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Effect of solid boundaries on swimming dynamics of microorganisms in a viscoelastic fluid

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Abstract

We numerically study the effect of solid boundaries on the swimming behavior of a motile microorganism in viscoelastic media. Understanding the swimmer-wall hydrodynamic interactions is crucial to elucidate the adhesion of bacterial cells to nearby substrates which is precursor to the formation of the microbial biofilms. The microorganism is simulated using a squirmer model that captures the major swimming mechanisms of potential, extensile, and contractile types of swimmers, while neglecting the biological complexities. A Giesekus constitutive equation is utilized to describe both viscoelasticity and shear-thinning behavior of the background fluid. We found that the viscoelasticity strongly affects the near-wall motion of a squirmer by generating an opposing polymeric torque which impedes the rotation of the swimmer away from the wall. In particular, the time a neutral squirmer spends at the close proximity of the wall is shown to increase with polymer relaxation time and reaches a maximum at Weissenberg number of unity. The shear-thinning effect is found to weaken the solvent stress and therefore, increases the swimmer-wall contact time. For a puller swimmer, the polymer stretching mainly occurs around its lateral sides, leading to reduced elastic resistance against its locomotion. The neutral and puller swimmers eventually escape the wall attraction effect due to a releasing force generated by the Newtonian viscous stress. In contrast, the pusher is found to be perpetually trapped near the wall as a result of the formation of a highly stretched region behind its body. It is shown that the shear-thinning property of the fluid weakens the wall-trapping effect for the pusher squirmer.

Keywords

Microswimmer; Viscoelastic fluid; Biocomotion

Introduction

Bacteria primarily live within microscopic colonies embedded inside a self-secreted matrix of polymers and proteins. These microbial biofilms form on natural and man-made surfaces and interfaces and play important roles in various health and environmental issues (Hall-Stoodley et al. 2004). Previous experimental studies have indicated the significance of bacterial motility mechanisms in the colonization process and the subsequent biofilm formation (O'Toole and Kolter 1998; Pratt and Kolter 1998; Watnick and Kolter 1999; Lemon et al. 2007; Merritt et al. 2007; Kim et al. 2008; Houry et al. 2010). In particular, flagellar mediated swimming is crucial in approaching the surface and initiating the adhesion process (Tuson and Weibel 2013) and pili-mediated motility highly promotes the surface exploration (Burrows 2012). The swimming capability of a subpopulation of cells endures even after the establishment of the biofilm structure. For instance, the epifluorescence microscopic observations by Tolker-Nielsen et al. (2000) showed that the *Pseudomonas putida* cells rapidly swim in circular trajectories inside the microcolonies and some of them may swim out of the “liquefied” inner region of the biofilm. Furthermore, (Houry et al. 2010) showed that during the growth of *Bacillus cereus* biofilms, the recruited motile planktonic cells penetrate deeply inside the biomass instead of staying at its surface. The locomotion of cells may lead to their accumulation on the surface of the biomass as shown by Vlamakis et al. (2008) for the *Bacillus subtilis* aggregates where the newly born motile cells move to the edge and the base of the biofilm.

The biofilm structure is strengthened by a protective matrix which is primarily composed of bacteria-produced extracellular polymeric substances (EPS). Dispersion of associated polysaccharides and proteins in the surroundings impart viscoelasticity into the ambient fluid. In addition, there exist ubiquitous examples in nature where fluid habitat of microorganisms is complex and shows non-Newtonian behavior, such as the spermatozoa in the mammalian female reproductive tract swimming through the cervical mucus (Suarez and Pacey 2006), *Helicobacter pylori* colonizing the mucus layer covering the stomach (Montecucco and Rappuoli 2001), spirobacteria such as *Borrelia burgdorferi* penetrating the connective tissues in skin (Wolgemuth et al. 2006; Harman et al. 2012), and the nematode *Caenorhabditis elegans* swimming in the water-saturated soil (Jung 2010). In marine environments, bacteria abundance and productivity is elevated within aggregates mainly composed of transparent exopolymer particles (TEP) referred to as oceanic gel (Azam 1992; Alldredge et al. 1993; Passow 2002). TEP contribute to fluxes of carbon into the deep ocean (Azam 1992) and significantly affect the world's carbon balance. Thin phytoplankton layer is another example, where high concentrations of marine microorganisms are present in a mucus-rich thin layer (Cunliffe et al. 2013). In these instances, the elastic effects become predominant when the Deborah number, De , defined as the ratio of the polymer relaxation time to the characteristic time scale of the swimming, is larger than unity. Based on the rheological measurements of the biofilms, the corresponding relaxation time ranges from 10^{-2} s to 10^2 s (Wloka et al. 2012; Klapper et al. 2002), or even up to 10^3 s (Shaw et al. 2004). Also, the typical relaxation time of the mucus layer varies in the 1 – 10 s range (Lauga 2009). Given the oscillation frequency of cilia $f \sim 5 - 50$ Hz (Brennen and Winet 1977) or the actuation frequency of spermatozoa $f \sim 20 - 50$ Hz

(Brennen and Winet 1977), we can deduce that the associated Deborah number is $O(1)$ or much larger.

The study of motile microorganisms swimming in complex fluids has received significant attention in recent years. It has been shown that in viscoelastic media, both enhancement and inhibition of swimming speed occurs depending on the swimming strategy and the rheological characteristics of the background fluid. For example, helical bacteria such as *Leptospira* and *B. burgdorferi* swim faster in a viscoelastic fluid compared to a Newtonian fluid of the same viscosity (Berg and Turner 1979; Kimsey and Spielman 1990), whereas *C. elegans* which undulates its body in a planar wave swims with a slower pace (Shen and Arratia 2011). Taylor's waving sheet (Taylor 1951) as an idealized model of an undulating swimmer has been utilized in several theoretical studies to investigate the kinematics and energetics of swimming in viscoelastic environments. The corresponding outcomes exhibit strong dependence on the waving stroke and the constitutive properties of the fluid. While the analytical study of Lauga (2007) indicates that the viscoelasticity hinders the locomotion of an infinite swimming sheet oscillating with small amplitude, numerical results of Teran et al. (2010) demonstrates enhancement of swimming speed and efficiency of a free waving sheet with finite length and large tail undulations within a favorable range of undulation pattern and polymer relaxation time. For an undulating swimmer, the maximum speed emerges at $De \sim 1$ (Teran et al. 2010) where the decaying time of elastic stresses matches the period of swimming strokes. For self-propelled helical bodies, both experiments (Liu et al. 2011) and simulations (Spagnolie et al. 2013) show that the swimming speed peaks at Deborah number of $O(1)$, and the speed enhancement with respect to Newtonian fluids is more pronounced for helices with large pitch angles. On the other hand, the swimming speed reduces compared to the Newtonian fluid, for small helical pitch angles with large filament radius. Simulations conducted on axisymmetric bodies with tangential squirming motion (Zhu et al. 2011, 2012) indicate that for ciliated cells, the swimming speed in shear-thinning polymeric solutions is always smaller compared to Newtonian fluids and the Weissenberg number Wi , defined as the product of the fluid relaxation time with the typical shear rate in the flow, associated with minimum velocity depends on the specific swimming gait of the microorganism. The hydrodynamic efficiency, however, is enhanced in viscoelastic fluids regardless of the squirming mode or the value of Weissenberg number.

