Effective viscosity of dilute bacterial suspensions: a two-dimensional model

Brian M Haines, Igor S Aranson, Leonid Berlyand and Dmitry A Karpeev

1 Department of Mathematics, Pennsylvania State University, 418 McAllister Building, University Park, PA 16802, USA
2 Materials Science Division, Argonne National Laboratory, 9700 South Cass Avenue, Argonne, IL 60439, USA
3 Mathematics and Computer Science Division, Argonne National Laboratory, 9700 South Cass Avenue, Argonne, IL 60439, USA

Received 3 April 2008
Accepted for publication 20 October 2008
Published 24 November 2008
Online at stacks.iop.org/PhysBio/5/046003

Abstract
Suspensions of self-propelled particles are studied in the framework of two-dimensional (2D) Stokesian hydrodynamics. A formula is obtained for the effective viscosity of such suspensions in the limit of small concentrations. This formula includes the two terms that are found in the 2D version of Einstein’s classical result for passive suspensions. To this, the main result of the paper is added, an additional term due to self-propulsion which depends on the physical and geometric properties of the active suspension. This term explains the experimental observation of a decrease in effective viscosity in active suspensions.

1. Introduction

Recently there has been considerable interest in understanding the dynamics of systems of active interacting biological agents (active systems, for short), such as flocking birds, schooling fish, swarming bacteria, etc [1–6]. Properties of these strongly self-organizing dissipative systems are of fundamental interest to nonequilibrium statistical mechanics [7–12] and to potential technological applications [13].

Common swimming (motile) bacteria, such as Bacillus Subtilis, Escherichia coli, and many others, are rod-shape microorganisms (length about 5 μm, diameter of the order of 1 μm), propelled by the input of mechanical energy at the smallest scales by the rotation of helical flagella attached to the cell wall. Suspensions of swimming bacteria (active suspensions) are a convenient representative of self-organizing biological systems. At relatively high filling fractions bacteria interact mostly through hydrodynamic entrainment induced by their swimming with respect to the ambient fluid [4, 14]. These hydrodynamic interactions are instrumental in the establishment of long-range order in active suspensions. At the same time, these systems are amenable to accurate experimental studies, control, and manipulation [14]. In the dense regime, the dynamics of active suspensions is dominated by the multiple body interactions and long-range self-organized coherent structures, such as recurring whirls and jets with the spatial scale exceeding the size of an individual bacterium by an order of magnitude. This regime, however, makes the analysis rather challenging.

In the dilute regime, the hydrodynamic interactions between bacteria (or passive particles) are often ignored as the interparticle distance exceeds the range of the flows resulting from the particle motion. Therefore, in this case it is possible to isolate the effect of the particle–fluid interactions on the effective behavior of active suspensions. This constitutes a step towards the full understanding and utilization of the novel properties of such systems.

The first step was taken in [15] by Einstein, who derived an explicit asymptotic formula for the effective viscosity of a dilute suspension of passive spheres. This formula shows an increase of the viscosity over that of the ambient fluid alone. The correction to the effective viscosity is to the first order in the volume fraction of the inclusions. Later, Batchelor and Greene obtained the second order asymptotic formula, which takes into account pairwise interactions between particles [16]. Jeffrey calculated the effective viscosity of a suspension of ellipsoidal particles to first order in [17].

Unlike the spherical case, yet akin to the case for ellipsoidal particles, the value of the viscosity is affected...
by the distribution of orientations of the inclusions and is dependent on the rate of shear. Thus, a viscosity for use in a constitutive (stress rate of strain) relation must be a tensor and the constitutive relation itself may be nonlinear. Indeed, it will be seen that the suspension is a non-Newtonian fluid. In this paper, no attempt will be made to fully describe the rheology of an active suspension, but only to derive an effective viscosity as the constant of proportionality between rates of energy dissipation with and without the inclusions. However, it is also shown that this effective viscosity is equivalent to the result obtained by defining a shear effective viscosity (used in [18]) as the ratio of the off-diagonal component of the bulk deviatoric stress to the rate of shear.

In this work, Einstein’s classical dilute limit result is extended to the case of self-propelled disk inclusions in a 2D Stokesian fluid. The choice of two-dimensional hydrodynamics is motivated by the tractable nature of calculations involving Green’s functions in 2D and also by the quasi-two-dimensional thin film geometry of the experiment [14]. In particular, the correction to the effective viscosity is explicitly calculated as a function of the orientations of the bacteria (direction of force of self-propulsion), the intensity of their force of self-propulsion, and the volume fraction of the suspension. In the case of an absence of self-propulsion and, alternatively, the case of a uniform distribution of orientations, the result recovers the 2D version of Einstein’s result (see, e.g., [19, 20]).

The model of self-locomoting bacterium and the corresponding hydrodynamics are described in section 2. Following Batchelor [21], the effective viscosity of a dilute suspension is defined in section 2, in terms of a suitable background flow and the relative increase in the energy dissipation due to the disturbance produced by the inclusion of a bacterium in the background flow. In the case of self-propulsion the disturbance flow is due both to the passive response of the background flow to the inclusion of a particle as well as the response of the stationary fluid to the particle’s self-propulsion. Because of the linearity of Stokesian hydrodynamics, the two components of the disturbance flow can be computed independently using the Green’s function for the disk.

