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Front Propagation in the Pearling Instability of Tubular Vesicles

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Abstract. Recently Bar-Ziv and Moses discovered a dynamical shape transformation in-
duced in cylindrical lipid bilayer vesicles by the action of laser tweezers. We develop a hydrody-
namic theory of fluid bilayers in interaction with the surrounding water and argue that the effect

of the laser is to induce a

sudden tension in the membrane. We refine our previous analysis to
account for the fact that the shape transformation is not uniform but propagates outward from
the laser trap. Applying the marginal stability criterion to this situation gives us an improved
prediction for the selected initial wavelength and a new prediction for the propagation velocity,
both in rough agreement with the experimental values. For example, a

tubule of initial radius

0.7 ~m has a predicted initial sinusoidal perturbation in its diameter with wavelength S-S /Lm,
as observed. The perturbation propagates as a front with the qualitatively correct front velocity
a bit less than 100 ~m/s. In particular we show why this velocity is initially constant, as ob-
served and so much smaller than the natural scale set by the tension. We also predict that the
front velocity should increase linearly with laser power. Finally we introduce an approximate
hydrodynamic model applicable to the fully nonlinear regime. This model exhibits propagating
fronts as well as fully-developed "pearled" vesicles similar to those seen in the experiments.

1. Introduction and Summary

The study of artificial biomembranes has opened a window into the machinery of real cells
by giving us physical systems which are simple enough to describe from first principles, yet
complicated enough to display lifelike behavior. The study of the equilibrium configurations
of closed bags of lipid bilayers ("vesicles") is by now well advanced Ii, 2]. Most interesting
biophysical phenomena, however, are not in equilibrium, and the study of the dynamics of
vesicle shapes is somewhat less developed. For example, budding and vesiculation [3] and
instabilities crucial for understanding adhesion [4], are all inherently dynamical processes.

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To gain a physical understanding of non-equilibrium membrane dynamics we must begin
with experiments in which some physical intervention brings about a dynamical shape trans-
formation (~). Several such techniques are by now well developed. Budding and other shape
transformations can be induced by adjusting temperature in closed vesicles IS, 6]. Strings of
beads can be induced by relieving tension using micropipettes [7], by sudden hydration of dry
lipid [8], and by the incorporation of a

small object which is subsequently pulled away with
laser tweezers [9]. One can even create tension inside a vesicle by polymerizing a

stiff rod inside

it [10], whereupon a cylindrical structure modulated with pearls can emerge ii Ii.
Recently Moses and Bar-Ziv have introduced a new class of experiments in which laser
tweezers act directly on single lipid bilayers [12]. It is already perhaps surprising that there
should be any action at all, since the optical absorption of a single bilayer is so small. As we
will recall in Section 3 below, we argued in [13] that the effect of the tweezers is to induce
a
tension L in the membrane proportional to the laser power. Our argument relied only
on basic electrodynamics, and while it does not give the precise value of the constant of
proportionality, it does imply that the effect of the laser is extremely simple; unlike other
more mechanical probes, the possibility of complicated parasitic effects seems minimal. More
importantly, laser tweezers provide for the first time the fast, delicate, and highly localized
probe needed to understand membrane dynamics in detail. For example, while beaded tubes
have been seen in some of the other techniques mentioned above (see Sect. 2), a unique feature
of the tweezer experiment is the controlled ability to excite a "small-amplitude" (quasilinear)
peristaltic modulation.
We recall the basic results of [12] in Section 2 below. The most intriguing phenomenon for us
was the fact that when laser tweezers are applied to previously stable long cylindrical vesicles,
they excite an instability ending with a "string of pearls" state. The initial wavelength of
the instability is ~

= 2~Ro/k, where Ro is the initial cylinder radius and the dimensionless
wavenumber is typically k

=

0.8. Remarkably, a purely local excitation due to the laser trap
creates (in a certain regime) a

i~niformly modulated state, which invades the initial cylindrical
region at a

roughly constant velocity of about uf r~ 30 ~tm Is. This is not the sort of behavior
we usually associate with pulling a stretchy object in a viscous fluid, and so we have a very
interesting dynamical system.
The pearling phenomenon bears a superficial resemblance to the instability of a cylindrical
column of ~vater in air, studied in the classical works of Plateau and Rayleigh [14-16]. In this
situation surface tension destabilizes the cylinder, since the same volume per unit length can be
contained with less surface area as a string of spherical droplets. As in other pattern-forming
systems, a competition ensues: the lowest surface-to-volume ratio comes from a

small number

of large droplets, but the formation of such a state is kinetically suppressed because it requires
the motion of water (a conserved quantity) over long distances. For a macroscopic system
the water may be treated as inviscid (high Reynolds numbei~); Rayleigh calculated that the
fastest-growing instability set in at wavenumber k

=

0.70 [15]. At micron scales. however, we
are in a regime of low Reynolds number; here Rayleigh found the fastest-growing instability to
be at k

=

0 [16], totally different from what is seen in [12].
Of course the situation studied in reference [12] is not a

thread of liquid surrounded by air.
Long ago Tomotika considered a

two-fluid model, in which a column of one viscous fluid is
initially immersed in another with a certain positive surface tension II?]. One could imagine
that these two fluids correspond to the interior and exterior water, so that both viscosities are
equal. Specializing Tomotika's result to this case, one finds the fastest-growing mode to be at

(~) Experiments in which a biological intervention is introduced (for example, mutating a single pro-
tein) are comparatively abundant [3].

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k

=

0.56. Unfortunately this simple picture is not obviously adequate for the pearling problem,
nor indeed is its predicted value for kmax ever observed; experimentally the initial wavenumber
is always a bit larger, and then increases still further with time. What is missing?
For one thing, the two-fluid model neglects the presence of a material object between the inner
and outer fluids, namely the membrane, except insofar as the latter somehow communicates
tension induced at the trap to the entire surface. In particular Tomotika imposed continuity of
the shear stress Tpz across the boundary, while a material object located there will in general
be capable of exerting tangential forces and hence causing a discontinuity in Tpz.
A more realistic treatment of membrane dynamics requires a

three-fluid model, in which

a
two-dimensional fluid (the bilayer) separates t~vo three-dimensional fluids (the water). The
"tension" on the membrane can then more precisely be regarded as minus the 2d pressi~re If of
the intermediate fluid, which in turn emerges from the appropriate hydrodynamic equations.
The key early works on membrane dynamics used models of this type to study equilibrium
fluctuations [18]. In the pearling experiment the laser takes the system far from equilibrium
by suddenly imposing a boi~ndary condition on IT. In other ~vords, the laser trap is regarded as
a
lipid reservoir located at z =

0 in cylindrical coordinates, whose chemical potential suddenly
jumps from zero to a negative value as the laser is switched on.
The idea that the laser effectively induces a

tension L, and that a Rayleigh-type instability
ensues, was first proposed by Moses and Bar-Ziv [12]. We substantiated this picture of the laser
action in [13], showed ho~v to estimate L from the laser power, and found the fastest-growing
mode kmax = 0.68, at the low end of the observed values (~).
The most serious lacuna in the analysis of reference [13] were that (a) we neglected the prop-
agating character of the pearling instability, assuming instead that the tension was everywhere
a constant, and (b) we neglected the fact that the lipid fluid is conserved. These points are
related, of course. For a shape transformation to propagate out~vard from the trap, leaving
behind a stationary shape, lipid must constantly be transported away from the moving front
and into the trap. Assumption (a) gave us no possibility at all of predicting the front velocity,
a readily accessible experimental quantity.
In this paper we will present a more detailed analysis addressing these and many other
points. After reviewing the experimental facts in Section 2, we will build up a physical picture
of the pearling system in Section 3. In particular we will show that assumption (b) above is a
good approximation during the time regime of the experiment, so that pearling is essentially
the invasion of a saturating front into a uniform linearly-unstable state. To get to the point as
quickly as possible we will construct in Section 4

a very simple form of the three-fluid model
which captures most of the essential physics without lengthy formulas. We then analyze the
front propagation in Section 5 using the marginal stability criterion (or "MSC") jig, 20] and
show how it gives qualitati~~ely correct results for vf and k when applied to our simple model.
As we will recall, the ~/ISC allows one to compute the front velocity using only the linearized
dynamics.
To get quantitatively accurate predictions we will construct a more realistic model in Sec-
tion 6. The reader may wish to skip to the end of this rather technical section. In it we first
solve the hydrodynamics exactly, then resolve the bilayer into its t~vo monolayers, to get a
four-fluid model. The motivation for this is that dynamical friction between the two leaves
of the bilayer has been shown to be quite significant for a

related class of membrane prob-
lems [21-23], though as we will see the actual effect on our answers will be slight. Again using
the MSC, we first find that the initial wavenumber is ko = 0.80, which agrees with experiment
some~vhat better than the result of [13]. In particular the initial wavenumber is insensitive to

(~) Actually we quoted k,nax =

0.65 due to an error ~vhich we will correct in equation (4.2) below.

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changes in the laser power or tubule radius, as observed. Secondly the exact hydrodynamics
gives a

front velocity vf equal to 0.06L/~ where ~ is the viscosity of water, another prediction
in rough agreement with experiment. While this prediction isn't precise due to our imprecise
knowledge of L, it does explain why the magnitude of vf is observed to be so much smaller than
the natural velocity scale L/~. Moreover, the linear dependence of the initial front velocity on
the laser power should be verifiable in the future (3).
Since the MSC uses only the linearized equations it must assume, rather than proving, the
existence of a uniformly-propagating front. One could take the phenomenological attitude that
such behavior is observed experimentally, but this and other qualitative facts should emerge
from the solution of the full nonlinear equations. In Section 7

we introduce a

third model,
with most of the simplifications of the first, simple model (Sect. 4) but retaining the nonlinear
structure of the elasticity. We show the results of numerical studies that indicate that it indeed
supports propagating front solutions, and that it produces stationary pearled structures like
those seen in experiment. More details will appear elsewhere.
Appendix A contains a glossary of symbols used for physical constants, and their values.
Granek and Olami were the first to attempt a

realistic treatment of pearling without the
simplifying assumptions (a), (b) above [24]. While our physical picture and conclusions are
different from theirs, we are indebted to them for emphasizing these issues. We are also
grateful to Moses and Bar-Ziv, who first suggested to us that marginal stability might be applicable to this problem. Finally, others have suggested that the laser could have other effects
besides inducing tension, for example effectively inducing a bilayer asymmetry (spontaneous
curvature) [24, 25].We don't see how this could happen, and in any case we will see that no
such effect is needed in order to explain the observed phenomena.

