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Periodic lipidic membrane tubes

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Abstract – We investigate the formation of two-phase lipidic tubes of membrane in the framework of the Canham-Helfrich model. The two phases have different elastic moduli (bending and Gaussian rigidity), different tensions and a line tension prevents the mixing. For a set of parameters close to experimental values, periodic patterns with arbitrary wavelength can be found numerically. A wavelength selection is detected via the existence of an energy minimum. When the chemical composition induces an important enough size disequilibrium between both phases, a segregation into two half infinite tubes is preferred to a periodic structure.

Introduction. – Inhomogeneous lipid membranes have received increasing attention recently [1,2]. They are formed by multiple lipid components which laterally separate into coexisting liquid phases with specific composition. In cell biology, this separation is responsible for cholesterol-enriched micro-domain formation. These domains, called rafts, are believed to concentrate important biological functions such as polarized sorting of proteins [3,4], cellular signaling [5], viral entry and budding [6].

In this letter, we focus on inhomogeneous tubular membranes and we ask the question of the existence of periodic and steady patterns. Tubular membranes exist in the cell, allowing transport functions from an intracellular compartment to another. They also appear during cell development and motility. Made of a ternary mixture of lipids (sphingomyelin, dioleoylphosphatidylcholine and cholesterol) in varying composition, these vesicles exhibit various and complex shapes and domain organizations, as the temperature approaches the mixing/demixing composition temperature. For a composition which favors cholesterol-enriched phases, periodic tubular vesicles have been observed [7]. Here, in the framework of the Canham-Helfrich model, we explain the existence of periodic membrane tubes and the selection of the wavelength in terms of physical parameters such as the elastic coefficients, the surface and line tensions. Other non-periodic inhomogeneous tubes have been experimentally observed [8,9] like quasi-semi infinite tubes where the complete separation seems to be energetically preferred: each half-infinite tube is made with a unique phase separated from the neighbor by a unique junction. Our goal is also to explain this duality between periodicity or homogeneity when the chemical composition between both phases is approximately balanced.

Variational treatment for biphasic tubes. – The physics of membrane tube formation has been studied both theoretically and experimentally [10–12]. We will use the variational free energy minimization that we adapt to an infinite periodic biphasic tube with a prescribed chemical ratio composition $S_{\mathrm{Lo}}/S_{\mathrm{Ld}}$ (see fig. 1). The free energy is obtained by extending the tubular energy with an effective force acting at some ends, giving

$$\mathcal{F} = \sum_{i=\mathrm{Ld,Lo}} \int_{\Omega_i} \left[2\kappa_i(\mathsf{H}-\mathcal{C}_\mathrm{i})^2 + \kappa_{\mathrm{G},i}\,\mathsf{K} + \tilde{\sigma}_i\right] \mathrm{d}S + \oint_{\partial\Omega} \tau\,\mathrm{d}\ell + \int f\,\mathrm{d}z. \qquad (1)$$

We denote the two phases by Lo or Ld following the classical terminology which distinguishes a liquid-ordered and a liquid-disordered phase. Both phases will be treated in the same way but the Lo-phase is more rigid. For each phase, we integrate the free energy over its membrane area. The length of each phase i measured on the z-axis is λ_i and the total wavelength is thus $\lambda = \lambda_{\mathrm{Ld}} + \lambda_{\mathrm{Lo}}$. We choose as

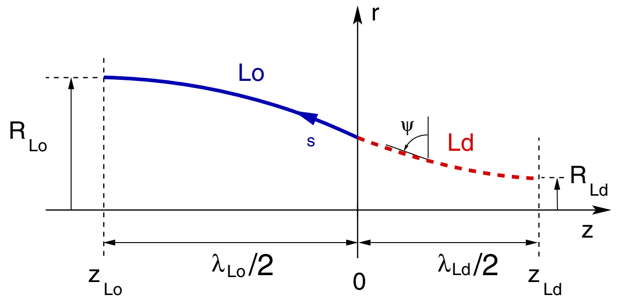


Fig. 1: Geometry sketch of a periodic biphasic membrane tube. The z-axis is the axis of symmetry of the tubes. Half of the wavelength of both Ld and Lo phases is depicted. The $\{r,\psi\}$ parametrization used when deriving the Euler-Lagrange equations is shown. The interface is located at $s=z=0$.

