The effect of curvature and topology on membrane hydrodynamics

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received 11 July 2008; accepted in final form 5 October 2008
published online 10 November 2008

PACS 87.16.dp – Transport, including channels, pores, and lateral diffusion
PACS 47.63.-b – Biological fluid dynamics
PACS 68.05.-n – Liquid-liquid interfaces

Abstract – We study the mobilities of point-like and extended objects (rods) on a spherical membrane to show how these quantities are modified in a striking manner by the curvature and topology of the membrane. We also present theoretical calculations and experimental measurements of the membrane fluid velocity field around a moving rod bound to the crowded interface of a water-in-oil droplet. By using different droplet sizes, membrane viscosities, and rod lengths, we show that the viscosity mismatch between the interior and exterior fluids leads to a suppression of the fluid flow on small droplets that cannot be captured by the flat-membrane predictions.

Introduction. – The dynamics of membrane-bound inclusions is important in many biological and soft matter systems. Mobile inclusions in lipid membranes, such as proteins [1] or lipid “rafts” [2], are fundamental to a variety of biological processes, including signal transduction [3] and the endocytosis of bacterial toxins [4]. Also, the mobilities and hydrodynamic interactions of colloidal particles on crowded fluid-fluid interfaces have ramifications on the design and formation of colloidosomes [5].

Both lipid membrane inclusions and colloidal particles are generically large enough that their motion through the membrane can be treated using continuum hydrodynamics. One can consider the membrane to be a viscous two-dimensional fluid separating two (perhaps dissimilar) solvents and neglect any internal degrees of freedom in the membrane. This description takes into account the distinct nature of the incompressible two-dimensional fluid separating the surrounding solvents. The flows in this fluid can support stresses and thus lead to a discontinuity in the bulk fluid stress across the membrane; furthermore, flows which transport fluid from the membrane to the bulk are not allowed, since the membrane fluid is confined to the surface. This is in marked contrast to an interface between two immiscible fluids, such as oil and water, where the bulk fluid stress is continuous across the interface and there is no distinct fluid confined there.

The low-Reynolds-number hydrodynamics of viscous membranes differs substantially from the better-known problem of 3D hydrodynamics. The hydrodynamics of an isolated 2D fluid suffers from the same problem as 2D elasticity theory: namely, the response to a point force is log divergent at long length scales [6]. Membrane hydrodynamics, however, is not a purely two-dimensional theory, since flows in the membrane are viscously coupled to flows in the surrounding three-dimensional fluids. This coupling has two principal effects: 1) in-plane momentum in the membrane is not locally conserved, since membrane flows generate bulk fluid flows that transfer momentum out of the membrane; and 2) non-local interactions between points in the membrane, mediated by the flows in the solvents, are generated. The coupling of the membrane to the solvents introduces a new, inherent length scale into membrane hydrodynamics that is unrelated to inertia (i.e. Reynolds number). This “Saffman-Delbrück” (SD) length, which is given by the ratio of the (2D) membrane viscosity \( \eta_m \) to the (3D) fluid viscosity \( \eta \), \( \ell_0 \sim \eta_m/\eta \) [7], cuts off the logarithmic divergence mentioned above. For cellular plasma membranes \( \ell_0 \approx 1 \mu \text{m} \) [8]. The existence of
an inherent length scale in membrane hydrodynamics has
cumplex and rather subtle effects on a variety of problems,
including protein diffusion in cell membranes [7,9], the
flow of monolayers through channels [10], the dynamics
of monolayer domains [11], the membrane micro-
rheology [12], and the mobilities of both rigid and flexible
extended objects in membranes [13].

In this letter, we examine the effects of membrane
gometry and topology on membrane hydrodynamics [14].
Specifically, we present both experimental and theoretical
results that elucidate these effects on particulate transport
in spherical membranes. Our theoretical results show that
there are two main effects: first, the spherical topology
of the membrane fundamentally alters the membrane
velocity field. On a sphere, any non-vanishing vector field
must include at least two singularities [15], which can
be vortices, sources, or sinks. However, only vortices are
allowed for flows on an incompressible membrane, since
sources and sinks require compression of the membrane.
No such singularities appear on a flat membrane. The
compact topology of a spherical membrane also gives
rise to an asymmetry between the surrounding 3D
fluids that is absent for a flat membrane. Second, the
curvature of the membrane introduces a new length scale
—the radius of curvature, $R$—that competes with $\ell_0$ in
determining the hydrodynamics of particles embedded
in the membrane. This length scale acts as a long-distance
cutoff in the system, though its unique geometric nature
distinguishes it from other long-distance cutoffs in
membrane hydrodynamics [7,16,17]. These two effects
can exert opposing influences on the transport properties
of the membrane. Indeed, their competition results in
particulate mobility that exhibits a surprisingly complex
and non-monotonic dependence on the membrane
radius.

