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# Fluctuating hydrodynamics and microrheology of a dilute suspension of swimming bacteria

A. W. C. Lau
*Department of Physics, Florida Atlantic University, Boca Raton, Florida 33431, USA*

T. C. Lubensky
*Department of Physics and Astronomy, University of Pennsylvania, Philadelphia, Pennsylvania 19104, USA*

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A bacterial bath is a model active system consisting of a population of rodlike motile or self-propelled bacteria suspended in a fluid environment. This system can be viewed as an active, nonequilibrium version of a lyotropic liquid crystal or as a generalization of a driven diffusive system. We derive a set of phenomenological equations, which include the effects of internal force generators in the bacteria, describing the hydrodynamic flow, orientational dynamics of the bacteria, and fluctuations induced by both thermal and nonthermal noises. These equations violate the fluctuation dissipation theorem and the Onsager reciprocity relations. We use them to provide a quantitative account of results from recent microrheological experiments on bacterial baths.

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## I. INTRODUCTION

Many species of bacteria, such as *E. coli*, are rodlike, single-celled organisms that actively navigate their environment by swimming [1]. A common mechanism for motility is based on the rotation of bacterial flagella propelled by the action of rotary motors embedded in the cell wall. When all the motors rotate counterclockwise, the flagella bundle up and propel a bacterium forward in the direction of its long axis. This is called "run." When some of the flagella rotate clockwise, the flagella unbundle and the cell body spins or "tumbles." On average, a bacterium tumbles for about 0.1 s before it "runs" in a different (random) direction; the typical run time is about 1 s. Therefore, at long time, a bacterium appears to perform a sort of random walk [2,3]. With a typical size of a bacterium of the order of microns and a typical speed of the order of 10 $\mu$m/s, the Reynolds number $\mathcal{R}$ is much less than 1.

Early experimental studies utilizing light-scattering technique demonstrated that the velocity distribution of motile microorganisms, in general, and bacteria, in particular, is not Maxwellian [4], indicating that their motion is far more complex than that of Brownian particles [5]. A large concentration of these microorganisms constitutes a state that is far from equilibrium, exhibiting self-organized collective motion with spatial and temporal patterns such as swirls and jets [6–11].

More quantitative information about a bacterial bath (e.g., of *E. coli*) can be extracted from microrheological measurements, which track the motion of passive micron-sized beads dispersed in it [6,7,12]. Interestingly, the mean-squared displacement (MSD) of these passive beads is superdiffusive at short time and diffusive at long time, with a diffusion constant that is a few orders of magnitude greater than that of the same beads in water. These studies of the microrheology of bacterial baths clearly demonstrate that the motility of bacteria drastically alters the physical properties, i.e., response and fluctuations of the fluid environment in which they are suspended. The phenomena of superdiffusion and self-organized behaviors have been either observed or predicted in other active systems as well [13–20].

The experiments on baths of *E. coli* [6,7,12] cited above did not address the violation of the fluctuation-dissipation theorem (FDT), the effects of spatial heterogeneities in the bath, or the effects of different bacterial swimming modes. These issues are crucial to a consistent interpretation of microrheological experiments in active systems in general and in bacterial baths in particular [14] (see also Appendix A). They were addressed in a recent experimental study by *Chen et al.* [21]. In that study, two strains of *E. coli*, a rod-shaped bacterium with dimensions $3\times 1$ $\mu$m, were used: one strain is the wild type, which tumbles and runs, and the other is the tumbler, which predominantly tumbles. In contrast to previous experiments, these experiments [21] carried out simultaneous measurements of both one- and two-point passive microrheology. One-point measurements are sensitive to the local environment of the probe colloidal particle. Two-point measurements, on the other hand, automatically average over system inhomogeneities and provide an unambiguous measure of the parameters characterizing bulk rheological properties [14,22]. The Chen study [21] also carried out independent measurements of the response of beads in the bath to controlled external forces and from it extracted the effective viscosity of the bath. The results of this study are that, even at low bacterial volume fraction ($\phi\sim 10^{-3}$), fluctuations in the bath are considerably enhanced over those of pure water and that tracer particles exhibit superdifussive behavior, even though the viscosity of the bath was indistinguishable from that of water. This indicates that FDT is strongly violated and, thus, that a bacterial bath is a far-from-equilibrium system. The Chen experiments found in addition that, for the wild-type bacteria, MSDs extracted from one- and two-point measurements are different, providing strong evidence that spatial heterogeneities, possibly in the form of vortices and spirals, are present. For the tumblers, the power spectrum, $\Delta(\omega)$, was found to be Lorentzian, whereas for the wild type, it was found to scale with frequency $\omega$ as $\Delta(\omega)\sim\phi/\sqrt{\omega}$. These stress fluctuations, whose functional form is different from that of thermal fluctuations, arise from the active process of tumbling or swimming of bacteria. The purpose of this paper is to derive the long-wavelength low-frequency

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equations governing the dynamics of a bacteria bath and use them to provide quantitative explanations of the Chen microrheological experiments.

Early theoretical models of bacterial baths focus on hydrodynamical phenomena at a macroscopic level [23] and on modeling the bulk motion of chemotatic bacteria via an advection-diffusion-type equation [24]. Recently, there has been considerable progress in developing theoretical models [25–28] to describe collective coherent motion and related phenomena in nonequilibrium systems with many particles or degrees of freedom. Motivated by the observation of collective behavior and spatial patterns in schools of fish and flocks of birds, Vicsek *et al.* introduced and carried out numerical studies of a model in which each particle (modeled as a point) moves at a constant speed but with a velocity direction determined by averaging over the directions of a large collection of particles in its neighborhood plus a small random perturbation [25]. This model in two dimensions (2D) exhibits a nonequilibrium phase transition: at sufficiently high concentration, all particles spontaneously move in a single direction, thus breaking the rotational symmetry of the low-concentration state in which particles move in random directions. This phase transition, which is prohibited in equilibrium systems by the Mermin-Wagner theorem [29], is rationalized within a phenomenological dynamical *xy* model [26,27], which predicts that the MSD of a tagged particle in two dimensions exhibits superdiffusion at the transition. In addition, computer simulation of the bird-flocking model [30] shows that a passive bead, interacting with a sea of "birds," exhibits superdiffusion.

The simple bird-flocking model treats only the vector order associated with particle velocity and it assumes that the particles move relative to a rigid rather than a fluid background. Recent work [31,32] proposes a theory, allowing for the possibility of nematic rather than vector order, to describe the dynamics of anisotropic self-propelled particles suspended in a background fluid with its own dynamics. This theory generalizes the equilibrium hydrodynamics of nematogens to a nonequilibrium situation and predicts that an ordered suspension of self-propelled nematics is unstable at long wavelength, possibly giving rise to vortices and jets. This instability has been confirmed in a recent simulation [33]. The theory also predicts that an isotropic suspension of self-propelled rods exhibits a viscoelastic enhancement when macroscopically sheared [32]. In a related study, Joanny and co-workers derived a set of phenomenological hydrodynamic equations for an active polar gel, constructed to model the dynamics of the cytoskeleton [34–36]. Starting with a microscopic model for a system of cross-linked active long filaments, Marchetti and Liverpool [37–39] derived a set of hydrodynamic equations for active gels that provide considerable physical insight into various instabilities and ordered phases in these active systems. Continuum equations have also been derived from the Boltzmann equation [40,41] and from the results of simulations [33,42–45] directed at understanding pattern formation, instabilities, and giant density fluctuations of a concentrated bacterial bath. Despite all these theoretical studies, there has so far been no theoretical attempt to quantitatively link phenomenological continuum hydrodynamiclike theories to the results from microrheological experiments and, indeed, there is as yet no satisfactory analytical theory that explains superdiffusion and related phenomena in a bacterial bath.

One of the major purposes of this paper is to formulate a continuum theory, following Ref. [32], for the dynamics of bacterial baths and, more importantly, to provide a much-needed link between theories and microrheological experiments. We provide a simple derivation of the hydrodynamic equations governing a dilute bacterial bath and show that the active stress tensor is indeed proportional to the alignment tensor [31,32] and that there is an active contribution to the mass flow. Reference [46] argued that this contribution to the mass flow was allowed by symmetry and that it leads to giant fluctuations as has been confirmed numerically [43,47].

To describe the local orientation of the bacteria in the isotropic phase, we use the Maier-Saupe–de Gennes nematic alignment tensor rather than the vector order parameter that one might expect from the fact that individual bacteria swim in a well-defined local direction and, therefore, have tendency, such as the particles in flocking models, to develop *polar* rather than the nematic order. However, a recent simulation [33] provides evidence that a system of mobile rods, depending on how the active force is applied to them, might be dominated by nematic fluctuations. Theoretical studies of active gels [37] also suggest that there is a region in the phase space where a system of active polar objects has a preference for nematic rather than *polar* order. More importantly, incipient polar order yields a power spectrum which scales $\Delta(\omega) \sim \omega^{-3/2}$, in clear disagreement with the experiment of Ref. [21]. A detailed theory of how the orientational order should be described in terms of a microscopic model of the swimming behavior of bacteria is a subject of another study.

Having derived nonequilibrium continuum equations, we linearize them to calculate harmonic-order correlation functions for the velocity field, alignment tensor, and concentration field of the bacteria. In addition to a renormalization of the viscosity by active forces propelling the bacteria, as found previously [32], we find that a bacterial bath can support long-wavelength shear waves, which are directly controlled by an activity parameter. Furthermore, we find that there is an active contribution to the long-time tail in the velocity autocorrelation function [48] and that the velocity field is correlated over a finite distance in space. Finally, we argue that in order to explain microrheological data for the wild-type bacteria, we must include nonlinear terms, ignored in Ref. [32], in the active stress arising from the concentration fluctuations of the bacteria that we show lead to a noise spectrum, $\Delta(\omega) \sim \phi/\sqrt{\omega}$, in excellent agreement with experiments.

This paper is organized as follows. In Sec. II, we give a simple derivation of the continuum equations for a bacteria bath. These equations are expected to be valid in the isotropic phase. In Sec. III, we analyze the physics of the bacteria bath as described by the linearized theory. In Sec. IV, we show how the theory explains recent experimental observations. In the Appendix A, we give an exposition of the theory behind microrheology for active systems. In the Appendix B, we address briefly noises of nonthermal origins.

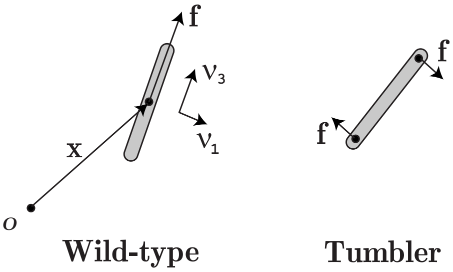

FIG. 1. A cartoon of a "bacterium" as modeled by an anisotropic rod. For the wild types, the movements of the flagella (not shown) of the bacterium create a stress field which exerts an average force (the drag force) on the center-of-mass of the bacterium along its long axis and by Newton's third law, there is a reaction force (the thrust force) exerted on the fluids through its surface. Thus, the resulting active stress tensor for the effective medium (bacteria +fluid) is that of a force dipole, which is proportional the uniaxial order parameter $Q_{ij}$. For the tumblers, there are opposite forces exerted on both ends of the rod in the direction perpendicular to its long axis. The resulting active stress for tumblers is the biaxial order parameter.

## II. DERIVATION OF THE FLUCTUATING HYDRODYNAMIC EQUATIONS

In this section, we derive a set of equations describing the continuum dynamics of an active bacterial bath. As discussed in Sec. I, in order to understand recent microrheological experiments, we need a two-fluid description that treats both the active bacteria and the solvent in which they are suspended. The standard hydrodynamical variables for such a two-fluid system are the mass density of the active particles $\rho_A(\mathbf{x},t)$, the mass density of the solvent $\rho_S(\mathbf{x},t)$, and the total momentum density $\mathbf{g}(\mathbf{x},t)$. For simplicity, we ignore the energy density field, the temperature field, and the nutrient fields. To describe the local orientation of the bacteria, we employ a nonhydrodynamic variable, the symmetric-traceless alignment tensor $Q_{ij}(\mathbf{x},t)$, which, as expected, decays to zero in finite time in the isotropic phase. We first develop the phenomenological equations for an equilibrium two-component nematic liquid crystal in its isotropic phase. We then add to these equations the forces and torques arising from the active sources propelling the bacteria. Each bacterium is modeled as an anisotropic rod with force generators that create a stress field that exerts an average force on and an average torque about the center-of-mass of a bacterium (see Fig. 1). By Newton's third law, there must also be an equal and opposite force exerted on the fluid by the bacterium at its surface. The resulting active stress for the effective medium is obtained simply by adding up these forces for a collection of bacteria. In agreement previous studies [32,37], we find that the active stress is proportional to the alignment tensor.

