Transport and Collective Dynamics in Suspensions of Confined Swimming Particles

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The past decade has seen growing interest in the dynamical properties of interacting, self-propelled organisms. This classical, "many-body problem" is motivated by phenomena in biology, but is now recognized to encompass issues in nonequilibrium statistical mechanics, nonlinear dynamics and applied mathematics. As outlined so eloquently in the classic work of Vicsek, *et al.* (1995) and Toner and Tu (1995), we are all familiar with the self-organization of flocks of flying birds, schools of fish, and the like, but the mathematical description of this cooperative behavior is far from clear. Those early phenomenological models invoked local rules of interactions between moving objects, or postulated local PDEs to explore the possible ordering of an ensemble of particles.

Suspensions of swimming bacteria serve as model systems with which to study this problem. The familiar lab workhorses *E. coli* and *B. subtilis* (Fig. 1) display complex swimming dynamics at the single-cell level, associated with the stochastic bundling and unbundling of their multiple rotating helical flagella during the course of chemotaxis. Experiments by Wu and Libchaber (2000) on *E. coli* swimming in suspended soap films showed that small whorls and jets of cooperative swimming were responsible for greatly-enhanced diffusion and even superdiffusion of passive tracers, establishing the idea of a "bacterial bath" for such tracers akin to the molecular bath responsible for Brownian motion. Even in the restricted geometry of a soap film it was clear that recurring, coherent structures were important on scales exceeding those of individual bacteria.

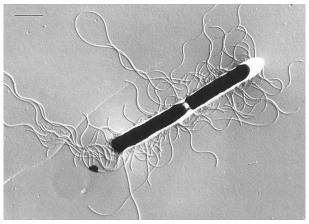

Figure 1: *Electron micrograph of B. subtilis about to divide into two cells. Scale bar is* 1 *μm.*

More recently, Dombrowski, *et al.* used particle imaging velocimetry (PIV) to map out the swimming velocity field of *B. subtilis* in fluid drops sitting on or hanging from surfaces. They found that this self-organization took the form of coherent jets and swirls (even vortex streets, as in high Reynolds number flows) with spatial correlations extending outward to hundreds of microns (Fig. 2). Recalling that the body of a single bacterium is about 4×0.7 μm, we see that there are thousands of cells in a vortex. They conjectured that hydrodynamic interactions were responsible for these effects, by analogy with similar phenomena in sedimentation. This has remained an untested hypothesis until now. The recent paper by Hernandez-Ortiz, Stoltz, and Graham is a very important contribution to the field because it shows that hydrodynamic interactions alone can produce the kinds of coherent structures seen in experiment. They present numerical studies of the dynamics of a suspension of self-propelled swimmers (around which the far-field velocity field is that surrounding a fluid-dynamical singularity known as a stresslet) whose only dynamical couplings are through their mutually-interacting velocity fields. Beyond a critical volume fraction, their results show a fairly sharp transition to a state characterized by greatly accelerated velocities and passive tracer diffusivities. Moreover, the system spontaneously generates vortical structures on scales much larger than the swimmers. In fact, they span the container. This suggests that the finite-size of the box actually sets the vortex size.

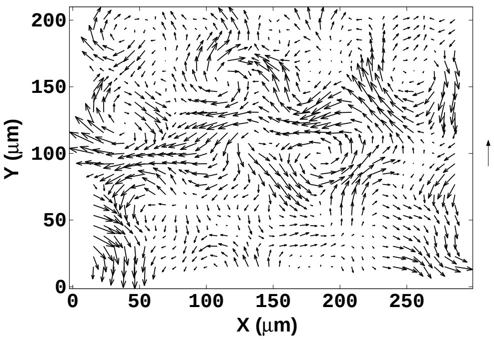

Figure 2: *Bacterial swimming velocity field in a suspension of B. subtilis. Vortices contain thousands of cells.*

Both the experimental results and those from the simulations are at odds with the original idea of a phase transition to truly long-range swimming order. Yet, they are consistent with more recent continuum models by Ramaswamy, *et al.* (2002, 2004) which predict an intrinsic instability due to long-range hydrodynamic interactions. Within that model, the fate of the system beyond that instability is not yet known. For instance, we do not know what determines the lifetime of the vortices. As the characteristic velocities U and length scales L found in the collective regime are so much greater than those for an isolated bacterium, the role of fluid advection in molecular transport is dramatically different. This is embodied in the Peclet number $Pe = UL/D$, where $D \sim 10^{-5}$ cm^2/s is a solute diffusion constant. In these systems, Pe can be as large as 10^2 at high cell concentration. This implies that the conventional description of intercellular signaling as governed by diffusion alone fails (miserably). What are the implications of this new regime for the transport of nutrients and chemical messengers, particularly for such processes as quorum sensing and biofilm formation? In light of the results of Hernandez-Ortiz, Stoltz, and Graham a natural related question is: What is the continuum limit of the discrete-particle description of a suspension of self-propelled swimmers?