To experimentally test our theoretical results, we create
a two-dimensional colloid liquid at the spherical interface
of a water-in-oil droplet and measure the membrane
flow fields created by the motion of a colloidal rod
on the membrane. These flow fields show unambiguous
deviations from the flat-membrane theory [13] that are
consistent with our theoretical predictions for a spherical
membrane.

Theoretical model. — Consider a spherical membrane
of radius $R$ consisting of a distinct, incompressible fluid of
viscosity $\eta_m$. We ignore inertial effects and impose force
balance at the membrane. We apply a tangential point
force $\mathbf{F} = F \hat{y}$ to a rigid disk of radius $a$ at the north pole
of the membrane, as illustrated in fig. 1(a). We assume
that $a$ is the smallest length scale in the problem, so that
we can treat the force on the particle as a point force
(we account for the finite particle size via a short-distance
cutoff; see below). This force gives rise to an applied force
density $\mathbf{f}_{\text{app}} = F\theta / (2\pi R^2)$ on the membrane. Because
of the curvature of the membrane, the in-plane force
balance equation must be written in a manifestly covariant
form [18]:

\[
 f_{\alpha}^{\text{app}} = -\eta_m \left[ D^2 D_{\beta} v_{\alpha} + K v_{\alpha} \right] + \sigma_{\alpha\beta}^- - \sigma_{\alpha\beta}^+, \tag{1}
\]

where $D_{\alpha}$ is the covariant derivative and $K = 1/R^2$ is
the Gaussian curvature of the sphere; the Greek indices
run over the polar and azimuthal angles $\theta, \phi$, respectively.
Here, we have assumed that the membrane is
incompressible, $D^\alpha v_{\alpha} = 0$. The term in brackets in eq. (1)
is the viscous force density resulting from gradients in the
membrane velocity field $v_{\alpha}$; the last two terms are
the viscous stresses due to the solvents inside ($\sigma^-$)
and outside ($\sigma^+$) the spherical surface, $\sigma_{\alpha\beta}^\pm = \eta \pm [D_\beta v_{\alpha}^\pm +
D_\alpha v_{\beta}^\pm - P_\beta \delta_{\alpha\beta}]$ where $P_{\beta}$, $\eta$, and $v^\pm$ are the dynamic
pressures, viscosities, and velocities, respectively, of the
solvents inside ($-$) and outside ($+$) the sphere. We can
see from eq. (1) that geometry can have a dramatic effect
on membrane hydrodynamics. In particular, the term
$-\eta m K v_{\alpha\beta}$ in eq. (1) shows that position-independent flows
generate stress in membranes with non-zero Gaussian
curvature, such as spheres, but not on membranes with
no Gaussian curvature, such as planes and cylinders.

The bulk fluid velocities and pressures satisfy the incompressible
Stokes equation: $\nabla^2 \mathbf{v} = \nabla P$, $\nabla \cdot \mathbf{v} = 0$, with boundary conditions $\lim_{r \to \infty} \mathbf{v} = \lim_{r \to 0} \mathbf{v} = 0$.
These boundary conditions in effect provide arbitrary
constraint forces that prevent the rigid translation of
the membrane and interior fluid. We also impose “stick”
boundary conditions at the membrane: $\mathbf{v} = 0$.

It is convenient to decompose this dynamical system
into normal modes consisting of the combined flows of the
membrane and the external solvents. The deformations
of a 2D membrane can be decomposed into bending,
compression, and shear modes. The incompressibility of
the membrane suppresses the compression modes. Thus,
the bending modes are prevented by the incompressibility of the interior fluid, since any bending deformation in the membrane would increase the interior volume of the sphere. The remaining shear modes, which automatically satisfy the membrane incompressibility constraint, can be written as \( v_\alpha = \epsilon_{\alpha\beta} D^\beta \Psi \), where \( \epsilon_{\alpha\beta} \) is the alternating tensor. The combined membrane and solvent system is diagonalizable in a basis of spherical harmonics [18,19].