The disturbance flow \( u'_p \) due to the active locomotion of a single bacterium is calculated in section 3. This flow is responsible for the propulsion of the bacterium. It is also shown that this disturbance flow decays at infinity. This result is emphasized since the lack of such decay is a common point of deficiency of 2D hydrodynamics. Indeed, while the translation of a ball in 3D produces no flow at infinity, in the well-known Stokes paradox, the 3D flow due to an infinite cylinder (described by the corresponding force monopole) translating transversely to its axis generates a non-zero flow at infinity (see, e.g., [22]). This prevents the decoupling of rods, which is needed for the dilute limit, where it is assumed that the flow due to a suspension can be approximated by the sum of solutions due to a single inclusion. However, a self-propelled particle is constrained by the viscous drag force opposing the propulsion force, thus producing a force dipole which decays at infinity, unlike the force monopole in the case of the moving disk.

In calculating the other component of the disturbance flow, \( u'_p \), due to the bacterium’s passive response to a background flow, care must be taken to ensure that no flow is produced at infinity. Thus, in section 4 an appropriate background flow is selected to ensure the disturbance decays at infinity. Once it has been done, the effective viscosity is calculated as a function of the bacteria’s orientations relative to the background flow. This allows the effective viscosity of a suspension with a given distribution of orientations to be computed. The effective viscosity for the steady-state distributions arising from the alignment of bacteria to the flow in different regimes is also discussed. Conclusions and the outlook are presented in section 5. Finally, the details of calculations are included in the appendices.

2. Model and its homogenization

A 2D dilute suspension of bacteria is modeled as a collection of discs of radius \( a \), each of which has an associated point force, representing the flagellum, placed at a distance \( \lambda a \) from the disk, as shown in figure 1. The point force is directed radially outward from the center of the bacterium and has some orientation angle \( \alpha \), measured from the x-axis. The bacteria are distributed throughout an ambient fluid of viscosity \( \eta \) which takes up the entire domain \( \mathbb{R}^2 \). A single bacterium in an infinite fluid moves with respect to the fluid with constant velocity driven by the point force \( \vec{c} \).

The suspension is assumed to contain sufficiently many bacteria so as to produce appreciable changes in the properties of the equivalent homogenized fluid. At the same time, the size of the bacteria and the propulsion force are assumed to be sufficiently small, so that the disturbance flow produced by bacteria is negligible at inter-bacterial distances and hence can be ignored at the locations of other bacteria. Therefore, in the following calculations, it is sufficient to consider a single bacterium with orientation \( \alpha \) in an unbounded volume of fluid. This is analogous to Einstein’s assumptions for passive suspensions.

This unbounded volume is an idealization of the microscopic volume element surrounding a single one of the particles located within a macroscopic fluid element. Because of the decay assumption, this idealization is permissible for the solution of the Stokes’ equation within that region. The viscous dissipation in the macroscopic fluid element is then the
sum of the dissipations in all of the subordinate microscopic volumes, jointly containing a collection of particles having some prescribed distribution of orientations. Analogous to the method of Batchelor in [21], the effective viscosity $\eta^\ast$ of a suspension in an ambient fluid of viscosity $\eta$ is defined as the viscosity of an equivalent fluid with no inclusions that produces the same energy dissipation in each macroscopic volume element.

For a suspension of passive particles, the existence of an equivalent Newtonian fluid with the scalar effective viscosity $\eta^\ast$ is a classical result of homogenization theory (see e.g., [23] and references therein). The analysis for active particles is more subtle and has not been carried out in a rigorous mathematical context. The assumption is made that the effective viscosity of an active suspension can be defined as was done for passive particles. Namely, $\eta^\ast$ is a scalar quantity characterizing the additional energy dissipation due to the presence of inclusions. This technique, albeit standard for passive suspensions, is presented somewhat cryptically in the literature. To clarify the main points, the conceptual side of the calculation is presented here; the technical details can be found in appendix A (also see [21] for the derivation in the passive case).

Since the effective viscosity is to be defined in terms of energy dissipation, a background flow, which describes the flow throughout the homogenized fluid and on the boundary of the suspension, is chosen so that it has a non-zero rate of energy dissipation (i.e., requiring a non-zero strain rate). In the plane $\mathbb{R}^2$, representing the microscopic volume with coordinates $\{x_i\}_{i=1,2}$, the velocity components of the background flow are defined as $u_i = \epsilon_{ij}x_j$. Here $\epsilon_{ij}$ is a constant and symmetric strain rate tensor but otherwise left to be specified later. Adding a single self-propelled disk inclusion $V_b$ somewhere in the plane produces the disturbance flow $\vec{u}_d$. Provided that the background flow with strain rate $\epsilon$ is selected properly, $\vec{u}_d$ vanishes at infinity, decoupling the bacteria, as required of the dilute limit. The disturbance flow can be computed explicitly and it is done below. The total flow of the suspension is $\vec{u} = \vec{u} + \vec{u}_d$ and in principle it should be possible now to compare the dissipation rates of $\vec{u}$ and $\vec{u}$ by integrating over $\mathbb{R}^2$ and $\mathbb{R}^2 - V_b$, respectively.

As shown in [21], the integration over unbounded volumes leads to technical difficulties because the disturbance flow does not decay fast enough rendering the additional energy dissipation rate infinite. This in part is due to the premature passage to the dilute limit, which requires each inclusion to be individually surrounded by an infinite volume of background fluid. This motivates the more efficient method of comparing the dissipation rates within a bounded domain $\vec{V}$ which contains sufficiently many bacteria and passing to the dilute limit later.

Figure 2 shows such a domain encompassing two bacteria. Inside $\vec{V}$ are the regions representing the bodies of the bacteria, $V_b$, and, for each, an $\epsilon$-disk $V_{\epsilon,i}$ around the corresponding point force.

The disturbance flow in the domain $\vec{V} = \bigcup_i V_b - \bigcup_i V_{\epsilon,i}$ is required to vanish at the outer boundary $\partial \vec{V}$. This models a finite container with the background flow applied at the boundary and the disturbance flow vanishing there.

