EFFECTIVE VISCOSITY AND DYNAMICS OF SUSPENSIONS OF MICRO-SWIMMERS

A Dissertation in Mathematics
by Vitaliy Gyrya

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Abstract

This dissertation explores two problems, all related to modeling and analysis of hydrodynamic interactions between microswimmers, most common example of which are swimming microorganisms, e.g. *Bacillus subtilis*. Results for both problems were published in peer-reviewed journals.

In Chapter 1 we introduce the subject of the study, its origins and goals, as well as its current state of development.

In Chapter 2 we present the first problem, in which we study the dynamics and interaction of two microswimmers, modeled by self-propelled dumbbell-type structures. We focus on alignment dynamics of a coplanar pair of elongated swimmers, which propel themselves either by “pushing” or “pulling” both in three- and quasi-two-dimensional geometries of space. We derive asymptotic expressions for the dynamics of the pair, which, complemented by numerical experiments, indicate that the tendency of bacteria to align with one another strongly depends on the position of the propulsion force. In particular, we observe that positioning of the effective propulsion force inside the dumbbell results in qualitative agreement with the dynamics observed in experiments, such as mutual alignment of converging bacteria.

In Chapter 3 we present the second problem, where we develop a 2D model for a suspension of microswimmers in a fluid and analyze it analytically in the dilute regime when swimmer-swimmer interactions can be neglected and numerically in the moderate concentration regime accounting for all hydrodynamic interactions, using a Mimetic Finite Difference method – efficient method for problems with complex geometries. Our analysis shows that in the dilute regime (in the absence of rotational diffusion) the effective shear viscosity is not affected by self-propulsion. But at the moderate concentrations (due to swimmer-swimmer interactions) the effective viscosity decreases linearly as a function of the propulsion strength of the swimmers. These results prove that (i) a physically observable decrease of viscosity...
for a suspension of self-propelled microswimmers can be explained purely from the view of hydrodynamics, i.e. “higher order” phenomena such as chemotaxis and chemical constitution of fluid can be neglected (ii) self-propulsion and interactions among swimmers are both essential to the reduction of the effective shear viscosity.

In Chapter 3 we also present a number of numerical experiments for the dynamics of swimmers resulting from pairwise interactions at moderate distances from one another. The numerical results agree with the physically observed phenomena (e.g., attraction of swimmer to swimmer and swimmer to the wall). This is viewed as an additional validation of the model and the numerical scheme.
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Chapter 1

Introduction

In recent years modeling of suspensions of microswimmers has become an increasingly active area of research. This dissertation explores two problems in this area related to modeling microswimmers and analyzing hydrodynamic interactions between them. In the first problem we study the dynamics of two elongated swimmers in the asymptotic limit of large distance between them. In the second problem we focus on the effective shear viscosity of suspensions of microswimmers at small and moderate concentrations.

To begin, we present some motivations for the active interest in suspensions of microswimmers. In section 1.2 we present some interesting known phenomena observed experimentally for suspensions of microswimmers. In section 1.3 we discuss key features of modeling microswimmers and the related problem of modeling suspensions of passive inclusions. Finally, in section 1.4 we review existing approaches to modeling microswimmers.

1.1 Microswimmers

Microswimmers are actively swimming microparticles typically on the scale of $0.1 - 10$ micrometers ($\mu$m). Although there are examples of engineered microswimmers (e.g., [1]), by far the predominant examples of microswimmers are swimming microorganisms, also called microbes. Although invisible to a naked eye, microbes are omnipresent and constitute the majority of the Earth’s biomass.

According to the biological classification all microorganisms are divided into
three domains: archaea, bacteria, and eukarya. Eukarya are uni- or multi-cellular microorganisms that contain a nucleus. Bacteria and archaea are mostly uni-cellular microorganisms that do not contain a nucleus and until 1990 were viewed as members of the same domain – prokaryotes.

Bacteria are the dominant part of the Earth’s biomass. The number of bacteria cells together is estimated at around $4 - 6 \times 10^{30}$, [2]. As a reference, this can be compared to the number of atoms in one hundred people. Bacteria are omnipresent. One milliliter of fresh water typically contains $10^6$ bacteria. A surprising fact is that inside and on the surface of human body, typically, there are ten times more bacteria cells than there are human cells. This seems counterintuitive at first, but it can be explained by the size difference between human and bacteria cells. Typical bacteria cells are $0.5 - 5.0 \mu m$ in length, which is ten times smaller than human cells. This translates into a factor of 1000 in weight/volume difference. So, a typical adult human contains only around two pounds of bacteria cells, which are mostly contained in the digestive tract.

The shape of bacteria varies a lot and is adapted to the living environment to optimize nutrient intake, convenience of attachment, etc. The typical shapes of bacteria spherical (coccis) and rod-shaped (bacilli).

In this dissertation we discuss bacteria and other microorganisms that can swim. Such microorganisms propel themselves through fluid by rotating or beating flagella – hair-like growth on the surface of the cell. Currently there are three types of flagella that have been identified: bacterial, archaeal, and eukaryotic (also called cilia). Bacterial and archaeal flagella are classified different due to evolutionary differences and certain differences in the details of the structure, but are very similar in terms of their functionality.

Bacterial and archaeal flagella rotate like cork-screws, driven by the torque generating motors located within the cell membrane. The rotation of the flagella pushes fluid back behind the cell body. This results in a forward hydrodynamic drag onto the flagellum. To offset the forward hydrodynamic drag onto flagella (forces acting on the swimmer have to be balanced) the body of the swimmer has to experience a backward hydrodynamic drag of the same magnitude. For this the body of the swimmer has to be moving forward through the fluid.

The rotation of the flagellum, also, causes the body of the bacterium to rotate
in the opposite direction around its axis of symmetry. The rotating flagella exert a hydrodynamic torque onto the fluid. One of the consequences of the torque generated by the flagella motor is that the body and the flagella are rotating in the opposite direction around the axis of symmetry of bacteria. The axis of symmetry is not changed as a result of such motion. The effects of this torque can be observed in the experiments where bacteria are close to one another or close to the wall of container. For example it is known [3] that a bacterium swimming next to a solid wall will swim in circles in the plane parallel to the wall. The direction of the swimming is determined by the chirality of the flagellum, since the body and the flagellum of bacteria interact differently with the wall, making bacteria swim in circles.

![Figure 1.1](http://www.nsf.gov/news/mmg/media/images/ecoli_h.jpg)

**Figure 1.1.** An illustration of *Escherichia coli* bacterium rotating its flagella to propel it through the fluid. Note that flagella and the body rotate in the opposite directions.

All known bacteria have flagella that are left-handed helices. During the “swimming phase” all flagella rotate in a counterclockwise direction. This makes flagella wrap around each other in a single bundle that propels bacteria forward. During the “tumble phase” all flagella rotate in a clockwise direction. This makes flagella unwrap and push the bacteria violently in opposite directions, resembling tumbling, hence the name. Tumbling motion allows bacteria to randomly reorient in space.

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Figure 1.2. An illustration of displacement of the scallop as it opens and then closes its shells attempting to swim.

Eukaryotic flagella (cilia) are generally shorter than bacterial and archaeal flagella and exhibits a different motion. Instead of rotating, cilia lash back and forth in an irreversible manner, usually slightly out of phase with the adjacent cilia. The out of phase motion generates a so-called metachronal wave on the surface of the cell, leading to the propulsion of the microorganism.

The irreversible motion (motion that does not replicate itself if viewed backward in time) of all types of flagella is essential on microscale. According to Purcell’s Scallop theorem [4] any reciprocal motion (motion that looks the same if viewed forward and backward in time) in Stokes fluid (see section 1.3 on the discussion of Stokes fluid) cannot lead to a locomotion. The name of the theorem is due to the original example of a scallop that can only open and close its shells, thus producing a reciprocal motion. The displacement of scallop opening the shells is exactly nullified by the displacement of a scallop closing its shells. The velocities with which scallop opens and closes its shells at zero Reynolds number (see section 1.3) is irrelevant to its displacement due to absence of inertia terms.
1.2 Physically observed phenomena for suspensions of microswimmers

Here we discuss two phenomena that of particularly interested to us. One phenomenon is related to pattern formations in suspensions of microswimmers on scales much larger than individual swimmers. The other phenomena is related to rheology, in particular effective viscosity of suspensions of microswimmers.

1.2.1 Pairwise interactions of swimmers

One of the current research areas in the field of suspensions of microswimmers is the study of the dynamics of large populations of aquatic single-cellular [5, 6, 7, 8, 9] and multicellular [10, 11] microorganisms. In particular, there is a significant interest in understanding the mechanisms of formation of coherent structures such as whorls and jets of cooperative swimming in suspension on scales much larger than individual microorganisms (see, e.g., [12, 9, 13]). For example, the correlation lengths of collective motion in suspensions of \textit{E. coli} bacteria can exceed the size of individual cells by more than an order of magnitude. Similarly, the collective flow speeds, of the order $50 - 100 \ \mu \text{m/sec}$, significantly exceed the speed of individual bacteria, $15 - 20 \ \mu \text{m/sec}$.

The principal organizing role in the formation of large-scale patterns (e.g., [6, 14, 7, 9]) is believed to be played by hydrodynamic interactions between individual swimmers and the environment. This includes the boundary effects as well as the hydrodynamic interaction with other swimmers [12, 8]. These effects and interactions are also believed to set the spatial and temporal scales of the patterns. At the same time, fundamental questions about the hydrodynamics of a single swimmer have been studied by many researchers over several decades (e.g., [15, 16, 17, 18, 19] and references therein). Here one of the central features is the very low Reynolds number $Re$ of a typical microscopic swimmer [20, 17], making the governing dynamics Stokesian (see section 1.3). Since Stokesian dynamics are time-reversible, the very possibility of propulsion at low Reynolds numbers had to be clarified in general (see, e.g., [18]), with some of the early important contributions made by Purcell [4].
Modeling the propulsion mechanism of flagellates includes the work by Phan-Thien et al. [21, 22]. In particular, Ref. [21] presents the numerical results based on the boundary element method for the interactions of two nearby microswimmers with rotating tails. We also address the question of pairwise hydrodynamic interactions of swimmers at large distance in Chapter 2 and at moderate distances in section 3.4.4 of Chapter 3. Unlike in [21], however, our models abstract from the method of propulsion (e.g., rotating helix, water jet) and are applicable to a wider class of swimmers. Also, being simpler structurally, our models allow for analysis with fewer number of parameters defining the dynamics (e.g., phase shift for rotating helixes).

Studies of the fundamental interactions of small numbers (e.g., pairs) of swimming particles are also important for validating phenomenological mean-field theories of large-scale pattern formation in active suspensions [23]. The continuum phenomenological models proposed in such studies typically rely on a two-phase formulation of the problem: the particle phase interacts with the fluid phase via a postulated coupling mechanism. It should be possible, at least in principle, to derive or verify the proposed coupling mechanisms against the fundamental particle-particle dynamics.

Saintillan and Shelley [24] modeled swimmers as slender rods with tangential traction prescribed on a part of the boundary. For such swimmers they analyzed the stability of the nematicallg ordered state (all swimmers facing the same direction) numerically, based on slender-body theory. Even though nematicallg ordered state is not normally observed for swimming microorganisms, the results of the numerical analysis fit well with the physical experiments of [9, 13]. Saintillan and Shelley [24] observed: instabilities of nematicallg ordered state in long wavelengths (length on the scale of the size of the container), reminiscent of the long correlation lengths in physical experiments, and significant impact of the nematic ordering on the mean swimming velocity of the swimmers, reminiscent to the significant increase of the mean swimming velocities in physical experiments.

In Chapter 2 we focus on the mechanisms of alignment of a pair of elongated swimmers, with the aim of shedding light on a possible mechanism of large-scale ordering in dilute bacterial suspensions. We derive the simplified PDE-ODE model for the suspensions of dumbbell-shaped microswimmers from the Navier-Stokes
equation and Newton's laws in the limit of small Reynolds number. This model is further reduced to a much simpler model applicable to the case of large separation between elongated swimmers. Three main ingredients in this reduction are basic solutions of the Stokes equation for a point force, for a moving ball, and Stokes drag law for a moving ball. For the reduced model we found formal asymptotic expansions for the velocities of the swimmers as functions of their positions. Next we applied these asymptotic formulas to a number of test cases to see whether two swimmers starting from those initial positions and orientations will swim in or swim off. It was observed that the dynamics of swimmers crucially depends on the position of the point-force relative to the dumbbell body of the microswimmer. This discovery is important for understanding the differences in dynamics of various types of microswimmers based on the position of their propulsion apparatus.

1.2.2 Effective viscosity of suspensions of microswimmers

Recently, bacterial suspensions have also emerged as a prototypical systems for the study and engineering of novel biomaterials with unusual rheological properties [25, 26]. Here the idea is to exploit the active nature of the particles in the suspension in order to generate specific effects, such as enhancement of transport and diffusion of tracers relative to that of the solvent [25, 10, 9]. In [5] it was shown that self-propelled bacteria (Escherichia coli; 1µm wide and 2-3µm long; concentration around 10% by volume) enhanced the diffusion of tracer particles (1-10µm in size) by 2–3 orders of magnitude in the quasi-two-dimensional setting of a freely suspended soap film. Further analysis of this enhanced diffusion in the flow created by self-propelled microswimmers (Chlamydomonas reinhardtii) was performed recently in [27]. In [28, 29] it was demonstrated that self-propelled bacteria (Bacillus subtilis; .7µm wide and 5µm long; concentration around 3% – 5% by volume) could reduce the viscosity of the suspension by up to seven times when compared to passive/dormant bacteria. The experiments were also performed in a thin film. The activity of the bacteria was controlled by changing the supply of oxygen.

The above experiments demonstrate that suspensions of active swimmers may have drastically different properties than suspensions of passive inclusions. Ex-
ploiting these properties may lead to new or improved engineering solutions (e.g., self-replicating micromixers). Explaining and quantifying the changing viscosity for a suspension of microswimmers is the goal of Chapter 3. We identify the following key features affecting this viscosity and the difficulties related to modeling and analysis of microswimmers: 

(i) inhomogeneity of the fluid due to inclusions,
(ii) elongated shape of the inclusions,
(iii) particle-particle interactions, and the new feature – (iv) self-propulsion.

The rheological properties of passive suspensions have been studied extensively for over a century and are part of the homogenization theory – study of differential equations concerned with effective (homogenized) properties of inhomogeneous materials with high frequency and high contrast inhomogeneities. The analysis of the effective viscosity for passive suspensions dates back to the famous work of Einstein [30], where he computed the linear (in volume fraction \(\phi\)) correction to the viscosity for a suspension of neutrally buoyant inert hard spheres in a Newtonian fluid in the dilute limit (\(\phi \rightarrow 0\)). In the 1922 Jeffery [31] extended the analysis from spherical to ellipsoidal inclusions, where he demonstrated the dependence of the viscosity on the distribution of orientations of the inclusions. In the 1971-72 Hinch and Leal [32, 33] analyzed the limiting distribution of orientations of ellipsoids in a shear flow in the presence of a rotational Brownian motion and used this to obtain the effective viscosity for a suspension of ellipsoids. In the 1972 Batchelor and Green [34] were the first to consider pairwise particle interactions in order to find the \(O(\phi^2)\) correction to Einstein’s result [30]. Up to this point, all works have involved formal asymptotics.

In the 1980s, rigorous homogenization results were first obtained for moderate concentrations of particles by Levy and Sanchez-Palencia in [35] and asymptotic results by Nunan and Keller in [36] for periodic distributions of inclusions. Results for the densely-packed regime in 2000s were proven in [37, 38, 39].

For suspensions of microswimmers, the new feature compared to suspensions of passive particles is the active nature of the inclusions. Due to the linearity of the instantaneous problem, given by Stokes PDE, the solution to the instantaneous problem for microswimmers can be represented as a sum of solutions of the instantaneous problem for passive inclusions and the solution due to the active component of the inclusions. The later solution significantly depends on the
distribution of microswimmers, making the dynamics of microswimmers a crucial factor in the analysis of the rheology for suspensions of microswimmers.

One of the first works on the rheology of suspensions of microswimmers and closest to our analysis of Chapter 3 is by Ishikawa and Pedley [40]. Ishikawa and Pedley model microswimmers, daubed “squirmers”, as spheres (hence they ignore elongated shape of many microswimmers, e.g. *Bacillus subtilis*) with a prescribed relative velocity of fluid on the surface. The analysis of effective shear viscosity has been performed numerically using the database of pairwise interactions computed using boundary integral method. Authors observed no decrease of effective viscosity for swimmers with centers of gravity coinciding with geometric centers of the swimmer. For swimmers with center of gravity shifted towards the back (bottom-heavy swimmers) effective shear viscosity could take values larger or smaller than those of suspension of passive spheres depending on the orientations of the shear flow. For vertical shear flow (i.e., velocity of the background flow is constant along vertical lines) smaller values of the effective viscosity were observed. For horizontal shear flow larger values of the effective viscosity were observed. Thus there was no definitive answer for why decrease of the effective viscosity is observed in experiments such as [28, 29]. We believe that the two reasons why Ishikawa and Pedley did not observe definite decrease of viscosity is in their model of a swimmers: (i) their swimmers are round and thus do not have a preferred direction unless they have shifted center of gravity; (ii) squirmers is an example of a puller, as can be seen by the flow it creates (back in front of the swimmer and forward behind it).

In [41] authors consider a phenomenological model of active gels, treating them from the perspective of liquid crystals. In particular, they are interested in the effective viscosity of active gels near “nematic” phase. They view a suspension of microswimmers as an example of an active gel. In our view, attainability of the “nematic” phase understood as an almost perfect alignment in suspensions of swimming microorganisms is debatable. On the other hand, the “nematic” phase may be feasible for suspensions of engineered microswimmers that swim due to externally applied alternating magnetic field (e.g. [1]) and, therefore, could be synchronized to swim in the same direction.

Another notable work presenting phenomenological arguments relating the viscosity of suspensions to the activity of particles is [42]. In [42], a tensor order
parameter $Q$ is used to characterize the local ordering of the system (i.e., the alignment of swimming particles to each other). The governing dynamics for $Q$ is borrowed from the theory of systems with nematic ordering and is phenomenological. In particular, the relationship of the evolution of the order parameter to the microscopic alignment dynamics has not been clarified, and the very possibility of arriving at macroscopic expressions for the effective viscosity from first-principle arguments has not been established. In this work, we begin to fill this gap by proposing a model that allows for an analytic and numerical analysis of the dynamics and ultimately explains the observed effects of decreasing viscosity.

In the recent work [43] Haines, Aranson, Berlyand and Karpeev obtained an analytic formula for the instantaneous apparent viscosity of a suspension of swimmers in 2D as a function of distribution of swimmers in the limit of small concentrations. In [43] a swimmer is modeled as a disk with the propulsion force applied to the fluid at a point fixed distance away from the center. The analytic formula for the instantaneous apparent viscosity can be used to obtain effective viscosity if the orientational distribution of swimmers with time is known. Similarly to the work of Ishikawa and Pedley [40] no decrease of viscosity is observed without imposing alignment externally (e.g. by hand or gravitational field).

A three-dimensional extension of [43] was considered in [44]. Here a body of a swimmer is a slightly elongated sphere (which has a preferred direction) with a propulsion force applied to the fluid at a point fixed distance away from the center. A Brownian rotational noise is added (designed to model tumbling of bacteria) to guaranty unique limiting distribution of orientations of swimmers. Various analytic formulae for the effective viscosity were obtained in the dilute limit for shear and extensional background flows showing the decrease of viscosity. In fact, for extensional background flow one can consider a model without Brownian rotational noise and still obtain the decrease of effective viscosity. On the other hand, for shear background flow and swimmers without the Brownian rotational noise no reduction (or increase) of viscosity would be observed as will be proved in Chapter 3. Thus, Brownian noise is essential to the decrease of effective shear viscosity and is not just a simplifying assumption for unique limiting orientational distribution of swimmers.

In Chapter 3, we present a two-dimensional mathematical model of suspen-
sion of microswimmers. The elongated body of the swimmer is modeled by an ellipse. The front half of the ellipse represents the solid surface and the back half represents the surface covered with flagella or cilia (e.g. *Paramecium*) that exert the propulsion force onto the fluid. This model is similar to that of Saintillan and Shelley [24] with the difference that in [24] swimmers have zero thickness. A model identical to ours has recently appear in [45]. The analysis of our model in Chapter 3 has a very different aim from the analysis in [24] and [45]. Our main focus is on rheology, while [24] focuses on stability of nematically ordered suspension of swimmers and [45] focuses on pairwise interactions of swimmers in infinite space.

We consider both dilute and moderate concentration regimes. In the dilute regime (no swimmer-swimmer interactions) we analytically demonstrate that self-propulsion has no effect on the effective shear viscosity. Therefore, we show that the elongated shape of the swimmers and the propulsion force are not sufficient to change the effective viscosity as compared to the passive suspensions.

On the other hand, the numerical analysis of the moderate concentration regime, taking into account all interactions, showed a decrease of the effective viscosity with increase of the propulsion strength of the swimmers. At this concentration regime all of the above features (ii–iv) are present: the elongated shape of the swimmers, the propulsion force and the swimmer-swimmer interactions. Both concentration regimes are discussed to pinpoint the importance of interactions between swimmers for reduction of viscosity.

We performed a number of numerical simulations at the moderate concentrations where we computed the effective shear viscosity of a suspension of swimmers in a layer between two solid walls undergoing a shearing motion with relative velocity $2\nu$. We analyzed the dependence of the effective viscosity on the velocity $\nu$ and the propulsion strength of the swimmers, $f_p$. Using an analytical scaling argument we demonstrated that the effective viscosity depends only on the propulsion-shear ratio $\frac{f_p}{\mu\nu}$ ($\mu$ is viscosity of the ambient fluid) for a fixed shape of the domain and the swimmers. The simulations indicate that the effective shear viscosity decays linearly as a function of the propulsion-shear ratio (for small values of $\frac{f_p}{\mu\nu}$). The same linear trend continues for negative values of the propulsion strength, which corresponds to microswimmers with propulsion apparatus ahead of the body, i.e. pullers instead of pushers. For larger values of the propulsion-shear ratio a devi-
tion from the linear trend was observed and explained by the finite size of the container.

1.3 Key features of modeling microswimmers

One of the main features of suspensions of microswimmers is a low Reynolds number

$$\mathcal{R}e = \frac{\rho V L}{\mu} \ll 1,$$

(1.1)

where $\rho$ is the density of the fluid, $V$ is the mean fluid velocity, $L$ is the characteristic length, $\mu$ is the dynamic viscosity of the fluid. Based on the typical swimming velocities ($V \approx 20 \mu m/\text{sec}$) and typical length of swimming bacteria ($L \approx 5 \mu m$), the Reynolds number of the fluid flow induced by the motion of the swimming bacteria is typically of the order $10^{-4} - 10^{-6}$ and usually is less than $10^{-2}$ (see, e.g., [20]).

The Reynolds number (1.1) by definition is the ratio of inertial forces $\rho V L$ to viscous forces $\mu$. Therefore $\mathcal{R}e \ll 1$ indicates that the inertial forces on the fluid elements are entirely dominated by viscous forces. Ignoring the inertial effects of the fluid in our model is reflected by reducing the Navier-Stokes equation written in the non-dimensional form (see Appendix A)

$$\mathcal{R}e \left( u_t + u \cdot \nabla u \right) = -\nabla p + \Delta u + F$$

(1.2)

to the Stokes equation

$$0 = -\nabla p + \Delta u + F$$

(1.3)

by setting $\mathcal{R}e = 0$.

1.3.1 Balance of forces and torques

When Reynolds number is small one can show that inertial terms are small compared to viscous terms not just for the fluid element, but also for any inclusion $B$ emersed in the fluid $\Omega$. From Newton’s second law of motion

$$m \dot{\mathbf{v}}_c = \mathbf{F}_B := \int_{\partial B} \sigma(u, p) \, dx,$$

(1.4)
where the stress tensor $\sigma(u)$ is defined in terms of the strain rate (symmetrized gradient) $D(u)$,

$$
\sigma(u) = 2 \mu D(u) - p I, \quad 2 D(u) = \nabla u + (\nabla u)^T,
$$

and $\hat{n}(x)$ is the unit inward normal to $\partial B_*$. Here $v_c = \dot{x}_c$ is the velocity of the center of mass $x_c$ of the particle, $I$ is the moment of inertia for the particle with respect to $x_c$. The force $F_B$ is due to the viscous drag exerted onto the fluid by the particle; likewise, $T_B$ is the torque due to the viscous force. The force is applied at the center of mass $x_c$ of the particle and the torque is calculated with respect to $x_c$.

In the preceding section we described the dynamics of a swimmer. In this section we derive the PDE and ODE models for a collection of swimmers interacting with a fluid. We consider several neutrally buoyant swimmers (indexed by a superscript $i = 1, \ldots, N$) immersed in a Newtonian fluid (water) that occupies the domain $\Omega$. We are concerned with instantaneous velocities of swimmers and fluid due to propulsion forces. The head and the tail balls of the $i$th bacterium are denoted by $B^i_H$ and $B^i_T$, respectively. The corresponding coordinates, velocities, forces, and torques are labeled accordingly. The swimmers occupy the domain $\Omega_B = \bigcup_{i=1}^N B^i$ while the fluid occupies the domain $\Omega_F = \Omega \setminus \Omega_B$.

In the Stokesian framework, the Stokes drag law is applicable, stating that the viscous drag on a ball is proportional to the radius $R$, while the mass of the ball is proportional to $R^3$. Indeed, a neutrally-buoyant swimmer has the density of the surrounding fluid $\rho$, so its mass is $\frac{4}{3} \pi R^3 \rho$. For sufficiently small radius $R$ and finite density $\rho$ and viscosity $\mu$, the inertial terms $m \dot{v}_c$ and $I \omega$ in (1.4-1.5) can therefore be neglected to obtain the balance of forces and torques:

$$
0 = F_B := \int_{\partial B} \sigma(u, p) \, dx, \quad (1.6)
$$

$$
0 = T_B := \int_{\partial B} (x - x_c) \times \sigma(u, p) \, dx, \quad (1.7)
$$

Note that the reduction of (1.4-1.5) to (1.6-1.7) does not mean that the linear
and angular acceleration of inclusions are always zero. Instead the reduction of (1.4-1.5) to (1.6-1.7) represents the zero-order approximation, which means there is a boundary layer in time in which the flow is established. Since the size of the boundary layer is of order $Re \ll 1$, physically this means that the flow is established instantaneously on the time scale of appreciable changes in the position of the inclusions, and the distribution of fluid velocities at any time is governed by the steady Stokes equation. Mathematically this means that the fluid velocities are the fast variables in a system with two time scales. They are slaved to the slow variables – the positions of the dumbbell balls – and in the singular limit instantaneously relax to their quasi-stationary state for each value of the slow variables.