By applying the force balance condition eq. (1), we determine the amplitude of each normal mode of the combined membrane/solvent system generated by the applied force. Then the membrane velocity is given by [18]

\[
\mathbf{v} \cdot \hat{\varphi} = -V \sin \phi \sum_{l=1}^{l_{\text{max}}} \frac{1}{s_l} \csc \theta P_l^1(\cos \theta),
\]

\[
\mathbf{v} \cdot \hat{\theta} = -V \cos \phi \sum_{l=1}^{l_{\text{max}}} \frac{1}{s_l} \left[ \cot \theta P_l^1(\cos \theta) + P_l^2(\cos \theta) \right],
\]

where \( V = \eta / (4\pi \eta_m) \), \( l_{\text{max}} \) is defined below, \( P_l^m(x) \) is the \( l \)-th associated Legendre function, and

\[
s_l = \frac{l(l+1)}{2l+1} \left[ (l+1)-2+\frac{R}{\ell_+}(l-1)+\frac{R}{\ell_-}(l+2) \right].
\]

In eq. (4) we have defined two lengths in analogy to the SD length: \( \ell_\pm = \eta_m / \eta_\pm \). In contrast, only one length scale, the SD length \( \ell_0 \equiv \eta_m / (\eta_- + \eta_+) \), controls the membrane hydrodynamics of a flat membrane. In other words, the viscosities of the two solvents surrounding a flat membrane enter symmetrically, as they must. For a spherical membrane, the asymmetry between the exterior and interior solvents causes these two length scales to enter independently. The most striking manifestation of this asymmetry occurs in the limit of a large interior viscosity, \( \eta_+ \gg \eta_- \). In that limit eq. (4) shows that the \( l = 1 \) term dominates the sums in eqs. (2) and (3), corresponding to a rigid rotation of the membrane and interior fluid. The opposite limit \( \eta_- \gg \eta_+ \) will not have an analogous effect. In addition to introducing this asymmetry between the external fluids, we can see from eq. (4) that the geometry of the membrane has another effect: it introduces a new length scale —the membrane radius \( R \)— that effectively rescales the SD lengths \( \ell_\pm \). Indeed, for a small enough sphere, \( R \ll \ell_+ \), the same rigid body rotation seen in the limit \( \eta_- \gg \eta_+ \) is observed. Thus, geometry alone can have a dramatic effect on membrane hydrodynamics.

In order to investigate the transport properties of the membrane, we need to isolate the motion of the particle within the membrane from the overall motion —specifically, the rigid rotation discussed above— of the entire membrane. To do so, we apply a constraint force \( \mathbf{F}_0 \) at the south pole that forces the membrane velocity to vanish there, see fig. 1(a). This force also mimics the adsorption of the membrane onto the substrate in the experiments, see below. Because of the linearity of the Stokes equation, the total response of the fluids is simply the sum of the individual responses to each force. A typical solution for the membrane velocity field on the sphere is shown in fig. 1(a). The appearance of a vortex in the upper hemisphere is required by topological constraints; there is a similar one placed symmetrically on the backside of the sphere (not shown).

The particle’s mobility, defined by \( \mathbf{v}|_{\theta=0} = \mu \mathbf{F} \), is

\[
\mu = \frac{1}{4\pi \eta_m} S_+ \left[ 1 - \left( \frac{S_-}{S_+} \right)^2 \right],
\]

where

\[
S_\pm = \sum_{l=1}^{l_{\text{max}}} (\pm 1)^{l+1} l(l+1) \eta(l+2) = \frac{1}{2s_l}.
\]

The first term in eq. (5) is generated by the force exerted on the particle itself (see eqs. (2) and (3)), while the second term is generated by the pinning force [18]. The finite particle radius \( a \) acts as a cutoff, setting the upper limit \( l_{\text{max}} \) on the sums in eqs. (2), (3), and (5). In particular, we set the exact value of \( l_{\text{max}} \) by requiring that the \( R \to \infty \) limit of eq. (5) agrees with the mobility of a disk of radius \( a \ll \ell_0 \) in a flat membrane [7,9,12]:

\[
\mu_{\text{flat}} = \frac{1}{4\pi \eta_m} \ln \left[ 1 + \frac{2\ell_0}{a} e^{-\gamma} \right],
\]

where \( \gamma = \text{Euler’s constant} \). It is straightforward to show that eq. (5) has the correct limiting behavior if we set \( l_{\text{max}} \) equal to the largest integer less than \( 2e^{-\gamma} R/a \).

