

# Effective Viscosity of Dilute Bacterial Suspensions: A Two-Dimensional Model

Brian M. Haines<sup>1</sup>, Igor S. Aranson<sup>2</sup>, Leonid Berlyand<sup>1</sup>, Dmitry A. Karpeev<sup>3</sup>

<sup>1</sup> Department of Mathematics, Pennsylvania State University, 418 McAllister Building, University Park, PA 16802

<sup>2</sup> Materials Science Division, Argonne National Laboratory, 9700 South Cass Avenue, Argonne, IL 60439

<sup>3</sup> Mathematics and Computer Science Division, Argonne National Laboratory, 9700 South Cass Avenue, Argonne, IL 60439

**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.

PACS numbers: 87.16.-b, 05.65.+b, 87.17.Jj

## 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, 2, 3, 4, 5, 6]. Properties of these strongly self-organizing dissipative systems are of fundamental interest to nonequilibrium statistical mechanics [7, 8, 9, 10, 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  $5 \mu m$ , diameter of the order  $1 \mu m$ ), 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 whorls and jets with the spatial scale exceeding the size of 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 non-linear.

\*\*\*\*\* While it is obvious that for ellipsoidal particles the eff viscosity is tensor, it is not at all obvious why the constitutive relation should be non linear, requires some explanation\*\*\*\*\*

In particular, 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 a relation between rates of energy dissipation.\*\*\*

\*\*\*\*\*Non quite clear what is full rheology as oppose to just effective viscosity. What do you mean “effective viscosity as a relation between rates of energy dissipation”, do you mean ”defined as a relation between rates of energy dissipation” specify which rates. Here the referee may ask is it legitimate to define effective viscosity like that for NON Newtonian fluid, I suggest that you discuss this question with Igor. This is a very important point where our paper may be volnurable: we have to justify the definition of effective viscosity which we use, otherwise a critique can say that we computed something which is not really effective viscosity. Bottom line here: we need to clearly justify our definition of effective viscosity why it is relevant in NONnewtonian case, here erelevancy may mean why it would describe the experimental observations\*\*\*\*\*

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., [18]).

The model of the bacterium and the corresponding hydrodynamics are described in Section 2. Following Batchelor [19], 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  $u'_a$  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., [21]). 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 time-dependent nature of the effective viscosity, arising from the evolution of this distribution due to the active alignment of the inclusions to the flow, is also discussed. Conclusions are discussed in Section 5. Finally, the details of calculations are discussed 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

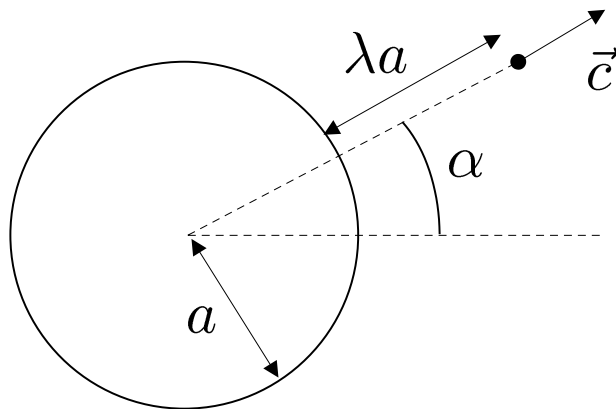
the center of the bacterium and has some orientation angle  $\alpha$ , measured from the  $x$ -axis. The bacteria are distributed throughout an ambient fluid of viscosity  $\eta$  which takes up the entire domain  $\mathbb{R}^2$ . A single bacterium in an infinite fluid moves with respect to the fluid 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 [19], the effective viscosity  $\eta^*$  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  $\eta^*$  is a classical result of homogenization theory (see e.g., [20] 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 it was done for passive particles. Namely,  $\eta^*$  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 [19] 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 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  $\vec{u}'$ . Provided that  $\epsilon$  is selected properly,  $\vec{u}'$  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



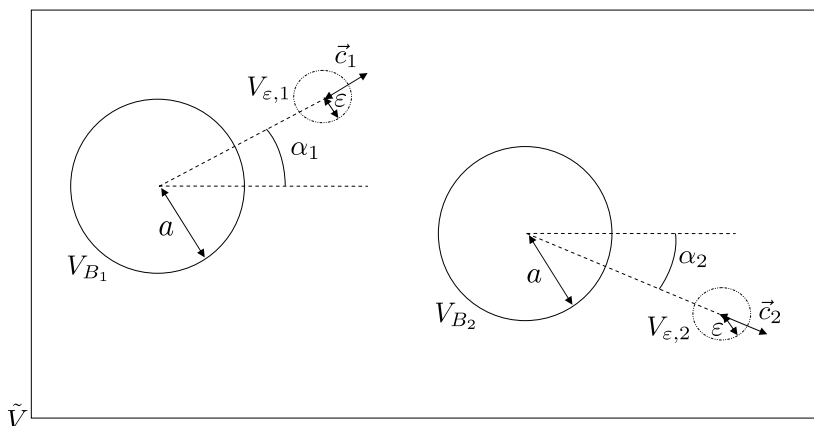
**Figure 1.** Schematic presentation of a bacterium with orientation  $\alpha$ .

total flow of the suspension is  $\vec{u} = \vec{u} + \vec{u}'$  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 [19], 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  $\tilde{V}$  which contains sufficiently many bacteria and passing to the dilute limit later.