2. Relevant Experimental Facts

Briefly the observed phenomena of interest to us are as follows [12]. Initial preparation of
the system yields stable, nearly straight cylinders up to hundreds of microns long, anchored
at both ends by large globules of lipid. In contrast to multilamellar vesicles, in which laser
tweezers induce visible delamination [26j, each tube in these experiments consists of a single
bilayer of DMPC or DGDG, with water on the inside and outside. The tubules are polydisperse,
~vith initial radii Ro between 0.3-5 ~tm. The high temperature used (45 °C) implies that the
membrane is in its pure fluid state. Initially the system is somewhat flaccid, as seen from
visible thermal undulations and the fact that the tubes are not quite straight.
Application of a

laser spot localized to r~ 0.3 ~tm produces a dramatic transformation to a
stationary "peristaltic" figure, I.e. a cylindrical shape with radius r(z) at first varying roughly
sinusoidally with distance z

from the trap. Greater laser power is required for larger-radius
tubules, but nothing seems to depend on the length of the tube, so long as the trap is initially
many radii from the ends. The shape transformation propagates outward from the laser trap,
with a well-defined velocity uf which varies between experimental trials but is typically about
30 ~tm/s and roughly constant for at least a couple dozen wavelengths. Remarkably, after
a very short illumination the shape transformation continues to propagate ajter the laser is
shut off, leading to a uniform, small-amplitude peristaltic shape. Longer excitation leads
to the eponymous pearled state. Sometimes tubes intersect each other; in this case the shape
transformation can actually cross from one tube to the other upon reaching the intersection [27j.
Once formed, the peristaltic shape has a well-defined initial wavelength ~ which is uniform
over many microns. The dimensionless initial wavenumber ko " 2~Ro/~ is always found in

(~) See the Note Added at the end.

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the range 0.64-1.0, and is typically about 0.8 (Ref. [12], Fig. I), whatever the initial radius
Ro. After prolonged tweezing some buildup of lipid becomes visible at the point of application
of the laser. The associated lipid structure is not optically resolvable; its exact nature is
presently unknown. As the modulation grows more pronounced, k

grows from ko to become

slightly greater than I and deviations from a simple sinusoidal profile become pronounced. The
modulated state is tense: visible thermal fluctuations are suppressed and the tube draws itself
straighter than initially.
We pause to contrast the above phenomena with other related results. Deuling and Helfrich
studied aged red blood cells, which had different interior and exterior fluids; in this situation it
is reasonable to invoke a spontaneous curvature co expressing the chemical asymmetry of the
bilayer environment. In our case there is no such asymmetry; as we will recall in Section 3.I
below, the fact that each leaf of the bilayer is initially in equilibrium with a common lipid
reservoir then implies that co =

0 [28].
Evans and Rawicz, and recently Pouligny, have rapidly formed thin tethers coming from large
vesicles, respectively by adjusting the internal pressure or by pulling out a

small inclusion in the

membrane [7,9]. Such tethers sometimes contain pearls. Also lower-temperature experiments,
where in-plane order is important, can give pearled shapes [29]. All of these experiments
have in common that the formation of pearls is coterminous with the formation of the tethers
themselves, and small-amplitude sinusoidal modulations are not seen. Finally, experiments in
mixed surfactant systems have shown eqi~ilibrii~m peristaltic shapes [30]. This is presumably due
to shape-composition coupling, which is known to lead to an instability towards an asymmetric
bilayer [31, 32] and thence to the mechanism of [33].

3. Physical Picture

In Rayleigh's problem, the tension was a material parameter characterizing the air-water in-
terface, and hence trivially constant. In our case we argued in the Introduction that tension is
instead a dynamical variable, and so its spread must be self-consistently determined along with
the change of shape. Our main objective in this section is to justify the assumption [12,13]
that tension initially spreads so rapidly that it effectively becomes constant and uniform as
soon as the laser is turned on (4). Thus the spread of tension is not what limits the speed of
initial propagation of the shape pulse. Our arguments in this section will all be rather crude.
We can only emphasize that the field of membrane dynamics is not yet fully developed, and
buttress our arguments whenever possible with the observed phenomenology.
In this section we will for simplicity assume axial symmetry everywhere. We will return to
this point in Section 6.3. Thus all scalars are functions of radius p, distance z

from the trap,
and time t; all velocity vectors have vanishing azimuthal component.

3.I. INITIAL EQUILIBRIUM. We begin with a discussion of the initial equilibrium, before
turning on the laser.
Initially some preparation protocol has created long cylindrical vesicles constrained to stretch
between the terminal blobs and in thermal equilibrium with them. We will speculate as little
as possible about the nature of the blobs. Since they are far from the illumination spot,
their only role is to determine the nature of the initial equilibrium, not the subsequent fast
dynamics. We will simply assume that the blobs furnish lipid reservoirs and that both leaves
of the bilayer membrane are in equilibrium with these common reservoirs, with a

chemical

potential for exchange close to zero.

(~) As mentioned earlier, Granek and Olarni first studied this issue [24].

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With this assumption we find that initially the membrane has tension close to zero, consistent
with the initially observed thermal motion [12]. We also get that the spontaneous curvature
co = 0, since in a chemically symmetric bilayer co can only arise as the difference in chemical
potentials between the two constituent monolayers (~) [28]. co #

0 is consistent with the

observed absence of any preferred initial tubule radius [12]. Nonzero spontaneous curvature
can lead to eqi~ilibrii~m unduloid shapes [33, 34], but as we mentioned earlier these are not
observed in the experiments in question. Moreover, these "Delaunay surfaces" begin with an
initial wavenumber k

=

I, larger than what is observed (see Appendix B).
The physical boundary condition imposed by the terminal blobs will not matter in our
analysis, but for concreteness suppose that they seal off the tubule, imposing fixed volume.
This constraint then creates a physical pressi~re difference, with a very small negative constant
pressure inside the tube pa =

- ~/2R(land p =

0 outside), where ~

is the usual bending
modulus. po balances the tendency of a cylinder to increase in diameter to reduce its bending
energy. One can either solve the volume constraint explicitly and substitute into the bending
energy (as in [12,13]), or else regard po as a Lagrange multiplier (as in [34] to see that then
the cylindrical shape is stable to all small perturbations. This is the initial equilibrium state.

3. 2. LASER ACTION. Next we recall our model of the laser action from reference [13]. When
the laser comes close to the membrane, nothing happens: local heating is not important. When
the laser spot toi~ches the membrane, it pulls material in by the dielectric effect. While it is
hard to calculate the exact tension so induced, we may easily estimate it as follows (~): the
applied laser power of r~ 50 mW, spread over a spot of diameter 0.3 ~tm, corresponds to an
energy density in vacuum £ of 2.3 x104 erg cm~3. Taking the dielectric contrast between water
and lipid at this frequency to be of order be =

0.23 [35j, we see that when a

lipid molecule falls
into the trap displacing water ~ve gain an energy [36j +~ £be aoD, where ao is the area of the
molecule's head and D is its total length. Taking 2D +~ 40 I, we get that each unit of bilayer
area sucked into the trap yields an energy gain of L

+~ 2

x
10~3 erg cm~~
Actually this figure is surely an overestimate. If the action of the laser is really to pack more
lipid into the trap, there must be an offsetting cost per unit area to fold it up or otherwise
put it into a more compact configuration than a single nearly-flat bilayer. (For more details
see [37].) Still, we see that the trap generates a

tension well in excess of the critical value [12]

Lcrjt +~ ~/R(+~ 1.2 x

10~~ erg cm~~ needed to trigger shape transformations (see Sect. 6.3
below), where ~ +~ 0.6 x

10~~~ erg is the bending stiffness of DMPC bilayers and we took

Ro "

0.7 pm for illustration. Let a e LR(/~ denote the dimensionless tension; thus

a e LR(/~ +~ 2 x 10~, (3.1)

and larger for largAr tubules. Such large tensions are qualitatively corroborated by other
experiments involving laser-induced expulsion of vesicles [37].
One could imagine that the details of how the bilayer gets packed into the optical trap could
effectively create different boundary conditions for the chemical potential of each layer and
hence induce a sort of symmetry breaking, a spontaneous curvature for the layer. For example,
tiny vesicles could get pinched off preferentially from the inner layer. We will resist such
speculations, as we have no theoretical or experimental evidence in favor of such a mechanism,

(~) See Appendix E. The situation is quite different in systems without free exchange of lipid between
the two leaves of the bilayer, such as vesicles of spherical topology. Here indeed the initial preparation
leads to a new parameter describing vesicles, the fixed area difference between the two monolayer
leaves [6].
(~) We thank R. Bruinsma for suggesting this estimate.

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nor will such a spontaneous curvature be needed to understand the phenomena. We will also
assume that the laser creates no major disruption to the integrity of the bilayer, I-e- the
membrane remains impermeable on the time scale (tenths of a second) in question (~), and
transfer of lipid from one leaf to the other ("flipflop") also remains too slow to be of interest,
as in unstressed membranes [38].
Further support for our model of the origin of pearling by laser-induced tension comes from
the observation that mechanical tension applied suddenly to a cylindrical vesicle (by dragging
an end attached to a movable pipette) creates a pearling instability similar to the one seen
with the laser [27]. Whichever excitation one uses, when it stops the tension reverts slowly to
zero, thermal fluctuations resume, and the tubule relaxes back to its initially stable cylindrical
shape [12].

3.3. INITIAL TENSION PROPAGATION. As we mentioned in the Introduction, the induced
tension L is properly to be regarded as a boi~ndary condition on the pressi~re IT of the lipid
fluid (~):
lI(Z # 0,t > 0) #

-L.