Figure 2 shows the dimensionless mobility \( \eta_m \mu \) of a particle at the north pole of a pinned spherical membrane as a function of the membrane radius \( R \) for a variety of interior viscosities \( \eta_- \). As expected, the flat-membrane SD result eq. (7) (horizontal dashed lines) is recovered in the limit \( R \to \infty \) in all cases. The approach to this limit, however, is dependent on the viscosity ratio \( \eta_+ / \eta_- \). For \( \eta_+ / \eta_- < 1 \) (green/gray curve), the mobility in a spherical membrane is larger than in
a flat membrane because here the more viscous fluid is bounded, causing it to dissipate less energy. Conversely, when \( \eta_+ / \eta_- > 1 \) (dotted curve), the mobility in a spherical membrane is suppressed relative to the flat case.

In the limit of high membrane curvature, \( R/\ell_+ \ll 1 \), \( \eta_{m,H} \rightarrow \ln(R/a)/2\pi \) (dot-dashed line). The appearance of \( R \) as the long-distance cutoff in the logarithm is generally expected [7,16,17], but the prefactor is determined by the spherical geometry. Hence, particle mobilities in high-curvature membranes, \( R/\ell_+ \ll 1 \), are depressed relative to the SD result.

For intermediate curvatures, the mobility exhibits an interesting non-monotonic behavior on the particle radius. In particular, there is a clear maximum in the mobility for moderately small values of \( R/\ell_+ \), independent of the viscosity ratio \( \eta_+ / \eta_- \). In contrast, the corresponding mobilities on a cylindrical membrane exhibit no such peaks [18]. Therefore, this maximum is a striking illustration of the effects of the geometry of the sphere on the transport properties of the membrane. In particular, the presence of the Gaussian curvature term in the force balance equation (1) alters the mobility for membranes with non-zero Gaussian curvature. The different roles of topology and geometry in membrane hydrodynamics will be investigated further in a future publication [18].

We now turn to the problem of the mobility of, and fluid flows around, extended objects embedded in the membrane. Specifically, we consider a rod of length \( L \) embedded in the membrane. Using the Kirkwood approximation [20], we model the rod as a linear array of \( N+1 \) disks of radius \( a \) separated by a distance \( b \), where \( L = Nb + 2a \). We also apply a pinning force at the south pole. Using the superposition principle, the total membrane velocity is \( v_{\alpha}^{\text{tot}}(\theta, \phi) = \sum_{i=0}^{N+1} F_{\beta}^{(i)}(\chi_{\alpha,\beta}(\theta, \phi_i, \theta_i, \phi_i)) \). Here, \( F^{(i)} \) is the force applied to the disk at the point \((\theta_i, \phi_i)\); \( i = 0 \) corresponds to the south pole, and \( i = 1, \ldots, N+1 \) labels the disks in the rod. We choose our coordinate system so that the rod lies along the great circle \( \phi = \pi/2 \) of the sphere with its center at the north pole, so that \( \theta_i = b(N/2 + 1 - i) \) for \( i \neq 0 \). We consider only forces parallel to the rod axis. The response function \( \chi_{\alpha,\beta}(x,y) \) gives \( v_{\alpha}(x) \) due to a unit force in the \( \beta \)-direction applied at \( y \).

To determine the forces \( F^{(i)} \), we require the total fluid velocity to vanish at the south pole and each disk in the rod to move with unit velocity. These constraints provide a set of \( N+2 \) linear equations that determine \( F^{(i)} \). Summing the \( N+1 \) forces acting on the rod moving at unit velocity gives the inverse mobility of the rod. Using these forces, we can determine the entire velocity field in response to the rod’s motion, both on the sphere and in the surrounding fluids.