### 1.4 Self-propulsion

Some of the earlier works in modeling the swimming at low Reynolds number were done by Taylor [15], who studied self-propulsion of a waving sheet, and Purcell [4], who studied the basics of self-propulsion of microswimmers.

Throughout the years two different approaches to modeling microswimmers have been identified based on whether the bodies representing microswimmers change their shape or not. Examples of models of swimmers changing their shape are a three-linked sphere swimmer [18, 46] and a swimmers with rotating tail [21].

These models are attractive because the real-world swimmers (bacteria, fish, etc.) swim due to shape changes (rotation of flagella, waving of the tail, etc.). Unfortunately, the analysis of these models is difficult, so far the analysis of these models was limited to studying the dynamics of pairs of such swimmers due to their pairwise interactions (e.g., [21, 47]).

The other approach, emerging as the main way of modeling microswimmers [24, 20, 48, 19], typically abstracts away the details of the actual propulsion mechanism and use simple, tractable, rigid geometries to model a microswimmer. In general “higher-order” effects such as signaling between bacteria and chemotaxis are ignored, the emphasis being on the basic hydrodynamic interactions. The propulsion here is either due to a prescribed effective force or an effective relative velocity of the fluid on a part of the surface of the swimmer. We believe
that prescribing effective force closer resembles mechanisms of propulsion by microorganisms, where the propulsion is due to the torque generating motor. For fixed-shape swimmers, self-propulsion is enforced by the balance of force (1.6) and torque (1.7) on each of the swimmers.

Both [24] and [48] model swimmers as elongated bodies; the former employs slender body theory for cylindrical rods, while the latter models the elongated body as a dumbbell consisting of a pair of balls. Our model of microswimmers presented in Chapter 2 resembles that of [48], although for the later one the exact mathematical formulation is difficult to uniquely deduce based on its formulation [48]. In section 2.2.2 we present the exact mathematical formulation of the model for dumbbell-shaped microswimmer. In the aforementioned studies the self-propulsion mechanism is modeled by a prescribed force, concentrated at a point inside the dumbbell ball, as in [48], or distributed over a part of the surface of the body in the form of a specified tangential traction, as in [24, 19]. Both of these studies ultimately rely on numerical simulations with the goal of studying the emergence of large-scale coherent patterns predicted by continuum theories such as [23, 13] or observed in experiments [7, 9]. By contrast, the main tool of our work in Chapter 2 is an asymptotic analysis followed by straightforward numerical simulations.

A different structural and dynamic approach is taken by Pedley and coworkers (see [20, 40, 49]). Here a basic swimmer is modeled as a squirming sphere, with a prescribed tangential velocity as the model of the propulsion by motile cilia (short hair on the surface of the cell beating in the same direction). As with the dumbbell model, a spherical squirmer allows for the use of fundamental solutions and relations (e.g., the Stokeslet solution and the Faxén relations) to approximate the dynamics of the swimmers. Saintillan and Shelley [24] model microswimmers as slender rods with tangential traction prescribed on a part of the boundary, for which they observed behavior reminiscent of that in the physical experiment for Bacillus subtilis [9, 7, 50]. In particular, they observed local nematic ordering of rod-like swimmers that had a significant impact on their mean swimming speed. In Chapter 3 we model microswimmers as ellipsoids with tangential tractions prescribed on part of the boundary. This model is similar to that Saintillan and Shelley [24], except that in our model microswimmers have non-zero thickness,
which is a better approximation for microswimmers in real life.

1.5 Outline of the dissertation

The remaining part of the dissertation is structured as follows.

In Chapter 2 we present the results previously published in [51]. The structure of the presentation was reworked to accommodate the questions and comments raised during numerous presentations of these results. Section 2.3 is the most significantly changed one. We begin by presenting a model of dumbbell-shaped microswimmer in a fluid. For two such swimmers we perform formal asymptotic analysis in the limit of large interswimmer distances. The asymptotic analysis is then used to answer the question of mutual alignment of swimmers due to hydrodynamic interactions.

In Chapter 3 we present the results previously published in [52]. We begin by presenting a model of ellipsoid-shaped microswimmer in a fluid. This model is better suited for the analysis of suspensions of microswimmers that can be arbitrarily close to one another. For this model we consider the dynamics of swimmers resulting from hydrodynamic interactions between two swimmers and between swimmer and a wall. The main result of this dissertation is the analysis of the effective shear viscosity of suspension of microswimmers at small (pairwise hydrodynamic interactions are neglected) and moderate concentrations (all hydrodynamic interactions are accounted for). For moderate concentration the analysis has been performed using Mimetic Finite Difference method for solving Stokes differential equation [53] developed by Beirão da Veiga, Gyrya, Lipnikov, and Manzini in 2009.
Chapter 2

Hydrodynamic interactions between dumbbell microswimmers at large pairwise distances

2.1 Introduction

In this chapter we focus on the mechanisms of alignment of a pair of elongated swimmers, with the aim of shedding light on a possible mechanism of large-scale ordering in dilute bacterial suspensions. The principal organizing role in the formation of large-scale patterns (e.g., [6, 14, 7, 9]) is believed to be played by hydrodynamic interactions between individual swimmers and the environment. This includes the boundary effects as well as the hydrodynamic interaction with other swimmers [12, 8]. These effects and interactions are also believed to set the spatial and temporal scales of the patterns.

In developing our model for a microswimmer we follow the main emerging approaches [24, 20, 48, 19] that typically abstract away the details of the actual propulsion mechanism and use simple, tractable, rigid geometries to model a swimmer. Effects such as signaling between bacteria and chemotaxis are ignored, the emphasis being on the basic hydrodynamic interactions. For simplicity we consider the model where there is no randomness in the propulsion mechanism (e.g., no tumbling). This is both physically meaningful (swimming microorganisms do
not tumble for extended periods of time when food sources are abundant) and important for forming a complete picture of the hydrodynamic interactions between microswimmers (e.g., understanding which phenomena are due to self-propulsion and which are due to randomness).

The model in [48] is the closest to our model. The authors represent the elongated body of a microswimmer as a *rigid dumbbell* consisting of a pair of balls constant distance apart. One of the balls is intended to model the body and the other is intended to model the “propeller”. At the same time the “propeller” ball in [48] experiences the drag of the fluid, thus functioning as part of the body as well. Unfortunately, the precise mathematical formulation cannot be uniquely deduced from the formulation of the model in [48].

In section 2.2.2 we present a complete mathematical model of a microswimmer. Analogously to [48] we model a microswimmer as a *rigid dumbbell*. In contrast to [48] the function of a “propeller” and elongated body is no longer ambiguously taken by one ball. In our model both of the balls in the dumbbell are rigid balls with no-slip conditions on them representing the body of the microswimmer. The role of the “propeller” is played by a prescribed propulsion force applied to the fluid outside of the dumbbell balls (as in [48] vs. prescribed velocities on the boundary, as in [20]; see also recent work [43] on the rheology of bacterial suspensions). The relative position of the propulsion force to the dumbbell body of the swimmer is a parameter of the model. This allows us to investigate the dependence of mutual dynamics (swim in/off) of neighboring bacteria on the position of this force (which roughly can be interpreted as the effect of the shape of the microorganism and the method of propulsion or distribution of cilia). We study the hydrodynamic interaction for well-separated swimmers. For this reason we say that two swimmers *swim in*, starting from a given mutual orientation, if at some point the distance between them decreases to the order of their size, (i.e., they become not well separated). Two swimmers, starting from a given mutual orientation, *swim off* if the distance between them increases to infinity without *swim in* happening first. We observe that positioning the propulsion force between the dumbbell balls results in attractive behavior of swimmers. On the other hand, positioning the propulsion force outside the dumbbell results in repulsive behavior. For comparison, in the earlier work [48] the position of the propulsion force was fixed (center of a ball in
In this Chapter we study the alignment of a coplanar pair of three-dimensional elongated swimmers, which propel themselves by “pushing” or “pulling”, mimicking a variety of self-propelled microorganisms, from sperm cells and bacteria to algae. We derive asymptotic expressions for the dynamics of the pair, which, complemented by numerical experiments, indicate that the tendency of bacteria to get closer together or to get further apart from one another strongly depends on the position of the propulsion force. In particular, we observe that positioning of the propulsion force inside the dumbbell results in the qualitative agreement with the dynamics observed in experiments [13]. We also observe that the dynamics of bacteria in a thin film (with no-slip boundary conditions on the top and bottom) is qualitatively similar to that for the whole space.

One of our objectives is to develop a well-posed PDE model of an active suspension derived from first principles (unlike many engineering models that use ad hoc assumptions). Our proposed model is simple enough to allow for theoretical analysis (asymptotics) yet captures basic features observed in experimental studies.

This chapter is organized as follows. In section 2.2 we present a full PDE model for the dynamics of swimmers based on Stokesian hydrodynamics and motivate our decisions.

In section 2.3 we introduce an asymptotic reduction of the PDE model in the dilute limit of swimmer concentration. Here we show how to solve the reduced model numerically and give an analytic (asymptotic) solution for a pair of swimmers. Then we analyze two basic (physically interesting) configurations of swimmers based on the asymptotic formulas and numerical calculations. In section 2.6 we make some concluding remarks and indicate areas for future study.
2.2 Model for microswimmers

2.2.1 Structure of the swimmer

Let $S^i$ be the $i$-th swimmer. Here and in the future we reserve the superscript $i$ for swimmer index, $i = 1, \ldots, N$. We model the elongated body of a microswimmer $S^i$ as a dumbbell (see Fig. 2.1). It consists of two neutrally buoyant balls of equal radius $R$ rigidly connected to one another a distance $2L$ apart. The balls are denoted $B^i_H$ (head) and $B^i_T$ (tail), with their centers located at $x^i_H$ and $x^i_T$, respectively. The unit vector directed from $x^i_T$ to $x^i_H$ is denoted by

$$d^i := \frac{(x^i_H - x^i_T)}{|x^i_H - x^i_T|}, \quad (2.1)$$

indicating the direction of the swimmer’s motion, and the line connecting the centers of the balls is referred to as the dumbbell axis. The action of the flagellum –

![Figure 2.1. Model of a single bacterium: two balls (labeled head and tail) and the propulsion force (red ball with arrow) connected by a rigid rod (that does not interact with the fluid).](image)

the bacterial propulsion apparatus – is represented either by a smooth volume force density $\mathbf{F}(\mathbf{x})$ with support in the balls $B^i_P$ of small radii $\varrho$ ($\varrho \ll 1$), with the centers $x^i_P$, located on the dumbbell axis, or by a sum of delta-functions concentrated at $x^i_P$. This force and its support will sometimes be referred to as the propulsion force. The location $x^i_P$ of the propulsion forces relative to the positions $x^i_H$ and $x^i_T$ of the balls in the dumbbell is defined by the parameter

$$\zeta = \frac{(x^i_P - x^i_C)}{L}, \quad \text{where} \quad x^i_C = \frac{x^i_H + x^i_T}{2}. \quad (2.2)$$
For instance $\zeta = \mp 1$ corresponds to the center of the tail or head ball, respectively, and $\zeta = 0$ corresponds to the center of the dumbbell.

Depending on the value of $\zeta$, swimmers are classified into pushers/pullers and inner/outer swimmers. A swimmer is called a pusher if $\zeta < 0$ and puller if $\zeta > 0$. A swimmer is called outer if $|\zeta| > 1$ and inner if $|\zeta| < 1$.

The total force exerted onto the fluid in the ball $B^i_p$ has magnitude $f_p = \text{const}$ and is directed along the axis $d^i$, that is,

$$\int_{B^i_p} F(x) dx = F^i_p = -f_p d^i. \quad (2.3)$$

Here $F^i_p$ models the effective force of the flagellum on the fluid. For simplicity of presentation, we assume that the propulsion force is a delta function

$$F(x) = \sum_{i=1}^{N} \delta(x - x^i_p) F^i_p. \quad (2.4)$$

### 2.2.2 PDE-ODE model of a suspension of swimmers

At any time $t$ the fluid-swimmers system satisfies the so-called instantaneous problem (2.5-2.10), consisting of the PDE (2.5) and the boundary conditions (2.7-2.10).

The PDE is the steady incompressible Stokes equation

$$\begin{align*}
\mu \Delta u(x) - \nabla p(x) &= -F(x) = -\sum_i \delta(x - x^i_p) F^i_p, \\
\text{div} (u(x)) &= 0
\end{align*} \quad (2.5)$$

in the fluid domain

$$\Omega_F := \Omega \setminus \Omega_B, \quad \Omega_B = \bigcup_{i=1}^{N} S^i = \bigcup_{i=1}^{N} (B^i_H \cup B^i_T). \quad (2.6)$$

The boundary conditions are

$$\begin{align*}
u(x) &= 0, & x &\in \partial \Omega, \\
u(x) &= v^i_c + \omega^i \times (x - x^i_c), & x &\in \partial B^i_*, * = H, T, \quad (2.7)\end{align*}$$
\[\int_{\partial B_H \cup \partial B_T} \sigma(u, p) \, dx + F^i = 0, \quad \text{ (2.9)}\]

\[\int_{\partial B^+_H \cup \partial B^+_T} (x - x^i_C) \times \sigma(u, p) \, dx = 0, \quad \text{ (2.10)}\]

where \(v^i_C\) is the velocity of the center of the \(i\)-th swimmer, \(\omega^i\) is the rotational velocity of the \(i\)-th swimmer and the stress tensor \(\sigma(u, p)\) is defined by

\[\sigma(u, p) := 2\mu D(u) - pI, \quad D(u) := \frac{1}{2} \left( \nabla u + (\nabla u)^T \right)\]

where \(I\) is the identity matrix.

The evolution of the fluid-swimmers system is given by the ODE initial value problem

\[
\begin{cases}
\dot{x}^i_C = v^i_C \left( x^j_C, d^j_C; f_p \right), \\
\dot{d}^i_C = \omega^i \left( x^j_C, d^j_C; f_p \right) \times d^i_C,
\end{cases}\]

\[
\begin{cases}
x^i_C(0) = x^i_C, \\
d^i_C(0) = d^i_C.
\end{cases}\]

Here \(v^i_C \left( x^j_C, d^j_C; f_p \right)\) and \(\omega^i \left( x^j_C, d^j_C; f_p \right)\) are the solutions of the instantaneous problem (2.5-2.10) with given positions \(x^j\) and orientations \(d^j\) of the swimmers, as well as prescribed propulsion strength \(f_p\).

### 2.2.3 Discussion of the model

Bacteria swim by rotating the flagellum, driven by the torque generating motors located within the bacterial membrane. The rotation of the flagellum causes the body of the bacterium to rotate in the opposite direction around its axis of symmetry. This rotation exerts a hydrodynamic torque on the fluid. The major consequence of the torque generated by the flagella motor is that the body and the flagella are rotating in the opposite direction around the axis of symmetry of bacteria. The axis of symmetry is not changed as a result of such motion. Experiments for which this torque is important are those where bacteria are close to one another or to the wall of container. For example it is known [3] that a bacterium swimming next to a solid wall will swim in circles in the plane parallel to the wall. The direction of the swimming is determined by the chirality of the flagellum. In fact for all known
bacteria the flagellum rotates counterclockwise during the propulsion phase.

On the other hand, for well-separated swimmers the effects of the torque around the axis of symmetry can be neglected because the disturbance due to it decays as \( r^{-3} \), faster than the decay \( r^{-2} \) of the disturbance due to self-propulsion. Ignoring the motor torque simplifies the model, making it readily amenable to analytical treatment while still capturing the key features of the experimental observations in the dilute limit.

Note that our model is in fact a model of a \textit{self-propelled} swimmer as opposed to a body propelled by an external force, such as gravity or the magnetic field. The propulsion of our swimmer is due to the point force that models the effective action of flagellum on the fluid. This force is balanced – see equations (2.9-2.10) – by an equal and opposite force of the fluid onto the flagellum transmitted to the body of the swimmer. Therefore the propulsion force is not external since all external forces (e.g., gravity) are unbalanced.

Another issue of concern at very small scales is Brownian motion. How reasonable is it to ignore such motion? The rotational diffusion coefficient \( D_{\text{rot}} \) for an ellipsoid of length \( l \) and diameter \( d \) (see [54, 55]) is

\[
D_{\text{rot}} = \frac{12}{\pi} \frac{k_B T}{l^3 \ln(l/d) \mu},
\]

where \( k_B \) is the Boltzmann constant

\[
k_B = 1.3806503 \times 10^{-23} \text{m}^2 \cdot \text{kg} \cdot \text{s}^2 \cdot \text{K},
\]

\( T \) is temperature, and \( \mu \) is the viscosity of the fluid.

Computing the value of the diffusion coefficient \( D_{\text{rot}} \) for \textit{Bacillus subtilis} \((l \approx 4 - 5 \mu \text{m} \text{ and } d \approx 0.7 - 1.0 \mu \text{m})\) in water at near-room temperature \((T \approx 300 \text{ K}) \text{ and } \eta = 0.8 \times 10^{-3} \text{N} \cdot \text{s} \cdot \text{m}^{-2})\), we obtain

\[
D_{\text{rot}} \approx \frac{12}{\pi} \frac{1.3806503 \times 10^{-23} \cdot 300}{(5 \cdot 10^{-6})^3 \cdot \ln(5) \cdot 8 \cdot 10^{-3}} \frac{\text{m}^2 \cdot \text{kg} \cdot \text{K} \cdot \text{m}^2 \cdot \text{N} \cdot \text{s}}{\text{s}^2 \cdot \text{K} \cdot \text{m}^3 \cdot \text{N} \cdot \text{s}} \approx 10^{-2} \text{s}^{-1}.
\]

An isolated swimmer in the absence of Brownian motion will swim in a straight line. In the presence of Brownian motion, the expected time \( T(\theta) \) to deviate by an
angle $\theta$ from a given orientation can be computed by using the appropriate first passage time as

$$T(\theta) = \frac{\theta^2}{D_{\text{rot}}}.$$ 

Thus, for “interior” swimmers in the “mirror image” configuration (see section 2.5.0.1) the expected time to leave the basin of attraction of the “swim in” configuration due to the described thermal effects becomes comparable to the interaction time (the “swim in” time) at distances of $100\mu$m and larger. At smaller separations we can, therefore, ignore thermal effects, at least at the qualitative level.

### 2.3 Asymptotic reduction of the PDE model

In the dilute limit the problem of determining the drag forces and velocities on the individual balls can be effectively approximated by using three classical relations (building blocks for asymptotic reduction): the basic solutions for the flow due to a point force (see Appendix B.1), for the flow due to a moving sphere (see Appendix B.2) and the Stokes drag law (see Appendix B.3). We assume that the bacteria are

- sufficiently long ($2L \gg R$) and
- far apart ($|x_i^c - x_j^c| \gg 2L$, $i \neq j$), so that all the balls and the point of application of propulsion forces are well separated ($|\zeta - 1|, |\zeta + 1| \sim 1$).

#### 2.3.1 Weak additivity: example with two moving balls

In this section we illustrate weak additivity on a minimal example. Suppose we want to construct an approximate solution $\hat{u}(x)$ to the flow due two balls $B^1$ and $B^2$ with centers at $x^1$ and $x^2$ moving in Stokesian fluid with velocities $v^1$ and $v^2$. The velocity of the fluid at infinity is zero.

$$\begin{cases}
\mu \Delta u = \nabla p & \text{in } \mathbb{R}^3 \setminus (B^1 \cup B^2) \\
\text{div } u = 0 & \text{in } \mathbb{R}^3 \setminus (B^1 \cup B^2)
\end{cases}$$ (2.12)
subject to
\[ u(x) = v^i \quad \text{for } x \in \partial B^i, \quad i = 1, 2. \tag{2.13} \]

One possible way of approximating the solution \( u(x) \) would be to write it as a sum of two solutions \( H(x - x^i; R)v^i, i = 1, 2, \) where only one ball is present and it is moving with velocity \( v^i \) (see Appendix B.2 for definition of \( H(x; R) \))

\[ u(x) \approx \tilde{u}(x) = H(x - x^1; R)v^1 + H(x - x^2; R)v^2, \tag{2.14} \]

This approximation is good in the sense that it exactly satisfies the PDE (2.12). The error in the approximation is due to the boundary conditions (2.13) not being satisfied. In particular notice that the approximation (2.14) consistently overestimates the velocity of the fluid when \( v^1 \) and \( v^2 \) point in the same direction.

The quality of the approximation can be improved dramatically if instead we write

\[ u(x) \approx \tilde{u}(x) = H(x - x^1; R)\tilde{v}^1 + H(x - x^2; R)\tilde{v}^2, \tag{2.15} \]

where velocities \( \tilde{v}^1, \tilde{v}^2 \) are chosen so the error of approximation on each ball is zero in average

\[ \int_{\partial B^i} (u(x) - \tilde{u}(x)) \, dx = 0, \quad i = 1, 2. \tag{2.16} \]

The velocities \( \tilde{v}^1, \tilde{v}^2 \) satisfy the equations (the second equation has indexes 1 and 2 switched)

\[ \int_{\partial B^i} (u(x) - \tilde{u}(x)) \, dx = \int_{\partial B^i} \left( v^1 - [\tilde{v}^1 + H(x - x^2; R)\tilde{v}^2] \right) \, dx = 0. \tag{2.17} \]

Equation (2.17) can be written as a symmetric positive definite system for \( \tilde{v}^1 \) and \( \tilde{v}^2 \)

\[ \begin{cases} \tilde{v}^1 + H^{1,2}\tilde{v}^2 = v^1, \\ H^{2,1}\tilde{v}^1 + \tilde{v}^2 = v^2, \end{cases} \tag{2.18} \]

where

\[ H^{1,2} = H^{2,1} = \frac{1}{|\partial B^1|} \int_{\partial B^1} H(x - x^2; R) \, dx \approx H(x^1 - x^2; R). \tag{2.19} \]

The last part of (2.19) is made precise by the following lemma.
Lemma 1. For large distances $|x^2 - x^1|$ between balls we have approximation

$$\frac{1}{|\partial B^1|} \int_{\partial B^1} H(x - x^2; R) \, dx = H(x^1 - x^2; R) + O(|x^1 - x^2|^{-3}). \quad (2.20)$$

Proof. Define

$$r := (x^1 - x^2), \quad r := |r| \quad \text{and} \quad n := r/r$$

and use the expression (B.2) for $H(x; R)$

$$\frac{1}{|\partial B^1|} \int_{\partial B^1} H(x - x^2; R) \, dx = \frac{1}{4\pi R^2} \int_{|x|=R} H\left(x + (x^1 - x^2); R\right) \, dx = \frac{1}{4\pi R^2} \int_{|x|=R} \frac{3R}{4|x + r|} \left[ \alpha I + \beta \frac{(x + r)(x + r)^T}{|x + r|^3} \right] \, dx. \quad (2.21)$$

Use the Taylor expansions in powers of $r^{-1}$

$$H\left(x + r; R\right) = \frac{3R}{4} \left[ \frac{\alpha}{|x + r|} I + \beta \frac{(x + r)(x + r)^T}{|x + r|^3} \right] = \frac{3R}{4} \left[ \alpha \left(r^{-1} - r^{-2}(x \cdot n)\right) I + \beta \left(r^{-1}nn^T + r^{-2}M\right) \right] + O(r^{-3}) = \frac{3R}{4} \left[r^{-1}(\alpha I + \beta nn^T) + r^{-2}((x \cdot n)I + M)\right] + O(r^{-3}), \quad (2.22)$$

where

$$M = \begin{bmatrix} M_{1,1} & M_{1,2} \\ M_{2,1} & M_{2,2} \end{bmatrix}, \quad \begin{cases} M_{1,1} = -n_1(n_1^2x_1 - 2n_2^2x_1 + 3n_1n_2x_2), \\ M_{2,1} = -n_2(3n_1n_2x_1 - 2n_1^2x_2 + n_2^2x_2), \\ M_{1,2} = M_{2,1} = -2n_1^2n_2x_1 + n_2^3x_1 + n_1^3x_2 - 2n_1n_2^2x_2. \end{cases}$$

Note, that from the symmetry $x \leftrightarrow -x$

$$\int_{|x|=R} ((x \cdot n)I + M) \, dx = 0. \quad (2.23)$$

Combining (2.21), (2.22) and (2.23) we get the desired result (2.20). \qed
2.3.2 Weak additivity for microswimmers

The construction of the approximate solution $\tilde{u}$ for the problem of dumbbell-point-force swimmers (2.5-2.10) is similar to the approximation (2.15,2.18) for two balls moving in the fluid. The novel part for dumbbell-point-force swimmers is the presence of point-forces. Because of this, it is convenient to write the approximate solution $u(x) \approx \tilde{u}(x)$ not based on the velocities $\tilde{v}_i$, but rather based on the drag forces

$$\tilde{u}(x) = \sum_{i=1}^{N} \left( H(x - x^i_H; R)\tilde{v}_i^H + H(x - x^i_T; R)\tilde{v}_i^T + G(x - x^i_{p})F^i_p \right) \approx$$

$$\approx \sum_{i=1}^{N} \left( G(x - x^i_H)F^i_H + G(x - x^i_T)F^i_T + G(x - x^i_{p})F^i_p \right)$$

(2.24)

where we used the approximation

$$H(x; R) = \gamma_0 G(x) + O(|x|^{-3}), \quad \gamma_0 = 6\pi \mu R,$$

(2.25)

$$F^i_* = \gamma_0 \tilde{v}_i^*, \quad * = H \text{ or } T.$$  

(2.26)

The forces $F^i_H$ and $F^i_T$ are the drag forces of the balls onto the fluid (B.3).

