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Drift in supported membranes

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An object moving in a fluid transports the fluid along the direction of its motion. Using the concept of drift, i.e., the net motion of a small volume of fluid or a tracer particle due to a moving body, we quantify this entrainment for an inclusion in a supported lipid bilayer membrane. Our analysis demonstrates that a moving object in a supported membrane transports a small volume of fluid by a significant distance only when the initial position of the fluid volume in question is within a distance ξ from the line of motion, where ξ is the screening length of the membrane. The total area swept out by a line of such fluid volume elements, initially at rest and oriented perpendicular to the direction of motion, is the drift area. We show that the drift area is related quadratically to the screening length. These calculations suggest that dynamic domains of entrained lipids of size ξ form spontaneously around moving objects in supported membranes due to hydrodynamic interactions. This effect is potentially important for transport processes in biological and artificial membranes. © *2007 American Institute of Physics*. [DOI: 10.1063/1.2805843]

The motion of particles through fluids has been studied in areas as diverse as oceans, industrial mixers, colloidal systems, and protein transport in cells and membranes. One aspect of this transport that is often neglected concerns the entrainment of the local fluid environment by the moving body. An elegant way of quantifying this effect, introduced by Darwin,[1] involves calculating the total distortion in an initially planar fluid surface after a moving object has passed through it. The total permanent distortion in this material surface, after the object has moved far away, is a measure of the amount of fluid that the moving particle is dragging along with it, and is called drift [see Fig. 1(A)]. Prior work on drift has largely concentrated on inviscid flows, primarily due to interest in Darwin's theorem, which states that the total mass of the drift volume is equal to the added mass of the body,[2,3] that is the force per unit acceleration, exerted by the fluid on the moving body. This result is intuitively reasonable, since, by assumption, internal dissipation is neglected for inviscid flows. Drift has been shown to be important in a number of flow phenomena, such as thermal mixing due to drift caused by bubbles, and transport by sedimenting particles.[4] It was also shown that fluid structures such as vortices could transport fluid, and that the drift was related to the added mass of a moving vortex.[4,5]

In viscous flows Darwin's theorem no longer holds, since the work done is also dissipated by internal friction. Nevertheless, drift still occurs and is perhaps the simplest way to conceptualize the hydrodynamic effect of particle motion on the fluid itself. The first investigation of drift in viscous flow was undertaken by Eames *et al.*,[3] who calculated the drift produced by a translating droplet.

In this paper, motivated by the importance of transport of inclusions, such as proteins and protein clusters, in biological and synthetic membranes, we examine drift due to a moving particle in the common laboratory configuration of supported lipid membranes,[6] where a planar lipid bilayer is separated from a supporting solid substrate by a thin film of fluid, referred to as the subphase. We focus on supported membranes [Fig. 1(B)] since they are emerging as important model systems in the laboratory.[6–8] The coupling between the membrane and the surrounding fluid can be treated phenomenologically by introducing an additional velocity-dependent friction term in the two-dimensional Stokes equations for the fluid membrane, which can then be analytically solved for the case of a moving disk.[9]

The detailed structure of velocity fields due to particles moving in the membrane depends upon all the relevant length scales, i.e., the particle radius, the distance to the substrate, and the ratio between the two-dimensional membrane viscosity and the shear viscosity of the subphase fluids.[10] For the case of an object moving at low Reynolds number in an unbounded fluid, the velocity field decays as the inverse of the distance from the particle. However, for an object moving in a membrane, provided the characteristic length scale of the object is smaller than the screening length of the membrane, the velocity field decays logarithmically near the moving body, and as the square of the radial distance further away.[11] This logarithmic decay, which in ideal two-dimensional flows is the origin of Stokes' paradox,[12] is cut