The sudden introduction of a gradient of IT causes the lipid to move toward the laser spot; this
motion in turn stretches the membrane, causing the tension to spread outward. We will first
argue that this initial spreading of tension is very fast, and essentially complete long before
shape changes have had a chance to begin. Hence in this subsection only let us at first neglect
shape changes altogether and ask what happens in a

linearized analysis when we begin to pull
on a cylinder of 2d fluid, then later check the self-consistency of this picture. Our arguments
in this subsection amount to little more than dimensional analysis. We simply point out that
tension propagates rapidly in a nearly unstretchable medium.
Since the shape is fixed and the water is incompressible, there can be no net flow of water
across a cross-section of the tube. As the bilayer begins to move toward the trap, it entrains
the surrounding water. Focusing our attention on the interior volume, this entrainment sets
up a velocity profile uz(p,z,t). For this estimate we will use Poiseuille (or "lubrication")
approximation, where all gradients in z are assumed much smaller than those in p. (We will
also temporarily neglect the exterior fluid.) The incompressible conservation law T7 u =

0

then implies that the radial velocity is small, up < uz, and by the equations of motion the
pressure p is constant across the cross-section of the tube. Solving the remaining equation of
motion ~i7~uz =

i7zp in this approximation then gives us the usual parabolic velocity profile
of Poiseuille flow,
"ZIP, z,t) "

f(z>t)P~ 9(z>t), j3.2)

where f is related to the pressure gradient and g = R] f/2 because there can be no net flow of
water down the tube.

The membrane itself is a compressible 2d fluid. Its velocity must match that of the water:

= uz(Ro) " ~R(f
2

(?) This amounts to assuming that the volume is effectively clamped by dissolved macromolecules. It
is reasonable since large laser-induced tension can pressurize vesicles with no significant loss of interior
volume, even long after the laser is shut off [37]. Indeed far greater tensions than those considered
here can be applied mechanically with no observed loss of interior volume nor other breakdown in the
bilayer model [7].
(~) The pressure of a 2d fluid has dimensions of tension.

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For its equation of motion, we can neglect the 2d viscosity of the lipid on these scales [22j and
write the force-balance equation as

v~n(z, t) = T~~jRo, z, t) =

- ~o~u~j ~~ =

-2~Ro fjz, t),

where Tzj is the 3d stress tensor of water. Gradients in the velocity must in turn affect the
density of lipid, by another conservation law. We write the lipid density as #

= #o(I + x)
where #o is the equilibrium density and x is the areal strain; then

~

[dz 2~Ro40 (1 + x)] =

dz i7z [2~Ro@ #o(I + x)] (3.3)

To close the equations we need the constitutive relation

IT=Kx,

where K is the 2d bulk modulus of the lipid layer.
Combining we find
~~
=

~~°i7(IT, (3.4)
°t 4~

whose solution IT(z,t) indeed spreads rapidly until it is essentially equal to the boundary
condition -L throughout the observed tens of microns. To estimate how rapidly, we need
the value of K. We argue in Appendix C that K is effectively much smaller than its "bare"
value (~) Ko ~

IA x 10~ erg cm~~; instead we will argue for K~~ r~ 10~~ erg cm~~ Even so,
K~~ » L. Combined with (3.I) we get the hierarchy of scales

~Ro~~ < L < K~~, (3.5)

which we will use repeatedly.
The large modulus means that the tension profile will rapidly outrun any front of shape
transformation traveling at uf < L /~ (in fact we will find in Sect. 6 that uf is much smaller than
this). For technical reasons the observable region must contain the laser spot, so propagation is
not observed for values of L larger than about 50 ~tm. Scaling (3A) we see that at a distance L
from the trap the tension approaches its saturation value in a

time of order tL ~ L2~/K~~RO.
Taking L

=

50 ~tm gives tL ~

4 x

10~~ s, about one video frame, and much faster than the
time L/uf r~ 2

s needed for the observed front propagation.
We conclude that after a very short time the tweezers create a uniform, tense, stretched
state of the lipid in the region of interest. If the tension L is great enough, this state will
be everywhere linearly unstable to shape perturbations, just as in the Rayleigh instability.
Of course it remains to show that a uniform stretched state will indeed change shape via a
uniformly propagating front as assumed above.

3.4. FRONT PROPAGATION. We have just argued that initially the tension spreads rapidly,
before the shape has had a chance to change. To see what happens to tension as the instability
progresses, we will continue to assume that this proceeds by the propagation of a well-defined
front, leaving behind a stationary modulated state. Later, this is shown to be a

self-consistent

picture.

(~) Were we to use the bare value Ko, we would have to include inert.ial effects in the above derivation,
leading to a

different dispersion relation from 3A [22], but with the same qualitative conclusion: tension
spreads more quickly than shape change.

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The energy which drives the pearling instability comes from delivering lipid to the trap.
But where does this lipid come from? Certainly very little comes from stretching the bilayer,
since we just asserted that its bare bulk modulus is much greater than the applied tension.
Likewise, the excess area associated with thermal fluctuations, and related to the effective bulk
modulus, is shown in Appendix C to be quite small. Instead, the change in area comes from
a shape transformation, in which the initial cylindrical shape gets replaced by something with
less area land hence fewer lipid molecules) per length. It may at first be hard to see how such
a
transformation could propagate at a constant velocity. After all, lipid must constantly be
transported to the trap, entraining water as in the previous subsection and incurring viscous
dissipation. Much as in Poiseuille flow through a pipe, shouldn't we expect a decrease of
pressure (IT(as the front moves away from the trap?
To address the question, consider first a case in which the cylinder gets converted at a moving
front to a modulated shape, with a change of its area per unit length from 2~Ro to 2~Ro II a).
The front is located at z = L, so to advance it at a velocity uf = dL/dt lipid must flow toward
the trap at velocity = auf.
The laser does work on the membrane at a rate 2~Roau f

L. This energy is lost due to viscous

dissipation, which scales as ~

f dV(i7u)~. Still assuming that the shape change propagates as a
well-defined front, we can separate this loss into two components: (I) dissipation at the front,
and (it) dissipation everywhere from z =

0 to L. Let us compare these losses. (I) The front
is moving at velocity uf. If the amplitude of the shape modulation is large (~°), the velocity
gradient near the front will be of magnitude uf /Ro. Anticipating our later result that the front
is well-defined (only a

few times Ro in length), we can thus estimate the volume factor to be
~R(, so the first loss is ~uf~~Ro. (ii) The second loss will be mainly due to entrainment of
water by lipid moving at velocity uz r~ auf. By the remarks in the previous subsection, the
entrainment of water creates a

shear 0puz r~ auf /Ro in a volume ~RO~L, for a

loss rate of

~a~uf~~L. Comparing the total loss rate to the power input, we find that

"~ ~

(+

~~L/Ro'
~~'~~

Here (collects various order-one factors neglected in our rough estimates. We see that indeed
the front cannot propagate at a constant velocity forever. But uf can stay roughly constant
until L >

(a~~Ro, and the regime in which this happens is characterized by the fact that drag
on the membrane behind the front is negligible. (The late-time asymptotics have been studied
by Granek and Olami [24].)
What is the fractional area loss a? Suppose first that the modulation saturates behind the

front at a

small amplitude, so that its radius is (Fig. I)

rjz,t) m Roji + ~jz, t)) j3.7)

with (u(< I. Requiring that the new shape have the same volume per unit length as the old
(no global transport of fluid), we find that a must be O(u~), so that Rola~ is enormous. We

will argue that this case is relevant for the case of a

short laser pulse, when full pearls never

form at all.

If on the other hand the laser is kept on for a

long time, we expect the final state to be of
large amplitude u r~ I, so one might worry that a r~ I. But we know a

lot about the final

state: it must be a string of pearls on thin tethers. After all, neglecting bending stiffness the
system minimizes area at fixed volume, leading to spherical pearls. Kinetic limitations prevent

(") If the amplitude is small, it turns out that the drag behind the front is even less important than
estimated here.

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Fig. 1. Modulated cylinder.

the pearls from all mergingj instead we expect a periodic structure with some wavelength ~.
The effect of the curvature stiffness is to prevent the tethers from shrinking to zero size. Since

a
thin cylinder of radius RI < Ro and length t has curvature energy](2~Rot) (1/Ri)~, RI will
stabilize at a nonzero value. Indeed if the tension is large (as we have argued), L/Lcrit » I
where Lcrit = ~/R], then we expect tethers of small radius, as seen (~~). In this case we can
neglect the volume and area of the tethers altogether.
Thus volume conservation says that a string of pearls of radius R2, separated by thin tethers
of length t (so that the wavelength 1

= 2R2 +t)~ must have volume per length 4~(R2)~/(31) =
~(Ro)~. The area per unit length is then just 4~(R2)~/l. For the wavelengths I

r~ 2~Ro

characteristic of the observed nonlinear regime, this corresponds to a

fractional area loss a of

just 10%. In other words, the constraint of volume conservation has kept a

small. If we carry

over the estimate leading to (3.6) (even though now the amplitude is not small), we see that
once again a~~ is very large and since (is O(1), we can neglect the drag along the length of
the tube for the initial propagation. Any gradient of the tension must be due to the drag, and
moreover we argued in Sect. 3.3 that the tension starts out uniform, so the continued smallness
of the drag means that the tension stays uniform in the initial propagation regime.
The conclusion of this subsection and the previous one is that in the regime of interest we
may reasonably model the effect of the laser as generating a constant uniform tension on the
membrane, just as was assumed in [12,13]. Lipid cannot literally disappear locally, but in the
observed initial regime we may act as though this were the case. In other words, the pearling
system behaves as if it were suddenly quenched into a uniform i~nstable state. This is the sort
of situation in which we expect front propagation, as we recall in Section 5 below.
As mentioned earlier, our conviction doesn't rest solely on these crude arguments, but also
on the experimental fact that indeed a

front does form and propagate at constant velocity; at
least initially [12]. Later in Section 7

we will see the front formation again in the numerical
solution to a simplified model.

3.5. OTHER ASSUMPTIONS. Here we collect other assumptions we are making. Our ax-
isymmetric assumption (3.7) could be generalized to allow i~(z, ~2, t) = £~ i~m(z, t)e~"~' The
peristaltic mode is m =

0. In Section 6.3 we will see that the m > 2 modes are stable. There i-e-
mains the m =

I mode, which corresponds to wandering of the cylinder centerline. The m =

I

mode is always soft, or critical, since it corresponds to the broken symmetry of displacement
normal to the tube. As we mentioned, such ~vandering is indeed obsen~ed initially. Hol~~ever

(~~)In fact the minimization gives a

tether radius of fi, times some constants of order unity,
which is qualitatively correct. There is thus no need to invoke spontaneous curvature to explain tether

formation.

