Fluctuation-Induced Interactions between Rods on a Membrane

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(May 31, 2021)

We consider the interaction between two rods embedded in a fluctuating surface. The modification of fluctuations by the rods leads to an attractive long-range interaction between them. We consider fluctuations governed by either surface tension (films) or bending rigidity (membranes). In both cases the interaction falls off with the separation of the rods as $1/R^4$. The orientational part of the interaction is proportional to $\cos^2[\theta_1 + \theta_2]$ in the former case, and to $\cos^2[2(\theta_1 + \theta_2)]$ in the latter, where $\theta_1$ and $\theta_2$ are angles between the rods and the line joining them. These interactions are somewhat reminiscent of dipolar forces and will tend to align collections of such rods into chains.

I. INTRODUCTION AND SUMMARY

In addition to their structural role of forming the exterior frames of the cell and its interior organelles and vesicles, lipid bilayers act as the host and regulator of many biophysical and biochemical reactions. Inter- and intracellular recognition and transport, adhesion, regulation of ion concentrations, and energy conversion, are but a few of the processes taking place at the membrane. These tasks are carried out by a variety of proteins, glycolipids, and other macromolecules that move through the many different lipids that make up the bilayer. The resulting membrane is thus far from uniform; there are even examples in which inhomogeneities occur on a larger scale, e.g. domains of phase separated lipids or two-dimensional protein assemblies. In modeling the physical properties of the cell, it is thus essential to have a good understanding of the interactions between inclusions in fluid membranes.

The pursuit of “biologically inspired” materials, which do not possess the full complexity of their natural counterparts, yet retain some of their useful features, is quite active. Artificial protein assemblies within lipid membranes are now routinely produced in the laboratory. Such model-membrane systems have potential applications for targeted drug delivery and may also lead to novel applications such as nano-scale pumps, templates, functionalized interfaces, and chemical reactors. The appropriate design of such artificial membranes again requires an understanding of how inclusions modify the physical properties of the bilayer, and how the membrane in turn contributes to the interactions between inclusions. The forces between the inclusions can be broadly subdivided into two categories. The first category includes interactions that are present in the bulk of the solvent. They include the van der Waals interaction, which falls off with separation $R$ as $1/R^6$ at long distances. The Coulomb interaction is strongly screened under physiological conditions. (Typical ion concentrations are a few hundred millimolar, which give a screening length of less than 10 Å.) Hydration and structural forces are also short-ranged. The second category includes interactions which are mediated by the membrane itself: the inclusion disturbs the lipid bilayer and this disturbance propagates to neighboring inclusions (c.f. and references therein). When macroscopic thermal fluctuations are unimportant (we refer to this case as $T = 0$), the resulting interactions tend to be short-ranged. For example, if in the region around an inclusion the membrane is forced to deviate from its preferred thickness ($\sim$ 40 Å), the resulting disturbance in the bilayer decays (heals) over a length of order this thickness. Two nearby inclusions then feel an interaction that falls off exponentially with this characteristic length.

There are also long-range interactions that are mediated by the membrane. To describe such interactions, it should be possible to neglect the microscopic properties of the membrane, and its molecular lipid bilayer structure, and focus

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on its macroscopic properties. In the long-distance limit, the membrane is well-described by the elastic Hamiltonian
\[ H = \int dS \left[ \sigma + \frac{\kappa}{2} H^2 + \bar{\kappa} K \right], \] (1)
where \( dS \) is the surface area element, and \( H, K \) are the mean and Gaussian curvatures respectively. The elastic properties of the surface are then described by the tension \( \sigma \), and the bending rigidities \( \kappa \) and \( \bar{\kappa} \). A finite surface tension is in general the strongest coupling in Eq.(1) and dominates the bending terms at long wavelengths. This term is present for films on a frame, interfaces at short distances, and possibly membranes subject to osmotic pressure differences between their interior and exterior. On the other hand, for unstressed vesicles, the surface tension is quite small, and may be neglected at wavelengths well below the size of the vesicle [12–14]. In this case, the energy cost of fluctuations is controlled by the rigidity terms. For simplicity we shall refer to surface dominated surfaces as films, and to rigidity controlled ones as membranes.

The long-range interactions between inclusions in a membrane that result from Eq.(1) were examined in Ref. [8]. If the inclusions are asymmetric across the bilayer and impose a local curvature, even at \( T = 0 \), there is a long-ranged repulsive interaction that falls off with distance as \( 1/R^4 \). The energy scale of this interaction is set by \( \kappa \) and \( \bar{\kappa} \). On the other hand, if thermal fluctuations of the membrane are included \((T \neq 0)\), there is a \( 1/R^4 \) interaction for generic inclusions. The only requirement is that the rigidity of the inclusion differs from that of the ambient membrane [8]. In particular, the interaction is attractive if the inclusions are stiffer than the membrane. The magnitude of this fluctuation–induced interaction is set by \( k_B T \), and is totally independent of the rigidities \( \kappa \) and \( \bar{\kappa} \) (see also Appendix D).

In a recent report, we considered the dependence of the fluctuation–induced \((T \neq 0)\) interaction between rod-like inclusions on their orientations [15]. The rods are assumed to be sufficiently rigid so that they do not deform coherently with the underlying membrane. They can thus only perform rigid translations and rotations while remaining attached to the surface. As a result, the fluctuations of the membrane are constrained, having to vanish at the boundaries of the rods. Consider the situation depicted in Fig. 1, with two rods of lengths \( L_1 \) and \( L_2 \) at a separation \( R \gg L_i \). For fluctuating films \((\sigma \neq 0)\), there is an attractive fluctuation-induced interaction given by,
\[ V_T^F(R, \theta_1, \theta_2) = -\frac{k_B T L_1^2 L_2^2}{128 R^4} \cos^2 [\theta_1 + \theta_2] + O \left(1/R^6\right), \] (2)
where \( \theta_1 \) and \( \theta_2 \) are the angles between the rods and the line adjoining their centers, as indicated in Fig.1. This angular dependence is actually the square of that of a dipole-dipole interaction in two dimensions, with \( L_1 \) and \( L_2 \) as the dipole strengths. The fluctuation-induced interaction on a membrane \((\sigma = 0)\) is very similar and given by
\[ V_M^T(R, \theta_1, \theta_2) = -\frac{k_B T L_1^2 L_2^2}{128 R^4} \cos^2 [2(\theta_1 + \theta_2)] + O \left(1/R^6\right). \] (3)
The orientational dependence is the square of a quadrupole–quadrupole interaction, with the unusual property of being minimized for both parallel and perpendicular orientations of the rods. Note that the strength of the interaction is the same in both cases. The above fluctuation-induced interactions decay less rapidly at large distances than van der Waals forces and may play an important role in aligning asymmetric inclusions in biomembranes. Since orientational correlations are often easier to measure than forces, this result may also be useful as a probe of the fluctuation-induced interaction. Finally, this interaction could give rise to novel two-dimensional structures for collections of rodlike molecules. In particular, the resemblance of the orientational part of the interaction to dipolar forces suggests that a suitable way to minimize the energy of a collection of rods is to form them into chains. (If the rods are not colinear, the interactions cannot be minimized simultaneously.) Such chain-like structures are observed for ferromagnetic particles controlled by similar forces [17].