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

The disturbance flow in the domain  $\tilde{V} - \sum_l V_{B_l} - \sum V_{\varepsilon,l}$  is required to vanish at the outer boundary  $\partial\tilde{V}$ . This models a finite container with the background flow applied



**Figure 2.** Bounded domain  $\tilde{V}$  for which the modified dissipation rate is computed; includes the complement of two  $a$ -disks (bacteria) and  $\varepsilon$ -disks (neighborhoods of point forces).

at the boundary and the disturbance flow vanishing there.

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

$$\int_{\partial V} \sigma_{ij} u_i n_j dA = \int_{\partial V} \tilde{\sigma}_{ij} \tilde{u}_i n_j dA. \quad (1)$$

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  $\partial\tilde{V}$  can be reduced to integrals over the boundary of the bacterial domain only:  $\partial V_b + \partial V_\epsilon$ . The domain of integration of these integrals is independent of  $\partial\tilde{V}$  and upon passing to the limit  $\tilde{V} \rightarrow \mathbb{R}^2$  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:

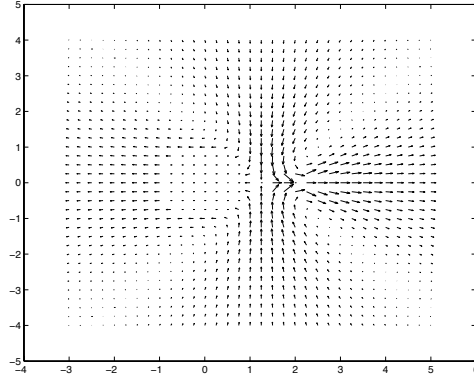
$$\begin{aligned} & 2(\eta^* - \eta) \epsilon_{ij} \epsilon_{ij} \\ &= \frac{\epsilon_{ik}}{A} \sum_l \int_{\partial V_{B_l} \cup \partial V_{\epsilon,l}} (\sigma'_{ij} x_k n_j - 2\eta u'_i n_k) dA. \end{aligned} \quad (2)$$

### 3. Flow due to a single bacterium

Let  $\Omega$  be the exterior of the unit disk in  $\mathbb{R}^2$  and  $\delta_{\vec{r}_0}$  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

$$\begin{cases} \eta \Delta \vec{u}'_a = \nabla p'_a + \vec{c} \delta_{\vec{r}_0} & \text{in } \Omega \\ \nabla \cdot \vec{u}'_a = 0 & \text{in } \Omega \\ \vec{u}'_a = 0 & \text{on } \partial\Omega \end{cases}, \quad (3)$$

where  $\vec{c}$  is the force strength and  $\partial\Omega$ . For simplicity of calculations, set  $\vec{c} = c\hat{x}$  and  $\vec{r}_0 = (1 + \lambda)\hat{x}$ . Note that here,  $\vec{u}'_a$  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.



**Figure 3.** Velocity field produced by a bacterium moving from right to left in 2D geometry.

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

$$\begin{cases} \Delta^2 \Phi(x, y) = \frac{\partial}{\partial y} \frac{c}{\eta} \delta_{\vec{r}_0} & \text{in } \Omega \\ \Phi = \frac{\partial \Phi}{\partial n} = 0 & \text{on } \partial \Omega \end{cases} \quad (4)$$

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

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

Explicitly, in polar coordinates,

$$\begin{aligned} \Phi(r, \theta) = & \quad (6) \\ & \frac{cr \cos(\theta)}{8\pi\eta} \left[ \frac{((1 + \lambda)^2 - 1)(r^2 - 1)}{1 + (1 + \lambda)^2 r^2 - 2(1 + \lambda)r \cos(\theta)} \right. \\ & \left. + \log \left( \frac{(1 + \lambda)^2 + r^2 - 2(1 + \lambda)r \cos(\theta)}{1 + (1 + \lambda)^2 r^2 - 2(1 + \lambda)r \cos(\theta)} \right) \right]. \end{aligned}$$

It is easy to see that  $u'_a \rightarrow u_\infty = \text{const}$  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

$$\begin{aligned} \vec{u}(r, \theta) = & \quad (7) \\ & \left( \begin{array}{l} \frac{ca^2\lambda^2(2+\lambda)^2}{8\pi\eta(1+\lambda)^3} \frac{1}{r} (\cos(\theta) + \cos(3\theta)) + O\left(\frac{1}{r^2}\right) \\ \frac{ca^2\lambda^2(2+\lambda)^2}{8\pi\eta(1+\lambda)^3} \frac{1}{r} (\cos(2\theta) \sin(\theta)) + O\left(\frac{1}{r^2}\right) \end{array} \right). \end{aligned}$$