The viscoelasticity of the ambient fluid, not only alters the swimming behavior of a single microorganism, but also affects the hydrodynamic interactions and collective motion of a population of motile cells. For example, (Ardekani and Gore 2012) demonstrated that in a suspension of microorganisms subjected to a background vortical flow, viscoelasticity results in aggregation of microorganisms on a limit cycle. Also, using a mean-field kinetic model, (Bozorgi and Underhill 2011, 2013) analyzed the effect of viscoelasticity on the instability conditions of a suspension of extensile microwimmers.

Understanding the swimming strategy of bacteria in confined geometries is shown to be a decisive factor in identifying the adhesion rate and elucidating the subsequent colonization process. However, a large majority of studies focused on the swimming behavior of motile cells in complex fluids have been conducted assuming the cells' habitat to be an unbounded domain and thus, the boundary induced effects, such as surface trapping and wall

accumulation, are poorly understood. On the contrary, the significance of the solid boundaries is well received in the context of particulate viscoelastic flows. Several computational (Ardekani et al. 2007; D'Avino et al. 2009; Despeyroux and Ambari 2012; Padhy et al. 2013) and experimental (Tatum et al. 2007; Ardekani et al. 2009; Eisenberg et al. 2013) investigations have been carried out to shed light on the dynamical behavior of rigid particles moving in close proximity of a solid surface in non-Newtonian fluids. In particular, it is found (Ardekani et al. 2007) that in the second-order fluids, a strong attraction force is developed which draws a solid sphere towards the corresponding wall. Also, the shear-thinning effects are shown (Eisenberg et al. 2013) to be determinant in raising the acceleration of the particles moving away from the nearby surfaces. Although the physical mechanisms underlying the interaction of solid surfaces with rigid particles are different than those affecting the dynamics of self-propelled cells, the experimental and computational methodologies developed in the aforementioned studies are of potential use in order to explore the impact of the walls on the swimming motion of motile microorganisms in viscoelastic media.

In the current study, we conducted a series of three-dimensional direct numerical simulations in order to investigate the near-wall swimming motion of a squirmer in viscoelastic fluids. We scrutinize the effects of fluid elasticity, shear-thinning, and polymer viscosity on the swimming speed, inclination, and trapping period of various types of squirmers with different locomotive gaits. Utilizing a decomposition of force and torque exerted on swimmer's body, the dynamical behavior of a squirmer adjacent to a solid boundary is rationalized. To the best of our knowledge, the results presented below are the first three-dimensional simulations analyzing the effect of a rigid surface on the self-propelled motion in complex fluids.

Mathematical model and numerical method

Squirmer model

In this study, we adopt an axisymmetric model microswimmer with tangential velocity on its surface to characterize the swimming strategy of ciliated microorganisms, such as *Volvox* and *Paramecium*, near a solid wall. The so-called squirmer model, first proposed by Lighthill (1952) and Blake (1971), has been widely utilized in numerical investigations of biolocomotion in various environmental conditions e.g. see Ishikawa et al. (2006), Llopis and Pagonabarraga (2010), Zhu et al. (2011, 2012), Doostmohammadi et al. (2012), Wang and Ardekani (2012a, b, 2013), Ishimoto and Gaffney (2013). The overall ciliary movement can be idealized as a continuous velocity distribution along the exterior surface of a self-propelled spheroid,

$$u_s(\theta) = \sum_{n=1}^{\infty} B_n V_n(\cos\theta), \quad (1)$$

where θ is the polar angle measured from the swimming direction, B_n represents the magnitude of n th mode of squirming motion, and the function V_n is defined as,

$$V_n(x) = \frac{2\sqrt{1-x^2}}{n(n+1)} \frac{d}{dx} P_n(x), \quad (2)$$

with $P_n(x)$ denoting the n th order Legendre polynomial. In a Newtonian fluid under Stokes flow conditions, the swimming speed of a squirmer in an unbounded domain is $U_0 = 2B_1/3$ (Blake 1971). Conforming with previous studies employing this approach, we assume $B_n = 0$ for $n > 2$. Hence, we can define the ratio of the second to the first squirmering mode, $\beta = B_2/B_1$, to distinguish three types of swimming mechanisms: $\beta > 0$ corresponds to pullers generating thrust by pulling fluid in front of their body such as *Chlamydomonas nivalis*, $\beta < 0$ corresponds to pushers propelling forward by pushing fluid behind their body such as *Escherichia coli*, and $\beta = 0$ corresponds to a neutral squirmer with net ciliary motion such as *Volvox*. Figure 1 demonstrates the flow field arisen from the swimming motion of these three types of squirmers in the unbounded Newtonian fluids. While a neutral squirmer gives rise to a potential flow in the surrounding fluid, the squirmering motion of a puller (pusher) results in a formation of a positive (negative) force dipole. Since the sedimentation velocity of the microorganisms is commonly much smaller than their swimming speed (Ishikawa et al. 2006), we assume the squirmer to be neutrally buoyant.

Governing equations

The governing equations of the incompressible flow in a viscoelastic fluid in dimensionless form are,

$$\nabla \cdot \mathbf{u} = 0, \quad (3a)$$

$$Re \left(\frac{\partial \mathbf{u}}{\partial t} + \mathbf{u} \cdot \nabla \mathbf{u} \right) = -\nabla p + \nabla \cdot \boldsymbol{\tau}, \quad (3b)$$

where $Re = \rho U_0 a / \mu$ is the Reynolds number, ρ is the fluid density, $\mathbf{u}$ is the fluid velocity, and p is the pressure. Here, the length is scaled by the radius of the spherical squirmer a , velocity by U_0 , time by a/U_0 , and pressure and stresses by $\mu U_0 / a$, where $\mu = \mu_s + \mu_p$ is the zero-shear viscosity of the fluid, and μ_s and μ_p are the viscosity of the solvent and the polymer, respectively. The deviatoric stress, $\boldsymbol{\tau}$ can be split into solvent and polymer components as $\boldsymbol{\tau} = \boldsymbol{\tau}^s + \boldsymbol{\tau}^p$. The Newtonian viscous stress is defined as $\boldsymbol{\tau}^s = \beta_s (\nabla \mathbf{u} + \nabla \mathbf{u}^T)$ with $\beta_s = \mu_s / \mu$ being the ratio of the solvent viscosity to the zero-shear viscosity of the polymeric solution. To characterize the evolution of the polymer stress, we adopt the Giesekus constitutive model (Giesekus 1982) which specifies the constrained elongation of the polymers and the shear-thinning behavior of the polymeric solution. In dimensionless form, the associated equation can be written as,

$$\boldsymbol{\tau}^p + Wi \frac{\nabla}{\partial t} \boldsymbol{\tau}^p + \frac{Wi \alpha_m}{1 - \beta_s} \boldsymbol{\tau}^p \cdot \boldsymbol{\tau}^p = (1 - \beta_s) (\nabla \mathbf{u} + \nabla \mathbf{u}^T), \quad (4)$$

where $Wi = \lambda U_0 / a$ is the Weissenberg number with λ being the polymer relaxation time. The mobility factor, α_m , represents the anisotropic hydrodynamic drag exerted on the polymer molecules by the surrounding solute molecules. Based on the thermodynamic analysis, the

mobility factor must lay in the range of 0 to 1/2 (Schleiniger and Weinacht 1991). For special case of $\alpha_m = 0$, the Giesekus model reduces to the Oldroyd-B model. In this work, unless otherwise stated, we set $\alpha_m = 0.2$ in accordance with previous studies regarding the squirming motion in unbounded viscoelastic media (Zhu et al. 2011; Zhu et al. 2012). The notation $\overset{\nabla}{\mathbf{A}}$ represents the upper-convected derivative,

$$\overset{\nabla}{\mathbf{A}} = \frac{\partial \mathbf{A}}{\partial t} + \mathbf{u} \cdot \nabla \mathbf{A} - \nabla \mathbf{u}^T \cdot \mathbf{A} - \mathbf{A} \cdot \nabla \mathbf{u}. \quad (5)$$

The range of parameters considered in the current study are $Re = 0.1$, $Wi = 0 - 6$, $\beta_s = 0.1 - 0.3$, $\alpha_m = 0 - 0.3$, and $\beta = -3, 0, 3$. Unless otherwise stated $\beta_s = 0.1$, $\alpha_m = 0.2$.