In this article we provide the calculational details that lead to the above results. The remainder of the paper is organized as follows. Due to its richer complexity, the detailed calculation for the force between rods on membranes is presented first in Sec. II. The corresponding calculation for films is described more succinctly in Sec. III. This is followed by a discussion of the results, and comparison with other work in Sec. IV. Various calculational details are relegated to the appendices. Asymmetric inclusions have also been recently considered in [18], where results similar to ours are reported.

II. MEMBRANES

We start with a thermally fluctuating planar membrane subject to the Hamiltonian in Eq.(1). We assume that the size of the membrane \( d \), is well below the persistence length \( \xi \) [14]. In this limit, the membrane undergoes only
small fluctuations about a flat state. We may then parametrize the membrane surface with a height function \( u(r) \) and approximate the full coordinate-invariant Hamiltonian of Eq. (1) by the quadratic form

\[
\mathcal{H}_0 = \frac{\kappa}{2} \int_{\mathbb{R}^2} d^2 r \left( \nabla^2 u(r) \right)^2.
\]

(4)

Since we assume \( d \) is large (compared with \( R \) and \( L_i \)), we denote the (finite but large) reference plane by \( \mathbb{R}^2 \).

Now consider the situation depicted in Fig. 1, where two rigid, rod-like objects, are attached to the membrane. We shall represent the rods by narrow rectangles of lengths \( L \) of \( \epsilon \), just as in the case of anharmonic terms that have been neglected in Eq. (4), the higher order terms in the same spirit as the gradient expansion for the Hamiltonian in Eq. (4). In Appendix B we further demonstrate that, as described in Appendix B, higher order terms come from the projection of \( L_i \) onto the \( x \)-\( y \) plane, as well as from the integration measure for \( \mathbb{R}^2 \), which is on the sphere of unit normals. Since \( \mathbf{b}_i \) controls the gradient of \( u(r) \) at the boundary of \( L_i \), the expansion in \( \mathbf{b}_i \) is in the same spirit as the gradient expansion for the Hamiltonian in Eq. (4). In Appendix B we further demonstrate that, just as in the case of anharmonic terms that have been neglected in Eq. (4), the higher order terms in \( \mathbf{b}_i \) left out from Eq. (4) are suppressed in the limit \( d \ll \xi \). Expressing the delta functions as functional integrals over auxiliary fields \( k_i(r) \) defined on the rods, we obtain

\[
Z = \int D\mathbf{u}(r) \prod_{i=1}^2 \int da_i d^2 b_i \int Dk_i(r) \exp \left[ -\frac{\mathcal{H}_0}{k_B T} \right].
\]

(6)

In Eq. (6) we have included only the leading term in an expansion in powers of \( \mathbf{b}_i \). As described in Appendix B, higher order terms come from the projection of \( L_i \) onto the \( x \)-\( y \) plane, as well as from the integration measure for \( \mathbf{b}_i \), which is on the sphere of unit normals. Since \( \mathbf{b}_i \) controls the gradient of \( u(r) \) at the boundary of \( L_i \), the expansion in \( \mathbf{b}_i \) is in the same spirit as the gradient expansion for the Hamiltonian in Eq. (4). In Appendix B we further demonstrate that, just as in the case of anharmonic terms that have been neglected in Eq. (4), the higher order terms in \( \mathbf{b}_i \) left out from Eq. (4) are suppressed in the limit \( d \ll \xi \). Expressing the delta functions as functional integrals over auxiliary fields \( k_i(r) \) defined on the rods, we obtain

\[
Z = \prod_i \int Dk_i(r) \delta \left( \int_{L_i} d^2 r_i k_i(r_i) \right) \delta^2 \left( \int_{L_i} d^2 r_i \mathbf{r} k_i(r_i) \right)
\]

\[
\times \exp \left[ -\frac{k_B T}{2\kappa} \sum_{i,j=1}^2 \int_{L_i} d^2 r_i \int_{L_j} d^2 r_j G(\mathbf{r}_i - \mathbf{r}_j) k_j(r_j) \right],
\]

(8)

where

\[
G(\mathbf{r} - \mathbf{r}') = \left( \frac{1}{\mathbf{r} \cdot \mathbf{r}'} \right) = \frac{1}{8\pi} |\mathbf{r} - \mathbf{r}'|^2 \ln |\mathbf{r} - \mathbf{r}'|.
\]

(9)

Equation (8) is analogous to the partition function for a pair of plasmas confined to the interior of rods \( L_1 \) and \( L_2 \). The delta functions impose the constraints that the net charge and dipole moments vanish within each rod. When the distance \( R \) between rods is much bigger than their size (i.e. \( L_i \ll R \)), we may approximate \( G(\mathbf{r}_1 - \mathbf{r}_2) \) in Eq. (8) by a multipole expansion and keep only the leading term, which comes from the quadrupole moments (see Appendix A)

\[
Q^{(i)}_{ab} = \int_{L_i} d^2 r \mathbf{r}_a \mathbf{r}_b k_i(r).
\]

(10)
After inserting
\[ I = \prod_{i=1}^{2} \int dQ^{(i)} d\mathbf{g}^{(i)} \exp \left[ i \sum_{ab} g_{ab}^{(i)} \left( Q_{ab}^{(i)} - \int_{L_i} d^2 r \ r_a r_b k_i(r) \right) \right], \tag{11} \]
into Eq. (8) and performing the multipole expansion, we obtain
\[
Z = \prod_{i} \int Dk_i(r) \int dQ^{(i)} d\mathbf{g}^{(i)} da_i d^2 b_i \times \exp \left\{ -\frac{k_B T}{2\kappa} \int_{L_i} d^2 r d^2 r' k_i(r) G(r - r') k_i(r') \right. \\
- i \sum_{i} \int_{L_i} d^2 r k_i(r) \left[ a_i + b_i \cdot r + r \cdot \mathbf{g}^{(i)} \cdot r \right] \\
+ i \sum_{ab} g_{ab}^{(i)} Q_{ab}^{(i)} - \frac{k_B T}{2\kappa} \left[ Q^{(1)} \cdot Q^{(2)} \right] \right\}, \tag{12} \]
where we have recast the delta functions in Eq. (8) in terms of integrals over \( a_i \) and \( b_i \). The quadrupole-quadrupole interaction
\[
\nu \left[ Q^{(1)}, Q^{(2)} \right] = \frac{1}{8\pi R^2} \left[ Q_{aa}^{(1)} Q_{bb}^{(2)} + 2Q_{ab}^{(1)} Q_{ab}^{(2)} - 2Q_{aa}^{(1)} \mathbf{R} \cdot Q^{(2)} \mathbf{R} \cdot Q^{(1)} \cdot \mathbf{R} \right. \\
- 8\mathbf{R} \cdot Q^{(1)} \cdot Q^{(2)} \mathbf{R} + 8\mathbf{R} \cdot Q^{(1)} \cdot \mathbf{R} \cdot Q^{(2)} \cdot \mathbf{R} \left. \right] + O(1/R^3), \tag{13} \]
(with implicit summation over repeated \( a \) and \( b \)) is calculated in Appendix A. Note that the Green’s function in Eq. (11) should also contain homogeneous terms, which reflect the boundary conditions at the outer edge of the membrane, \( r = d \). However, we have only used the explicit form of the Green’s function in computing the leading terms in the multipole expansion. As long as \( L_1 \) and \( L_2 \) are sufficiently far (compared to \( R \)) from the edge, the particular choice of boundary conditions at \( r = d \) does not modify the leading terms in this expansion. The homogeneous terms can therefore be safely suppressed in Eq. (11).