We assume that the active particles, as well as the solvent molecules, are conserved

$$\partial_t \rho_A = -\nabla \cdot \mathbf{g}_A, \tag{1}$$

$$\partial_t \rho_S = -\nabla \cdot \mathbf{g}_S. \tag{2}$$

These two equations imply the conservation of the total mass density $\rho=\rho_A+\rho_S$: $\partial_t\rho=-\nabla\cdot\mathbf{g}$, where $\mathbf{g}\equiv\mathbf{g}_A+\mathbf{g}_S$ is total momentum density. Following the standard procedure, we set [49]

$$\mathbf{g}_A = \rho_A \mathbf{v} + \mathbf{J}, \tag{3}$$

$$\mathbf{g}_S = \rho_S \mathbf{v} - \mathbf{J}, \tag{4}$$

where $\mathbf{v}=\mathbf{g}/\rho$ is the velocity of the effective fluid and $\mathbf{J}$ is the dissipative mass current (or relative momentum), which, as we show below in Sec. II A, contains a crucial active contribution. Note that $\mathbf{J}$ can be expressed in terms of the velocity difference $\mathbf{w}=\mathbf{v}_A-\mathbf{v}_S$ as

$$\mathbf{J} = \frac{\rho_A\rho_S}{\rho}\mathbf{w}. \tag{5}$$

The conservation of the total momentum implies that

$$\partial_t g_i = -\partial_j \pi_{ij} + \partial_j \sigma^A_{ij}, \tag{6}$$

where $\pi_{ij}=p\delta_{ij}+\rho v_i v_j-\sigma'_{ij}-\sigma^N_{ij}$ is the (passive) current for the total momentum density, which consists of the pressure $p$, the standard convective term, the viscous stress $\sigma'_{ij}=\eta(\partial_i v_j+\partial_j v_i)$ with a shear viscosity coefficient $\eta$, and the reversible couplings between orientation and flow, $\sigma^N_{ij}$, given by

$$\sigma^N_{ij} = \sigma^0_{ij} + \lambda_{klij}(\mathbf{x})\frac{\delta\mathcal{F}}{\delta Q_{kl}}, \tag{7}$$

where $\sigma^0_{ij}=-(\partial f/\partial\nabla_j Q_{kl})\nabla_i Q_{kl}$ is the Ericksen-Leslie elastic stress tensor, $\lambda_{ijkl}$ is a matrix of coefficients describing the orientation-flow couplings, and $\mathcal{F}\equiv\int d^3\mathbf{x} f(Q_{ij},\partial_k Q_{ij})$ is the Landau–de Gennes free-energy functional for the nematics. Equation (7) can be derived using the Poisson-bracket formalism, as was done in Ref. [50]. In Eq. (6), $\sigma^A_{ij}$ is the active contribution to the stress arising from the swimming of the bacteria. We will discuss this important term in Sec. II A.

We assume that the dynamics of $Q_{ij}$ is governed by the same equation as that for an equilibrium nematics in the isotropic phase. It can be written as

$$\partial_t Q_{ij} = -\frac{\mathcal{L}_{ijkl}}{2\gamma}\frac{\delta\mathcal{F}}{\delta Q_{kl}} - \mathbf{v}\cdot\nabla Q_{ij} + \lambda_{ijkl}(\mathbf{x})\partial_l v_k, \tag{8}$$

where $\mathcal{L}_{ijkl}\equiv\delta_{ik}\delta_{jl}+\delta_{il}\delta_{jk}-\frac{2}{3}\delta_{ij}\delta_{kl}$ which ensures the tracelessness of $Q_{ij}$. The first term in Eq. (8) is the dissipative term, the second term is the convective term, and the last term describes the coupling between orientation and flows. Note that $\lambda_{ijkl}$ appears in both Eqs. (7) and (8), as required for Onsager symmetry. Finally, it will be useful to use the unitless concentration field of the bacteria defined as $c(\mathbf{x},t)\equiv\rho_A/\rho$, whose equation of motion can be written as

$$\partial_t c = -\mathbf{v}\cdot\nabla c - \frac{1}{\rho}\nabla\cdot\mathbf{J}. \tag{9}$$

Note that only in the incompressible limit, i.e., $\rho$=const. does the concentration field obey a conservation law.

### A. Derivation of the active stress and the active mass current

Active fluids have extra stresses. The existence and form of these extra stresses were argued in Refs. [31,32] to follow from simple symmetry arguments and derived from a microscopic model for a similar system in Ref. [37]. Here, we present a simple and general derivation of these active stresses and show how they give rise to an additional driven mass-flow term. We first consider the effect of active forces alone, then we include other forces that are present when active forces are not present.

Consider a system of active anisotropic particles, with internal force generators, imbedded in a fluid background. We will call these the $A$ particles and we will refer to the solvent fluid as the $S$ system. Let the center-of-mass (CM) of $A$ particle $\alpha$ be at position $\mathbf{x}^\alpha$. Let $\mathbf{r}^\alpha(\tilde{u})$ be a vector from the particle's CM to a position $\tilde{u}$ on its surface. The internal forces generated by the active particle give rise to forces exerted on the surrounding medium across surface elements on the particle. These forces in general vary with position the surface. We define $-\tilde{f}_i^\alpha(\tilde{u})dS^\alpha$ to be the force exerted on the surrounding medium by the surface element $dS^\alpha$ at $\tilde{u}$. The force exerted at $\tilde{u}$ by the medium on the particle is then $\tilde{f}_i^\alpha(\tilde{u})dS^\alpha = -dS^\alpha N_j^\alpha \sigma_{ij}^\alpha$, where $N_j^\alpha$ is the unit *outer* normal to the surface at $\tilde{u}$ pointing from the particle to the medium and $\sigma_{ij}^\alpha$ is the stress tensor of the medium just outside the point $\tilde{u}$ on the surface. Thus, internal force generators give rise to a force $\mathbf{f}^\alpha$ and a torque $\boldsymbol{\tau}^\alpha$ about the CM of the particle

$$f_i^\alpha = -\int dS_j^\alpha \sigma_{ij}^\alpha \equiv \int dS^\alpha \tilde{f}_i^\alpha, \tag{10}$$

$$\tau_i^\alpha = -\epsilon_{ijk}\int dS_l^\alpha r_j^\alpha \sigma_{kl}^\alpha \equiv \epsilon_{ijk}\int dS^\alpha r_j^\alpha \tilde{f}_k^\alpha. \tag{11}$$

The equations of motion for the momentum, $p_i^\alpha$, of the active particle and its angular momentum, $\ell_i^\alpha$, about its CM arising from the active forces are, respectively, $dp_i^\alpha/dt = f_i^\alpha$ and $d\ell_i^\alpha/dt = \tau_i^\alpha$. The momentum density of the active particles is thus

$$g_{Ai}(\mathbf{x},t) = \sum_\alpha p_i^\alpha \delta[\mathbf{x} - \mathbf{x}^\alpha(t)] + \frac{1}{2}\epsilon_{ijk}\partial_j \sum_\alpha \ell_k^\alpha \delta[\mathbf{x} - \mathbf{x}^\alpha(t)]. \tag{12}$$

Note that we have included the angular momentum in Eq. (12) in order to satisfy the requirement that time derivative of total angular momentum, $\mathbf{L} = \int d^3\mathbf{x}\mathbf{x} \times \mathbf{g}$, be equal to the total torque on the system from all sources, including the internal total internal torque $\Sigma_\alpha \tau_i^\alpha$.

Next, we discuss the forces on the fluid in which the particles are embedded. As discussed above, each surface element $dS_j^\alpha(\tilde{u})$ exerts a force $dS_j^\alpha \sigma_{ij}^\alpha = -dS^\alpha \tilde{f}_i^\alpha$ on the fluid at the point $\mathbf{x}^\alpha + \mathbf{r}^\alpha(\tilde{u})$. Thus, the active particles give rise to the following contributions to the rate of change of the momentum density of the fluid:

$$\partial_t g_{Si}(\mathbf{x},t) = -\sum_\alpha \int dS^\alpha \tilde{f}_i^\alpha \delta(\mathbf{x} - \mathbf{x}^\alpha - \mathbf{r}^\alpha). \tag{13}$$

Therefore, the equation for the time rate of change of the total momentum density $g_i(\mathbf{x},t) = g_{Ai}(\mathbf{x},t) + g_{Si}(\mathbf{x},t)$ is

$$\begin{aligned}\partial_t g_i(\mathbf{x},t) &= -\sum_\alpha \int dS^\alpha \tilde{f}_i^\alpha \delta(\mathbf{x} - \mathbf{x}^\alpha - \mathbf{r}^\alpha)\\ &\quad + \sum_\alpha \left(f_i^\alpha + \frac{1}{2}\epsilon_{ijk}\partial_j \tau_k^\alpha\right)\delta(\mathbf{x} - \mathbf{x}^\alpha)\\ &= \frac{1}{2}\partial_j \sum_\alpha \int dS^\alpha(\tilde{f}_i^\alpha r_j^\alpha + \tilde{f}_j^\alpha r_i^\alpha)\delta(\mathbf{x} - \mathbf{x}^\alpha) + \cdots ,\end{aligned} \tag{14}$$

where we have Taylor expanded the delta function with respect to $\mathbf{r}^\alpha$ in the first line and retained only the first nontrivial term [51]. Therefore, the stress tensor arising from the active particles has a force-dipole contribution of the form $\sigma_{ij}^A \equiv \Sigma_\alpha d_{ij}^\alpha \delta(\mathbf{x} - \mathbf{x}^\alpha)$, with

$$d_{ij}^\alpha \equiv \frac{1}{2}\int dS^\alpha(\tilde{f}_i^\alpha r_j^\alpha + \tilde{f}_j^\alpha r_i^\alpha), \tag{15}$$

a symmetric force dipole generated by the active forces.

The properties of the forces $\tilde{f}_i^\alpha$ are best discussed in the body frame of the active particles. These forces will have a nonvanishing average component along specific directions locked to the body. For example, the force might act only along the three-direction in the body along the unit vector $\boldsymbol{\nu}_3^\alpha$. If the body has a center of inversion, the force densities $\tilde{f}_i^\alpha(\tilde{u})$ at point $\tilde{u}$ and $\tilde{f}_i^\alpha(\tilde{u}_I)$ at the inversion point $\tilde{u}_I$ can be decomposed into odd and even components and only the odd component contributes to $d_{ij}^\alpha$. The forces, in general, also have stochastic components $\delta\tilde{f}_i^\alpha$ that will be sources of noise in the final continuum equations for the active medium. The nature of noise and its spectrum will depend on the specifics of the active particle motion. In particular, the tumbling and running behavior of wild-type bacteria can be expected to have a different noise spectrum from that of the tumblers. For the moment, we will ignore the stochastic parts of the active forces and focus on the part with fixed value in the body frame, which we will continue to denote simply as $\tilde{f}_i^\alpha$. In Appendix B, we will derive the contribution to the continuum equation noise for a particular model for stochastic active forces.

We model the active particles as rigid biaxial rods with orthonormal sets of body axes $\nu_{1,i}^\alpha$, $\nu_{2,i}^\alpha$, and $\nu_{3,i}^\alpha$ locked to the particle $\alpha$, where we take $\nu_{3,i}^\alpha$ to be along the longest axis of the particle and $\nu_{1,i}^\alpha$ to be along the shortest (see Fig. 1). We consider two cases.