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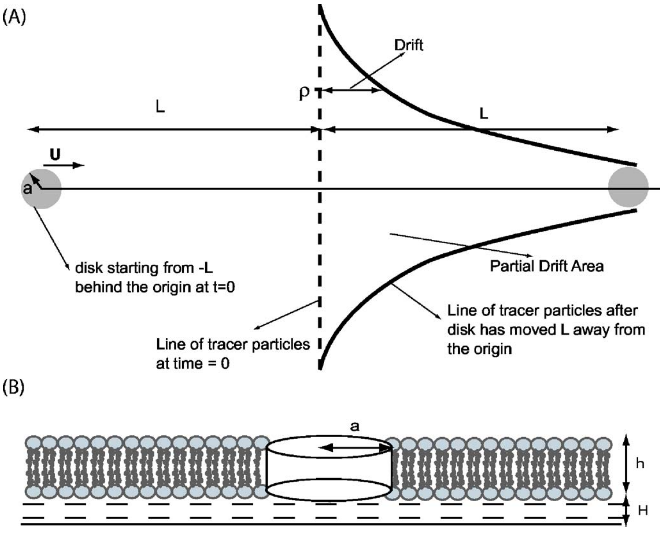

FIG. 1. (A) A schematic illustrating the concepts of drift and partial drift area. (B) A disk of radius a in a supported lipid membrane of thickness h, above a thin subphase of liquid of depth H.

off due to the coupling between the membrane and the subphase.[13] This structure of the membrane velocity fields, and in particular the localized (logarithmic) feature of the flow, gives rise to the possibility that entrainment of the local fluid may be important for transport processes in membranes. This observation is the primary motivation for this work, and is considered further in the discussion in Sec. IV.

It should be noted that the description of flow fields in supported membranes using the modified Stokes equation of Evans and Sackmann[9] is well known in the engineering literature as Brinkman's equation,[14] which describes viscous flow in a bed of immobile obstacles at low area fraction of the obstacles. We note that it has been argued that Brinkman's equation is the appropriate approximation to the hydrodynamics of cell membranes, due to the frictional contribution of the immobile proteins.[15,16] Our results, therefore, may be applicable to diffusing proteins and protein clusters in real cell membranes.

I. MEMBRANE HYDRODYNAMICS AND DRIFT

We consider a supported membrane of thickness h, containing a disk of radius a, resting on a thin Newtonian fluid layer of thickness H and viscosity η. The membrane is characterized by a surface viscosity, η_m, that is given by the three-dimensional shear viscosity of the lipid times the membrane thickness. The disk is moving to the right with a constant velocity $\boldsymbol{U}$ [Fig. 1(B)]. Let us choose the centerline of the disk as the positive x axis, and let the disk start its motion from $x=-L$. Consider a small volume of fluid (or equivalently a tracer particle that does not perturb the flow) initially at rest at $x=0$ and $y=\rho$ [see Fig. 1(A)]. As the disk moves from $-L$ to L, this volume of fluid will be disturbed, and, depending upon ρ, it will undergo a net horizontal displacement. This net displacement of the fluid element for a disk that moves an infinite distance, i.e., as $L\to\infty$, is defined as the *drift*.[2] Now imagine labeling a line of fluid elements or tracer particles at the origin along the y axis. The integral of the drift over this line has the dimensions of area, and represents the net area of fluid displaced as the disk travels from $-\infty$ to ∞. This integral is called the drift area (volume in three dimensions). We use *total* drift area when we integrate over an infinite line, but if we restrict the integration to a finite line, we call this the *partial* drift area, following Eames *et al.*[3,17] We focus on the partial drift area, since it is of greater interest for our purposes to examine the net motion of fluid elements close to the line of motion of the disk.

For steady motions, we consider the equivalent problem of a uniform flow of velocity $-\boldsymbol{U}$ incident upon a stationary disk. The drift of a fluid element is then the difference between the net displacement of the fluid element in the presence of the stationary disk and in its absence.