Numerical method

In order to capture the motion of a spherical squirmer in a fluid environment, we employed the distributed Lagrange multiplier method based on the finite volume scheme. The details of this approach are delineated elsewhere (Ardekani and Rangel 2008; Ardekani et al. 2008; Li and Ardekani 2014) and here we only present a brief description of the method. In the distributed Lagrange multiplier method, the momentum equation with an additional forcing term is solved on the entire computational domain. The forcing term is only added inside the particle domain and is iteratively calculated to rigidify the body of the particle and to impose the prescribed velocity profile on the outer surface of the squirmer which causes self-propulsion. When the squirmer approaches the wall, a short-range repulsive force (Glowinski et al. 2001) is implemented to prevent the squirmer-wall overlaps. It has been verified that the value of the repulsive force does not affect the dynamics of the near-wall motion of the squirmer (see Appendix A.4). The viscoelastic stress is solved using a commonly used formulation denoted as elastic and viscous stresses splitting (EVSS) method (Guenette and Fortin 1995). The benchmarks used to validate the aforementioned method and the computational code are provided in the Appendix A.1 and A.2.

Simulations are conducted in a rectangular domain of $60 \times 40 \times 40$ dimensionless units and stretched grids are used for spatial discretization. As illustrated in Fig. 2, the distance between the center of the squirmer and the wall is h , the orientation angle of the squirmer is α , and the no-slip wall is located at $y = 0$. The far-field boundary condition is considered at other boundaries of the domain. In order to describe the dynamics of the squirmer, we define two frames of reference: an inertial coordinate system xyz attached to the wall and a non-inertial coordinate system XYZ moving with the squirmer with X axis indicating the swimmer's inclination (see Fig. 2). The region covering the body of the squirmer is discretized using a uniform grid with at least 32 grid points across the squirmer diameter. The spatial derivatives in the convection term are evaluated using the quadratic upstream interpolation for convective kinetics (QUICK) scheme (Leonard 1979) and the diffusion terms are discretized using the central difference scheme. A second-order Crank-Nicolson time differencing is employed for temporal discretization with a computational time step $\Delta t = 2.5 \times 10^{-4}$. To ensure the consistency and accuracy of the results, several numerical tests have been conducted as shown in the Appendix A.3.

Results and discussion

In this section, the effects of the fluid viscoelasticity on the swimming motion of different types of squirmers near a rigid wall is investigated. In our previous study, two types of swimming modes are distinguished for the near wall motion of a single squirmer at $Re = 0.1$ in a Newtonian fluid: (a) the squirmer with $\beta \leq 3$ escapes the wall and (b) the squirmer with $\beta > 3$ swims in the close proximity of the wall (Li and Ardekani 2014). In present study, the initial height and the initial orientation of the squirmer are fixed at $h_0 = 2$ and $\alpha_0 = -\pi/4$ except otherwise mentioned, and we only focus on the effect of the viscoelasticity of the background fluid on the interaction of the model swimmer and the solid surface.

Neutral squirmer

Dynamical behavior—The time history of the vertical position of a neutral squirmer in Newtonian and viscoelastic fluids are shown in Fig. 3a. In general, the viscoelasticity of the background fluid does not alter the near-wall swimming behavior of a neutral squirmer qualitatively. At all Weissenberg numbers, the squirmer initially approaches the wall in an oblique direction and then collides with the surface at time t_i . Next, due to synergetic effects of hydrodynamic interactions and collision, the squirmer reorients and swims parallel to the wall for a limited time interval. Whilst the squirmer is trapped by the surface, it gradually rotates away from the wall and thus, the orientation angle α increases. Finally the squirmer escapes the wall at time t_e where α becomes positive. Here, we define the impact time t_i and the escape time t_e of the squirmer at which the distance to the surface is $h_c = 1.1$. Based on this value of h_c , in the contact regime, the squirmer is 10% of a cell size away from the wall which agrees with experimental observation of Drescher et al. (2011). They found that, while trapped by the nearby surface, an *Escherichia coli* cell is about 1–3 μm away from the wall. The specific choice of h_c affects the residence time quantitatively, but the qualitative trend will remain the same. As the inset in Fig. 3a demonstrates, the impact time t_i of the squirmer is postponed in the viscoelastic fluid since the overall swimming speed of the squirmer is smaller compared to the Newtonian fluid (see Fig. 3c) (Zhu et al. 2012). The trapping period $t_e = t_e - t_i$ in which the squirmer is in a close contact with the wall increases for $Wi < 1$ and reaches a peak value around $Wi = 1$. The prolonged trapping time at $Wi = 1$ originates from the diminished angular velocity of the squirmer in this case as delineated in Fig. 3d.

In order to elucidate the hydrodynamic interaction of the squirmer with the nearby wall, the temporal profiles of the torque and the vertical force exerted on the squirmer are calculated and illustrated in Fig. 4. After collision with the wall and reorientation of the squirmer, the polymer stress momentarily induces a large torque in negative z direction which reduces the angular velocity and impedes the growth of the inclination angle α . As demonstrated in the inset of Fig. 4a, the magnitude of this opposing torque reaches its maximum at $Wi = 1$ and decays for higher values of Wi . The slower rotation and longer residence time of the squirmer when its swimming characteristic time is on the order of the polymer relaxation time can be rationalized considering the inhibiting effect of the polymer stress which generates an adverse torque at the early stage of swimmer-wall interaction. In order to illustrate the elastic wake around the squirmer, we calculated the first normal stress

difference, $N_1 = \tau_{XX} - \tau_{YY}$, which is a measure of the polymer stretching. The snapshots of N_1 around the cell body immediately after the impact, as shown in Fig. 5, exhibit a larger region of elongated polymers and a pronounced elastic wake in case of $Wi = 1$. For higher values of polymer relaxation time corresponding to $Wi > 1$, the region of largest elongation becomes thinner (see Fig. 5b) and thus, the squirmer encounters reduced elastic resistance against reorientation.

During the trapping period, the region of elongated polymers shrinks and thereby, the magnitude of the polymeric torque exerted on the squirmer diminishes. On the other hand, a high shear region in the gap between the swimmer and the wall is developed for the case of $Wi = 1$, leading to a strong torque in z direction which counteracts the impeding effect of the polymeric torque. The overall effects of Newtonian and polymeric stresses on the surface of the squirmer result in counter-clockwise rotation of the cell and facilitates propelling towards the bulk fluid (see Fig. 4c). As soon as the inclination of the squirmer becomes horizontal, a large vertical force arising from the asymmetric distribution of the Newtonian shear stress is developed which negates the wall attraction effect and leads to departure from the vicinity of the surface (see Fig. 4d). Comparing Figs. 3b and 4b indicates that this driving force emerges at the time when the squirmer starts to swim parallel to the wall. Hence, the residence time of the swimmer is contingent upon the torque balance and angular kinetics of the ciliated cell.