Case (1): Wild type. The active force points on average along the long or "three" axis. In this case, we can set $d_{ij}^\alpha = \tilde{W}\nu_{3,i}^\alpha \nu_{3,j}^\alpha$, where $\tilde{W}$ has units of energy (force times distance) and we obtain the microscopic contribution

$$\sigma_{ij}^A(\mathbf{x},t) = \tilde{W}\sum_\alpha \nu_{3,i}^\alpha \nu_{3,j}^\alpha \delta(\mathbf{x} - \mathbf{x}^\alpha) \tag{16}$$

to the active stress, which on course-graining can be expressed in the incompressible limit, when $\rho(\mathbf{x}) = \rho$ is a constant, as

$$\sigma^A_{ij}(\mathbf{x},t) = Wc(\mathbf{x},t)Q_{ij}(\mathbf{x},t) + \frac{1}{3}\delta_{ij}Wc(\mathbf{x},t), \tag{17}$$

where $W \equiv \widetilde{W}\rho/m_A$, $m_A$ is the mass of an active particle, $c(\mathbf{x},t)=\rho_A(\mathbf{x})/\rho$ is its concentration field, and

$$Q_{ij}(\mathbf{x},t) \equiv \frac{1}{n_A(\mathbf{x},t)}\sum_\alpha \left(\nu^\alpha_{3,i}\nu^\alpha_{3,j} - \frac{1}{3}\delta_{ij}\right)\delta[\mathbf{x}-\mathbf{x}^\alpha(t)] \tag{18}$$

is the standard nematic order parameter [49], where $n_A(\mathbf{x},t) = \rho_A(\mathbf{x})/m_A$ is the number density of the active particles. The second term in Eq. (17), while contributing to the pressure, does not play a role in an incompressible medium. Thus, the stress tensor arising from active forces of the bacteria is indeed proportional to $Q_{ij}$, reflecting the symmetric force-dipole density.

Case (2): Tumblers. The active particles produce a torque, which is generated by a force in the $\boldsymbol{\nu}^\alpha_1$ direction at one end of the long axis and a force of equal magnitude in the $-\boldsymbol{\nu}^\alpha_1$ direction at the opposite end of the long axis. This leads to $d^\alpha_{ij}=\widetilde{W}(\nu^\alpha_{1,i}\nu^\alpha_{3,j}+\nu^\alpha_{1,j}\nu^\alpha_{3,i})$ and to a coarse-grained active stress

$$\sigma^A_{ij}(\mathbf{x},t) = Wc(\mathbf{x},t)B_{ij}(\mathbf{x},t), \tag{19}$$

where

$$B_{ij} \equiv \frac{1}{n_A(\mathbf{x},t)}\sum_\alpha (\nu^\alpha_{1,i}\nu^\alpha_{3,j} + \nu^\alpha_{1,j}\nu^\alpha_{3,i})\delta[\mathbf{x}-\mathbf{x}^\alpha(t)] \tag{20}$$

is the "biaxial" nematic order parameter. Thus, the active stress tensor of the tumblers is proportional to a different order parameter than that of wild-type bacteria. This fact is crucial to the explanation to the different microrheology of the two systems because the decay time and the spatial correlation length are much larger for $Q_{ij}$, which has a tendency to order with increasing rod concentration, than for $B_{ij}$, which does not.

We now include interactions that are present when active forces are turned off. To be specific, we add a frictional force describing the dissipative slowing down of the motion of particles $A$ relative to solvent particles $S$ if their velocities are not equal. The equations for $\mathbf{g}_A$ and $\mathbf{g}_S$ are, respectively,

$$\partial_t g_{Ai} = -\partial_j\pi^A_{ij} - \Gamma w_i + \sum\nolimits_\alpha \left(f^\alpha_i + \frac{1}{2}\epsilon_{ijk}\partial_j\tau^\alpha_k\right)\delta(\mathbf{x}-\mathbf{x}^\alpha),$$

$$\partial_t g_{Si} = -\partial_j\pi^S_{ij} + \Gamma w_i - \sum_\alpha \int dS^\alpha \tilde{f}^\alpha_i\,\delta(\mathbf{x}-\mathbf{x}^\alpha-\mathbf{r}^\alpha),$$

where $\pi^A_{ij}$ and $\pi^S_{ij}$ are the (passive) currents for the momentum densities of the active particles and solvent molecules, respectively, and $\Gamma$ is a friction coefficient. Adding the equations for $\mathbf{g}_A$ and $\mathbf{g}_S$ yields the equation for the total momentum density for wild-type bacteria

$$\partial_t g_i = -\partial_j\pi_{ij} + W\partial_j c(\mathbf{x},t)Q_{ij}(\mathbf{x},t), \tag{21}$$

where $\pi_{ij}=\pi^A_{ij}+\pi^S_{ij}$ is the total passive momentum current of Eq. (6) and the active stress (assuming wild-types active particles) is $\sigma^A_{ij}=Wc(\mathbf{x},t)Q_{ij}(\mathbf{x},t)$. For tumblers, $Q_{ij}(\mathbf{x})$ is replaced by $B_{ij}(\mathbf{x})$ in this expression. The equation for the difference of the two momentum densities is

$$\partial_t(g_{Ai}-g_{Si}) = -\partial_j(\pi^A_{ij}-\pi^S_{ij}) - 2\Gamma w_i + 2\mathcal{F}_i(\mathbf{x}) - W\partial_j c(\mathbf{x})Q_{ij}(\mathbf{x}), \tag{22}$$

where $\mathcal{F}_i(\mathbf{x},t) \equiv \Sigma_\alpha f^\alpha_i\delta(\mathbf{x}-\mathbf{x}^\alpha)$ is the coarse-grained average force density. Thus, in the low-frequency limit, we can set the left-hand side of Eq. (22) to zero and solve for the velocity difference $\mathbf{w}$ as

$$w_i = -\frac{1}{2\Gamma}\partial_j(\pi^A_{ij}-\pi^S_{ij}) + \frac{1}{\Gamma}\mathcal{F}_i(\mathbf{x}) - \frac{W}{2\Gamma}\partial_j c(\mathbf{x})Q_{ij}(\mathbf{x}).$$

In the isotropic phase, we expect that the average active force $\mathcal{F}_i(\mathbf{x})$ should be zero and this yields

$$J_i = -\frac{\rho_A\rho_S}{2\rho\Gamma}\partial_j(\pi^A_{ij}-\pi^S_{ij}) - \frac{\rho_A\rho_S}{2\rho\Gamma}W\partial_j cQ_{ij}, \tag{23}$$

where we have made used of Eq. (5). The first term in Eq. (23) gives the passive contribution, which must be of the form $\mathbf{J}^p=-\rho D\nabla c$ [52], where $D$ is the diffusion coefficient of the active particles when the active force is turned off. The second term is the active contribution to the mass current. It is proportional to $Q_{ij}$ as expected. Its dependence on the densities is slightly different from what a simple generalization of mass-flow term in Ref. [31] would give: it has the extra factor of $\rho_A\rho_S/\rho$ in front of $\partial_j cQ_{ij}$. In the limit of low volume fraction of the active particles, the prefactor is not simply a constant.

### B. Final equations

Now, we collect all the results from the previous section and add noise to describe fluctuations of microscopic origin. We assume that the effective medium is incompressible, expressed by the condition $\nabla\cdot\mathbf{v}=0$. The final set of equations reads

$$\partial_t g_i = -\partial_j\left(\frac{g_i g_j}{\rho}\right) - \partial_i p + \eta\nabla^2 v_i + \partial_j\sigma^0_{ij} + \partial_j\left(\lambda_{klij}\frac{\delta\mathcal{F}}{\delta Q_{kl}}\right) + W\partial_j cQ_{ij} + \partial_j\sigma^T_{ij}, \tag{24}$$

$$\partial_t Q_{ij} = -\frac{\mathcal{L}_{ijkl}}{2\gamma}\frac{\delta\mathcal{F}}{\delta Q_{kl}} - \mathbf{v}\cdot\nabla Q_{ij} + \lambda_{ijkl}\partial_l v_k + s_{ij}, \tag{25}$$

$$\partial_t c = -\mathbf{v}\cdot\nabla c + D\nabla^2 c + \alpha_2\partial_i c(1-c)\partial_j cQ_{ij} + \nabla\cdot\delta\mathbf{J}, \tag{26}$$

where $\alpha_2=W/(2\Gamma)$ and $\sigma^T_{ij}$, $s_{ij}$, and $\delta J_i$ are random noise sources whose thermal components have the following correlations:

$$\langle\sigma^T_{ij}(\mathbf{q},\omega)\sigma^T_{kl}(\mathbf{q}',\omega')\rangle = 2\eta k_B T\mathcal{L}_{ijkl}\delta(\mathbf{q}+\mathbf{q}')2\pi\delta(\omega+\omega'), \tag{27}$$

$$\langle s_{ij}(\mathbf{q},\omega)s_{kl}(\mathbf{q}',\omega')\rangle = \frac{k_B T}{\gamma}\mathcal{L}_{ijkl}\delta(\mathbf{q}+\mathbf{q}')2\pi\delta(\omega+\omega'), \tag{28}$$

$$\langle \delta J_i(\mathbf{q},\omega)\,\delta J_j(\mathbf{q}',\omega')\rangle = 2c_0 D(m_A/\rho)\,\delta_{ij}\,\delta(\mathbf{q}+\mathbf{q}')2\pi\delta(\omega+\omega'), \tag{29}$$

where $k_B$ is the Boltzmann constant and $T$ is the temperature. Note that we have assumed that these noises are the same as those in the equilibrium system. In Appendix B, we consider the renormalization of the above noise sources from the model for active stochastic forces. We find that their dominant contributions have exactly the same forms as those in Eqs. (27)–(29). Thus, their effect is simply to replace $T$ by an effective temperature depending on magnitude of fluctuations in the random active forces. We will simply use the symbol $T$ in what follows to signify the effective temperature. Our estimate based on a simple model of running and tumbling suggests the effective temperature is of order 1.25 times the thermal temperature. The active stochastic forces also contribute other multiplicative terms that depend on the local value of the density and orientational fields to the noise correlators. We will ignore these terms in our current analysis. Thus, the noise sources in active media violate FDT as expected. As we shall see in Sec. III, active stresses also violate FDT by breaking the Onsager reciprocity symmetry of transport coefficients. This effect appears to have greater impact in the present problem than the form of the noise terms.

## III. LINEARIZED THEORY FOR AN ISOTROPIC ACTIVE BACTERIAL BATH

In this section, we present an analysis of the linear theory for bacterial bath. In particular, we discuss all the correlation functions and highlight those behaviors that are different from those of an equilibrium liquid crystal in the isotropic phase. We assume the order parameter to be given by the uniaxial $Q_{ij}$, since we expect that its effects to be more important than those arising from the biaxial order parameter $B_{ij}$.

In the isotropic phase, we expect $\delta\mathcal{F}/\delta Q_{ij} = aQ_{ij} - L\nabla^2 Q_{ij}$ in the one-constant approximation and $\lambda_{ijkl} = \lambda\mathcal{L}_{ijkl}$ to the zeroth order in $Q_{ij}$. The parameter $\lambda$ characterizes the extent to which a velocity gradient exerts a torque on the order parameter. Therefore, the equations of motion for the bacterial bath in the isotropic phase may be written, after further linearizing Eqs. (24)–(26), as

$$\rho\partial_t v_i = \eta\nabla^2 v_i - \partial_i p + \lambda\partial_j(a - L\nabla^2)Q_{ij} + Wc_0\partial_j Q_{ij} + \partial_j\sigma^T_{ij}, \tag{30}$$

$$\partial_t Q_{ij} = -\frac{1}{\tau}(1-\xi^2\nabla^2)Q_{ij} + \lambda\mathcal{L}_{ijkl}\partial_l v_k + s_{ij}, \tag{31}$$

$$\partial_t\delta c = D\nabla^2\delta c + \alpha_2 c_0^2(1-c_0)\partial_i\partial_j Q_{ij} + \nabla\cdot\delta\mathbf{J}, \tag{32}$$

where $c_0$ is the mean concentration (or mass fraction) of the bacteria, $\tau \equiv \gamma/a$ is the relaxation time, and $\xi \equiv \sqrt{L/a}$ is the coherence length. $\tau$ and $\xi$, respectively, set the time and length for the interpretation of the microrheology of active baths to be detailed in Sec. IV. From the above equations, we can identify differences between the active theory and the equilibrium theory: the presence of the active stress term introduced in Refs. [31,32] $\sigma^A_{ij} = Wc_0 Q_{ij}$ and the active mass current term $\alpha_2 c_0(1-c_0)\partial_j Q_{ij}$. As argued by the above references, these terms are allowed by symmetry and absent in the equilibrium theory. Indeed, we see that these terms break the Onsager reciprocal theorem and this violation underlies all the nonequilibrium features in the linear theory of the model.