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we will neglect it since (at least in the linearized analysis) it decouples from the interesting
peristaltic mode.
We also assume in our hydrodynamic analysis no-slip boundary conditions between the fluid
bilayer and the surrounding water. This is a standard assumption and no evidence exists to
make us relax it; essentially it rests on the fact that applied shear tends to spread out to
length scales much longer than the molecular scale. However, the two leaves of the bilayer are
two separate objects in contact; they can slip relative to each other, with a

friction coefficient

measured in the experiments of Evans and collaborators [21,23j. We will incorporate this effect
in Section 6 below.

3.6. SUMMARY. Let us summarize this long section. We have given a qualitative, intuitive
argument for a physical picture in which the laser creates a nearly uniform, tense state, both
before and during the subsequent shape changes. We assi~med that the latter proceeded by the
propagation of a

front, which then must initially move at a velocity uf considerably smaller
than the dimensional combination L/~ (see Eq. (3.6)), as observed. We still need to show that
this is the case and get a precise formula for uf.
Since front propagation in general leaves behind a state of wavenumber ko different from the
fastest-growing mode kmax [19,20j, we will also need to revisit our estimate of reference [13j to
see what happens to that prediction. We do this for a simple model in Section 5, then for a

more accurate model in Section 6.

4. Very Simple Model

To get as quickly as possible to the heart of the matter we first develop a simple truncated model

without a

lot of algebra. In this ti~torial model only we will make some expedient additional
assumptions, each of which we will justify or improve in the sequel. The assumptions are:

. I) As in [13j, we will temporarily neglect the propagating character of the modulation until
Section 5. Instead we will just find the wavenumber of the fastest-growing Fourier mode.
Our goal here is to show in the simplest possible way how tension leads to wavenumber
selection.

.

ii) We will neglect altogether the bending stiffness of the membrane as well as all bilayer
effects until Section 6.2. This will prove to be a good approximation if the applied tension
L greatly exceeds the threshold value for instability, as we have argued is the case (see
Eq. 13.5)).

.

iii) We will neglect the finite compressibility of the membrane. This is legitimate as
long as L is much smaller than the effective elastic modulus K~~ (see Eq. (3.5) and
Appendix C).

.

iv) We will use lubrication approximation as in (3.2). This is certainly not justified, since
the wavenumber kmax of the mode we will find is not much smaller than unity and hence
z derivatives are not much smaller than p derivatives, but it will make our equations very
simple. Similarly we will neglect the exterior fluid altogether.

We argued that as soon as the laser switches on, very quickly a nearly uniform tension L
appears. Volume conservation then implies that the pressure inside jumps to a constant positive
value, pi # L/Ro (the Laplace pressure of a cylinder under tension) to prevent the tube from
collapsing. As the tube starts to change shape, described by the small quantity i~ in (3.7),

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the Laplace pressure /hpLapiace(z,t) =

-L 2H gets new contributions from the change in the
mean curvature H [34j:

/hP~apia~~ =

~ji u Rlvl~tl + °i~J~). 14.1)

Since we temporarily neglect the exterior fluid, the interior fluid must move in such a way
as to give the pressure p(r(z, t), z, t) =

/hpLapiace, which we just computed. To linear order we
again have the fluid flow (3.2), where now f, g are functions of z and time. We can no longer
fix g by demanding that the net flow of water across any cross-section vanish, since now the
tube is getting fatter in some places and thinner in others. Instead, conservation of the interior
water gives
~

[dz ~r(z, t)~) =

dz i7z (2~pdp)uz,

(4.2)
dt /
or fi =

-i7z[(fRo~ 9).

2

To eliminate g we need the lipid conservation law. While we argued earlier that global
lipid conservation, and the net flow it creates towards the trap, could be neglected, still local
conservation is important. Generalizing (3.3) to variable radius but fixing the density gives
(for nearly-cylindrical surfaces)

(

[dz 2~r(z, t)] =

- dz i7z [2~r(z, t)@] (4.3)

t

where the boundary velocity @z = uz (r(z, t), z, t) =

fr~ g. Thus linearizing in small quantities
we get fi =

-i7z fRo~ 9). Comparing the previous equation we eliminate g to find (~~)

fi = R(i7z f. (4A)

Since we are linearizing, let us take u(z, t) to be a single Fourier mode:

~~jt) cosjkz/Ro). j4.s)

The fluid equation of motion ~i7~uz =

i7zp, together with (4.I) then gives (neglecting z
derivatives compared to p derivatives) 4 f

=

-)i7z(1 k~)i~, or (see Fig. 2)

fi =
j

k~(I k~)u, (4.6)
8~ o

so that the mode with the largest growth rate fi Iv is at kmax =

I/vi. Note that the tension
needed to get an appreciable growth rate increases with tubule radius, as observed.
Note the structure of the dispersion relation (4.6) the growth rate is the product of a
term (~ (l k~)) arising from the perturbation to the pressure in (4.I), times an additional
overall factor of k~ representing the two z derivatives from the hydrodynamics. The first is
due to the conservation of fluid volume, and the second from the usual Poiseuille-flow relation
between fluid flux and pressure gradients. In the more refined hydrodynamic theory derived
below the general structure is retained, in the sense that the growth rate is the product of a
hydrodynamic factor and a pressure term, but the former has a more complicated wavevector
dependence than k~ as a consequence of the details of flow in cylindrical geometry.

(~~) Note that in [13] we mistakenly set the boundary velocity to zero instead of fixing it with (4.3)-
(4.2). The formula for kmax below is however unaffected.

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Fig. 2. Exact and lubrication approximation dispersion relations, neglecting stiffness and bilayer
structure. Circles indicate fastest-growing modes.

5. Velocity and Wavelength Selection

We saw in our very simple model that tension destabilizes a cylinder. More generally when
we incorporate bending stiffness in Section 6 we'll see the same thing, with a

finite threshold
Lcrit. We now want to know what becomes of such an unstable state.

We argued in Section 3 that in the regime in question our problem could be regarded as
a
i~niform, qi~enched unstable state: the membrane elastically transmits the laser-induced
tension everywhere. The uniform unstable state changes its conformation until it saturates in
one of two ways. For brief tweezing, we suppose that the laser pulls out about I% of the area
(see Appendix C), then shuts off; even when the laser stops pulling the shape transformation
proceeds to an amplitude such that the projected area is reduced by about I%, I.e. u r~
/@. This fits with the observation of a small-amplitude peristaltic shape which continues
to propagate after shutoff. For sustained tweezing, there is no such limitation, and the shape
transformation continues until checked by the curvature energy of the thin tethers, as we argued
in Section 3A.

In either case a uniform quenched unstable state rolls off a potential hill to saturate non-
linearly. In this class of problems one typically finds that the instability proceeds via the
propagation of a

front from an initial disturbance into the unstable medium (~3). The question
of the precise conditions under which an equation has such a

front solution are ticklish and

require a more reliable knowledge of the full nonlinear equation than we possess (for example,
at nonlinear orders the effects of thermal fluctuations are surely more subtle than the picture
in Appendix C). However, if we take the existence of the front as an empirical fact, we can
use the analysis of [20] to determine its main properties solely from the linearized dynamical
equations.

(~~) In the present case the laser itself provides the initial disturbance; for another example see the
photographs in [26].

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The shape is governed by some nonlinear, translation-invariant equation in u(z, t) We sup-
pose a

family of solutions whose envelopes are functions of z ut, for various values of the
velocity u. Only one of these solutions can correspond to the actual observed front; thus we seek
the dynamically selected value u*. The selected value must at least be stable to perturbations,
in an appropriate sense which we now recall.
Suppose the front moves from negative to positive z at velocity u* and consider the leading
edge, where u

is still small. We need to examine the effect of small perturbations bu. In this
region we may use the linearized equations, so that superposition holds and the perturbation
belongs to a

family bu r~ exp(uJ(q)t qz) for various values of a complex wavenumber q, where
uJ(q) is the dispersion relation of the linearized equation. The envelope of this blip is then
exp(tReuJ zReq), which is itself translating at uniform velocity uq = ReuJ/Req. Of this
family of perturbations, not all are dangerous to the stability of the front. A wavenumber q is
dangerous only if

.

I) Re q > 0, so that this is a

leading edge solution,

.

ii) ReuJ > 0, so that it is growing, and

.

iii) uq >u*.

Without (iii), the blip just gets left behind by the front and never gets a chance to destabilize
it. If any complex q meets all these conditions we will call the front unstable in its comoving

frame.

Of course the assumed front solution itself corresponds at its leading edge to one particular
linear solution with some q*, and so

u* = ReuJ~ /Re q~ (5.1)

where uJ~ = uJ(q*). Let us now consider values of q very close to q*, q = q* + a + ib for small
a, b. Then we find

uq =

u* (1+

~

(ReuJ' u*)

muJ[j
ReuJw ReuJw ,

where uJ[=

(" Since a, b

were arbitrary, and q~ obeys (I), (it) above, we can always satisfy

~

q~

(iii)

as well unless

~~ ~j

~~

~ ~~ ~~ ~j

~~

~~'~~

The three equations (5.1)-(5.2) are necessary conditions for the linear stability of a propagating
front in its comoving frame [20]. We will refer to them as the "marginal stability criterion for
u~" or simply "the MSC", and use them to fix the three real variables u*, Req*, Irn q*. Note
that the leading edge may be oscillating in time if uJ~ has an imaginary part. This of course
does not imply that the saturated pattern far behind the front is also oscillating, for it cannot
be described by the linearized analysis above.
We can also use (5.1)-(5.2) to determine the selected wavenumber qo of the stationary pattern
behind the front. In the comoving frame of the front, the saturated pattern is continuously
created at the front and moves rigidly with velocity -u". Nodes are created in the leading edge
of the front at a rate Q

=

Irn(uJ~ -q*u~). We can interpret Q as the flux of nodes moving toward
the saturated pattern; if nodes are not created or destroyed as they pass into the non-linear
region, then ~ve must have qou~ = Q, or

qo =

Irn(uJ~ q*u~)/u* (5.3)

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for the wavenumber of the pattern jig]. Note that qo is generally different from both the
fastest-growing mode qmax and from q*.
Let us apply (5.3) to our very simple model. We found in Section 4 that uJ(k) =

fik~(I

k~), equation (4.6). Extending this formula to complex values of k and applying (5.1)-(5.3), we find ko + qoRo = 0.77, a decay length of 3.8Ro, and u* =

0.20L/~ r~ 4 x

10~ ~tm Is. In fact we
~vill see in Section 6 that our more accurate calculation of ko is quite close to the very simple
model, while our prediction for u* will be much smaller (~4). We note that the decay length
is indeed only a

few times Ro, as observed and as assumed in our estimates (Sect. 3). The
selected wavenumber ko is purely geometrical since we can form no length scale from tension
and viscosity; in particular ko is independent of laser power.
Of course the very simple model is still rather crude, even with the refinement we just made.
We will upgrade it to a more accurate model in Section 6. Since the algebra is a bit involved,
the reader may want to skip this section and pass directly to the simulation results in Section 7.

