mathbf{r})^2\), \(B = (\partial_\phi \mathbf{r}) \cdot (\partial_\zeta \mathbf{r})\), \(C = (\partial_\zeta \mathbf{r})^2\), \(a = \mathbf{\nu} \cdot \partial^2_\phi \mathbf{r}\), \(b = \mathbf{\nu} \cdot \partial_\phi \partial_\zeta \mathbf{r}\), \(c = \mathbf{\nu} \cdot \partial^2_\zeta \mathbf{r}\), \(\mathbf{\nu} = (\partial_\phi \mathbf{r} \times \partial_\zeta \mathbf{r})/(|\partial_\phi \mathbf{r} \times \partial_\zeta \mathbf{r}|)\) being the normal to the surface.

To second order, we get \(dS = R^2 d\phi d\zeta\left[1 + u + \frac{1}{2} \partial_\phi^2 + \frac{1}{2} \partial_\zeta^2\right] d\phi d\zeta\) and \(H^2 dS = d\phi d\zeta\left[1 - u + \frac{1}{2} \partial_\phi^2 + \frac{1}{2} \partial_\zeta^2\right] + 2u \partial_\phi \partial_\zeta\), where \(\nabla^2 = \partial^2_\phi + \partial^2_\zeta\).

Fluctuation free energy.—The undeformed tube is an equilibrium solution only if \([17]\)

\[
R = \sqrt{\frac{\kappa}{2 \sigma}}.
\]

With this value of \(R\), the excess energy relative to the undeformed tube becomes

\[
\Delta F = \kappa \int d\phi d\zeta \left[ \frac{1}{2} u^2 - \nabla^2 u + \frac{1}{2} (\partial_\phi u)^2 + (\partial_\zeta u)^2 + 2u \partial^2_\phi u \right].
\]

For periodic or clamped \((u = \partial_\phi u = 0)\) boundary conditions along \(\zeta\), Eq. (4) can be rewritten as \(\Delta F = \frac{1}{2} \kappa \int \mathbf{L} d\phi d\zeta\), where \(\mathbf{L} = (1 + \partial^2_\phi)^2 + \partial^2_\zeta^2 + 2\partial_\phi\partial_\zeta^2\) is a self-adjoint operator. Here, for simplicity, we consider periodic boundary conditions. The eigenfunctions of \(\mathbf{L}\) being then the Fourier modes, we expand the deformation field according to

\[
u(\phi, \zeta) = \sqrt{\frac{R}{2\pi L}} \sum_{m,q} u_{m,q} e^{i(m\phi + q\zeta)}.
\]

Here \(m = 0, \pm 1, \pm 2, \pm M\) and \(q = 2\pi n R/L\), with \(n = 0, \pm 1, \pm 2, \ldots, \pm N\) is the normalized wave vector along the tube. The upper limits are set by the small length...
cutoff $\ell$, of the order of the membrane thickness, to $M = 2\pi R/\ell$ and $N = L/\ell$. Then, the fluctuation energy becomes [18]
\[
\Delta F = \frac{K}{2} \sum_{m,m_0}(m^2 - 1)^2 + \tilde{q}^2(\tilde{q}^2 + 2m^2)|u_{m,m_0}|^2.
\]
Since $\Delta F \geq 0$, the tube is indeed stable against all local deformations. At equilibrium at temperature $T$, it follows from equipartition that $\langle |u_{m,m_0}|^2 \rangle = 0$ and
\[
\langle |u_{m,m_0}|^2 \rangle = \frac{k_B T}{\kappa} \left( \frac{1}{(m^2 - 1)^2 + \tilde{q}^2(\tilde{q}^2 + 2m^2)} \right).
\]

**Soft modes.**—Note that the modes $m = \pm 1$ and $\tilde{q} = 0$ give no contribution to $\Delta F$. Indeed, they correspond to a rigid translation of the tube; here and in the following we shall exclude them. Similarly, the long-wavelength modes with $m = \pm 1$ and $\tilde{q} \neq 0$ describe local translations of the axis of the tube: they are Goldstone modes (see Fig. 1). These modes are extremely soft for thin tubes ($L \gg R$), since the factor weighing $|u_{m,m_0}|^2$ in Eq. (6) is $O[(R/L)^2] \ll 1$ for $m = \pm 1$, while it is $O(1)$ when $m \neq \pm 1$.