### A. Velocity correlations

Fourier transforming in space and time and imposing the incompressibility condition, the momentum equation can be written as

$$\begin{aligned} G_v^{-1}(\mathbf{q},\omega)v_i = {}& -2\lambda^2(a_R + Lq^2)G_Q(\mathbf{q},\omega)q^2 v_i \\ & + \imath\mathcal{M}_{ikl}[2\lambda(a_R+Lq^2)G_Q(\mathbf{q},\omega)s_{kl} + \sigma^T_{kl}], \end{aligned} \tag{33}$$

where $a_R = a + Wc_0/(2\lambda)$, $\mathcal{M}_{ikl} \equiv (\delta_{ik} - q_i q_k/q^2)q_l$, and $G_v(\mathbf{q},\omega) = 1/(-\imath\omega\rho + \eta q^2)$, and $G_Q(\mathbf{q},\omega) = \tau/(-\imath\omega\tau + 1 + \xi^2 q^2)$ are the bare propagators for the velocity and the alignment tensor, respectively. Thus, the propagator for the velocity field is renormalized

$$G_{Rv}^{-1}(\mathbf{q},\omega) = G_v^{-1}(\mathbf{q},\omega) + 2\lambda^2 q^2(a_R + Lq^2)G_Q(\mathbf{q},\omega). \tag{34}$$

In particular, we identify a renormalized viscosity

$$\eta_R(\mathbf{q},\omega) = \eta + \frac{2\lambda^2\tau(a_R + Lq^2)}{-\imath\omega\tau + (1+\xi^2 q^2)}. \tag{35}$$

Thus, the effective response of the bacteria bath becomes viscoelastic, as is the case in an equilibrium nematics in the isotropic phase [53]. However, unlike an equilibrium nematics in the limit when $a \to 0$, i.e., when the nematics starts to develop order, Eq. (35) implies a finite shear modulus $G^*(\omega) = -\imath\omega\eta_R(\mathbf{q}=0,\omega) = \lambda Wc_0$. This effect has been pointed out in Ref. [32].

From Eq. (33), we see that the random stress for the fluid is also renormalized $\sigma^R_{ij}(\mathbf{q},\omega) \equiv \sigma^T_{ij}(\mathbf{q},\omega) + 2\lambda(a_R + Lq^2)G_Q(\mathbf{q},\omega)s_{ij}$, whose correlation can be readily obtained $\langle\sigma^R_{ij}(\mathbf{q},\omega)\sigma^R_{kl}(\mathbf{q}',\omega')\rangle = 2\pi\delta(\mathbf{q}+\mathbf{q}')\,\delta(\omega+\omega')\Delta_R(q,\omega)\mathcal{L}_{ijkl}$, where

$$\Delta_R(q,\omega) \equiv 2\eta k_B T + \frac{4\lambda^2 k_B T}{\gamma}\frac{(a_R + Lq^2)^2}{\omega^2 + (1+\xi^2 q^2)^2/\tau^2}. \tag{36}$$

Comparing this to the real part of Eq. (35), we see that FDT is broken for a bacterial bath, signifying that the system is far from equilibrium. The origin of the violation of FDT comes from the breaking of the Onsager symmetry introduced by the active forces. Indeed, it is easy to show that the FDT is restored when $W=0$. We note that the violation of FDT in bacterial bath has been demonstrated experimentally in Ref. [21].

It is straightforward to obtain the velocity-velocity correlation function, which can be written as $\langle v_i(\mathbf{q},\omega)v_j(\mathbf{q}',\omega')\rangle = 2\pi\delta(\mathbf{q}+\mathbf{q}')\,\delta(\omega+\omega')S_{vv}(q,\omega)(\delta_{ij} - q_i q_j/q^2)$ with

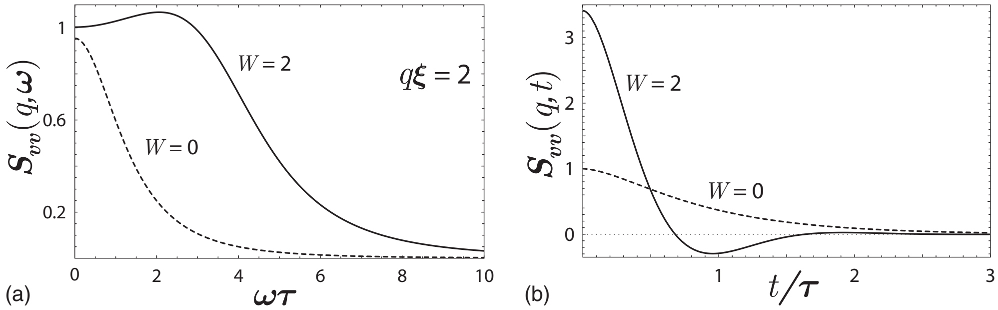

FIG. 2. Plots of the velocity-velocity correlation functions in frequency space (a) $S_{vv}(q,\omega)$ (in units of $k_BT\tau/\rho$) and in time (b) $S_{vv}(q,t)$ (in units of $k_BT/\rho$) with no active force $W=0$ (dashed lines) and with active force $W'=2$ (solid lines) with wave numbers $q\xi=2$, $a'=0.237$, and $\nu'=0.025$.

$$S_{vv}(q,\omega) = \frac{2q^2k_BT \,\mathrm{Re}\, \eta_R(q,\omega)}{|-\imath\omega\rho + \eta_R q^2|^2} + \frac{(2\lambda Wc_0k_BT/\gamma)(a_R + Lq^2)q^2}{|-\imath\omega\rho + \eta_R q^2|^2[\omega^2 + \tau^{-2}(1 + \xi^2q^2)^2]}. \tag{37}$$

The first term in Eq. (37) is the "equilibrium" correlation function but with the activity renormalized viscosity of Eq. (35), whereas the second term is the nonequilibrium contribution arising from the activity of the bacteria. We note that Eq. (37) cannot be written so that a proper effective temperature can be defined. The time-dependent correlation function of the velocity field, $\langle v_i(\mathbf{q},t)v_j(-\mathbf{q},0)\rangle \equiv (\delta_{ij}-q_iq_j/q^2)S_{vv}(\mathbf{q},t)$, follows from $S_{vv}(\mathbf{q},t) = \int d\omega S_{vv}(\mathbf{q},\omega)e^{-\imath\omega t}/(2\pi)$, which can be explicitly integrated to give

$$S_{vv}(\mathbf{q},t) = (k_BT/\rho)[\tilde{S}^P_{vv}(\mathbf{q},t) + \tilde{S}^A_{vv}(\mathbf{q},t)], \tag{38}$$

where

$$\tilde{S}^P_{vv}(\mathbf{q},t) = \frac{(\omega_+ - \nu q^2)e^{-\omega_- t} - (\omega_- - \nu q^2)e^{-\omega_+ t}}{\omega_+ - \omega_-}, \tag{39}$$

$$\tilde{S}^A_{vv}(\mathbf{q},t) = \left(\frac{\lambda Wc_0\tau^2}{\rho}\right)\frac{q^2\left(1 + \frac{Wc_0}{2\lambda a} + \xi^2q^2\right)}{(\omega_t\tau)^2(\omega_c\tau)(\omega_+ - \omega_-)} \times(\omega_+e^{-\omega_- t} - \omega_-e^{-\omega_+ t}), \tag{40}$$

where $\nu \equiv \eta/\rho$ is the kinematic viscosity, $\omega_c(\mathbf{q}) \equiv \nu q^2 + \tau^{-1}(1+\xi^2q^2)$,

$$\omega_t^2(\mathbf{q}) \equiv q^2\left[\frac{\lambda Wc_0}{\rho} + \frac{1}{\tau}(1 + \xi^2q^2)\left(\nu + \frac{2\lambda^2\tau a}{\rho}\right)\right], \tag{41}$$

and $\omega_\pm(\mathbf{q}) \equiv \frac{1}{2}(\omega_c \pm \sqrt{\omega_c^2-4\omega_t^2})$ are the two modes of the system.

Let us first analyze the spatial correlation of the velocity field at equal time. Setting $t=0$ in $\tilde{S}^P_{vv}(\mathbf{q},t)$ and $\tilde{S}^A_{vv}(\mathbf{q},t)$ and Fourier transforming back to real space, we find

$$\langle \mathbf{v}(\mathbf{r},t)\cdot\mathbf{v}(0,t)\rangle = \frac{2k_BT}{\rho}\delta(\mathbf{r}) + \frac{2k_BT}{\rho}\left(\frac{W'}{4\pi\xi^2 r}\right) \times\left[\left(\frac{W'}{a'} + \frac{\nu'}{1+\nu'}\right)e^{-r/\xi_+} - \frac{W'}{a'}\left(\frac{\nu'}{\nu'+a'}\right)e^{-r/\xi_a}\right],$$

where $\xi_+^2 \equiv \xi^2(1+\nu')$, $\xi_a^2 \equiv \xi^2(\nu'+a')/(\nu'+a'+W')$, and we have defined dimensionless quantities $W' \equiv \lambda Wc_0\tau^2/(\rho\xi^2)$, $a' \equiv 2\lambda^2\tau^2 a/(\rho\xi^2)$, and $\nu' \equiv \nu\tau/\xi^2$. Thus, in contrast to an equilibrium system, the velocity field for the bacterial bath is correlated over a region whose size is of the order of $\xi$.

In Fig. 2, we have plotted the velocity fluctuation spectrum, which illustrates interesting physics that is specific to an active system. For equilibrium nematics in the isotropic phase [54], $W=0$, we expect that on the time scales of seconds and length scales of microns, $\omega_\pm(\mathbf{q})$ are real and $S_{vv}(\mathbf{q},\omega)$ has a peak centered at zero frequency and $S_{vv}(\mathbf{q},t)$ decays exponentially in time (see Fig. 2). In contrast, for an active system, there is a peak in $S_{vv}(\mathbf{q},\omega)$ at nonzero frequency when $W$ is sufficiently large as illustrated in Fig. 2(a). Indeed, $S_{vv}(\mathbf{q},t)$ becomes oscillatory in time [see Fig. 2(b)]. This signals the onset of shear waves in the system [55] and it occurs roughly when $W' > W'_c \equiv 1-a' + \sqrt{1+\nu'-2a'}$. The existence of shear waves is intimately related to the renormalization of the viscosity from the active stress and it might be related to the spatially correlated structures, such as vortices and jets, often observed in these systems. Indeed, available data on velocity correlation show oscillatory behavior in time, consistent with above [7]. Note that in order to observe the effects of shear wave, the flow-alignment coupling parameter, $\lambda$, should not be too small. However, even for systems in which $\lambda=0$, the activity would enhance the amplitude of the long-time tails $\langle \mathbf{v}(\mathbf{r},t)\cdot\mathbf{v}(\mathbf{r},0)\rangle \sim W^2t^{-3/2}$ as $t\to\infty$, as can be calculated from Eq. (40). This enhancement of the long-time tail in the velocity field has also been pointed out in Ref. [32].