6. Complete Linear Model

Now that we have some confidence from our very simple model, we need to address some of
the oversimplifications listed in Section 4. First we will replace the lubrication approximation
with the exact solution to the Navier-Stokes equation. Then we resolve the bilayer structure
of the membrane to get the four-fluid model mentioned in the Introduction.

6.1. HYDRODYNAMICS: EXACT LINEAR THEORY. Now we go beyond the lubrication
theory and use the full linearized hydrodynamic equations for the interior and exterior fluids.
We begin with Stokes's observation that the axial symmetry we have assumed makes our
problem effectively two-dimensional. This, along with the incompressibility of the water,

)

+

i

+
1

= 0> (6.i)

allows us to write the interior and exterior water velocity in terms of the cylindrical stream
function ifi:

"~

~

'

"~ ~~'~~

The Navier-Stokes equations are now two equations in two unknowns, ifi and the pressure
p. We eliminate the latter by differentiating ~i7~up = 0pp with respect to z, differentiating
~i7~uz = 0zp with respect to p, and subtracting the two resulting equations to obtain

(i7~

~ ~ ~ifi
=

0. (6.3)
P °P

In Appendix D we find the stream function ifi required by a single mode of shape distortion
u(t) exp ikz /Ro, enforcing the no-slip boundary condition and lipid conservation. This yields u
and p in terms of fi, and ultimately the stress tensor T(inside and outside of the tube which
determines the normal force balance equation to relate u

and fi, I.e. to determine the growth
rate fi Iv = uJ(k). As mentioned in the Introduction, our boundary conditions differ from 11?]

(~~) It is interesting to note that the MSC prediction for the velocity is considerably larger than the
estimate w(qmax)/qm~x based on dimensional analysis and the assumption that the fastest-growing
mode dominates. This conclusion is implicit in the results of Dee and Langer [19] on the Swift-
Hohenberg equation, which for a particular parameter value has a

linear growth rate identical to that
given above for lubrication theory.

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Fig. 3. Dynamical factor as a

function of k, with fastest-growing modes indicated.

and [24], where the shear stress Tzp is taken to be continuous across the surface of the cylinder.
This boundary condition is appropriate for two viscous fluids that meet at an interface ii?] in
our case, however, there is a material object at the interface that supplies whatever forces are
necessary to ensure lipid conservation and the no-slip condition (~~).
The results for the growth rate have the form that generalizes (4.6) by the introduction of a
more complicated "dynamical factor" A(k),

uJ(k) = £A(k)(I k~) (6.4)

o~

with A(k) given by equation ID-g) of Appendix D. Figure 3

compares this function with the

lubrication approximation Ajub =

k~ /8. Our dynamical factor A(k) differs from the one given
in [13] due to the correction mentioned below equation (4.3); however the A(k) of Figure 3
leads to a kmax of 0.68 (see Fig. 2), very close to the value in [13j.
We see that for all wavenumbers the exact dynamical factor lies below that given by lubrica-
tion theory. This implies slower growth of instabilities given the same material parameters L,
~, and ~

(see Fig. 2). This increased drag relative to the lubrication approximation is sensible;
the lubrication model neglects some components of the velocity gradients and hence underes-
timates the rate of viscous dissipation. The same conclusion holds for the ordinary Rayleigh
instability of a

fluid column, as considered by Tomotika ii?]. We see a direct consequence of
this increased dissipation upon inserting the growth rate (6.4) into the MSC (5.1)-(5.2) and
solving the equations numerically. This yields ko =

0.75 and u~ =

0.06L Ii the latter indeed
being much slower than L Ii consistent with our discussion of (3.6).
We see that taking the propagating character of the instability into account has slightly
improved the agreement with the experimentally observed ko. Using our estimated value for

(~~) In Section 6.3 we also address the effect of the two-dimensional membrane viscosity and show that
it is dominated by the traction of the water.

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Fig. 4. Schematic of the bilayer showing various variables.

a, equation (3.I), we also get the front velocity uf r~ loo ~tm Is. Since our value for L is an
overestimate we get uf squarely in the observed range.

6.2. BILAYER MODEL. We now need a more realistic model of the bilayer. For one thing,
we have so far neglected bending stiffness, which as we saw is eventually crucial to stabilize the
tethers between pearls. But stiffness effects are comparable to effects involving the differential
stretching of the two leaves of the bilayer [6, 28], so we must include these as well. This means
introducing more continuum degrees of freedom, the densities #+ of lipid molecules per unit
area in each monolayer.
In fact one must sometimes retain #+ even in equilibrium problems, for example in closed
systems where the numbers of molecules are separately constrained. This situation leads to the
"area-difference elasticity" model studied for example in reference [6]. We can simply quote
their intermediate formula for the elastic energy:

(For completeness we rederive this formula in Appendix E.) Here ~ and Ko are the bilayer
stiffness and compression moduli, and dS is the area element of the midplane. H is the mean
curvature of the bilayer midplane; in our convention H

=

- 1/2Ro for a cylinder. We measure
the lipid density #+ at the neutral surface of the outer monolayer, assumed a distance d away
from the bilayer midplane, and similarly #~ See Figure 4. Thus the parameters of the model
are ~, Ko, d, and the full bilayer thickness 2D (see Appendix A). Since D and d are much
smaller than any other length scale in the problem, we will work to leading nontrivial order in
them, as indeed we have already done to get (6.5).
We begin in equilibrium at zero tension. Here the densities #+ take their preferred value #o.
Actually we will find it useful to recast our equations in terms of the densities referred not to the
monolayer neutral surfaces~ but to the bilayer midplane. If we imagine each molecule casting
its shadow on the midplane, the new density variables x+ are the excess density fluctuations
of those shadows (~~), relative to the equilibrium densities it projected to the midplane of
the unperturbed surface. Due to the curvature, it are no longer equal, but instead it =
#o II ~ 2Hod), where Ho is the equilibrium curvature. Thus we have I + x+ = #+11 ~ 2Hd) lit,
or

#+ /#o =

I + x+ + 2(bH)d, (6.6)

(~~) In [13] we called these variables p~.

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where bH = H Ho is the change of curvature. Substituting in (6.5) above yields [13]

F[H, x+, x~j =

/

dS lf(2H)~ +

j°

[(x+ + 2(bH)d)~ + (x~ 2(bH)d)~) + L),

(6.7)
2

Were we to consider fluctuations about flat membranes, we would set Ho # o; then (6.7)
reduces to the formula in [22].
Later we will want to rephrase (6.7) in terms of the mean density and density difference,

and rescale:
I

"

lR0/d)lx~ + x~) I

"

lR0/d)lx~ x~). 16'8)

We argued in Section 3 that the mean density adjusts quickly to its preferred value j

= o, since

only hydrodynamic drag obstructs this, and initially it is not effective. We cannot be quite so
sure about density difference, however. The two monolayers are like a pair of polymer brushes in
contact, and so the friction coefficient between the two layers can be land is) enormous [23,39].
Leaving (free, we then finally obtain the elastic energy

F[H, ii =

/

dS(f(2H)~ + ~/ (2H 2Ho)~

2

~

+

~° ((()~i~ + ~~ (H Ho)I) + L) (6.9)

2 2 o o

To gain a physical feeling for (6.9), consider two limiting cases. If the interlayer friction is small
(or time scales long), we can minimize (6.9) with respect to (also, and recover once again
the Canham-Helfrich model. If the friction is very large (or time scales very short) then (
cannot change at all from its initial value of zero, and we drop the third term of (6.9). For flat
membranes, Ho "

o and the first two terms combine to give the effective increase of stiffness
found in [22].

6.3. CYLINDER PERTURBATIONS. Let us instead specialize (6.9) to the case of a cylindrical

initial state and a

small sinusoidal perturbation of ~t and x of wavenumber k. Working to
quadratic order in fluctuations of shape and density difference one has [34]