The velocity of the ball $B^i_H$ in terms of the forces, thus, is

$$v^i_H \approx \tilde{v}_i^H + H(x^i_H - x^j_H; R)\tilde{v}_j^H + G(x^i_H - x^j_T)\tilde{v}_j^T + G(x^i_H - x^j_{p})F^j_p +$$

$$+ \sum_{j \neq i} \left( H(x^i_H - x^j_H; R)\tilde{v}_j^H + H(x^i_H - x^j_T; R)\tilde{v}_j^T + G(x^i_H - x^j_{p})F^j_p \right) \approx$$

$$\approx \gamma_0^{-1}F^i_H + G(x^i_H - x^j_H)F^j_H + G(x^i_H - x^j_T)F^j_T + G(x^i_H - x^j_{p})F^j_p +$$

$$+ \sum_{i=1}^{N} \left( G(x^i_H - x^i_H)F^i_H + G(x^i_H - x^i_T)F^i_T + G(x^i_H - x^i_{p})F^i_p \right)$$

(2.27)

The velocity $v^i_T$ of the ball $B^i_T$ satisfies similar equation. Thus, knowing the forces $F^i_i$ is enough to recover the velocities $v^i_i$.

The forces $F^i_H, F^i_T, i = 1, \ldots, N$ constitute $2 \times 3 \times N = 6N$ unknowns. In the remaining part of this section we explain how to obtain a closed system of 6N equations for the unknown forces.

The first 5N equations for the forces are the balance of forces and modified
balance of torque equations (2.9-2.10)

\[ F^i_H + F^i_T + F^i_p = 0, \quad i = 1, \ldots, N, \quad (2.28) \]
\[ d^i \times (F^i_H - F^i_T) = 0, \quad i = 1, \ldots, N. \quad (2.29) \]

Equations (2.28) give \( 3N \) equations. Each of the equations (2.29) has a one-dimensional kernel, hence they give \( 2N \) equations.

The transition from the original balance of torque equation (2.10) to the modified one (2.29) is as follows

\[
\int_{\partial B_H \cup \partial B_T} (x - x^i_C) \times \sigma(u, p) \, dx = L d^i \times (F^i_H - F^i_T) + \]
\[ + \int_{\partial B_H} (x - x^i_H) \times \sigma(u, p) \, dx + \int_{\partial B_T} (x - x^i_T) \times \sigma(u, p) \, dx. \quad (2.30) \]

The last two integrals, representing torques around each of the balls \( B_H \) and \( B_T \) can be neglected due to the assumption \( R \ll L \), thus obtaining the modified balance of torques equations (2.29).

The remaining \( N \) equations are the conditions on the rigidity of each of the swimmers

\[ d^i \cdot (v^i_H - v^i_T) = 0, \quad (2.31) \]

which have to be written in terms of forces using (2.27).

In particular, for a single swimmer that \( (N = 1) \) simple computations show

\[ v_H = v_T = v_0 d, \quad v_0 = \frac{f_P}{8\pi \mu L \left[ \frac{1}{2} + \frac{4L}{3R} + \frac{1}{|\zeta - 1|} + \frac{1}{|\zeta + 1|} \right]]. \quad (2.32) \]

The flow for a single swimmer, obtained from (2.24), is illustrated in Fig. 2.2.

### 2.3.3 Microswimmer as two force-dipoles

The above system (2.28-2.31) for \( 6N \) unknowns can be reduced to a smaller system for \( N \) unknowns if one makes the following observation.

From both balance equations (2.28-2.29) and the form of the propulsion force \( F^i_p = -f_P d^i \) it follows that \( F^i_H, F^i_T, \) and \( F^i_p \) are all collinear with \( d \). Indeed, \( F^i_p \) is
Figure 2.2. (a) Velocity field of the fluid, computed from (2.24), around a swimmer with $\zeta = -3$. Heuristics: The bacterium is moving left to right; hence the head ball pushes the fluid to the right. The force of the flagellum is pushing the fluid to the left. Because of incompressibility, the fluid is forced toward the bacterium from top and bottom. (b) Velocity field of the fluid, computed from (2.24), around a swimmer with $\zeta = 0$.

collinear with $d^i$ by definition. The balance equations (2.28-2.29) imply that both the sum and the difference of $F^i_H$ and $F^i_T$ are collinear with $d^i$. Hence, $F^i_H$ and $F^i_T$ themselves are collinear with $d^i$.

Therefore, for each swimmers there exists a scalar parameter $\alpha^i$ such that

$$F^i_T = \alpha^i F^i_p = \alpha^i f_p d^i, \quad F^i_H = -(1 - \alpha^i) F^i_p = (1 - \alpha^i) f_p d^i.$$ (2.33)

Effectively, the parameter $\alpha^i$ groups the forces $F^i_p$ in two “force-dipole” pairs as illustrated in Fig. 2.3. Since $F^i_p$ are given, $F^i_H$ and $F^i_T$ are completely determined by the scalar $\alpha^i$.

We obtain a linear system for $\alpha^i$ by substituting (2.33) into (2.27) and using
the rigidity constraint (2.31) for $v^i_H$ and $v^i_T$:

$$\alpha^i (d^i)^T \left[ G(x^i_H - x^i_T) + G(x^i_T - x^i_H) - \frac{2}{\gamma_0} \right] d^i +$$

$$+ \sum_{j \neq i} \alpha^j (d^j)^T \left[ -G(x^j_H - x^j_T) + G(x^j_T - x^j_H) + G(x^j_H - x^j_P) - G(x^j_T - x^j_P) \right] d^j =$$

$$= \sum_{j \neq i} (d^j)^T \left[ -G(x^j_H - x^j_T) + G(x^j_T - x^j_H) + G(x^j_H - x^j_P) - G(x^j_T - x^j_P) \right] d^j +$$

$$+ (d^i)^T \left[ G(x^i_T - x^i_P) + G(x^i_P - x^i_T) - G(x^i_H - x^i_P) - \frac{1}{\gamma_0} \right] d^i. \quad (2.34)$$

In the equation (2.34) the coordinates $x^i_*, x^j_*$ ($*=H,T,P$) and the directors $d^i, d^j$ are all known; $(d^i)^T$ stands for transpose of the vector $d^i$. The system is linear for $\alpha^i$, and the coefficients depend on the positions $x^i_*, x^j_*$ ($*=H,T,P$) in a nonlinear way.

We now return to the ODE, equations (2.11). As noted before, to find the explicit form for $V$, one has to find $F^i_H$ and $F^i_T$ in terms of $F^i_P$ and $x^i_*$. Thus, the explicit form of $V$ is determined by (2.33-2.34); see Appendix C.

2.4 Perturbation analysis for two swimmers

Notations

We next consider the PDE-ODE problem (2.5-2.11) for the particular case $N=2$. Specifically, we focus on the dynamics of a coplanar pair of swimmers, when $d^i, i=1,2$, lie in the $xy$-plane. To describe the relative positions of the two
swimmers, we use the angles $\theta_1$, $\theta_2$, and $\phi$ shown in Fig. 2.4. The angular velocity in this case is characterized by a single scalar (no rotation around the axis $d_i$ of the $i$th swimmer) and is completely determined by the velocities of the balls of the dumbbell:

$$\omega^i = \dot{\theta}^i = \frac{v_H^i - v_T^i}{2L} \cdot d_i^\perp,$$

(2.35)

where $d_i^\perp$ is obtained from $d_i$ by a 90° in-plane rotation. The velocity of the center of mass is

$$v_c^i = \frac{x_H^i + x_T^i}{2} = \frac{v_H^i + v_T^i}{2},$$

(2.36)

and, as mentioned before, the dynamics of the swimmer pair is completely determined by $(v_c^i, \omega^i)$.

**Asymptotic expressions for velocities**

As explained above, the velocities in the system (2.11) can be written explicitly in terms of $\alpha^i, x_c^i,$ and $f_P$. However, this system is too cumbersome for direct analysis.

But, since we confine ourselves to the dilute limit regime, we can satisfy ourselves with asymptotic expressions in terms of the natural small parameter $\varepsilon = a^{-1}$, where $a$ is the distance between the centers of the two swimmers: $a = |x_C^2 - x_C^1| \gg 1$. 
We consider the asymptotic expansion (C.6) for $\alpha^u$. After substituting it into equation (2.34) for $\alpha^i$ and equating the terms at the same orders of $\varepsilon = |x^2_c - x^1_c|^{-1}$ (see Appendix C.2), we obtain

$$\alpha^i = \alpha_0 + O(\varepsilon^2), \quad \text{where } \alpha_0^i = \frac{1}{2} \left( 1 + z(\zeta) \frac{R}{L} + z(\zeta) \left( \frac{R}{L} \right)^2 + \ldots \right), \quad (2.37)$$

where $z(\zeta)$ is defined by (C.16).

To this end, we consider the asymptotic expansions

\begin{align*}
v^i_c &= v^i_1 + v^i_2 \varepsilon + v^i_3 \varepsilon^2 + \ldots, \quad (2.38) \\
\omega^i &= \omega^i_0 + \omega^i_1 \varepsilon + \omega^i_2 \varepsilon^2 + \ldots \quad (2.39)
\end{align*}

and substitute them into the LHS of (2.35-2.36). In the RHS of (2.35-2.36) we express $v^i_*$ using (2.27) in terms of the drag forces (or, equivalently, in terms of $\alpha^i$) and expand the obtained formulas in $\varepsilon$ (see Appendix C).

Equating the terms at every order of $\varepsilon$ results in the following expressions for $v^i_c$, $\omega^i$:

\begin{align*}
O(\varepsilon^0) : & \quad \omega^i_0 = 0, \quad v^i_0 = v_0 d^i; \\
O(\varepsilon^1) : & \quad \omega^i_1 = 0, \quad v^i_1 = 0; \\
O(\varepsilon^2) : & \quad \omega^i_2 = 0, \quad v^i_2 = A^i(f_p, L, R, \mu, \zeta, \alpha_0) B^i(\theta^1, \theta^2, \phi); \\
O(\varepsilon^3) : & \quad \omega^i_3 = A^i(f_p, L, R, \mu, \zeta, \alpha_0) C^i(\theta^1, \theta^2, \phi), \\
O(\varepsilon^4) : & \quad \omega^i_4 = D^i(f_p, L, R, \mu, \zeta, \alpha_0) E^i(\theta^1, \theta^2, \phi),
\end{align*}

where $j \neq i$.

At the leading order ($\varepsilon^0$) $i$th swimmer swims straight along its axis $d^i$ with a constant velocity $v_0$ – as if there were no other swimmer. Also, each swimmer can be viewed as two “force dipoles”; see Fig. 2.3. The disturbance due to a point force, given by $G(\mathbf{x}) \mathbf{d}$, decays as $|\mathbf{x}|^{-1}$. Hence, the disturbance due to a “force dipole,” given by $(G(\mathbf{x} + \mathbf{d}L) - G(\mathbf{x} - \mathbf{d}L)) \mathbf{d}$, which is like a derivative of $G(\mathbf{x})$, decays as $|\mathbf{x}|^{-2}$. Therefore, the first nonzero correction in (2.38) is $v^i_2 \varepsilon^2$. The first nonzero correction to rotational velocity $\omega^i$ appears only at order $\varepsilon^3$. Heuristically, this can be seen from (2.35), since the RHS of (2.35) is like a finite-difference derivative of
the vector field, decaying as $\varepsilon^2 = |x|^2$.

Notice that all corrections starting from $\varepsilon^2$ are in a separable form

$$\text{Mat}(f_p, L, R, \mu, \zeta, \alpha_0) \text{Trig}(\theta^1, \theta^2, \phi).$$

(2.45)

Here the function $\text{Mat}(f_p, L, R, \mu, \zeta, \alpha_0)$ is determined by the properties $(f_p, L, R, \mu, \zeta, \alpha_0)$ and $\alpha_0 = \alpha(L, R, \zeta)$, given by (C.15)-(C.16), of swimmers and viscosity $\mu$ of the fluid (material properties); the function $\text{Trig}(\theta^1, \theta^2, \phi)$ depends only on the mutual orientations $(\theta^1, \theta^2, \phi)$ of swimmers.

The separable form (2.45) allows us to study separately two questions:

(a) For given material properties, how does the dynamics depend on the initial orientations of swimmers? Here we show that swim in or swim off is determined by the sign of $\text{Trig}(\theta^1, \theta^2, \phi)$.

(b) For given orientations, how does the dynamics depends on swimmer structure (primarily, the position $\zeta$ of the propulsion force)? Here we show that swim in or swim off is determined by the sign of $\text{Mat}(f_p, L, R, \mu, \zeta, \alpha_0)$.

In particular,

$$A^i(f_p, L, R, \mu, \zeta, \alpha_0) > 0 \quad \text{for pushers } (\zeta < 0),$$

$$A^i(f_p, L, R, \mu, \zeta, \alpha_0) < 0 \quad \text{for pullers } (\zeta > 0)$$

(2.46)

(see Appendix C.3).

For swimmer 1 we have

$$A^1(f_p, L, R, \mu, \zeta, \alpha_0) = \frac{f_p L}{32\pi \mu}(1 - \zeta - 2\alpha_0) > 0,$$

(2.47)

$$B^1(\theta^1, \theta^2, \phi) = -2(1 + 3 \cos(2(\theta_2 - \phi))) \begin{bmatrix} \cos(\phi) \\ \sin(\phi) \end{bmatrix},$$

(2.48)

and

$$C^1(\theta^1, \theta^2, \phi) = 3 \sin(\theta_1 - \phi) \left[ 5 \cos(\theta_1 + 2\theta_2 - 3\phi) + 2 \cos(\theta_1 - \phi) + (2.49) + \cos(\theta_1 - 2\theta_2 + \phi) \right],$$

(2.49)
\[
D^1(f_p, L, \mu, \zeta) = \frac{3f_p L^2(\zeta^2 - 1)}{256\pi\mu}, \quad (2.50)
\]
\[
E^1(\theta^1, \theta^2, \phi) = 35 \sin(2\theta^1 + 3\theta^2 - 5\phi) + 5 \sin(2\theta^1 + \theta^2 - 3\phi) + \\
+ 5 \sin(2\theta^1 - \theta^2 - \phi) - 4 \sin(\theta^2 - \phi) - \\
- 20 \sin(3\theta^2 - 3\phi) + 3 \sin(2\theta^1 - 3\theta^2 + \phi). \quad (2.51)
\]

To obtain the corresponding expressions for swimmer 2, we simply switch the indexes 1,2 and replace \(\phi\) with \((\pi + \phi)\), since \(\phi\) is the angle between \((x_2^c - x_1^c)\) and the \(x\)-axis. Note that from (2.47), the sign of \(C^i\) and \(B^i\), given by (2.49,2.48), will give the sign of the first-order corrections to \(v^i_c\) and \(\omega^i\).

### 2.5 Dynamics for two swimmers

The asymptotic formulas (2.40)-(2.44) describe the dynamics of a well-separated pair of swimmers. The difficulty with interpreting these equations is the number of independent parameters \((\theta^1, \theta^2, \phi)\), which does not allow having a single, comprehensive graph for the trajectories of two swimmers. Therefore, we consider two basic, yet representative, configurations (see Fig. 2.5) where there is only one free parameter and the remaining parameters are fixed.

The motivation for the choice of these basic configurations is twofold. First, the evolution of simple symmetric states, such as “mirror image,” provides an insight into the behavior of the pair of swimmers in the course of collisions. Second, these configurations allow for at least qualitative comparison with experimental data (on swim in/swim off of a pair of swimmers as shown in [13]).

#### 2.5.0.1 “Mirror image”

We first consider the case with the two swimmers positioned symmetrically with respect to the \(x\)-axis (see Fig. 2.5(a)). Because of the symmetry, the positions of the swimmers will remain symmetric relative to the \(x\)-axis at all times. Then the factors (2.48,2.49,2.51) in the asymptotic expressions (2.42)-(2.44) become

\[
C^1(\theta^1, \theta^2, \phi) = C^1(\theta^1, -\theta^1, \pi/2) = -3 \sin(2\theta^1)[3 - \cos(2\theta^1)], \quad (2.52)
\]
\[
C^2(\theta^1, \theta^2, \phi) = C^1(-\theta^1, \theta^1, -\pi/2) = 3 \sin(2\theta^1)[3 - \cos(2\theta^1)] = -C^1(\theta^1, -\theta^1, \pi/2),
\]
(a) “Mirror image” configuration  (b) “Parallel” configuration

Figure 2.5. Two basic configurations for the relative position of two swimmers. Configuration 1 is called the “mirror image” configuration, because swimmers are symmetric relative to $x$-axis. Configuration 2 is called the “parallel” configuration, because swimmers are parallel to one another.

\[
B^1(\theta^1, \theta^2, \phi) = B^1(\theta^1, -\theta^1, \pi/2) = \begin{bmatrix}
0 \\
-2(1 - 3 \cos(2\theta^1))
\end{bmatrix}, \quad (2.53)
\]
\[
B^2(\theta^1, -\theta^1, \pi/2) = B^1(\theta^1, -\theta^1, \pi/2)
\]

and

\[
E^1(\theta^1, -\theta^1, \pi/2) = \cos(\theta^1) \left[ 2 - 56 \cos(2\theta^1) + 6 \cos(4\theta^1) \right], \quad (2.54)
\]
\[
E^2(\theta^1, -\theta^1, \pi/2) = -E^1(\theta^1, -\theta^1, \pi/2). \quad (2.55)
\]

**Analysis of steady states**

If a steady (invariant) configuration of two swimmers exists (determined by $\theta^1$), it has to be rotationally steady,

\[
\omega^1(\theta_1) = 0 = \omega^2(\theta_1), \quad (2.56)
\]

and translationally steady,

\[
v^1(\theta^1) = v^2(\theta^1). \quad (2.57)
\]

We show below that no value of $\theta^1$ satisfies both (2.56) and (2.57) (while each of these conditions can be satisfied separately).
Figure 2.6. Figures (a) and (b) correspond to the swimmers for which the position of the propulsion force is given by \( \zeta = -2 \). (a) Schematic illustration of the dynamics of the angle \( \theta^1 \) (angle between the axis \( d^1 \) of the first swimmer and the \( x \)-axis) in the “mirror image” configuration. Arrows on the unit circle indicate the direction of change of the angle \( \theta^1 \). The states \( \theta^1 = \pm \pi/2 \) (empty circles) are the unstable steady states for pushers (\( \zeta < 0 \)) and stable for pullers (\( \zeta > 0 \)), from (2.46). The states \( \theta^1 = -\varepsilon \theta^1_1 \) and \( \theta^1 = \pi + \varepsilon \theta^1_1 \) (solid circles) are the stable steady states for pusher (\( \zeta < 0 \)) and unstable for pullers (\( \zeta > 0 \)), from (2.46). (b) The angle \( \theta^1 \) is plotted against the distance \(|x_{1C} - x_{2C}|\) between swimmers. For \( \theta^1 > 0 \) (swimmers oriented inward) the dynamics indicated by arrows shows that swimmers move toward each other (\(|x_{1C} - x_{2C}|\) decreases) and rotate outward (\( \theta^1 \) decreases). This action corresponds to the first part (\( T_0 < t < T_1 \)) of trajectories in Fig. 2.7(a). The bold red curve indicates the rotationally steady states, obtained from (2.56) and (2.43)-(2.44). The dashed blue curve indicates the translationally steady states, obtained from (2.57) and (2.40)-(2.42). These curves never intersect – no state is rotationally and translationally steady at the same time.

The trivial rotationally steady states are \( \theta^1 = \pm \pi/2 \) (respectively, swimmers moving toward or away from one other on a vertical line). These configurations are rotationally steady, since the configuration and the PDE (2.5) are invariant under reflection across the \( yz \)-plane:

\[
\begin{bmatrix}
u_x(-x, y, z) \\
u_y(-x, y, z) \\
u_z(-x, y, z)
\end{bmatrix} =
\begin{bmatrix}
-u_x(x, y, z) \\
u_y(x, y, z) \\
u_z(x, y, z)
\end{bmatrix},

p(-x, y, z) = p(x, y, z). \quad (2.58)
\]

Hence the trajectories and orientations of swimmers will also be invariant under this reflection. Thus, swimmers starting with their centers \( x_{1C} \) on a vertical line (\( x = z = 0 \)) and oriented vertically (\( \theta^1 = \pm \pi/2 \)) will move vertically on that line.
Hence, these configurations are, indeed, rotationally steady.

But, since the distance between swimmers is not preserved, these configurations are not translationally steady. Thus, these configurations are not steady.

Two other rotationally steady angles (both are stable under variations of $\theta^1$ for pushers and unstable for pullers, due to (2.46)) are

$$\theta^1 = 0 - \theta_1^1 \varepsilon + O(\varepsilon^2), \quad \text{and} \quad \theta^1 = \pi + \theta_1^1 \varepsilon + O(\varepsilon^2),$$

where

$$\theta_1^1 = 4 A^1(f_p, L, \mu, \zeta, \alpha^2) D^1(f_p, L, \mu, \zeta) = \frac{-3L(\zeta + 1)(1 - \zeta)}{2(1 - \zeta - 2\alpha^2)} > 0.$$

The angles (2.59) are found by setting

$$\omega^1 = \varepsilon^3 \omega_3^1 + \varepsilon^4 \omega_4^1 + O(\varepsilon^5) = O(\varepsilon^5).$$

For these angles $\theta^1$, the vertical component of the translational velocity has the form

$$\mathbf{v}^1 \begin{bmatrix} 0 \\ 1 \end{bmatrix} = |\mathbf{v}_0^1| \sin(\theta^1) + O(\varepsilon^2) = -|\mathbf{v}_0^1| \frac{2A^1(f_p, L, \mu, \zeta, \alpha^2)}{D^1(f_p, L, \mu, \zeta)} \varepsilon + O(\varepsilon^2) < 0$$

for $\varepsilon \ll 1$. Thus swimmers are moving apart and the states are not translationally steady.

Therefore, there is no steady “mirror image” configuration of swimmers under the assumptions of the model.

**Dynamics of the swimmers as a function of the position $\zeta$ of the propulsion force**

Next, we plot the trajectories of two swimmers in the “mirror image” configuration.

We choose an initial orientation of swimmers parallel to the $x$-axis ($\theta^1 = 0$). The trajectories of the centers of swimmers are shown in Fig. 2.7.

We observe that when the propulsion force is applied between the dumbbell balls ($-1 < \zeta < 1$), swimmers initially move apart and rotate inwards (see Fig. 2.7.c). After time $t_0$ (when swimmers have rotated sufficiently inwards) they start approaching each other and swim in. Eventually, the distance between the
swimmers decreases, and the assumptions about well-separated swimmers become invalid, so more accurate representations of the drag forces and velocities are needed to address evolution of the pair in this state. Remarkably, this behavior is consistent with the experimentally observed attraction between two nearby bacteria; see Fig. 1 in [13]. While experiments suggest the existence of long-living states of a close pair of bacteria swimming on parallel tracks, it is likely that this state cannot be properly captured in the asymptotic far-field approximation for the velocity fields of moving spheres used in this chapter.

![Figure 2.7](image)

**Figure 2.7.** Trajectories of initially parallel swimmers in the “mirror image” configuration (radius of dumbbell balls $R = 1$). (a) External pushers ($\zeta < -1$) at first ($T_0 < t < T_1$) attract and rotate outward. When rotated sufficiently outward ($t > T_1$), the swimmers swim off. (b) External pullers ($\zeta > 1$) swim off. (c) Internal swimmers ($|\zeta| < 1$) at first ($T_0 < t < T_1$) repel and rotate inward. When rotated sufficiently inward ($t > T_1$), the swimmers swim in.

The detailed explanation of this behavior is as follows. Initially, at the leading order ($\varepsilon^0$) the translational motion is along the $x$-axis ($\mathbf{v}_0^i = v_0 \mathbf{d} \parallel \mathbf{a}_x$). The next correction $\varepsilon^2 \mathbf{v}_2^i$ is directed outwards; hence, initially the swimmers move apart. This can be seen by substituting (2.40)-(2.42) and (2.47,2.53) into the expansion (2.38). As the swimmers move apart they are rotating inwards due to the $\varepsilon^3 \omega_3^i$ term in (2.39). The rotation changes the orientation of $\mathbf{d}^i$ and hence of the leading-order translational motion $\mathbf{v}_0^i = v_0 \mathbf{d}$. At $t = t_0$, which solves

$$\left( \mathbf{v}_0^i(t_0) + \varepsilon^2 \mathbf{v}_2^i(t_0) \right) \cdot e_2 = 0,$$

(2.60)
the swimmers rotated sufficiently inwards that the terms $v_0^i$ and $\varepsilon^2 v_2^i$ balance each other. After this moment ($t > t_0$) the contribution of $v_0^i$ to the motion along $oy$-axis dominates $\varepsilon^2 v_2^i$. Hence, swimmers start approaching each other (swim in).

We also observe that when the propulsion force is not between the dumbbell balls ($|\zeta| > 1$), the swimmers swim off (see Fig. 2.7(a) and 2.7(b)). These observations emphasize the fact that the dynamics of the pair of swimmers depends sensitively on the position of the propulsion force and, consequently, on the shape of the microorganisms and the structure of its propulsion apparatus.

**Stability of the “mirror image” configuration:**

The “mirror image” configuration is a reduction that allows us to describe the state of the swimmer pair with only two parameters ($a$ and $\theta^1$). How generic is this subset within the space of all configurations? Appendix D address this question in some detail and shows that the “outward” configuration ($\theta^1 < 0$) is stable whereas the “inward” configuration ($\theta^1 > 0$) is unstable, so that nearby configurations in the “general position” tend to approach the “outward mirror image” state but not the “inward mirror image,” at least when the interswimmer distance is large: $a \gg 1$. Since the “inward mirror image” is central to our description of asymptotic scattering of swimmers, we briefly comment on its validity. We regard this configuration as representative of the general asymptotic dynamics in that if a “swim off” (see below) occurs for the interaction of swimmers in the “inward mirror image” position, it will certainly occur in the “general position” case. At the same time, if a “swim in” occurs in the “inward mirror image” situation (as is shown below for specific choices of the force location), it is likely to occur for the nearby “general position” configurations, since the crucial “inward” character of the configuration is robust to perturbations. We plan to investigate this matter more closely in the future by considering a wider subspace of swimmer pair configurations.

