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Hydrodynamic interactions of swimming microorganisms can lead to coordinated behaviors of large groups. Using a mean-field theory and the Oldroyd-B constitutive equation, we show how linear viscoelasticity of the suspending fluid alters the hydrodynamic interactions and therefore the ability of the group to coordinate. We quantify the ability to coordinate by the initial growth rate of a small disturbance from the uniform isotropic state. For small wavenumbers the response is qualitatively similar to a Newtonian fluid but the Deborah number affects an effective viscosity of the suspension. At higher wavenumber, the response of the fluid to small amplitude oscillatory shear flow leads to a maximal growth rate at a particular wavelength unlike the Newtonian result.

In this Letter, we consider the collective behavior of a large group of swimming microorganisms. There is a long history of studying how microorganisms move through fluids including non-Newtonian fluids. Mucus is an important coating on surfaces, often as a barrier to infection [1–3]. Infections of *H. pylori* in the intestines occur when the bacterium is able to move through the mucus and not be flushed [4–6]. *H. pylori* are able to change the rheological properties of the mucus by changing the local pH [7]. The properties of saliva are also known to play a role in the process of biofilm formation on teeth [8].

Most models have shown that the presence of viscoelasticity usually reduces the swimming speed [9–14]. However, the swimming speed of some bacteria varies with viscosity and viscoelasticity [15–19]. It is particularly interesting that swimming speed is not a monotonic function of viscosity. For a large class of organisms, as the viscosity increases, the swimming speed first increases, reaches a maximum, then decreases [20, 21]. It has been speculated that this results from the non-Newtonian nature of the polymer solutions used. Although the influence of viscosity and viscoelasticity on a single organism is not completely understood, the focus of this Letter is the collective behavior of large groups.

As an organism swims through a fluid, it causes a long-ranged disturbance that moves and rotates the other organisms. This hydrodynamic interaction (HI) plays an important role in the collective behavior of the group. Previous results in a Newtonian solvent have shown that hydrodynamic interactions lead to long-ranged orientational correlations between organisms and coordination in communities of bacteria [22–31]. Using a linear stability analysis of a mean-field theory, it has been shown that the uniform isotropic state is stable if the organisms pull themselves forward (pullers) while it is unstable if they push themselves forward (pushers).

To understand how a non-Newtonian fluid can alter the stability (or instability) of the uniform isotropic state, we will couple the dynamics of the swimming microorganisms with a non-Newtonian constitutive equation. We have chosen the Oldroyd-B constitutive equation, which consists of a Newtonian solvent with viscosity η_s and a polymer stress which satisfies a single mode upper-convected Maxwell model [32]. The two parameters in the Maxwell model are the polymer contribution to the viscosity η_p and the relaxation time λ. This model has been used previously to understand single organisms in biofluids [12]. It represents the generic changes to the linear stability due to viscoelasticity, and therefore the long-ranged correlations of the group. Note that in the linear stability analysis, the nonlinear terms of the constitutive model do not contribute.

Our model consists of $\Psi(\boldsymbol{x}, \boldsymbol{n}, t)$, the probability density of an organism with position $\boldsymbol{x}$ and unit vector orientation $\boldsymbol{n}$ at time t, which satisfies the equation

$$\frac{\partial \Psi}{\partial t} = -\nabla_{\boldsymbol{x}} \cdot (\dot{\boldsymbol{x}} \Psi) - \nabla_{\boldsymbol{n}} \cdot (\dot{\boldsymbol{n}} \Psi), \qquad (1)$$

where $\dot{\boldsymbol{x}}$ is the effective velocity of the organism and $\dot{\boldsymbol{n}}$ is the effective angular velocity. We model the effective velocity as the isolated swimming speed v_{is} in the direction of its orientation plus the fluid velocity $\boldsymbol{u}$ plus a contribution to model diffusion of the center of mass

$$\dot{\boldsymbol{x}} = v_{is} \boldsymbol{n} + \boldsymbol{u} - D\nabla_{\boldsymbol{x}}(\ln\Psi), \qquad (2)$$

where D is the translational diffusivity. As a model of the effective angular velocity we will use Jeffery's equation for the rotation of a rigid ellipsoid in a linear flow to write