H

= Ro~~ [-I + ~t + R(V~~t ~t~) 2

~ ~~° ~~~~~ ~~~~~ ~ ~~~~~~ ~

~~~~~

'

ds =

jRo dzd~2) ii + t~ + Ro2jvt~)2). 2

In these formulas V

=

(Vz, RO~~V~) is the gradient on the unperturbed cylinder. Substituting
gives (~~)

F[~t, ii = ~~ 21rRo dz const. + (2a 1)~t + Q(-R(V~)~t~ +

~

(~ + @(l k~)(~t
2R~ ,

/

4

(6.10)

(~~) This formula differs from the one in [13] because we no longer need to replace the linear terms
using the ansatz u =

- (uk)~ + 2uk cos(kz/Ro). Instead we will see how the terms linear in u determine
the constant part of the pressure difference. This rearrangement of the algebra has no effect on the
answers, but the presentation here emphasizes that global volume conservation is not needed and hence
the detailed structure of the terminal blobs is unimportant.

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where e Kod~ /~ and

Q(z) e

I + (a)z + x~ + @(1 ~)~. (6.ll)

This is our final formula for the elastic energy. As we increase the dimensionless tension a

(Eq. (3. I)) from zero, eventually at some dent this quadratic form acquires a negative eigenvalue
and the system becomes unstable. (In Sect. 4

we dropped all but the a

terms.)
We note in passing that for non-axisymmetric shapes, ~t(z, ~J,t) = ~tkm cos(kz/Ro + m~J),
for m > I the polynomial (6.11) remains stable until larger values of a

than for the peristaltic

m =

0 modes.

Having found the energy cost F for small distortions in shape and relative density difference
(6.10)-(6.ll), we now need the dynamical equations for the two monolayers, the 2d fluids of
our four-fluid model. These equations are the equations of tangential force balance. Each
monolayer feels forces due to inhomogeneities in density, the traction T(of the 3d water, 2d
viscous forces, and the friction between the two leaves of the bilayer [22]

- 3z$ + T(+ ~3)@~ ~ b(fl+ @~) = 0. (6.12)

X

Here ~ is the 2d lipid viscosity; we have written the frictional force per unit area as b(@+ @~)
where b is a constant and @~ are the tangential layer velocities [21-23]. Although the change
in I may be neglected just as in Section 6.2, now we must keep elastic terms corresponding to
changes in (, since these are in principle of the same order as the friction term. The second and
third terms of (6.12) are negligible compared to the first and the last. Indeed, since @~ -~ filk,
and @+ @~ -~ £filk, the last three terms are of magnitude ~fi, (fi, bdfi respectively, so that
on micron scales the last term dominates (see Appendix A).

°

To get an equation for 3ti, we use the difference in lipid conservation laws 3z(@+ @~) =
-£31i to write the difference of the dominant terms of (6.12) as

3j ($ ~) =

-2b3z(@+ @~),
X X~

Or

k~ bF

3tX j6 13) " ~qfi.

Next we need the equation of normal force balance analogous to (D.7). The Laplace force
law, equation (4.I), needs to be modified to account for bending stillness. To find the right
expression we have only to recall the origin of the Laplace law itself: the pressure jump is
bF/bV, the change in the elastic free energy due to a

small change in shape which changes
the volume by bV. To get (4.I) we used = @ with ((= ROE(I RO~V~~t) + and
= Ro~(I + ~t +.). Now we simply use the full elastic energy (6.10)-(6.ll).
We may neglect the difference in monolayer velocities for the purposes of computing the
hydrodynamic factor A(k). Once again, this difference is suppressed by d/Ro relative to the
central flow velocity and therefore does not significantly modify the energy dissipated in the
3d fluids. Thus we again have fi given by -A(k) /~ times the nonconstant part of the pressure
jump, just as in (D.8). Combining with (6.13), our linearized hydrodynamic equations are

fi ~ ~ fi(~) Q(k~) + a

- @(I k~)

~

~ = -j ~~ ,

(6.14)
t X oil E p(1 k2) fl /~ X
2

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o.oi

a=50

io

- 5
/~

~

0.00

~4

~
~

~$

~0.0i

o-I .5

-o

k

Fig. 5. Growth rate versus wavenumber in the full linear model for various values of the dimen-
sionless tension a. A typical experimental value is a rw 20.

where e e Roil/bd~ is a measure of the importance of interlayer friction. The desired dispersion
relation is then given by the positive eigenvalue, if any, of this linear problem, I-e- w -~
(-180 s~~ ~, where we took a

typical Ro " 0.7~m and ~ solves ~~ ~(gi + y) + gall "

0. Here

go " A(k) [) a + k~(a)) + k~] is the growth rate with zero friction, gi " go + A(k)@(I k~)~
is the growth rate at infinite friction, and y e @ek~ /4.
Figure 5 shows the growth rate with e = o-S, = 3.5, and various values of tension. Clearly
there is little effect of stillness on the curve w(k) when the tension is as large as its experimental
value a -~ 20 (compare with Fig. 2). For this value we read oil a

fastest growing mode with

km~x =

0.68 for a = 20, but as we argued in Section 5 km~x is not the expected wavenumber.
Instead inserting the above formulas for the dispersion w(k) into the equations for the MSC
is-1)-(5.2) gives ko " 0.80, a decay length of 4.0Ro, and ~f = 0.06E/~ -~ 100 ~m Is. The perfect
agreement of ko with Figure 1 of [12] is fortuitous, but certainly the MSC gives reasonable values
for the pattern wavenumber, front width, and front velocity, and as promised these values are
not very different from those found in Section 6.1 since at large tension both the stillness and
the layer friction are unimportant (see Eq. (3.5)).

7. Model for the Nonlinear Regime

We turn finally to a model for the development of pearls beyond the linear instability. A model
based on the exact hydrodynamics coupled to the elastic forces presents a

rather formidable

computational challenge. It is therefore of interest to define a simplified model which nev-
ertheless maintains certain central features of the full problem. Chief among these are ii)
conservation of fluid volume within the vesicle, (it) the monotonic decrease in energy associ-
ated with low Reynolds number flow, and (iii) the fully nonlinear structure of the elastic energy
needed to arrive at a true minimum of the energy functional.

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The simplest model consistent with these constraints utilizes the lubrication approximation,
thus yielding a

local evolution equation for the vesicle radius r(z, t). One goal of this investiga-
tion is to determine whether propagating fronts of constant velocity are indeed possible within
such a model. Their existence would be strongly suggestive that such fronts are supported by
the full hydrodynamics. A second goal is to test the validity of the marginal stability criterion.
While the assumptions of lubrication theory may not be quantitatively correct in comparison
with experiment, the issue at hand is one of internal consistency; within the assumptions of
lubrication theory, how accurate is the MSC?
In the model, the diffusion of tension is ignored, so that E is assumed to be uniform along
the vesicle. The bilayer bending stillness is included to stabilize pearls against pinching oil,
but the small effects of membrane compressibility and bilayer friction are omitted. Rather
than introducing the optical trap explicitly, we consider an initial condition of uniform tension
with a

localized shape perturbation. Thus in this model, the flow of lipid to the trap is not
included. We justified this approach at length in Section 3.
We first need some formulas for the elastic force beyond linear approximation. The pressure
difference across the membrane is the change in energy with respect to volume, so now our
generalization of (4.1) becomes

AP = Ill)) =

$

=

2 1-EH + ~ l<~H + 2H~ 2HKl1 ii-1)

where if~ is the covariant Laplacian on the curved surface, and K is the Gauss curvature. Ax-
ially symmetric shapes described by a

radius r(z) (Fig. 1) have mean and Gaussian curvatures
given by

~ Ill ~~))3/2 r(i

~l)1/2

~

T(I ~j))~

Likewise, for these shapes the determinant g of the metric tensor and the covariant Laplacian

are

g # Tfi~

j~ 1 3

T 3

T/@fiZfifiZ

For uniform tubular states of radius Ro we see from ii-I) that the balance of forces yields an
equilibrium radius Ro "

(~/2E)~/~, as discussed earlier in the context of the thin "tethers"
between pearls.
Recalling the derivation of the lubrication theory results in Section 4, in particular equa-
tion (4.2), we know that the equation of motion for the radius r(z, t) should have the form of
a
local conservation law,

~~~~ ~~' ~~~~

where J is the axial current. For this we appeal to our previous (linearized) result on lubrication
theory that relates J to the gradient of pressure,

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30

20

S~
2$ 10

o-O 0.2 0A 0.6 0.8 1-O

z/3Zn

Fig. 6. Numerical solution of the lubrication equation (7.4) with a = 10, showing the formation of
pearls. Time increases from bottom to top in increments of AT =

1.0.

Recall that the factor of 4 in the denominator differs from the usual Poiseuille result due to

the imposition here of lipid conservation. The pressure is just that determined by the energy
functional, equation ii-I). Combining equations (7.2), (7.3), and ii-I), and rescaling both r
and z with the unperturbed radius Ro and introducing the rescaled time T =

(~R(/4~)t we
obtain the partial differential equation

r) =

) r~)

(-aH +

if~H + 2H~
2HK)j,

(7.4)
T z z

where a

is again the rescaled tension (3.1).
It is easily demonstrated that this is a gradient flow, for the time derivative of the functional

F is

dF j

~

bF fir j

~

bF 1
~ ~ ~

1 bF

$ ~

br 3T

~

br r

~

~

~r br

=

/

dz r~ 3z $ ~

§ 0,
r r

where the last line follows by an integration by parts. Thus, provided r > 0 (I.e. the interface
does not pinch oil), F is driven strictly downhill. Furthermore, when F is constant in time
the functional derivative bF/br =

0 and the system is at an energetic extremum. Since the
model (7A) also contains the proper linear stability result of the lubrication approximation,
it provides a dynamics that interpolates between the basic Rayleigh-like instability and the
stationary final states, while obeying the relevant hydrodynamic conservation laws.
The flux form of the equation of motion and the relation between pressure gradients and
velocity in (7.4) are features found as well in models introduced recently for interface motion
leading to topology transitions and singularities in viscous flows [40]. In all of these systems,
despite the simplicity of the physical ingredients, the equation of motion is highly nonlinear
and of very high degree (sixth order in z-derivatives in the present case). These features
make numerical studies quite delicate, but with care a stable and accurate algorithm may
be developed. Here we report preliminary results of simulations illustrating that propagating
fronts of peristalsis are supported by the model.
Figure 6 shows the evolution of a cylindrical vesicle with a =

10 perturbed initially with a
localized distortion. The computational domain has a

length 16 x 21r, and periodic boundary
conditions are imposed by use of a pseudospectral algorithm. The figure clearly shows that

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following an initial "induction" period there is a propagating peristaltic pattern moving sym-
metrically outward from the initial perturbation. A nonlinear least-squares fit of the leading
edge of the front at successive times to the product of a decaying exponential and a cosine
function shows that the position of the front increases linearly with time over the duration of
the simulation, during which it has moved about six pearl lengths. This constant velocity is in
accord with our physical arguments of Sections 3, 4. We find the dimensionless wavenumber of
the pattern in the leading edge of the front to be ko " 0.78, and the decay length to be m 5A.
Applying the techniques of the earlier sections to the model of this section, one finds that the
MSC predicts a wavenumber ko " 0.77; the decay length of 4.3 is somewhat smaller than the
value observed in the numerical solution, but is still on the order of a pearl size. Thus the
front is "sharp." Finally, in the rescaled units of (7.4), the front velocity at the value a =

10 is

found to be ~f m 13, close to but somewhat smaller than the marginal stability criterion value
of17. Work is in progress to understand the origins of these discrepancies.
In addition to these quantitative aspects of front propagation, we see that the state left
behind the front indeed has the appearance of a string of pearls, with very narrow tethers
between somewhat prolate ellipsoids. These are quite similar to ones seen in the experiments
of Bar-Ziv and Moses. It is also interesting to note that a slight shift between the selected
wavelength near the leading edge of the front and that found well behind, where the pearls
are fully formed. This difference is in qualitative accord with what one finds in other more
familiar examples of propagating pattern selection [19].