The “mirror image” configuration is stable under small perturbations in orientations of the swimmers when they are rotated outward from one another. The “mirror image” configuration is unstable under small perturbations in orientations of the swimmers when they are rotated inward to one another (see Appendix D).

Nevertheless, the swim in or swim off of swimmers in the “mirror image” configuration (as can be seen from Fig. 2.8 and Fig. 2.9) is representative of their
Figure 2.8. Pictures (a)-(c) show the trajectories for inner swimmers ($\zeta = 0$) starting from a perturbed parallel “mirror image” configuration. The measure of perturbation $\delta$ is defined by (D.2). The picture (a) corresponds to $\delta(0) = 0$, that is, the unperturbed “mirror image.” The picture (b) corresponds to $\delta(0) = 0.01$, and the picture (c) corresponds to $\delta(0) = 0.1$. The unit of length here is the radius $R = 1$ of a ball in the swimmer dumbbell.

Figure 2.9. Distance between two swimmers, starting from a perturbed parallel “mirror image” configuration distance 200 apart, at time $T$ ($T \approx 100$ seconds) as a function of the initial perturbation $\delta(0)$. The unit of length here is the radius $R = 1$ of a ball in the swimmer dumbbell.

mutual dynamics, resulting from hydrodynamic interactions.

2.5.0.2 “Parallel” configuration

Here we consider a pair of swimmers in a “parallel” configuration (see Fig. 2.5): one located ahead of the other parallel to one another ($\theta^1 = \theta^2$) and initially
parallel to the $x$-axis. The parameter $\phi$ measures the angle between $(x^2_C - x^1_C)$ and the $x$-axis. As swimmers may not be aligned with the $x$-axis for $t > 0$, we introduce another parameter $\tilde{\phi}$ – the angle between $(x^2_C - x^1_C)$ and the axis of the first swimmer $d^1(t)$. Thus, $\tilde{\phi}(t) = \phi(t) - \theta^1(t)$.

The factors (2.42)-(2.44) in the asymptotic expressions (2.38)-(2.39), when written in terms of $\tilde{\phi}$ instead of $\phi$, become

\[
C^1(\theta^1, \theta^2, \tilde{\phi}) = C^1(0, 0, \tilde{\phi}) = 3\sin(2\tilde{\phi}) \left[1 - 5\cos(2\tilde{\phi})\right]
\] (2.61)

\[
C^2(\theta^1, \theta^2, \tilde{\phi}) = C^1(0, 0, \tilde{\phi} + \pi) = 3\sin(2\tilde{\phi}) \left[1 - 5\cos(2\tilde{\phi})\right] = C^1(0, 0, \tilde{\phi})
\] (2.62)

and

\[
B^1(\theta^1, \theta^2, \tilde{\phi}) = B^1(0, 0, \tilde{\phi}) = -2(1 + 3\cos(2\tilde{\phi})) \begin{bmatrix} \cos(\tilde{\phi}) \\ \sin(\tilde{\phi}) \end{bmatrix}, \quad (2.63)
\]

\[
B^2(\theta^1, \theta^2, \tilde{\phi}) = B^1(0, 0, \tilde{\phi} + \pi) = 2(1 - 3\cos(2\tilde{\phi})) \begin{bmatrix} \cos(\tilde{\phi}) \\ \sin(\tilde{\phi}) \end{bmatrix}, \quad (2.64)
\]

\[
E^1(\theta^1, \theta^1, \tilde{\phi}) = -\frac{1}{2}\sin(\tilde{\phi}) \left[9 + 20\cos(2\tilde{\phi}) + 35\cos(4\tilde{\phi})\right], \quad (2.65)
\]

\[
E^2(\theta^1, \theta^1, \tilde{\phi}) = -E^1(\theta^1, \theta^1, \tilde{\phi}). \quad (2.66)
\]

Since for a general angle $\tilde{\phi}$ term $E^1(0, 0, \tilde{\phi}) \neq 0$, equation (2.66) implies that

\[
\omega^1(\phi) \neq \omega^2(\phi). \quad (2.67)
\]

This means that a pair of swimmers in the “parallel” configuration may not remain in the “parallel” configuration at some later time. In other words, the “parallel” configuration may not be preserved in time (unlike the “mirror image” configuration, which is preserved in time).

The only angles $\tilde{\phi}$ for which swimmers remain in the “parallel” configuration are $\tilde{\phi} = 0$ and $\tilde{\phi} = \pi$. These angles correspond to a pair of swimmers one following another on the same straight line; we call this the head-to-tail configuration. The difference between $\tilde{\phi} = 0$ and $\tilde{\phi} = \pi$ is only in assigning numbers to swimmers ($\tilde{\phi} = \pi$ means that the leading swimmer is called the first, while $\tilde{\phi} = 0$ means that
the trailing swimmer is called the first). Next, w.l.o.g. we consider the case \( \tilde{\phi} = 0 \).

**“Head-to-tail” configuration**

From the top-bottom symmetry, it follows that for \( \tilde{\phi} = 0 \) the rotational corrections at all orders vanish. For instance, to the order \( \varepsilon^4 \) this can be checked by plugging \( \tilde{\phi} = 0 \) into (2.43)-(2.44) using (2.47),(2.49) and (2.51)

The stability (under variations in \( \tilde{\phi} \)) of the “head-to-tail” configuration of swimmers is determined by the sign of the leading-order correction terms \( C_1 \) and \( C_2 \) in the rotational velocities \( \omega_1 \) and \( \omega_2 \); see (2.61,2.62).

Take \( \theta_1(0) = \theta_2(0) \) (swimmers initially aligned with \( x \)-axis) and \( \tilde{\phi}(0) = \phi(0) \) small positive (the second swimmer is ahead and slightly above the first one). Then \( C_1 = C_2 < 0 \), which means \( \omega_1, \omega_2 < 0 \): the swimmers are rotating clockwise. The angle \( \tilde{\phi} = \phi - \theta_1 \) increases. Similarly, take \( \tilde{\phi}(0) = \phi(0) \) small negative. Then \( C_1 = C_2 > 0 \), which means \( \omega_1, \omega_2 > 0 \): the swimmers are rotating counterclockwise and \( \tilde{\phi} = \phi - \theta_1 \) decreases.

Therefore, from (2.46), for pushers (\( \zeta < 0 \)) the “head-to-tail” configuration is unstable and for pullers (\( \zeta > 0 \)) it is stable. This result is in fact consistent with the simulations of [48] indicating formation of close “head-to-tail” pairs of puller dumbbells.

**Dynamics of swimmers as a function of the position \( \zeta \) of the propulsion force**

We study the dependence of the dynamics of two swimmers in the “head-to-tail” configuration, depending on the position \( \zeta \) of the propulsion force. Since the two swimmers are positioned on the same line (there is no preferred direction other than this line), will stay on this line and can either get closer together or get farther apart as they move on this line.

We observe that pushers (\( \zeta < 0 \)) always swim off and pullers (\( \zeta > 0 \)) always swim in (see Fig. 2.10).

### 2.5.1 Quasi-two-dimensional model

In this section we consider two swimmers swimming in a thin film (quasi-two-dimensional fluid, abbreviated Q2D). The interest in studying this case is due to a number of physical experiments (e.g., [5, 7, 13, 9]) observing the motion of bacteria in a thin film (in particular, in experiments in [9] the thickness of the film was of
**Figure 2.10.** Dependence of the relative velocities of two swimmers in the “head-to-tail” configuration on position $\zeta$ of the propulsion force. Pushers ($\zeta < 0$) swim off; pullers ($\zeta > 0$) swim in. The asymptotic technique used by us cannot be applied to the uncharacterized regions (between dashed lines) of $\zeta$ close to $\pm 1$.

The same order as the thickness of the bacteria). The thin film allows one to focus a microscope on individual bacteria and track their motion with time.

The modeling in a thin film (of thickness $2h$) differs from the above model in the whole space because the boundary conditions on the top and bottom of the thin film must be taken into account. While the experiments in [5, 9] were performed with free-standing fluid film, suggesting free slip boundary conditions on the interfaces, the experiment in [9] indicates formation of thin, solid-like walls on the fluid-air interfaces due to the byproducts of bacterial metabolism. Therefore, in fact, the correct boundary conditions for the in-plane velocities are no-slip.

Hence, instead of the fundamental solution $G(\cdot)$ of the Stokes equation in the whole space, we use its Q2D analog – the Green’s function $\tilde{G}(\cdot)$ with no-slip boundary conditions on the horizontal walls ($z = \pm h$):

$$\tilde{G}(x, y, h) = \tilde{G}(x, y, -h) = 0. \quad (2.68)$$

The series expansion for the velocity of the fluid due to a point force $\delta(r)e_1$ is obtained in [56]:

$$u(r) = \tilde{G}(r)e_1. \quad (2.69)$$
Taking the leading term in this series (as $|\mathbf{r}| \to \infty$), we get an approximation

$$\mathbf{u}(\mathbf{r}) = \begin{bmatrix} u_x(\mathbf{r}) \\ u_y(\mathbf{r}) \\ u_z(\mathbf{r}) \end{bmatrix} \approx \frac{f(z)}{|\mathbf{r}|^4} \begin{bmatrix} x^2 - y^2 \\ 2xy \\ 0 \end{bmatrix},$$

(2.70)

where $f(z)$ is a known function (see [56] and Appendix B.4).

Analogously to the 3D approximation (2.25), we want to approximate the fluid flow due to a sphere moving (in the $xy$-plane) midway between the walls by

$$\mathbf{u}(\mathbf{r}) \approx -\gamma_0 \tilde{G}(\mathbf{r}) \mathbf{F},$$

(2.71)

where $\mathbf{F}$ is the drag force on the sphere. The approximation (2.71) is valid when $R \ll h$. It applies here, because we are concerned with the following scaling regime: $R \ll h \ll L \ll \varepsilon^{-1}$, where $\varepsilon^{-1} = |\mathbf{x}_C^2 - \mathbf{x}_C^1|$ is the distance between the two swimmers.

The solution procedure is exactly the same as for the 3D fluid, except that $G(\mathbf{r})$ is replaced by $\tilde{G}(\mathbf{r})$. Using a Q2D analog of (2.27), we obtain the velocity field of the Q2D fluid due to a swimming bacterium (see Fig. 2.11).

Note that the asymptotic Green’s function $\tilde{G}(\cdot)$ for the Q2D fluid is qualitatively different from the Green’s function $G(\cdot)$ in a 3D fluid. For instance, they have different rates of decay: $G(\mathbf{r}) \sim |\mathbf{r}|^{-1}$ and $\tilde{G}(\mathbf{r}) \sim |\mathbf{r}|^{-2}$. In addition, since the shear modes in the Q2D geometry decay exponentially with the decay rate determined by the spacing between the wall $2h$, (see, e.g., [57]), only curl-free “pressure modes” decay powerlike survive far away from the origin. But, most importantly, $\tilde{G}$ has negative coupling, $e_1^T \tilde{G}(e_2)e_1 < 0$. This means that by applying force to the Q2D fluid in the positive direction along the $x$-axis some of the fluid will actually be moving in the negative direction (unlike in 3D, where the coupling is positive and all fluid moves in the positive direction). In spite of these qualitative differences, the velocity of the fluid due to a swimming bacterium in Q2D and 3D fluids have similar structures (compare the bold arrows on Figs. 2.2 and 2.11). This similarity of the velocity fields suggests that the dynamics of swimmers may also be similar for 3D and Q2D fluids. Indeed, we find this to be the case.

Note that the velocity field (2.70) due to the point force is curl-free. Therefore,
the velocity fields (a) and (b) are also curl-free as superpositions of velocity fields of the form (2.70). It appears that circulation of the velocity fields in Figs. 2.11(a) and (b) along closed contours passing through dumbbell balls is not zero, since vector fields point counterclockwise along some curves. This situation leads to an apparent contradiction with the Stokes formula. However, all such curves pass through a singular point of the vector field in the center of the ball, and the Stokes theorem does not apply (compare to classical electrostatics where all field lines pass through point charges).

**Asymptotic expressions for velocities**

Substitute the asymptotic expansion (2.38)-(2.39) into the LHS of (2.35)-(2.36). Write the velocities of the balls in the RHS of (2.35)-(2.36) in terms of $\alpha_0$; see (C.1)-(C.2) and (C.6). Expand $G(\cdot)$ in powers of $\varepsilon$ and solve the equations at like powers of $\varepsilon$,

\[
\begin{align*}
O(1) : & \quad \omega_0^1 = 0, \quad v_0^1 = v_0 d^i, \\
O(\varepsilon) : & \quad \omega_1^1 = 0, \quad v_1^1 = 0, \\
O(\varepsilon^2) : & \quad \omega_2^1 = 0, \quad v_2^1 = 0, \\
O(\varepsilon^3) : & \quad \omega_3^1 = 0, \quad v_3^1 = \frac{f_p L (1 - \zeta - 2\alpha_0)}{4\pi\mu} \left[ \begin{array}{c} -\cos(2\theta^2 - 3\phi) \\ \sin(2\theta^2 - 3\phi) \end{array} \right],
\end{align*}
\]
\[ O(\varepsilon^4) : \quad \omega_1^4 = \frac{3f_p L(1 - \zeta - 2\alpha_0)}{4\pi \mu} \sin \left(2\theta_1^1 + 2\theta_2 - 4\phi\right), \]  
\[ O(\varepsilon^5) : \quad \omega_3^5 = \frac{3f_p L^2(\zeta^2 - 1)}{2\pi \mu} \sin \left(2\theta_1^1 + 3\theta_2^1 - 5\phi\right). \]  

Next, we analyze the dynamics of two well-separated swimmers in the “mirror image” and “head-to-tail” configurations (see Fig. 2.5) in the Q2D fluid. We observe that the dynamics of swimmers is qualitatively the same as that of a 3D fluid. The robustness of the dynamics can be explained by the similarity between the velocity fields due to swimmers (compare Figs. 2.2 and 2.11).

**Dynamics of the swimmers as a function of the position \( \zeta \) of the propulsion force**

**A. (“Mirror image” configuration, Q2D fluid)**

We analyze the dynamics of swimmers depending on the position \( \zeta \) of the propulsion force for the “mirror image” configuration of swimmers. We observe that (as in 3D, see Fig. 2.7(c)) when the propulsion force is positioned between the dumbbell balls (\(|\zeta| < 1\)) the swimmers swim in (see Fig. 2.12(c)).

Also, (as in 3D, see Fig. 2.7(a) and Fig. 2.7(b)) when the propulsion force is positioned outside the dumbbell (\(|\zeta| > 1\)) the swimmers swim off (see Fig. 2.12(a) and Fig. 2.12(b)).

**B. “Head-to-tail” configuration, Q2D fluid**

![Figure 2.12](image-url)  
**Figure 2.12.** Trajectories of two swimmers in a Q2D fluid in the “mirror image” configuration, starting from \((T_0)\) parallel orientation \((\theta_1 = \theta_2 = 0; \text{radius of dumbbell balls } R = 1)\). Initially in (a) through (c) the swimmers are parallel to each other \(\theta_1 = \theta_2 = 0\): (a) \(\zeta < -1\), the outer pushers swim off; (b) \(\zeta > 1\), the outer pullers swim off; (c) \(|\zeta| < 1\), the inner swimmers swim in.
Figure 2.13. Dependence of the relative velocities of two Q2D swimmers in the “head-to-tail” configuration on $\zeta$, which determines the position of the propeller. Pushers ($\zeta < 0$) swim off, and pullers ($0 < \zeta$) swim in. The asymptotic technique used by us cannot be applied to the uncharacterized regions (between dashed lines) of $\zeta$ close to $\pm 1$.

For two swimmers in the “head-to-tail” configuration in the Q2D fluid we observe the same dynamics as for the 3D fluid – pushers ($\zeta < 0$) swim off and pullers ($0 < \zeta$) swim in (see Fig. 2.13).

2.6 Conclusions

In this chapter we studied the hydrodynamic interaction between two microscopic swimmers, modeled as self-propelled dumbbells, in two distinct settings: three-dimensional and quasi-two-dimensional fluid domains. The interaction in a three-dimensional fluid domain models the interaction of swimmers in the bulk (away from the walls of the container), while the interaction in a quasi-two-dimensional fluid domain models the interaction of swimmers in a thin film. Qualitatively, models in both settings produced the same results, thus suggesting that the hydrodynamic interaction of a pair of swimmers is robust under the change of geometry of the fluid domain.

At the same time, the shape of the swimmer, that is, the position ($\zeta$) of the effective propulsion force, proved to have a critical effect on the character of the
hydrodynamic interaction of swimmers. In the “mirror-image” configuration the
dynamics of swimmers differentiates inner ($|\zeta| < 1$) and outer swimmers ($|\zeta| > 1$).
Inner swimmers ($|\zeta| < 1$) in the “mirror-image” configuration experience a swim in, approaching each other and perfectly matching the swim in experimentally
observed in [13] for the rod-shaped bacterium *Bacillus subtilis*, which has multiple
flagella distributed over the cell surface. Unlike inner swimmers, outer swimmers
($|\zeta| > 1$) in the “mirror-image” configuration experience a swim off, due to outward
rotation.

In the “head-to-tail” configuration the dynamics of the swimmers differentiates
pushers ($\zeta < 0$) and pullers ($\zeta > 0$). Pushers ($\zeta < 0$) in the “head-to-tail”
configuration experience a swim off; that is, while they remain oriented along the
same straight line, the distance between them gradually increases. Unlike pushers,
pullers ($\zeta > 0$) in the “head-to-tail” configuration experience a swim in; that is,
while they remain on the same straight line, the distance between them gradually
decreases. Moreover, for pushers the “head-to-tail” configuration is not stable,
whereas for pullers it is stable. Thus, our model predicts a formation of “head-to-
tail” structures by pullers and no such structures for pushers.

The surprising sensitivity of the observed hydrodynamic interaction of swim-
mers to the flagellum position (more generally to the structure of the propulsion
apparatus) and, therefore, to the structure and the shape of the swimmer may
explain the wide range of behaviors exhibited by microorganisms (see, e.g., [58] for
a study of a sperm cell with a very long flagellum and [59] for a study of algae that
pull themselves forward with flagella positioned in the forward part of the body)
and different models of microscopic swimmers, such as dumbbells [48], squirmers
[40], self-locomoting rods [24], and three-sphere swimmers [60].

Further refinements of our model are keenly needed. In particular, our calcula-
tions are conducted in the dilute limit, where the distance between the swimmers
is large compared to their size. However, as we demonstrated, pushers have a
tendency to converge, thus eventually violating this approximation. Therefore,
nontrivial regularizations of the interaction at small distances using, possibly, lu-
brication forces and hard-core repulsion must be included into the model in order
to obtain agreement with experiments and simulations. Further, at high con-
centration, deviations from the pairwise interaction may also become important,
especially because hydrodynamic forces decay very slowly in the three-dimensional geometry of the sample.
Chapter 3

Effective shear viscosity and dynamics of suspensions of micro-swimmers from small to moderate concentrations

3.1 Introduction

In this chapter, we present a two-dimensional mathematical model of the suspension of microswimmers in fluid and its analysis. The results of this Chapter were published in [52].

We model the elongated body of the swimmer as an ellipse. The front half of the ellipse represents the solid surface and the back half represents the surface covered with flagella or cilia (e.g. Paramecium) that exert the propulsion force onto the fluid.

We consider both dilute and moderate concentration regimes. In the dilute regime (no swimmer-swimmer interactions) we demonstrate analytically that self-propulsion has no effect on the effective viscosity. Therefore, we show that the elongated shape of the swimmers and the propulsion force are not sufficient to change the effective viscosity as compared to the passive suspensions.

On the other hand, the numerical analysis of the moderate concentration
regime, taking into account all interactions, showed a decrease of the effective viscosity with propulsion strength of the swimmers. At this concentration regime all of the above features (ii-iv) are present: the elongated shape of the swimmers, the propulsion force and the swimmer-swimmer interactions. Both concentration regimes are discussed to pinpoint the importance of interactions between swimmers for reduction of viscosity.

To reflect the settings of the physical experiments in [28] and [5] further, we studied the suspension at moderate concentrations of approximately 10% by volume. At such concentrations, computational analysis is the only available tool. The major difficulty in the theoretical analysis is the dependence of the apparent instantaneous viscosity on the distribution of the swimmers in the fluid domain. The distribution changes with time due to interaction of the swimmers with the ambient flow and other swimmers. In direct numerical simulations, to obtain accurate values for the effective viscosity, we average the instantaneous apparent viscosity over extended periods of time.

First, to validate the model and to analyze accuracy of the numerical method we performed a number of tests for the dynamics of a swimmer in the proximity of a wall or another swimmer. We observed the attraction of a swimmer to another swimmer and a swimmer to the wall. The attraction in both cases is only short term. A swimmer next to a wall, while getting closer to the wall, will slowly rotate and swim away from the wall. Two nearby swimmers will swim away from one another once their positions become offset from the mirror image configuration (see Fig. 3.6). These numerical results agree with the physical observations for *Escherichia coli* [61], *Bacillus subtilis* [29], and *Volvox* [47]. At the same time, the results shed light on the details of the swimmer-swimmer and swimmer-wall interactions.

Second, we performed a number of numerical simulations at moderate concentrations where we computed the effective shear viscosity of a suspension of swimmers in a layer between two solid walls undergoing a shearing motion with relative velocity $2v$. We analyzed the dependence of the effective viscosity on the velocity $v$ and the propulsion strength of the swimmers, $f_p$. Using an analytical scaling argument we demonstrated that the effective viscosity depends only on the propulsion-shear ratio $\frac{f_p}{\mu v}$ ($\mu$ is viscosity of the ambient fluid) for a fixed shape of
the domain and the swimmers. The simulations indicate that the effective shear
viscosity decays linearly as a function of the propulsion-shear ratio (for small val-
ues of $f_p/\mu$). The same linear trend continues for negative values of the propulsion
strength, which corresponds to microswimmers swimming in the opposite direc-
tion, i.e. pullers instead of pushers. For larger values of the propulsion-shear ratio
a deviation from the linear trend was observed and explained by the finite size of
the container.

The outline of this chapter is as follows. In section 3.2 we present a mathemat-
ical model for a swimmer in a fluid. We write down the complete set of PDEs and
motivate each of the modeling assumptions. In section 3.2.3 we prove dependence
of the effective shear viscosity on the propulsion-shear ratio. In Section 3.3.1 we
define the instantaneous apparent viscosity and the effective shear viscosity, which
coincide for homogeneous fluids but are generally different for inhomogeneous ones.
In Section 3.4 we briefly describe the numerical method, technical difficulties and
their solutions followed by the computational results for dynamics of interacting
swimmers and the effective shear viscosity for a suspension of swimmers. Section
3.4.5 relates the time and size units in our numerical simulations to the units in
physical experiments [29]. Finally, in Section 3.5 we summarize the results of our
analysis. In appendix E we present the variational formulation for the model and
demonstrate its well-posedness.
3.2 Mathematical model of a swimmer

We present the PDE model for a microswimmer in a Stokesian fluid in Section 3.2.1 and motivate model assumptions in Section 3.2.2. The model is written in two dimensions but it can be readily extended to three dimensions. Although this PDE model was developed independently, reference should be made to the earlier works of Saintillan and Shelley [24] as well as Short, et al. [10]. Notable differences with [24] and [10] are that collisions rules are different (no collisions in [10]).

3.2.1 The PDE model for the swimmer

Let $\Omega \subset \mathbb{R}^2$ be a bounded domain with a smooth boundary representing the container of the fluid with swimmers. Each swimmer is modeled as an ellipse $S^i$, $i = 1, \ldots, N$, with the center at $x^i_C$, and the orientation $d^i$ of the longest semiaxis, see Fig. 3.1. Here and below the superscript $i$ indicates the index of the swimmer.

![Illustration of an i-th swimmer with two parts of the boundary: $\Gamma_H^i$ and $\Gamma_P^i$. On the front part $\Gamma_H^i$ of the swimmer (H stands for “head”) the fluid sticks to the surface. On the back part of the swimmer $\Gamma_P^i$ (P stands for “propeller”) the fluid cannot penetrate the boundary of the swimmer. Also, the fluid is pushed backwards on $\Gamma_P^i$ due to a prescribed tangential component of traction.](image)

The motion of the fluid surrounding the swimmers is governed by the incompressible stationary Stokes equation

$$
\begin{align*}
\mu \Delta u &= \nabla p \\
\text{div}(u) &= 0
\end{align*}
$$

in $\Omega_F := \Omega \setminus \bigcup_i \bar{S}^i$.

(3.1)
where \( \mathbf{u} \) is the fluid velocity, \( p \) is the pressure, and \( \mu \) is viscosity. The boundary of the fluid domain \( \Omega_F \) includes boundaries of the swimmers, \( \Gamma_H^i \) and \( \Gamma_P^i \), and the boundary of the container, \( \partial \Omega \). The following boundary conditions are imposed:

\[
\begin{align*}
\mathbf{u}(\mathbf{x}) &= g(\mathbf{x}) \quad \text{for } \mathbf{x} \in \partial \Omega, \\
\mathbf{u}(\mathbf{x}) &= \mathbf{u}_c^i + \mathbf{\omega}^i \times (\mathbf{x} - \mathbf{x}_c^i) \quad \text{for } \mathbf{x} \in \Gamma_H^i, \\
\{ (\mathbf{u}(\mathbf{x}) - [\mathbf{u}_c^i + \mathbf{\omega}^i \times (\mathbf{x} - \mathbf{x}_c^i)]) \cdot \mathbf{n} = 0 \}
\end{align*}
\]

(3.2) 

\[
\begin{align*}
\tau \sigma(\mathbf{u}, p) \mathbf{n} &= -f((\mathbf{x} - \mathbf{x}_c^i) \cdot \mathbf{d}^i) \quad (\tau \cdot \mathbf{d}^i) \\
\mathbf{F}_H^i + \mathbf{F}_P^i &= 0 \quad (balance \ of \ forces), \\
\mathbf{T}_H^i + \mathbf{T}_P^i &= 0 \quad (balance \ of \ torques).
\end{align*}
\]

(3.3) 

Here, the instantaneous translational, \( \mathbf{u}_c^i \), and rotational, \( \mathbf{\omega}^i \), velocities are additional unknowns. The symbols \( \mathbf{n} \) and \( \tau \) denote the unit normal and unit tangent to the surface. The stress tensor \( \sigma(\mathbf{u}, p) \) is defined by

\[
\sigma(\mathbf{u}, p) := 2 \mu D(\mathbf{u}) - p \mathbf{I}, \quad D(\mathbf{u}) := \frac{1}{2} (\nabla \mathbf{u} + (\nabla \mathbf{u})^T),
\]

(3.7) where \( \mathbf{I} \) is the identity matrix.