Due to history effects induced by the relaxation of the polymers, the influence of the wall is sensed by the squirmer even after it swims a distance away from the surface. Figure 6a shows the temporal evolution of the cell's swimming speed normalized with respect to steady state velocity in an unbounded domain. At $t = 30$ where the squirmer is more than four body lengths away from the surface, the swimmer velocity exhibits minute fluctuations in time and reaches to its value in an unbounded domain. However, as shown in Fig. 6b, the distribution of the first normal stress difference is still slightly asymmetric with respect to the inclination of the squirmer and the polymer stretching and elastic wake are less developed on the portion of the squirmer facing the wall. This asymmetry impacts the angular kinematics of swimming even at large separation distances as indicated in Fig. 3b, however, in the Newtonian case, the swimming inclination of the squirmer reaches a steady state for $t > t_e$ (see Fig. 3b).

Effect of constitutive properties—In this section, the effect of the constitutive properties of the background fluid on the squirmer dynamics near a wall is investigated. The impact of shear-thinning behavior on the residence time of the squirmer is depicted in Fig. 7a. It is evident that by increasing the degree of shear-thinning, the trapping period of the squirmer will grow. This is closely related to the escaping mechanism of the swimmer resulting from the imbalance in the distribution of the Newtonian viscous stress. In fluids with a high degree of shear-thinning, the elevated shear rate in the constriction between the squirmer and the wall leads to a local decline in the fluid viscosity and consequently, a lower value of the Newtonian torque. Thus, the squirmer should spend a longer period of time near the wall to become capable of overcoming the impeding effect of the polymeric torque and reorienting away from the surface. In particular at $Wi = 1$, the residence time of a neutral

squirmer swimming in a Giesekus fluid with $\alpha_m = 0.2$ is about 25% longer compared to an Oldroyd-B fluid.

The other important characteristic of the viscoelastic fluids is the viscosity ratio which describes the relative importance of the Newtonian and polymeric contributions in the fluid viscosity. By increasing the value of β_s , the role of solvent viscosity in kinetics of the swimmer gains more significance which leads to earlier release of the cell from the wall attraction (see Fig. 7b). Since the inhibiting impact of the polymeric torque is lessened for elevated values of β_s , the squirmer reorientation enhances and the cell escapes the wall faster.

Puller

In this section, the dynamical behavior of a puller with $\beta = 3$ in the vicinity of a solid surface is investigated. The swimming trajectory of the puller swimmer is qualitatively akin to the neutral squirmer, i.e. it approaches the wall due to hydrodynamic interactions, spends a brief period of time in the close proximity of the wall, and eventually escapes the wall. The temporal evolution of the vertical distance and inclination angle, shown in Fig. 8a and b, clearly demonstrate this swimming strategy. However, the residence time of the puller swimmer is about one order of magnitude smaller compared to a neutral squirmer (see Fig. 9). Also, viscoelasticity of the background fluid does not alter the trapping time of a puller substantially, in contrast to a neutral squirmer with analogous conditions. This discrepancy stems from the absence of polymeric negative torque after the impact of the puller with the wall as shown in Fig. 10a. Due to specific swimming gait of a puller which imposes inward surface deformation, the polymer stretching around the swimmer poles is more symmetric compared to a neutral squirmer and no sizable elongated region is established behind the squirmer to pull it backward. The trace of the polymer conformation tensor, $\mathbf{C}$, defined as,

$$\mathbf{C} = \frac{Wi}{1 - \beta_s} \boldsymbol{\tau}^p + \mathbf{I}, \quad (6)$$

indicates the intensity of polymer stretching. The snapshot of $\text{tr}(\mathbf{C})$ shown in Fig. 11 shows that the locomotion of a puller, instead of rendering an elastic wake in the rear side, engenders stretching of the polymers mainly around its lateral sides perpendicular to the swimming direction. After a brief time interval, due to the growth of shear rate in the separating gap, the Newtonian shear stress significantly amplifies; leading to development of a vertical force, as depicted in Fig. 10b, which provides sufficient thrust to escape the wall attraction.

Pusher

Dynamical behavior—The fluid viscoelasticity has a more dramatic effect on the near wall swimming motion of a pusher with $\beta = -3$. As depicted in the time history plots of the vertical distance and orientation angle shown in Fig. 12a and b, after approaching the surface, the pusher swimmer is strongly trapped by the wall and continues its swimming trajectory while maintaining a constant distance from the nearby boundary. Although in steady state, the pusher holds a small orientation angle ($\sim 5^\circ - 10^\circ$) away from the wall, it is

incapable of escaping the confining effect of swimmer-wall hydrodynamic interaction. This behavior is in stark contrast with swimming strategy of a pusher in a Newtonian fluid wherein the swimmer eventually reorients away and departs the nearby wall. The time scale of arriving at steady state decays with increasing the Weissenberg number. The steady state values of the vertical distance, inclination angle, and the velocity components for various values of Wi are depicted in Fig. 13a and b. The separation length scale dramatically decays with increasing Wi , however, the angle α varies within a limited range. Figure 13b shows that in viscoelastic fluids, unlike the Newtonian case, the pusher swims along the horizontal direction parallel to the attracting boundary. The viscoelasticity also hinders the swimming speed compared to a Newtonian fluid. Further, by increasing the polymer relaxation time, the swimming speed grows and reaches a peak at $Wi = 4$.

In order to quantify the boundary effects on the pusher swimmer, we calculated the temporal profiles of torque and vertical force exerted on the squirmer. The results are shown in Fig. 14a and b. Immediately after the impact, analogous to the neutral squirmer, a large polymeric torque is developed in negative z direction which impedes the reorientation of the cell towards the fluid bulk. Subsequently, high values of shear rate arise in the constriction between the wall and the squirmer, leading to the formation of a positive torque due to the Newtonian viscous stress. The balance of these two torques leads to rotation of the cell away from the wall while maintaining a close distance with the surface. Contrary to the neutral squirmer where the viscous force becomes sufficiently strong to overcome the elastic drag, in case of the pusher swimmer, a wide region of stretched polymers is developed behind the squirmer's body which results in high elongational viscosities and thus, a large elastic drag which the Newtonian viscous force is unable to overcome. Since at steady state, the pusher is oriented away from the wall, the force generated due to the concentration of stretched polymers behind the squirmer draws it toward the nearby surface. On the other hand, the viscous force tends to separate the pusher from the wall and lessen the shear rate in the gap region. Therefore, the squirmer attains a kinetic balance and continues to swim in the vicinity of the surface. The distribution of the trace of the conformation tensor at steady state as depicted in Fig. 15 displays the strong elastic wake in the aft of the squirmer.

Effect of initial conditions—By varying the values of h_0 and α_0 , the effect of initial conditions on the near-wall behavior of a pusher is analyzed and the corresponding results are demonstrated in Fig. 16. Since the surface-associated effects become negligible when $\alpha_0 > 0$ as the squirmer swims away from the wall, we concentrated our study on the cases of $\alpha_0 < 0$. It is evident that, in general, the dynamical behavior of a pusher approaching the wall in an oblique angle is independent of the initial conditions. While in a Newtonian fluid, pushers can escape the wall, they are trapped by the nearby surface in a viscoelastic fluid. In this regard, it is noticeable that the pusher with $\alpha_0 = -\pi/3$ does not collide with the wall in a viscoelastic fluid, however, its equilibrium distance from the wall is of the same order as the other cases. If the pusher initially approaches the wall at $\alpha_0 = -\pi/2$, it collides with the wall in the normal direction and stays perpendicular to the wall for a relatively long time, but eventually starts to rotate and finally escapes the wall and continues to swim at a constant distance away from the wall.