**Excess area.**—With the decomposition (5) and the expression of $dS$, we calculate the average excess area:
\[
\Delta S = \left( \int dS \right) - S_0 = R^2 \sum_{m,m_0} \frac{1}{2} (m^2 + \tilde{q}^2) \langle |u_{m,m_0}|^2 \rangle.
\]
where $S_0 = 2\pi RL$ is the projected area, i.e., the area in the absence of thermal fluctuations ($T = 0$). Using Eq. (7), we obtain the normalized excess area:
\[
s = \frac{\kappa \Delta S}{k_B T S_0} = \frac{R}{4\pi L} \sum_{m,m_0} \frac{m^2 + \tilde{q}^2}{(m^2 - 1)^2 + \tilde{q}^2(\tilde{q}^2 + 2m^2)}.
\]
In general, the double sum giving $s$ (limited by the cutoffs $M$ and $N$) can be calculated numerically. In Fig. 2 we show the behavior of $s$ for different fixed lengths $L$ as a function of the reduced tension $\tilde{\sigma} = 2\ell^2 \sigma/\kappa$ ($\tilde{\sigma} \approx 1$ corresponding to the lysis tension of the membrane [19]). Unexpectedly, the relative excess area increases with increasing tensions, contrary to planar membranes, in which the tension suppresses the fluctuations [10]. Indeed, for a square membrane of the same projected area $S_0$, $s = (8\pi)^{-1} \log[(\sigma + \kappa/\Lambda^2)/(\sigma + 4\pi^2 \kappa/S_0)]$, which decreases with $\sigma$, as shown in Fig. 2. Note that in this harmonic approximation the excess area diverges as $L \to \infty$ at fixed tension. This divergence suggests a critical behavior and implies that anharmonic terms become important, as we shall discuss later on.

A reasonably accurate analytical approximation of $s$ can be obtained in the following way. We split $s = s_0 + s_1 + s_2$, where $s_0$ contains the terms with $m = 0$, $s_1$ those with $m = \pm 1$, and $s_2$ those with $|m| \geq 2$. We find $s_0 = 1/(8\pi\sqrt{2})$ by approximating, for $L \gg R$, the sum over $\tilde{q}$ by an integral running from $-\infty$ to $\infty$. For $L \gg \ell$, $s_1$ can be summed exactly by replacing $N$ by $\infty$, yielding
\[
s_1 \approx \frac{L}{48\pi R} - \frac{R}{8\pi L} + \frac{1}{8\pi \sqrt{2}} \coth \left( \frac{L}{2\sqrt{2}} \right).
\]
Finally, for $L \gg R \gg \ell$, we replace the sum over $\tilde{q}$ in $s_2$ by an integral, we retain the dominant contribution for $m \gg 1$, and we take the limit $M \to \infty$, which gives
\[
s_2 \approx \frac{1}{2\pi^2} \sum_{m=2}^{\infty} \frac{1}{m} \arctan \left( \frac{\Lambda R}{m} \right)
\]
\[
= -\frac{1}{2\pi^2} \arctan(\Lambda R) + \frac{1}{4\pi^2}
\]
\[
\times \int_0^{\Lambda R} d\lambda \pi \lambda \coth(\pi \lambda) - \frac{1}{\lambda^2}.
\]

**FIG. 2** (color online). Relative normalized excess surface $s$ as a function of the normalized tension $\tilde{\sigma}$ for $L = 10^2\ell$ (circles, blue), $L = 10^3\ell$ (squares, green), and $L = 10^4\ell$ (diamonds, red). Note that $L/R = \sqrt{\tilde{\sigma} L/\ell}$. The continuous lines correspond to the analytical approximation given in the text. The dashed line (green) corresponds to a square planar membrane with the same projected area as the tube having $L = 10^3\ell$.  

**FIG. 1** (color online). The first soft, Goldstone modes ($m = 1$). From top to bottom: $n = 1$, $n = 2$, and $n = 3$. 

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where \( \Lambda = 2\pi/\ell \) is the wave vector cutoff. The increase \( s \sim \sigma^{1/2} \) at high tensions comes from the dominant contribution of the soft modes \( s_1 = L/(48\pi R) \) [see Eq. (10)].

Vanishing differential surface tension.—The astonishing increase of the relative excess area with tension is due to the vanishing of the differential surface tension \( \gamma_{m,q} \) of the soft modes: we define the latter, for each mode, as the ratio between the free energy \( \Delta F_{m,q} = \frac{1}{2} \kappa ([m^2 - 1] + \tilde{q}^2(\tilde{q}^2 + 2m^2))|u_{m,q}|^2 \) and the excess surface \( \Delta S_{m,q} = \frac{1}{2} R^2(m^2 + \tilde{q}^2)|u_{m,q}|^2 \):

\[
\gamma_{m,q} = \frac{\Delta F_{m,q}}{\Delta S_{m,q}} \sim \frac{1}{\sigma^2} 4\sigma \tilde{q}^2 = 2\kappa \sigma^2,
\]

where \( \tilde{q} = \tilde{q}R^{-1} \) is the true wave vector. For the soft modes, this quantity thus vanishes as \( \sigma^2 \), contrary to planar membranes, for which \( \Delta F_q/\Delta S_q = (\sigma|q|^2 + \kappa|q|^4)/|q|^2 \sim \sigma \) tends to its tension. Note that in both cases \( \Delta F \propto q^2 \); the difference comes from \( \Delta S_q \), which is \( \propto q^2 \) for the flat membrane and \( \propto R^{-2} \propto q^2 \) for the tube (the transverse wave vector of the soft modes is \( \propto R^{-1} \)).