We first isolate the integration over \( k_1(r) \) in Eq. (12),
\[
I_1 = \int Dk_1(r) \exp \left\{ -\frac{k_B T}{2\kappa} \int_{L_1} d^2 r d^2 r' k_1(r) G(r - r') k_1(r') \right. \\
- i \int_{L_1} d^2 r k_1(r) \left[ a_1 + b_1 \cdot r + r \cdot \mathbf{g}^{(1)} \cdot r \right] \right\}. \tag{14} \]
To perform the above integration, the Green’s function in Eq. (14) has to be inverted in the finite region \( L_1 \). In order to do this, we introduce an auxiliary field \( h(r) \) and write
\[
I_1 = \int Dh(r) \exp \left[ -\frac{\kappa}{2k_B T} \int_{R^2} d^2 r \left( \nabla^2 h(r) \right)^2 \right] \\
\times \prod_{r' \in L_1} \delta \left( h(r') - a_1 - b_1 \cdot r - r \cdot \mathbf{g}^{(1)} \cdot r \right). \tag{15} \]
This is just the partition of a membrane constrained by a single curved rod. After evaluating the contribution on \( L_1 \) (via the delta function), we are left with
\[
I_1 = \exp \left[ -\frac{2\kappa}{k_B T} \epsilon_1 L_1 \left( g_{aa}^{(1)} \right)^2 \right] \int Dh(r) \exp \left[ -\frac{\kappa}{2k_B T} \int_{R^2 - L_1} d^2 r \left( \nabla^2 h(r) \right)^2 \right], \tag{16} \]
where the prime indicates that the function \( h(r) \), and its normal gradient, are constrained to satisfy the following conditions on the boundary \( \partial L_1 \), of \( L_1 \),
\[
h(r) \left|_{r \in \partial L_1} = a_1 + b_1 \cdot r + r \cdot \mathbf{g}^{(1)} \cdot r, \right. \\
\partial h(r) \left. \right|_{r \in \partial L_1} = \frac{\partial}{\partial n} \left( a_1 + b_1 \cdot r + r \cdot \mathbf{g}^{(1)} \cdot r \right). \tag{17} \]
Now let \( h_0(r) \) denote a solution to the biharmonic equation,
\[
\nabla^4 h_0 = 0
\]
on \( \mathbb{R}^2 - L_1 \) with the boundary conditions of Eqs. \((17)\). We then set
\[
h(r) = h_0(r) + \delta h(r),
\]
where both \( \delta h(r) \), and its normal gradient, are zero on the boundary of \( L_1 \). Following this change of variables,
\[
I_1 = A \exp \left\{ -\frac{2\kappa}{k_B T} \epsilon_1 L_1 \left( g^{(1)}_{aa} \right)^2 \right\} \exp \left\{ -\frac{\kappa}{2k_B T} \int_{\mathbb{R}^2 - L_1} d^2 r \left( \nabla^2 h_0(r) \right)^2 \right\},
\]
where
\[
A = \int \mathcal{D} \delta h(r) \exp \left\{ -\frac{\kappa}{2k_B T} \int_{\mathbb{R}^2 - L_1} d^2 r \left( \nabla^2 \delta h(r) \right)^2 \right\},
\]
is a normalization constant, independent of \( a, b, \) and \( g \), which does not affect the remaining computations. In order to solve Eq. \((13)\) we must specify the boundary conditions at \( r = d \), which are the same as those for \( u(r) \). As discussed earlier, the results should be independent of this choice, and it is convenient to select
\[
\delta h(0) = 0.
\]
As shown in Appendix \( \mathbb{C} \), the solution for the case when the rod is along the \( y \)-axis, in the limit \( d \gg L_1 \), gives
\[
\int_{\mathbb{R}^2 - L_1} d^2 r \left( \nabla^2 h_0(r) \right)^2 = 2\pi \left( L_1 g^{(1)}_{xy} \right)^2 + \frac{1}{\ln(4d/L_1)} \left[ b_1^2 + b_2^2 \right] + O(L_1/d),
\]
where \( s_i \) are numerical constants. The second term on the right hand side of Eq. \((21)\) is examined in Appendix \( \mathbb{B} \), where the irrelevance of higher order terms in \( b \) is demonstrated. In the limit \( d \gg L_1 \), it suffices to keep only the first term on the right-hand side of Eq. \((21)\), which gives
\[
I_1 = A \exp \left\{ -\frac{\kappa}{k_B T} \epsilon_1 L_1 \left( g^{(1)}_{aa} \right)^2 + \pi \left( L_1 g^{(1)}_{xy} \right)^2 \right\}. \tag{22}
\]
The result of the \( k_2(r) \) integration in Eq. \((12)\) is similar, with the index 2 replacing 1, and with the coordinate axis appropriately rotated to align with the second rod. The overall expression for the partition function now reads (dropping unimportant multiplicative constants)
\[
Z = \prod_{i=1}^2 \int dQ^{(i)} d\mathbf{g}^{(i)} \exp \left\{ -\frac{\pi K}{k_B T} \left[ \left( L_1 g^{(1)}_{xx} \right)^2 + \left( L_2 g^{(2)}_{xy} \right)^2 \right] \right\} \times \exp \left\{ -i \sum_i g^{(i)2}_{ab} - \frac{k_B T}{2\kappa} v \left[ Q^{(1)}, Q^{(2)} \right] \right\}, \tag{23}
\]
where we have set the widths of the rods to zero (i.e. taken the \( \epsilon_i \to 0 \) limit). The primed indices \( x', y', x'', y'' \) indicate that the corresponding components are with respect to the coordinate frames where \( L_1 \parallel y' \) and \( L_2 \parallel y'' \). We define an un-primed coordinate system such that the \( x \)-axis is parallel to \( \mathbf{R} \) and the two rods make angles of \( \theta_1 \) and \( \theta_2 \) with respect to the \( x \)-axis as in Fig. \( \mathbb{E} \). Integration over \( \mathbf{g} \) yields
\[
Z = \prod_{i=1}^2 \int dQ^{(i)} \delta \left( Q^{(i)}_{xx} \cos^2 \theta_i + Q^{(i)}_{xy} \sin 2\theta_i + Q^{(i)}_{yy} \sin^2 \theta_i \right) \times \delta \left( Q^{(i)}_{xy} \sin^2 \theta_i - Q^{(i)}_{yy} \sin 2\theta_i + Q^{(i)}_{xx} \cos^2 \theta_i \right) \times \exp \left\{ -\frac{k_B T}{2\kappa} \sum_i \frac{1}{2\pi L_1} \left[ \frac{1}{2} \left( Q^{(i)}_{yy} - Q^{(i)}_{xx} \right) \sin 2\theta_i + Q^{(i)}_{xy} \cos 2\theta_i \right]^2 \right\} \times \exp \left\{ -\frac{k_B T}{2\kappa} v \left[ Q^{(1)}, Q^{(2)} \right] \right\}. \tag{24}
\]
Since we are working in the large-$R$ limit, the $Q$ integrations are most easily performed by expanding Eq. (24) to second order in $v$. After expanding $-k_B T \log Z$, we find the $(R, \theta_1, \theta_2)$-dependent part of the free energy given in Eq. (3). We can re-write this interaction in a coordinate invariant form, in terms of the vector $\hat{R}$ and the directors $\hat{L}_1$ and $\hat{L}_2$ along the rods as 