Calculating the dissipation rate of a suspension as a volume integral over $\vec{V}$, however, requires knowledge of the disturbance flows $\vec{u}_d$ throughout the fluid and, thus, involves solving a boundary value problem in the two-dimensional domain $\vec{V} = \bigcup_i V_b$. To avoid this, the total dissipation rate in this domain is calculated equivalently as the integral of the work of forces at the boundary $\partial \vec{V}$. The density of work at the boundary is $\sigma_{ij}\epsilon_{jk}x_k$ and $\sigma_{ij}\epsilon_{jk}x_k$ for the homogenized and total suspension flows, respectively. While the flows of the homogenized fluid and total flow of the suspension agree on the boundary $\partial \vec{V}$, $u_i = \vec{u}_i = \epsilon_{ij}x_j$, the corresponding values of the stress tensors $\sigma$ and $\dot{\sigma}$ are not necessarily the same. The effective viscosity is defined as the parameter entering into $\dot{\sigma}$ that makes the integrals of the above densities over $\partial \vec{V}$ equal:

$$\int_{\partial \vec{V}} \sigma_{ij}u_i n_j dA = \int_{\partial \vec{V}} \sigma_{ij}\vec{u}_i n_j dA.$$  \hfill (1)

Using the Stokes equation $\nabla \cdot \sigma' = -\nabla p' + \eta \Delta u' = 0$ and repeatedly applying the divergence theorem (see appendix A), the integrals of these densities over $\partial \vec{V}$ can be reduced to integrals over the boundary of the bacterial domain only: $\partial V_b + \partial V_{\epsilon,i}$. The domain of integration of these integrals is independent of $\partial \vec{V}$ and upon passing to the limit $\vec{V} \to \mathbb{R}^2$ they
are expressed in terms of the appropriate limiting disturbance flow $\vec{u}$ vanishing at infinity.

As the container is magnified and approaches all of $\mathbb{R}^2$ the interparticle distances increase and the dilute assumption allows one to replace the solution to (A.5) by a superposition of solutions for the flow due to a single bacterium, derived in the next section. The effective viscosity is then determined from the expression resulting from summing over all inclusions:

$$2 (\eta^* - \eta) \epsilon_{ij} \epsilon_{ij} = \frac{\epsilon_{ik}}{A} \sum_{l} \int_{\partial V_{B_l} \cup \partial V_{i,j}} (\sigma_{ij} x_k n_j - 2 \eta u'_i n_k) \, dA.$$  \hspace{1cm} (2)

3. Flow due to a single bacterium

Let $\Omega$ be the exterior of the unit disk in $\mathbb{R}^2$ and $\delta_{0}$ be the Dirac delta evaluated at $\vec{r} - \vec{r}_0$, where $\vec{r}_0$ is the location of the point force. In the low Reynolds number limit, the flow due to the bacterium obeys the Stokes equation

$$\begin{align*}
\eta \Delta \vec{u}_0 &= \nabla p_0 + \vec{c} \delta_{0} \quad \text{in } \Omega \\
\nabla \cdot \vec{u}_0 &= 0 \quad \text{in } \Omega \\
\vec{u}_0 &= 0 \quad \text{on } \partial \Omega,
\end{align*}$$  \hspace{1cm} (3)

where $\vec{c}$ is the force strength, $\partial \Omega$ is the surface of $\Omega$ and $\vec{u}_0 \rightarrow \text{const}$ as $x \rightarrow \infty$. For simplicity of calculations, set $\vec{c} = c \hat{\vec{x}}$ and $\vec{r}_0 = (1 + \lambda) \hat{\vec{x}}$. Note that here $\vec{u}_0$ is set to 0 on $\partial \Omega$. This is the reference frame in which the bacterium is at rest—for the purpose of finding the total flow of the suspension, the reference frame in which the fluid is at rest at infinity must be used.

By writing $\hat{\vec{u}}$ as the curl of a stream function $\Phi$ and taking the curl of (3), this reduces to the inhomogeneous biharmonic equation (see appendix B for more details):

$$\begin{align*}
\Delta^2 \Phi(x, y) &= \frac{\partial}{\partial y} c \frac{\delta_{0}}{\eta} \quad \text{in } \Omega \\
\nabla \cdot \Phi &= 0 \quad \text{on } \partial \Omega.
\end{align*}$$  \hspace{1cm} (4)

The Green’s function $\Gamma(x + iy, x - iy)$ for the domain $\Omega$ with these boundary conditions is known (see appendix C) and yields the solution

$$\Phi(x, y) = -\frac{c}{\eta} \frac{\partial \Gamma}{\partial y} (x + iy, 1 + \lambda).$$  \hspace{1cm} (5)

Explicitly, in polar coordinates,

$$\Phi(r, \theta) = \frac{1}{a} \frac{c r \cos \theta}{8 \pi \eta} \left[ \frac{(1 + \lambda)^2 - 1}{1 + (1 + \lambda)^2 r^2 - 2 (1 + \lambda) r \cos \theta} \right].$$

$$+ \log \left[ \frac{(1 + \lambda)^2 + r^2 - 2 (1 + \lambda) r \cos \theta}{1 + (1 + \lambda)^2 r^2 - 2 (1 + \lambda) r \cos \theta} \right].$$  \hspace{1cm} (6)