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

$$\begin{cases} \Delta p = -c \frac{\partial}{\partial x} \delta_{\vec{r}_0} & \text{in } \Omega \\ \nabla p \cdot \hat{n} = \eta \Delta \vec{u} \cdot \hat{n} & \text{on } \partial \Omega \end{cases} \quad (8)$$

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

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

#### 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  $p'$  are the solutions to

$$\begin{cases} \eta \Delta \vec{u}' = \nabla p' + \vec{c} \delta_{\vec{r}_0} \\ \nabla \cdot \vec{u}' = 0 \end{cases} \quad (10)$$

subject to the boundary conditions

$$\begin{aligned} u'_i &\rightarrow \epsilon_{ij} x_j \quad \text{as } r \rightarrow \infty \\ \vec{u}' &= \text{const} \quad x \in \partial\Omega. \end{aligned} \quad (11)$$

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 (except for the effect of particle orientation, which will be seen) because the bacterium would rotate rigidly with the background flow and produce no additional dissipation.\*\*\*

\*\*\*\*\* (except for the effect of particle orientation, which will be seen) –not clear what it means, looks like it would alter viscosity due to particle orientation, then why this is not important – a clarification is needed.\*\*\*\*\*

Third, upon placing a disk (i.e., bacterium) in the flow, it is necessary that the disturbance flow  $\vec{u}'_p \rightarrow 0$  as  $r \rightarrow \infty$ . If this were not the case, the dilute assumption that this flow is negligible at the locations of other bacteria would be violated. In 2D, this is only possible for a background flow that satisfies the conditions for existence of such a decaying flow derived in [22]. The background flow is chosen to be the simplest flow that matches these criteria—the sum of two perpendicular shearing flows,

$$\epsilon = 2\epsilon_0 \begin{pmatrix} 0 & 1 \\ 1 & 0 \end{pmatrix}. \quad (12)$$

where  $\epsilon_0 = \text{const}$  is the amplitude of the strain rate.



The disturbance flow due to the presence of a bacterium will be

$$\vec{u}' = \vec{u}'_a(\alpha) + \vec{u}'_p \quad (13)$$

with the pressure given by

$$p' = p'_a(\alpha) + p'_p \quad (14)$$

where, using notation,  $\vec{u}'_a(\alpha) := \vec{u}'_a(r, \theta - \alpha)$  as a polar vector and  $p'_a(\alpha) := p'_a(r, \theta - \alpha)$ , rotated to allow for an arbitrary orientation of a bacterium in the background flow.

For a suspension of bacteria that are not fully aligned, the effective viscosity can be written in terms of the function  $P(\alpha)$  which gives the probability density of orientations of the bacteria  $\alpha_l$ , which are assumed to be independent identically distributed random variables. In this case, (2) becomes

$$\begin{aligned} 2(\eta^* - \eta)\epsilon_{ij}\epsilon_{ij} = & \quad (15) \\ \epsilon_{ik}\phi \int_0^{2\pi} \int_{\partial V_B \cup \partial V_\varepsilon} & (\sigma'_{ij}(\alpha)x_k n_j \\ - 2\eta u'_i(\alpha)n_k) dA & P(\alpha)d\alpha, \end{aligned}$$

where  $\phi$  is the volume fraction occupied by bacteria. Performing the integration over  $\partial V_B \cup \partial V_\varepsilon$  and passing to the limit  $\varepsilon \rightarrow 0$ , one obtains the following formula for the effective viscosity:

$$\begin{aligned} \eta^* = \eta [1 + 2\phi & \quad (16) \\ + \frac{c}{2\pi\eta\epsilon_0} \frac{1 + 2\lambda(2 + \lambda)}{(1 + \lambda)^3} \phi \int_0^{2\pi} & \sin(2\alpha) P(\alpha)d\alpha], \end{aligned}$$

where  $\phi$  is the two-dimensional volume fraction.