$$V_M^T = - \frac{k_B T}{128} \frac{L_1^2 L_2^2}{R^4} \left[ 2 \left( 2(\hat{L}_1 \cdot \hat{R})(\hat{L}_2 \cdot \hat{R}) - \hat{L}_1 \cdot \hat{L}_2 \right)^2 - 1 \right]^2 + O(1/R^6). \quad (25)$$

### III. FILMS

We now turn to the analogous calculation for films. Again we use a Gaussian approximation for the Hamiltonian in Eq. (1), but keep only the surface tension this time,

$$\mathcal{H}_0 = \frac{\sigma}{2} \int d^2 r (\nabla u(r))^2. \quad (26)$$

All anharmonic corrections to the above expression are unimportant in the limit $\sigma a^2 \gg k_B T$, where $a$ is a microscopic length. We follow a procedure similar to that described in Sec. (II) but with the differences noted below. The expression for the partition function is similar to Eq. (3), with $\mathcal{H}_0$ now given by Eq. (26). For films however, we cannot justify keeping only the leading terms in an expansion in $b_i$. Thus the full rotationally-invariant measure of integration on the sphere of slopes $b_i$ should be employed (see Appendix B). Also, the appropriate domain replacing $L_i$ is the projected length $\bar{L}_i \equiv L_i/\sqrt{1 + b_i^2}$. After introducing auxiliary fields $k_i(r)$ as in Sec. (II), the analog of Eq. (8) may be written as

$$Z = \prod_i \int \frac{d^2 b_i}{(1 + b_i^2)^{3/2}} \int Dk_i(r) \delta \left( \int_{L_i} d^2 r k_i(r) \right) \times \exp \left[ -\frac{k_B T}{2\sigma} \sum_{i,j=1}^2 \int_{L_i} d^2 r_i \int_{L_j} d^2 r_j k_i(r_i) G(r_i - r_j) k_j(r_j) - i \sum_i b_i \cdot \int_{L_i} d^2 r_i k_i(r_i) \right], \quad (27)$$

where

$$G(r - r') = \left( \frac{1}{\nabla^2} \right)_{rr'} = \frac{1}{2\pi} \ln |r - r'|. \quad (28)$$

Note that for films, the dipole moment of $k_i(r)$ does not vanish. Expanding $G(r - r')$ in a multipole expansion and keeping only the leading term, which now comes from the dipole moments $p_i \equiv \int r k_i(r)$, we find

$$Z = \prod_i \int Dk_i(r) \int dp^{(i)} dp^{(i)} \frac{d^2 b_i}{(1 + b_i^2)^{3/2}} \times \exp \left\{ -\frac{k_B T}{2\sigma} \sum_i \int_{L_i} d^2 r d^2 r' k_i(r) G(r - r') k_i(r') - i \int_{L_i} d^2 r k_i(r) [a_i + (b_i + g_i) \cdot r] + i \sum_i g_i \cdot p^{(i)} \right\} \times \frac{k_B T}{2\sigma} u \left[ p^{(1)}, p^{(2)} \right], \quad (29)$$

where

$$u \left[ p^{(1)}, p^{(2)} \right] = \frac{1}{\pi R^2} \left[ p^{(1)} \cdot p^{(2)} - 2(p^{(1)} \cdot \hat{R})(p^{(2)} \cdot \hat{R}) \right], \quad (30)$$

is the effective dipole-dipole interaction, analogous to Eq. (13), and $g_i$ is the variable conjugate to $p^{(i)}$. We integrate out $k_i(r)$ as in Sec. (II) by introducing an auxiliary field $\delta_i(r)$. In this case we must solve a harmonic equation on $IR^2 - L_i$, instead of the biharmonic Eq. (18), with the boundary condition on $L_i$.
\[
  h_0(r)_{|r \in \partial L_i} = a_i + (b_i + g_i) \cdot r .
\]

The harmonic problem can be solved either by a method similar to that described in Appendix D or by conformal mapping. The resulting expression for the partition function reads

\[
  Z = \prod_i \int dp^{(i)} dg \frac{d^2b_i}{(1 + b_i^2)^{3/2}}
  \times \exp \left[ -\frac{\sigma}{2k_BT} \left( \frac{\pi}{4} \tilde{L}_1^2 (b_1y' + g_1y')^2 + \frac{\pi}{4} \tilde{L}_2^2 (b_2y' + g_2y')^2 \right) + i \sum_i g_i \cdot p^{(i)} - \frac{k_BT}{2\sigma} u \left[ p^{(1)}, p^{(2)} \right] \right],
\]

where the meaning of the primes is the same as in the previous section. One can now see explicitly that the higher order terms in the expansion in \( b_i \) are important in this case. The remaining integrations, except those of \( b_1y' \) and \( b_2y' \), can be performed in a straightforward manner. The latter two integrals are rather complicated and in order to get a simple result, we restrict to the case \( \sigma L^2 \left( L^2/R^2 \right) \ll k_BT \). In this limit, the integrals can be approximated by Gaussian forms. After expanding \(-k_BT \log Z\), we find Eq.(B), which can be expressed in a coordinate invariant form, in terms of the vector \( \tilde{R} \) and the directors \( \hat{L}_1 \) and \( \hat{L}_2 \) along the rods, as

\[
  V_F^T = -\frac{k_BT L_1^2 L_2^2}{128 R^4} \left( 2(\hat{L}_1 \cdot \tilde{R})(\hat{L}_2 \cdot \tilde{R}) - \hat{L}_1 \cdot \hat{L}_2 \right)^2 + O(1/R^6).
\]

**IV. DISCUSSION**

We shall now discuss some general aspects of the fluctuation-induced interactions in Eqs.(2) and (3). The magnitude of the interaction is solely determined by \( k_BT \) and is independent of the tension and rigidity coefficients \( \sigma \) and \( \kappa \). Thus the effect persists even for rather stiff membranes with \( \kappa \gg k_BT \). The only assumption is that the inclusions are much more rigid than the embedding surface, thus limiting its fluctuations in their neighborhood.

