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## **Squeezing and stretching of vesicles**

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**Abstract.** We propose and solve a model problem concerning the squeezing and stretching of vesicles between two adhesive plates. Our model is two-dimensional: the vesicle's contour is represented through a closed curve. It has, however, the potential to represent the behaviour of the average section of a vesicle in space. In particular, we compute the gap width that must be reached in stretching the vesicle to make it snap into the loose, undistorted configuration. Detecting this snapping would provide an independent measure for the *adhesion potential* of the plates.

In the past years, much effort has been devoted to study how lipid membranes adhere either to rigid walls or to other membranes. Most papers deal with the adhesion of a closed membrane, also called a *vesicle*. The simplest model to describe the adhesion of a vesicle to a wall employs an adhesion free energy  $\mathcal{F}_a$  proportional to the area of the membrane  $\mathcal{S}_*$  in contact with the wall, that is,

$$\mathcal{F}_a := -w \operatorname{area}(\mathcal{S}_*)$$

where the positive, constitutive parameter w is usually referred to as the *adhesion potential*. The elastic properties of a lipid membrane are described by a free energy  $\mathcal{F}_e$  which depends on the principal curvatures of the surface that represents it. The simplest form for  $\mathcal{F}_e$ , also known as the Canham–Helfrich Hamiltonian, reads as

$$\mathcal{F}_e = \frac{\kappa}{2} \int_{\mathcal{S}} (2H)^2 \,\mathrm{d}a \tag{1}$$

where *H* is the *mean curvature* of the whole membrane *S*, possibly discontinuous along the border of  $S_*$ , *a* denotes the area-measure, and  $\kappa$  is a positive, constitutive parameter, called the *bending rigidity*. The stable equilibrium configurations for an adhering membrane minimize the functional  $\mathcal{F} := \mathcal{F}_e + \mathcal{F}_a$  subject to the isoperimetric constraint on the area of *S*, which reflects the fact that a lipid membrane does not leak molecules. A similar constraint is often imposed on the volume enclosed within the membrane, when this is impermeable to the environment fluid. This requirement can, however, be dropped when the osmotic pressure is low enough, as is presumed here for simplicity. Adhesion in two dimensions has also been explored by Seifert in [1], who studied transitions between free and bound vesicles. So far the Euler–Lagrange equations for this functional have mainly been solved numerically (see, e.g., [2]). Recently, we found a method which gives *exact* solutions to these equations when the membrane is represented as a plane curve in a simple two-dimensional model [3, 4]. Clearly, such a model would be unable to describe the wealth of all possible equilibrium shapes of a membrane, but it provides a good approximation to their qualitative features when a single

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Figure 1. A vesicle between two parallel plates.

curve can be regarded as the *average section* of the membrane. One merit of this model is illustrated below: it allows one to estimate the adhesion potential w. It is known (see section 6.1 of [5], and references therein) that measuring the interaction forces between two adhering membranes should eventually result in measuring the adhesion potential w. Here, we take a different path. We solve an equilibrium problem for the curve that models a membrane: we first squeeze and then stretch it between two parallel plates, to which it can adhere. The total stretch  $\varepsilon$  needed to make the curve lose contact with the plates and snap into a circle depends on the adhesion potential w, and is in general quite large. Measuring  $\varepsilon$  should provide an independent means to access w. The developments below apply provided the value of w is not exceedingly high, since in that case the membrane might break up.

Consider a closed curve c with fixed length 4L that adheres to two parallel plates, 2d apart (see figure 1). The same geometric setting was considered by Lipowsky and Seifert [6], who were, however, concerned with the appropriate definition of an effective contact angle for an open membrane between two plates. For equilibrium shapes symmetric with respect to both coordinate axes, the free energy of the curve is given by

$$\mathcal{F} = \frac{\kappa}{2} \int_c \sigma^2 \,\mathrm{d}s - 4w L_* \tag{2}$$

where s is the arc-length along c and  $2L_*$  is the length of each adhering segment. Here, both  $\kappa$  and w are scaled to a characteristic length, which, however, does not affect their ratio. We require the length of c to be prescribed, as is the area of a closed membrane, but we impose no constraint upon the area enclosed by c. Mathematically, the adhesion affects the equilibrium configurations of a membrane through a boundary condition on the points where the membrane detaches itself from the plates: there, the curvature  $\sigma$  of c suffers a discontinuity, while the unit tangent t remains continuous. For a flat plate,  $\sigma$  jumps from 0 to

