



Hydrodynamic interaction of two unsteady model microorganisms

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ARTICLE INFO

Article history:

Received 7 December 2009

Received in revised form

2 August 2010

Accepted 2 August 2010

Available online 7 August 2010

Keywords:

Bio-fluid mechanics

Cell locomotion

Ciliates

Diffusion

Stokes flow

ABSTRACT

The study of pair-wise interactions between swimming microorganisms is fundamental to the understanding of the rheological and transport properties of semi-dilute suspensions. In this paper, the hydrodynamic interaction of two ciliated microorganisms is investigated numerically using a boundary-element method, and the microorganisms are modeled as spherical squirmers that swim by time-dependent surface deformations. The results show that the inclusion of the unsteady terms in the ciliary propulsion model has a large impact on the trajectories of the interacting cells, and causes a significant change in scattering angles with potential important consequences on the diffusion properties of semi-dilute suspensions. Furthermore, the analysis of the shear stress acting on the surface of the microorganisms revealed that the duration and the intensity of the near-field interaction are significantly modified by the presence of unsteadiness. This observation may account for the hydrodynamic nature of randomness in some biological reactions, and supersedes the distinction between intrinsic randomness and hydrodynamic interactions, adding a further element to the understanding and modeling of interacting microorganisms.

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1. Introduction

The application of biomechanics to the world of microorganisms, such as bacteria, has produced in recent years a fecund research activity that has fostered a valuable and unique understanding of their locomotion mechanisms and collective motions. In this sense, biomechanics is complementary to biology, ecology and chemistry in unraveling the secrets behind the various phenomena pertaining to microorganisms.

Microorganisms play a vital role in many biological, technical and medical phenomena and applications. The influence of plankton blooms on the oceanic ecosystem, their role in absorbing CO₂ from the atmosphere, the use of microorganisms in the food and chemical industries, and the importance of the bacterial flora in the human intestines for the digestion and absorption of food are all examples of the vast number of natural phenomena regulated by microorganisms and of their considerable impact on human life.

One of the most interesting manifestations to analyze is a suspension of microorganisms. In order to understand the macroscopic properties of a suspension, we need to adopt a *bottom-up* strategy, i.e. from a cellular to a continuum level, and consider the role played by the hydrodynamic interactions between individual microorganisms. It goes without saying that

to model the motion of any real microorganism mathematically is an overwhelming task, such is the vast variety of shapes and environmental parameters upon which their behavior depends. Nevertheless, it is possible to make the problem mathematically tractable by imposing simplifying assumptions that do not preclude a non-trivial analysis of the cells locomotion and interaction process.

Since the theory of infinite oscillating sheets was first proposed by Taylor in 1951 to model the swimming motion of fish, a variety of theoretical models have been developed to model swimming microorganisms, partly in response to the variety of self-propelling structures developed by nature, and partly as concepts for the construction of artificial robotic micro-swimmers (Dreyfus et al., 2005). At the low Reynolds numbers that characterize micro-swimming, two major types of locomotion can be observed: flagellar and ciliary. In the former, one or more long and slender organelle, called *flagella*, beat independently in a complex undulating or helical motion that propels the organism.

In ciliary motion, a large number of small hair-like appendages covering the surface of the organism, *cilia*, generate the propulsive force by beating in phase (isochronal rhythm) or slightly out of phase (metachronal rhythm). This regular motion generates the propulsive forces that enable the organism to swim, notably without a drastic alteration of its shape. This aspect makes ciliary propulsion amenable to a mathematical analysis, especially when the microorganism is assumed spherical in shape. In this case, the so-called *squirmers* model (Blake, 1971), in which the individual cilia are replaced by a spherical progressive waving envelope, is

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often employed to describe real microorganisms, especially ciliates such as *Opalina*, and colonies of flagellates such as *Volvox*. The same modeling approach can be used also for cyanobacteria (Stone and Samuel, 1996), such as *Synechococcus*, which have no external organelles, and swim using surface traveling waves without altering their external shape (Pitta and Berg, 1995; Samuel et al., 2001). Recently, an important experimental confirmation of the validity of the squirming model was found by Ishikawa and Hota (2006) in the case of interacting ciliated protozoa *Paramecia*. Their results showed a good agreement between the measured and the predicted trajectories when the *Paramecia* were modeled as squirmers. For its versatility and range of applicability, the squirming model will be used in the present paper to investigate the hydrodynamic interaction of ciliates.

The seminal work of Lighthill (1952), and, in particular, the subsequent extension of the theory due to Blake (1971) represents the starting point in the study of the squirming motion of spherical organisms. Blake provides analytical results for the velocity field, the swimming speed and the hydrodynamic efficiency of a solitary squirmer in a quiescent fluid, which can then be used to solve numerically more complex problems. A squirmer model microorganism is assumed to propel itself by generating tangential velocities on its surface. When the surface velocities do not depend on time the squirmer is termed *steady*, whereas when these depend on time, the expression *unsteady squirmer* is commonly used. Although we will come back to this point in Section 2, it is important to observe that the term *unsteady* is simply used to indicate that the tangential velocity on the surface of the squirmer is time-dependent; the Stokes equations are still solved in the assumption of quasi-steady flow and therefore do not possess any intrinsic notion of time.