The known scalar function \( f \) in (3.4) defines the propulsion model (see e.g., (3.12)). The known vector function \( g \) in (3.2) is the velocity of the container boundary. The viscous forces \( \mathbf{F}_H^i, \mathbf{F}_P^i \) and torques \( \mathbf{T}_H^i, \mathbf{T}_P^i \) on \( \Gamma_H^i \) and \( \Gamma_P^i \), respectively, are given by

\[
\begin{align*}
\mathbf{F}_H^i &= \int_{\Gamma_H^i} \sigma(\mathbf{u}, p) \mathbf{n} \, d\mathbf{x}, \quad \mathbf{F}_P^i := \int_{\Gamma_P^i} \sigma(\mathbf{u}, p) \mathbf{n} \, d\mathbf{x} \\
\mathbf{T}_H^i &= \int_{\Gamma_H^i} (\mathbf{x} - \mathbf{x}_c^i) \times \sigma(\mathbf{u}, p) \mathbf{n} \, d\mathbf{x}, \quad \mathbf{T}_P^i := \int_{\Gamma_P^i} (\mathbf{x} - \mathbf{x}_c^i) \times \sigma(\mathbf{u}, p) \mathbf{n} \, d\mathbf{x}.
\end{align*}
\]

(3.8) 

The PDE problem (3.1-3.6) defines the so-called instantaneous problem. The proof of existence and uniqueness of the solution is outlined in Appendix E.

The dynamics of the swimmers, defining the evolution of the fluid domain
\( \Omega_F(t) \), is given by the following ODEs:

\[
\begin{align*}
\frac{d}{dt} x^i_C(t) &= u^i_C(t), \\
\frac{d}{dt} d^i(t) &= \omega^i(t) \times d^i(t)
\end{align*}
\]  

(3.10)

with the initial conditions

\[
x^i_C(0) = x^{i,0}_C, \quad d^i_C(0) = d^{i,0}_C, \quad \|d^{i,0}_C\| = 1.
\]  

(3.11)

### 3.2.2 Discussion and motivation for the PDE model

Modeling of the fluid motion by the incompressible stationary Stokes equations (3.1) is a standard reduction from the Navier-Stokes equations for small Reynolds number, \( \mathcal{R}e := \frac{\sqrt[3]{V L}}{\rho} \ll 1 \). Here \( \rho \) is the density of the fluid (\( \rho \approx 1 \text{g/cm}^2 \)), \( V \) and \( L \) are representative velocity and size in the problem. For instance, on the scale of self-propelled bacteria, such as \( \textit{Bacillus subtilis} \) (5 \( \mu \text{m} \) in length and 7 \( \mu \text{m} \) in width) swimming with the velocity up to 100 \( \mu \text{m/sec} \), we obtain \( \mathcal{R}e \approx 10^{-4} \ll 1 \).

The boundary condition (3.2) indicates that the fluid sticks to the walls of the container \( \Omega \), which are moving with velocity \( \mathbf{g} \). This is the standard boundary condition for solid walls. It can also be applied to the case of microswimmers in a thin film. The boundary \( \partial \Omega \), here, would be the fluid-air interface. The reason for using the no-slip boundary condition would be the experimental evidence that microorganisms produce a surfactant that solidifies the interface [9] and effectively creates no-slip conditions. The solid-like behavior of the interface was also evidenced in [62], where dry friction like behavior was observed for a micro gear touching interface, which manifests solid surface.

The boundary condition (3.3) is similar to the condition (3.2) in that the fluid sticks to the surface \( \Gamma^i_h \). But unlike \( \partial \Omega \), the boundary \( \Gamma^i_h \) is moving with translational velocity \( \mathbf{u}^i_C \) and rotational velocity \( \omega^i \) that are not known a priori and need to be found in the process of solving (3.1-3.6).

The first boundary condition in (3.4) indicates that the fluid cannot flow through the surface of the swimmer. The second condition describes a force that acts on the fluid and pushes it backward, as a result propelling the swimmer forward. Thus, we have just enough boundary conditions on \( \Gamma^i_p \) for solvability of
the problem. Note that the form of the right-hand side in (3.4) indicates that the propulsion of the swimmer is coordinate invariant. An example of the scalar function $f$ is the “uniform” distribution of force along the boundary:

$$
\tau \sigma(u, p) \mathbf{n} = -f((\mathbf{x} - \mathbf{x}_{C}^i) \cdot \mathbf{d}^i) \mathbf{n} := \frac{-f_p}{|\Gamma^i_p|} (\tau \cdot \mathbf{d}^i),
$$

where $f_p$ is the total force of the propulsion:

$$
f_p = \int_{\Gamma^i_p} f((\mathbf{x} - \mathbf{x}_{C}^i) \cdot \mathbf{d}^i) \, dx.
$$

Boundary conditions (3.5-3.6) indicate that all swimmers are self-propelled as opposed to moving due to an external force (e.g., gravity). One can obtain these equations from Newton’s second law, noting that in the Stokes regime the inertial forces are negligible compared to the viscous forces (see [51] for more details).

From a modeling point of view an important feature of microswimmers propelled by flagella is the clockwise rotation of the swimmer’s body around its axis due to hydrodynamic torque resulting from the counter-clockwise rotation of the flagella. In two-dimensional model there cannot be rotation around the axis. Also, the rotation of bacteria in thin films can be freely neglected due to proximity of the fluid-air interface above and below versus only on side of bacteria, as considered in [61]. On the other hand, should an analogous three-dimensional model be constructed this feature should be added in the definition of the tangential component of tractions on the part of the boundary responsible for the self-propulsion.

### 3.2.3 Scaling observation

The following observation will simplify the future analysis. Consider two initial value problems (3.1)-(3.11) in the same domain $\Omega$ and with the same initial data (i.e., positions of the swimmers $\{\mathbf{x}_C^i(0), \mathbf{d}^i(0)\}_{i=1}^N$) but with different boundary conditions:

**Problem I:** The boundary data are

$$
g^I(t, \mathbf{x}) \quad \text{and} \quad f^I(s).
$$

(3.14)
**Problem II:** The boundary data are

\[ g^{II}(t, x) = \lambda g^I(t/\lambda, x) \quad \text{and} \quad f^{II}(s) = \lambda f^I(s). \]  

(3.15)

We use superscripts I and II to denote solutions to the above problems. The following result is verified by the direct substitution.

**Lemma 2** (Scaling). Let functions \( u^I(t, x), p^I(t, x) \) and positions of the swimmers \( \{x_i^I(t), d_i^I(t)\}_{i=1}^N \) be solution to the first problem. Then, the functions

\[ u^{II}(t, x) := \lambda u^I(t/\lambda, x), \quad p^{II}(t, x) := \lambda p^I(t/\lambda, x) \]  

(3.16)

and the positions of the swimmers,

\[ x_{c}^{ii}(t) = x_{c}^{i}(t/\lambda), \quad d_{i}^{ii}(t) = d_{i}^{i}(t/\lambda), \]  

(3.17)

are solutions to the second problem.

**Remark 1.** The statement of Lemma 2 can be phrased as follows. Simultaneously increasing the propulsion force \( f(\cdot) \) of the swimmers and the fluid velocity \( g(x) \) by a factor of \( \lambda \) leads to swimmers moving along the same trajectories but \( \lambda \) times faster. The corresponding viscous forces are increased by a factor \( \lambda \).

**Remark 2.** A rotational diffusion may be used to model the Brownian motion or tumbling. This diffusion introduces a new time-scale which breaks up the scaling result of Lemma 2.

### 3.3 Effective viscosity

In the theory of fluid dynamics one of the primary objects of interest is the relation between the applied forces (stress) and the observed fluid flow (strain rate). For Newtonian fluids this relationship is linear:

\[ \sigma(x) = 2\mu D(u(x)) - p(x)I \quad \text{for} \ x \in \Omega_F. \]  

(3.18)

For non-Newtonian fluids (3.18) does not hold with the same value of \( \mu \). Hence, assuming that one still desires to characterize the relation between the stress and
the strain rate in the form similar to (3.18), the viscosity \( \mu \) should be permitted to vary.

In the most general case, \( \mu \) will depend on the form of the flow, i.e. \( \mu(D(u)) \). This is not very informative, as in this case the relation (3.18) is equivalent to \( \sigma = F(D(u)) \), where \( F(\cdot) \) is some function. Thus, to characterize the relation between the stress and the strain rate, one should specify the function \( F(\cdot) \).

To avoid this problem, we accept the fact that the general relation between the bulk stress and the bulk strain rate greatly depends on the type of the fluid flow. Thus, we will limit ourselves to a rather specific, but experimentally intuitive definition along the lines, proposed by Batchelor [63]:

“We shall consider here only the important and representative case in which the suspension is confined between two parallel rigid planes in steady relative shearing motion, with the stress being observed as the force per unit area on a section of one boundary with linear dimensions large compared with particle spacing.”

3.3.1 Definition of effective viscosity and instantaneous apparent viscosity

Consider a fluid (or a complex fluid, such as a suspension of active or passive particles in the fluid) between two solid plates a distance \( 2H \) apart, see Fig. 3.2. We induce a shearing motion on the boundary by moving the top plate to the right with velocity \( v \mathbf{e}_1 \) and the bottom plate to the left with velocity \( -v \mathbf{e}_1 \). We prescribe the periodic conditions on the vertical left and right boundaries. The effective shear viscosity, being a measure of friction in the fluid, should be defined in terms of the total viscous forces

\[
F_T := \int_{\Gamma_T} \sigma(u, p) \mathbf{n} \, dx \quad \text{and} \quad F_B := \int_{\Gamma_B} \sigma(u, p) \mathbf{n} \, dx,
\]

acting on the top (\( \Gamma_T \)) and the bottom (\( \Gamma_B \)) plates, respectively, and should scale correctly with the dimensions of the domain. These considerations suggest the
following quantity, dubbed as the *instantaneous apparent viscosity*:

\[ \bar{\mu}(v; t) := \frac{H}{Lv} \left( \mathbf{F}_T(t) - \mathbf{F}_B(t) \right) \cdot \mathbf{e}_1, \quad (3.20) \]

where \( L \) is the length of the plate on which viscous forces \( \mathbf{F}_T \) and \( \mathbf{F}_B \) are acting and \( \frac{\dot{\gamma}}{2H} = \dot{\varepsilon} \) is the shear rate of the background flow created by the motion of the top and bottom plates.

**Figure 3.2.** Schematic illustration of shear flow between two plates.

For homogeneous fluids the quantity (3.20) does not depend on time since the viscous forces \( \mathbf{F}_T \) and \( \mathbf{F}_B \) do not change with time. For inhomogeneous fluid there are additional challenges. For instance, for a suspension of passive or active inclusions, the value of \( \bar{\mu}(v; t) \) will be different depending on the concentration and distribution of inclusions. For a suspension of active inclusions, such as swimmers, it will also depend on the propulsion strength of the swimmers. Moreover, changing the propulsion strength from \( f_p \) to \(-f_p \) will change the value of \( \bar{\mu}(v; t) \) in a nontrivial way. In general, this value will not remain the same and will not simply change sign. For this reason, we call the quantity in (3.20) the instantaneous apparent viscosity and not the effective viscosity, which will be defined later. The word *instantaneous* indicates that \( \bar{\mu}(v; t) \) is computed at a particular instant of time and depends on a particular configuration of swimmers. The word *apparent* indicates the nontrivial dependence on the propulsion strength \( f_p \). This dependence will be analyzed later.
in section 3.3.2.1.

We would like to define the effective viscosity as a material property independent of the configuration of swimmers. Thus, we define the effective viscosity as a time average of the instantaneous apparent viscosity

\[ \hat{\mu}(v) := \lim_{T \to \infty} \frac{1}{T} \int_0^T \bar{\mu}(v; t) \, dt. \]  

(3.21)

We assume that this time-averaged quantity does not depend on the initial configuration of swimmers. Verifying this assumption is a separate research topic, which we leave for possible future analysis.

### 3.3.2 Estimates and observations for the instantaneous apparent viscosity

Here we make some analytic observations regarding the instantaneous apparent viscosity. First, we make use of the scaling observation, Remark 1. This observation tells us that the instantaneous apparent viscosity, as defined by (3.20), takes the same value for problems I and II, (3.14)-(3.15), at times \( t/\lambda \) and \( t \), respectively:

\[
\bar{\mu}^I(\lambda v, \lambda f_p; t/\lambda) = \frac{H}{L \lambda v} (F^I_T(t/\lambda) - F^I_B(t/\lambda)) \cdot e_1 =
\]

\[
= \frac{H}{L v} (F^I_T(t) - F^I_B(t)) \cdot e_1 = \bar{\mu}^I(v, f_p; t).
\]  

(3.22)

Hence, the effective viscosities, being time averages of the instantaneous apparent viscosities, also, match for the problems I and II:

\[
\hat{\mu}^I(\lambda v, \lambda f_p) = \lim_{T \to \infty} \frac{1}{T} \int_0^T \bar{\mu}^I(\lambda v, \lambda f_p; t/\lambda) \, dt =
\]

\[
= \lim_{T \to \infty} \frac{1}{T} \int_0^T \bar{\mu}^I(v, f_p; t) \, dt = \hat{\mu}^I(v, f_p).
\]  

(3.23)

This means that the effective viscosity of a suspension of swimmers depends only on the ratio of the propulsion strength \( f_p \) to the shear rate defined by \( v \), i.e.

\[
\hat{\mu} \left( \frac{v}{f_p} \right) := \hat{\mu} \left( \frac{v}{f_p}, 1 \right) = \hat{\mu} \left( 1, \frac{f_p}{v} \right).
\]  

(3.24)
The nondimensional analog of $\frac{f_p}{v}$ is $\frac{\bar{f}_p}{\bar{\mu}v}$. Due to its importance we shall refer to the ratio $\frac{f_p}{\bar{\mu}v}$ as the *propulsion-shear ratio*.

### 3.3.2.1 The apparent viscosity for the instantaneous problem

In this section we identify the dependence of the instantaneous apparent viscosity on the propulsion strength $f_p$ of the swimmers for a given distribution of swimmers. We will consider three instantaneous problems A, B and C given by (3.1-3.6) in the same fluid domain $\Omega_F$ but with different boundary conditions:

**A. Active swimmers + Shear**: \( v^A = v \) and \( f^A_p = f_p \).

**B. Passive/dormant swimmers + Shear**: \( v^B = v \) and \( f^B_p = 0 \).

**C. Active swimmers + No shear**: \( v^C = 0 \) and \( f^C_p = f_p \).

Due to linearity of the Stokes equations (3.1) the solution \((u^A, p^A)\) to the problem A is a sum of the solutions \((u^B, p^B)\) and \((u^C, p^C)\) to the problems B and C:

$$u^A(x) = u^B(x) + u^C(x) \quad \text{and} \quad p^A(x) = p^B(x) + p^C(x). \quad (3.25)$$

We have a similar relation for the forces on the top and bottom plates. Thus, the expression that enters the definition (3.20) of the instantaneous apparent viscosity is

$$F^A_T(v, f_p) - F^A_B(v, f_p) = (F^B_T(v) - F^B_B(v)) + (F^C_T(f_p) - F^C_B(f_p)). \quad (3.26)$$

Here we explicitly indicated that the forces depend on the shear velocity $v$ and the propulsion strength of the swimmers. Inserting this in definition (3.20), we obtain

$$\bar{\mu}^A(v, f_p) = \frac{H}{Lv} (F^A_T(v, f_p) - F^A_B(v, f_p)) \cdot e_1 =$$

$$= \frac{H}{Lv} (F^B_T(v) - F^B_B(v)) \cdot e_1 + \frac{H}{Lv} (F^C_T(f_p) - F^C_B(f_p)) \cdot e_1 = \bar{\mu}^B(v) + \frac{1}{v} \bar{\eta}(f_p), \quad (3.27)$$

where

$$\frac{1}{v} \bar{\eta}(f_p) := \bar{\mu}^A(v, f_p) - \bar{\mu}^B(v) = \frac{H}{Lv} (F^C_T(f_p) - F^C_B(f_p)) \cdot e_1 \quad (3.28)$$
is the contribution to the instantaneous apparent viscosity due to self-propulsion.

### 3.3.3 Effective shear viscosity for a suspension of swimmers in the dilute regime

Consider a suspension of swimmers in the dilute regime: the fluid domain is sufficiently large and swimmers are sufficiently far apart from one another. Thus, the dilute assumptions are as follows: (i) individual swimmers interact only with the background flow and do not interact with one another, (ii) only orientations of swimmers play role in the effective viscosity. We use decomposition (3.27) of the instantaneous apparent viscosity to derive the following results.

Let $\omega(\theta)$ be the rotational velocity of a swimmer as a function of angle $\theta$ between the swimmer major semiaxis and the $x$-axis. Assume that shear motion is along the $x$-axis.

**Lemma 3.** The rotational velocity of swimmers is an even function of $\theta$, i.e.

$$\omega(\theta) = \omega(-\theta).$$

**Proof.** Indeed, the rotation of swimmers is entirely due to the background flow and does not depend on the propulsion strength $f_p$ of the swimmers. That is the rotational velocity $\omega = \omega(\theta, \dot{\varepsilon})$ is only a function of the orientation of the swimmer and the shear rate $\dot{\varepsilon}$ of the background flow.

Due to reversibility of the Stokes flow, we get

$$\omega(\theta, -\dot{\varepsilon}) = -\omega(\theta, \dot{\varepsilon}).$$

(3.30)

Consider the reflection of the problem across $x$-axis. Such reflection maps

1. orientation $\theta$ to $-\theta$,

2. the flow with shear rate $\dot{\varepsilon}$ to the flow with shear rate $-\dot{\varepsilon}$,

3. angular velocity $\omega$ to $-\omega$ (due to change of the clockwise orientation)

Using the mapping 1-3 above and (3.30) we get the desired result (3.29)

$$\omega(-\theta, \dot{\varepsilon}) = -\omega(\theta, -\dot{\varepsilon}) = -( -\omega(\theta, \dot{\varepsilon})) = \omega(\theta, \dot{\varepsilon}).$$
Let \( p(\theta) \) be the density function for the portion of time that a swimmer spends at the angle \( \theta \),

\[
\int_{-\pi}^{\pi} p(\theta) \, d\theta = 1.
\]

Here the average can be taken over the time it takes a swimmer to complete a full rotation in the shear flow. Note that \( p(\theta) \) is the same for all swimmers regardless of their initial orientation.

**Lemma 4.** The density function \( p(\theta) \) is an even function of \( \theta \), i.e.

\[
p(\theta) = p(-\theta).
\]  

(3.31)

**Proof.** The statement (3.31) follows from Lemma 3 and the conservation of angular flux condition

\[
p(\theta)\omega(\theta) = \text{constant for all } \theta,
\]  

(3.32)

which says that the average flux of orientations of swimmers through the angle \( \theta \) does not depend on \( \theta \).

Indeed, (3.32) holds due to every swimmer rotating periodically in the same direction (clockwise for \( v > 0 \), counter-clockwise for \( v < 0 \)). Thus, the number of swimmers passing through orientations \( \theta_1 \) and \( \theta_2 \) on average over time is the same.

From (3.32) and (3.29) we have

\[
p(\theta)\omega(\theta) = p(-\theta)\omega(-\theta) = p(-\theta)\omega(\theta).
\]

Dividing through by \( \omega(\theta) \) we get (3.32). \( \square \)

Now we consider the contribution of self-propulsion to the instantaneous apparent viscosity \( \bar{\mu}(f_p; t) \) as introduced in (3.26) and (3.28).

**Lemma 5.** The total contribution, \( \frac{1}{v} \bar{\eta}(f_p) := \bar{\mu}(v, f_p) - \bar{\mu}(v, 0) \), of self-propulsion
to the effective viscosity is zero:

\[
\frac{1}{v} \tilde{\eta}(f_p) = \frac{1}{v} \lim_{T \to \infty} \frac{1}{T} \int_0^T \tilde{\eta}(f_p; t) \, dt = H \frac{L v}{T} \lim_{T \to \infty} \frac{1}{T} \int_0^\infty \left( F^C_T(f_p; t) - F^C_B(f_p; t) \right) \cdot e_1 \, dt = 0.
\]

(3.33)

Proof. The active contribution of \( N \) swimmers \( \tilde{\eta}(f_p; t) \) to the effective viscosity is a sum of contributions \( \tilde{\eta}_1(f_p, \theta_i(t)) \) of individual swimmers:

\[
\tilde{\eta}(f_p; t) = \sum_{i=1}^N \tilde{\eta}_1(f_p, \theta_i(t)).
\]

From the symmetry of the flow, the contribution \( \tilde{\eta}_1(f_p, \theta) \) is an odd function of \( \theta \):

\[
\tilde{\eta}_1(f_p, \theta) = -\tilde{\eta}_1(f_p, -\theta).
\]

Hence, the contribution of all swimmers to the instantaneous apparent viscosity due to self-propulsion is

\[
\tilde{\eta}(f_p) = \lim_{T \to \infty} \frac{1}{T} \int_0^T \sum_{i=1}^N \tilde{\eta}_1(f_p, \theta_i(t)) \, dt = N \int_{-\pi}^{\pi} p(\theta) \tilde{\eta}_1(f_p, \theta) \, d\theta =
\]

\[
= N \int_{-\pi}^{0} p(\theta) \tilde{\eta}_1(f_p, \theta) \, d\theta + N \int_{0}^{\pi} p(\theta) \tilde{\eta}_1(f_p, \theta) \, d\theta =
\]

\[
= -N \int_{0}^{\pi} p(\theta) \tilde{\eta}_1(f_p, \theta) \, d\theta + N \int_{0}^{\pi} p(\theta) \tilde{\eta}_1(f_p, \theta) \, d\theta = 0.
\]

(3.34)

This proves the assertion of the lemma. \( \square \)

Note that \( \tilde{\eta}(f_p) = 0 \) independently of the initial orientations of the swimmers. This is due to the first line of (3.34), which says that the time average of the contribution of each swimmer \( \tilde{\eta}_1(f_p, \theta_i(t)) \) is equal to the average over one full rotation of the swimmer. The latter one does not depend on the initial orientation of the swimmer.

From the definition of the effective viscosity (3.21), decomposition of instantaneous apparent viscosity (3.26), independence of the dynamics of the orientations of swimmers of the propulsion strength and, finally, Lemma 5 we get the following
statement.

**Theorem 1.** The effective viscosity \( \hat{\mu}(v, f_p) \), defined by (3.21), of a suspension of swimmers with propulsion strength \( f_p \), defined by (3.13), interacting only with the background shear flow (i.e., no swimmer-swimmer interactions) is independent on the propulsion strength \( f_p \).

**Remark 3.** The immediate consequence of Theorem 1 is that in the dilute limit the effective viscosities of suspensions of active and passive swimmers are the same.

**Remark 4.** The result of Theorem 1 is based on a different set of assumptions than Ishikawa and Pedley [40], where swimmers have a shifted center of gravity. Our swimmers centers of gravity is the same as their geometric center. In fact, our result explains why Ishikawa and Pedley could not obtain decrease of viscosity for swimmers with “neutral” center of gravity.

**Remark 5.** Adding to the model the rotational diffusion (either due to Brownian motion or tumbling), in the absence of the swimmer-swimmer interactions, would break up the symmetry (3.31) and lead to a preferential alignment of swimmers. Depending on the sign of the propulsion strength \( f_p \), the flow due to swimmers helps \((f_p > 0)\) or resists \((f_p < 0)\) the background shearing motion. This explains the results of [44], where the decrease of effective viscosity is observed in the presence of rotational diffusion.

### 3.4 Numerical modeling and analysis

We solve the ODEs (3.10) using the forward Euler method with variable time step \( \Delta t_n \) (see more on the choice of the time-step in Section 3.4.2). On each time step \( t_n \), using positions \( x^i_c(t_n) \) and orientations \( d^i(t_n) \) of swimmers, we find their new translational and rotational velocities by solving the problem (3.1-3.6). After that, we update positions of the swimmers, assuming constant velocities on the time interval \( (t_n, t_n + \Delta t_n) \):

\[
x^i_c(t_{n+1}) = x^i_c(t_n) + \Delta t_n v^i_c(t_n).
\]  

(3.35)
Since our spatial discretization method is first-order accurate for stresses in terms of the mesh size, the first-order accurate time integration method is sufficient to balance spatial and temporal errors.

3.4.1 Solution of the instantaneous problem

Efficient and accurate solution of the PDE problem (3.1-3.6) on each time step is required for computing the viscosity of the suspension. We use the recently developed Mimetic Finite Difference (MFD) method [53]. Since the MFD method for the Stokes problem is a new method, we give a short comparative description of this method and some other popular methods.

3.4.1.1 Short description of MFD method

The MFD method combines mesh flexibility of the Finite Volume (FV) methods with analytical power of Finite Element (FE) methods. To some extent it can be viewed as an extension of FE methods to unstructured polygonal (polyhedral in three dimensions) meshes. The mesh flexibility simplifies mesh generation around swimmers that may have complicated shapes. The major difference between the MFD and FE methods lies in definition of basis functions. The FE methods define them explicitly everywhere in the computational domain. The MFD method specifies the basis functions only on mesh edges. This reduction of topological complexity has a number of important consequences for numerical modeling of complex phenomena.

First, the MFD method minimizes the number of discrete unknowns (compared to the FE method) (a) by partitioning of the computation domain into smaller number of elements that are polygons and (b) by using velocity and pressure degrees of freedom only where they are needed for accuracy and stability of the discretization. For example, the MFD method on a square mesh with \( N \) mesh vertices uses about \( 2.5N \) velocity and \( N \) pressure unknowns. The FE methods on the same mesh and with roughly the same accuracy uses about \( 4N \) velocity and \( N \) pressure unknowns.