$$\dot{\boldsymbol{n}} = (\boldsymbol{\delta} - \boldsymbol{nn}) \cdot [(\gamma\Gamma + \Omega) \cdot \boldsymbol{n} - D_r \nabla_{\boldsymbol{n}}(\ln\Psi)], \quad (3)$$

where D_r is the rotational diffusivity, $\Gamma = (\nabla\boldsymbol{u} + \nabla\boldsymbol{u}^\dagger)/2$ is the rate of strain tensor, $\Omega = (\nabla\boldsymbol{u} - \nabla\boldsymbol{u}^\dagger)/2$ is the vorticity tensor, and $\gamma = (A^2 - 1)/(A^2 + 1)$ where A is the aspect ratio of the ellipsoid. Most bacteria with long flagellar bundles have a large enough aspect ratio including the body and bundle such that γ is near one.

The fluid velocity $\boldsymbol{u}$ is generated by the motion of the other organisms. At low Reynolds number conservation of mass and momentum in the fluid give $\nabla_{\boldsymbol{x}} \cdot \boldsymbol{u} = 0$ and

$$-\eta_s \nabla_{\boldsymbol{x}}^2 \boldsymbol{u} + \nabla_{\boldsymbol{x}} q + \nabla_{\boldsymbol{x}} \cdot \boldsymbol{\tau}_p = \nabla_{\boldsymbol{x}} \cdot \boldsymbol{\Sigma}, \qquad (4)$$

where q is the pressure, $\boldsymbol{\Sigma}$ is the stress from the organisms pushing on the fluid and $\boldsymbol{\tau}_p$ is the stress due to the "polymers" which give rise to the non-Newtonian behavior of the fluid. In the mean-field approximation, the stress $\boldsymbol{\Sigma}$ is the orientational average over the other organisms using the distribution Ψ in a self-consistent model

$$\boldsymbol{\Sigma} = dN \int_S \Psi \left(\boldsymbol{nn} - \frac{1}{3}\boldsymbol{\delta} \right) \mathrm{d}\boldsymbol{n}, \qquad (5)$$

where S is the surface of a unit sphere, d is the dipole moment exerted by a swimmer, and N is the number of organisms in the domain of volume V. In this mean-field approximation, the stress $\boldsymbol{\Sigma}$ accounts for the HI between organisms which leads to the instability and collective behavior. We assume that d is constant and not affected by the flow due to the other organisms. The stress $\boldsymbol{\tau}_p$ is assumed to follow the upper-convected Maxwell model $\boldsymbol{\tau}_p + \lambda\hat{\boldsymbol{\tau}}_p = -2\eta_p\Gamma$, where $\hat{\boldsymbol{\tau}}_p$ is the upper convected derivative $\hat{\boldsymbol{\tau}}_p = \partial\boldsymbol{\tau}_p/\partial t + \boldsymbol{u}\cdot\nabla\boldsymbol{\tau}_p - (\nabla\boldsymbol{u}^\dagger \cdot \boldsymbol{\tau}_p + \boldsymbol{\tau}_p \cdot \nabla\boldsymbol{u})$. Equations 1 to 5 form a closed system, for which the uniform isotropic state is a steady state solution. Other than the inclusion of the polymer stress, this system is the same as that used by previous researchers [27, 29–31]. Using our knowledge of the Newtonian problem, we non-dimensionalize the system using a characteristic time scale $t_c = \eta_s/(|d|c)$, where we have used the absolute value of the dipole moment d and the concentration $c = N/V$. This time scale represents the characteristic time needed for HI between organisms to rotate the orientation of an organism. We choose a characteristic length scale $l_c = v_{is}t_c$ and characteristic stress scale $\eta_s/t_c = |d|c$. We will also rescale Ψ such that the uniform isotropic state corresponds to $\Psi = 1/(4\pi)$. Unless otherwise stated, for the remainder of the Letter, we will use dimensionless variables with these scales.

We will neglect both translational diffusion and rotational diffusion for simplicity. It is known for Newtonian fluids that translational diffusion stabilizes high wavenumber perturbations but does not affect the stability of low wavenumber perturbations. Rotational diffusion is known to stabilize all perturbations. We expect both to be true for non-Newtonian fluids. In our linear stability analysis, primed variables represent the deviation of the variable from the steady state solution.