Fluctuation-induced shortening.—Let us now investigate how the length of a tube with a fixed surface \( S_{\text{tot}} \) is shortened by the fluctuations. We define the relative shortening \( \epsilon = (L_0 - L_T)/L_0 \), where \( L_T \) is the length of the tube at temperature \( T \), and \( L_0 = S_{\text{tot}}/(2\pi R) \) the length of the straight tube in the absence of fluctuations. Identifying in the thermodynamic limit the total surface \( S_{\text{tot}} \) with its average, we determine numerically, using Eq. (9), the length \( L_T \) for which \( S_0 + \Delta S = S_{\text{tot}} \). As is shown in Fig. 3, \( \epsilon \) increases as the tube is stretched by increasing the tension. Again, this is counterintuitive: one would expect the tension to flatten the thermal ripples. Note that this behavior should depend on the boundary conditions, since it is dominated by the long-wavelength soft modes; thus, we have recalculated the fluctuations for clamped boundary conditions \( (u = \partial_z u = 0) \); we find qualitatively the same behavior (see Fig. 3).

Correlation function.—To test the critical behavior suggested by the divergence of the fluctuating area, we calculate the correlation function \( C(\phi, \zeta) = \langle u(\phi)u(\zeta) \rangle \) of the modes, we get

\[
C(\phi, \zeta) = \frac{k_B T R}{2\pi \kappa L} \sum_{m,q} \cos(m\phi) \cos(q\zeta) \frac{\cos(m\phi) \cos(q\zeta)}{(m^2 - 1)^2 + \tilde{q}^2(\tilde{q}^2 + 2m^2)}. \tag{13}
\]

In Fig. 4 we show the normalized correlation function \( c(\xi, \zeta) = C(0, \zeta)/C(0, 0) \) at two different tensions for the same length \( L \). For a flat tense membrane, the correlations decay on the characteristic length \( \xi_{\text{flat}} = \sqrt{k_B T \sigma} \), that corresponds in our case to the tube radius. Here, instead, the correlations always extend over the whole length of the tube; i.e., the correlation length is \( \xi \approx L \). Hence, in the thermodynamic limit \( \xi \to \infty \): the system, within the harmonic approximation, is indeed critical.

As shown in Fig. 4, the critical behavior originates from the modes \( m = \pm 1 \); the other modes decay on \( \xi_{\text{flat}} \) and give a negligible contribution for long tubes. In this limit, neglecting the modes with \( |n| \neq 1 \) and keeping the dominant terms for \( \tilde{q} \to 0 \) yields the analytical approximation, excellent for \( |z| > R \) (see Fig. 4):

\[
\text{FIG. } 3 \text{ (color online). Relative shortening } \epsilon \text{ as a function of the reduced tension } \tilde{\sigma}, \text{ for } \kappa = 25k_B T \text{ and fixed total surface } S_{\text{tot}}. \text{ The continuous lines refer to periodic boundary conditions, the dashed ones to clamped boundary conditions. The two lower curves (blue) are for } S_{\text{tot}} = 10^5 \ell^2, \text{ the two upper ones (red) for } S_{\text{tot}} = 10^6 \ell^2. \]

\[
\text{FIG. } 4 \text{ (color online). Normalized correlation function } c \text{ as a function of } z/L, \text{ for } L = 10^3 \ell. \text{ The correlation function is periodic with period } z = L \text{ and is an even function of } z. \text{ Only half a period is shown for two different normalized tensions: } \tilde{\sigma} = 10^{-2} \text{ (yielding } L'/R = 100) \text{ on the left (} 0 \leq z/L \leq 0.5 \text{), } \tilde{\sigma} = 2 \times 10^{-4} \text{ (yielding } L'/R \approx 14 \text{) on the right (} 0.5 \leq z/L \leq 1 \text{). Continuous lines (red): exact numerical calculation; dashed lines (blue): approximate analytical expression (14) normalized by the true value } C(0,0). \text{ Dash-dotted lines (green): contribution from the modes } m \neq \pm 1: \text{ for } \tilde{\sigma} = 10^{-2} \text{ (left curve), the curve is magnified 10 times.} \]

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This expression is identical to the correlation function of a tense string [1] with line tension $\gamma = 2 \pi \kappa / R$. The latter coincides with the free energy per unit length of the undeformed tube.