It is easy to see that $u'_0 \rightarrow u_{\infty} = \text{const}$ as $r \rightarrow \infty$. Subtracting this flow (moving to the reference frame where the water is at rest at $\infty$) and rescaling to a disk of radius $a$, is shown in figure 3 and is given asymptotically by

$$\vec{u}(r, \theta) \rightarrow \frac{1}{a} \left[ \frac{(a/2)^3 (2 \lambda) + 1}{8 \pi \eta (a/2)^3} \frac{1}{(\cos \theta + \cos(3 \theta))} + O \left( \frac{1}{a} \right) \right].$$  \hspace{1cm} (7)

Now, by taking the divergence of (3), one obtains

$$\begin{align*}
\Delta p &= -c \frac{\partial}{\partial x} \delta_{0} \quad \text{in } \Omega \\
\nabla p \cdot \hat{n} &= \eta \Delta \vec{u} \cdot \hat{n} \quad \text{on } \partial \Omega.
\end{align*}$$  \hspace{1cm} (8)

The solution to (8) is found using complex function theory (see appendix D), and is the real part of the complex function

$$\Pi(z) = -\frac{1}{a} \frac{c}{2 \pi (1 + \lambda)} \frac{a^2 z^2 (2 + \lambda)^2}{(1 + \lambda)(1 + \lambda - z)((1 + \lambda)z - a)^2}.$$  \hspace{1cm} (9)

4. Calculation and interpretation of the effective viscosity

In order to calculate the effective viscosity, it remains to perform the integration in (2). In (2), $\vec{u}'$ and $\vec{p}'$ are the solutions to

$$\begin{align*}

\eta \Delta \vec{u}' &= \nabla \vec{p}' + \vec{c} \delta_{0} \quad \text{in } \Omega \\
\nabla \cdot \vec{u}' &= 0 \quad \text{on } \partial \Omega,
\end{align*}$$  \hspace{1cm} (10)

subject to the boundary conditions

$$u'_i \rightarrow \epsilon_{ij} x_j \quad \text{as } r \rightarrow \infty$$

$$\vec{u}' = \text{const} \quad x \in \partial \Omega.$$  \hspace{1cm} (11)

Note that, as mentioned in section 3, one is not free to choose the value of the constant that $\vec{u}$ takes on $\partial \Omega$.

As will be seen, the effective viscosity is dependent on the background flow (i.e., the choice of the strain rate tensor $\epsilon_{ij}$ in (11)). However, the choice of this flow cannot be completely arbitrary. First, since the effective viscosity is defined in terms of energy dissipation, a non-zero rate of strain is required so that there is energy being dissipated due to viscosity. Second, the background flow is chosen without vorticity so that it does not rotate bacteria, which allows for the computation of the effective viscosity for a fixed (time-independent) distribution of orientations of bacteria (see figure 1). It should be noted that adding uniform vorticity to the background flow would not alter the effective viscosity.
through its dependence on produces a torque on the bacteria (see, e.g., [17]), which will spherical and an interaction with the background flow thus are assumed to be independent identically distributed random interaction of the bacteria with the background flow), which orientation of a bacterium in the background flow.

The coefficient where \( \phi \) is chosen to be the simplest flow that matches these criteria, for a background flow that satisfies the conditions for existence of other bacteria would be violated. In 2D, this is only possible aspherical bacteria to the flow. Then, we can expect that, after a steady-state distribution has been established, it can be expanded as follows (see [18] for more general results):

\[
P(\alpha, \epsilon_0) = \frac{1}{2\pi} + P_1(\alpha)\epsilon_0 + P_2(\alpha)\epsilon_0^2 + \cdots. \tag{17}
\]

The zeroth-order term corresponds to an isotropic distribution of orientations \( (P(\alpha, \epsilon_0) = 1/2\pi = \text{const}) \) arising in the limit of a negligible aligning background flow. This diffusion-dominated limit integrates to zero in (16) and recovers the classical result for the effective viscosity of a two-dimensional suspension of inert disks (see, e.g., [20]):

\[
\eta^* = \eta(1 + 2\phi). \tag{18}
\]

Further, the linear term in (17) cancels \( \epsilon_0 \) in the denominator of (16) and to the leading order the suspension exhibits a linear response (quasi-Newtonian, in Batchelor’s terminology; see [31]). Higher order terms result in a weakly-non-Newtonian response, largely negligible for small \( \epsilon_0 \).

For larger \( \epsilon_0 \) expansion (17) need not hold and thus the non-Newtonian effects suggested by (20) can be expected to be strong. Here, too, one cannot use (16) to infer a blow up in \( \eta^* \) as \( \epsilon_0 \) bounded away from 0. We can expect, however, that such background flows will result in substantial alignment of inclusions along one of the preferred directions \( \alpha_0 \): \( P(\alpha, \epsilon_0) \approx \delta(\alpha - \alpha_0) \). Substituting this into (16), we formally obtain

\[
\eta^* \approx \eta \left[ 1 + 2\phi + \frac{c}{2\pi \eta_0} \frac{1 + 2\lambda(2 + \lambda)}{(1 + \lambda)^3} \phi \sin 2\alpha_0 \right]. \tag{19}
\]

For the background flow (12), the corresponding preferred directions are \( \alpha_0 = -\frac{\pi}{4}, \frac{\pi}{4} \). Thus, after (approximate) alignment has been established, we obtain

\[
\eta^* \approx \eta \left[ 1 + 2\phi - \frac{c}{a} \frac{1 + 2\lambda(2 + \lambda)}{(1 + \lambda)^3} \phi \right]. \tag{20}
\]

This formula predicts a reduction in the overall effective viscosity relative to the inert case (18) and can be used to explain the experimental data on the reduction of viscosity in bacterial suspensions observed in recent experiments [26].