$$\sigma^* = \sqrt{\frac{2w}{\kappa}} \tag{3}$$

as proved by Seifert and Lipowsky [2]. We denote by  $\vartheta$  the angle that t makes with the unit vector  $e_x$  orthogonal to the plates, so that for the quarter curve we concentrate on,  $\vartheta$  ranges in the interval  $[0, \frac{\pi}{2}]$  (see figure 1). Since the gap between the plates is fixed, the energy

functional in (2) is further subject to the constraint

$$\int_{0}^{L^{*}} \cos \vartheta(s) \,\mathrm{d}s = \int_{0}^{\frac{\pi}{2}} \frac{1}{\sigma} \cos \vartheta \,\mathrm{d}\vartheta = d \tag{4}$$

where  $L^* := L - L_*$  is the length along which *c* is not in contact with the plate at x = d, and use has also been made of the identity

$$\sigma = \frac{\mathrm{d}\vartheta}{\mathrm{d}s}.\tag{5}$$

It is shown in [4] that under these assumptions the curvature of the equilibrium shape of c is given by

$$\sigma = \sigma^* \sqrt{1 + \nu \cos \vartheta} \tag{6}$$

where  $\nu > -1$  is the Lagrange multiplier associated with the constraint (4).

Let  $\xi$  and  $\beta$  be the dimensionless parameters defined as

$$\xi := d\sqrt{\frac{2w}{\kappa}} \qquad \beta := L\sqrt{\frac{2w}{\kappa}}.$$
(7)

The former is a scaled measure of d, while the latter is better interpreted as a dimensionless measure of w. By (3) and (7), making use of (6) in (4), we arrive at

$$\xi = \int_0^{\frac{\pi}{2}} \frac{\cos\vartheta}{\sqrt{1 + \nu\cos\vartheta}} \,\mathrm{d}\vartheta =: \xi_0(\nu). \tag{8}$$

Similarly, the requirement that  $L \ge L^*$  is expressed as

$$\beta \geqslant \int_0^{\frac{\pi}{2}} \frac{\mathrm{d}\vartheta}{\sqrt{1+\nu\cos\vartheta}} =: \beta_0(\nu). \tag{9}$$

Since  $\xi_0$  is a strictly decreasing function which ranges in the whole positive real line for  $-1 < \nu < +\infty$ , there is a unique root  $\nu_{\xi}$  of (8) for every dimensionless half-width  $\xi$  of the gap between the plates. This indeed corresponds to an adhering shape of *c*, provided that  $\beta$  satisfies (9) for  $\nu = \nu_{\xi}$ : if  $\beta > \beta_0(\nu_{\xi})$ , the adhering length  $L_*$  is positive, whereas if  $\beta = \beta_0(\nu_{\xi})$ , the membrane touches each plate at a single point. Whenever (9) fails to be satisfied, there is no possible equilibrium shape of *c* adhering to the plates. By (6) and (2), the dimensionless energy  $e := \frac{\mathcal{F}}{\sqrt{8\kappa w}}$  of an adhering membrane is obtained by evaluating the function

$$e(\nu) := \int_0^{\frac{\pi}{2}} \sqrt{1 + \nu \cos \vartheta} \, \mathrm{d}\vartheta + \int_0^{\frac{\pi}{2}} \frac{1}{\sqrt{1 + \nu \cos \vartheta}} \, \mathrm{d}\vartheta - \beta \tag{10}$$

on the root  $v_{\xi}$  of (8) for the chosen  $\xi$ . This function attains its minimum at  $\nu = 0$ , while it diverges when  $\nu \to -1$ . For an adhering shape of *c*, *e* can also be expressed as a function of  $\xi$ , by inverting equation (8): it then attains its minimum at  $\xi = 1$ ; it diverges to  $+\infty$  for  $\xi \to 0^+$ , whereas it grows linearly at infinity.

These general facts will now serve to solve a specific problem. Let the plates be initially so far apart that the membrane can freely acquire its circular equilibrium shape. Then, imagine bringing them closer, so that the circular membrane just fits in the gap between them: this amounts to setting  $\xi = \xi_c := \frac{2\beta}{\pi}$ . We ask for which values of the adhesion potential the membrane would then climb and adhere along the plates to reduce the total energy. Since here the prescribed  $\xi$  also depends on  $\beta$ , the answer requires some analysis. From (8) and (9), we first arrive at the estimate

$$\frac{\pi}{2} \geqslant \frac{\beta_0(\nu_c)}{\xi_0(\nu_c)} \tag{11}$$



**Figure 2.** The energy difference  $\Delta e = e - e_c$  for  $\beta = 10$  as a function of the scaled half-width  $\xi$ .