Second, the MFD method is built the same way on general polygonal meshes as on triangular meshes. Thus, it can be used on locally refined meshes with
hanging nodes and on moving meshes with non-convex elements that are frequently used in numerical modeling. It was shown in [64] that the MFD method can be employed even when the mesh elements have curved faces. In this work, we use polygonal meshes near boundary of the swimmers (see Section 3.4.1.2) and make the computational mesh coarser far away from the swimmers. This approach increases accuracy in the areas of interest. The MFD method is the second-order accurate (with respect to the local mesh size) for the velocity and the first-order accurate for the pressure.

3.4.1.2 Mesh construction

In the simulations, we used a three-step algorithm for construction of the computational mesh. First, we construct a uniform square background mesh, i.e. the square domain of size 1 by 1 is divided into $N^2$ squares with sides $h = 1/N$.

![Figure 3.3. A sample mesh near a swimmer. The computational domain is around the swimmer and is colored light blue. The mesh is coarsened away from the swimmer. Notice that the mesh elements adjacent to the swimmer are polygons with 3, 4 and 5 vertices.](image)

Second, we overlap the background mesh with the ellipses representing swimmers. For this, we find the points of intersection of the ellipses with the edges of the background mesh. These points are connected by straight edges and added to the new mesh. The mesh elements inside the ellipses are then thrown out. As a
result, the boundary of the ellipses is approximated with the second-order accuracy and the resulting mesh is polygonal (see Fig. 3.3).

Third, we coarsen the mesh by grouping the mesh elements those centers are at least $2h$ away from the swimmers into square mesh elements with sides $2h$. This process can be repeated by grouping the mesh elements those centers are at least $4h$ away from the swimmers into square mesh elements with sides $4h$. This strategy leaves the mesh intact in the neighborhood of swimmers where spacial variation of flow is the largest.

### 3.4.2 Choosing the time step

There are several factors that determine the size of the time step $\Delta t_n$. For moderate concentrations of swimmers ($\sim 10\%$ by volume) the crucial point to be addressed is collision of swimmers. For this, the relative displacements of swimmers on each time step should be small compared to their pairwise distances. Due to the hydrodynamic attraction of swimmers it is common to see pairs of swimmers arbitrarily close to one another. This requires to use extremely small time steps; therefore, such an approach is not practical.

We implemented a balanced algorithm for choosing the time step. First, we fix the upper $\Delta t_{\text{upper}}$ and the lower $\Delta t_{\text{lower}}$ bounds for the time step. Then, we pick the size of the time step $\Delta t$ such that

$$\Delta t_{\text{upper}} \geq \Delta t \geq \Delta t_{\text{lower}}$$

and the swimmers cannot get closer than the mesh size $h$ to one another. If both criteria cannot be satisfied, we set $\Delta t := \Delta t_{\text{lower}}$ and apply the collision algorithm described in the next subsection.

Numerical experiments have shown that $\Delta t_{\text{upper}} := .01$ and $\Delta t_{\text{lower}} := .001$ for the propulsion strength of swimmers $f_p = 1$ and the shear rate $\dot{\varepsilon} = 1$ lead to smooth dynamics of the apparent viscosity (see Fig. 3.7). When $f_p > 1$, the time step is selected based on the scaling observation (see Remark 1). This remark implies that trajectories of swimmers for the case with $\dot{\varepsilon} = 1$, $f_p = f_p^0$, $\Delta t = \Delta t^0$ will be close to that in the case with $\dot{\varepsilon} = 1/\lambda$, $f_p = f_p^0/\lambda$, $\Delta t = \Delta t^0/\lambda$. We choose the scaling constant $\lambda = f_p$, i.e. we fix the propulsion strength of the swimmers.
This leads to smaller values of the shear rate than in the base case. Therefore, our choice of the upper and lower bounds for the time step is \( \Delta t_{upper} := .01/f_p \) and \( \Delta t_{lower} := .001/f_p \).

### 3.4.3 Implementing collisions of swimmers

Dynamic change of the time step only minimizes probability of collisions and does not eliminate them completely. There are two popular methods for dealing with collisions of rigid objects. A group of methods use a short range repulsive force to push swimmers away from one another. The method employed in our simulations is used commonly in modeling of granular media [65] and is better suited for the problems with many bodies close to one another, where long time simulations are necessary.

Lubrication theory can be used to make asymptotically correct predictions for small pairwise distances \( \delta \ll 1 \) between swimmers. But the smallest allowed pairwise distance is tied together with the size of the time step, \( \Delta t \sim \delta \). Since at concentrations around 9% by volume almost always there are swimmers next to one another, allowing pairwise distances to bee too small would make time stepping prohibitively slow. In our analysis, we require swimmers to be approximately one mesh size apart. Lubrication theory would be more appropriate for a very detailed, short-term analysis of two swimmers near contact, than for an analysis of many swimmers where long-term collection of statistics is essential.

To avoid additional technical difficulties, we consider a small exclusion region around each swimmer. The exclusion region for the ellipse with major semi-axis \( a \) and \( b \) is defined as the ellipse with major semi-axis \( a + h \) and \( b + h \), respectively. Therefore, if the exclusion regions of two swimmers do not overlap, then these swimmers are guaranteed not to have a common mesh element adjacent to both. The collision is implemented as a soft collision of exclusion regions.

That is, suppose that at time \( t_0 \) we solved the Stokes problem (3.1-3.6) for two swimmers \( S^1 \) and \( S^2 \) and found their velocities \( \mathbf{u}_C^i \) and \( \omega^i \), \( i = 1, 2 \). The positions of the swimmers at time \( t_1 = t_0 + \Delta t \) are computed as follows:

\[
\mathbf{x}_C^i(t_1) = \mathbf{x}_C^i(t_0) + \Delta \mathbf{x}^i, \quad \Delta \mathbf{x}^i = \Delta t \mathbf{u}_C^i(t_0).
\]
Their orientations are incremented similarly by values $\Delta \theta^i$. By our assumptions, $\Delta t = \Delta t_{\text{lower}}$ and new positions result in overlap of exclusion regions.

Before solving the instantaneous problem again (3.1-3.6), we will displace the swimmers $S^i$, $i = 1, 2$, according to

$$x^i \rightarrow x^i + \delta_t \left( u^i_a d^i + u^i_b d^i_\perp \right),$$

$$d^i \rightarrow \begin{bmatrix} \cos(\omega^i \delta_t) & -\sin(\omega^i \delta_t) \\ \sin(\omega^i \delta_t) & \cos(\omega^i \delta_t) \end{bmatrix} d^1,$$

where $\delta_t$, given by (3.42), is chosen so the exclusion regions of swimmers no longer overlap. The motivation for this displacement and definition of all terms in (3.36–3.37) is given below.

Consider two ellipses in contact. The force of their interaction is directed along the normal to their surfaces at the point of the contact. The force $F_{1,2}$ of the first swimmer $S^1$ onto the second swimmer $S^2$ is equal in magnitude and opposite in direction to $F_{2,1}$, the force of $S^2$ onto $S^1$.

$$F^{1,2} = -F^{2,1}. \quad (3.38)$$

**Figure 3.4.** Two ellipsoidal exclusion regions (containing swimmers) in contact (a) and two overlapping ellipsoidal exclusion regions (b).

To estimate the effect of the interaction force $F^{2,1}$ on the motion of the swimmer
we compute the net force and the net torque applied to the swimmer:

\[ \mathbf{F}_{\text{net}}^1 = \mathbf{F}^{2,1} \quad \text{and} \quad T_{\text{net}}^1 = (\mathbf{x} - \mathbf{x}_C^1) \times \mathbf{F}^{2,1}. \quad (3.39) \]

The force \( \mathbf{F}^{2,1} \) will be acting on swimmer \( S^1 \) as long as \( S^1 \) and \( S^2 \) are in contact. In the Stokes regime (where inertia is negligible compared to the viscous forces) the forces \( \mathbf{F}^{2,1} \) and \( \mathbf{F}^{1,2} \) will be only as strong as necessary to prevent mutual penetration of swimmers. Since in the Stokes regime inertial terms are dominated by viscous terms, the treatment of collision is based on the following drag coefficients: two for translational motion along the major axes, \( \gamma_a \) and \( \gamma_b \), and one for the rotational motion, \( \gamma_{\theta} \).

If \( \mathbf{d}^1 \) is the direction of the major axis and \( \mathbf{d}_{\perp}^1 \) is the direction of the minor axis, we may write the net force as \( \mathbf{F}_{\text{net}}^1 = f_a \mathbf{d}^1 + f_b \mathbf{d}_{\perp}^1 \) and the motion of the ellipse as \( \mathbf{u}_C^1 = u_a^1 \mathbf{d}^1 + u_b^1 \mathbf{d}_{\perp}^1 \) and \( \omega^1 \). The drag coefficients relate the forces acting on the ellipse with the motion of the ellipse as follows:

\[ f_a^1 = \gamma_a u_a^1, \quad f_b^1 = \gamma_b u_b^1, \quad T_{\text{net}}^1 = \gamma_{\theta} \omega^1. \quad (3.40) \]

In general, for two overlapping ellipses, there will be two points of intersection denoted by \( P_1 \) and \( P_2 \) (see Fig. 3.4(b)). The midpoint \( M := (P_1 + P_2)/2 \) will be considered as the point of the interaction. The interaction force (denoted by \( \mathbf{n}_{(P_1,P_2)} \)) will be assumed to act perpendicular to the line \((P_1, P_2)\) as shown on the figure. Based on this, we can compute the corrected velocities of the swimmers (along major/minor axis and rotational velocity):

\[ u_a^1 = \gamma_a^{-1} f_a = \gamma_a^{-1} \mathbf{d} \cdot \mathbf{n}_{(P_1,P_2)}, \]
\[ u_b^1 = \gamma_b^{-1} f_b = \gamma_b^{-1} \mathbf{d}_{\perp} \cdot \mathbf{n}_{(P_1,P_2)}, \]
\[ \omega^1 = \gamma_{\theta}^{-1} T_{\text{net}}^1 = \gamma_{\theta}^{-1} \mathbf{n}_{(P_1,P_2)} \times (M - \mathbf{x}_C^1). \quad (3.41) \]

We are left to answer the question: How big should be the displacements \( \Delta \mathbf{x}^1 \) and \( \Delta \theta^1 \)? Since we already computed the direction of the displacements the above question is reduced to the question of scaling: How big should be the scaling \( \delta_t \) in \( \Delta \mathbf{x}^1 = \delta_t \mathbf{u}_C^1 \) and \( \Delta \theta^1 = \delta_{\theta} \omega^1 \)?

We suggest to take \( \delta_t \) so that the swimmers are slightly out of contact. For
this, we select two points $O^1$ and $O^2$ on the boundaries of $S^1$ and $S^2$, respectively, that are between $P_1$ and $P_2$. For example, let us take $O^1$ to be the point, where the tangent line is parallel to the line passing through $P_1$ and $P_2$. We choose the point $O^2$ in a similar fashion. Denoting the velocities of points $O_1$ and $O_2$ by $u_{O_1}$ and $u_{O_2}$, respectively, we take

$$
\delta_t := (1 + \alpha) \frac{(O^1 - O^2) \cdot n_{(P_1, P_2)}}{(u_{O_1} - u_{O_2}) \cdot n_{(P_1, P_2)}}.
$$

(3.42)

Here $\alpha \geq 0$ is an analogue of a restitution coefficient (measure of bounce, i.e. elastic vs inelastic collision). It can, also, serve as a “reserve” to guarantee that after the procedure the ellipses do not overlap. In numerical simulations, we use $\alpha = 0.1$, which corresponds to soft collisions.

### 3.4.4 Dynamics: Interaction of swimmers

Here we present two numerical experiments for the hydrodynamic interaction of swimmers at the intermediate distances (distances of order of the size of the swimmer): a swimmer next to a wall (see Fig. 3.5a) and two side-by-side swimmers (see Fig. 3.5b). In both cases attraction due to a hydrodynamic interaction was observed.

This behavior can be explained, heuristically, by the fact that each swimmer acts as a force dipole (see (3.5)). It pushes fluid forward (ahead of itself) due to the no-slip condition on $\Gamma_H$ and backward (behind itself) due to the thrust condition on $\Gamma_P$. Since the fluid is incompressible, it is being forced towards the swimmer on its sides creating lateral suction of sorts.

#### 3.4.4.1 A swimmer next to a wall

In this numerical experiment, the swimmer was positioned distance 0.1 away parallel to a wall (see Fig. 3.5a). The lengths of the semi-axes of the swimmer were $a = 0.048$ and $b = 0.024$. The propulsion force is given by (3.12) with the propulsion strength $f_p = 1$.

The computed initial translational and rotational velocities of the swimmer
were
\[
\mathbf{u}_c^1 = \begin{bmatrix} 0.065 \\ -0.016 \end{bmatrix}, \quad \omega^1 = 0.061.
\] (3.43)

The vertical swimmer’s velocity is roughly quarter of its horizontal velocity indicating rather strong interaction with the wall. Over time the swimmer approaches the wall while simultaneously rotating away from it. When it has rotated sufficiently, it begins moving away from the wall.

We conclude that a swimmer positioned parallel to the wall is attracted to it and spends a significant amount of time swimming parallel to it. But it will not remain next to the wall indefinitely. The entire time spent near the wall, the swimmer rotates away and eventually swims away.

Figure 3.5. Figure (a) shows the fluid flow for a single microswimmer next to a wall. Figure (b) shows the fluid flow for two swimmers side by side. The bold blue arrows indicate the direction of the fluid that pushes the swimmer closer to the wall (a) and the two swimmers closer to one another (b). The bold red lines with arrows indicate the trajectories that each of the swimmers will follow. Both (a) and (b) show the initial period of attraction (red line getting closer to the wall and two red lines getting closer to one another). The two swimmers in the mirror image configuration remain close to one another after this. The swimmer next to the wall rotates away from the wall to eventually get further and further away from it.
3.4.4.2 Two adjacent “mirror image” swimmers

In this experiment, we consider two swimmers with the length of the semi-axes \( a = 0.048 \) and \( b = 0.024 \), initially positioned parallel to the \( x \)-axes, with the centers on the same vertical line (see Fig. 3.5b):

\[
x_1^c = \begin{bmatrix} 0.5 \\ 0.4 \end{bmatrix} \quad \text{and} \quad x_2^c = \begin{bmatrix} 0.5 \\ 0.6 \end{bmatrix}.
\]

The swimmers are mirror images of one another with respect to the horizontal line \( y = 0.5 \).

The computed initial translational and rotational velocities of the swimmers were

\[
u_1^{1,2} = \begin{bmatrix} 0.066 \\ \pm 0.014 \end{bmatrix}, \quad \omega_1^{1,2} = \mp 0.02.
\]

With time the swimmers approach one another, simultaneously rotating away from one another. This dynamics of two side-by-side swimmers is reminiscent of the dynamics of two well-separated “external pushers” in a similar configuration [51]. There is a difference between the well-separated and moderately separated regimes, however. In the well separated regime, the swimmers have enough time to rotate sufficiently away from one another for the translational correction (to swimming straight) due to the suction to be dominated by the vertical velocity for a free swimmer. In the moderate regime, the suction is too strong and the swimmers do not have enough time to rotate sufficiently outwards.

One can also compare the velocities (3.44) and (3.43). While the translational velocities in both cases are almost the same, the rotational velocity in (3.43) is roughly three times larger than in (3.44). This may explain the difference in the dynamics between a swimmer next to a wall and two “mirror image” swimmers.

In Fig. 3.5(b) one can clearly see the trajectories of the swimmers converge and experience a sharp turn after which they become parallel. The swimmers will remain in this symmetrical configuration with distance 0.0664 between their centers and at the angles \( \mp 0.28 \) (turned somewhat outwards) with the \( x \)-axes.

If the swimmers are initially not in a perfectly symmetric configuration, they eventually separate and swim away from one another. This type of dynamics is
presented below.

3.4.4.3 Two adjacent “offset” swimmers

In this computation, we consider two swimmers parallel to the $x$-axes with the centers offset from the same vertical line:

\[
\mathbf{x}_c^1 = \begin{bmatrix} 0.55 \\ 0.40 \end{bmatrix} \quad \text{and} \quad \mathbf{x}_c^2 = \begin{bmatrix} 0.45 \\ 0.60 \end{bmatrix}.
\]

This initial configuration of swimmers can be thought of as a perturbation of the “mirror image” configuration.

The computed initial translational and rotational velocities of the swimmers are

\[
\mathbf{u}_c^1 = \begin{bmatrix} 0.0626 \\ 0.0047 \end{bmatrix}, \quad \omega^1 = -0.12, \quad \mathbf{u}_c^2 = \begin{bmatrix} 0.0740 \\ -0.0064 \end{bmatrix}, \quad \omega^2 = -0.11. \quad (3.45)
\]

Initially, both of the swimmers rotate in the same direction, clockwise. The direction of the rotation is determined by the swimmer which is ahead of the other one, the bottom swimmer in this configuration. Thus, the second (top) swimmer rotates towards the first one (see the streamlines in Fig. 3.6). The second swimmer will cross the trajectory of the first swimmer, behind it, and will swim away. This demonstrates that there is no stable configuration of swimmers where they stay close to one another indefinitely. Note that in Fig.3.5(b) the swimmers stayed together due to mirror image conditions being enforced. Any small perturbation from this condition will lead to swimmers eventually swimming away from one another.

3.4.5 Time and size scales in the physical and numerical experiments

In an attempt to relate the physical and numerical units, we recall the physical parameters of bacteria such as *Bacillus subtilis*. The length of the bacterium is around $5\mu\text{m}$ and the typical swimming speed is $\sim 20\mu\text{m/sec}$. The length of a
Figure 3.6. Figure illustrates the fluid flow for two “offset” parallel microswimmers. Bold red lines show the trajectories each of the swimmers will follow.

swimmer in the above numerical experiments is $2a = 0.096$. In these experiments, (3.43) and (3.44), the typical forward component of the velocity of a swimmer is

$$0.065 \approx \frac{2 \text{ swimmer body length}}{3 \text{ computer unit of time}}. \quad (3.46)$$

Since the typical speed of the bacterium is 4 body lengths per second, the unit of computer time for $f_p = 1$ corresponds to

$$\left(\text{unit of computer time for } f_p = 1\right) = \frac{2/3}{4} \text{ sec} = 1/6 \text{ sec}. \quad (3.47)$$

Now we compute the physical analogue of the shear rate for the computational experiment with $f_p = 1$. The size of the container is $1/0.096 \approx 10$ lengths of a swimmer, which corresponds to $50 \mu$m. The speed of the top plate relative to the bottom plate is $2 \frac{50 \mu m}{1/6 \text{ sec}} = 600 \frac{\mu m}{\text{sec}}$. Thus, the shear rate is $\frac{600 \mu m \cdot \text{sec}^{-1}}{50 \mu m} = 12 \text{ sec}^{-1}$.

3.4.6 Effective viscosity

For a homogeneous fluid, the instantaneous apparent viscosity defined by (3.20) and the effective viscosity defined by (3.21) are the same. For an inhomogeneous fluid (e.g., suspensions) (3.20) takes different values depending on the distribution
of inclusions. Figure 3.7 illustrates sample values of the instantaneous apparent viscosity for a suspension of swimmers as a function of time.

\[ \text{Instantaneous measurement of viscosity} \]
\[ \text{Average viscosity} \]
\[ \text{Fluid viscosity} \]

Figure 3.7. The green horizontal line indicates the viscosity of the ambient fluid (\( \mu = 1 \)). The blue (oscillating) line shows the instantaneous apparent viscosity as defined by (3.20). The red horizontal line indicates the time average of the instantaneous apparent viscosity. The computations are performed for the suspension of 25 swimmers at 9\% volume fraction in a 1 \times 1 \text{ square with periodic boundary conditions in the } x\text{-direction. The propulsion of each swimmer is defined by (3.12) with the total propulsion strength } f_p = 1 \text{ as defined by (3.13).}

Since in practice the instantaneous apparent viscosity is computed on a finite interval of time it is important to derive an error estimate for the effective viscosity, which is a non-trivial task. Intuitively, the more evaluations one makes (longer simulation time), the more accurate is the estimate of the effective viscosity. However, the same number of samples (time steps) can be done with small or large time step \( \Delta t \). Small \( \Delta t \) is important for capturing correctly the dynamics of the suspension. Long simulation time is important for the accuracy of the overall estimate of the effective viscosity. Both extremes, million samples with \( \Delta t = 10^{-12} \) or hundred samples with \( \Delta t = 10 \) may be equally poor at predicting the effective viscosity. In the first case, one would get a very accurate dynamics of the suspension, but would miss the range of values. In the second case, one would get a rather broad range of values for completely inaccurate dynamics of the suspension. Since the interaction of swimmers is assumed to play a key role in the effective viscosity the last choice is not satisfactory as well.

We begin by identifying an acceptable time step, which may be a subjec-
Figure 3.8. Autocorrelation function for propulsion force $f_p = 1$ and time step $\Delta t = 0.02$.

A mean of $N$ independent identically distributed random variables approaches normal distribution with the standard deviation $s/\sqrt{N}$, where $s$ is the standard deviation of the underlying distribution. In our analysis, all evaluations of the instantaneous apparent viscosity $\bar{\mu}(v; t)$ do not represent independent samples. For example, the correlation between the values of $\bar{\mu}(v; t)$ on two consecutive time steps is more than 0.8 for $\frac{f_p \mu_{p}}{\mu_{w}} = 1$. Let $n_{\text{lag}}$ be the smallest lag for which the autocorrelation equals to zero. As shown in Fig. 3.8, the zero-autocorrelation lag is $n_{\text{lag}} = 58$ for $\frac{f_p \mu_{p}}{\mu_{w}} = 1$. This number indicates that the samples $n_{\text{lag}}$ time steps apart are essentially uncorrelated and may be viewed as independent samples.

The total number of time steps divided by $n_{\text{lag}}$ is the sample size $N$. The error in estimating the effective viscosity is then assumed to have a normal distribution with the standard deviation

$$\sqrt{\frac{N_{\text{total}}}{n_{\text{lag}}}}.$$ (3.48)
The standard deviation of the error, computed according to (3.48), is shown as vertical error bars on Figure 3.9.

### 3.4.6.1 Effective viscosity as a function of the propulsion-shear ratio

In this section, we analyze the dependence of the effective viscosity of the suspension of microswimmers on the propulsion-shear ratio \( \frac{f_p}{\mu v} \). To compute the effective viscosity, we consider a \( 1 \times 1 \) container with periodic boundary conditions on vertical sides and set the shear velocity \( v = 1 \) on horizontal sides. We fix the size and number of swimmers and vary only their propulsion strength \( f_p \). For each value of \( f_p \), we simulate the dynamics of the swimmers and compute the viscous forces acting on the top and bottom plates and then the instantaneous apparent viscosity as defined by (3.20).

The effective viscosity as a function of the propulsion strength is shown in Fig. 3.9. Generally, the standard deviation of the estimates for the effective viscosity is much larger for larger values of the propulsion-shear ratio \( \frac{f_p}{\mu v} \). This is due to the fact that the standard deviation of the instantaneous apparent viscosity is proportional to the propulsion strength of the swimmers. Therefore, according to the error estimate (3.48) to compute the effective viscosity for \( \frac{f_p}{\mu v} = 10 \) with the same accuracy as for \( \frac{f_p}{\mu v} = 1 \) it requires not 10 but \( 10^2 \) more time steps.

The red line on Figure 3.9 is given by

\[
\alpha \left( \frac{f_p}{\mu v} \right) + \beta, \quad \alpha = -0.046, \quad \beta = 1.141, \quad (3.49)
\]

and represents the weighted least square fit to the data. The weights are inversely proportional to the square of the estimated error in computing each of the data points. Thus, the data points corresponding to larger values of the propulsion-shear ratio and having larger errors affect \( \alpha \) and \( \beta \) significantly less than the than data points corresponding to smaller values.

The linear decrease of the effective viscosity is observed for the propulsion-shear ratio ranging from negative one to five. Around \( \frac{f_p}{\mu v} \approx 5 \) this linear trend changes. We explain this change by the finite size of the fluid domain. More precisely, we show how the finite size of the container affects the dynamics of a single swimmer. In Fig. 3.10, we show the trajectory of a single swimmer when the propulsion-shear
Figure 3.9. The points marked by circles indicate the numerically obtained values of the effective viscosity for a given propulsion-shear ratio $f_p/\mu v$. These points are combined into two groups: A and B. Points in group A exhibit linear trend. Points in group B exhibit finite domain effects. The solid horizontal line shows the viscosity of the ambient fluid ($\mu = 1$). The dashed horizontal line shows the effective viscosity of a suspension of passive inclusions ($f_p = 0$). The decline straight line shows the weighted least square interpolation to all shown data points. The weights are the standard deviations of the error.

A single swimmer in a shear background flow swims along an ellipse-like trajectory. The larger is the propulsion-shear ratio, the larger is the vertical semi-axis of this trajectory. For $f_p/\mu v \sim 6$, this semi-axis is half of the container size and no longer fits into the fluid domain. Due to the swimmer-wall interaction, the elliptic-like trajectory of the swimmer deforms significantly at larger values of the propulsion-shear ratio. This explains smooth transition from the linear trend (points in group A in Fig. 3.9) to the finite domain effect (points in group B).

Extrapolating the linear trend (3.49) to the propulsion-shear ratio $f_p/\mu v = 24$, corresponding to the measurements in [28] (shear rate $0.5\text{sec}^{-1}$), we get an 8.5-fold
Figure 3.10. Sample trajectory of a single swimmer with the propulsion strength $f_p = 1$ in the shear flow $v = 1$. The swimmer’s position and orientation at time moments $T_0 = T_1, T_2, T_3$ are shown.

decrease in the effective viscosity from 1.1408 to 0.1327. This is close to the 7-fold decrease in the viscosity observed in experiments [28].