In fact, experimental observations on bacterial suspensions made in [14] can even be construed as manifestations of a negative effective viscosity, consistent with (20) for moderate \( \epsilon_0 \) and suitable \( c \) and \( \lambda \). This evidence includes the observed formation of non-decaying whirls and jets of collective locomotion (see also simulations [27–30] for dense suspensions), which are indicative of long-wave instability, potentially signaling a change in sign of the effective viscosity. Indeed, while positive viscosity results in preferential damping of high wavenumbers, when the viscosity changes sign to negative, low wave number modes get destabilized and saturate at large-scale coherent structures.

Reduction of effective viscosity is observed in a quasi-two-dimensional experiment with a free-standing bacterial film, geometry similar to that described in [14].
This effect is best illustrated with a linear scalar model of the form

\[ v_i = \eta^* \Delta v - \beta \Delta^2 v. \]

Here the growth rate for the kth mode is \( \lambda_k = -k^2(\eta^* + \beta k^2) \) so for \( \eta^*, \beta > 0 \) all modes decay, while for \( \eta^* < 0, \beta > 0 \) the small wavenumber modes (\( |k| < \sqrt{|\eta^*|/|\beta|} \)) will either grow or simply not decay.

Some of the previous works have discussed the possibility of a reduced effective viscosity. In particular, heuristic arguments in [32] anticipated the reduction in viscosity predicted by equation (20). Additionally, the dependence of effective viscosity on orientation can explain the results of recent simulations [33]. There, to linear order in \( \phi \), a reduction in viscosity was observed only in the presence of a uniform external aligning field (gravity for bottom-heavy swimmers). This is due to the fact that the swimmers in [33] were modeled as spherical squirming particles, unaffected by a shear flow. Hence, in the absence of an external entraining field, the only alignment was due to pairwise interactions between the squirmers, naturally leading to an order \( \phi^2 \) correction to \( \eta^* \). This result underscores the importance of the bacterial shape to the leading order effects on the effective viscosity of dilute suspensions. In particular, a significant order \( \phi \) effect is expected for elongated particles (ellipsoids or cylinders with large aspect ratios (of the order of 1:5 for swimming bacteria).

In this work, we used one of the accepted definitions of effective viscosity, which characterizes the additional rate of energy dissipation due to the inclusions. The conventional definition of the viscosity involving the constitutive relation between the strain rate and the stress is more revealing, but harder to obtain in general, as the suspension has a strongly non-Newtonian rheology. Indeed, for Newtonian fluids, the \( \eta^* \) is more representative of experimental settings. The inclusion of orientation effects will provide models that are more representative of experimental settings. The puzzling phenomenon of reduced viscosity in bacteria-laden fluids may find rather unexpected technological applications in bio-medical research and chemical technology, such as microscopic bacterial mixers and chemical reactors [13].

Acknowledgments

The work of B Haines was supported in part by NSF grant DMS-0708324. The work of L Berlyand was partially supported by NSF grant DMS-0708324 and DOE grant DE-FG02-08ER25862. 1S Aranson and D Karpeev were supported by US DOE, grant DOE grant DE-AC02-06CH11357. We would also like to thank Andrey Sokolov, Srima Ramaswamy, Raymond Goldstein and Michael Graham.

Appendix A. Calculation of dissipation rate and definition of effective viscosity

Following [21], the rate of work being done at the boundary \( \partial \Omega \) is given by

\[ \int_{\partial \Omega} \sigma_{ij} u_i n_j \, dA = e_{ik} \int_{\partial \Omega} \left( -p \delta_{ij} + 2\eta e_{ij} \right) x_k n_j \, dA, \quad (A.1) \]

where \( \sigma_{ij} \) is the stress tensor, \( u \) is the velocity of the fluid, \( n \) is the unit outward normal for the surface \( \partial \Omega \), \( p \) is the pressure of the fluid and \( e_{ij} \) is the rate of strain tensor. Henceforth, primed quantities will denote the disturbance values due to the presence of a bacterial suspension. The new stress tensor can be expressed as \( \delta_{ij} = \sigma_{ij} + \sigma'_{ij} \). Additionally, on \( \partial \Omega \), \( e_{ij} = e'_{ij} \).

Thus, the effective viscosity of the suspension \( \eta^* \) is defined by setting

\[ e'_{ik} \int_{\partial \Omega} \left( -p \delta_{ij} + 2\eta e'_{ij} \right) x_k n_j \, dA = e_{ik} \int_{\partial \Omega} \left( -p \delta_{ij} + 2\eta e_{ij} + \sigma'_{ij} \right) x_k n_j \, dA. \quad (A.2) \]

Noting that the terms involving \( p \) are identical on both sides and employing the divergence theorem yields

\[ 2A (\eta^* - \eta) e_{ij} e_{ij} = e_{ik} \int_{\partial \Omega} \sigma'_{ij} x_k n_j \, dA, \quad (A.3) \]

where \( A \) is the area of the surface \( \partial \Omega \). The right-hand side of \( (A.3) \) is the additional rate of dissipation due to the suspension. Employing the divergence theorem yet again, this integral is
transformed into an integral over the surfaces of the particles, producing

$$\epsilon_{ik} \int_{\Omega} \sigma'_{ij} x_k n_j \, dA = \epsilon_{ik} \int_{\Omega - \sum V_b \cup V_c} \left( \frac{\partial \sigma'_{ij}}{\partial x_j} x_k + \sigma'_{ik} \right) \, dV$$

$$+ \epsilon_{ik} \sum_{\partial V_b \cup \partial V_c} \sigma'_{ij} x_k n_j \, dA,$$