### B. Correlation functions for the alignment tensor and the concentration of the bacteria

Next, we explore the dynamics of the alignment tensor. Because of the couplings to the velocity field, the five originally identical modes for the components of the alignment tensor split into three identical longitudinal and two identical transverse components and the correlation function for the alignment tensor can be written as $\langle Q_{ij}(\mathbf{q},\omega)Q_{kl}(\mathbf{q}',\omega')\rangle = (2\pi)^4\delta(\mathbf{q}+\mathbf{q}')\delta(\omega+\omega')[S^L_{QQ}(q,\omega)(\mathcal{L}_{ijkl}-\mathcal{P}_{ijkl}) + S^T_{QQ}(q,\omega)\mathcal{P}_{ijkl}]$, where

$$\mathcal{P}_{ijkl} = \hat{q}_i\hat{q}_l\delta_{kj} + \hat{q}_j\hat{q}_l\delta_{ki} - 2\hat{q}_i\hat{q}_j\hat{q}_k\hat{q}_l + (k \leftrightarrow l), \tag{42}$$

with $\hat{q}_i \equiv q_i/q$ and

$$S^L_{QQ}(q,\omega) \equiv \frac{(k_BT/\gamma)}{\omega^2 + \tau^{-2}(1+q^2\xi^2)^2}, \tag{43}$$

$$S^T_{QQ}(q,\omega) \equiv \frac{k_BT \,\mathrm{Re}\, \gamma_R^{-1}}{|-\imath\omega + \gamma_R^{-1}[a + L_R(\mathbf{q},\omega)q^2]|^2}, \tag{44}$$

where $\gamma_R^{-1}(\mathbf{q},\omega) = \gamma^{-1} + 2\lambda^2q^2/(-\imath\omega\rho + \eta q^2)$ is the renormalized dissipation coefficient for the alignment tensor. Equation (44) has a renormalized elastic constant for the active nematics given by

$$L_R(\mathbf{q},\omega) \equiv L + \frac{\lambda W c_0\gamma}{-\imath\omega\rho + (\eta + 2\lambda^2\gamma)q^2}. \tag{45}$$

It is interesting to note that only the transverse part of the nematic fluctuations is renormalized as a result of the couplings to the flow. Note also that unlike velocity field correlations, Eqs. (43) and (44) do respect FDT.

Finally, the concentration fluctuation is coupled to $Q_{ij}$ via the novel activity-driven mass-flow term in Eq. (32). Therefore, we expect that the concentration fluctuations are greatly enhanced. Note that the concentrations only coupled to the longitudinal part of the $Q_{ij}$. The concentration correlation function can be written as $\langle\delta c(\mathbf{q},\omega)\delta c(\mathbf{q}',\omega')\rangle = 2\pi\delta(\mathbf{q}+\mathbf{q}')\delta(\omega+\omega')S_{cc}(\mathbf{q},\omega)$, with

$$S_{cc}(\mathbf{q},\omega) = \frac{2c_0Dq^2}{\omega^2 + D^2q^4} + \frac{4\alpha_2^2c_0^4(1-c_0)^2q^4S^L_{QQ}(\mathbf{q},\omega)}{3(\omega^2 + D^2q^4)}. \tag{46}$$

Note that the second term in Eq. (46) is proportional to $c_0^4$, which signifies that for high concentration of bacteria, the concentration fluctuations become significant. This is because this term in the static correlations

$$\langle\delta c(\mathbf{q})\delta c(-\mathbf{q})\rangle = c_0 + \frac{2(k_BT/\gamma)\tau^2c_0^4(1-c_0)^2\alpha_2^2q^2}{3D(1+q^2\xi^2)[1+q^2(\xi^2+D\tau)]} \tag{47}$$

goes like $1/q^2$ when the correlation length $\xi$ diverges. These giant fluctuations in the ordered phase were pointed out in Ref. [31].

## IV. MICRORHEOLOGY OF AN ACTIVE BACTERIAL BATH: THE ROLE OF NONLINEARITY

Microrheology [56–59] has recently emerged as an important experimental tool for probing the mechanical properties of *equilibrium* soft materials, requiring access to only miniscule sample volumes while probing a broader range of frequencies than conventional rheometry. In a typical microrheology experiment, the complex shear modulus of a material is extracted from the microscopic motions of micron-sized tracer particles dispersed in it. There are two common techniques. In *active microrheology*, the shear moduli of soft materials are inferred from the displacements of tracer particles produced by external forces of either optical or magnetic origin. In *passive microrheology*, the displacement correlation function is instead measured by tracking the *thermal* motion of the tracers. In equilibrium systems, the FDT [49] assures us that both techniques yield the same information. Recently, the conventional one-point passive microrheology, i.e., tracking of *single* isolated particles, was shown to be inadequate for extracting bulk properties of inhomogeneous materials [22]. This limitation has been overcome by a new method, two-point microrheology, in which the cross-correlated *thermal* motion of pairs of embedded tracer particles is used to determine the complex shear modulus of the surrounding medium [22,60]. Its success has been demonstrated in a variety of model systems, such as DNA solutions [61] and F-actin solutions [22] in thermal equilibrium. The theoretical justification of one-point and two-point microrheology in a thermal setting is given by Refs. [60,62,63].

To extend these new experimental techniques to active biological systems such as living cells or bacterial bath, we must first address two fundamental questions. (i) Given that active systems are nonequilibrium systems in which the FDT does not apply, what useful information can one extract from passive microrheological data? (ii) Given the high degree of heterogeneity of biological systems such as the cell cytoplasm, does two-point microrheology apply equally well to active inhomogeneous media? In Ref. [14], we have successfully generalized the equilibrium framework of microrheology to nonequilibrium situations to justify passive microrheology for active systems (for a brief exposition, see Appendix A). Our main result is that active elements give rise to additional stress fluctuations in the medium, with a power spectrum $\Delta(\omega)$ that can actually be extracted using passive two-point microrheology via [14]

$$D_{rr}(R,\omega) = \frac{\Delta(\omega)}{6\pi R|G^*(\omega)|^2}, \tag{48}$$

where $D_{rr}(R,\omega)$ is the cross correlation of pairs of tracer particles a distance $R$ apart and $G^*(\omega)$ is the shear modulus of the material. Note that $G^*(\omega)$ must be measured by an independent response measurement. It is important to emphasize that a hydrodynamic theory is related to $\Delta(\omega)$, which equals to the stress fluctuation spectrum of the medium in the long-wavelength limit. Note that the latter limit is valid if $R$ is greater than the typical length scale of the medium, i.e., the coherence length. This framework was successfully applied to living cells, providing important insight into the intracellular stress fluctuations arising from motor activities [14,64].

In Ref. [21], this framework was used to interpret microrheological experiments on a bacterial bath. First, from the response measurements, the viscosity for a bacterial bath at low volume fraction was found not to differ from that of pure water at the low volume fractions under study for both wild-type and tumbler baths. Using Eq. (48), the power spectrum thus extracted is Lorentzian for the tumblers and scales such as $\Delta(\omega)\sim\phi/\sqrt{\omega}$ for the wild type. The former observation implies that the flow-orientation coupling parameter λ is small ($\lambda\ll 1$) and, therefore, we can set $\lambda=0$ in Eqs. (30) and (31), so that there is no renormalization of the viscosity from activity even in the presence of the active stress. The role of the active stress then is to provide an additional source of stress fluctuations. From Eq. (36), we see that the power spectrum is Lorentzian $\Delta(\omega)=\Delta_T+W^2c_0^2\tau^2(k_BT/\gamma)/[1+(\omega\tau)^2]$, where $\Delta_T\equiv 2\eta k_BT$ is the "thermal" contribution. While it explains the data for tumblers, a linear theory cannot explain the $1/\sqrt{\omega}$ behavior for the wild types. What is missing? One of the key assumptions of the linearized theory is that we assumed $c(\mathbf{x},t)=c_0$ in the equations for $v_i$ and $Q_{ij}$, i.e., bacteria are homogeneously distributed. While this assumption seems reasonable for tumblers, since they do not move around much, it can hardly be justified at all for the wild type. Since the wild types are swimming around, it is conceivable that their density fluctuates significantly in space and time. Indeed, recent numerical work confirms the giant fluctuations in the nematic phase. Here, in the isotropic phase, we expect that the contribution is not negligible. This suggests that we have to include density fluctuations of the bacteria.

The full active stress $\sigma_{ij}^A(\mathbf{x},t)=Wc_0Q_{ij}(\mathbf{x},t)+W\delta c(\mathbf{x},t)Q_{ij}(\mathbf{x},t)$ has an average part $\langle\sigma_{ij}^A(\mathbf{x},t)\rangle=W\langle\delta c(\mathbf{x},t)Q_{ij}(\mathbf{x},t)\rangle$, which is zero in the isotropic phase. The Fourier transform of $\langle\delta\sigma_{ij}^A(\mathbf{x},t)\delta\sigma_{kl}^A(\mathbf{x}',t')\rangle$ has the form $\langle\delta\sigma_{ij}^A(\mathbf{q},\omega)\delta\sigma_{kl}^A(\mathbf{q}',\omega')\rangle=2\pi\Delta_A(q,\omega)\mathcal{L}_{ijkl}\delta(\mathbf{q}+\mathbf{q}')\delta(\omega+\omega')$, where

$$\begin{aligned}\Delta_A(\mathbf{q}=0,\omega)&=\frac{W^2c_0^2\tau^2(k_BT/\gamma)}{1+(\omega\tau)^2}\\&\quad+W^2\int\frac{d^3\mathbf{k}}{(2\pi)^3}\int\frac{d\omega'}{2\pi}S_{cc}(k,\omega')S_{QQ}(k,\omega-\omega')\\&\quad+\frac{W^2}{15}\int\frac{d^3\mathbf{k}}{(2\pi)^3}\int\frac{d\omega'}{2\pi}S_{cQ}(k,\omega')S_{cQ}^*(k,\omega-\omega')\end{aligned}\tag{49}$$

and $S_{cQ}(q,\omega)\equiv 2\alpha_2c_0^2(1-c_0)q^2S_{QQ}^L(q,\omega)/(-\imath\omega+Dq^2)$. Note that the last two terms arise specifically from density fluctuations of the bacteria. Using Eq. (46), we see that the second term in Eq. (49) has a term proportional $c_0$ and a term proportional to $c_0^4$. The third term in Eq. (49) is also proportional to $c_0^4$. Thus, we find that $\Delta(\omega)=\Delta_T+\Delta_A(\mathbf{q}=0,\omega)$, as measured by passive two-point microrheology can be written as

$$\Delta(\omega)=\Delta_T+\Delta_0\left[f_1(\omega\tau;b)+\frac{k_1}{1+(\omega\tau)^2}+k_2f_2(\omega\tau;b)\right],\tag{50}$$

where $\Delta_0\equiv\widetilde{W}^2\phi_0\tau^2k_BT/(4\pi v_B\gamma\xi^3)$, $k_1\equiv 4\pi\phi_0\xi^3/v_B$, $k_2\equiv 2\widetilde{W}^2\phi_0^3\tau k_BT/(3\gamma v_B^3\Gamma^2D^2)$, $v_B$ is the volume of a bacterium, $b\equiv D\tau/\xi^2$, and

$$f_1(x;b)\equiv\frac{1}{\pi\sqrt{1+b}}\int_1^\infty du\frac{u(u-1)^{1/2}}{(u+b)(x^2+u^2)},\tag{51}$$

$$\begin{aligned}f_2(x;b)\equiv&\frac{b}{\pi\sqrt{1+b}}\int_1^\infty du\frac{(u-1)^{3/2}}{(u+b)(x^2+u^2)}\\&\times\frac{1}{[(1-b)u+2b]}\left[1+\frac{2b(u-1)}{5(1+b)u}\right]\\&-\frac{2b^2}{\pi}\int_1^\infty du\frac{(u-1)^{5/2}}{u[(1+b)u-b](x^2+4u^2)}\\&\times\frac{1}{[(1-b)u+b]}\left[1-\frac{b(u-1)}{5u}\right].\end{aligned}\tag{52}$$

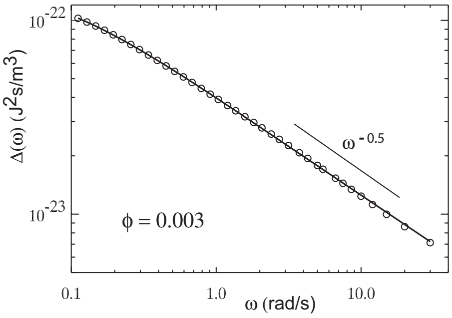

FIG. 3. The power spectrum of the stress fluctuations, $\Delta(\omega)$, as measured by two-point passive microrheology of a wild-type bacterial bath with a volume fraction of $\phi\sim 10^{-3}$. Solid line is the best fit of our theoretical model, Eq. (50), to data from Ref. [21]. The best-fit values are $b=0.1$, $k_1=0.29$, $k_2=8.9$, $\Delta_0=10^{-22}$ J$^2$ s/m$^3$, and $\tau=7.54$ s.

Note that each of these integrals can be done analytically, but their expressions are too complicated to reproduce here. However, it is straightforward to see that the power spectrum is dominated by $f_1$ which scales as $f_1(x)\sim 1/\sqrt{x}$ for $x\gg 1$ and this explains the $1/\sqrt{\omega}$ spectrum observed in experiments and, hence, superdiffusion exhibited by tracer particles in a bacterial bath.