8. Conclusion

Laser tweezers are an important new experimental tool for understanding membrane dynamics;
they furnish a precisely controllable, local, physical intervention. In this paper and [13] we have
proposed a simple model for the effective laser-membrane interaction and used it to explain
much of the phenomenology of the pearling instability discovered in this context by Bar-Ziv
and Moses.

Various aspects of the pearling phenomenon remain to be explained. For example, we have
not attempted to study the migration of the pearls which develop after prolonged tweezing.
What we did show was how a cylindrical vesicle under tension is unstable to states with a
periodic modulation in diameter. We refined our previous prediction for the initial wavelength
of this perturbation using the marginal stability criterion and predicted a

selected wavenumber

in good agreement with the experiments of reference [12]. We also explained the observed front
behavior and predicted a

front velocity in qualitative agreement with the experiments. Along
the way we showed how to incorporate the bilayer membrane structure into the dynamics.
Although this structure did not significantly affect our results, it may matter in dynamics
problems at lower tension and on shorter length scales. Finally, our numerical calculations
have demonstrated that the lubrication approximation is rich enough to capture the essential
physics of the pearling phenomena, such as the existence of an initial uniform front propagation
velocity and the shape of the fully developed pearls. These calculations were in reasonable
agreement with the predictions of the MSC, thus bolstering our faith in this approach and
suggesting that the MSC can be reasonably applied to other fluid dynamics problems. One
particularly relevant problem is the propagation of the ordinary Rayleigh instability along a
column of fluid, as seen in recent experiments on droplet fission [41].
We are not aware of any naturally-occurring biological process to which the pearling insta-
bility literally applies. Our goal was rather to create a simple theory of membrane dynamics
and test its many underlying assumptions by applying it to a well-controlled dynamical shape
transformation. We expect that the approach developed in this paper can provide a starting

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point for understanding other phenomena of more direct biological interest, for instance the
dynamics of shape instabilities during adhesion.
Note added: In more recent experiments [27], Bar-Ziv and Moses have found that the pearling
propagation velocity is indeed linear in laser power, as predicted here, though with a

somewhat
smaller numerical coefficient than our estimate.

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Society, for the partial support of this research.

Appendix A

A Compendium of Constants

Here we list the values of various physical constants for DMPC bilayers. We take:
the bilayer bending stillness to be ~ =

0.6 x

10~~~ erg [43],
the bilayer thickness to be 2D =

40 1

[44],
the distance from bilayer midplane to each monolayer neutral surface to be d rw D/3 =

12

I

[6,39],
the bare bilayer compression modulus to be Ko "

144 erg cm~~ [43],
the interlayer friction constant b to be 10~ ergs cm~~ [21],
the viscosity of water ~ to be x

10~~ erg s

cm~~,

and the 2d viscosity of the lipid layer to be ~

=10~6 ergs cm~~ [45].

In addition for concreteness we sometimes take:

the typical tubule radius Ro "

0.7 ~m (Ref. [12], Fig. I),
the typical laser power 50 mW [12],
and the temperature to be kBT =

4.2 x

10~~~ erg.

Thus we get the derived quantities:
kBT/41r~ = 0.006,
Ecrit e ~/Ro~ "

1.2 x 10~~ erg cm~~,
e e Ro~/bd~ rw 0.5,
e Kod~ /~ -~ 3.5.
Also, we estimated the induced tension E

-~ 2

x 10~~ erg cm~~ in Section 3.2, so E/~ rw

2

x 10~~m/s and the dimensionless tension a e ERO~/~ -~ 20.
The values of E, b, d

are not known very accurately, but fortunately our formula for ko is not

very sensitive to them.

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Appendix B

The Delaunay Surfaces

We argued in the text against the introduction of a spontaneous curvature term in the elastic
free energy. In the presence of such a term we may add and subtract a constant to recast the
energy in the form

F[shape] =

2~ /

((H Ho)~ + a'j.

Large thermal fluctuations then imply that initially a' = 0, and the free energy then simply
prefers conformations with constant mean curvature everywhere equal to Ho
Remarkably there is a one-parameter family of such shapes with axial symmetry. These are
the "unduloid" or "Delaunay" surfaces. They obey a nonlinear equation expressing H

= Ho

Deuling and Helfrich used this equation in reference [33]. There is however a very simple
geometrical characterization of these surfaces [46]:

Draw a

line I in the plane. Construct any ellipse, tangent at one point to I. Let the ellipse
roll without slipping along I, and follow the path of one focus to get a curve C. The figure
of revolution obtained by rotating C about the axis I is a

surface of constant mean curvature

1/2r+, where r+ is the larger semimajor axis of the ellipse.

Let us see what this says for nearly-cylindrical shapes. Such shapes are generated from
nearly-circular ellipses, with foci near the center. The radius Ro of the near-cylinder is thus
equal to that of the near-circle. Rolling the near-circle along the axis of course gives a periodic
shape with period ~

= 21rRo. In our language, this is a

small perturbation with wavenumber
k

=

I, larger than the initial wavenumber seen experimentally.

Appendix C

Thermal Fluctuations

In subsection 3.3 we quoted an estimate for the effective stretching modulus of the bilayer.
Generally the effects of thermal fluctuations on the conformations of still membranes are
quite small unless one carefully adjusts to the threshold of a shape transformation. One simply
replaces the elastic constants by effective values corrected by terms of relative order kBT/41r~,
about half a percent for DMPC (~~). We will neglect such effects. One notable exception,
however, is the susceptibility K~~, whose "bare" value is so small that thermal corrections can
be significant. At modest values of tension, the membrane effectively becomes elastic, because
significant area can hide in invisible short-scale wrinkles excited by thermal agitation ii, 48].
(The tiny value reported for the bare Kp~ in iii is attained only at extremely large values of applied tension, where these wrinkles have been extinguished.)
Following Helfrich and Servuss, let us estimate the magnitude of this effect in our case. We
consider a membrane thermally fluctuating about a cylindrical shape, and evaluate the average

true area Ao +

(I dS) in terms of the "projected" or apparent area 21rRoL. We would like
to know how Ao changes as we adjust the tension, at fixed projected area; this tells us how
much area we can pull out of our membrane at fixed apparent shape, and hence the effective

(~~) Something similar happens with dynamic couplings [47].

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modulus. Follo~v-ing [48], the relative area extension as we change the dimensionless tension a
is

~~~~
~

~ /j~ ~~~~
In our case a -~ 20 (Appendix A). The lo~ver bound of the integral should be either the initial
tension or unity, whichever is larger, to account for the cylindrical geometry; since we take the
initial tension to vanish and a rw 20 we get bA/A -~ (kBT/81r~) log 20 rwl$io. This estimate
is not very sensitive to the actual value of a. Then the effective modulus is given by the
constitutive relation E

= Kea(bA/A), or Kea rw 100 E

-~ 2 x10~~ ergcm~~, so that the
hierarchy (3.5) we assumed earlier is still preserved.

Appendix D

Computation of the Dynamical Factor A(k)

Equation (6.3) is solved by separating variables as ~l =

il(p)exp(wt + ikz/Ro). il satisfies
(3) p~~3p (k/Ro)~)~il = 0, which has solutions of the form

il(p) = AIPII (kp/Ro + BIPKI (kp/Ro) + A2P~IO (kp/Ro) + B2P~KO (kp/Ro), (D.I

where I~(~), K~(z) are modified Bessel functions [49]. Demanding that il(p) be well-behaved
at p =

0 and p = co forces Bi " 82 "

0 in the interior fluid and Ai " A2 "

0 in the exterior

fluid. The no-slip boundary conditions, together with the lipid conservation law (4.3), give us
four equations for the four unknowns Ai, A2, Bi, B21

~) (p = Ro) " Rob,

~j (p = Ro) " Rob,

(D.2)

~t(p=Ro)=i= (Ii, ~i(p=Ro)=i= (Ii, (D.3)
where + (-) denotes the exterior (interior) fluid. Note that in (D.3) we have assumed that the
lipid velocity has no constant part, in accord with the arguments of Section 3 that after the
tension has spread the 2d pressure (tension) is practically uniform and we can take any net
flow of lipid to be small. Also, we have taken the lipid to be incompressible since the applied
tension is much smaller than the membrane compressibility (Eq. (3.5)). Plugging (D.I) into
(D.2)-(D.3), and using the relations

Ii(z) =

Ii(z),

Ii(z) =

Io(z))Ii(z), (D.4)

Ki(z) =

- Ki(z),

Ki(z) =

- Ko(z))Ki(z), (D.5)
we find

I)(Aili(k)+A2RoIo(k)) = Rob

o

I)(BiKi(k)+B2RoKo(k)) = Rob

o

Ai)Io(k) + A2(2Io(k) + kli(k)) =

I) fi

o '

El)Ko(k) + 82(klfi (k) 2Ko(k)) =

I)fi, (D.6)

o '

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I-e- the A's and the B's are proportional to fi, with proportionality constants which are rational

functions of the modified Bessel functions.

To relate fi to ~t and thus determine the growth rate fil~t, we examine the normal force
balance equation at the membrane:

T£ Tp ApLaplace ~ o, (D.I)

where T~j is the 3d stress tensor of water and -ApLapiace is the pressure jump due to the
surface tension, given by (4.I). The z component of the Navier-Stokes equation relates the
pressure to the velocity, p~ = @V~~) + pt. The NS equation does not fix the constants p);
we must choose p(=

0 and pi = E/Ro. Using

lp~~3pp3p + (k/Ro)~) f

"

0

for f(p) =

lo (kp/Ro), Ko (kp/Ro) (49], we find at the membrane (~~)

T£ Tj =

- 2i~

~

(Bi

~

(Ko(k) + Ki(k)) + B2kKi (k))
Ro Ro k

- 2i~

~

(Ai)(Io(k))Ii(k)) + A2kIi(k)) + E/Ro (D.8a)

Ro o

e
-~A(k)~~fi + E/Ro (D.8b)

Equations (D.8b) defines what we call the "dynamical factor" A(k) in equation (6.4). Taking
the values for the A's and B's determined by (D.6), we find

~ ~

l [k(K(K)) + 2KoKi) (kill -1)) 2IoIi)

~

2k 3IoKo/k Kili /k + k(I)K(I(K)) '~~

In equation (D.9) all Bessel functions are to be evaluated at k.

Appendix E

Membrane Elasticity

Here we briefly derive equation (6.5). Following previous authors (e.g. is, 6] we visualize each
monolayer as a fluid of compressible cylinders, each of length D. One end (the "chain" touches
the bilayer midplane and resists compression and extension with a modulus Kc and preferred
area/molecule at the end of aco. The other end (the "head") is a normal distance +D from
the midplane with modulus Kh and preferred area aho. All of the parameters introduced are
the same for each monolayer, since the two layers and their respective solvents are identical.
We thus consider a monolayer elastic energy per molecule of

f~[shape,a), all =

~Khaoh

~~

l)

~

+ ~Kcaoc

~~)~
const.. (E.1)
2

aoh 2

aoc

Here the constant includes the chemical potential for extracting additional molecules from any
reservoir; it will of course turn out to be related to the physical tension.

(~~) We have used Tq =

-p6~~ + ~(3~u~ +)u~) for incompressible fluids [50].

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It's convenient to introduce a pair of imaginary "neutral" surfaces at normal distance +d
from the midplane, where d will be specified in a moment, and to measure the densities #~ of
lipid molecules in the two monolayers relative to these surfaces. Thus the areas a)~ above are

al =

(#~)~~ [l ~ 2H~(D d))
at =

(#~)~~ [l + 2H~d).

Here H~ are the mean curvatures of the two neutral surfaces. We dropped terms involving
Gauss curvature, as well as those of order (HD)~. Substituting in (E.I) we get

~ ~ ~~ ~ ~~

f~ = 140)~~ (i12H~ ~ Cm) ~ ~cm ~j)

2H~ +
I

~j i) crust", iE.2)
where K, lo, ~, cm, the new constant, and the neutral surface location d

are various combina-

tions of the original parameters chosen to put (E.I) into the form (E.2). In particular d is
chosen to set the coefficient of the cross-term in the convenient form shown. Since the original
parameters weren't directly observable anyway, we abandon them now in favor of the new
ones. This is actually progress. Note that again the new parameters are the same for each
monolayer.
The monolayer free energy is now f dS~ #~ f~, where dS~ are the areas of the two neutral
surfaces. Rewriting in terms of the area element dS of the midplane we get

dS~ #~ f~ = dS(1 ~ 2Hd)

~j~ i j~ K j~ 2

~

4jo