In fig. 3, we plot the membrane velocity field \( v_\perp = v_\perp(\theta) y \) along the line that perpendicularly bisects the rod (i.e. the line \( \phi = 0, \pi, 0 < \theta < \pi \)) in fig. 1(b)), as a function of the polar angle \( \theta \), for various values of the membrane radius \( R \) (black, green, and dashed curves). For comparison, we also plot a projection of the flat-membrane result [12] onto the largest sphere (dotted curve); that is, we map the flat-plane distance \( d \) onto an angle \( \theta \) using the arc-length \( R\theta \) as the flat-space distance.

![Fig. 3: (Color online) membrane velocity \( v_\perp \) surrounding a membrane-bound rod of length \( L = 2\mu m \), measured along the axis indicated by the dotted line in the schematic illustration (inset), as a function of the polar angle \( \theta \) for various values of the membrane radius \( R \). For all curves, \( a = 0.1\mu m, \ell_+ = 20\mu m, b = 2a, \) and \( N = 9 \); the membrane radii are \( R = 2\mu m \) (black curve), \( R = 10\mu m \) (green/grey curve), and \( R = 50\mu m \) (dashed curve). We also show the flat-membrane result (dotted curve), which has been mapped onto the largest sphere using the arc-length \( R\theta \) as the flat-space distance.](image-url)

**Experiments.** – To test our model, we performed experiments to measure the flow fields on spherical droplets caused by the motion of a rod-like object confined to the droplet surface. Water droplets (\( \eta_\perp = 10^{-3} \text{Ns/m}^2 \)), typically 30–100 \( \mu m \) in diameter, suspended in hexadecane (\( \eta_\perp = 3.34 \times 10^{-3} \text{Ns/m}^2 \)) provided the spherical interface. The interface was coated with a monolayer of small (370 nm diameter, measured by scanning electron microscopy) poly(methyl methacrylate) (PMMA) spheres, which were sterically stabilized by poly(hydroxystearic acid) and labeled with NBD fluorescent dye (7-chloro-4-nitrobenzofurazan) [21]. This monolayer is confined to
the interface [22], effectively creating a distinct membrane fluid there. The PMMA particles served dual roles: to set the membrane viscosity and to allow measurement of the membrane flow field using video microscopy and particle-tracking software. Spheres were imaged using bright-field optical microscopy (not fluorescence) using a Zeiss Axiolicht 200 with a 100× objective and a numerical aperture equal to 1.3. Images were captured at 30 frames/s and analyzed with particle-tracking code written in IDL [23]. A representative image is shown in fig. 1(b). Finally, the glass coverslips were treated with dichloromethylsilane before the experiments to prevent wetting of the water droplet on the glass. During the measurements, the droplets lay on the bottom of the viewing cell and the PMMA particles at the bottom of the droplet adhered to the coverslip, preventing the rotation of the droplet as a whole.

To create the rod, we added paramagnetic polystyrene spheres that absorbed to the interface. These 0.95 µm diameter spheres were made of carboxylate-functionalized, divinylbenzene- (DVB-) crosslinked polystyrene containing iron oxide (Bangs Laboratories item # MC04N, lot 3251). In the presence of a magnetic field, the spheres aligned into a single rod-shaped aggregate, see fig. 1(b). The rod was moved at speeds of approximately a few µm/s along the surface by a permanent magnet brought close to the sample. To measure the flow field, $O(10^2)$ PMMA particles were tracked during the rod’s motion. For each droplet, the process was typically repeated twelve times, and the mean and statistical uncertainty of the flow velocities were measured. Droplets of different radii, rod lengths, and viscosities were used.

In fig. 4 we plot the measured membrane velocity (open points) along the line that perpendicularly bisects the rod—that is, the velocity $v_\perp$ plotted in fig. 3—as a function of the absolute distance $|x| = R|\sin \theta|$ from the north pole in the $x$-direction. By symmetry, we expect the velocity field to be symmetric about the rod axis. However, as shown in fig. 4, the data can exhibit asymmetries due to random experimental error and asymmetries in the colloidal suspension. Therefore, to compare with the theoretical predictions we indicate the average velocity value by the solid points.