Note that for isotropically oriented bacteria ( $P(\alpha) = 1/2\pi = \text{const}$ ), the angular term goes to zero and the effective viscosity reduces to the result in [18] for the effective viscosity of a two-dimensional dilute suspension of disks,

$$\eta^* = \eta(1 + 2\phi). \quad (17)$$

Nevertheless, using heuristic arguments (see [23]) and in preliminary experiments ([24]), a reduction in viscosity is anticipated. In reality, bacteria are not spherical. An interaction with the background flow thus produces a torque on the bacteria which will tend to align them in particular preferred directions (see e.g. [25]). For a fully aligned suspension of bacteria, one obtains, from (16),

$$\eta^* = \eta \left[ 1 + 2\phi + \frac{c}{2\pi\eta\epsilon_0} \frac{1 + 2\lambda(2 + \lambda)}{(1 + \lambda)^3} \phi \sin 2\alpha \right]. \quad (18)$$

For the background flow (12), the corresponding preferred directions are  $\alpha = -\frac{\pi}{4}, \frac{3\pi}{4}$ . Thus, after aligning,

$$\eta^* = \eta \left[ 1 + 2\phi - \frac{c}{2\pi\eta\epsilon_0} \frac{1 + 2\lambda(2 + \lambda)}{(1 + \lambda)^3} \phi \right]. \quad (19)$$

This formula can be used to explain the experimental data on the reduction of viscosity in bacterial suspensions observed in [24].

\*\*\*\*\* the following correction needs to be discussed\*\*\*\*\* \*\*\*In fact, experimental observations on bacterial suspensions made in [14] can be construed as manifestations of a *negative* effective viscosity. This includes the formation of non-decaying whorls and jets of collective locomotion (see also simulations [27, 28, 29, 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.

\*\*\*\*\* modes get destabilized and saturate at large-scale coherent structures— not clear\*\*\*\*\*

This effect is best illustrated with a linear scalar model of the form

$$v_t = \eta^* \Delta v - \beta \Delta^2 v.$$

Here the growth rate for the  $k$ -th 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 ( $|k| < \sqrt{|\eta^*|/|\beta|}$ ) are destabilized.

\*\*\*\*\* what precisely means destabilized here? do you simply mean growth (nondecay)? if so then just say it or explain\*\*\*\*\*

It is also notable that the coefficient  $\epsilon_0$ , which characterizes the strength of the background flow, appears in formulas (16) and (19) for the effective viscosity, unlike in a Newtonian fluid. However, it must be noted that the probability distribution  $P(\alpha)$  depends on  $\epsilon_0$  as well, which affects the overall dependence on  $\epsilon_0$ . Indeed, bacteria are not perfectly spherical and will tend to align to the principal axes of the shear flow. At the same time, random effects, such as tumbling will counteract this alignment, attempting to drive the system to the isotropic state. The overall steady-state distribution  $P(\alpha)$  will depend on the relative strength of these two effects.

For  $\epsilon_0$  relative to the noise strength \*\*\*\*\*not cleat what means relative here, be more specific, relative means larger? explain what is noise strength\*\*\*\*\*

random effects \*\*\*\*\* such as .....\*\*\*\*\*

dominate the alginment of aspherical bacteria to the flow. In this case we can expect (see [31] for more general results)

$$P(\alpha) = \frac{1}{2\pi} + P_1(\alpha)\epsilon_0 + P_2(\alpha)\epsilon_0^2 \dots \tag{20}$$

Since the zeroth order term denotes an isotropic distribution of orientations, it integrates to zero in (16). The next order term  $\epsilon_0 P_1$  cancels  $\epsilon_0$  in the denominator and to the leading order in  $\epsilon_0$  the suspension exhibits a linear response (quasi-Newtonian, in Batchelor’s terminology; see [32]). In particular, in the limit of  $\epsilon_0 \rightarrow 0$ , the steady state is in fact an isotropically oriented suspension  $P(\alpha) = 1/2\pi$ , which recovers the classical result for disks Eq. (17). On the other hand, for  $\epsilon_0$  large relative to the noise strength, an expansion such as (20) will not hold and, thus, the non-Newtonian effects suggested by (19) will be strong. Furthermore, since that equation, which assumes complete

alignment, is only valid for values of  $\epsilon_0$  large relative to the diffusive random effects, one cannot use it to infer a blow up in  $\eta^*$  as  $\epsilon_0 \rightarrow 0$ .

The dependence of effective viscosity on orientation can also 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 results 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).\*\*\* \*\*\*\*\* here the reader may be confused, since it looks like we only consider spherical particles nevertheless we see decrease to the first order— this is ket point and worth of clear explanation\*\*\*

## 5. Conclusion and Outlook

Here a rather puzzling result has been obtained: the effective viscosity of active bacterial suspension *may decrease* with the increase in volume fraction of particles. The reduction of effective viscosity can be interpreted as a result of transformation by swimming bacteria of chemical energy of the surrounding nutrient medium into mechanical energy of fluid motion, and thus replacing energy loss due to viscous dissipation. Moreover, the viscosity may even become formally negative (when the flagella add more energy than is being due to viscous effects dissipated) if the volume fraction  $\phi$  and the magnitude of the propulsion force  $c$  exceed critical values.