We have fit Eq. (50) to the experimental data of Ref. [21] for the wild-type bacteria at volume fraction of $\phi=3\times 10^{-3}$, with excellent agreement (see Fig. 3). The best-fit values are $\tau\sim 7.51$ s, $\Delta_0=1.6\times 10^{-22}$ J$^2$ s/m$^3$, $k_1=0.29$, $k_2=8.9$, and $b=0.1$. The quality of the fit depends sensitively on the values of $\tau$ and $\Delta_0$, but not on $k_1$, $k_2$, and $b$ as long as they are not too big. Using the fact that $k_1=4\pi\phi_0\xi^3/v_B\sim 0.29$ and $v_B\approx 20$ μm$^3$, the effective volume of an *E. coli* bacterium, we find that $\xi\approx 10$ μm, which is consistent with experimental observation. Next, using $b=D\tau/\xi^2\sim 0.1$, we find $D\sim 1$ μm$^2$/s, consistent with that of a diffusion coefficient for a passive micron-sized passive particle [see Eq. (23) above]. Additionally, estimating that $\gamma\sim k_BT\tau/v_B$, we have $\Delta_0\approx\widetilde{W}^2\phi_0\tau/(4\pi\xi^3)$. Interpreting $\widetilde{W}$ as the energy scale for a typical bacterium to swim with a typical speed of $v\sim 20$ μm/s against the frictional force arising from the fluid for a typical distance of $d\sim v\tau$, we find $\widetilde{W}\sim 10^{-17}$ J. Therefore, we find $\Delta_0=\widetilde{W}^2\phi_0\tau/(4\pi\xi^3)\sim 10^{-22}$ J$^2$ s/m$^3$, which agrees with experiments. Finally, estimating that $\Gamma \sim \eta/\xi^2$, we find $k_2 \approx 2\tilde{W}^2\phi_0^3\tau^2/(3v_B^2 b^2\eta^2) \sim 10$, agreeing with the experiments. Given these agreements, we are convinced that our model captures the essential nonequilibrium fluctuating hydrodynamics of a bacterial bath.

## ACKNOWLEDGMENTS

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## APPENDIX A: MICRORHEOLOGY FOR ACTIVE SYSTEMS

In this appendix, we show, based on a phenomenological model, how two-point microrheology experiments in conjunction with response experiments extract information about the activity of active elements in the form of a power spectrum of stress fluctuations in active systems despite their heterogeneity. Microrheology relies on the generalized Langevin equation (GLE) [49] for the velocity $\mathbf{v}$ of a tracer particle

$$m\partial_t \mathbf{v}(t) = -\int_{-\infty}^{t} dt'\,\gamma(t-t')\mathbf{v}(t') + \mathbf{f}_E(t) + \mathbf{f}_R(t), \qquad \text{(A1)}$$

where $m$ is the mass of the tracer particle, $\mathbf{f}_E(t)$ is the external force, and $\mathbf{f}_R(t)$ is the random force arising from the medium. The friction function $\gamma(\tau)$ is related to the viscoelasticity of the embedding medium through boundary conditions at the surface of the tracer particle. If the medium is incompressible and isotropic, its mechanical response is characterized by a frequency-dependent complex shear modulus $\mu(\omega) \equiv -i\omega\eta(\omega) = \mu'(\omega) - i\mu''(\omega)$ [65], where $\eta(\omega) = \eta'(\omega) + i\eta''(\omega)$ is the complex shear viscosity. Thermodynamic stability requires $\mu''(\omega) = \eta'(\omega) \geq 0$. In such a medium, Stokes law states that $\gamma(\omega) = 6\pi a\mu(\omega)/(-i\omega)$ [57], where $a$ is the radius of the particle. In the active scheme, $\mathbf{f}_R(t)$ can be set to zero; Fourier transforming the GLE equation, we obtain the displacement $\mathbf{r}(\omega) = \chi(\omega)\mathbf{f}_E(\omega)$, where $\chi(\omega) = -1/(i\omega[-im\omega + \gamma(\omega)])$ is the response function.

Passive microrheology measures quantities related to the correlation function $C_{r_ir_j}(t,0) = \langle r_i(t) r_j(0)\rangle$, whose Fourier transform can be calculated with the aid of Eq. (A1) in terms of the random noise spectrum $\mathcal{I}_R(\omega)$,

$$C_{r_ir_j}(\omega) = \delta_{ij}\frac{\mathcal{I}_R(\omega)}{\omega^2|-im\omega + \gamma(\omega)|^2}. \qquad \text{(A2)}$$

In thermal equilibrium, this correlation function is related through the FDT to the response function $\chi(\omega)$,

$$C_{r_ir_j}(\omega) = \delta_{ij}\frac{2k_BT}{\omega}\,\text{Im}\,\chi(\omega) = \frac{2k_BT\gamma'(\omega)\delta_{ij}}{\omega^2|-im\omega + \gamma(\omega)|^2} \qquad \text{(A3)}$$

$$\approx \delta_{ij}\frac{k_BT}{3\pi a}\frac{\mu''(\omega)}{\omega|\mu(\omega)|^2}. \qquad \text{(A4)}$$

Comparing Eqs. (A2) and (A3), we conclude that $\mathcal{I}_R(\omega) = 2k_BT\gamma'(\omega)$. The final form in Eq. (A4) is valid in the window $\omega_a < \omega < \omega_b$, with the lower frequency $\omega_a \sim 10^{-2}$ Hz set by the compressional mode of the network and upper frequency $\omega_b \sim 10^5$ Hz by inertial effects [63].

In an active system, active elements not only modify the viscoelastic response of the medium, they also give rise to random, nonthermal stress fluctuations that cause tracer particles to be subjected to random nonthermal forces. In what follows, we relate one- and two-particle correlation functions measured in passive microrheology experiments to stress fluctuations and response to external forces. We start by postulating that an active system at large length scale effectively is an incompressible, viscoelastic medium characterized by a displacement field $\mathbf{u}(\mathbf{x},t)$, whose equation of motion is given by

$$\rho\frac{\partial^2 u_i}{\partial t^2} = \partial_j\sigma_{ij}(\mathbf{x},t) + f_i(\mathbf{x},t), \qquad \text{(A5)}$$

where $\rho$ is the coarse-grained mass density and $f_i(\mathbf{x},t)$ is the nonthermal random force density arising from the active particles, such as motors or bacteria, and $\sigma_{ij}(\mathbf{x},t)$ is the stress tensor. Within linear-response theory, the stress $\sigma_{ij}(\mathbf{x},t)$ is related to the strain by $\sigma_{ij}(\mathbf{x},\omega) = 2\mu(\omega)u_{ij}(\mathbf{x},\omega)$, where $u_{ij} = (\partial_j u_i + \partial_i u_j)/2$ is the strain tensor and $\mu(\omega)$ the frequency-dependent shear modulus describing the elastic response of the cytoplasm. To construct the random force $f_i(\mathbf{x},t)$, we note that there should be no net external force in a stationary cell and, therefore, it must take the form $f_i(\mathbf{x},t) = \partial_j s_{ij}(\mathbf{x},t)$, where $s_{ij}(\mathbf{x},t)$ is a random stress tensor whose average is zero. If we assume that stress fluctuations are local in space, then the stress correlation function is given by

$$\langle s_{ij}(\mathbf{x},\omega) s_{kl}(\mathbf{x}',\omega')\rangle = 2\pi\Delta(\omega)\delta(\omega+\omega')\delta^3(\mathbf{x}-\mathbf{x}') \times\left[\delta_{ik}\delta_{jl} + \delta_{il}\delta_{jk} - \frac{2}{3}\delta_{ij}\delta_{kl}\right], \qquad \text{(A6)}$$

where $\Delta(\omega)$ is the power spectrum of the stress fluctuations whose microscopic origin is the activity of the motors. The form of Eq. (A6) is not surprising. Stress fluctuations in thermal equilibrium systems [66] have an identical form but with $\Delta(\omega)$ replaced by $2k_BT\mu''(\omega)/\omega$.

### 1. One-point microrheology

To relate our phenomenological model to microrheology experiments, we put a tracer particle of radius $a$ in this random medium and ask: what forces are exerted on this particle by random stress fluctuations? Let us assume that the tracer particle situated at the origin undergoes a displacement $\varepsilon_i(t)$. First, we decompose $\mathbf{u}(\mathbf{x},t)$ into an average part and a fluctuating part $\mathbf{u}(\mathbf{x},t) = \bar{\mathbf{u}}(\mathbf{x},t) + \tilde{\mathbf{u}}(\mathbf{x},t)$. The equations of motion in term of these variables are $-\rho\omega^2\bar{\mathbf{u}}_i(\mathbf{x},\omega) = \partial_j\bar{\sigma}_{ij}(\mathbf{x},\omega)$ and $-\rho\omega^2\tilde{\mathbf{u}}_i(\mathbf{x},\omega) = \partial_j\tilde{\sigma}_{ij}(\mathbf{x},\omega) + f_i(\mathbf{x},\omega)$, with the boundary conditions that $\bar{\mathbf{u}}_i(|\mathbf{x}| = a,\omega) = \varepsilon_i(\omega)$ and $\bar{\mathbf{u}}_i(|\mathbf{x}|,\omega) \to 0$, as $|\mathbf{x}| \to \infty$, and $\tilde{\mathbf{u}}_i(|\mathbf{x}| = a,\omega) = 0$ and $\tilde{\mathbf{u}}_i(|\mathbf{x}|,\omega) \to 0$, as $|\mathbf{x}| \to \infty$. The total force exerted by the medium on the particle has two components: the systematic (average), $\bar{F}_i(\omega) = \int_{S_0} dS\hat{n}_j\bar{\sigma}_{ij}(\mathbf{x},\omega)$, and random parts, $\tilde{F}_i(\omega)$

$=\int_{S_0} dS\hat{n}_j\tilde{\sigma}_{ij}(\mathbf{x},\omega)$, where $\bar{\sigma}_{ij}=2\mu(\omega)\bar{u}_{ij}$ and $\tilde{\sigma}_{ij}=2\mu(\omega)\tilde{u}_{ij}$ are, respectively, the average and fluctuating stresses and $\hat{n}_j$ is the unit surface normal pointing toward the center of the particle. It is straightforward to compute $\bar{F}_i(\omega)$ $=6\pi a\mu(\omega)\varepsilon_j(\omega)\delta_{ij}$ [52]. The evaluation of the spectrum $\mathcal{I}^R_{ij}(\omega)\equiv\langle\tilde{F}_i(\omega)\tilde{F}_j(-\omega)\rangle$ of the random force is more complicated. Consider the following integral [67]:

$$\mathcal{J}=\int_{V_0} d^3\mathbf{x}[\bar{\mathbf{u}}_i(\mathbf{x},\omega)\partial_j\tilde{\sigma}_{ij}(\mathbf{x},\omega)-\tilde{\mathbf{u}}_i(\mathbf{x},\omega)\partial_j\bar{\sigma}_{ij}(\mathbf{x},\omega)],$$

where $V_0$ is all space excluding the region occupied by the particle. After integrating by parts and using Green's theorem, we can transform this integral into $\mathcal{J}=\varepsilon_i(\omega)\tilde{F}_i(\omega)$. Alternatively, we can make use of Eq. (A5) to obtain $\mathcal{J}$ $=\int_{V_0} d^3\mathbf{x}\bar{\mathbf{u}}_i(\mathbf{x},\omega)f_i(\mathbf{x},\omega)$. Through these two forms of $\mathcal{J}$, we find

$$\varepsilon_i(\omega)\tilde{F}_i(\omega)=\int_{V_0} d^3\mathbf{x}\bar{\mathbf{u}}_i(\mathbf{x},\omega)f_i(\mathbf{x},\omega), \tag{A7}$$

from which $\mathcal{I}^R_{ij}(\omega)$ can be directly computed

$$\varepsilon_i(\omega_1)\varepsilon_j(\omega_2)\langle\tilde{F}_i(\omega_1)\tilde{F}_j(\omega_2)\rangle$$
$$=\int_{V_0} d^3\mathbf{x}d^3\mathbf{x}'\bar{\mathbf{u}}_i(\mathbf{x},\omega_1)\bar{\mathbf{u}}_j(\mathbf{x}',\omega_2)\langle f_i(\mathbf{x},\omega_1)f_j(\mathbf{x}',\omega_2)\rangle.$$