Effect of constitutive properties—The effect of the shear-thinning behavior and the viscosity ratio on the wall attraction of the pusher is shown in Fig. 17. The equilibrium distance of the pusher from the wall grows as the mobility factor and the viscosity ratio increase. The higher viscosity ratio leads to the dominance of the Newtonian viscous force over the elastic force and leads to the reduced trapping effect. The increase in the mobility factor reduces the extensibility of the polymers behind the swimmer by imposing a limit on the extensional viscosity of the solution and consequently weakens the wall trapping effect.

Concluding remarks

In this work, we presented numerical results to demonstrate how the fluid viscoelasticity affects the swimming behavior of small organisms in the vicinity of rigid surfaces. Studying this phenomenon is of prime importance in order to gain fundamental insights regarding the hydrodynamic interplay of motile cells with nearby substrates. Using the Giesekus constitutive model, we elucidated the near-wall dynamics of three types of squirmers with different swimming gaits, i.e. neutral squirmer (potential swimmer), puller (contractile swimmer), and pusher (extensile swimmer). These model swimmers cover a wide range of locomotion strategies typical of motile cells. Employing direct numerical simulations, the characteristics of the polymeric flow arising from swimmer-wall interactions are revealed and the underlying physical mechanisms affecting the swimmer dynamics are analyzed in depth.

In case of the neutral squirmer, we showed that the swimmer is capable of escaping the wall attraction due to the synergetic effects of the Newtonian viscous torque and vertical force. The former reorients the squirmer away from the surface, and subsequently the latter counterbalances the restraining effect of the stretched polymers. To better illustrate the spatial structure of the viscoelastic stresses and the configuration of elongated polymers, in Fig. 18, we have plotted ellipsoids that represent the geometric structure of the conformation tensor. The principal axes of the ellipsoids are aligned with the eigenvectors of $\mathbf{C}$, the axis lengths are scaled by corresponding eigenvalues, and the coloring is based on the value of the first normal stress difference (N_1) at the center of the ellipsoids. This visualization illustrates the distribution of polymer stretching and the associated stresses around the swimmer's body. All the snapshots are obtained at $t = 2$ immediately after the collision with the wall. Figure 18a shows a strong polymer stress concentration and relatively high elongational viscosities in the aft of the neutral squirmer. The elongation field is asymmetric in vertical direction with more stretching in the lower portion of the swimmer near the rigid surface. The elastic drag generated by the elevated values of polymer stress behind the squirmer results in backward pulling and relatively long residence time of the swimmer in the proximity of the nearby wall.

Figure 18b depicts the elongation and stress fields around a puller swimmer after its impact with the wall. Due to inward surface deformation of the puller, around the swimmer's poles little stretching arise which is mostly in the tangential direction. In this case, polymer stretching predominantly occurs perpendicular to the swimming plane in the neighborhood of the squirmer's equator in YZ plane. This kinetic configuration of the polymers combined with excessive shear stress beneath the squirmer lead to shorter trapping time and faster

release of the puller compared to the neutral squirmer. Thus, the contractile ciliated microorganisms are expected to be least affected by the wall attraction and exhibit lower surface accumulation.

The geometric distribution of the eigenstructure of the conformation tensor for a pusher, as shown in Fig. 18c, reveals that due to outward tangential deformation of an extensile swimmer, the polymers become highly stretched on the cell surface along the swimming direction. In particular, a largely elongated localized region is formed around the rear pole of the pusher, inducing an elastic drag which resists the locomotion of the swimmer. This configuration remains unchanged after reorientation of the cell and counteracts the releasing force which stems from the Newtonian viscous contribution. Hence, unlike the Newtonian case, the pusher is unable to escape the wall attraction in viscoelastic fluids. It is noticeable that, compared to other swimming gaits, the self-propulsion of the pusher engenders the highest rate of polymer elongation, especially around the swimmer's poles.

While the near-wall motion of bacteria in Newtonian fluids has been experimentally investigated in numerous studies (DiLuzio et al. 2005; Li et al. 2008; Drescher et al. 2011), to the best of our knowledge, the cell-surface interactions in complex fluids still await experimentation. The insights gained through the present study can be corroborated by comparing the simulation results with experimental measurements in terms of the residence time and the cell trajectory after collision with the wall. However, employing microorganisms incorporates complex biological factors in the experimental investigation and renders further difficulty to compare the outcomes with the results stemming from the simulation of squirmers. To remedy this problem, (Thutupalli et al. 2011) introduced a novel experimental technique which utilizes self-propelling liquid droplets to mimic the surface deformations of a squirmer. This methodology can be employed to further our knowledge regarding the hydrodynamic interaction solid walls with nearby squirmers swimming in viscoelastic media.

In this study, we quantified the impact of the Weissenberg number on the residence time of the swimmers in the proximity of solid surfaces. The associated outcomes can be utilized to enhance our understanding regarding the adhesion rate of the bacterial cells constituting a microbial community in viscoelastic media. In addition, this investigation sheds light on the polymeric effects opposing the locomotion of three types of self-propelled particles near rigid walls. The insights gained through this study pave the way to design more efficient artificial swimmers via minimizing the unfavorable concentration of stretched polymers. The results presented in this work can be extended in several directions. For example, instead of using an idealized model of cell locomotion, more accurate models of microorganisms could be taken into account. Specifically, the helical structure and the rotation of flagella should be considered in more comprehensive simulations of motile bacteria. Finally, hydrodynamic interactions of a group of swimmers pose an important theoretical challenge in order to resolve the collective behavior of microorganisms in viscoelastic media.

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Appendix: Verification of the numerical method

A.1 Rotation of a single sphere in an Oldroyd-B shear flow

In an Oldroyd-B fluid, we simulate the rotation of a single sphere in a shear flow to verify our numerical platform. Simulation is conducted in a rectangular domain of $[-2a, 2a] \times [-2a, 2a] \times [-4a, 4a]$ where a is the radius of the sphere and the sphere is centered at $(0,0,0)$. The flow is driven by two parallel plates at $z = -4a$ and $z = 4a$ moving opposite in x -direction with the same speed U . Periodic boundary conditions are applied in x and y directions. The mesh size is $\Delta x = a/16$ and the time step is $\Delta t = 10^{-3}a/U$. The shear rate of the flow is $\dot{\gamma} = U/4a$, the Weissenberg number $Wi = \lambda \dot{\gamma}$, the Reynolds number $Re = \rho \dot{\gamma} a^2 / \mu = 0.025$ and the viscosity ratio $\beta_s = 0.5$. Figure 19a shows the time evolution of the angular velocity of the sphere at different Wi . It is seen that for the Newtonian case, the sphere asymptotically reaches to its steady state of $\omega_y = 0.5\dot{\gamma}$ while for viscoelastic cases, overshoots can be observed around $t\dot{\gamma} = 0.2$. In Fig. 19b, the steady angular velocity as a function of Wi is compared with previous experimental (Snijkers et al. 2011) and numerical (Goyal and Derksen 2012) results. It is evident that our simulation results are in good agreement with the previous results.