(A.4)

where $V_b$ is the volume occupied by a single bacterium, $V_c$ is a ball of radius $\epsilon$ around its corresponding point force, and the summation is taken over all bacteria inside $\Omega$. Now, the fluid in $\Omega$ obeys the inhomogeneous Stokes equation

$$\eta \Delta \bar{\nu} = \nabla \cdot \bar{\nu} + \sum_i c_i \delta \bar{r}_i \text{ in } \Omega \quad \nabla \cdot \bar{\nu} = 0 \text{ in } \Omega - \sum V_b$$

$$\bar{\nu} \cdot n = 0 \text{ on } \partial V_b$$

$$\bar{\nu} = \epsilon_{ij} x_j \text{ on } \partial \Omega,$$

(A.5)

where the subscript $l$ has been added to all quantities that can vary among the bacteria. In particular, $\bar{v}_l$ is the velocity of the $l$th bacterium, $\bar{r}_l$ is the location of its point force and $\delta \bar{r}_l$ indicates the strength and orientation of each point force. Thus, $\frac{\partial \sigma'_{ij}}{\partial y_j} = 0$ in $\Omega - \sum V_b \cup V_c$. Additionally, $\epsilon_{ik}$ can vary among the bacteria. In particular, $\bar{v}_l = \epsilon_{ij} x_j$ on $\partial \Omega$. Since $\nabla \cdot \bar{\nu} = 0$, the velocity can be expressed as the (2D) curl of a scalar stream function $\Phi(x, y)$. This curl, which operates on scalar functions and produces a vector function, is defined as

$$\text{Curl}_S \Phi(x, y) = \left( \frac{\partial \Phi}{\partial y}, -\frac{\partial \Phi}{\partial x} \right).$$

The scalar curl $\text{Curl}_S$, which operates on vectors, is defined as

$$\text{Curl}_S \bar{\nu} = \frac{\partial u_k}{\partial y} - \frac{\partial u_y}{\partial x},$$

so that $\text{Curl}_S \text{Curl}_S \Phi(x, y) = \Delta \Phi(x, y)$. Substituting $\bar{\nu} = \text{Curl}_S \Phi(x, y)$ into (3) and taking the scalar curl of both sides yields the inhomogeneous biharmonic equation

$$\Delta^2 \Phi(x, y) = \text{Curl}_S \frac{c}{\eta} \delta \bar{r}_0 = \frac{\partial}{\partial y} \left( \frac{c}{\eta} \delta \bar{r}_0 \right)$$

(B.2)

with boundary conditions

$$\Phi = \frac{\partial \Phi}{\partial n} = 0 \text{ on } \partial \Omega.$$

The Green’s function for the domain $\Omega$ with these boundary conditions is derived in the exact same fashion as that for the unit disc (see appendix C), and has a simple form as a function of the complex variables $z = x + iy$ and $\xi = x + iy$, taken from [34]:

$$\Gamma(z, \xi) = \frac{1}{8\pi} |z - \xi|^2 \log |z - \xi| + \frac{1}{16\pi} ((z|^2 - 1)|(|\xi|^2 - 1).$$

(B.4)

This yields the solution formula

$$\Phi(x, y) = \int_{\Omega} \Gamma(x + iy, \xi + iy) \frac{\partial}{\partial y} \frac{c}{\eta} \delta \bar{r}_l (\xi + iy) \, d\xi \, dy$$

$$= -\frac{c}{\eta} \int_{\Omega} \frac{\partial}{\partial y} \Gamma(x + iy, \xi + iy) \delta \bar{r}_l \, d\xi \, dy$$

and hence

$$\Phi(x, y) = -\frac{c}{\eta} \frac{\partial}{\partial y} (x + iy, 1 + \lambda).$$

(B.5)

Appendix C. Green’s function

This derivation follows that in [34], with the only difference being that, in this case, the domain is the outside of the unit disk $D$. Nevertheless, the mathematical details are identical. The fundamental solution of the biharmonic equation is

$$\Lambda(z, \xi) = \frac{1}{8\pi} |z - \xi|^2 \log |z - \xi|,$$

(C.1)

and the general solution of the biharmonic equation is

$$\Upsilon(z) = 2 \text{Re} [\bar{z} \Phi(z) + \Psi(z)],$$

(C.2)

where $\Phi$ and $\Psi$ are arbitrary analytic functions. Thus, the problem is to find a function of the form (C.2) that cancels (C.1) and its normal derivative on $\partial D$. To facilitate this, (C.2) can be equivalently written as

$$\Upsilon(z) = 2 \text{Re} [\bar{z}^2 - 1] \Phi(z) + \Psi(z).$$

(C.3)

Let $\Gamma(z, \xi) = \Lambda + \Upsilon$. Then, the condition $\Gamma = 0$ on $\partial D$ is equivalent to

$$\text{Re} [\Psi(z)] = -\frac{1}{8\pi} \log |z - \xi|$$

$$= \text{Re} \left\{ -\frac{1}{8\pi} \frac{1}{1 - \xi} \left( \frac{1}{z} - \frac{1}{\xi} - \log \left| \frac{1}{z} - \frac{1}{\xi} \right| \frac{1}{z} - \frac{1}{\xi} \right) \right\},$$