Using Eq. (A6) and again Green's theorem, we obtain

$$\varepsilon_i(\omega_1)\varepsilon_j(\omega_2)\langle\tilde{F}_i(\omega_1)\tilde{F}_j(\omega_2)\rangle$$
$$=2\pi\Delta(\omega_1)\delta(\omega_1+\omega_2)\varepsilon_i(\omega_1)\frac{\bar{F}_j(\omega_2)}{\mu(\omega_2)}+O(\omega_2^2). \tag{A8}$$

From the result for $\bar{F}_i(\omega)$ above, Eq. (A8) implies that the spectrum of the random noise on the tracer particle is given by $\mathcal{I}^R_{ij}(\omega)\equiv\langle\tilde{F}_i(\omega)\tilde{F}_j(-\omega)\rangle=6\pi a\Delta(\omega)\delta_{ij}$. These results combined with the effective Langevin equation for the tracer particle, $-m\omega^2\varepsilon_i(\omega)=-6\pi a\mu(\omega)\varepsilon_i(\omega)+\tilde{F}_i(\omega)$, imply that if inertial effects can be ignored, the correlation function of the tracer displacements is

$$\langle\varepsilon_i(\omega)\varepsilon_j(-\omega)\rangle=\frac{\Delta(\omega)}{6\pi a|\mu(\omega)|^2}\delta_{ij}, \tag{A9}$$

a quantity that is directly measured in passive *one-point* microrheology experiments. This result shows that (i) the tracer can exhibit superdiffusive behavior provided $\Delta(\omega)$ diverges sufficiently at small $\omega$ and (ii) if an independent measure of $\mu(\omega)$ exists, then $\Delta(\omega)$ can be sensibly extracted from passive correlations of tracer particles. However, this argument based on one-point data may not accurately reflect continuum fluctuations because of the heterogeneities in the medium, an issue that we now address.

### 2. Two-point microrheology

It has recently been shown theoretically that two-point microrheology which measures the correlated fluctuations of two tracers, separated in space, extracts bulk rheological properties [60]. However, the derivation of this result is also based on FDT; thus, we must now show that within our phenomenological approach, our main conclusion from Eq. (A9) above, where we have assumed a homogeneous medium, still holds for a heterogeneous medium using two-point microrheology. For simplicity, we assume that the heterogeneities near the vicinity of the tracers are well reflected by a local effective shear modulus $\mu^*(\omega)$ which may be different from $\mu(\omega)$ in the bulk. Let particle 1 (2) at $\mathbf{x}(\mathbf{x}')$ undergo a displacement $\varepsilon_i^{(1)}(\omega)[\varepsilon_i^{(2)}(\omega)]$. Generalizing the argument above for the single particle, we have the relation

$$\varepsilon_i^{(1)}(\omega)\tilde{F}_i^{(1)}(\omega)+\varepsilon_i^{(2)}(\omega)\tilde{F}_i^{(2)}(\omega)=\int_{V_0} d^3\mathbf{x}\bar{\mathbf{u}}_i(\mathbf{x},\omega)f_i(\mathbf{x},\omega),$$

where the integration is over all space excluding the regions occupied by both particles. Multiplying the above equation by its complex conjugate and making use of Eq. (A6), the noise correlators can be formally identified

$$\langle\tilde{F}_i^{(n)}(\omega)\tilde{F}_j^{(m)}(-\omega)\rangle=\Delta(\omega)\chi_{ij}^{-1(n,m)}(-\omega)/\mu(-\omega), \tag{A10}$$

where $\chi_{ij}^{(n,m)}(\omega)$ is the two-particle response matrix [62] given by $\chi_{ij}^{(1,1)}(\omega)=\frac{\delta_{ij}}{6\pi a\mu^*(\omega)}$ and $\chi_{ij}^{(1,2)}(\omega)=\frac{\hat{R}_i\hat{R}_j}{4\pi R\mu(\omega)}+\frac{\delta_{ij}-\hat{R}_i\hat{R}_j}{8\pi R\mu(\omega)}$ to the lowest order in $1/R$, where $R\equiv|\mathbf{x}-\mathbf{x}'|$, the distance between the two particles and $\hat{\mathbf{R}}\equiv\mathbf{R}/R$. For identical particles, symmetry implies that $\chi_{ij}^{(1,1)}(\omega)=\chi_{ij}^{(2,2)}(\omega)$ and $\chi_{ij}^{(1,2)}(\omega)=\chi_{ij}^{(2,1)}(\omega)$, which in turn implies $\mathcal{I}_{ij}^{(1,1)}(\omega)$ $=\mathcal{I}_{ij}^{(2,2)}(\omega)$ and $\mathcal{I}_{ij}^{(1,2)}(\omega)=\mathcal{I}_{ij}^{(2,1)}(\omega)$. It is straightforward to invert the response matrix to obtain the noise correlators using Eq. (A10). The results show that if inertial effects are not important, the equation of motion for $\varepsilon_i^{(1)}(\omega)$ and $\varepsilon_i^{(2)}(\omega)$, $\varepsilon_i^{(m)}(\omega)=\Sigma_n\chi_{ij}^{(m,n)}(\omega)\tilde{F}_j^{(n)}(\omega)$, implies that the one-particle correlation function $\langle\varepsilon_i^{(1)}(\omega)\varepsilon_j^{(1)}(-\omega)\rangle$ depends in a complicated way on $\mu^*(\omega)$ and $\mu(\omega)$, which may not yield reliable results. In contrast, the cross-correlation function, which is measured directly by two-point microrheology [22] and which to the lowest order in $1/R$ satisfies

$$D_{rr}(R,\omega)\equiv\frac{1}{2}\langle\varepsilon_i^{(1)}(\omega)\varepsilon_i^{(2)}(-\omega)\rangle=\frac{\Delta(\omega)}{6\pi R|\mu(\omega)|^2}, \tag{A11}$$

depends only on $\mu(\omega)$ and $\Delta(\omega)$ in the bulk and, moreover, does not depend on the tracers' size, shape, or boundary conditions.

## APPENDIX B: NONTHERMAL NOISES FROM ACTIVE FORCES

In this appendix, we discuss briefly the renormalization of the noises, Eqs. (27)–(29), arising from nonthermal sources. These nonthermal sources may come from fluctuations in the active forces exerted across the surface of an active particle, in general, and from the run-and-tumble dynamics of *E. coli*, in particular [68]. We find below that there are additive as well as multiplicative noises that contribute to the random noises of the momentum equation, Eq. (24), and of the concentration equation, Eq. (26). The multiplicative noises, which depend on the local values of the alignment tensor and the concentration field of the active particles, require a more elaborate analysis and we defer its study for a future publication. Here, we are only interested in those terms that have the same structures as those in Eqs. (27) and (29). Note also that in our (simple) treatment of the bacterial bath, the noise term for the alignment tensor equation, Eq. (28), remains unchanged. In order to estimate the order of magnitude for nonthermal contributions, we briefly study a simple model of the force fluctuations arising from the run-and-tumble switching dynamics of *E. coli*. We find that all the noises are proportional to the number density of active particles, which we take to be small, and thus conclude that for the system we are studying, they should not be important, justifying ignoring these active force-generated noises to the order that we are calculating in Secs. III and IV.

### 1. Stress

Using the definition of the active stress, $\sigma_{ij}^A(t) \equiv \Sigma_\alpha d_{ij}^\alpha(t)\,\delta[\mathbf{x}-\mathbf{x}^\alpha(t)]$, we can write its fluctuations at time $t$ arising from surface force fluctuations as

$$\delta\sigma_{ij}^A(t) = \sum_\alpha \delta d_{ij}^\alpha(t)\,\delta[\mathbf{x}-\mathbf{x}^\alpha(t)], \tag{B1}$$

with

$$\delta d_{ij}^\alpha(t) = \frac{1}{2}\int dS^\alpha[\delta\tilde{f}_i^\alpha(t) r_j^\alpha(t) + \delta\tilde{f}_j^\alpha(t) r_i^\alpha(t)], \tag{B2}$$

where $\delta\tilde{f}_i^\alpha(t) = \tilde{f}_i^\alpha(t) - \langle\tilde{f}_i^\alpha(t)\rangle_f$ is the deviation of the local force at point $\tilde{u}^\alpha$ from its average $\langle\tilde{f}_i^\alpha(t)\rangle_f$. We assume that $\delta\tilde{f}_i^\alpha(t)$ is Gaussian distributed with variance $\langle\delta\tilde{f}_i^\alpha(\tilde{u}^\alpha,t)\,\delta\tilde{f}_j^\beta(\tilde{u}'^{\beta},t')\rangle_f = \delta^{\alpha\beta}\Delta_{ij}^f(\tilde{u}^\alpha)\,\delta(\tilde{u}^\alpha - \tilde{u}'^{\alpha})\,\delta(t-t')$ and a noise strength $\Delta_{ij}^f(\tilde{u}^\alpha)$ given by

$$\begin{aligned}\Delta_{ij}^f(\tilde{u}^\alpha) &= \Delta_1(\tilde{u}^\alpha) N_i(\tilde{u}^\alpha,t) N_j(\tilde{u}^\alpha,t) \\ &\quad + \Delta_2(\tilde{u}^\alpha)[\delta_{ij} - N_i(\tilde{u}^\alpha,t) N_j(\tilde{u}^\alpha,t)],\end{aligned} \tag{B3}$$

where $N_i(\tilde{u}^\alpha,t)$ is the unit normal to the surface of the active particle at point $\tilde{u}^\alpha$. Of course, more complicated tensorial forms for $\Delta_{ij}^f$ are possible: in Eq. (B3), we treat the two directions on the surface perpendicular to the normal as equivalent. Using Eqs. (B1)–(B3), we can calculate the stress fluctuations as $\langle\delta\sigma_{ij}^A(\mathbf{x},t)\,\delta\sigma_{kl}^A(\mathbf{x}',t')\rangle_f = \Delta_{ijkl}^f(\mathbf{x},t)\,\delta(\mathbf{x}-\mathbf{x}')\,\delta(t-t')$, with

$$\begin{aligned}\Delta_{ijkl}^f(\mathbf{x},t) &= \frac{1}{4}T_{ijkl}(\mathbf{x},t) + \frac{1}{4}[\delta_{ik}R_{jl}(\mathbf{x},t) + \delta_{il}R_{jk}(\mathbf{x},t) \\ &\quad + \delta_{jk}R_{il}(\mathbf{x},t) + \delta_{jl}R_{ik}(\mathbf{x},t)],\end{aligned} \tag{B4}$$

where $T_{ijkl}(\mathbf{x},t) \equiv \Sigma_\alpha T_{ijkl}^\alpha(t)\,\delta[\mathbf{x}-\mathbf{x}^\alpha(t)]$, $R_{ij}(\mathbf{x},t) \equiv \Sigma_\alpha R_{ij}^\alpha(t)\,\delta[\mathbf{x}-\mathbf{x}^\alpha(t)]$,

$$\begin{aligned}T_{ijkl}^\alpha(t) &= \int dS^\alpha\{[\Delta_1(\tilde{u}^\alpha) - \Delta_2(\tilde{u}^\alpha)][N_i^\alpha(t)N_k^\alpha(t)r_j^\alpha(t)r_l^\alpha(t) \\ &\quad + N_j^\alpha(t)N_l^\alpha(t)r_i^\alpha(t)r_k^\alpha(t) + ij \leftrightarrow kl]\},\end{aligned} \tag{B5}$$

and

$$R_{ij}^\alpha(t) = \int dS^\alpha\Delta_2(\tilde{u}^\alpha) r_i^\alpha(t) r_j^\alpha(t). \tag{B6}$$