Obviously, more dedicated controlled experiments with bacterial suspensions and further generalizations of the obtained result to more general flow geometries, such as three-dimensional films and slabs, are keenly needed. Additionally, analysis of more dense suspension and direct 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 L. Berlyand was partially supported by NSF grant DMS-0708324. I.S. Aranson and D. Karpeev were supported by US DOE, grant DOE grant DE-AC02-06CH11357. We would also like to thank Andrey Sokolov, Sriram Ramaswamy, Raymond Goldstein, and Michael Graham. \*\*\*\*\* usually it says thanks for what, e.g., useful discussions, suggestions\*\*\*

## Appendix A. Calculation of Dissipation Rate and Definition of Effective Viscosity

Following [19], the rate of work being done at the boundary  $\partial\Omega$  is given by

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

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  $\tilde{\sigma}_{ij} = \sigma_{ij} + \sigma'_{ij}$ . Additionally, on  $\partial\Omega$ ,  $e_{ij} = \epsilon_{ij}$ . Thus, the effective viscosity of the suspension  $\eta^*$  is defined by setting

$$\begin{aligned} \epsilon_{ik} \int_{\partial\Omega} (-p\delta_{ij} + 2\eta^* \epsilon_{ij}) x_k n_j dA = \\ \epsilon_{ik} \int_{\partial\Omega} (-p\delta_{ij} + 2\eta \epsilon_{ij} + \sigma'_{ij}) x_k n_j dA. \end{aligned} \quad (\text{A.2})$$

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

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

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

$$\begin{aligned} \epsilon_{ik} \int_{\partial\Omega} \sigma'_{ij} x_k n_j dA = \\ \epsilon_{ik} \int_{\Omega - \sum V_B \cup V_\epsilon} \left( \frac{\partial \sigma'_{ij}}{\partial x_j} x_k + \sigma'_{ik} \right) dV \\ + \epsilon_{ik} \sum \int_{\partial V_B \cup \partial V_\epsilon} \sigma'_{ij} x_k n_j dA, \end{aligned} \quad (\text{A.4})$$

where  $V_B$  is the volume occupied by a single bacterium,  $V_\epsilon$  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

$$\begin{cases} \eta \Delta \vec{u}' = \nabla p' + \sum_l \vec{c}_l \delta_{\vec{r}_l} & \text{in } \Omega - \sum_l V_{B_l} \\ \nabla \cdot \vec{u}' = 0 & \text{in } \Omega - \sum_l V_{B_l} \\ \vec{u}' = \vec{v}_l & \text{on } \partial V_{B_l} \\ \vec{u}' = \epsilon_{ij} x_j & \text{on } \partial\Omega \end{cases}, \quad (\text{A.5})$$

where the subscript  $l$  has been added to all quantities that can vary among the bacteria. In particular,  $\vec{v}_l$  is its velocity of the  $l$ th bacterium,  $\vec{r}_l$  is the location of its point force, and  $\vec{c}_l$  indicates the strength and orientation of each point force. Thus,  $\frac{\partial \sigma'_{ij}}{\partial x_j} = 0$  in

$\Omega - \sum V_B \cup V_\epsilon$ . Additionally,

$$\begin{aligned}
 & \epsilon_{ik} \int_{\Omega - \sum V_B \cup V_\epsilon} \sigma'_{ik} dV \\
 &= \epsilon_{ik} \int_{\Omega - \sum V_B \cup V_\epsilon} 2\eta \frac{\partial u'_i}{\partial x_k} dV \\
 &= -\epsilon_{ik} \sum \int_{\partial V_B \cup \partial V_\epsilon} 2\eta u'_i n_k dA,
 \end{aligned} \tag{A.6}$$

since the surface integral over  $\partial\Omega$  vanishes. Applying these observations to (A.3) produces

$$\begin{aligned}
 & 2(\eta^* - \eta)\epsilon_{ij}\epsilon_{ij} \\
 &= \frac{\epsilon_{ik}}{A} \sum_l \int_{\partial V_{B_l} \cup \partial V_{\epsilon,l}} (\sigma'_{ij} x_k n_j - 2\eta u'_i n_k) dA.
 \end{aligned} \tag{A.7}$$

## Appendix B. Velocity

Recall that the velocity field  $\vec{u}$  solves the Stokes equation,

$$\begin{cases} \eta \Delta \vec{u} = \nabla p + \vec{c} \delta_{\vec{r}_0} & \text{in } \Omega \\ \nabla \cdot \vec{u} = 0 & \text{in } \Omega \\ \vec{u} = 0 & \text{on } \partial\Omega \end{cases}. \tag{B.1}$$

For simplicity, it is assumed that  $\vec{c} = c\hat{x}$  and  $\vec{r}_0 = (\lambda + 1)\hat{x}$ . Since  $\nabla \cdot \vec{u} = 0$ , 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 by

$$\text{Curl}_V \Phi(x, y) = \begin{pmatrix} \frac{\partial \Phi}{\partial y} \\ -\frac{\partial \Phi}{\partial x} \end{pmatrix}.$$

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

$$\text{Curl}_S \vec{u} = \frac{\partial u_x}{\partial y} - \frac{\partial u_y}{\partial x}$$