To generate the theoretical velocity profiles for these measurements, we need to determine the membrane viscosity $\eta_m$, which in turns sets the value of $\ell_0$. To do so, the positions $r$ of the PMMA spheres were measured as they underwent thermal motion on the surface of the droplet (i.e. in the absence of any applied forces). A typical set of measurements tracked 40 particles over a total period of 20–40 s. The mean-square displacements, $\langle [r(t-t_0) - r(t_0)]^2 \rangle = \Delta r^2(t)$, were computed by averaging over all PMMA spheres and all times $t_0$. The slope of $\Delta r^2(t)$ in the linear (long-time) regime was measured, and the diffusion constant $D$ was obtained from the relation $\Delta r^2(t) = 4Dt$. For the three samples shown in fig. 4, we obtained the following diffusion constants $D$: (a) 0.28 µm$^2$/s; (b) 0.21 µm$^2$/s; and (c) 0.037 µm$^2$/s. Using these values for $D$, the Saffman-Delbrück length $\ell_0$ for each sample was determined from the Stokes-Einstein relation $D = k_B T \mu$ and the mobility of a point-like particle in a membrane. For a spherical membrane, this mobility is given by eq. (5); for a flat membrane, it is given by eq. (7).

In figs. 4(a)–(c), we show a sequence of droplets demonstrating the increasing effect of curvature. We show the predictions of the flat-membrane theory (FMT, dashed lines) [13] and the spherical membrane theory (SMT, solid lines); each curve is obtained by direct calculation using no adjustable parameters. We account for the rod thickness in the theory by setting $v_\perp$ equal to the rod velocity $v_0$ everywhere within the rod. The substrate pins the fluid velocity at the south pole (we do not account for any additional hydrodynamic interactions between the sphere and the substrate). In fig. 4(a), where $R \gg \ell_0$, we see that both the FMT and SMT are close to the data. In fig. 4(b), where $R \gg \ell_0$, but is now comparable to $L$, the
effects of curvature begin to be seen. However, only when $\ell_0$ approaches $R$, as in fig. 4(c), does the effect of curvature become dramatic. Here the velocity field decays more rapidly away from the rod than the FMT predictions. In this case the SMT prediction is a significant improvement over that of the FMT. This is in marked contrast to the behavior shown in fig. 3, where the velocity field exhibits smaller gradients as the curvature is increased. However, that behavior is seen in the limit $R/\ell_+ \ll 1$, whereas for all the data in fig. 4 the droplet radii $R$ are larger than the SD lengths $\ell_+$. We can understand the suppression of the velocity fields in fig. 4 by first considering the case in which the interior viscosity is much larger than the exterior viscosity. In this case, large gradients in the velocity field of the interior fluid are suppressed. These nearly spatially homogeneous flows generate large gradients in the velocity field of the exterior fluid. This is seen most clearly when the membrane and interior fluid rotate as a rigid object, where all of the dissipative flows occur in the exterior fluid. When the situation is reversed—that is, when the interior fluid is less viscous—the flows of the membrane and interior fluid become more localized around the rod in order to minimize long-range flow in the more viscous exterior fluid. Thus, the viscosity mismatch between the less viscous interior fluid (water) and the more viscous exterior fluid (oil) enhances the localization of the membrane velocity field around the rod, as seen in fig. 4(c).

Conclusion. – This work demonstrates the considerable effect of membrane curvature and topology on the transport of particles embedded in the membrane. The compact topology of the sphere requires the formation of vortices in steady-state, zero-Reynolds-number flow; it also implies an asymmetry between the interior and exterior solvents, which can enhance or suppress particulate transport relative to that of a flat membrane. Furthermore, the diffusivity of particles bound to membranes of high curvature is significantly reduced. The experimental data, while somewhat noisy, do show a decay in the velocity field away from the rod that is faster than the FMT predictions and consistent with the SMT. The conclusions of this work should be relevant to understanding the kinetics of particulate aggregates on the surface of droplets and the transport of proteins on membranes separating the viscous cytosol from extracellular fluids.

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AJL thanks T. Liverpool for enjoyable and enlightening discussions. MLH and AJL were supported in part by NASA NRA 02-OBPR-03-C. ADD acknowledges support through a Faculty Research Grant from the University of Massachusetts, Amherst. ADD and RM thank Kan Du and the microscopy facilities of the NSF-funded UMass Materials Research Science and Engineering Center on Polymers for technical assistance.

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