The velocity field around a stationary disk of radius a in a supported membrane, subject to a uniform velocity of $-U$ in the x direction, is given by[9]

$$u_r(r,\theta)=U\left[-1+\frac{C_1}{r^2}+\frac{C_2}{r}K_1\left(\frac{r}{\xi}\right)\right]\cos\theta, \tag{1a}$$

$$u_\theta(r,\theta)=U\left\{1+\frac{C_1}{r^2}+\frac{C_2}{r}\left[\frac{r}{\xi}K_0\left(\frac{r}{\xi}\right)+K_1\left(\frac{r}{\xi}\right)\right]\right\}\sin\theta, \tag{1b}$$

where r and θ are the usual polar coordinates, and ξ represents the typical length scale of fluid disturbances in the supported membrane,[9,10]

$$\xi=\left(\frac{\eta_m H}{\eta}\right)^{1/2}. \tag{2}$$

We refer to ξ as the screening length. The constants C_1 and C_2 are

$$C_1=a^2\left(1+\frac{2aK_1(a/\xi)}{\xi K_0(a/\xi)}\right), \tag{3a}$$

$$C_2=-\frac{2\xi}{K_0(a/\xi)}, \tag{3b}$$

where K_0 and K_1 are the modified Bessel functions.

It is instructive to examine this velocity field in the two limits of being either very close or very far from the disk. Consider again the system with the disk moving in the membrane with a velocity of U. When the disk radius $a\ll\xi$, then very close to the disk, $r/\xi\ll 1$. In this limit, it can be shown that the velocity field as a function of r behaves to leading order as $\log(r/\xi)$. The far field, when $r/\xi\gg 1$, however, decays as r^{-2}. The initial logarithmic decay is a well-known result of two-dimensional hydrodynamics, which for a perfect two-dimensional flow yields the Stokes paradox.[12] However, for a membrane coupled to a surrounding fluid, the logarithmic decay occurs over the length scale $r\sim\xi$.

Estimates of the length scale ξ can be made from published values of the parameters involved. Most lipid bilayer membranes are about 5 nm in thickness, and supported by a film of water of about 1–1.5 nm.[18] There appears to exist some ambiguity regarding membrane viscosity measurements,[19] which range from 1 to 2 poise[20] to at least

150 poise.[21,22] Assuming that the bilayer rests on water (viscosity 1 centipoise), the membrane screening length from Eq. (2) lies between about 20 and 270 nm for the lower and upper estimates of the membrane viscosity, respectively.

We therefore expect that the motion of an object such as a disk in a fluid membrane is likely to impact the motion of other objects within a distance ξ, which would tend to be dragged along by hydrodynamic entrainment. Drift, as introduced by Darwin,[1] is one way to quantify this phenomenon.

II. CALCULATING DRIFT

The drift, Δ, due to the translation of the disk, is the integrated motion of a fluid element belonging to a particular streamline, along the streamline,[3] i.e.,

$$\Delta = \int_0^\infty \mathrm{dt}(u_x + U). \tag{4}$$

Here we have added the constant velocity U to cancel out the effect of the uniform flow of velocity $-U$ in Eq. (1). Note that the drift as defined by Eq. (4) measures displacement only in the x direction. As can be easily seen from symmetry considerations, the net displacement in the y direction is zero if the disk travels from $-\infty$ to ∞. The streamfunction, $\psi(r,\theta)$, defined by the equations $u_r = 1/r\partial\psi/\partial\theta$ and $u_\theta = -\partial\psi/\partial r$, can be written down by inspection as

$$\psi(r,\theta) = U\left[-r + \frac{C_1}{r} + C_2 K_1\left(\frac{r}{\xi}\right)\right]\sin\theta. \tag{5}$$

Far away from the disk, when $x \to \infty$ and $y \to \rho_0$, the streamfunction reduces to $-U\rho_0$. Streamlines, i.e., lines of constant ψ, that correspond to an initial position, $y = \rho_0$, are therefore given by the curve $r(\theta)$, which satisfies

$$\rho_0 = \left[r - \frac{C_1}{r} - C_2 K_1\left(\frac{r}{\xi}\right)\right]\sin\theta. \tag{6}$$

Some illustrative streamlines are plotted in Fig. 2.