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

$$\Delta^2 \Phi(x, y) = \text{Curl}_S \frac{c}{\eta} \hat{x} \delta_{\vec{r}_0} = \frac{\partial}{\partial y} \frac{c}{\eta} \delta_{\vec{r}_0} \tag{B.2}$$

with boundary conditions

$$\Phi = \frac{\partial \Phi}{\partial n} = 0 \text{ on } \partial\Omega. \tag{B.3}$$

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 Appendix C), and has

a simple form as a function of the complex variables  $z = x + iy$  and  $\zeta = \xi + i\gamma$ , taken from [26]:

$$\begin{aligned} \Gamma(z, \zeta) &= \frac{1}{8\pi} |z - \zeta|^2 \log \left| \frac{z - \zeta}{1 - \bar{\zeta}z} \right| \\ &+ \frac{1}{16\pi} (|z|^2 - 1) (|\zeta|^2 - 1). \end{aligned} \quad (\text{B.4})$$

This yields the solution formula

$$\begin{aligned} \Phi(x, y) &= \int_{\Omega} \Gamma(x + iy, \xi + i\gamma) \frac{\partial}{\partial \gamma} \frac{c}{\eta} \delta_{\vec{r}_0}(\xi, \gamma) d\xi d\gamma \\ &= -\frac{c}{\eta} \int_{\Omega} \frac{\partial}{\partial \gamma} \Gamma(x + iy, \xi + i\gamma) \delta_{\vec{r}_0} d\xi d\gamma \end{aligned}$$

and hence

$$\Phi(x, y) = -\frac{c}{\eta} \frac{\partial \Gamma}{\partial \gamma}(x + iy, 1 + \lambda). \quad (\text{B.5})$$

### Appendix C. Green's Function

This derivation follows that in [26], 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

$$\Lambda(z, \zeta) = \frac{1}{8\pi} |z - \zeta|^2 \log |z - \zeta|, \quad (\text{C.1})$$

and the general solution of the biharmonic equation is

$$\Upsilon(z) = 2\text{Re} \{ \bar{z}\Phi(z) + \Psi(z) \}, \quad (\text{C.2})$$

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

$$\Upsilon(z) = 2\text{Re} \{ [z^2 - 1] \Phi(z) + \Psi(z) \}. \quad (\text{C.3})$$

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

$$\begin{aligned} \text{Re} \{ \Psi(z) \} &= -\frac{1}{8\pi} (z - \zeta)(\bar{z} - \bar{\zeta}) \log |z - \zeta| \\ &= \text{Re} \left\{ -\frac{1}{8\pi} (z - \zeta) \left( \frac{1}{z} - \bar{\zeta} \right) \log(1 - \bar{\zeta}z) \right\}, \end{aligned} \quad (\text{C.4})$$

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  $\Gamma = \frac{\partial \Gamma}{\partial n} = 0$  on  $\partial D$  implies  $\frac{\partial \Gamma}{\partial x} = \frac{\partial \Gamma}{\partial y} = 0$  there, and so

$$\begin{aligned} \frac{\partial \Gamma}{\partial z} &= \bar{z} \text{Re} \{ \Phi(z) \} + \frac{1}{2} \Psi'(z) + \frac{1}{16\pi} (\bar{z} - \bar{\zeta}) \\ &+ \frac{1}{16\pi} (\bar{z} - \bar{\zeta}) \log(z - \zeta)(\bar{z} - \bar{\zeta}) = 0. \end{aligned} \quad (\text{C.5})$$

Substituting  $\Psi$  yields

$$\begin{aligned} \operatorname{Re}\{\Phi(z)\} &= \\ \operatorname{Re}\left\{\frac{|\zeta|^2 - 1}{16\pi} - \frac{1}{8\pi}\left(1 - \frac{\zeta}{z}\right)\log(1 - \bar{\zeta}z)\right\}, \end{aligned} \quad (\text{C.6})$$

and hence, using  $\bar{z} = \frac{1}{z}$  on  $\partial D$  once more,

$$\Phi(z) = \frac{|\zeta|^2 - 1}{16\pi} - \frac{1}{8\pi}\left(1 - \frac{\zeta}{z}\right)\log(1 - \bar{\zeta}z). \quad (\text{C.7})$$

Thus,

$$\begin{aligned} \Gamma(z, \zeta) &= \frac{1}{8\pi} |z - \zeta|^2 \log\left|\frac{z - \zeta}{1 - \bar{\zeta}z}\right| \\ &+ \frac{1}{16\pi} (|z|^2 - 1)(|\zeta|^2 - 1). \end{aligned} \quad (\text{C.8})$$

## Appendix D. Pressure

By taking the divergence of (3), one obtains

$$\begin{cases} \Delta p = -\nabla \cdot c\hat{x}\delta_{\vec{r}_0} = -c\frac{\partial}{\partial x}\delta_{\vec{r}_0} \\ \nabla p \cdot \hat{n} = \eta\Delta\vec{u} \cdot \hat{n} \text{ on } \partial\Omega \end{cases}. \quad (\text{D.1})$$