For both membranes and films, the interaction falls off with distance as \( 1/R^4 \). This is a general feature of fluctuation-induced forces, including the (finite \( T \)) van der Waals interactions, which in \( d \) dimensions fall off as \( 1/R^{2d} \). Since the direct van der Waals interactions between inclusions still fall off as \( 1/R^6 \), the forces mediated through the two-dimensional surface will always asymptotically dominate. Of course the dimensional dependence of \( R^4 \) is canceled by a product of lengths in the numerator. For spherical inclusions, this is given by the product of two inclusion areas (see Ref. [8] and Appendix D) and for rods by the product of the squares of their lengths. Presumably, for general shapes, there is a formula that interpolates between these two limits. Another potential extension is to a polymer floating on a membrane. The interplay between the elasticity and shapes of a polymer and membrane, neglecting membrane fluctuations, have been examined in [20]; an extension to the case of a fluctuating membrane has also recently appeared [21]. There is also interesting behavior in the opposite limit of \( R \ll L \) for the interaction between two parallel semiflexible polymers [22].

Finally, the most interesting aspect of our calculation is the orientational dependence of the force. This is most easily discussed for the film, where an intermediate stage involves calculating the angular dependence of a dipole-dipole interaction, which is subsequently squared. The final angular dependence is thus that of squared dipolar interactions. Similarly, the result for the membrane corresponds to squared quadrupolar interactions. The minimal-energy orientations are shown in Fig.2; note there is a large degeneracy. We also note that these interactions cannot be obtained by adding two-body potentials on the rods; To find the orientational dependence of additive forces, let us consider an interaction \( U(|r_1 - r_2|) du_1 du_2 \), between any two infinitesimal segments of two rods of length \( L \) at a distance \( R \gg L \). Expanding \(|r_1 - r_2| \), and integrating over the two rods, leads to the interaction

\[
  V(R, \theta_1, \theta_2) = L^2 U(R) + \frac{L^4}{6} \left( \frac{U'(R)}{R} + U''(R) \right) - \frac{L^4}{12} \left( \frac{U'(R)}{R} - U''(R) \right) \left( \cos 2\theta_1 + \cos 2\theta_2 \right).
\]

Note that the angular dependence is now completely different, and minimized when the two rods are parallel to their axis of separation. Presumably both interactions are present for rods of finite thickness; the additive interaction is proportional to \( L^2(L \epsilon/R)^2 \), where \( \epsilon \) is the thickness. The previously calculated interactions are thus larger by a factor proportional to \( (R/\epsilon)^2 \) and should dominate at large separations.

The unusual dependence on orientation in Eqs.(2) and (3) could lead to new types of orientational ordering in ensembles of rod-shaped particles. Of course, due to the non-additive nature of the forces, the fluctuation-induced
interaction should be calculated separately for each arrangement. However, a cursory examination suggests that three-body and higher order interactions fall off with separation as \(1/R^6\). Thus for \(R \gg L\), a collection of rods can be treated as if they interact through additive pair potentials. It is amusing to examine the minimum of such an interaction for three rods placed on the vertices of an equilateral triangle. One possible equilibrium configuration is a three arm star with the relative angles of \(2\pi/3\) between the rods. Interestingly, this so-called “triskelion” structure is indeed formed by three rod-like “clathrin” proteins [1]. (Another stable configuration has each rod parallel to the corresponding side of the equilateral triangle.) Of course, given the relative proximity of the three proteins, it is not clear that the asymptotic interactions of Eq. (3) are applicable to this case. Another generic aspect of dipole and quadrupolar interactions is that they are frustrated (i.e. cannot be simultaneously minimized with respect to the orientations) if the rod centers are not aligned. There may thus be an overall tendency to arrange rod shaped molecules into chains. (Naturally this effect competes with the tendency to aggregate the inclusions together.) We hope that the orientational dependent interactions calculated in this paper will provide a fresh perspective on the behavior of inclusions in biological membranes.

ACKNOWLEDGMENTS

MK and MG acknowledge the hospitality of the ITP at Santa Barbara where this work was initiated (supported by NSF Grant No. PHY-89-04035). The work at MIT is supported by the NSF grant DMR-93-03667. RG acknowledges support from the Institute for Advanced Studies in Basic Sciences, Gava Zang, Zanjan, Iran.

APPENDIX A: THE QUADRUPOLE QUADRUPOLE INTERACTION

In this appendix we derive the quadrupole-quadrupole interaction in Eq. (13). The starting point is the pairwise interaction

\[
v = 2 \int_{L_1} d^2 r \int_{L_2} d^2 r' k_1(r) G(r - r' - R) k_2(r').
\]  
(A1)

The Green’s function may be written as

\[
G(r - r' - R) = \frac{1}{8\pi} |r - r' - R|^2 \ln |r - r' - R| \quad \text{(A2)}
\]

\[
= \frac{1}{16\pi R^2} \left(1 + \frac{r^2}{R^2} + \frac{r'^2}{R^2} - 2\frac{r \cdot r'}{R^2} - 2\frac{r \cdot \hat{R}}{R} + 2\frac{r' \cdot \hat{R}}{R} \right) \quad \text{(A3)}
\]

\[
\times \left[ \ln \left(1 + \frac{r^2}{R^2} + \frac{r'^2}{R^2} - 2\frac{r \cdot r'}{R^2} - 2\frac{r \cdot \hat{R}}{R} + 2\frac{r' \cdot \hat{R}}{R} \right) + \ln(R^2) \right].
\]

Since \(r\) and \(r'\) are limited to the interior of \(L_1\) and \(L_2\), we can expand the above expression in powers of the small quantities \(|r/R|, |r'/R|\). Because of the constraints

\[
\int_{L_i} d^2 r k_i(r) = 0,
\]

\[
\int_{L_i} d^2 r a k_i(r) = 0,
\]  
(A4)

