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# Hydrodynamic interactions among large populations of swimming micro-organisms

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## 1. Introduction

Bio-convection, biofilm forming or mechanics of reproduction are connected to the motility and collective behaviour of micro-organisms. For instance, spermatozoa suspensions exhibit coherent motion whose frequency and lifespan are strongly correlated to semen fertility (Moore et al. 2002). As interplays in many-bodied systems result in intricate patterns, the understanding of these requires an in-depth knowledge of the suspension microstructure and statistics. Representative and reliable statistics require a large number  $N_p$  of interactive swimmers that many simulation methods can hardly afford [e.g.  $N_p = 40$  in Mehandia and Nott (2008) or  $N_p \leq 216$  in Ishikawa et al. (2008)]. In the following, a spherical swimmer model is derived from the classical low Reynolds number framework and implemented in the force-coupling method (FCM) for large populations. Resulting statistics reveals non-trivial spatial arrangements of swimmers depending on their swimming gait.

## 2. Methods

### 2.1 Swimmer model

The modelling of a swimming micro-organism highly depends on the length scale of its description. Former experimental observations reveal that collective motion arise for length scales much larger than the swimmer characteristic length  $l$ . On the contrary to fish or birds, micro-organisms display rudimentary sensory abilities. Consequently, the coupling between individuals is mainly mediated through hydrodynamic interactions. The size  $a$  and swimming velocities  $V_0$  of most micro-swimmers are such that the Reynolds number is very small and they can be modelled using Stokes equations. A simple classification of micro-organisms consists in differentiating them according to the hydrodynamic perturbation they exert on the quiescent surrounding fluid. In the far-field description ( $r \gg 2a$ ), active swimmers can be considered a permanent

symmetric moving force dipole: the thrust exerted by its propulsive apparatus on the fluid counterbalances the drag exerted by the fluid on its head. The resulting swimming dipole is constant and reads:

$$S = aF^h \left( p \otimes p - \frac{1}{3} I \right),$$

where  $p$  is the swimming direction,  $F^h = \pm 6\pi\mu a V_0 p$  the drag force exerted on the spherical swimmer given by the Stokes law and  $I$  the  $\mathcal{R}^3$  identity matrix. If the swimmer propels itself by pushing the fluid from aft part (e.g. spermatozoa), it is called a *pusher*; the drag force is therefore negative. If it pulls the fluid from the fore part, it is called a *puller* (e.g. *Chlamydomonas*), and the drag is positive. The induced fluid velocity disturbance due to the presence of an isolated spherical pusher  $\alpha$  is shown in Figure 1(a),(b).

Drescher et al. (2011) evidenced the good agreement between the disturbed velocity field of a single bacteria and its dipolar approximation.

In the literature, combining detailed hydrodynamic interactions and finite-sized active particle systems proved to be computationally costly. For instance, Stokesian dynamics simulations are limited to  $O(10^2)$  swimmers, thereby drastically slowing statistical convergence, restricting 3D simulations to small computational domains and reducing the scale of observed collective motion if any. An alternative numerical method is introduced as a new paradigm for the modelling of active particles: the FCM.

### 2.2 The force coupling method

Originally developed by Maxey and Patel (2001), and largely developed since then, the FCM is a numerical solution method designed for particulate flows. Each particle is modelled via a 3D Gaussian function whose

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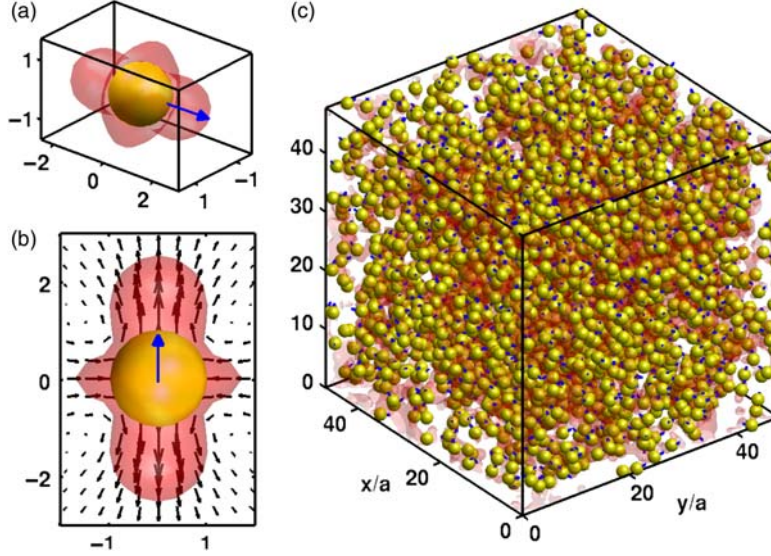


Figure 1. Light red: isocontour  $\|U\| = 0.5V_0$ . Blue arrows: swimming direction. (a) Fluid velocity disturbances induced by a spherical swimmer. (b) Velocity field induced around a ‘pusher’. For the ‘puller’ case, the arrows are just reversed. (c) Simulation box with  $N_p = 2664$ .

width is set to match analytical results. For each swimmer, the swimming dipole is distributed over the Gaussian envelope and a supplementary dipole is added to ensure the particle rigidity. Steric and analytical lubrication forces are eventually incorporated. Then, Stokes equations for the quiescent fluid forced by  $N_p$  swimming dipoles are solved for a 3D periodical domain using parallelised Fourier transforms. The resulting fluid disturbances are averaged over the Gaussian envelopes to obtain translational and rotational velocities of the swimmer. The FCM holds a high computational efficiency allowing simulations of

large populations:  $N_p \approx O(10^3)$ . Figure 1(c) shows a periodic box of size  $L^3 = (48a)^3$  with  $N_p = 2664$  swimmers, and the isocontour  $\|U\| = 0.5V_0$  of the velocity disturbances that evidence the long-range hydrodynamic interactions between swimmers.