A.2 Free swimming of a squirmer in a Giesekus fluid in an unbounded domain

The simulation is performed on a non-uniform structured grid with the smallest mesh size of $\Delta x = D/40$ near the squirmer, where D is the diameter of the spherical squirmer. The computational domain is $[-40a, 40a] \times [-40a, 40a] \times [-40a, 40a]$ and the squirmer is initially placed at $(0,0,0)$. The time step is $\Delta t = 10^{-5}$. The Reynolds number, defined as $Re = U_0 a / \nu$, is 0.01 in all the simulations, and $U_0 = 2B_1/3$. According to the analysis of a squirmer in a Newtonian fluid at finite Reynolds number, the swimming speed of a squirmer is determined by $U/U_0 \simeq 1 - 0.15\beta Re$ (Wang and Ardekani 2012a), thus the effects of the inertia on the swimming speed can be neglected in our simulation. The viscosity ratio is $\beta_s = 0.5$ and mobility factor is $\alpha_m = 0.2$. The Weissenberg number is defined as $Wi = \lambda B_1/a$. The swimming speed of the squirmer U is plotted in Fig. 20 for squirmers with $\beta = -5, 0$, and 5 . Our results show good agreement with the results obtained by Zhu et al. (2012).

A.3 Convergence study

Convergence studies have been performed for the near-wall motion of squirmers with $\beta = 0$ and -3 under different grid sizes and different time steps. Figure 21 shows the time history of the distance h away from the wall, orientation angle α and the swimming speed U of the

squirmers. The results from these different computations agree well with each other. It is confirmed that the computed results are independent of the mesh size and the time step.

A.4 Repulsive force

When the squirmer lies in the close proximity of the surface, due to the lubrication effect and other non-hydrodynamic phenomena such as electrostatic charges, a repulsive force is developed which prevents intrusion of the swimmer's body into the wall. To capture the associated hydrodynamic squeezing effect, exceedingly fine grid resolutions are needed which make the corresponding simulations computationally highly demanding. In addition, as indicated by Spagnolie and Lauga (2012), hydrodynamic interactions are inadequate to prevent the swimmer-wall interference in some settings. Hence, in order to avoid overlapping of the squirmer's body and the nearby wall, we impose a short-range repulsive force (Glowinski et al. 2001) defined as,

$$\mathbf{F}_r = \frac{C_m}{\varepsilon} \left(\frac{h - h_{\min} - h_r}{h_r} \right) \mathbf{e}, \quad (7)$$

where $h_{\min} = a$ is the minimum possible distance from the wall and h_r represents the range over which the force is acting and is normally set to be the smallest grid size in the computational domain (Glowinski et al. 2001). The direction of the repulsive force $\mathbf{e}$ is considered to be perpendicular to the wall. The parameters $C_m = M_p U_0^2 / a$ and $\varepsilon = 10^{-4}$ denote a scaling factor and a small positive number, respectively, with M_p being the mass of the squirmer. As demonstrated in Fig. 21, changing the value of ε have a negligible impact on the simulation results.

References

- Allredge AL, Passow U, Logan BE. The abundance and significance of a class of large, transparent organic particles in the ocean. *Deep-Sea Res Pt I*. 1993; 40:1131–1140.
- Ardekani A, Gore E. Emergence of a limit cycle for swimming microorganisms in a vortical flow of a viscoelastic fluid. *Phys Rev E*. 2012; 85:056,309.
- Ardekani AM, Rangel R. Numerical investigation of particle-particle and particle-wall collisions in a viscous fluid. *J Fluid Mech*. 2008; 596:437–466.
- Ardekani AM, Rangel RH, Joseph DD. Motion of a sphere normal to a wall in a second-order fluid. *J Fluid Mech*. 2007; 587:163–172.
- Ardekani AM, Dabiri S, Rangel RH. Collision of multi-particle and general shape objects in a viscous fluid. *J Comput Phys*. 2008; 227:10,094–10,107.
- Ardekani AM, Joseph DD, Dunn-Rankin D, Rangel RH. Particle-wall collision in a viscoelastic fluid. *J Fluid Mech*. 2009; 633:475–483.
- Azam F. Intense hydrolytic enzyme activity on marine aggregates and implications for rapid particle dissolution. *Nature*. 1992; 359:10. [PubMed: 1489415]
- Berg HC, Turner L. Movement of microorganisms in viscous environments. *Nature*. 1979; 278:349–351. [PubMed: 370610]
- Blake JR. A spherical envelope approach to ciliary propulsion. *J Fluid Mech*. 1971; 46:199–208.
- Bozorgi Y, Underhill PT. Effect of viscoelasticity on the collective behavior of swimming microorganisms. *Phys Rev E*. 2011; 84:061,901.
- Bozorgi Y, Underhill PT. Role of linear viscoelasticity and rotational diffusivity on the collective behavior of active particles. *J Rheol*. 2013; 57:511–533.

- Brennen C, Winet H. Fluid mechanics of propulsion by cilia and flagella. *Ann Rev Fluid Mech.* 1977; 9:339–398.
- Burrows LL. *Pseudomonas aeruginosa* twitching motility: Type IV pili in action. *Ann Rev Microbiol.* 2012; 66:493–520. [PubMed: 22746331]
- Cunliffe M, Engel A, Frka S, Gasparovic B, Guitart C, Murrell JC, Salter M, Stolle C, Upstill-Goddard R, Wurlm O. Sea surface microlayers: A unified physicochemical and biological perspective of the air-ocean interface. *Prog Oceanogr.* 2013; 109:104–116.
- D’Avino G, Cicale G, Hulsén MA, Greco F, Maffettone PL. Effects of confinement on the motion of a single sphere in a sheared viscoelastic liquid. *Journal of Non-Newtonian Fluid Mechanics.* 2009; 157:101–107.
- Despeyroux A, Ambari A. Slow motion of a sphere towards a plane through confined non-newtonian fluid. *J. Non-Newtonian Fluid Mech.* 2012; 167:38–45.
- DiLuzio WR, Turner L, Mayerm M, Garstecki P, Weibel DB, Berg HC, Whitesides GM. *Escherichia coli* swim on the right-hand side. *Nature.* 2005; 435:1271–1274. [PubMed: 15988531]
- Doostmohammadi A, Stocker R, Ardekani AM. Low-Reynoldsnumber swimming at pycnoclines. *Proc Natl Acad Sci USA.* 2012; 109:3856–3861. [PubMed: 22355147]
- Drescher K, Dunkel J, Cisneros LH, Ganguly S, Goldstein RE. Fluid dynamics and noise in bacterial cell–cell and cell–surface scattering. *Proc National Academy Sci.* 2011; 108(27):10,940–10,945.
- Eisenberg DA, Klink IM, Phillips RJ. Axisymmetric sedimentation of spherical particles in a viscoelastic fluid: Sphere-wall and sphere-sphere interactions. *J Rheol.* 2013; 57:857–880.
- Giesekus H. A simple constitutive equation for polymer fluids based on the concept of deformation-dependent tensorial mobility. *J Non-Newtonian Fluid Mech.* 1982; 11:69–109.
- Glowinski R, Pan TW, Hesla TI, Joseph DD, Periaux J. A fictitious domain approach to the direct numerical simulation of incompressible viscous flow past moving rigid bodies: application to particulate flow. *J Comput Phys.* 2001; 169:363–426.
- Goyal N, Derksen JJ. Direct simulations of spherical particles sedimenting in viscoelastic fluids. *J Non-Newton Fluid Mech.* 2012; 183:1–13.
- Guenette R, Fortin M. A new mixed finite element method for computing viscoelastic flows. *J Non-Newtonian Fluid Mech.* 1995; 60:27–52.
- Hall-Stoodley L, Costerton JW, Stoodley P. Bacterial biofilms: from the Natural environment to infectious diseases. *Nature Rev Microbiol.* 2004; 2:95–108. [PubMed: 15040259]
- Harman MW, Dunham-Ems SM, Caimano MJ, Belperron AA, Bockenstedt LK, Fu HC, Radolf JD, Wolgemuth CW. The heterogeneous motility of the Lyme disease spirochete in gelatin mimics dissemination through tissue. *Proc Natl Acad Sci USA.* 2012; 109:3059. [PubMed: 22315410]
- Houry A, Briandet R, Aymerich S, Gohar M. Involvement of motility and flagella in *Bacillus cereus* biofilm formation. *Microbiol.* 2010; 156:1009–1018.
- Ishikawa T, Simmonds MP, Pedley TJ. Hydrodynamic interaction of two swimming model micro-organisms. *J Fluid Mech.* 2006; 568:119–160.
- Ishimoto K, Gaffney EA. Squirmer dynamics near a boundary. *Phys Rev E.* 2013; 88:062–702.
- Jung S. *Caenorhabditis elegans* swimming in a saturated particulate system. *Phys Fluids.* 2010; 22:031–903.
- Kim TJ, Young BM, Young GM. Effect of flagellar mutations on *Yersinia enterocolitica* biofilm formation. *Appl Environ Microbiol.* 2008; 74:5466–5474. [PubMed: 18606789]
- Kimsey RB, Spielman A. Motility of Lyme Disease Spirochetes in Fluids as Viscous as the Extracellular Matrix. *J Infect Dis.* 1990; 162:1205–1208. [PubMed: 2230247]
- Klapper I, Rupp CJ, Cargo R, Purvedorj B, Stoodley P. Viscoelastic fluid description of bacterial biofilm material properties. *Biotechnol Bioeng.* 2002; 80:289–296. [PubMed: 12226861]
- Lauga E. Propulsion in a viscoelastic fluid. *Phys Fluids.* 2007; 19:083,104.
- Lauga E. Life at high Deborah number. *Europhysics Letters.* 2009; 86(6):64,001.
- Lemon KP, Higgins DE, Kolter R. Flagellar Motility Is Critical for *Listeria monocytogenes* Biofilm Formation. *J Bacteriol.* 2007; 189:4418–4424. [PubMed: 17416647]
- Leonard BP. A stable and accurate convective modelling procedure based on quadratic upstream interpolation. *Comput Meth Appl Mech Engng.* 1979; 19:59–98.