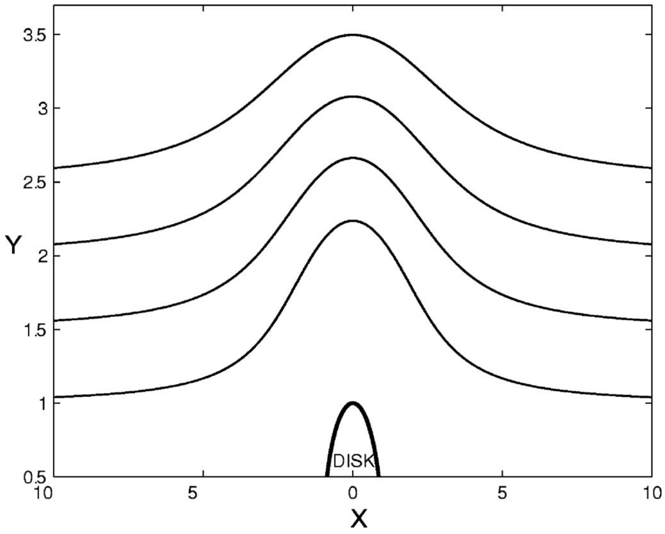

FIG. 2. Streamlines of a circular disk in a membrane subject to a uniform unperturbed flow in the $-x$ direction. The membrane screening length $\xi = a$. The elliptical appearance of the disk is due to differences in the scales of the axes.

Next, to express Eq. (4) as an integral over space, we use $u_\theta = r d\theta/dt$ and so we have

$$\Delta(\theta_0,\theta_f,\rho_0) = \int_{\theta_0}^{\theta_f} \mathrm{d}\theta \frac{r(U+u_x)}{u_\theta}. \tag{7}$$

Here θ_0 and θ_f are, respectively, the initial and final values of the angular coordinate, and the integration is over the streamline along which the streamfunction takes the value $-U\rho_0$.

From Eq. (1), after transforming to Cartesian coordinates, we obtain

$$\Delta(\theta_0,\theta_f,\rho_0) = \int_{\theta_0}^{\theta_f} \mathrm{d}\theta r \frac{[C_1\cos 2\theta + C_2 r\cos 2\theta K_1(r/\xi) - (C_2/\xi)r^2 K_0(r/\xi)\sin^2\theta]}{[r^2 + C_1 + C_2 r K_1(r/\xi) + (C_2/\xi)r^2 K_0(r/\xi)]\sin\theta}. \tag{8}$$

To calculate the net effect of the motion of the disk on a line of fluid elements, initially at $x=0$ in the plane, we integrate over the initial positions ρ_0 of the fluid element. Since we are interested in capturing the effect of the disk motion close to the disk, we choose the limits of integration to be some value, say ρ_f, where the drift is effectively negligible. This integral is called the partial drift area, A, and is defined as

$$A(\theta_0,\theta_f) = \int_{-\rho_f}^{\rho_f} \mathrm{d}\rho\Delta(\theta_0,\theta_f,\rho). \tag{9}$$

III. DRIFT, PARTIAL DRIFT, AND SCREENING LENGTH

To calculate the drift Δ for a fluid element on a particular streamline, we numerically compute the integral in Eq. (8) by using the trapezoid method.[23] A particular streamline is picked by its y coordinate, ρ, and the polar angle, θ_0, of this point from the starting point of the disk at $x = L = -100a$ is computed. The upper limit of the integration is then chosen to be $\theta_f = \pi - \theta_0$. At each step, the relevant values of the (r,θ) coordinates are obtained from Eq. (6). We tested for accuracy by changing the stepsize between 10^{-4} and 10^{-1} radians and found that the value of drift changes less than 1%. In order to