(C.4)

since $\bar{z} = \frac{1}{z}$ there. Since the equation inside the braces is analytic in the unit disk, it must be $\Psi(z)$. Additionally, the condition that $\Gamma = \frac{\partial \Phi}{\partial n} = 0$ on $\partial D$ implies $\frac{\partial \Phi}{\partial n} = 0$ there, and so

$$\frac{\partial \Gamma}{\partial z} = \frac{1}{8\pi} \frac{1}{1 - \xi} \log |z - \xi| \left| (z - \xi) \right| \frac{1}{z} - \frac{1}{\xi} \frac{1}{1 - \xi}$$

and

$$+ \frac{1}{16\pi} (\bar{z} - \bar{\xi}) \log |z - \xi| (\bar{z} - \bar{\xi}) = 0.$$
Substituting $\Psi$ yields
\[
\text{Re}(\Phi(z)) = \text{Re}\left\{ \frac{1}{16\pi} \left( 1 - \frac{\xi}{z} \right) \log(1 - \bar{z}) \right\},
\] (C.6)
and hence, using $\bar{z} = \frac{1}{z}$ on $\partial D$ once more,
\[
\Phi(z) = \frac{1}{16\pi} \left( 1 - \frac{\xi}{z} \right) \log(1 - \bar{z}) \log(1 - \bar{z}).
\] (C.7)

Thus,
\[
\Gamma(z, \zeta) = \frac{1}{8\pi} \left| z - \zeta \right|^2 \log \left| \frac{z - \zeta}{1 - \bar{z}z} \right| + \frac{1}{16\pi} (|\zeta|^2 - 1)(|\zeta|^2 - 1).
\] (C.8)

Parameter $\Gamma$ needs to be rescaled to suit a disc of radius $a$.

**Appendix D. Pressure**

By taking the divergence of (3), one obtains
\[
\begin{cases}
\Delta p_a = -\nabla \cdot \mathbf{c} \delta \eta_0 = -\frac{\partial}{\partial x} \delta \eta_0, \\
\nabla \cdot \mathbf{p}_a \cdot \hat{n} = \eta \Delta \mathbf{u} \cdot \hat{n} \quad \text{on } \partial \Omega.
\end{cases}
\]

Thus $p_a(x, y)$ is the real part of some function $\Pi(z)$, which is holomorphic in $\Omega$, such that $\Pi'(z) = \eta(\Delta u_x - i\Delta u_y)$ on $\partial \Omega$. In fact, viewing $u_x$ and $u_y$ as functions of $x$ and $y$,
\[
\Pi(z) = \eta \int_{\gamma} [\Delta u_x(X(\zeta), Y(\zeta)) - i\Delta u_y(X(\zeta), Y(\zeta))] \, d\zeta,
\] (D.2)
where $X(z) = \frac{1}{2}(z + \frac{1}{z})$, $Y(z) = \frac{1}{2}(z - \frac{1}{z})$, and $\gamma$ is any path from the origin to $z$. It is clear that $p_a = \text{Re}(\Pi)$ satisfies the compatibility condition and is harmonic, except where the integrand has singularities, so it remains to check that $\Delta \text{Re} \Pi(z) = -c^2 \frac{\partial}{\partial x} \delta \eta_0$. Performing the integration in (D.2) gives
\[
\Pi(z) = -\frac{1}{8\pi} \frac{c}{a^2} \frac{\lambda^2}{(1 + \lambda)(a(1 + \lambda) - z)(a(1 + \lambda) - z)^2}.
\] (D.3)

Taking the real part of (D.3) and expanding it about $x = a(1 + \lambda)$ yields
\[
p_a(r, \theta) = -\frac{\cos(\theta)}{2\pi r} + O(1),
\] (D.4)

thus, indeed, $\Delta p_a(r, \theta) = -c^2 \frac{\partial}{\partial x} \delta \eta_0$.

**Appendix E. Disturbance flow**

In terms of the stream function of the background flow, $\Psi_0(r, \theta) = r^2(\cos^2 \theta - \sin^2 \theta)$, the stream function for the disturbance flow $\tilde{\Psi}$, from [24], is given by
\[
\Psi = \frac{r^4 - 2r^2 \lambda^2}{a^4} \Psi_0 \left( \frac{a^2}{r}, \theta \right) + \frac{r^3}{a^3} (r^2 - a^2) \frac{\partial}{\partial r} \Psi_0 \left( \frac{a^2}{r}, \theta \right) - \frac{(r^2 - a^2)^2}{4a^4} \nabla^2 \left[ r^2 \Psi_0 \left( \frac{a^2}{r}, \theta \right) \right].
\] (E.1)

This yields the velocity
\[
\tilde{u}_p = \left( -\frac{1}{r} \frac{\partial \Psi}{\partial \varphi}, \frac{\partial \Psi}{\partial r} \right).
\] (E.2)

The corresponding pressure $p_p$ is, once more, the real part of
\[
\Pi(z) = \eta \int_{\gamma} [\Delta u_{p,x}(X(\zeta), Y(\zeta)) - i\Delta u_{p,y}(X(\zeta), Y(\zeta))] \, d\zeta.
\] (E.3)

Performing this integration gives
\[
p_p(x, y) = -c^2 \eta \frac{a^2 \eta x y}{r^4}.
\] (E.4)

**Appendix F. Glossary**

This paper addresses effects of the activity of self-propelled particles on the effective viscosity of the suspension of the said particles in the ambient Stokesian Newtonian fluid (e.g., water). Here we explain some of the main terms pertaining to this topic.

- **Effective viscosity** $\eta^*$ is defined in this paper for a suspension as a scalar quantity that characterizes the average rate of energy dissipation in a volume of the suspension. $\eta^*$ is the viscosity of an equivalent homogeneous Stokesian Newtonian fluid, that is, a fluid without inclusions with the same dissipation rate as the suspension. Observe that as defined here apparent viscosity does not characterize the constitutive relation for the suspension, which is typically non-Newtonian and is given by a rheological effective viscosity tensor.

- **Rheological effective viscosity** of a suspension is a tensor $\Theta^*$ relating the bulk stress and strain-rate tensors. In a Newtonian suspension $\Theta^* = \eta^* I$, where $I$ is a rank-4 identity tensor.