**Wandering exponent.**—The fractal rugosity of critical interfaces is measured by the wandering exponent $\nu$ [11], defined by $\langle h^2(\xi) \rangle^{1/2} \sim |\xi|^\nu$, where $h(\xi) = u(0, \xi) - u(0, 0)$. At distances $R < |\xi| \ll L$, $\langle h^2(\xi) \rangle = 2\langle C(0, 0) - C(0, \xi) \rangle \sim k_B T |\xi| / (2 \pi \kappa)$. Hence, we find $\nu = 1/2$. This is the same as for a tense interface in two dimensions (e.g., Ising). Note that there is no roughness exponent for tense flat membranes ($\nu = 0$), while tensionless membranes have $\nu = 1$ (see Ref. [2]).

**Thermal Casimir forces.**—An interesting manifestation of the correlation function is the so-called Casimir effect, i.e., the interaction between two objects constraining a fluctuating medium [20]. To investigate the simplest situation, we model the constraint by the confining potential $V = \frac{1}{2} \lambda u^2(\phi_1, \xi_1) + \frac{1}{2} \lambda u^2(\phi_2, \xi_2)$ (describing, e.g., optical tweezers). Expanding the partition function in the limit $\lambda \ll k_B T$ yields the Casimir interaction $\mathcal{F}_C = -\lambda^2 \int C(\phi_1 - \phi_2, \xi_1 - \xi_2) / (2k_B T)$. For $R \ll d \ll L$, the corresponding force $f_C = -\alpha \mathcal{F}_C / \alpha d$, where $d = R|\xi_1 - \xi_2|$ is constant:

$$f_C \approx -\frac{\lambda^2 k_B T}{96 \pi \kappa^2} \frac{L}{R^2} \cos \phi;$$

it is attractive for $|\phi| < \pi / 2$ and repulsive otherwise. Such long-range Casimir forces are characteristic of correlated media [21].

**Anharmonicity.**—To check the validity of the harmonic approximation (6), we have calculated up to fourth-order the energy of the softest mode $\epsilon(\phi, \xi) = U(\phi) + \cos(\phi) \times \cos(\xi)$, with $\phi = 1 = 2\pi R / L$; this yields $F = 2\pi \kappa L R^{-1} [1 + \frac{1}{2} \left( \xi_1^2 + \xi_2^2 \right) U^2 + \frac{1}{12} \left( 3 - 2 \xi_1^2 - 17 \xi_2^2 - 30 \xi_1^2 \xi_2^2 \right) U^4]$. Setting $\langle U^4 \rangle = \langle U^2 \rangle^2$, we find that the fourth-order term is negligible when $L / R \ll 4 \pi^{3/2} [\kappa / (k_B T)]^{1/3}$. Typically, for $\kappa \approx 50 k_B T$, this gives the validity condition for the harmonic approximation $L / R \ll 100$.

**Conclusions.**—The critical behavior and the long-range correlations that we have found in tubules are unexpected for a fluid membrane under tension. Indeed, critical behaviors are rather characteristic of tensionless membranes. The long-range character of the correlation function comes from the existence of a one-dimensional family of Goldstone modes: the correlation function is indeed the same as for a string with tension equal to the free energy per unit length of the undeformed tube. However, other unexpected consequences of the Goldstone modes, such as the behavior of the excess fluctuating area and length of membrane tubules, cannot be reproduced by an equivalent unidimensional string model. In any case, at the scale of the surface, tubules are two-dimensional objects: indeed, the critical behavior is not driven by $R \to 0$ but by $R \ll L$.

It would be interesting to study how the anharmonic terms affect the fluctuations. We believe that the correlation function should remain long-ranged because of the one-dimensional character of the Goldstone modes. Conversely, the excess surface and the related shortening of the tube length should be more sensitive to the anharmonic corrections.

Experiments could measure the force-extension relation on a tube held at both ends, thus testing the deviation $\epsilon$ from the mean-field behavior $L_0 = S_{\text{tot}} / (2 \pi R) \propto \sigma^{1/2}$. Indeed, for $S_{\text{tot}} = 10^5 \ell^2$ and $\sigma = 10^{-2}$, we found $\epsilon = 10\%$ (see Fig. 3), with $L_0 / R = S_{\text{tot}} \sigma / (2 \pi \ell^2) = 100$ still within the validity range of our harmonic approximation.

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