- Li G, Ardekani AM. Hydrodynamic interaction of microswimmers near a wall. *Phys Rev E*. 2014; 90:013,010.
- Li G, Tam LK, Tang JX. Amplified effect of brownian motion in bacterial near-surface swimming. *Proc National Academy Sci USA*. 2008; 105:18,359–35,518.
- Lighthill MJ. On the squirming motion of nearly spherical deformable bodies through liquids at very small Reynolds numbers. *Comm Pure Appl Math*. 1952; 5:109–118.
- Liu B, Powers TR, Breuer KS. Force-free swimming of a model helical flagellum in viscoelastic fluids. *Proc Natl Acad Sci USA*. 2011; 108:19,516–19,520.
- Llopis I, Pagonabarraga I. Hydrodynamic interactions in squirmer motion: Swimming with a neighbour and close to a wall. *J Non-Newtonian Fluid Mec*. 2010; 165:946–952.
- Merritt PM, Danhorn T, Fuqua C. Motility and Chemotaxis in *Agrobacterium tumefaciens* Surface Attachment and Biofilm Formation. *J Bacteriol*. 2007; 189:8005–8014. [PubMed: 17766409]
- Montecucco C, Rappuoli R. Living dangerously: How *Helicobacter pylori* survives in the human stomach. *Nat Rev Mol Cell Biol*. 2001; 2:457–466. [PubMed: 11389469]
- O'Toole GA, Kolter R. Flagellar and twitching motility are necessary for *Pseudomonas aeruginosa* biofilm development. *Mol Microbiol*. 1998; 30:295–304. [PubMed: 9791175]
- Padhy S, Rodriguez M, Shaqfeh ESG, Iaccarino G, Morris JF, Tonmukayakul N. The effect of shear thinning and walls on the sedimentation of a sphere in an elastic fluid under orthogonal shear. *J Non-Newtonian Fluid Mech*. 2013; 201:120–129.
- Passow U. Transparent exopolymer particles (TEP) in aquatic environments. *Prog Oceanogr*. 2002; 55:287–333.
- Pratt LA, Kolter R. Genetic analysis of *Escherichia coli* biofilm formation: roles of flagella, motility, chemotaxis and type I pili. *Mol Microbiol*. 1998; 30:285–293. [PubMed: 9791174]
- Schleiniger G, Weinacht RJ. A remark on the Giesekus viscoelastic fluid. *J Rheol*. 1991; 35:1157–1170.
- Shaw T, Winston M, Rupp CJ, Klapper I, Stoodley P. Commonality of Elastic Relaxation Times in Biofilms. *Phys Rev Lett*. 2004; 93:098,102.
- Shen XN, Arratia PE. Undulatory Swimming in Viscoelastic Fluids. *Phys Rev Lett*. 2011; 106:208,101.
- Snijkers F, D'Avino G, Maffettone PL, Greco F. Effect of viscoelasticity on the rotation of a sphere in shear flow. *J Non-Newton Fluid Mech*. 2011; 166:363–372.
- Spagnolie SE, Lauga E. Hydrodynamics of self-propulsion near a boundary: predictions and accuracy of far-field approximations. *J Fluid Mech*. 2012; 700:105–147.
- Spagnolie SE, Liu B, Powers TR. Locomotion of Helical Bodies in Viscoelastic Fluids: Enhanced Swimming at Large Helical Amplitudes. *Phys Rev Lett*. 2013; 111:068,101.
- Suarez SS, Pacey AA. Sperm transport in the female reproductive tract. *Human Reprod Update*. 2006; 12:23–37.
- Tatum JA, Finnis MV, Lawson NJ, Harrison GM. 3D particle image velocimetry of the flow field around a sphere sedimenting near a wall: Part 1. Effects of Weissenberg number. *J non-Newtonian Fluid Mech*. 2007; 141(2):99–115.
- Taylor G. Analysis of the swimming of microscopic organisms. *Proceedings of the Royal Society of London Series A-Mathematical. Phys Sci*. 1951; 209:447–461.
- Teran J, Fauci L, Shelley M. Viscoelastic Fluid Response Can Increase the Speed and Efficiency of a Free Swimmer. *Phys Rev Lett*. 2010; 104:038,101.
- Thutupalli S, Seemann R, Herminghaus S. Swarming behavior of simple model squirmers. *New J. Phys*. 2011; 13(7) 073–021.
- Tolker-Nielsen T, Brinch UC, Ragas PC, Andersen JB, Jacobsen CS, Molin S. Development and dynamics of *Pseudomonas* sp. biofilms. *J Bacteriol*. 2000; 182:6482–6489. [PubMed: 11053394]
- Tuson HH, Weibel DB. Bacteria-surface interactions. *Soft Matter*. 2013; 9:4368–4380. [PubMed: 23930134]
- Vlamakis H, Aguilar C, Losick R, Kolter R. Control of cell fate by the formation of an architecturally complex bacterial community. *Genes Dev*. 2008; 22:945–953. [PubMed: 18381896]
- Wang S, Ardekani A. Ciliates swimming near an interface. *Phys Rev E*. 2013; 87:063010.