To leading order, the primed variables satisfy

$$\frac{\partial\Psi'}{\partial t} = -\boldsymbol{n}\cdot\nabla_{\boldsymbol{x}}\Psi' + 3\gamma\boldsymbol{nn}:\Gamma', \qquad (6)$$

$$\nabla_{\boldsymbol{x}}\cdot\boldsymbol{u}' = 0, \qquad (7)$$

$$-\nabla_{\boldsymbol{x}}^2\boldsymbol{u}' + \nabla_{\boldsymbol{x}}q' + \nabla_{\boldsymbol{x}}\cdot\boldsymbol{\tau}_p' = \nabla_{\boldsymbol{x}}\cdot\boldsymbol{\Sigma}', \qquad (8)$$

$$\boldsymbol{\Sigma}' = \frac{p}{4\pi}\int_S \Psi' \left(\boldsymbol{nn} - \frac{1}{3}\boldsymbol{\delta} \right) \mathrm{d}\boldsymbol{n}, \qquad (9)$$
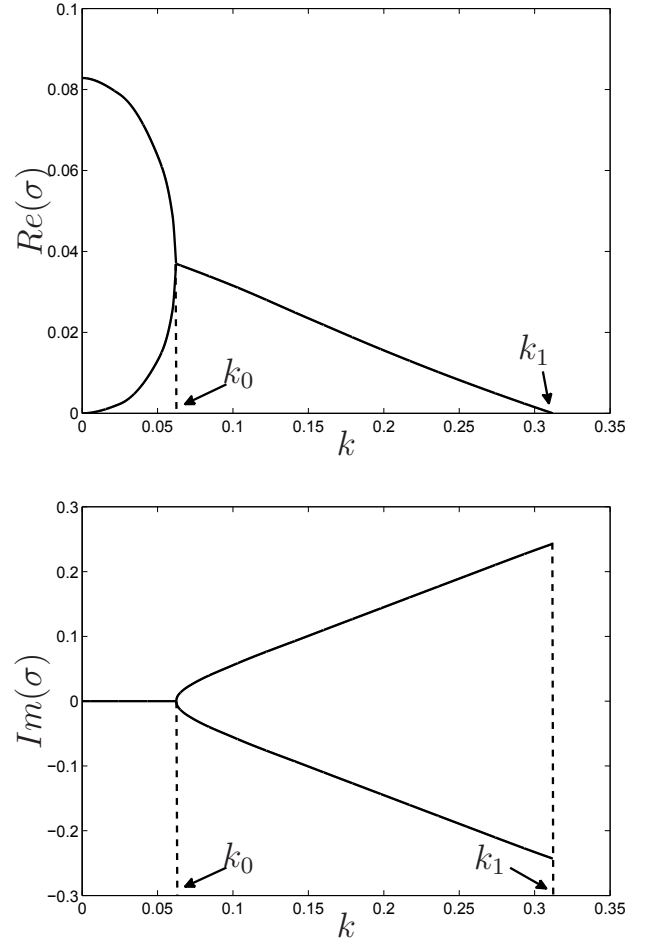

FIG. 1: Dispersion relation for pushers showing the real part of σ (a) and the imaginary part of σ (b) versus wavenumber k. The dimensionless parameters in the constitutive equation are $H = 2$ and De $= 1$.

$$\boldsymbol{\tau}_p' + 5\mathrm{De}\frac{\partial\boldsymbol{\tau}_p'}{\partial t} = -2H\Gamma', \qquad (10)$$

where p denotes the sign of the dipole moment ($p = -1$ for pushers and $p = 1$ for pullers), the ratio of the polymer viscosity to the solvent viscosity is $H = \eta_p/\eta_s$, and the Deborah number is De $= \lambda|d|c/(5\eta_s)$. We can solve these equations by postulating a plane wave solution with dependence $\exp(\imath\boldsymbol{k}\cdot\boldsymbol{x} + \sigma t)$ and determine the dispersion relation for σ. The dispersion relation is the solution to

$$\frac{3\imath p\gamma}{4k\left(1 + \frac{H}{1+5\mathrm{De}\sigma}\right)}\left[2a^3 - \frac{4}{3}a + (a^4 - a^2)\ln\left(\frac{a-1}{a+1}\right)\right] = 1 \qquad (11)$$

where $a = -\imath\sigma/k$.