Thus  $p(x, y)$  is the real part of some function  $\Pi(z)$ , which is holomorphic in  $\Omega^c$ , 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  $y$ ,

$$\begin{aligned} \Pi(z) &= \eta \int_{\gamma} [\Delta u_x(X(\zeta), Y(\zeta)) \\ &- i\Delta u_y(X(\zeta), Y(\zeta))] d\zeta, \end{aligned} \quad (\text{D.2})$$

where  $X(z) = \frac{1}{2}(z + \frac{1}{z})$ ,  $Y(z) = \frac{1}{2i}(z - \frac{1}{z})$ , and  $\gamma$  is any path from the origin to  $z$ . It is clear that  $p = \operatorname{Re}(\Pi)$  satisfies the compatibility condition and is harmonic, except where the integrand has singularities, so it remains to check that  $\Delta \operatorname{Re}\Pi(z) = -c\frac{\partial}{\partial x}\delta_{\vec{r}_0}$ . Performing the integration in (D.2) gives

$$\Pi(z) = \frac{-c}{2\pi} \frac{a^2\lambda^2(2 + \lambda)^2 z}{(1 + \lambda)(a(1 + \lambda) - z)((1 + \lambda)z - a)^2}. \quad (\text{D.3})$$

Taking the real part of (D.3) and expanding it about  $x = a(1 + \lambda)$  yields

$$p(r, \theta) = c\frac{\cos(\theta)}{2\pi r} + O(1), \quad (\text{D.4})$$

thus, indeed,  $\Delta p(r, \theta) = -c\frac{\partial}{\partial x}\delta_{\vec{r}_0}$ .

## 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  $\vec{u}_d$ , from [22], is given by

$$\begin{aligned} \Psi = & \frac{r^4 - 2r^2a^2}{a^4} \Psi_0 \left( \frac{a^2}{r}, \theta \right) \\ & + \frac{r^3}{a^4} (r^2 - a^2) \frac{\partial}{\partial r} \Psi_0 \left( \frac{a^2}{r}, \theta \right) \\ & - \frac{(r^2 - a^2)^2}{4a^4} \nabla^2 \left[ r^2 \Psi_0 \left( \frac{a^2}{r}, \theta \right) \right]. \end{aligned} \quad (\text{E.1})$$

This yields the velocity

$$\vec{u}_d = \begin{pmatrix} -\frac{1}{r} \frac{\partial \Psi}{\partial \theta} \hat{r} \\ \frac{\partial \Psi}{\partial r} \hat{\theta} \end{pmatrix}. \quad (\text{E.2})$$

The corresponding pressure  $p_d$  is, once more, the real part of

$$\begin{aligned} \Pi(z) = & \eta \int_{\gamma} [\Delta u_{d,x}(X(\zeta), Y(\zeta)) \\ & - i \Delta u_{d,y}(X(\zeta), Y(\zeta))] d\zeta. \end{aligned} \quad (\text{E.3})$$

Performing this integration gives

$$p_d(x, y) = -\frac{16a^2 \eta xy}{r^4}. \quad (\text{E.4})$$

## 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 suspensions  $\Theta^* = \eta^* I$ , where  $I$  is a rank-4 identity tensor.
- 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.



- 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.