- Wang S, Ardekani AM. Inertial squirmer. *Phys Fluids*. 2012a; 24:101,902.
- Wang S, Ardekani AM. Unsteady swimming of small organisms. *J Fluid Mech*. 2012b; 702:286–297.
- Watnick PI, Kolter R. Steps in the development of a *Vibrio cholerae* El Tor biofilm. *Mol Microbiol*. 1999; 34:586–595. [PubMed: 10564499]
- Wloka M, Rehage H, Flemming HC, Wingender J. Rheological properties of viscoelastic biofilm extracellular polymeric substances and comparison to the behavior of calcium alginate gels. *Colloid Polym Sci*. 2012; 282:1067–1076.
- Wolgemuth CW, Charon NW, Goldstein SF, Goldstein RE. The flagellar cytoskeleton of the spirochetes. *J Mol Microbiol Biotechnol*. 2006; 11:221–227. [PubMed: 16983197]
- Zhu L, Do-Quang M, Lauga E, Brandt L. Locomotion by tangential deformation in a polymeric fluid. *Phys Rev E*. 2011; 83:011,901.
- Zhu L, Lauga E, Brandt L. Self-propulsion in viscoelastic fluids: Pushers vs. pullers. *Phys Fluids*. 2012; 24:051,902.

Fig. 1.
(Color online) Flow streamlines around squirmers in the comoving frame of reference for **a** neutral squirmer, **b** puller, and **c** pusher. The *black arrow* indicates the swimming direction

Fig. 2.
Schematic configuration of a squirmer near a wall

Fig. 3.
(Color online) Temporal evolution of **a** distance from the wall, **b** orientation angle **c** swimming speed, and **d** angular velocity for the neutral squirmer with $\beta = 0$

Fig. 4. (Color online) Temporal evolution of the torque and the vertical force exerted on the neutral squirmer with $\beta = 0$. The panels show **a** variation of the torque for different values of Wi , **b** variation of the vertical force for various values of Wi , **c** decomposition of the torque for the case of $Wi = 1$, and **d** decomposition of the vertical force for the case of $Wi = 1$

Fig. 5.
(Color online) Distribution of the first normal stress difference at plane $z = 0$ around the neutral squirmer with $\beta = 0$. The snapshots are taken immediately after the impact at $t = 2$ and correspond to **a** $Wi = 1$, and **b** $Wi = 6$

Fig. 6.
 (Color online) **a** Temporal evolution of the swimming speed normalized with respect to the steady state value of the speed in an unbounded domain, and **b** distribution of the first normal stress difference around the swimmer at plane $z = 0$. The snapshot is taken at $t = 30$. The panels correspond to a neutral squirmer with $\beta = 0$ and $Wi = 6$

Fig. 7.
(Color online) Temporal evolution of the orientation angle and vertical distance of a neutral squirmer for various values of **a** mobility factor, and **b** viscosity ratio. The corresponding parameters are $\beta = 0$, $Wi = 1$, and **a** $\beta_s = 0.1$, and **b** $\alpha_m = 0.2$

Fig. 8.
(Color online) Temporal evolution of **a** vertical distance and **b** inclination angle for a puller swimmer with $\beta = 3$

Fig. 9.
(Color online) Residence time of the swimmer as a function of the Weissenberg number for puller $\beta = 3$ (squares, blue) and neutral squirmer $\beta = 0$ (circles, red)

Fig. 10.

(Color online) Time history of the **a** torque and **b** vertical force exerted on the puller swimmer with $\beta = 3$ and $Wi = 1$. The inset in panel **b** demonstrates the evolution of the vertical force in short time. The Newtonian and polymeric contributions to the total torque and force are also shown

Fig. 11.
 (Color online) Distribution of $\text{tr}(\mathbf{C})$ at plane $z = 0$ around the puller with $\beta = 3$. The snapshot is taken at $t = 2$ immediately after the impact and the corresponding Weissenberg number is $Wi = 1$

Fig. 12.

(Color online) Temporal evolution of **a** separation distance and **b** orientation angle for the pusher swimmer with $\beta = -3$. The inset in panel **a** illustrates the variation of the vertical distance over the trapping period

Fig. 13.
(Color online) Steady state values of **a** vertical distance (black circles) and orientation angle (blue squares), and **b** velocity components in x and y directions (black circles and blue squares, respectively) as functions of the Weissenberg number for the pusher with $\beta = -3$

Fig. 14.
(Color online) Time history of the decomposition of **a** torque and **b** vertical force exerted on the pusher with $\beta = -3$. The inset in panel **b** shows the evolution of the vertical force around the impact time

Fig. 15.

(Color online) Distribution of $\text{tr}(\mathbf{C})$ at plane $z = 0$ around the pusher squirmer with $\beta = -3$. The snapshot is taken at $t = 50$ and the corresponding Weissenberg number is $Wi = 1$

Fig. 16.

(Color online) Comparison of the temporal evolution of (a) vertical distance and (b) orientation angle of a pusher in Newtonian and viscoelastic fluids at different initial angles and positions. The Newtonian cases ($Wi = 0$) are shown with square symbols. The corresponding parameters for the viscoelastic cases (no symbols) are $Wi = 1$, $\beta_s = 0.1$ and $\alpha_m = 0.2$.

Fig. 17.
(Color online) Temporal evolution of the orientation angle and vertical distance of a pusher for various values of **a** mobility factor, and **b** viscosity ratio. The corresponding parameters are $\beta = -3$, $Wi = 1$, and **a** $\beta_s = 0.1$, and **b** $\alpha_m = 0.2$

Fig. 18.

(Color online) Snapshots of the conformation tensor and the polymer stress around **a** neutral squirmer with $\beta = 0$, **b** puller with $\beta = 3$, and **c** pusher with $\beta = -3$. The principal axis of each ellipsoid is aligned with the principal eigenvector of $\mathbf{C}$ and its length is scaled based on the associated eigenvalue. The minor axes correspond to the second and third eigenvectors of $\mathbf{C}$. The coloring is based on the value of the first normal stress difference at the centroid of each ellipsoid. The snapshots are taken at $t = 2$ after the collision and the corresponding Weissenberg number is $Wi = 1$

Fig. 19.
 (Color online) **a** Transient behaviour of a rotating sphere in an Oldroyd-B shear flow **b**
 Comparison of the steady angular velocity as a function of Wi with the results of Snijkers et
 al. (2011) and Goyal and Derksen (2012)

Fig. 20.
 (Color online) Swimming speed U as a function of the Weissenberg number Wi , for the neutral squirmer $\beta = 0$ (solid line: (Zhu et al. 2012) and circles: present results), pusher $\beta = -5$ (dashed line: (Zhu et al. 2012) and squares: present results) and puller $\beta = 5$ (dashdot line: (Zhu et al. 2012) and triangles: present results). The Reynolds number is $Re = 0.01$ and the swimming speed is scaled by the squirmer's speed U_0 in a Newtonian fluid

Fig. 21.

(Color online) Time history of **a** vertical distance h and orientation angle α and **b** swimming speed U of the neutral squirmer calculated using different grid sizes, different time steps and different values of the parameter ε . The corresponding parameters are $Wi = 6$ and $Re = 0.1$ and the squirmer is initialized at $h_0 = 2$ and $\alpha_0 = -\pi/4$.