length unit the radius $R_{\rm Lo}$, which is the value of the radius at its extremal value in the Lo-phase (see fig. 1). Our study will fix all the lengths of the pattern as a function of $R_{\rm Lo}$, which is fixed by the total available mass of lipids. The free energy (1) includes the membrane bending energy at the lowest order in its principal curvatures: the mean curvature H, and the Gaussian curvature K with characteristic elastic coefficients κ_i and $\kappa_{{\rm G},i}$, respectively the bending and Gaussian rigidities. One can also include the spontaneous curvature of the phase i, $\mathcal{C}_i$, if the two leaflets of the membrane are different. This occurs by anchoring amphiphilic molecules in vesicles for example, which may induce a tubular instability [13]. In each phase $\tilde{\sigma}_i$, the tension of the membrane in phase i, remains constant if the area per lipid does not vary, so the surface of each phase remains constant. Not included here, a small pressure effect may be incorporated. The interface between the two phases is described by a jump in the values of the bending and Gaussian rigidities and in the values of the surface tension. Moreover, a line energy is associated to this interface with a line tension τ. Since we describe the tube shape by the angle ψ and the local radius r as a function of the arclength s, one needs a Lagrange multiplier $\Gamma(s)$ to impose the relation ${\rm d}r/{\rm d}s=\cos\psi$. Equation (1) does not depend on s explicitly, the Hamiltonian $\mathcal{H}_i$ is a constant in each phase. The mechanical equilibrium at the junction imposes that $\mathcal{H}_{\rm Lo}=\mathcal{H}_{\rm Ld}$. For a detailed discussion on the Hamiltonian, see Appendix A of [14]. Moreover, and as it is frequently done in standard experiments, we assume that at least one end of the tube is connected to a reservoir of lipids (a vesicle for example) at ∞ so no force is required for an extension of the tube length. This imposes that $\mathcal{H}_{\rm Lo}=\mathcal{H}_{\rm Ld}=0$ and gives a first relation between the force f, the radius at the dip $r_{\rm min}=R_{\rm Ld}/R_{\rm Lo}$ and the tensions $\sigma_{\rm Lo}=\tilde{\sigma}_{\rm Lo}R_{\rm Lo}^2$ and $\sigma_{\rm Ld}=\tilde{\sigma}_{\rm Ld}R_{\rm Lo}^2$. As f is a constant, we get

$$\begin{aligned} R_{\rm Lo}f/\pi &= \frac{\kappa_{\rm Ld}}{r_{\rm min}}[(1-2\mathcal{C}_{\rm Ld}r_{\rm min})^2+2\sigma_{\rm Ld}r_{\rm min}^2/\kappa_{\rm Ld}] \\ &= \kappa_{\rm Lo}[(1-2\mathcal{C}_{\rm Lo})^2+2\sigma_{\rm Lo}/\kappa_{\rm Lo}]. \end{aligned} \tag{2}$$

In addition, $\Gamma(s)$ can be eliminated to derive the shape equation in each phase [8,10–12], it reads

$$\begin{aligned} \dddot{\psi} = &-\frac{\dot{\psi}^3}{2}-\frac{2\cos\psi}{r}\ddot{\psi}+\frac{3\sin\psi}{2r}\dot{\psi}^2+\frac{3\cos^2\psi-1}{2r^2}\dot{\psi} \\ &-\frac{\cos^2\psi+1}{2r^3}\sin\psi+\frac{\sigma_i}{\kappa_i}\dot{\psi}+\frac{\sigma_i}{\kappa_i}\frac{\sin\psi}{r} \\ &+\mathcal{C}_i^2\dot{\psi}+\mathcal{C}_i^2\frac{\sin\psi}{r}-2\mathcal{C}_i^2\dot{\psi}\frac{\sin\psi}{r}, \end{aligned} \tag{3}$$