- [1] X.-L. Wu and A. Libchaber, *Particle Diffusion in a Quasi-Two-Dimensional Bacterial Bath*, Phys. Rev. Lett. **84**, 3017 (2000).
- [2] M.J. Kim and K.S. Breuer, *Enhanced diffusion due to motile bacteria*, Phys. Fluids, **16**, 78 (2004)
- [3] N.H. Mendelson *et al.*, *Organized Cell Swimming Motions in Bacillus subtilis Colonies: Patterns of Short-Lived Whirls and Jets*, J. Bacteriol. **181**, 600 (1999).
- [4] C. Dombrowski *et al.*, *Self-Concentration and Large-Scale Coherence in Bacterial Dynamics*, Phys. Rev. Lett. **93**, 0980103 (2004).
- [5] I.H. Riedel, K. Kruse, and J. Howard, *A Self-Organized Vortex Array of Hydrodynamically Entrained Sperm Cells*, Science **309**, 300 (2005).
- [6] Ch. Becco *et al.*, *Experimental evidences of a structural and dynamical transition in fish school*, Physica (Amsterdam) **A367**, 487 (2006); J. Buhl *et al.*, *From Disorder to Order in Marching Locusts*, Science **312**, 1402 (2006).
- [7] T. Feder, *Statistical Physics is for the Birds*, Physics Today, p. 28, Oct 2007
- [8] J. Toner and Y. Tu, *Long-Range Order in a Two-Dimensional Dynamical XY Model: How Birds Fly Together*, Phys. Rev. Lett **75**, 4326 (1995).
- [9] G. Grégoire and H. Chaté, *Onset of Collective and Cohesive Motion* Phys. Rev. Lett. **92**, 025702 (2004).
- [10] T. Vicsek, A. Czirók, E. Ben-Jacob, I. Cohen, and O. Shochet, *Novel Type of Phase Transition in a System of Self-Driven Particles*, Phys. Rev. Lett **75**, 1226 (1995); A. Czirók, H.E. Stenley, and T. Vicsek, *Spontaneously ordered motion of self-propelled particles*, J. Phys. **A 30**, 1375 (1997).
- [11] D. Grossman, I. S. Aranson, and E. Ben-Jacob, *Emergence of agent swarm migration and vortex formation through inelastic collisions*, New J. Phys. **10** 023036 (2008)
- [12] R.A. Simha and S. Ramaswamy, *Hydrodynamic Fluctuations and Instabilities in Ordered Suspensions of Self-Propelled Particles*, Phys. Rev. Lett. **89**, 058101 (2002).
- [13] M.J. Kim and K.S. Breuer, *Use of Bacterial Carpets to Enhance Mixing in Microfluidic Systems*, Jour. Fluids Engin. **129**, 319 (2007).
- [14] A. Sokolov, I. S. Aranson, J. O. Kessler, R. E. Goldstein, *Concentration Dependence of the Collective Dynamics of Swimming Bacteria*, Phys. Rev. Lett. **98**, 158102 (2007)
- [15] A. Einstein *Investigations on the theory of the Brownian movement*, Dover Publications, New York, 1956
- [16] G.K. Batchelor and J.T. Green, *The determination of the bulk stress in a suspension of spherical particles to order  $c^2$* , J. Fluid Mech. **56**, 401-427 (1972).
- [17] G.B. Jeffery, *The Motion of Ellipsoidal Particles Immersed in a Viscous Fluid*, R. Soc. London Ser. A **102**, 161-79 (1922).
- [18] M. Belzons, R. Blanc, J.L. Bouillot, and C. Camoin, *Viscosité d'une suspension diluée et bidimensionnelle de sphères*, C.R. Acad. Sc. Paris Serie II **292**, 939-44 (1981).
- [19] G.K. Batchelor, *An Introduction to Fluid Dynamics*, Cambridge University Press, Cambridge, 1967.
- [20] T. Levy, E. Sanchez-Palencia, *Suspension of solid particles in a newtonian fluid*, J. Non-Newt. Fluid Mech. **13** (1983) 63-78.
- [21] L.D. Landau and E.M. Lifshitz, *Fluid Mechanics*, Elsevier, Oxford, 1987.
- [22] A. Avudainayagam and B. Jothiram, *A Circle Theorem for Plane Stokes Flows*, Q. J. Mechanics Appl. Math. **41**, 383-93 (1988).

- [23] Y. Hatwalne, S. Ramaswamy, M. Rao, R.A. Simha, *Rheology of Active-Particle Suspensions*, Phys. Rev. Lett. **92**, 118101 (2004).
- [24] A. Sokolov, I.S. Aranson, in preparation.
- [25] T.J. Pedley and J.O. Kessler, *Hydrodynamic Phenomena in Suspensions of Swimming Microorganisms*, Annu. Rev. Fluid Mech. **24**, 313-58 (1992).
- [26] P. R. Garabedian, *Partial Differential Equations*, John Wiley & Sons, New York, 1964.
- [27] J.P. Hernandez-Ortiz, Ch. G. Stoltz, and M. D. Graham, *Transport and Collective Dynamics in Suspensions of Confined Swimming Particles*, Phys. Rev. Lett. **95**, 204501 (2005).
- [28] T. Ishikawa and T. J. Pedley, *Coherent Structures in Monolayers of Swimming Particles*, Phys. Rev. Lett. **100**, 088103 (2008)
- [29] P. T. Underhill, J. P. Hernandez-Ortiz, and M. D. Graham, *Diffusion and Spatial Correlations in Suspensions of Swimming Particles*, Phys. Rev. Lett. **100**, 248101 (2008).
- [30] I. Llopis and I. Pagonabarraga, *Dynamic regimes of hydrodynamically coupled self-propelling particles*, Europhys. Lett. **75** (6), pp. 999-1005 (2006).
- [31] E. Hinch and L. Leal, *The effect of Brownian motion on the rheological properties of a suspension of non-spherical particles*, J. Fluid Mech. **52** (4), pp. 683-712 (1972).
- [32] G. Batchelor, *The stress system in a suspension of force-free particles*, J. Fluid Mech. **41** (3), pp. 545-570 (1970).
- [33] T. Ishikawa and T. J. Pedley, *The rheology of a semi-dilute suspension of swimming model micro-organisms*, J. Fluid Mech. **588**, 399 (2007)