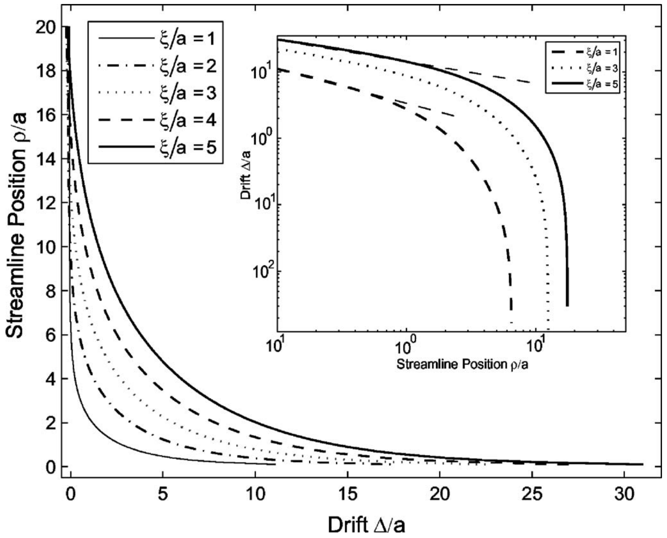

FIG. 3. The curve represents the net motion of fluid elements in the x direction from their initial position on the $x=0$ axis due to a translating disk. The disk has moved from $-100a$ to about $100a$ along the x axis. The inset shows three of these curves plotted with a log-log scale. Note the sharp drop as the initial streamline position becomes greater than ξ. The straight dashed lines are guides to the eye.

ensure that our choice of the starting point L is not influencing the results, we repeated the analysis for $L=200a$ and $1000a$ for selected values of ξ and found no appreciable difference. We therefore keep the stepsize at 10^{-3} radians and choose $L=100a$ for the rest of the paper.

We then investigate the influence of the screening length ξ on the drift. The results are shown in Fig. 3. Increasing ξ, which corresponds to increasing the effective viscosity of the membrane, increases the drift of each fluid particle. It can be observed that the drift is significant only for those fluid particles close to the line of motion of the disk, and rapidly becomes negligible for larger distances. This result can also be seen with a log-log scale in the inset to Fig. 3, where two distinct types of behavior, one near the line of motion and the other far away, are observed, with the crossover at about $\rho \approx \xi$. A semilog plot of the drift (Fig. 4) shows that for small ρ_0, the drift scales logarithmically with ρ_0. This behavior arises from the logarithmic decay of the velocity field close to the disk. It is noteworthy that the dependence of drift on ξ for a given value of ρ_0 is almost linear in ξ, as can be seen from Fig. 4.

We also calculate the partial drift area for the region by integrating the drift over each initial streamline position. The results are shown in Fig. 5. We find that the greater the screening length, the greater the partial drift area of the moving disk, and the relation between the partial drift area and the screening length, ξ, appears to be very nearly quadratic.

These calculations are consistent with the picture that the disk entrains a part of the fluid of dimensions of the order of the screening length ξ. As can be seen from Fig. 1, the drift is only significant for the fluid particles a distance $O(\xi)$ from the line of motion of the disk. The partial drift area appears to be a measure of the total area of the entrained flow due to the disk, which is proportional to the area of a ring of thickness ξ.

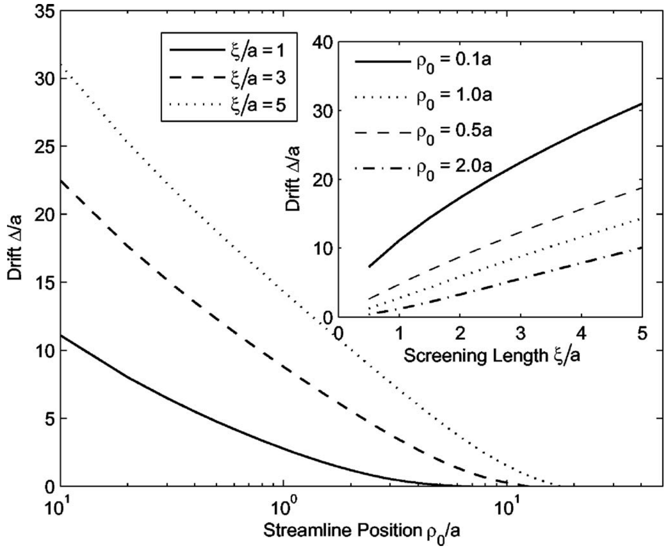

FIG. 4. A plot of the drift on a semilog scale that demonstrates that close to the centerline, the drift $\sim\log(\rho_0/a)$. The inset shows the almost linear relation between the drift and the screening length ξ for several values of ρ_0/a.