(for \(i = 1, 2\)) the leading terms in the integration vanish in Eq. (A1). The first non-vanishing term comes from the quadrupole moment

\[
\int_{L_i} d^2 r a r_b k_i(r) = Q_{ab}^{(i)},
\]  
(A5)

and is given by Eq. (13).
APPENDIX B: INTEGRATION OVER TILT ANGLES

In this appendix we examine the higher order terms in the tilts of the rods \( \mathbf{b}_i \), and show that they may be neglected. For simplicity we shall focus on \( \mathbf{b}_1 \); similar arguments apply to \( \mathbf{b}_2 \). Whenever possible we drop the index and use \( \mathbf{b} \equiv \mathbf{b}_1 \) and \( L \equiv L_1 \). The integration for \( \mathbf{b} \) must be performed over all possible orientations of the rod \( L \) in the three dimensional embedding space. The manifold of orientations is the unit sphere. In terms of the vector \( \mathbf{b} \), defined in Eq. (B1), the rotation invariant measure on the unit sphere is given by

\[
\mathrm{d}\Omega = \frac{\mathrm{d}^2 b}{(1 + b^2)^{3/2}}. \tag{B1}
\]

The leading term of the expansion of Eq. (B2) in \( \mathbf{b} \), \( \mathrm{d}^2 b \), was used as the integration measure in Eq. (B1). Additional \( \mathbf{b} \) dependence comes from the projection of the tilted rods onto the \( x-y \) reference plane. For example, the conditions imposed in Eq. (B1) do not really apply for \( r \in L \) but rather for \( r \) in the projected image of \( L \), which is a rod of length \( L/(1 + b_y^2)^{1/2} \). Again, in Eq. (B1) we have taken the leading order in an expansion in \( \mathbf{b} \) by setting \( 1/(1 + b_y^2)^{1/2} \approx 1 \).

We shall now demonstrate that the higher order terms in \( \mathbf{b} \) can be neglected (as discussed after Eq. (B1)). The argument is presented explicitly for terms of order \( b^2 \), but is easily extended to higher orders. Including the first corrections to Eq. (B1) results in

\[
Z \equiv \int \mathcal{D}u(r) \prod_{i=1}^{2} \mathcal{D}k_i(r) \mathrm{d}a_i \mathrm{d}^2 b_i \ (1 + \Gamma_x b_x^2 + \Gamma_y b_y^2) \tag{B2}
\]

\[
\times \exp \left[ -\frac{\kappa}{2k_B T} \int \mathrm{d}^2 r (\nabla^2 u(r))^2 + i \sum_i \int_{L_i} \mathrm{d}^2 r_i k_i(r_i) (u(r_i) - a_i - \mathbf{b}_i \cdot \mathbf{r}_i) \right],
\]

where \( \Gamma_x \) and \( \Gamma_y \) are independent of \( \mathbf{b} \). If, as in Sec. II, only the leading term is retained, the integration over \( \mathbf{b} \) leads to the constraint that the dipole moment \( k_1(r) \) must be zero (see Eqs. (B3)). Due to the higher order terms in \( \mathbf{b} \), this constraint is modified, and we have to take into account the dipole moment

\[
\mathbf{p} \equiv \int_{L_1} \mathrm{d}^2 r \mathbf{r} k_1(r). \tag{B3}
\]

Following the same procedure used for the quadrupole moment in Sec. II we introduce an auxiliary variable \( \mathbf{r} \), via

\[
1 = \int \mathrm{d} \mathbf{p} \mathrm{d} \mathbf{f} \exp \left[ i \mathbf{f} \cdot \left( \mathbf{p} - \int_{L_1} \mathrm{d}^2 r \mathbf{r} k_1(r) \right) \right]. \tag{B4}
\]

Inserting Eqs. (B4) and (B1) into Eq. (B2), and performing the multipole expansion, gives

\[
Z = \int \prod_i \mathcal{D}k_i(r) \mathrm{d}Q^{(i)}(\mathbf{r}) \mathrm{d}a_i \mathrm{d}^2 b_i \mathrm{d}^2 b \mathrm{d} \mathbf{f} \mathrm{d} \mathbf{p} (1 + \Gamma_x b_x^2 + \Gamma_y b_y^2) \tag{B5}
\]

\[
\times \exp \left[ -\frac{\kappa}{2k_B T} \int_{L_1} \mathrm{d}^2 r d^2 r' k_1(r) G(r-r') k_1(r') - i(\mathbf{b} - \mathbf{f}) \cdot \mathbf{p} - \frac{i}{\kappa} \int_{L_1} \mathrm{d}^2 r k_1(r) \left[ a_1 + \mathbf{f} \cdot \mathbf{r} + \mathbf{r} \cdot \mathbf{g}^{(1)} \mathbf{r} \right] \right] \times \cdots.
\]

In the above equation, \( \cdots \) denotes factors that are independent of \( k_1(r), \mathbf{b}, \mathbf{f}, \) and \( \mathbf{p} \), and identical to the corresponding terms in Eq. (B2) with the exception that \( v [Q^{(1)}, Q^{(2)}] \) is replaced by \( v [\mathbf{p}, Q^{(1)}, Q^{(2)}] \), i.e. the multipole energy now also depends on \( \mathbf{p} \). The integration over \( k_1(r) \) is the same as in Eq. (B1), except that \( \mathbf{b}_1 \) is replaced by \( \mathbf{f} \). Thus, after substituting \( \mathbf{f} \) for \( \mathbf{b}_1 \) in Eq. (B1), we are left with the modified integrals

\[
Z = \int \mathrm{d} \mathbf{f} \mathrm{d} \mathbf{p} \exp \left[ -\frac{\kappa}{2k_B T \ln(4d/L)} (s_1 f_x^2 + s_2 f_y^2) - i(\mathbf{b} - \mathbf{f}) \cdot \mathbf{p} \right] \tag{B6}
\]

\[
\times \left( 1 + \Gamma_x b_x^2 + \Gamma_y b_y^2 \right) \left( W_0 + W_{1x} p_x^2 + W_{1y} p_y^2 + \cdots \right).
\]

In the above equation, \( \{W_0, W_{1x}, W_{1y}, \cdots\} \) refer to the results of the remaining integrations, which are performed after expanding \( \exp[-\kappa/k_B T v(\mathbf{p}, Q^{(1)}, Q^{(2)})/2\kappa] \) in powers of \( \mathbf{p} \), and are independent of \( \mathbf{p}, \mathbf{b}, \) and \( \mathbf{f} \). After integrating over \( \mathbf{f} \), and dropping an unimportant constant, we obtain
\[ Z = \int d\mathbf{b} d\mathbf{p} \exp[-i\mathbf{b} \cdot \mathbf{p}] \]

\[ \times (1 + \Gamma_x b_x^2 + \Gamma_y b_y^2) \left[ W_0 - W_0 \frac{k_B T \ln(4d/L)}{2\kappa} \left( \frac{p_x^2}{s_1} + \frac{p_y^2}{s_2} \right) + \cdots \right]. \]

Note that the \( W_{1x} \) and \( W_{1y} \) have been dropped since they are subleading in the limit \( d \gg L \). Integrating over \( \mathbf{b} \) and \( \mathbf{p} \) then gives

\[ Z = W_0 + W_0 \frac{k_B T \ln(4d/L)}{\kappa} \left( \frac{\Gamma_x}{s_1} + \frac{\Gamma_y}{s_2} \right) + \cdots. \]  

As discussed in Sec.II, we assume that the size of the membrane is much less than the persistence length \( \xi \). Thus, the higher order terms in the expansion in Eq.(B8) are smaller by powers of \( k_B T \ln(4d/L) \kappa \approx \ln(d/L) \ln(\xi/a) \ll 1. \)  

Here we have used the result \[ \xi \approx a \exp(2\pi \kappa / k_B T), \] with a short-distance cutoff \( a \) of order molecular size, leading to the hierarchy of length scales \( a < L \ll d \ll \xi \). To leading order, then, we have \( Z = W_0 \), which is independent of \( \Gamma_x \) and \( \Gamma_y \) and therefore the lowest order term in the expansion in \( \mathbf{b} \). It is interesting to note that the above argument does not hold for films controlled by surface tension, as discussed in Sec.III.