- A Stokesian fluid is a fluid governed by the (steady-state) Stokes equation. It is an ideal model of a fluid at a low Reynolds number, that is when the inertial effects are dominated by viscous effects.

- A Newtonian fluid is a fluid whose stress at each point is linearly proportional to its strain rate at that point.

- Suspension denotes a collection of insoluble inclusions in a fluid, such as water.

- Active suspension denotes a suspension of self-propelled inclusions, such as bacteria.

©U.S. Govt

**References**

[1] Wu X-L and Libchaber A 2000 Particle diffusion in a quasi-two-dimensional bacterial bath Phys. Rev. Lett. **84** 3017

[2] Kim M J and Breuer K S 2004 Enhanced diffusion due to motile bacteria Phys. Fluids **16** 78

[3] Mendelson N H et al 1999 Organized cell swimming motions in Bacillus subtilis colonies: patterns of short-lived whirls and jets J. Bacteriol. **181** 600

[4] Dombrowski C et al 2004 Self-concentration and large-scale coherence in bacterial dynamics Phys. Rev. Lett. **93** 098103

[5] Riedel I H, Kruse K and Howard J 2005 A self-organized vortex array of hydrodynamically entrained sperm cells Science **309** 300
[6] Becco Ch et al 2006 Experimental evidences of a structural and dynamical transition in fish school Physica A 367 487
Buhl J et al 2006 From disorder to order in marching locusts Science 312 1402
[7] Feder T 2007 Statistical physics is for the birds Phys. Today p 28
[8] Toner J and Tu Y 1995 Long-range order in a two-dimensional dynamical XY model: how birds fly together Phys. Rev. Lett. 75 4326
[9] Grégoire G and Chaté H 2004 Onset of collective and cohesive motion Phys. Rev. Lett. 92 025502
[10] Vicsek T, Czirók A, Ben-Jacob E, Cohen I and Shochet O 1995 Novel type of phase transition in a system of self-driven particles Phys. Rev. Lett. 75 1226
Czirók A, Stanley H E and Vicsek T 1997 Spontaneously ordered motion of self-propelled particles J. Phys. A: Math. Gen. 30 1375
[11] Grossman D, Aranson I S and Ben-Jacob E 2008 Emergence of agent swarm migration and vortex formation through inelastic collisions New J. Phys. 10 023036
[12] Simha R A and Ramaswamy S 2002 Hydrodynamic fluctuations and instabilities in ordered suspensions of self-propelled particles Phys. Rev. Lett. 89 058510
[13] Kim M J and Breuer K S 2007 Use of bacterial carpets to enhance mixing in microfluidic systems J. Fluids Eng. 129 319
[14] Sokolov A, Aranson I S, Kessler J O and Goldstein R E 2007 Concentration dependence of the collective dynamics of swimming bacteria Phys. Rev. Lett. 98 158102
[15] Einstein A 1956 Investigations on the Theory of the Brownian Movement (New York: Dover)
[16] Batchelor G K and Green J T 1972 The determination of the bulk stress in a suspension of spherical particles to order c^2 J. Fluid Mech. 56 401–27
[17] Jeffery G B 1922 The motion of ellipsoidal particles immersed in a viscous fluid Proc. R. Soc. Lond. A 102 161–79
[18] Hinch E and Leal L 1972 The effect of Brownian motion on the rheological properties of a suspension of non-spherical particles J. Fluid Mech. 52 683–712
[19] Brady J 1983 The Einstein viscosity correction in n dimensions Int. J. Multiph. Flow 10 113–4
[20] Belzons M, Blanc R, Bouillot J L and Camoin C 1981 Viscosité d’une suspension diluée et bidimensionnelle de sphères C. R. Acad. Sci., Paris II 292 939–44
[21] Batchelor G K 1967 An Introduction to Fluid Dynamics (Cambridge: Cambridge University Press)
[22] Landau L D and Lifshitz E M 1987 Fluid Mechanics (Oxford: Elsevier)
[23] Levy T and Sanchez-Palencia E 1983 Suspension of solid particles in a Newtonian fluid J. Non-Newton. Fluid Mech. 13 63–78
[24] Avudainayagam A and Jothiram B 1988 A circle theorem for plane Stokes flows Q. J. Mech. Appl. Math. 41 383–93
[25] Pedley T J and Kessler J O 1992 Hydrodynamic phenomena in suspensions of swimming microorganisms Annu. Rev. Fluid Mech. 24 313–58
[26] Sokolov A and Aranson I S 2009 in preparation
[27] Hernandez-Ortiz J P, Stoltz Ch G and Graham M D 2005 Transport and collective dynamics in suspensions of confined swimming particles Phys. Rev. Lett. 95 204501
[28] Ishikawa T and Pedley T J 2008 Coherent structures in monolayers of swimming particles Phys. Rev. Lett. 100 088103
[29] Underhill P T, Hernandez-Ortiz J P and Graham M D 2008 Diffusion and spatial correlations in suspensions of swimming particles Phys. Rev. Lett. 100 248101
[30] Llopis I and Pagonabarraga I 2006 Dynamic regimes of hydrodynamically coupled self-propelling particles Europhys. Lett. 75 pp 999–1005
[31] Batchelor G 1970 The stress system in a suspension of force-free particles J. Fluid Mech. 41 pp 545–70
[32] Hatwalne Y, Ramaswamy S, Rao M and Simha R A 2004 Rheology of active-particle suspensions Phys. Rev. Lett. 92 118101
[33] Ishikawa T and Pedley T J 2007 The rheology of a semi-dilute suspension of swimming model microorganisms J. Fluid Mech. 588 399
[34] Garabedian P R 1964 Partial Differential Equations (New York: Wiley)