IV. CONCLUSION

We have used the concept of *drift* and *partial drift* to develop a quantitative theory of fluid entrainment by a disk moving uniformly in a supported fluid membrane. We find that for a given initial position of a fluid particle, the drift varies very nearly linearly with the screening length, ξ. The total area swept out by a line of initially stationary fluid elements is the partial drift area, and we find that it depends quadratically on the size of the membrane screening length, ξ. We argue that the partial drift area captures the phenomenon of entrainment of lipids by inclusions. The quadratic dependence of the partial drift area on ξ is in agreement with this view, as would be expected for a concentric ring of entrained lipids around a circular inclusion.

The hydrodynamic calculation we have presented lends itself to the following visualization. Imagine the fluid membrane as if it were made up of thin layers concentric to a

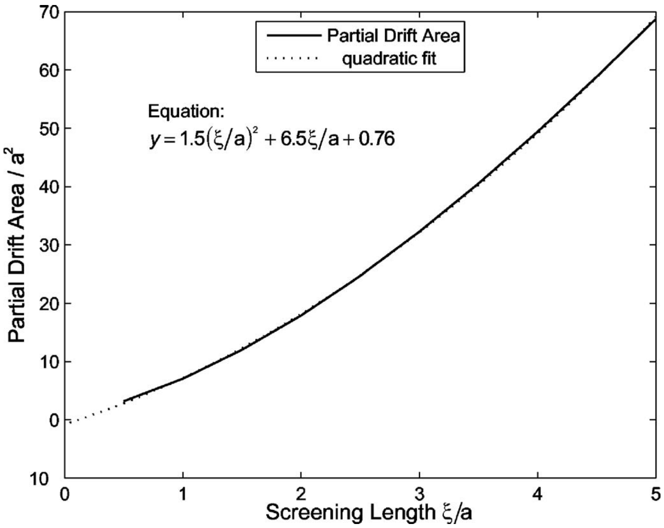

FIG. 5. The partial drift area plotted against the membrane screening length, ξ.

small circular disk at rest in the membrane. When the disk begins to move, these layers are dragged along some distance before slipping off and being replaced by a new layer of fluid. The rate at which a layer slips off is given by the difference between the disk velocity U and the velocity of the fluid at the layer. For distances of up to ξ from the center of the disk, due to the slow (logarithmic) decay of the velocity field, this difference in velocities is small, and fluid moves an appreciable distance before slipping off. For larger distances, the fluid hardly moves at all.

Thus the phenomenon of drift gives a measure of the entrainment of nearby fluid by a moving membrane-bound object. An obvious question to ask is if there are any possible consequences of the hydrodynamic drift on the dynamics of natural inclusions in membranes such as integral membrane proteins. For example, the phenomenon of drift may play some part in the dynamic recruitment of membrane-bound objects into clusters. Aggregation of receptor molecules, along with colocalized lipids and other proteins, into larger clusters on cell membranes is known to be a part of the signal-transduction process.[24,25] The mechanism for this aggregation is not fully understood and it is likely, as is common in biology, that several types of interactions are responsible. With respect to hydrodynamic interactions, assuming the estimates of length scales for model membranes also apply to biological membranes, a protein of about 5 nm in radius will be surrounded by a domain of $\xi \approx 20$ nm or greater in size. If two proteins approach each other to a distance less than ξ, hydrodynamic drift would tend to couple their motion, increasing the chances of a favorable binding event between the two.

Similarly, the presence of these inclusions in lipid membranes affects the physics of the membrane itself by creating domains of entrained fluid. Prior experiments, such as those of Zhang and Granick,[26] appear to be consistent with this picture of entrainment. However, it is noteworthy that the above picture we have presented also provides a physical process via which some kinds of specialized lipid domains[27] can form around membrane proteins. In a heterogeneous lipid membrane, all that is needed is some affinity of certain membrane lipids or protein molecules for certain other proteins arising, for example, due to geometric effects or electrostatic interactions. Since each membrane protein, as it diffuses around, is surrounded by an entrained domain, equilibrium considerations will guarantee that this domain is composed largely of the lipids, or other proteins, with favorable interactions. Such domains would be small and dynamic, existing on time scales that are limited by Brownian motion. These hypotheses, and the role of Brownian motion in drift-assisted segregation, are subjects of current investigation.

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