with boundary conditions at the interface located at $s=0$. In eq. (3), the dot means the derivative with respect to s. From eq. (3), at the middle of each phase ($r=R_i$ and $\psi=\pi/2$), we deduce two new relations: $\sigma_{\rm Lo}/\kappa_{\rm Lo}=1/2-\mathcal{C}_{\rm Lo}^2$ and $\sigma_{\rm Ld}/\kappa_{\rm Ld}=1/(2r_{\rm min}^2)-\mathcal{C}_{\rm Ld}^2$, which finally gives the value of both tensions σ_i as $r_{\rm min}$ knowing the bending rigidities. The boundary conditions are due to either geometrical constraints like the continuity of r and ψ, or to mechanical equilibrium, our approach being purely static. Continuity relations are expressed by

$$\psi(\epsilon)=\psi(-\epsilon), \tag{4}$$

$$r(\epsilon)=r(-\epsilon). \tag{5}$$

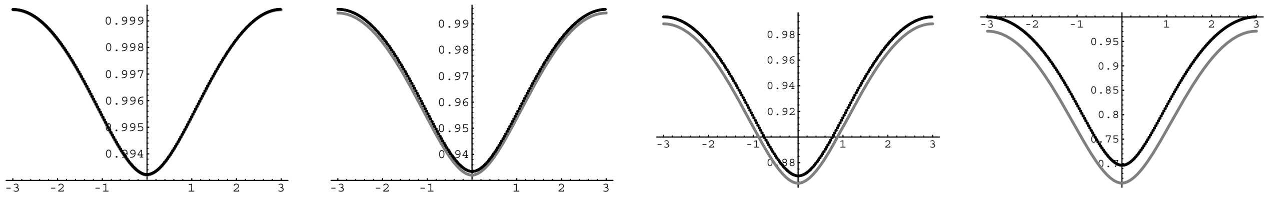
Mechanical equilibrium (momentum and force balance, (see appendix A of [14])) at the junction gives two other boundary conditions,

$$\begin{aligned} &\kappa_{\rm Ld}\left(\dot{\psi}(\epsilon)-\mathcal{C}_{\rm Ld}\right)-\kappa_{\rm Lo}\left(\dot{\psi}(-\epsilon)-\mathcal{C}_{\rm Lo}\right)= \\ &\quad(\kappa_{\rm Lo}+\kappa_{\rm G,\,Lo}-\kappa_{\rm Ld}-\kappa_{\rm G,\,Ld})\frac{\sin\psi(0)}{r(0)}, \end{aligned} \tag{6}$$

$$\begin{aligned} &\kappa_{\rm Ld}\ddot{\psi}(\epsilon)-\kappa_{\rm Lo}\ddot{\psi}(-\epsilon)=\tau\frac{\sin\psi(0)}{r(0)} \\ &+(2\kappa_{\rm Ld}+\kappa_{\rm G,\,Ld}-2\kappa_{\rm Lo}-\kappa_{\rm G,\,Lo})\frac{\sin\psi(0)\cos\psi(0)}{r(0)^2}, \end{aligned} \tag{7}$$

with $\mathcal{C}_i$ the spontaneous curvature if the bilayer is asymmetric. It is possible to transform eq. (3) by integrating once to obtain a second-order nonlinear equation for $\psi(r)$ with a free parameter [15,16]. That equation was useful to find explicit solutions and indicates that the space of possible solutions has 3 degrees of freedom for ψ and 4 for the profiles, which are necessary to solve the junction conditions.

Exact results. – It turns out that explicit solutions of eq. (3) have been found but they require a lipid membrane model incorporating both a spontaneous curvature and pressure effect. A simplification arises for a periodic tube since we do not have to consider non divergent asymptotes at infinity and in principle we can truncate the solutions. As an example, the catenoid, which is a solution of eq. (3), may be a good candidate to represent the concave phase of the tube. Exact known solutions have been discovered [15,16]; they include



(a) $\tau = 0.01$ (b) $\tau = 0.1$ (c) $\tau = 0.2$ (d) $\tau = 0.5$

(e) $\tilde{\kappa} = 0.01$ (f) $\tilde{\kappa} = 0.1$ (g) $\tilde{\kappa} = 0.2$ (h) $\tilde{\kappa} = 0.5$