### 3. Results and discussion

Large populations of *pushers* and *pullers* are simulated for volume fractions  $\varphi_v = N_p 4/3 \pi a^3 / L^3$  ranging from 10% to 30%. Not all the microstructure features can be explained

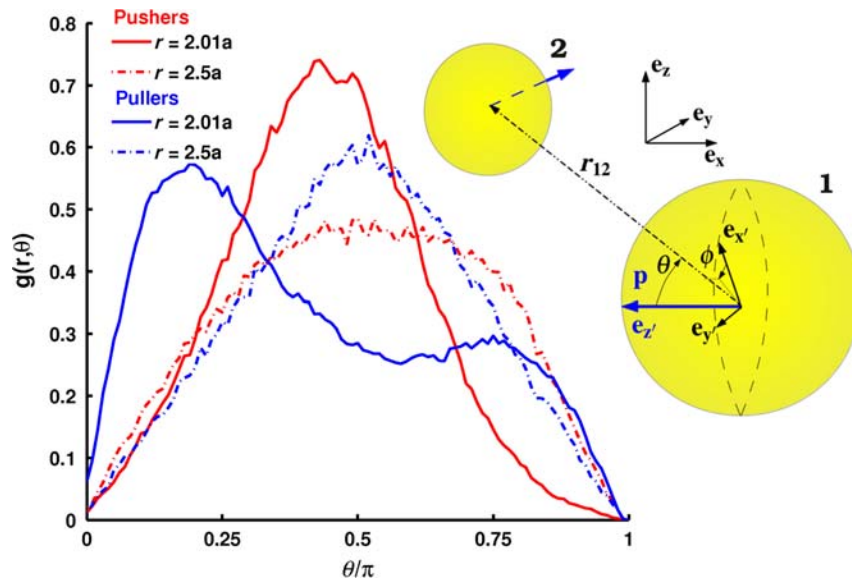


Figure 2. Left: normalised pair distribution depending on  $\theta$  for  $r = 2.01a$  and  $r = 2.5a$ . Right: swimmer body-fixed spherical coordinates.

with two-body analysis when the suspension is dense enough ( $\varphi_v \geq 0.2$ ) for multi-body ( $>2$ ) interactions to occur. Hence, there is a need for statistics on quantities of interest. Effects of steric and hydrodynamic interaction on the suspension microstructure are considered with the normalised pair distribution  $g$  centred on the local swimmer spherical coordinates defined on Figure 2. It provides the likelihood of finding a neighbour at the position  $(r, \phi, \theta)$  knowing there is a swimmer of radius  $a$  at the origin. The swimmer hydrodynamic disturbances are symmetric around their orientation vector  $\mathbf{p}$ , and the steric forces isotropic. Thus,  $g(r, \phi, \theta)$  is averaged over  $\phi$  and depends only on  $\theta$  and  $r$ . Figure 2 shows the pair distribution along  $\theta$  for  $r = 2.01a$  and  $r = 2.5a$  for both types of swimmers and  $\varphi_v = 0.2$ .

Concerning pushers (red curves), in close contact ( $r = 2.01a$ ) the presence probability is maximal where the swimming dipole is attractive ( $\theta = \pi/2$ ). Moving away from the surface,  $g$  flattens towards the recirculation regions ( $\theta = \pi/4$  and  $3\pi/4$ ); except in the repulsive directions, where contact is unlikely to occur.

The puller case exhibits a more complex behaviour. For  $r = 2.01a$ , the probability density function of pair relative orientations  $\langle \mathbf{p}_1 \cdot \mathbf{p}_2 \rangle$  (not shown here) reveals that, for  $\theta = 0$ , swimmers are either aligned or in opposition with equal probability. Even if it corresponds to the attractive region, it also corresponds to the most repulsive lubrication region. Hence the presence of zero probability.

Instead, contact occurs in more stable regions ( $\theta = \pi/4$  and  $3\pi/4$ ), where the residence time is longer due to the induced recirculation. The observed asymmetry comes from the fact that swimmers are more likely to be aligned for  $\theta = 3\pi/4$  than  $\theta = \pi/4$ . The far-field profile ( $r = 2.5a$ ) is different from the pusher case as  $g$  clearly sharpens around  $\theta = \pi/2$ .

## 4. Conclusions

In this study, the force coupling method has been implemented for large suspensions of pushers and pullers. Resulting statistics provide a good insight of the interplays and allow a reliable macroscopic description of the particulate media. Also, literature acknowledged that the spatial arrangement of particles acts on the suspension rheology. Preferential configurations and particle stresses confer the suspension shear-thinning or shear-thickening properties, which are currently being investigated.

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