Heuristically, the decrease of the viscosity due to interactions can be related to the reduction of viscosity in the dilute limit in the presence of the rotational Brownian noise [44]. In this work, it is observed that the rotational Brownian noise breaks up the symmetry (3.31) in the angular distribution of swimmers and leads to the preferential alignment of swimmers with the shearing flow. Crudely, one can view the interactions between the swimmers as a form of rotational (and translational) noise that has the same effect as the rotational Brownian noise in [44]. This parallel was, also, identified by Ishikawa & Pedley in [49]. The intensity of the rotational noise due to the interactions is proportional to the activity of the swimmers (that is the propulsion strength $f_p$). The break up of the symmetry (3.31) and shift of the peaks of the angular distributions of the swimmers can be observed in Fig. 3.11. The greater is the propulsion strength $f_p$ of the swimmers, the larger is the shift of the peaks in the distributions.

We compared the distribution $p(\theta, f_p)$ of swimmers by angles resulting from hydrodynamic interactions of swimmers with propulsion strength $f_p$ to the distribution $p_{\text{dil}}(\theta, D)$ of swimmers in the dilute limit in the presence of rotational
Figure 3.11. Top six plots show the distribution of swimmers by angles in the shear flow ($v = 1$) for different values of the propulsion strength: $f_p = 0, 1, \ldots, 5$. The horizontal axis indicates the angle $\theta \in (-\pi/2, \pi/2)$. The vertical axis indicates the distribution density. To remove focus from local irregularities and highlight the global pattern the angular distributions are smoothed by convolution with the Gaussian with mean zero and standard deviation $\pi/40$. Bottom six plots show the distribution of ellipses by angles, given by (3.50), in the shear flow in the presence of diffusion with strength $D$.

diffusion with coefficient $D$. The distribution $p_{\text{dil}}(\theta, D)$ solves the Fokker-Planck equation

$$\frac{\partial^2}{\partial \theta^2} \left[ D p_{\text{dil}}(\theta) \right] - \frac{\partial}{\partial \theta} \left[ -\frac{\gamma}{2} \left( 1 - \frac{3}{5} \cos(2\theta) \right) p_{\text{dil}}(\theta) \right] = 0,$$  \hspace{1cm} (3.50)

where $\gamma = 2$ is the shear rate in the numerical simulations. In both cases, in-
creasing \( f_p \) or \( D \) leads to the shift in the positive direction of the peak in the distributions \( p(\theta, f_p) \) and \( p_{\text{dil}}(\theta, D) \), respectively. The distribution \( p(\theta, f_p) \) has a more pronounced peak compared with distribution \( p_{\text{dil}}(\theta, D) \) and does not flatten as rapidly. The flattening part may be the explained by the interactions with the walls.

3.4.6.2 Distribution of swimmers in the domain

The distribution of swimmers in the domain and their orientations play a crucial role in determining the instantaneous apparent viscosity.

In physical experiments [61] and some numerical simulations [48, 66], it was observed that swimmers tend to aggregate near the walls. In our numerical experiments, we observed this aggregation through computing the time averaged volume density of swimmers as a function of distance from the bottom wall (see Fig. 3.12). For each horizontal line, we computed the portion of the line covered by swimmers. This number is the instantaneous volume fraction of swimmers and fluctuates with time. To eliminate the fluctuations we take a time average of the instantaneous volume fractions. Due to the top-bottom symmetry of the PDE and random initial conditions, the graph of the distribution is also symmetric.

![Figure 3.12](image)

**Figure 3.12.** The right figure shows a sample distribution of 25 swimmers with the propulsion strength \( f_p = 1 \). The volume fraction of swimmers is 0.09. The left figure shows the time-averaged volume fraction of swimmers as a function of the depth (distance from the bottom wall). Note the increase of the density near the top and bottom walls.

In [43], it was demonstrated that in the absence of pairwise interactions, shear
flow leads to a distribution of swimmers by the angles that decreases the viscosity. In the presence of the pairwise interactions and the swimmer-wall interactions the dynamics of the swimmers is much more complex.

### 3.5 Summary

In this work we formulated a well-posed PDE model for the suspension of swimmers which includes the propulsion strength $f_p$ of the swimmers as a parameter. We analyzed the effective shear viscosity of the suspension at the dilute (each swimmer interacts only with the background flow) and moderate concentration regimes.

Using the symmetries of the model, we demonstrated that in the dilute regime the effective shear viscosity of the suspension does not depend on the propulsion strength of swimmers. Hence, in the dilute regime the suspension of active microswimmers has the same effective viscosity as the suspension of passive inclusions of the same shape and at the same concentration. This argument is not specific to our choice of a swimmer and can be applied to a large class of swimmers without any changes. In particular, it can be applied to the swimmers in [40, 24, 43].

Adding rotational diffusion to the model breaks up the symmetry in the angular distribution of swimmers, leading to preferential alignment of swimmers, which in turn leads to decrease of the effective viscosity for pushers ($f_p > 0$) and increase for pullers ($f_p < 0$).

Using invariance of the PDE model under scaling, we observed the dependence of the effective shear viscosity on the propulsion-shear ratio $\frac{f_p}{\mu v}$ where $\mu$ is the fluid viscosity and $v$ is the shear rate of the background flow. This allowed us to analyze the effective viscosity as a function of one parameter.

The numerical simulations performed at the moderate concentrations ($\sim 10\%$ by volume) indicated that the effective shear viscosity decays linearly as a function of the propulsion-shear ratio. This remains true for negative values of the propulsion strength ($f_p < 0$), which corresponds to pullers instead of pushers. We observed the increase of effective shear viscosity for pullers. We found out that the size of the fluid container places an upper bound on the propulsion-shear ratio for which the effective shear viscosity changes linearly. Our numerical experiments indicated that the decrease of the effective viscosity observed in the physical exper-
iments can be explained entirely from the point of view of hydrodynamics. This is an important observation, since biological systems are very complex and include a variety of processes (chemotaxis, oxygen taxis, etc.) that could be hard to isolate in physical experiments. Our mathematical model does not include these phenomena and places the focus only on the hydrodynamic interactions.

Comparison of the results in the dilute and moderate concentration regimes, had shown that changes (increase or decrease) in the effective shear viscosity are not just due to self-propulsion but crucially depend on the swimmer-swimmer interactions. For this reason and as an additional validation of the model and verification of the numerical approach, we performed a number of simulations for two nearby swimmers and for a swimmer next to a wall. The observed results matched with the physically observed behavior for bacteria. The swimmers attract one another due to lateral suction of fluid induced by self propulsion. But neither two swimmers nor a swimmer next to a wall have a steady state configuration in terms of relative positions.

The method presented in this chapter is ideally suited for the complex problems involving swimming microorganisms (e.g. bacteria), where the nature of the experimentally observed phenomenon is not clear a priori. For instance, it may not be clear if the experiment can be explained purely from hydrodynamic considerations or chemotaxis and other phenomena should be considered as well. Our method allows to perform analysis only with hydrodynamic interactions (accurately handling all interactions) and later add chemotaxis if necessary. As an example of physical experiment that could be analyzed by our method we refer to a recent work [62] describing extraction of mechanical energy from “chaotically” swimming bacteria by means of asymmetric gears.
Chapter 4

Afterword

In this dissertation we presented two problems related to suspensions of microswimmers: dynamics of microswimmers resulting from pairwise interactions, and effective shear viscosity for suspensions of microswimmers. We identify the following as the major contributions:

- We developed two PDE models (Chapters 2 and 3) of microswimmers from the first principles. The dumbbell model of Chapter 2 is most appropriate for the analysis of well-separated swimmers, while the ellipsoid model of Chapter 3 is better suited for moderate to close separation regime. Both models contain as their parts well-posed instantaneous PDE problems.

- We identified a critical dependence of the dynamics of a pair of microswimmers (resulting from hydrodynamic interactions) on the position of the effective force of the propulsion. We identified the appropriate position for the propulsion apparatus to model for swimming microorganisms such as Bacillus subtilis.

- We reproduced the reduction of effective shear viscosity in suspensions of microswimmers in the moderate concentration regime. Identified the minimal set of key features responsible for the reduction of effective shear viscosity: (i) self-propulsion of the swimmers, (ii) elongated shape of the swimmers, and (iii) interactions or rotational noise.

- We analytically proved that for rather general swimmers in the dilute regime
(swimmer-swimmer interactions are neglected), effective shear viscosity does not depend on the strength of the propulsion of the swimmers. Thus, identified the connection between interactions and rotational noise as key (interchangeable) ingredients for reduction of viscosity.

- We explained the mechanism leading to the reduction of effective shear viscosity at moderate concentrations.

The results presented above and the ones published by other researchers in the last several years significantly improved understanding of suspensions of microswimmers. Still, there are many important aspects that are not well understood. Next, we would like to touch on some questions related to this dissertation that we believe to be interesting and important for better understanding of suspensions of microswimmers.

The mechanisms responsible for the reduction of effective shear viscosity in suspensions of microswimmers in PDE models with interactions (no rotational noise) and rotational noise (no interactions) are similar. Interactions or rotational noise lead to shift of the peak of the orientational distribution of swimmers, which in turn leads to reduction of viscosity. The two natural questions are

- How well can we estimate the effective viscosity for suspensions with interactions (no rotational noise) based only on the orientational distribution of swimmers? That is, if after long-time simulations only the average distribution of swimmers by orientations is retained and all information about positions of swimmers and orientational correlations are lost, is it still possible to accurately approximate the observed value of the effective viscosity?

- What is the appropriate way of approximating the interactions by rotational noise? What is the underlying rotational noise that produces the same orientational distribution of swimmers as the interactions in the shear flow?

Answering these two questions will drastically simplify the analysis of PDE models for swimmers with interactions and will make the analytical analysis of such models possible. As a consequence, it will be possible to identify the quantitative dependence of the effective shear viscosity on the propulsion strength of
the swimmers and the shear rate in the continuous range of parameters. For comparison, currently, it takes from several days to a month to numerically obtain one data point for the effective viscosity. Larger values of the propulsion strength present additional challenges, because to obtain the same confidence for the effective viscosity for swimmers that are twice as strong it takes four times more computational time. Thus, approximation of the interactions by rotational noise would allow to identify the quantitative dependence of the effective viscosity for a much broader range of propulsion strengths and swimmer densities.

Our preliminary computations showed that the contribution of self-propulsion to the effective shear viscosity computed crudely based on the orientational distribution of swimmers (positions of swimmers are not taken into account) is accurate within 10% for pusher as compared with accurate numerical simulations. For pullers the accuracy for the approximation is significantly worse. This could be due to more pronounced pattern formations for pullers: pullers tend to form long train-like structures (typically 3 – 7 together) while pushers tend to swim side by side (typically in pairs).

The goal of the following question is to elucidate the connection between the phenomenon of reduction of viscosity and another recently observed phenomena for suspensions of microswimmers [62]. Sokolov, Apodaca, Grzybowski, and Aranson in 2009–2010 performed a set of experiments [62] demonstrating that swimming microorganisms (e.g. *Bacillus subtilis*, 5µm in length) can rotate microscopic gears (size ∼ 100 microorganisms). The direction of rotation is not random and is determined by the asymmetry of the teeth of the gears (one of the edges of each tooth is shorter than the other). This experiment is interesting by itself as it highlights the differences between Brownian motion of molecules in an ideal gas, and seemingly random motion of swimming microorganisms – Brownian motion of molecules will not rotate the gears.

The question that we want to raise here is about the connection between rotation of gears and reduction of viscosity. Physical experiments [28] and our numerical solutions of the PDE model showed that microswimmers can reduce the effective shear viscosity. But how big a decrease can one expect? The experiment with gears suggests that the effective shear viscosity can be negative – indeed, the gears are rotating without an external force (e.g. magnetic field) being applied
to them. On the other hand the cause of the rotation is not to be found in the bulk, but rather in the interactions between swimming microorganisms and the boundary. Clarifying the connection between effective viscosity and rotation of asymmetric gears would benefit the general understanding of suspensions of microswimmers. A separate issue here is with pullers. In the preliminary physical experiments, swimming microorganisms such as algae, which are believed to be pullers, did not decrease the viscosity and did not rotate the gears. This is in contrast with our numerical analysis, which showed increase of effective viscosity for pushers at moderate concentrations. Results similar to ours were obtained for pullers in the dilute regime by [44].

The last question that we would like to raise here would be of interest to mathematicians rather than physicists or biologists, and is related to issues of existence of solutions. In Chapters 2 and 3 we present PDE models that consist of the instantaneous PDE problem (relating swimmer velocities to their positions) and the ODE problem for the positions of swimmers based on the solution of the instantaneous PDE problem. We proved that the instantaneous problems are well-posed (see Appendix E.2). One of the open questions is establishing global in time existence of solutions to the ODE describing the dynamics of the swimmers. For this we would like to show on a theoretical level that collisions between model swimmers in the PDE models of Chapters 2 and 3 are not possible in finite time. For this one can consider a simple representative example: position two swimmers (e.g., modeled according to Chapter 3) along the same line facing each other and allow them to swim. They will start moving towards each other, but the closer they get the slower they swim. We would like to demonstrate that the velocity of the swimmers is roughly inversely proportional to the distance between swimmers. If the inverse dependence between the velocity of the swimmers and the distance between them proves true it would mean that the distance between swimmers decays exponentially in time and hence does not become zero (no collisions) in finite time.

Showing that the PDE models of Chapters 2 and 3 do not allow collisions in finite time (or demonstrating otherwise) would help to identify the types of interactions that are possible between swimmers within these models. In particular, during the numerical simulations of suspensions of microswimmers at mod-
erate concentrations we often have to resolve interactions of swimmers at small
distances. Having a lower bound on the time step in the numerical simulations
inevitably leads to “numerical collisions” between swimmers. This question will
clarify whether the observed collisions are purely an artifact of finite time step in
the numerical simulations or are the result of the PDE models.
Reduction of Navier-Stokes to Stokes

Consider the Navier-Stokes equation

$$\rho \left[ \frac{\partial}{\partial t} u + u \cdot \nabla u \right] = -\nabla p + \mu \nabla^2 u + F,$$  \hspace{1cm} (A.1)

where $\rho$ is the fluid density, $t$ is time, $x$ is the spatial variable, $u$ is the fluid velocity, $p$ is the fluid pressure, and $\mu$ is the viscosity of the fluid. Scaling parameters

$$L \quad \text{characteristic length}, \hspace{1cm} (A.2)$$
$$V \quad \text{characteristic speed}, \hspace{1cm} (A.3)$$
$$T = \frac{L}{V} \quad \text{characteristic time}, \hspace{1cm} (A.4)$$
$$P \quad \text{characteristic pressure}, \hspace{1cm} (A.5)$$
$$\rho \quad \text{fluid density}, \hspace{1cm} (A.6)$$
$$f \quad \text{characteristic force}. \hspace{1cm} (A.7)$$

Introduce the non-dimensional (marked by *) parameters

$$x = Lx^*, \quad u = Vu^*, \quad t = Tt^*, \quad p = Pp^*, \quad F = fF^*, \hspace{1cm} (A.8)$$
and operators
\[
\frac{\partial}{\partial t} = \frac{1}{T} \frac{\partial}{\partial t^*}, \quad \nabla_x = \frac{1}{L} \nabla_{x^*}, \quad \triangle_x = \frac{1}{L^2} \triangle_{x^*}. \tag{A.9}
\]
Substituting (A.8) and (A.9) into (A.1) we obtain
\[
\rho \left[ \frac{V}{T} \frac{\partial}{\partial t^*} u^* + \frac{V^2}{L} u^* \cdot \nabla_{x^*} u^* \right] = -\frac{P}{L} \nabla_{x^*} p^* + \frac{V}{L^2} \mu \triangle_{x^*} u^* + f F^*.
\]

Remembering the scaling for time (A.4) and multiplying through by \( \frac{L^2}{V \mu} \) we obtain
\[
\frac{\rho V L}{\mu} \left[ \frac{\partial}{\partial t^*} u^* + u^* \cdot \nabla_{x^*} u^* \right] = -\frac{L P}{V \mu} \nabla_{x^*} p^* + \triangle_{x^*} u^* + \frac{f L^2}{V \mu} F^*.
\tag{A.10}
\]

Introduce the non-dimensional froups
\[
\mathcal{R}e := \frac{\rho V L}{\mu} \ll 1, \tag{A.11}
\]
\[
\eta := \frac{V \mu}{L P} \tag{A.12}
\]
\[
\text{taking } \frac{f L}{P} = 1. \tag{A.13}
\]

Multiplying (A.10) by \( \eta \) we obtain
\[
\eta \triangle_{x^*} u^* = \nabla_{x^*} p^* - F^* + \mathcal{R}e \left[ \frac{\partial}{\partial t^*} u^* + u^* \cdot \nabla_{x^*} u^* \right].
\]

Assuming
\[
\eta \mathcal{R}e \ll 1 \tag{A.14}
\]

we obtain the Stokes equation
\[
\eta \triangle_{x^*} u^* = \nabla_{x^*} p^* - F^*.
\]
Basic Stokes solutions

B.1 Point force

The velocity field due to a point force $\mathbf{F}$ in an unbounded fluid domain is

$$ u(x) = G(x) \cdot \mathbf{F}, \quad G(x) = \frac{1}{8\pi\mu|x|} \left( \mathbf{I} + \frac{xx^T}{|x|^2} \right). \quad (B.1) $$

Tensor $G$ (along with a suitable pressure tensor $P$) solves the Stokes problem with a point force

$$ \begin{cases} \mu \triangle G = \nabla P - \delta(x) \\ \text{div}(u) = 0 \end{cases}.$$

Therefore, it is the fundamental solution to the above problem, given in components by

$$ G_{ij}(x) = \frac{1}{8\pi\mu|x|} \left( \delta_{ij} + \frac{x_i x_j}{|x|^2} \right), $$

with the corresponding pressure, a vector, given by (up to an additive constant)

$$ P_i(x) = \frac{1}{4\pi} \frac{x_j}{|x|^3}. $$

The stress tensor corresponding to $G$ and $P$ is a triadic $\Sigma$:

$$ \Sigma_{ijk} = -P_j \delta_{ik} + \frac{\mu}{2} (G_{ij,k} + G_{kj,i}) = -\frac{3}{4\pi} \frac{x_i x_j x_k}{|x|^5}. $$
For more details see [67].

### B.2 A ball moving through fluid

A ball of radius $R$ moving with a constant velocity $\mathbf{v}$ through an unbounded fluid domain creates the velocity field:

$$
\mathbf{u}(\mathbf{x}) = H(\mathbf{x}; R) \mathbf{v}, \quad H(\mathbf{x}; R) = \frac{3R}{4\pi} \left[ \alpha \mathbf{I} + \beta \mathbf{n} \mathbf{n}^T \right], \quad (B.2)
$$

$$
\alpha = 1 + \frac{R^2}{3r^2}, \quad \beta = 1 - \frac{R^2}{r^2}, \quad r = |\mathbf{x}|, \quad \mathbf{n} = \frac{\mathbf{x}}{r},
$$

where $\mathbf{I}$ is the identity matrix and $(\mathbf{n} \mathbf{n}^T) \mathbf{v} = (\mathbf{v} \cdot \mathbf{n}) \mathbf{n}$ is the dyadic product.

Away from the origin ($r \gg R$)

$$
H(\mathbf{x}; R) \approx \gamma_0 G(\mathbf{x}), \quad \gamma_0 = 6\pi \mu R,
$$

where $\gamma_0$ is the inverse mobility of the ball, characterizing the applied force necessary to generate a steady translational velocity of unit magnitude.

### B.3 Stokes law for drag

The drag force from the fluid of viscosity $\mu$ on a ball of radius $R$, moving with a velocity $\mathbf{v}$ through unbounded fluid is

$$
\mathbf{F} = -\gamma_0 \mathbf{v}. \quad (B.3)
$$

More generally, suppose that a ball is added to given an initial background flow $\mathbf{u}$ and that under the influence of external forces the ball undergoes a steady translational motion of the ball with velocity $\mathbf{v}$. The Stokes law for drag states that the accompanying drag force $\mathbf{F}$ on the ball is proportional to the difference of the velocity of the ball and the velocity of the background flow, which would exist at the location of the ball $\mathbf{x}$ in its absence:

$$
\mathbf{F} = -\gamma_0 (\mathbf{v} - \mathbf{u}(\mathbf{x})). \quad (B.4)
$$
Since in the Stokes framework the drag on the ball must be balanced by the applied forces on the particle, (B.4) provides a means of calculating the net applied force that results in a given translation velocity $v$.

The Stokes law is an approximation to Faxén’s first law [67]:

$$
F = -\gamma_0 (v - \mathbf{u}(\mathbf{x})) + \gamma_0 \frac{R^2}{6} \nabla^2 \mathbf{u}(\mathbf{x}).
$$

(B.5)

If the background flow is due to a point force or another translating sphere at $\mathbf{x}$, far from $\mathbf{r}$, then it follows from (B.1) and (B.2) that the gradient is small $- \sim \frac{1}{|\mathbf{x} - \mathbf{r}|^2}$. In this case the Stokes law (B.4) is a good approximation to (B.5).

**B.4 Q2D Green’s function**

Take formula (51) in [56],

$$
\mathbf{u}_j^1 \approx -\frac{3z}{4\rho^2} \left(1 - \frac{z}{2h}\right) \left[1 \delta_{\alpha\beta} - \frac{r_{\alpha}r_{\beta}}{\rho^2}\right] \delta_{j\alpha} \delta_{1\beta} + \\
+ \delta_{j3} \delta_{k3} O\left(\rho^{-\frac{1}{2}} e^{-\rho_{\mu}/H}\right) + \left(\delta_{j3} \delta_{k3} + \delta_{k3} \delta_{j3}\right) O\left(\frac{r_{\alpha}r_{\beta}}{\rho} \rho^{-\frac{1}{2}} e^{-\rho_{\mu}/H}\right) + \\
+ \delta_{j\alpha} \delta_{k\beta} \left[O\left(\frac{r_{\alpha}r_{\beta}}{\rho} \rho^{-\frac{1}{2}} e^{-\rho_{\mu}/H}\right) + O\left(\frac{r_{\alpha}r_{\beta}}{\rho} \rho^{-\frac{1}{2}} e^{-2\rho_{\mu}/H}\right)\right].
$$

(B.6)

where $y_1 \approx 4.2$, and rewrite it in our notations. The point force is applied midway between the walls of the film. Replace $h = \frac{1}{2} H$; here $H$ is thickness of the film (replace by $h$). Assume $k = 1$, that is force is applied along $e_1$. Here $\rho$ is the radius vector from point force (replace by $r = |\mathbf{r}|$). Replace $x_3$ by $z$.

Performing the above changes, we obtain

$$
\mathbf{u}_j^1 \approx -\frac{3z}{4\rho^2} \left(1 - \frac{z}{2h}\right) \left[1 \delta_{\alpha\beta} - \frac{r_{\alpha}r_{\beta}}{\rho^2}\right] \delta_{j\alpha} \delta_{1\beta} + \\
+ \delta_{j3} \delta_{13} O\left(\rho^{-\frac{1}{2}} e^{-\rho_{\mu}/(2h)}\right) + \left(\delta_{j3} \delta_{1\alpha} + \delta_{13} \delta_{j\alpha}\right) O\left(\frac{r_{\alpha}}{\rho} \rho^{-\frac{1}{2}} e^{-\rho_{\mu}/(2h/2)}\right) + \\
+ \delta_{j\alpha} \delta_{1\beta} \left[O\left(\frac{r_{\alpha}r_{\beta}}{\rho} \rho^{-\frac{1}{2}} e^{-\rho_{\mu}/(2h)}\right) + O\left(\frac{r_{\alpha}r_{\beta}}{\rho} \rho^{-\frac{1}{2}} e^{-2\rho_{\mu}/(2h)}\right)\right].
$$

(B.7)
Note that only the first term in (B.7) does not decay exponentially in $\rho$:

$$u_j^1 \approx -\frac{3}{4\pi\mu} z \left(1 - \frac{z}{2h}\right) \frac{1}{\rho^2} \left[ \frac{r_{\alpha\beta}}{\rho^2} - \frac{1}{2} \delta_{\alpha\beta} \right] \delta_{j\alpha} \delta_{1\beta} =$$

$$= \frac{3}{4\pi\mu} z \left(1 - \frac{z}{2h}\right) \frac{1}{\rho^2} \left[ \frac{r_{\alpha\beta}}{\rho^2} \delta_{j\alpha} \delta_{1\beta} - \frac{1}{2} \delta_{\alpha\beta} \delta_{j\alpha} \delta_{1\beta} \right] =$$

$$= \frac{3}{4\pi\mu} z \left(1 - \frac{z}{2h}\right) \frac{1}{\rho^2} \left[ \frac{r_{j1}}{\rho^2} \delta_{11} - \frac{1}{2} \delta_{j1} \right].$$

(B.8)

Rewriting $u^3$ in components, we have

$$u^1 \approx \frac{3z}{4\pi\mu} \left(1 - \frac{z}{2h}\right) \frac{1}{\rho^2} \left[ \frac{r_{j1}}{\rho^2} - \frac{1}{2} \delta_{11} \right] = \frac{3z}{4\pi\mu} \left(1 - \frac{z}{2h}\right) \frac{1}{\rho^2} \left[ \frac{z^2}{\rho^2} - \frac{1}{2} \delta_{j1} \right].$$

(B.9)

Note that $\rho^2 \approx x^2 + y^2$. Hence, (B.8) takes the form

$$u^1 \approx \frac{3z}{8\pi\mu} \left(1 - \frac{z}{2h}\right) \frac{1}{\rho^4} \left[ \frac{x^2 - y^2}{\rho^2} \right] =$$

$$= \frac{3z}{8\pi\mu} \left(1 - \frac{z}{2h}\right) \frac{1}{\rho^2} \left[ \frac{x^2 - y^2}{\rho^2} \right].$$

(B.9)

Since $|z| < h \ll 1$, one has an approximation for the Green’s function in Q2D:

$$\tilde{G}(\mathbf{r}) \approx f(z) \begin{bmatrix} x^2 - y^2 & 2xy & 0 \\ 2xy & y^2 - x^2 & 0 \\ 0 & 0 & 0 \end{bmatrix},$$

where

$$f(z) = \frac{3}{8\pi\mu} z \left(1 - \frac{z}{2h}\right).$$

(B.10)

Here $f(z)$ satisfies no-slip boundary conditions: $f(z = 0) = 0$ and $f(z = 2h) = 0$. 
Asymptotic formulas

The velocities of the head and tail balls in terms of \( \{ \alpha^j \} \) and \( x^j_H \) are

\[
\frac{1}{f_p} v^i_H = \sum_{j \neq i} \left[ (1 - \alpha^j)G(x^i_H - x^j_H) + \alpha^jG(x^i_H - x^j_T) - G(x^i_H - x^j_P) \right] \tau^j + \\
\left[ \alpha^iG(x^i_H - x^i_T) + G(x^i_H - x^i_P) + \frac{1}{\gamma_0 I} \right] \tau^i,
\]

(C.1)

\[
\frac{1}{f_p} v^i_T = \sum_{j \neq i} \left[ (1 - \alpha^j)G(x^i_T - x^j_H) + \alpha^jG(x^i_T - x^j_T) - G(x^i_T - x^j_P) \right] \tau^j + \\
\left[ (1 - \alpha^i)G(x^i_T - x^i_H) + G(x^i_T - x^i_P) + \frac{1}{\gamma_0 I} \right] \tau^i.
\]

(C.2)

Note that

\[
G(-x) = G(x) \quad \forall x \in \mathbb{R}^3
\]

(C.3)

and

\[
\tilde{G}(-x) = \tilde{G}(x) \quad \forall x \in \mathbb{R}^3.
\]

(C.4)

Hence,

\[
G(x^i_T - x^i_H) = G(x^i_H - x^i_T) = G(2L\tau).
\]

(C.5)

Using the (C.1,C.2) and the relation

\[
v^i_c = \frac{1}{2}(v^i_H + v^i_T),
\]

\[
\omega^i = \frac{1}{2L}(v^i_H - v^i_T) \times \tau^i,
\]
we obtain

\[
\frac{2}{f_p} v^i_c = \sum_{j \neq i} \left[ (1 - \alpha^j) \left\{ G(x^i_H - x^j_H) + G(x^i_T - x^j_T) \right\} + \\
+ \alpha^j \left\{ G(x^i_H - x^j_p) + G(x^i_T - x^j_T) \right\} - \\
- \left\{ G(x^i_H - x^j_p) + G(x^i_T - x^j_T) \right\} \tau^j + \\
+ \left[ G(2L \tau^i) + G(x^i_H - x^j_p) + G(x^i_T - x^j_T) + \frac{2}{\gamma_0} I \right] \tau^i,
\]

\[
\frac{2L}{f_p} \omega^i = \tau^i \times \sum_{j \neq i} \left[ (1 - \alpha^j) \left\{ G(x^i_H - x^j_H) - G(x^i_T - x^j_T) \right\} + \\
+ \alpha^j \left\{ G(x^i_H - x^j_p) - G(x^i_T - x^j_T) \right\} - \\
- \left\{ G(x^i_H - x^j_p) - G(x^i_T - x^j_T) \right\} \tau^j + \\
+ \tau^i \times \left[ (2\alpha^i - 1)G(2L \tau^i) + G(x^i_H - x^j_p) - G(x^i_T - x^j_T) \right] \tau^i.
\]

### C.1 Expansion of \( G(\cdot) \)

The expansion of \( v^i_c \) in orders of \( \varepsilon \) is due to the expansions of the Green’s function \( G \), e.g.

\[
G(x^i_H - x^j_p) = G(x^i_H - x^i_p + x^i_C - x^j_C - x^j_p) = \\
= G \left( (x^i_H - x^i_p) + (x^i_C - x^j_C) + (x^j_C - x^j_p) \right).
\]

Here the quantities \( (x^i_H - x^i_p) \) and \( (x^i_C - x^j_C) \) measure the distances in the same bacteria, hence they do not depend on \( \varepsilon = |x^i_C - x^j_C|^{-1} \). The only quantity that depends on \( \varepsilon \) is \( (x^i_C - x^j_C) \).