Figure 1 shows the dispersion relation for a suspension of pushers ($p = -1$) with $\gamma = 1$ for a weakly non-Newtonian fluid for which $H = 2$ and De $= 1$. The result is qualitatively similar to a Newtonian fluid. For $k < k_0$, σ is real with three possible values, one positive value that approaches a finite value as $k \to 0$, one
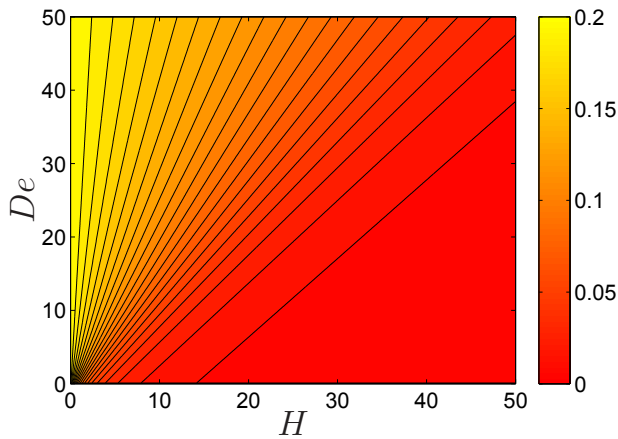
FIG. 2: (Color online) Contour plot and level curves of the positive σ for pushers as $k \to 0$ from equation 12 when $\gamma = 1$.

FIG. 3: (Color online) Scaled dispersion relation for pushers for $\gamma = 1$ and $H = 40$. The curves represent De = 0 (solid black), De = 14 (solid orange (gray)), De = 20 (dashed blue), De = 30 (dot-dashed red), De = 50 (dotted magenta), and De = 100 (solid green (lighter gray)). The scaling collapses the curves for De = 0 and De = ∞.

positive value that approaches zero as $k \to 0$, and one negative value that approaches a finite value as $k \to 0$ (not shown). The negative value does not occur in the Newtonian case and results from a stable decay of the polymer stress with time because of the relaxation time. The limit De $\to 0$ is a singular limit in which this negative root scales as De^{-1}. By expanding as $a \to \infty$ we find that as $k \to 0$ the finite values of σ solve

$$\text{De} = \frac{H}{-p\gamma - 5\sigma} - \frac{1}{5\sigma}. \tag{12}$$

Although this expression can be solved easily for both σ roots, the form of equation 12 illustrates a key feature; the level curves of σ are straight lines.

Figure 2 shows level curves for the positive root for pushers with $\gamma = 1$. The values of H and De can vary widely for biofluids. For saliva, H ranges from near zero to ~ 10 [33, 34]. De is proportional to λ and c. The relaxation time typically lies between $5ms$ and $1s$, though has been reported as high as $76s$. Relevant concentrations to expect possible collective behavior are from 10^9 to 10^{11} cells/mL. Using $1s$ as the maximum relaxation time and the dipole moment for *E. coli* ($\sim 2 \times 10^{-18}J$), De can range from near zero to ~ 40. For gastric mucus, the properties depend strongly on pH. Near neutral pH, it is fit well using $H = 32$ and $\lambda = 50ms$ [7]. Therefore De can range from near zero to ~ 2. At low pH, gastric mucus forms a gel with much higher viscosity and relaxation time. H can be in the thousands and De in the hundreds, though gels are typically not modeled using the Oldroyd-B constitutive equation.

In the limit $H \to 0$, the level curves approach $\sigma = 1/5$ which is the Newtonian result. This corresponds to a dimensional growth rate of $|d|c/(5\eta_s)$. When De = 0, we obtain $\sigma = 1/(5(1+H))$. In this limit, the polymer is able to relax fully during the growth process and therefore the fluid acts as an effective Newtonian fluid with viscosity $\eta_s + \eta_p$. Since the growth rate for a Newtonian fluid is
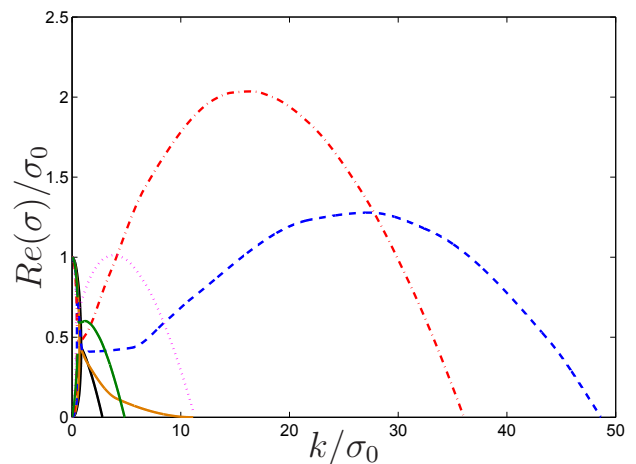
inversely proportional to the viscosity, the growth rate is scaled down by a factor $1 + H$. Finally, for any non-zero value of H, as the Deborah number is increased from zero, the polymer cannot relax fully during the growth process and contributes less to the instability. Therefore, for any finite H as De $\to \infty$ the value of σ approaches the Newtonian solvent result.