Figure 3. The total stretch  $\varepsilon$  of a circular membrane against the dimensionless adhesion potential  $\beta$ .

where  $\nu_c$  is the root of (8) corresponding to  $\xi_c$ . Then, since the ratio  $\beta_0/\xi_0$  is a strictly increasing function of  $\nu$  which ranges from 1 to  $\frac{\pi}{2}$  for  $-1 < \nu < 0$ , we conclude that  $\nu_c$  must fall in the latter interval for (11) to be valid. Finally, since  $\beta_0$  is strictly decreasing and  $\beta_0(0) = \frac{\pi}{2}$ , we learn that, whenever  $\beta > \frac{\pi}{2}$ , there is an adhering solution with  $\xi = \xi_c$ , whose adhering length  $L_*$  would be larger for larger values of  $\beta$ .

Besides this, when  $\beta > \frac{\pi}{2}$ , a circular membrane brought in contact with the plates will abruptly adhere to them. Indeed, let us compare the energy of the free circle  $e_c := \frac{\pi^2}{4\beta}$  and that of all possible adhering shapes. Figure 2 illustrates the graph of  $\Delta e := e - e_c$  against  $\xi$ for  $\beta = 10$ ; its qualitative features are the same for all  $\beta > \frac{\pi}{2}$ . It clearly shows the energy gain for the membrane in adhering to the plates at  $\xi = \xi_c$ . Since  $\xi_c > 1$ ,  $\Delta e$  would further decrease on squeezing the membrane between the plates, and the adhering length  $L_*$  would accordingly increase, as long as  $\xi > 1$ . Were the plates free, they would feel an *attractive* force



**Figure 4.** Stretched membrane, just before snapping, for  $\beta = 10$ . The adherent length  $L_*$  still fails to vanish.



Figure 5. A vesicle between two misaligned plates.

exerted by the membrane, which ceases when  $\xi = 1$ : that is, when  $d = d_0 := \sqrt{\frac{\kappa}{2w}}$ . Further squeezing the membrane would be hampered by a *repulsive* force which grows stronger as  $\xi$  approaches 0.

On stretching the membrane by pulling the plates apart,  $\xi$  keeps increasing also beyond  $\xi_c$ , whereas  $L_*$  decreases. The membrane stays adherent to the plates until it is so stretched that  $\xi$  reaches the critical value  $\xi_* > \xi_c$  where  $\Delta e$  vanishes. At  $\xi = \xi_*$  the free circle becomes energetically favourable for the membrane, though the adherent length  $L_*$  has not yet vanished. A *snapping* transition is thus predicted to take place when  $d = d_* := \xi_* \sqrt{\frac{2w}{\kappa}}$ . Figure 3 illustrates the total stretch  $\varepsilon := \frac{d_*}{d_c} - 1$  to which the circular membrane with radius  $d_c$  is subject before snapping back;  $\varepsilon$  is an increasing function of the adhesion potential, which saturates at  $\frac{\pi}{2} - 1$  as  $\beta \to +\infty$ . For  $\beta = 10$ ,  $\xi_* \cong 8.586$ , whereas  $\xi_c \cong 6.366$ . Moreover, figure 4



**Figure 6.** The total stretch  $\varepsilon$  of a circular membrane against the dimensionless adhesion potential  $\beta$ , when the angle  $2\alpha$  between the bounding plates is  $10^{\circ}$ .

shows the shape of the membrane under maximum stretch, just at the snapping transition. The relative elongation of a free circle in the *x*-direction is considerably high, as it amounts to 35% its initial extension.

We also studied the effect of a slight misalignment of the plates on the snapping of the membrane under stretch. The situation we envisage is shown in figure 5:  $2\alpha$  is the angle between the plates, and 2d is the largest gap between them. In this geometry, the adhesion also serves to keep the vesicle in place. The *scenario* we outlined for the parallel plates remains qualitatively unaffected. The graph of the total stretch  $\varepsilon$  against  $\beta$  is plotted in figure 6 for  $\alpha = 5^{\circ}$ : it differs from the one for  $\alpha = 0^{\circ}$  by less than 10%.

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