(i) $\Delta\tilde{\kappa}_G = 0.1$ (j) $\Delta\tilde{\kappa}_G = 0.1$ (k) $\Delta\tilde{\kappa}_G = 0.2$ (l) $\Delta\tilde{\kappa}_G = 0.5$

Fig. 2: Tube profiles $r(z)$ for the periodic tube where $z_{\mathrm{Lo}} = 3$, $z_{\mathrm{Ld}} = -3$, and $R_{\mathrm{Ld}} = 1$ (see fig. 1). The elastic coefficients of both Lo and Ld phases are the same, except those mentioned. In each figure, we present the solution for the linearized problem (dark curves) and for the complete non-linear problem (light curves). We can see there that for small enough relative parameters, both curves are almost the same in each case.

as special limits catenoids and unduloids. Taking into account our choice of length unit, they are represented by $\sin\psi = 1/\mathcal{C}_{\mathrm{Lo}}\left[(r+1/r) \pm \sqrt{4-2\mathcal{C}_{\mathrm{Lo}}^2}\right]$ for the Lo-phase, while the concave Ld-phase may be represented by $\sin\psi = 1/\mathcal{C}_{\mathrm{Ld}}\left[(r/r_{min}^2 + 1/r) \pm \sqrt{4/r_{min}^2 - 2\mathcal{C}_{\mathrm{Ld}}^2}\right]$. Since we have chosen as length unit R_{Lo} at its maximum, the spontaneous curvature $\mathcal{C}_{\mathrm{Lo}}$, which indeed is responsible for the length scale of the system, is equal to $4/3$ while $r_{min} = 4/3\mathcal{C}_{\mathrm{Ld}}$. Except for the catenoid, these solutions exist only in the case where the two layers of the membrane are asymmetric, the tension and the pressure being Lagrange multipliers function of the spontaneous curvatures in both phases. Nevertheless, it turns out to be impossible to satisfy the boundary conditions (6) and (7) simultaneously for arbitrary physical elastic coefficients since all the parameters of the solution are fixed by the spontaneous curvature of the bilayers. The only possibility remaining is the catenoid, $\sin\psi = r_{min}/r$, which may represent the concave phase when the spontaneous curvature $\mathcal{C}_{\mathrm{Ld}}$ vanishes.

Linear analysis and nonlinear numerical treatment. – From above, one notices that the known exact analytical solutions are too much constrained and one really need a family with 3 real degrees of freedom in ψ to solve the constraints at the interface. Moreover, we neglect the spontaneous curvature assuming the two leaflets of the membrane symmetric. Expanding the Euler-Lagrange equation (3) in both phases in the vicinity of the cylindrical exact solution, $r(z) = R_i(1+U_i(z))$ gives a fourth-order linear differential equation: $R_i^4(\partial_z^4 U_i) + U_i = 0$. Its solution, symmetric with respect to the middle of each domain $\epsilon\lambda_i/2$ is

$$U_i(z) = A_i\left(\cosh\frac{z+\epsilon\lambda_i/2}{\sqrt{2}}\cos\frac{z+\epsilon\lambda_i/2}{\sqrt{2}} + r_i\sinh\frac{z+\epsilon\lambda_i/2}{\sqrt{2}}\sin\frac{z+\epsilon\lambda_i/2}{\sqrt{2}}\right) \quad (8)$$

with $\epsilon = +1$ for the Lo-phase, and -1 for the Ld-phase. In a linear approach, A_i and r_i may be chosen arbitrarily, giving the 4 degrees of freedom needed to satisfy the junction conditions. Note that the wavelength of the pattern $\lambda = \lambda_{\mathrm{Ld}} + \lambda_{\mathrm{Lo}} = \lambda_{\mathrm{Ld}}(1 + S_{\mathrm{Ld}}/S_{\mathrm{Lo}})$, is a real degree of freedom at fixed composition ratio between phases, $S_{\mathrm{Ld}}/S_{\mathrm{Lo}}$: in principle, the problem can be solved without fixing the wavelength.