We can better understand the behavior near small k by calculating the small k expansion for each branch. Using these expansions, we find that if we scale σ by σ_0 (the positive root as $k \to 0$) we can almost collapse the data by also scaling k by σ_0. Figure 3 plots the scaled dispersion relation. The scaling collapses the curves exactly when De = 0 and De = ∞. For intermediate De, the curves do not collapse exactly but retain the same qualitative structure for $k < k_0$.

This qualitative collapse for $k < k_0$ in Figure 3 suggests that the dominant change in this region is a rescaling by an effective viscosity that depends on De and H. In the limit De $\to \infty$, the polymer does not have time to relax during the growth process and therefore has no impact on the growth rate of the unstable mode. When De $\to 0$ the polymer fully relaxes and therefore acts as an effective Newtonian fluid with a new viscosity. Therefore the growth rate is scaled down by a factor of $1 + H$ and is shifted to smaller k by a factor of $1 + H$.

At intermediate De, the dispersion relation for $k_0 < k < k_1$ is qualitatively different for a non-Newtonian fluid than for a Newtonian fluid. At large enough H and intermediate De the growth rate exhibits a maximum at a particular k. This is in sharp contrast to the Newtonian result in which the largest growth rate occurs for $k \to 0$ and is thought to lead to large scale coordination in sus-

pensions of microorganisms. This peak occurs because of the competition of two effects. As k increases towards k_1 for a Newtonian fluid, the real part of σ decreases as the imaginary part of σ increases. However, as k increases, the flow becomes dominated by oscillations (similar to small amplitude oscillatory shear (SAOS)) and the frequency of oscillation increases as k increases. As the frequency increases, the effective viscosity $\eta'(\omega)$ decreases, leading to an increase in the growth rate. The competition of these two phenomena leads to a peak.

This peak occurs for "large" H and intermediate De. H must be large enough that the low and high frequency values of η' differ significantly. The constitutive equation considered here does not "shear-thin" in steady shear flow, and any shear-thinning would not alter the results of the linear stability analysis. However, in the region $k_0 < k < k_1$ the relevant viscosity is η' which does decrease with increasing frequency. Even for large enough H, the peak does not occur for all De since for De $\to \infty$ the polymer does not contribute to the dynamics and for De $\to 0$ the polymer acts as a Newtonian fluid. The scale of De for which the peak does occur is approximately De $\propto H$ for large H. A predictive theory of the peak height and k at the peak is left for future work.

For Fig. 3 using De = 30 and σ_0 from equation 12, the value of k at the peak corresponds to a length scale approximately equal to $20l_c$. The value of l_c is inversely proportional to cell concentration. Using parameters for *E. coli* and c ranging from 10^9 to 10^{11} cells/mL gives a range of the lengthscale associated with the peak from $3\mu m$ to $300\mu m$. This lengthscale is larger than the typical separation between organisms, which represents large-scale collective behavior, although we expect these numbers would be altered slightly by fluctuations not in the mean-field assumption and nonlinear effects.

In conclusion, we have used a mean-field theory and viscoelastic constitutive equation to better understand how a non-Newtonian fluid alters the hydrodynamic interactions of swimming organisms and therefore their ability to form large scale structures. This naturally leads to the question of whether one role of non-Newtonian biological fluid barriers is to interrupt the HI of microorganisms. It also leads to the possibility that microorganisms could alter the properties of those barriers to enhance their ability to interact using HI. We hope this work helps in efforts to start addressing these questions.

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