### C.2 Asymptotic expansion for \( \alpha^i \)

Consider the asymptotic expansion

\[
\alpha^i = a^0 + \varepsilon \alpha^i_1 + \varepsilon^2 \alpha^i_2 + \ldots,
\] (C.6)
and substitute it into (2.34), where all terms are expanded in asymptotic series in 
\( \varepsilon = |x_c^2 - x_c^1|^{-1} \). Note that the terms like \( G(x^i_H - x^i_T) \) do not depend on \( \varepsilon \); hence, their expansion will have only \( \varepsilon^0 \) order term (itself). On the other hand, the terms like \( G(x^i_H - x^j_T) \) are of order \( \varepsilon^1 \) and will not have order \( \varepsilon^0 \) terms.

Thus, at the order \( \varepsilon^0 \) the equation (2.34) becomes

\[
\alpha^i_0 (\tau^i)^T \left[ G(x^i_H - x^i_T) + G(x^i_T - x^i_H) - \frac{2}{\gamma_0} \right] \tau^i = (\tau^i)^T \left[ G(x^i_H - x^i_T) + G(x^i_T - x^i_H) - G(x^i_T - x^i_P) - \frac{1}{\gamma_0} \right] \tau^i. \tag{C.7}
\]

Express the arguments of \( G(\cdot) \) in terms of \( \tau^i, L, \) and \( \zeta \):

\[
x^i_H - x^i_T = 2L\tau^i, \quad x^i_H - x^i_P = (1 - \zeta)L\tau^i, \quad x^i_T - x^i_P = (-1 - \zeta)L\tau^i, \tag{C.8}
\]

and substitute back into (C.7) to get

\[
\alpha^i_0 (\tau^i)^T \left[ G(2L\tau^i) + G(-2L\tau^i) - \frac{2}{\gamma_0} \right] \tau^i = (\tau^i)^T \left[ G(-2L\tau^i) + G((1 - \zeta)L\tau^i) - G((-1 - \zeta)L\tau^i) - \frac{1}{\gamma_0} \right] \tau^i. \tag{C.9}
\]

Using the definition of

\[
\gamma_0 = \frac{1}{8\pi\mu R} \tag{C.10}
\]

and the properties (C.17-C.18), simplify (C.9):

\[
\frac{1}{4\pi\mu} \alpha^i_0 \left[ \frac{1}{2L} + \frac{1}{2L} - \frac{1}{R} \right] = \frac{1}{4\pi\mu} \left[ \frac{1}{2L} + \frac{1}{1 - \zeta|L|} - \frac{1}{1 + \zeta|L|} - \frac{1}{2R} \right]. \tag{C.11}
\]

Multiply through by \( 4\pi\mu RL \):

\[
-\alpha^i_0 \left[ 1 - \frac{R}{L} \right] = -\left[ \frac{1}{2} - \frac{R}{2L} - \frac{R}{1 - \zeta|L|} + \frac{R}{1 + \zeta|L|} \right]. \tag{C.12}
\]

Pull out \( \frac{1}{2} \) from the RHS, and solve for \( \alpha^i_0 \)

\[
\alpha^i_0 = \frac{1}{2} \frac{1 - \frac{R}{L} \left( 1 + \frac{2}{|1 - \zeta|} - \frac{2}{|1 + \zeta|} \right)}{1 - \frac{R}{L}}. \tag{C.13}
\]
Denote
\[ \xi := \frac{R}{L} \ll 1, \tag{C.14} \]
and perform the expansion of (C.13) in terms of \( \xi \)
\[ a_0^i = \frac{1}{2} \left( 1 + z\xi + z\xi^2 + \ldots \right), \tag{C.15} \]
where
\[
z = z(\zeta) := 2 \left( \frac{1}{|1 + \zeta|} - \frac{1}{|1 - \zeta|} \right) = \begin{cases} 
\frac{4}{\zeta^2 - 1} & \text{if } \zeta < -1, \\
\frac{4\zeta}{\zeta^2 - 1} & \text{if } 1 < \zeta < 1, \\
-\frac{4\zeta}{\zeta^2 - 1} & \text{if } 1 < \zeta. 
\end{cases} \tag{C.16} \]

Lemma 6 (Properties of \( G(\cdot) \)). Note the following two properties of \( G(\cdot) \):

1. Let \( q \in \mathbb{R} \) and \( \tau \in \mathbb{R}^3 \), \( |\tau| = 1 \). Then
\[ G(q\tau) = \frac{1}{|q|} G(\tau). \tag{C.17} \]

2. Let \( \tau \in \mathbb{R}^3 \), \( |\tau| = 1 \). Then
\[ \tau^T G(\tau) \tau = \frac{1}{4\pi\mu}. \tag{C.18} \]

Proof. Property 1 follows simply from the definition of \( G(\cdot) \):
\[ G(q\tau) = \frac{1}{8\pi\mu |q|} \left( \mathbf{I} + \tau\tau^T \right) = \frac{1}{|q|} G(\tau). \tag{C.19} \]

Property 2 follows by simple substitution:
\[ \tau^T G(\tau) \tau = \frac{1}{8\pi\mu} \tau^T \left( \mathbf{I} + \tau\tau^T \right) \tau = \frac{1}{8\pi\mu} (1 + 1) = \frac{1}{4\pi\mu}. \tag{C.20} \]
\[ \Box \]
\section*{C.3 Sign of $A^i(f_p, L, R, \mu, \alpha_0)$}

\textbf{Lemma 7} (Properties of $(1 - \zeta - 2\alpha_0^i)$). Assume $f_p > 0$ in the expression

$$A^i(f_p, L, R, \mu, \alpha_0) = \frac{f_p L}{32\pi \mu} (1 - \zeta - 2\alpha_0),$$ \hfill (C.21)

where $\alpha_0$ is given by (C.15-C.16). For pushers ($\zeta < 0$)

$$A^i(f_p, L, R, \mu, \alpha_0) > 0.$$

\hfill (C.22)

For pullers ($\zeta > 0$)

$$A^i(f_p, L, R, \mu, \alpha_0) < 0.$$

\hfill (C.23)

\textit{Proof.} Use the formula (C.15) for $\alpha_0^i$ to rewrite

$$1 - \zeta - 2\alpha_0^i = 1 - \zeta - \left(1 + z\xi + z\xi^2 + \ldots\right) =$$

\hfill (C.24)

$$= -\left(\zeta + z\xi + z\xi^2 + \ldots\right) = -\left(\zeta + \frac{z\xi}{1 - \xi}\right).$$

Consider three case: $\zeta < -1$, $-1 < \zeta < 1$, $1 < \zeta$. For each of these cases use the formula (C.16) for $z(\zeta)$ to evaluate (C.24).

Case $\zeta < -1$: Here $z(\zeta) = \frac{4}{\zeta^2 - 1}$, and

$$-\left(\zeta + \frac{z\xi}{1 - \xi}\right) = -\left(\zeta + \frac{4}{\zeta^2 - 1} \frac{\xi}{1 - \xi}\right).$$ \hfill (C.25)

This expression is always positive when $(-\zeta - 1) \sim 1$ as $\xi \to 0$.

Case $-1 < \zeta < 1$: Here $z(\zeta) = \frac{4\zeta}{\zeta^2 - 1}$, and

$$-\left(\zeta + \frac{z\xi}{1 - \xi}\right) = -\left(\zeta + \frac{4\zeta}{\zeta^2 - 1} \frac{\xi}{1 - \xi}\right) = -\zeta \left(1 + \frac{4}{\zeta^2 - 1} \frac{\xi}{1 - \xi}\right).$$ \hfill (C.26)

This expression changes sign from positive to negative only as $\zeta$ passes through 0. So it is positive when $\zeta < 0$ and negative when $\zeta > 0$. 
Case 1 < \zeta: Here \( z(\zeta) = \frac{-4\xi}{\zeta^2 - \xi} \) and

\[
- \left( \zeta + \frac{z\xi}{1 - \xi} \right) = - \left( \zeta - \frac{4\xi}{\zeta^2 - 1} \frac{\xi}{1 - \xi} \right). 
\]

This expression is always negative when \((\zeta - 1) \sim 1\) as \(\xi \to 0\).
Stability of the “mirror image” configuration

Before analyzing the stability of the “mirror image” configuration we determine the quantity, which does not depend of the orientation of the $\vec{ox}$-axis (i.e., it does not depend on the choice of observer), that characterizes how close a given configuration is to a “mirror image” configuration. Then we perturb this parameter by a small amount and check whether this parameter is decreasing. If this parameter is decreasing, the configuration is stable; otherwise it is unstable.

Note that for two swimmer, in the “mirror image” configuration

$$\pi + 2\phi - (\theta^1 + \theta^2) = 2\pi n, \quad n \in \mathbb{N} \quad (D.1)$$

for any choice of the $\vec{x}$-axis. Moreover, if equation (D.1) holds, then two swimmers are in the “mirror image” configuration. Therefore, the quantity

$$\delta := \pi + 2\phi - (\theta^1 + \theta^2) \quad (D.2)$$

can be viewed as a measure of deviation from the “mirror image” configuration.

To perform the stability analysis, we perturb the “mirror image” configuration. That is, we choose $|\delta(0)| > 0$ small, and we check whether $|\delta(t)|$ decreases with time. If $\delta'(0)$ has the opposite sign to $\delta(0)$, then $|\delta(t)|$ decreases with time locally, and the configuration is stable; otherwise it is not stable.
We have
\[ \delta' = 2\phi' - (\theta^1 + \theta^2) = 2\phi' - (\omega^1 + \omega^2). \] (D.3)

The expressions for \( \omega^1 \) and \( \omega^2 \) can be found from (2.43,2.47,2.49). The expression
for \( \phi' \) can be found simply as a projection of the translational velocity difference
\((v_2^c - v_1^c)\) onto the unit circle
\[
\phi' = \varepsilon (v_2^c - v_1^c) \cdot \begin{bmatrix} -\sin(\phi) \\ \cos(\phi) \end{bmatrix} = \\
\varepsilon v_0 \left( -\sin(\phi)(\cos(\theta^2) - \cos(\theta^1)) + \cos(\phi)(\sin(\theta^2) - \sin(\theta^1)) \right) + O(\varepsilon^3),
\]
where we used
\[
v_i^c = v_0 \tau_i + O(\varepsilon^2), \quad i = 1, 2.
\]

Without loss of generality, choose the \( x \)-axis so that \( \pi + 2\phi = 0 \), that is, \( \phi = -\pi/2 \), which means the second swimmer is directly below the first swimmer. Then
\[
\delta' = \varepsilon v_0 \left( \cos(\theta^2) - \cos(\theta^1) \right) + O(\varepsilon^3) = \\
= -2\varepsilon v_0 \sin \left( \frac{\theta^2 - \theta^1}{2} \right) \sin \left( \frac{\theta^2 + \theta^1}{2} \right) + O(\varepsilon^3) = \\
= -2\varepsilon v_0 \sin \left( \frac{\theta^1 - \delta}{2} \right) \sin \left( \frac{\delta}{2} \right) + O(\varepsilon^3). \] (D.4)

Thus, for swimmers rotated outward \((0 < \theta^1 < \pi)\) the “mirror image” configuration is stable and for swimmers rotated inward \((0 > \theta^1 > -\pi)\) the “mirror image” configuration is unstable under small perturbations. The results of the stability analysis are not affected by the type of the swimmer; they are the same for all values of \( \zeta \).
Variational formulation and well-posedness of problem (3.1-3.6)

E.1 Variational formulation

There are a number of questions that are easier to answer working with the variational instead of the PDE formulation of the problem. Here we refer to the instantaneous PDE problem (3.1-3.6). The questions that we plan to answer are well-posedness (existence and uniqueness of the solution) of the instantaneous problem (3.1-3.6) and construction of the numerical scheme for approximating the solution to (3.1-3.6).

For simplicity of presentation, we will derive the variational formulation for a single swimmer. Obtaining the variational formulation for multiple swimmers after that will be straightforward.

First, we specify the admissible class \( A_g \) of solutions \( u \) and then the space \( A_0 \) of variations \( v \). The admissible class of velocity fields \( u \) is defined as

\[
A_g := \left\{ u \in H^1(\Omega_F) \mid \begin{array}{l}
u(x) = g(x) \quad \text{for} \ x \in \partial \Omega, \\
u(x) = u_c + \omega_u \times (x - x_c) \quad \text{for} \ x \in \Gamma_h, \\
u(x) = u_c + \omega_u \times (x - x_c) + \tau \tilde{u} \quad \text{for} \ x \in \Gamma_p \end{array} \right\}.
\]

(E.1)

Here \( \tau \) is a unit tangent to the surface and \( \tilde{u} \) is an unknown scalar function.
The linear space $\mathcal{A}_0$ of variations for the admissible class $\mathcal{A}$ is

$$
\mathcal{A}_0 := \left\{ v \in H^1(\Omega_F) \mid v(x) = 0 \quad \text{for} \quad x \in \partial \Omega, \right. \\
\left. v(x) = v_c + \omega v \times (x - x_c) \quad \text{for} \quad x \in \Gamma_H, \right. \\
\left. v(x) = v_c + \omega v \times (x - x_c) + \tau \tilde{v} \quad \text{for} \quad x \in \Gamma_P \right\}.
$$

(E.2)

Rewrite the Stokes equation $(3.1)$ by adding to its LHS

$$
\mu \text{div}(\nabla u)^T = \mu \nabla (\text{div} u) = 0.
$$

We obtain

$$
2\mu \text{div} \left( D(u) \right) = \nabla p. \tag{E.3}
$$

This is done to obtain symmetrized gradient $D(u)$ (and later a stress tensor $\sigma(u, p)$) in place of $\nabla u$. Multiply (E.3) by $v \in \mathcal{A}_0$ and integrate over $\Omega_F$

$$
\int_{\Omega_F} \left( 2\mu \text{div} \left( D(u) \right) - \nabla p \right) \cdot v \, dx = 0. \tag{E.4}
$$

Integrate (E.4) by parts (here $n$ is a unit outward normal to the boundary)

$$
-2\mu \int_{\Omega_F} D(u) : \nabla v \, dx + 2\mu \int_{\partial \Omega_F} nD(u)v \, dx + \\
+ \int_{\Omega_F} p \text{div}(v) \, dx - \int_{\partial \Omega_F} pvn \, dx = 0. \tag{E.5}
$$

Combining the second and forth terms in (E.5), using the definition of stress tensor

$$
\sigma(u, p) := 2\mu D(u) - pI, \tag{E.6}
$$

and rearranging the remaining terms we obtain

$$
2\mu \int_{\Omega_F} D(u) : \nabla v \, dx - \int_{\Omega_F} p \text{div}(v) \, dx = \int_{\partial \Omega_F} n\sigma(u, p)v \, dx. \tag{E.7}
$$
Consider the last integral $\int_{\partial \Omega_F} \mathbf{n} \sigma(u, p) \mathbf{v} \, d\mathbf{x}$ and note that
\[
\partial \Omega_F = \partial \Omega \cup \partial S,
\]
where $\partial S = \Gamma_H \cup \Gamma_P$.

Due to the boundary conditions (3.3-3.6) on the solution $u$ and the boundary conditions (E.2) on the test function $\mathbf{v}$ we have
\[
\int_{\partial \Omega} \mathbf{n} \sigma(u, p) \mathbf{v} \, d\mathbf{x} = 0.
\]

(E.8)

The integral over the surface of swimmer can be written as
\[
\int_{\partial B} \mathbf{n} \sigma(u, p) \mathbf{v} \, d\mathbf{x} = \int_{\partial B} \mathbf{n} \sigma(u, p) \left( \mathbf{v}_c + \omega \times (\mathbf{x} - \mathbf{x}_c) + \tau \hat{\mathbf{v}} \right) \, d\mathbf{x} = \mathbf{v}_c \cdot \int_{\partial B} \mathbf{n} \sigma(u, p) \, d\mathbf{x} + \omega \int_{\partial B} (\mathbf{x} - \mathbf{x}_c) \times \mathbf{n} \sigma(u, p) \, d\mathbf{x} + \int_{\Gamma_p} \mathbf{n} \sigma(u, p) \tau \hat{\mathbf{v}} \, d\mathbf{x}.
\]

(E.9)

From the balance conditions (3.5-3.6) and the prescribed values of the tangential component of traction (3.12) the RHS of (E.9) takes the form
\[
\int_{\Gamma_p} \mathbf{n} \sigma(u, p) \tau \hat{\mathbf{v}} \, d\mathbf{x} = - \int_{\Gamma_p} \frac{f_p}{|\Gamma_p|} (\mathbf{d} \cdot \tau \hat{\mathbf{v}}) \, d\mathbf{x} = - \int_{\Gamma_p} \frac{f_p}{|\Gamma_p|} \mathbf{d} \cdot \left[ \int_{\Gamma_p} \tau \hat{\mathbf{v}} \, d\mathbf{x} + \int_{\Gamma_p} \mathbf{v}_c \, d\mathbf{x} + \int_{\Gamma_p} \omega \times (\mathbf{x} - \mathbf{x}_c) \, d\mathbf{x} \right] +
\]

\[
\int_{\Gamma_H} \frac{f_p}{|\Gamma_p|} \mathbf{d} \cdot \left[ \int_{\Gamma_H} \mathbf{v}_c \, d\mathbf{x} + \int_{\Gamma_H} \omega \times (\mathbf{x} - \mathbf{x}_c) \, d\mathbf{x} \right] = \frac{f_p}{|\Gamma_p|} \mathbf{d} \cdot \left[ - \int_{\Gamma_p} \mathbf{v} \, d\mathbf{x} + \int_{\Gamma_H} \mathbf{v} \, d\mathbf{x} \right],
\]

which is a known linear functional of $\mathbf{v}$.

Introduce the notations
\[
a(u, v) := \mu \int_{\Omega_F} D(u) : \nabla v \, d\mathbf{x} = \mu \int_{\Omega_F} D(u) : D(v) \, d\mathbf{x},
\]

(E.10)

\[
(p, \text{div}(v)) := \int_{\Omega_F} p \, \text{div}(v) \, d\mathbf{x},
\]

(E.11)
\[ L(v) := \frac{f_p}{|\Gamma_p|} \mathbf{d} \cdot \left[ -\int_{\Gamma_p} \mathbf{v} \, dx + \int_{\Gamma_H} \mathbf{v} \, dx \right]. \quad (E.12) \]

In the notations (E.10-E.12) equation (E.7) takes the form

\[ 2a(u, v) - (p, \text{div} \, v) = L(v), \quad \forall v \in A_0. \quad (E.13) \]

Take the incompressibility equation in (3.1), multiply by \( q \in L^2_0(\Omega_F) \) and integrate over the fluid domain \( \Omega_F \) to get

\[ \int_{\Omega_F} \text{div}(u)q \, dx = (q, \text{div} \, u) = 0, \quad \forall q \in L^2_0(\Omega_F). \quad (E.14) \]

Combining equations (E.13-E.14) we have a complete variational formulation:
Find a pair \((u, p) , u \in A_g \text{ and } p \in L^2_0(\Omega_F)\), such that

\[ \begin{cases} 
2a(u, v) - (p, \text{div} \, v) = L(v), & \forall v \in A_0, \\
(q, \text{div} \, u) = 0, & \forall q \in L^2_0(\Omega_F). 
\end{cases} \quad (E.15) \]

The minimization problem, corresponding to the variational problem (E.15) is:

\[ \min_{u \in A_g^{\text{div}=0}} E[u], \quad \text{where } E[u] := a(u, u) - L(u) \quad (E.16) \]

and \( A_g^{\text{div}=0} \) consists of divergence free functions from \( A_g \).

### E.2 Well posedness of the instantaneous PDE problem (3.1-3.6)

The existence and uniqueness of minimizers of (E.16) is proved in a standard way provided that the coercivity of the bilinear form \( a(\cdot, \cdot) \) can be shown. The coercivity proof, using Korn’s inequality, is essentially contained in [68] as we now explain.

**Theorem 2.** The bilinear form \( a(\cdot, \cdot) \) is coercive on \( V \) with respect to the norm \( ||\cdot||_1 \), induced from \( H^1(\Omega_F) \). In particular, \( a(\cdot, \cdot) \) defines an equivalent inner product on \( V \).
Proof. Coercivity of $a(\cdot, \cdot)$ relies in an essential way on Korn’s inequality:

$$a(u, u) + ||u||^2 > c||u||^2_1,$$  \tag{E.17}\

for some $c > 0$ (here $|| \cdot ||$ denotes the $L_2$ norm). The proof of (E.17) found in [68] applies to the case for any subspace $U \subset H^1(\Omega_F)$ consisting of functions with a zero trace on a part of the boundary with nonzero two-dimensional measure. This applies to $V$ as its elements vanish on $\partial \Omega$ – the no-slip boundary conditions on the outer boundary of $\Omega_F$. In particular, $a(\cdot, \cdot)$ is nondegenerate, since the nontrivial kernel of $D(u)$, consisting of the rigid motions $u(x) = u_0 + \omega_0 \times x$, is excluded from $V$ due these boundary conditions. The result (E.17) is nontrivial, since the left-hand side contains only symmetric combinations of the derivatives of $u$.

The coercivity proof is completed by showing the existence of the following bound:

$$a(u, u) > d||u||^2,$$  \tag{E.18}\

for some $d > 0$. This replaces Poincare’s inequality in the case of the symmetrized gradient. It can be proved for $V$ as is done in [68], using the compactness of the embedding $V \hookrightarrow L_2(\Omega_F)$. This embedding is induced from the usual compact embedding $H^1(\Omega_F) \hookrightarrow L_2(\Omega_F)$, since $V$, being a closed subspace of $H^1(\Omega_F)$ is also weakly closed (see, e.g., [69]).

With the coercivity of $a(\cdot, \cdot)$ proved, the existence of minimizers for (E.16) can be proved by standard techniques. Since each minimizer satisfies (E.5), the difference of any two of them is $a(\cdot, \cdot)$-orthogonal to a dense subset of $V$, hence is zero, which proves uniqueness.

Finally, the unique field $u$ that solves (E.16) is a weak solution of the Stokes equation on a regular bounded domain. Therefore, once again by the standard theory (e.g., [70]), there exists a unique pressure field $p \in L_2(\Omega_F)$, which together with $u$ satisfies the a priori $L_2$ estimates [70]. Since the boundary of $\Omega_F$ and the is smooth, these estimates imply that $(u, p)$ are smooth too. By reversing the steps leading to the weak formulation (E.5), we now see that $(u, p)$ form a strong solution of the full system.
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