In order to check the validity of the former linear analysis and to show that solutions for periodic tubes exist, we have performed the numerical integration of the nonlinear differential equations (3), according to the matching relations (4), (6), (7), using the shooting to a fitting point numerical method [17]. Integrations in the regime of validity of the linear analysis have been performed in order to check the consistency of both calculations. A systematic study of the tube profile $r(z)$ when changing

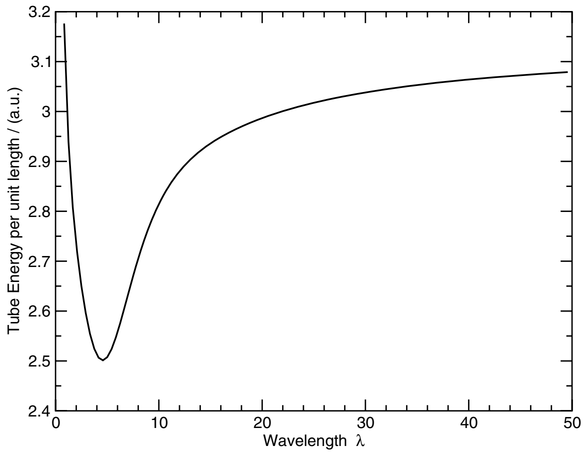
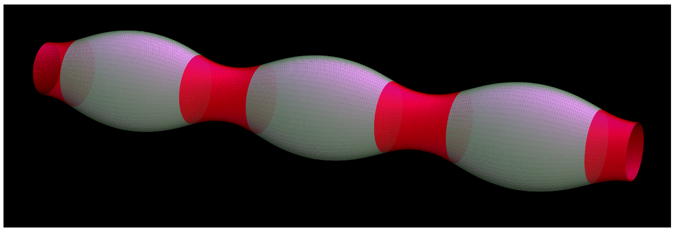
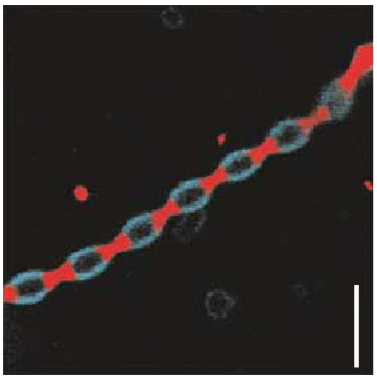


Fig. 3: Tube energy per unit length as a function of the imposed wavelength in units of R_{Lo}.



(a)



(b)

Fig. 4: (Colour on-line) (a) Three-dimensional representation of the numerical tube, with the energetically selected wavelength. Blue (light) phase stands for the Lo-phase, and red (dark) phase for the Ld-phase. (b) the periodic multiphase tube, from ref. [7]. Scale bar: $5\,\mu$m.

uniquely one of the three elastic dimensionless parameters (see fig. 2) allows to measure the effects of a mismatch between the physical constants of both phases. We systematically compare the non-linear solutions to the one found in the linear approximation, for double checking of our numerical procedure. As expected, we see that both solutions are almost equal when the differences between the elastic constants of the two phases are small ($\tilde{\kappa} = 1 + \delta\tilde{\kappa} = \kappa_{\mathrm{Lo}}/\kappa_{\mathrm{Ld}}$, $\Delta\tilde{\kappa}_{\mathrm{G}} = (\kappa_{\mathrm{G,Lo}} - \kappa_{\mathrm{G,Ld}})/\kappa_{\mathrm{Ld}}$, and $\tilde{\tau} = \tau R_{\mathrm{Ld}}/\kappa_{\mathrm{Ld}} \ll 1$). These figures illustrate the effects induced by the mismatch of elastic constants between the two phases and the line tension on the geometry of the periodic tube.