**APPENDIX C: SOLUTION OF THE BIHARMONIC EQUATION**

The biharmonic equation (Eq.(18)) for a single rod is discussed in detail in this appendix. The problem is to find the solution to

\[ \nabla^4 h = 0, \]  

on a finite disk of radius \( d \) from which a line segment of length \( L \) along the \( y \)-axis has been removed. The boundary conditions are

\[ h(x = 0, -\frac{L}{2} \leq y \leq \frac{L}{2}) = a + b_y y + g_{yy} y^2; \]

\[ \partial_x h(x = 0, -\frac{L}{2} \leq y \leq \frac{L}{2}) = b_x + 2g_{xy} y, \]

\[ h(d) = 0, \]

\[ \partial_r h(d) = 0. \]

Note that for the boundary conditions, the derivatives are taken before the limit \( \epsilon \to 0 \). It turns out to be easier to impose a weaker boundary condition at \( r = d \), namely

\[ h(d) = O \left( \frac{L}{d} \right), \quad \frac{\partial}{\partial r} h(d) = O \left( \frac{L}{d} \right). \]  

Since we have \( d \gg L \), it will suffice to keep the leading terms in the limit \( L/d \to 0 \). Performing the integration by parts yields,

\[ \int_{\mathbb{R}^2 - L} d^2 r \nabla^2 h \]  

\[ = \int_{\partial(\mathbb{R}^2 - L)} dl \left( \nabla^2 h \frac{\partial h}{\partial n} - h \frac{\partial \nabla^2 h}{\partial n} \right) \]

\[ = \int_{-L/2}^{L/2} dy \left( h(0, y)f_1(y) - \frac{\partial h}{\partial x}(0, y)f_2(y) \right), \]

where
The Green's functions of the unknown functions \( f \) differ by subleading terms at \( r = \sqrt{x'^2 + (y - y')^2} \). Note that the boundary conditions in Eq.(C3) do not uniquely specify \( G \). Indeed the asymmetry in \( G \), which satisfy
\[
\nabla^4 G_1(x; y; x' = 0, y') = \delta(x - x') \delta(y - y'),
\]
and obey the conditions in Eq.(C8) at \( r = d \), are given by
\[
G_1(x; y; y') = \frac{1}{16\pi} \left[ x^2 + (y - y')^2 \right] \ln \left[ \frac{x^2 + (y - y')^2}{4d^2} \right] + \frac{1}{8\pi} \frac{yy'}{d^2} (r^2 + r'^2) + \frac{1}{16\pi} \left[ a^2 - r^2 - r'^2 \right],
\]
\[
G_2(x; y; y') = \frac{x}{8\pi} \left\{ \ln \left[ \frac{x^2 + (y - y')^2}{4d^2} \right] + \frac{2yy'}{d^2} + 1 - \left( \frac{r^2 + r'^2}{d^2} \right) \right\}.
\]

Note that the boundary conditions in Eq.(C3) do not uniquely specify \( G_1 \) and \( G_2 \), but allow different choices which differ by subleading \( O(L/d) \) terms at \( r = d \). Indeed the asymmetry in \( G_1 \) with respect to interchange of \( x \) and \( y - y' \) is a result of this freedom. If we require \( h \) and \( \partial h/\partial r \) to vanish at \( r = d \) then \( G_1 \) would be rotationally symmetric. The unknown functions \( f_i \) in the above solution can now be obtained self-consistently by matching to the known forms of \( h \) and \( \partial h/\partial x \) on \( L \), as given by the boundary conditions in Eq.(C2). We thus end up with the following integral equations
\[
a + b y + g_{yy} y^2 = \int_{-L/2}^{L/2} dy' \, G_1(x = 0, y; x' = 0, y') f_1(y')
\]
\[
b_x + 2g_{xy} y = \int_{-L/2}^{L/2} dy' \, \frac{\partial}{\partial x} G_2(x = 0, y; x' = 0, y') f_2(y').
\]
(Note that at \( x = 0, G_2 \) and \( \partial G_1/\partial x \) are both identically zero.) We start with Eq.(C11) for \( f_2(y) \), which is somewhat easier to solve. After changing variables to \( y = (L \cos \phi)/2 \) and \( y' = (L \cos \phi')/2 \), this equation reads
\[
b_x + L g_{xy} \cos \phi = \frac{L}{2} \int_0^{\pi} d\phi' \sin \phi' \, f_2 \left( \frac{L}{2} \cos \phi' \right) G'(\phi, \phi'),
\]
where
\[
G'(\phi, \phi') = \frac{1}{8\pi} \left[ 2 \ln(2\cos\phi - \cos\phi') - 2 \ln \left( \frac{4d}{L} \right) + 1 \right].
\]
We now use the expansion [24]...
\[ \ln(2|\cos \phi - \cos \phi'|) = -\sum_{n=1}^{\infty} \frac{2}{n} \cos n\phi \cos n\phi', \quad (C14) \]

and define a series
\[ \sin \phi' f_2 \left( \frac{L}{2} \cos \phi' \right) = \sum_{m=0}^{\infty} a_m \cos m\phi'. \quad (C15) \]

Solving Eq. (C12) for the \( a_m \)'s gives, to leading order in \( d \gg L \),
\[ f_2 \left( \frac{L}{2} \cos \phi' \right) = \frac{1}{\sin \phi'} \left[ \frac{-8bx}{L \ln \left( \frac{4dL}{L} \right)} - 8g_{xy} \cos \phi' \right]. \quad (C16) \]

The integral equation for \( f_1 \) requires more care. First, note that the choice of \( G_1 \) in Eq. (C9) does not lead to a vanishing normal derivative at \( r = d \), unless the condition
\[ \int_{-L/2}^{L/2} dy' y'^2 f_1(y') = 0, \quad (C17) \]

is satisfied. Setting up the expansion
\[ \sin \phi' f_1 \left( \frac{L}{2} \cos \phi' \right) = \sum_{m=0}^{\infty} b_m \cos m\phi', \quad (C18) \]

for \( f_1 \), this requirement implies
\[ 2b_0 + b_2 = 0. \quad (C19) \]