~~~~~~ ~ 2~~~l~~~~ ~

jo 4 jo

~

~°~~~"'

~~

Here H is the mean curvature of the midplane: H~ = H + 2H~d plus a Gauss-curvature term
we drop.
We will be considering only values of the tension much smaller than K (Eq. (3.5)), so we
may use lo in place of #~ in the constant term above. Writing the other H~ in terms of H
and finally identifying the constant with the tension E then yields equation (6.5).
Before switching on the laser the terminal blobs serve as reservoirs, and we argued in the
text that then E should be taken to be close to zero. In equilibrium the densities will then
just take their preferred values, and we recover the Canham-Helfrich model, with ~

the bilayer
stillness. In particular, no spontaneous curvature appears, as argued in [21]. After switching
on the laser the system is no longer in equilibrium, and we need to work out dynamically what
happens.
We note in passing that in a

situation where the two bilayer leaves are not in equilibrium
with a common reservoir, the constant term in (E.I will not be equal for the two layers. Rather
than containing a

chemical potential for a

reservoir, these terms act as Lagrange multipliers
enforcing the constraint of fixed molecule numbers N~ in each layer. Letting A) e

aoN~ be

the "preferred area" of each layer, we then recover the area-difference elasticity model (Ref. [6]).
In particular the parameter aADE is essentially the same as our parameter @.

References

[1] Lipowsky R., Nat~tre 349 (1991) 475.
[2] Seifert U. and Lipowsky R., in "Structure and Dynamics of Membranes", R. Lipowsky
and E. Sackmann Eds. (Elsevier, 1995).

N°5 PEARLING INSTABILITY 795

[3] Rothman J., Nat~tre 372 (1994) 55-63.
[4] Gallez E. and Coakley W., Frog. Biophys. Mol. Biol. 48 (1986) 155-199.
[5] Seifert U., Bemdl K. and Lipowsky R., Phys. Re~. A44 (1991) 1182; Miao L., Fourcade
B., Rao M., Wortis M. and Zia R.K.P., Phys. Rev. A43 (1991) 6843.
[6] Miao L., Seifert U., Wortis M. and D6bereiner H.-G., Phys. Rev. E49 (1994) 5389-3407.
[7] Evans E. and Rawicz W.,Phys. Rev. Lett. 64 (1990) 2094.
[8] Needham D., private communication.
[9] Pouligny B., private communication; see also Angelova M., Pouligny B., Martinot-
Lagarde G., Grehan G. and Gouesbet G., Frog. Colloid Polym. Sci. 97 (1994) 293-297,
and in press.

[10] Miyata H. and Hotani H., Proc. Nat. Acad. Sci. USA 89 (1992) 11547-11551.
[11] Fygenson D., private communication.
[12] Bar-Ziv R. and Moses E., Phys. Rev. Lett. 73 (1994) 1392; Bar-Ziv R. and Moses E., to
appear.

[13] Nelson P., Powers T. and Seifert U., Phys. Rev. Lett. 74 (1995) 3384-3387.
[14] Plateau J., "Statique expArimentale et thAorique des liquides soumis aux seules forces
molAculaires" (Gautier-Villars, 1873).
[15] Lord Rayleigh, Proc. London Math. Soc. 10 (1879) 4.
[16] Lord Rayleigh, Philos. Mag. 34 (1892) 145.
[17] Tomotika S., Proc. Roy. Soc. London A150 (1932) 322.
[18] Brochard F. and Lennon J., J. Phys. France 36 (1975) 1035; Waxman A., St~td. Appl.
Math. 70 (1984) 63-86; Schneider M., Jenkins J. and Webb W., Biophys. J. 45 (1984)
891; J. Phys. France 45 (1984) 1457-1472; MiIner S. and Safran S., Phys. Rev. A36
(1987) 4371-4379.
[19] Dee G. and Langer J., Phys. Rev. Lett. 50 (1983) 383-386; Ben-Jacob E., Brand H., Dee
G., Kramer L. and Langer J., Physica 14D (1985) 348 -364; Langer J., in "Chance and
matter", J. Soulettie, J. Vannimenus and R. Stora Eds. (North-Holland, 1987).
[20] van Saarloos W., Phys. Rev. A37 (1988) 211-229; Phys. Rev. A39 (1989) 6367.
[21] Evans E., Yeung A., Waugh R. and Song J., in "Structure and conformation of am-
phiphilic membranes", R. Lipowsky et al. (Springer, 1992).
[22] Seifert U. and Langer S., E~trophys. Lett. 23 (1993) 71-76; Biophys. Chem. 49 (1994)
13-22.

[23] Evans E. and Yeung A., Chem. Phys. Lipids 73 (1994) 39-56.
[24] Granek R. and Olami Z., J. Phys. II France 5 (1995) 1348-1370.
[25] Svetina S., private communication.
[26] Bar-Ziv R., Menes R., Moses E. and Safran S., Phys. Rev. Lett. 75 (1995) 3356.
[27] Bar-Ziv R. and Moses E., to appear.
[28] Evans E., Biophys. J. 14 (1974) 923; Helfrich W., Z. Nat~trforsch. 29C (1974) 510.
[29] Thomas B., private communication.
[30] Chiruvolu S., Warriner H., Naranjo E., Idziak S., Radler J., Plano R., Zasadzinski J. and
Safinya C., Science 266 (1994) 1222-1225.
[31] Leibler S., J. Phys. France 47 (1986) 507-516.
[32] Seifert U., Phys. Rev. Lett. 70 (1993) 1335-1338.
[33] Deuling H. and Helfrich W., Blood Cells 3 (1977) 713; J. Phys. France 37 (1976) 1335. [34] Ou-Yang Zhong-can and Helfrich W., Phys. Rev. A39 (1989) 5280.
[35] Israelachvili J., "Intermolecular and surface forces" (Academic Press, 1992).
[36] Jackson J. D., "Classical electrodynamics" (Wiley, 1975) pp. 107, 160.
[37] Bar-Ziv R., Frisch T. and Moses E., Phys. Rev. Lett. 75 (1995) 3481-3484.
[38] Wimley W. and Thompson T., Biochemistry 30 (1991) 1702.

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[39] Waugh R., Song J., Svetina S. and Zeks B., Biophys. J. 61 (1992) 974.
[40] Goldstein R-E-, Pesci A-I- and Shelley M-J-, J~hys. Rev. Lett. 70 (1993) 3043; Eggers
J., Phys. Rev. Lett. 71 (1993) 3458; Bertozzi A-L-, Brenner M-P-, Dupont T-F- and
Kadanofl L.P., "Singularities and similarities in interface flows," in Centennial Edition,
Appl. Math. Series L. Sirovich, Ed. (Springer-Verlag Applied Mathematics Series, New
York, 1993).
[41] Shi X-D-, Brenner M-P- and Nagel S-R-, Science 265 (1994) 219.
[42] Bar-Ziv R. and Moses E., to appear.
[43] Evans E. and Needham D., J. Phys. Chem. 91 (1987) 4219.
[44] Marsh D., "CRC handbook of lipid bilayers" (CRC, 1990) p.166.
[45] Merkel R., Sackmann E. and Evans E., J. Phys France 50 (1989) 1535.
[46] Bouasse H., "Cours de math4matiques g4n4rales" (Paris, Delagrave, 1911).
[47] Cai W. and Lubensky T-C-, Phys. Rev. Lett. 73 (1994) 1186.
[48] Helfrich W. and Servuss R., N~tovo Cimento 3D (1984) 137.
[49] M. Abramo~vitz and I. Stegun Eds., "Handbook of mathematical functions" (Dover,
1965).
[50] Landau L. and Lifsitz E., "Fluid mechanics" (Pergamon, 1959).