To treat a relevant example, we compare our solution with the only experiment on periodic tubes we are aware of. We choose the physical parameters which are given in [7] (see fig. 4(b)). The ratio is fixed to $\kappa_{\mathrm{Lo}}/\kappa_{\mathrm{Ld}} \simeq 1.25$, and the line tension $\tau \simeq 9 \times 10^{-13}\,$N. The values of the Gaussian rigidities are hard to measure since the Gaussian elastic energy manifests itself only in topological changes for homogeneous membranes and as boundary contributions for inhomogeneous membranes. We use the values mentioned in ref. [18] of $\kappa_{\mathrm{G},(i)} = -0.83\kappa_i$. The chemical composition is set to keep the area ratio between both phases equal to $S_{\mathrm{Lo}}/S_{\mathrm{Ld}} = 1.5$. We perform different simulations for different values of the wavelength of the periodic tube. In all these calculations, the wavelength value is an input, it means that we can choose arbitrarily the domain size. In other words, solving the Euler-Lagrange equation (3) with the boundary conditions does not allow to find the wavelength, a situation which is commonly found in pattern formation such as rolls in Rayleigh-Bénard convection [19] or cells in directional solidification [20]. Since the wavelength can be chosen freely *a priori*, the wavelength selection for the periodic tube may result from the energy minimization. Fixing the surface ratio of both phases to the chemical composition, we calculate the energy per unit length incorporating in eq. (1) the numerical solutions given by the Euler-Lagrange equation (3). The plot of this energy density *versus* the domain size is presented in fig. 3. The energy minimum corresponds to $\lambda = 4.4$ times R_{Lo}, (see fig. 4a) the experimental value (ref. [7]) being $\lambda \sim 5$ in the same units. We can estimate that the results are in agreement since the determination of the experimental wavelength, not indicated by the experimentalists, is imprecise. Moreover, since tube formation occurs at a temperature close to the critical mixing temperature, one can expect some uncertainty on the value of the line tension, which vanishes at the critical temperature. Not surprisingly, for a variational treatment, fig. 3 shows that the competition between elastic and capillary energies occurs for a wavelength of the order of the tube radius, short and very large wavelength compared to this length scale being eliminated. Recall that long wavelengths correspond to a half-infinite tube, not selected for the parameters of ref. [7].

Imposing the bending rigidities and line tension as indicated previously, one can vary the composition value and calculate the selected wavelength. By changing the $S_{\mathrm{Lo}}/S_{\mathrm{Ld}}$ ratio, we can explore if a periodic tube is preferred to two half-infinite tubes. In fig. 5 we plot the inverse of the size of the Ld-domain with respect to the area fraction. We can see there that for high enough composition difference, there is no finite wavelength selection, and the tube is completely phase-separated into two phases separated by a unique junction.

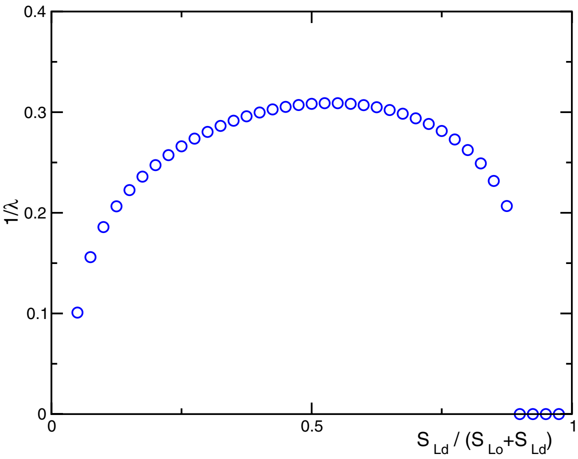


Fig. 5: Plot of the inverse of the selected wavelength as a function of the normalized chemical ratio. For extreme chemical ratios, semi-infinite tubes are preferred.

Conclusions. – In this letter, periodic membrane tubes have been found numerically for arbitrary wavelength once the physical parameters like the chemical composition, the elastic rigidities and the line tension are fixed. We show that periodic tubes are preferred to a complete phase separation as soon as the chemical composition does not favor too much one phase, for a realistic set of physical constants. It means that the periodicity allows a decrease of the elastic energy which compensates the increase of capillary energy. The agreement between the only reported experiment and the numerics confirms the validity of the model for tubular structures and the accuracy of the physical constants.

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