The integral equation (C10) can now be written as
\[ a + \frac{L^2}{8} g_{yy} + \frac{L}{2} b_y \cos \phi + \frac{L^2}{8} g_{yy} \cos 2\phi = \frac{L}{2} \int_0^\pi d\phi' \sin \phi' f_1 \left( \frac{L}{2} \cos \phi' \right) G(\phi, \phi'), \quad (C20) \]

where
\[ G(\phi, \phi') = \frac{L^2}{32\pi} \left[ (\cos \phi - \cos \phi')^2 \ln(2|\cos \phi - \cos \phi'|) \right. \]
\[ - (\cos \phi - \cos \phi')^2 \ln \left( \frac{4dL}{L} \right) + 2\frac{d^2}{L^2} \ln \left( \frac{4dL}{L} \right) \cos^2 \phi \]
\[ \left. - \frac{d^2}{L^2} \ln \left( \frac{4dL}{L} \right) \right] \cos 2\phi' \]
\[ + \cos \phi \left[ \left( \frac{5}{2} - 2 \ln \left( \frac{4dL}{L} \right) \right) \cos \phi' + \frac{1}{6} \cos 3\phi' \right] \]
\[ + \cos 2\phi \left[ - \frac{1}{2} + \frac{1}{2} \ln \left( \frac{4dL}{L} \right) - \frac{1}{3} \cos 2\phi' + \frac{1}{24} \cos 4\phi' \right] \]
\[ + \sum_{n=3}^{\infty} \cos n\phi \left[ \left( \frac{2}{n} - \frac{1}{n-1} - \frac{1}{n+1} \right) \cos n\phi' \right. \]
\[ \left. + \frac{1}{2} \left( \frac{1}{n+2} + \frac{1}{n} - \frac{2}{n+1} \right) \cos(n+2)\phi' \right] \]
\[ + \left. \frac{1}{2} \left( \frac{1}{n-2} + \frac{1}{n} - \frac{2}{n-1} \right) \cos(n-2)\phi' \right]. \quad (C21) \]

In going to the second form of \( G(\phi, \phi') \) in Eq. (C21), we have used the expansion in Eq. (C14) and rearranged the resulting expression as a series expansion so that it resembles the LHS of the integral equation. Substituting the
expansion of Eq.\( (\text{C18}) \) in the integral equation \( (\text{C20}) \) and equating the coefficients of \( \cos n\phi \) on both sides, we obtain the following set of linear equations for the \( b_n \),

\[
(I) : \quad \left( \frac{2}{n} - \frac{1}{n-1} - \frac{1}{n+1} \right) b_n + \frac{1}{2} \left( \frac{1}{n+2} + \frac{1}{n} - \frac{2}{n+1} \right) b_{n+2} \\
+ \frac{1}{2} \left( \frac{1}{n-2} + \frac{1}{n} - \frac{2}{n-1} \right) b_{n-2} = 0 \quad (n > 2),
\]

\[
(II) : \quad \left[ \frac{5}{2} - 2 \ln \left( \frac{4d}{L} \right) \right] b_1 + \frac{1}{6} b_3 = -\frac{64}{L^2} b_y,
\]

\[
(III) : \quad 2 \left[ -2 \frac{d^2}{L^2} + \ln \left( \frac{4d}{L} \right) \right] b_0 + \left[ -\frac{3}{4} + \frac{1}{2} \ln \left( \frac{4d}{L} \right) \right] b_2 = -\frac{128}{L^3} a - \frac{16}{L} g_{yy},
\]

\[
(IV) : \quad 2 \left[ -\frac{1}{2} + \frac{1}{2} \ln \left( \frac{4d}{L} \right) \right] b_0 - \frac{1}{3} b_2 + \frac{1}{24} b_4 = -\frac{16}{L} g_{yy}.
\]

The solution to the above equations is (to leading order in \( d \gg L \)),

\[
b_0 = \left( \frac{L^2}{d^2} \right) \left[ \frac{4}{L} g_{yy} + \frac{32}{L^3} a \right],
\]

\[
b_1 = \frac{32}{L^2} \ln \left( \frac{4d}{L} \right),
\]

\[
b_2 = -2 \left( \frac{L^2}{d^2} \right) \left[ \frac{4}{L} g_{yy} + \frac{32}{L^3} a \right],
\]

\[
b_3 = 0,
\]

\[
b_4 = -\frac{384}{L} g_{yy},
\]

and all other \( b_n \) are determined by the recursion relation (I). Putting the results for \( f_1 \) and \( f_2 \) into Eq.\( (\text{C4}) \), we find Eq.\( (\text{C7}) \), with \( s_1 = s_2 = 4\pi \).

**APPENDIX D: SPHERICAL INCLUSIONS**

In this appendix we correct an error in Ref.\[8\]. The expression for \( H \) below Eq.\( (\text{8}) \) in Ref.\[8\] should read

\[
H = \frac{(k_BT)^2}{64\kappa_0 A} \left( Q_{ij}^{(1)} Q_{ji}^{(1)} + 2Q_{ii}^{(1)} + Q_{ij}^{(2)} Q_{ji}^{(2)} + 2Q_{ii}^{(2)} \right) - \frac{(k_BT)^2}{2\kappa_0} V_1 \left( Q^{(1)}, Q^{(2)} \right).
\]

This changes the final answer by a factor of 1/2. Thus, Eq.(10) of Ref.\[8\] for the interaction between two inclusions of area \( A \), separated by a distance \( R \), becomes

\[
V^T(R) = -k_BT \frac{6A^2}{\pi^2 R^4}.
\]

[1] B. Alberts, J. Lewis, M. Raff, K. Roberts and J.D. Watson, *Molecular Biology of the Cell*, Garland, New York 1994.
[2] R.B. Gennis, *Biomembranes, Molecular Structure and Function*, Springer-Verlag, New York 1989.
[3] D.D. Lasic, *Liposomes from Physics to Applications*, Elsevier, Amsterdam 1993.
[4] Cevc and D. Marsh, *Phospholipid Bilayers: Physical Principles and Models*, John Wiley, New York 1987.
[5] J.H. Fendler, *Membrane mimetic chemistry. Characterizations and applications of micelles, microemulsions, monolayers, bilayers, vesicles, host-guest systems, and polymers*, John Wiley, New York 1982.
[6] J. Israelachvili, *Intermolecular and Surface Forces*, Academic Press, San Diego 1992.
FIG. 1. Two rod-shaped inclusions embedded in a membrane. The rods are separated by a distance $R$. The $i$th rod has length $L_i$, width $\epsilon_i$, and makes an angle $\theta_i$ with the line joining the centers of the two rods.

FIG. 2. The minimal-energy orientations for two rods in a membrane (a and b) and a film (a only). The energy is minimal for all values of $\theta$. 