In recent years, with the progress in numerical methods and the growing availability of computational resources, this theoretical model has started to be exploited to solve more complex problems. For example, Magar et al. (2003) used Blake's expressions to investigate the nutrient uptake by a self-propelled steady squirmer, and subsequently extended their work to include the effect of oscillating tangential surface displacements on the nutrient absorption (Magar and Pedley, 2005), showing, for instance, that an optimum swimming mode exists that minimizes energy dissipation for a given uptake rate.

The next natural stage in the bottom-up approach to cells suspensions has been to investigate two-body interactions as the simplest form of interactions. In fact, pair-wise interactions still represent a crucial step for a fundamental understanding of the influence of micro-swimming motion on the macroscopic properties of semi-dilute suspensions in which, by definition, cell-cell interactions represent the building blocks and cannot be neglected. Ishikawa et al. (2006) investigated the hydrodynamic interaction of spherical microorganisms by considering the time-averaged flow around each organism, which propels itself by axisymmetric and time-independent tangential displacements of its surface. This *steady squirmer* model allows one to analyze precisely the hydrodynamics of the interaction between cells, from the far field to the near field. It is important to stress that the near-field analysis, based on the lubrication theory, as well as the far field analysis remain valid also in the case of time-dependent surface deformations, i.e. for *unsteady* squirmers.

Another important study on squirmers' interaction is the computational and experimental investigations of Ishikawa and Hota (2006). As mentioned above, Ishikawa and Hota showed that a steady squirmer model is an appropriate mathematical vehicle to describe the hydrodynamic interaction of *Paramecia*. However, the experimental results also showed a large scattering of the cells' trajectories for a given initial configuration, differences that

a steady model cannot intrinsically reproduce. Excluding the "randomness" in the experiments due to the varying shapes of the interacting ciliated protozoa, it is reasonable to expect that the interaction process is strongly sensitive to the relative phase between the interacting organisms of the cilia beating, and therefore that unsteady hydrodynamics plays a major role in determining the observed behaviors.

In many real situations, in fact, the cilia's beat frequencies can be of the order of 30–80 Hz, hence the assumption of time-independent tangential deformations poses questions on the model accuracy and applicability, since the averaging process would include many beat cycles. In particular, if the time scale for the interaction process is of the same order or larger than the time scale for the unsteady squirming motion, unsteady effects can be expected to be important, and the hydrodynamic effects at time-scales shorter than the swimming stroke should be taken into account. If we define the time-scale of the beat motion as $t_{beat} = 1/f_{beat}$, where f_{beat} is the cilia's beat frequency (Hz), and the time-scale for the near-field interaction as $t_{int} = \text{cell body radius}/\text{swimming speed}$, the effect of the unsteady terms can only be neglected if $t_{beat} \ll t_{int}$. In reality, the two time-scales are comparable, as can be derived from the data showed in Brennen and Winet (1977), therefore unsteady effects are likely to be important and should not be neglected (a numerical example is given in Section 3 for *Paramecium caudatum*).

Recently (Pooley et al., 2007), the importance of such time-dependent terms was examined for a minimal swimming model of three linked spheres, and the results showed that these terms can influence significantly the dynamic behavior of the organism. The model micro-swimmer used in Pooley et al. (2007) is a very simplistic model with two degrees of freedom that is based on the Purcell's swimmer, and although the interest in such a model has increased recently due to its simplicity of implementation in robotic swimmers, the three linked sphere swimmer is not appropriate to investigate real microorganisms such as ciliates or flagellates.

In this paper, we investigate the hydrodynamic interactions of ciliated microorganisms using the so-called *unsteady squirmer model*. We demonstrate how modeling unsteadiness could be a key factor in the prediction of the diffusion properties of a semi-dilute suspension of cells, and how taking into account the mechanical stimulation arising from the hydrodynamic interaction may lead to more accurate locomotive models, which include, for instance, the avoiding reaction observed experimentally for some ciliates colliding with an obstacle.

In their experimental investigation, Ishikawa and Hota classified as hydrodynamic approximately 85% of the observed interactions, and as biological – that is showing a typical avoiding or escape reaction – the remaining 15%. In the case of interactions, biological reactions occur in response to mechanical stimuli that cause a change in the membrane potential and a consequent transient response of the ciliary apparatus. This response is usually activated by the opening (gating) of the ion channels covering the membrane, and the most common model used to describe this gating mechanism is the so-called stretch model, which considers the surface tension as the principal factor. In this paper, we show how the hydrodynamic forces acting on the surface during the near-field interaction process changes in duration and intensity for an unsteady squirmer compared to a steady one. Although the prediction of the membrane deformation due to the viscous stress is beyond the scope of this study, the changes in the shear stress due to unsteadiness, experienced by the cells during the hydrodynamic interaction, may be at the root of an hydrodynamic explanation of some biological reactions.

In the first part of this paper, we explain in mathematical terms how an unsteady squirmer is defined, and how this model

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