Therefore, fluctuations in the active forces in the bacteria contribute a nonthermal noise to Eq. (24) in addition to the thermal component, Eq. (27). The correlation of the nonthermal noise has the form given in Eq. (B4). Clearly, Eq. (B4) has a far more complicated structure than that of the thermal noise, as it contains terms that are proportional to the alignment tensors. Thus, we face the problem of multiplicative noise and an interpretation of which algebra the noise applies may be necessary [69]. To simplify our discussion, we will ignore these terms and extract from Eq. (B4) the isotropic part, whose correlation has the same structure as that of the thermal noise in Eq. (27). To that end, we decompose $T_{ijkl}(\mathbf{x},t)$ and $R_{ij}(\mathbf{x},t)$ into respective parts $\tilde{T}_{ijkl}$ and $\tilde{R}_{ij}$ that are fully symmetric and traceless and parts that are not, $\tilde{T}_{ijkk} = \tilde{T}_{iikl} = \tilde{T}_{ijil} = 0$ and $\tilde{R}_{ii} = 0$, and introduce the notation

$$T_{iikl} = T_{kl}^{(1)} = T_{klii}, \quad T_{ii}^{(1)} = T_{iikk} = T^{(1)},$$

$$T_{ikil} = T_{kl}^{(2)} = T_{kiil}, \quad T_{ii}^{(2)} = T_{ikik} = T^{(2)},$$

$$R_{ii} = R, \quad \tilde{T}_{ij}^{(a)} = T_{ij}^{(a)} - \frac{1}{3}\delta_{ij}T^{(a)}, \tag{B7}$$

where $a = 1,2$, so that

$$\begin{aligned}T_{ijkl} &= \tilde{T}_{ijkl} - \frac{2}{7}\Big[\delta_{ik}\tilde{T}_{jl}^{(1)} + \delta_{jl}\tilde{T}_{ik}^{(1)} + \delta_{il}\tilde{T}_{jk}^{(1)} \\ &\quad + \delta_{jl}\tilde{T}_{ik}^{(1)} - \frac{5}{2}(\delta_{ij}\tilde{T}_{kl}^{(1)} + \delta_{kl}\tilde{T}_{ij}^{(1)})\Big] \\ &\quad + \frac{3}{7}\Big[\delta_{ik}\tilde{T}_{jl}^{(2)} + \delta_{jl}\tilde{T}_{ik}^{(2)} + \delta_{il}\tilde{T}_{jk}^{(2)} \\ &\quad + \delta_{jl}\tilde{T}_{ik}^{(2)} - \frac{4}{3}(\delta_{ij}\tilde{T}_{kl}^{(2)} + \delta_{kl}\tilde{T}_{ij}^{(2)})\Big] \\ &\quad + \frac{1}{10}\left(\delta_{ik}\delta_{jl} + \delta_{il}\delta_{jk} - \frac{2}{3}\delta_{ij}\delta_{kl}\right)\left(T^{(2)} - \frac{1}{3}T^{(1)}\right) \\ &\quad + \frac{1}{9}\delta_{ij}\delta_{kl}T^{(1)},\end{aligned} \tag{B8}$$

$$R_{ij} = \tilde{R}_{ij} + \frac{1}{3}\delta_{ij}R, \tag{B9}$$

where $\tilde{T}_{ijkl}$ is traceless with respect to contraction of any pair of indices. Note that the only terms that survive averaging in the isotropic phase are those composed from the Kronecker $\delta$'s (the last two in $T_{ijkl}$ and the last one in $R_{ij}$). The other anisotropic terms would, however, contribute fluctuation corrections to correlation functions. In terms of these tensors, Eq. (B4) can be rewritten as

$$\Delta^{A}_{ijkl}(\mathbf{x},t) = \frac{1}{6}\left(\delta_{ik}\delta_{jl} + \delta_{il}\delta_{jk} - \frac{2}{3}\delta_{ij}\delta_{kl}\right) \times\left[R(\mathbf{x},t) + \frac{3}{20}T^{(2)}(\mathbf{x},t) - \frac{1}{20}T^{(1)}(\mathbf{x},t)\right] + \frac{1}{36}\delta_{ij}\delta_{kl}[4R(\mathbf{x},t) + T^{(1)}(\mathbf{x},t)] + \cdots, \quad \text{(B10)}$$

where we only display those parts of $\Delta^{A}_{ijkl}$ that are proportional $\mathcal{L}_{ijkl} \equiv \delta_{ik}\delta_{jl} + \delta_{il}\delta_{jk} - \frac{2}{3}\delta_{ij}\delta_{kl}$ and $\delta_{ij}\delta_{kl}$. They have exactly the same forms as those arising from thermal fluctuations. Note that $R(\mathbf{x},t) \equiv \Sigma_{\alpha} R^{\alpha}_{ii}(t)\delta[\mathbf{x} - \mathbf{x}^{\alpha}(t)]$ and

$$R^{\alpha}_{ii}(t) = \int dS^{\alpha}\Delta_2(\tilde{u}^{\alpha})\mathbf{r}^{\alpha}(t)\cdot\mathbf{r}^{\alpha}(t) = \mathcal{A}\overline{\Delta_2 r^2} \quad \text{(B11)}$$

does not depend on $t$. Here, $\mathcal{A}$ is the surface area of the active particles and $\bar{R} \equiv \overline{\Delta_2 r^2}$ is the average over the surface of $\Delta_2(\tilde{u}^{\alpha})$ times the squared distance from the center of mass to a point on the surface. Thus, $R(\mathbf{x},t) = \mathcal{A}\bar{R}n_A(\mathbf{x},t)$, where $n_A(\mathbf{x},t)$ is the number density of active particles. Similarly, we find $T^{(a)}(\mathbf{x},t) = \mathcal{A}\overline{T^{(a)}}n_A(\mathbf{x},t)$, where

$$\overline{T^{(1)}} \equiv \frac{4}{\mathcal{A}}\int dS[\Delta_1(\tilde{u}) - \Delta_2(\tilde{u})][N_i(t)r_i(t)]^2,$$

$$\overline{T^{(2)}} \equiv \frac{2}{\mathcal{A}}\int dS[\Delta_1(\tilde{u}) - \Delta_2(\tilde{u})]\{r^2 + [N_i(t)r_i(t)]^2\},$$

which are independent of $t$. Thus, there is a well-defined transverse noise with strength $\mathcal{A}n_A(\mathbf{x},t)(20\bar{R} + 3\overline{T^{(2)}} - \overline{T^{(1)}})/120$ and a well-defined longitudinal noise with strength $\mathcal{A}n_A(\mathbf{x},t)[4\bar{R} + \overline{T^{(1)}}]/36$ that directly renormalize the temperature.

### 2. Concentration current

Fluctuations in the active forces generated by the active particles also lead a nonthermal noise to the concentration equation, Eq. (26), in addition to the thermal component, Eq. (29). It follows from the definition of the concentration current,

$$\mathbf{J} = \frac{\rho_A\rho_S}{\rho}\mathbf{w}, \quad \text{(B12)}$$

and the velocity difference calculated in Sec. II A,

$$w_i = -\frac{1}{2\Gamma}\partial_i(\pi^{A}_{ij} - \pi^{S}_{ij}) + \frac{W}{2\Gamma}\partial_j(cQ_{ij}) + \frac{1}{\Gamma}\mathcal{F}_i(\mathbf{x},t), \quad \text{(B13)}$$

where

$$\mathcal{F}_i(\mathbf{x},t) = \sum_{\alpha} f^{\alpha}_i(t)\delta(\mathbf{x} - \mathbf{x}^{\alpha}). \quad \text{(B14)}$$

In Sec. II A, we ignore the average of $\mathcal{F}_i$ because it would be proportional to a polar order parameter. We cannot, however, ignore its fluctuations. Using Eq. (B3), we find

$$\langle\mathcal{F}_i(\mathbf{x},t)\mathcal{F}_j(\mathbf{x}',t')\rangle_f = \mathcal{A}\delta(\mathbf{x} - \mathbf{x}')\delta(t - t')n_A(\mathbf{x},t) \times\left[\left(\tfrac{1}{3}\bar{\Delta}_1 + \tfrac{2}{3}\bar{\Delta}_2\right)\delta_{ij} + \bar{P}Q_{ij}(\mathbf{x},t)\right],$$

where

$$\bar{P} = \frac{1}{2\mathcal{A}}\int dS[\Delta_1(\tilde{u}) - \Delta_2(\tilde{u})][3(N_i\nu_{3,i})^2 - 1]. \quad \text{(B15)}$$

The fluctuation in $\mathbf{J}$, which contributes an additional noise source for the concentration equation, follows directly from $\langle\mathcal{F}_i(\mathbf{x},t)\mathcal{F}_j(\mathbf{x}',t')\rangle_f$. The first term in this expression has the same form as the thermal noise, except that it is proportional to particle density, i.e., multiplicative noise. Note also that since we do not concern ourselves with polar order parameters, the cross correlation between $J_i$ and $\sigma^{A}_{ij}$ vanishes.

### 3. Simple model for wild-type bacteria

A simple model for the fluctuating active forces generated by a wild-type bacterium is to take account of its run-and-tumble dynamics. We write the surface force per unit area generated by the active particle as

$$\tilde{f}^{\alpha}_i(t) = f_r[1 - s^{\alpha}(t)]\nu^{\alpha}_{3,i}\delta^2(\mathbf{r}^{\alpha} - \ell_r\boldsymbol{\nu}^{\alpha}_3) + f_t s^{\alpha}(t)\{\nu^{\alpha}_{1,i}\delta^2(\mathbf{r}^{\alpha} - \ell_t\boldsymbol{\nu}^{\alpha}_3) - \nu^{\alpha}_{1,i}\delta^2(\mathbf{r}^{\alpha} + \ell_t\boldsymbol{\nu}^{\alpha}_3)\}, \quad \text{(B16)}$$

where $\ell_i$ are the length scales associated with the force and torque generated by an active particle, $f_r$ and $f_t$ are the average forces generated by the bacterium when it is running and tumbling, respectively, and $s^{\alpha}(t)$ is a stochastic variable which models the run-and-tumble dynamics of the bacteria. From Eq. (B16), it is clear that when a bacterium is in a running state, $s=0$, there is a force pointing along the long axis of the bacterium and when the bacterium is in a "tumbling" state, $s=1$, there is a torque about the CM of the bacterium. We assume that there is no correlation among the bacteria switching dynamics and that a bacterium switches its states at random times with a probability per unit time, $p_t$, to switch from running to tumbling and a probability per unit time, $p_r$, to switch from tumbling to running. For such a process, the correlation functions for $s^{\alpha}(t)$ are well known [70],

$$\langle s^{\alpha}(t)\rangle = \frac{p_t}{p_r + p_t}, \quad \text{(B17)}$$

$$\langle\delta s^{\alpha}(t)\delta s^{\beta}(t')\rangle = \frac{p_r p_t}{(p_r + p_t)^2}e^{-(p_r+p_t)|t-t'|}\delta_{\alpha\beta} \approx \frac{p_r p_t}{(p_r + p_t)^3}\delta(t - t')\delta_{\alpha\beta}, \quad \text{(B18)}$$

where in the last line, we have approximated the exponentially decay function in time by a delta function. Using these results, the fluctuations in the active stress arising from run-and-tumble dynamics can be calculated and it takes the form

$$\langle \delta\sigma^A_{ij}(\mathbf{x},t)\,\delta\sigma^A_{kl}(\mathbf{x}',t')\rangle_s = \frac{p_r p_t \Delta^s_{ijkl}(\mathbf{x},t)}{(p_r+p_t)^3}\,\delta(t-t')\,\delta(\mathbf{x}-\mathbf{x}'), \tag{B19}$$

with

$$\Delta^s_{ijkl}(\mathbf{x},t) = W_r^2 T^{(1)}_{ijkl}(\mathbf{x},t) - W_r W_t T^{(2)}_{ijkl}(\mathbf{x},t) + W_t^2 T^{(3)}_{ijkl}(\mathbf{x},t), \tag{B20}$$

where $W_r \equiv f_r \ell_r$, $W_t \equiv f_t \ell_t$,

$$T^{(1)}_{ijkl}(\mathbf{x},t) \equiv \sum_\alpha \nu^\alpha_{3,i}\nu^\alpha_{3,j}\nu^\alpha_{3,k}\nu^\alpha_{3,l}\,\delta[\mathbf{x}-\mathbf{x}^\alpha(t)], \tag{B21}$$

$$\begin{aligned} T^{(2)}_{ijkl}(\mathbf{x},t) \equiv \sum_\alpha \big[&\nu^\alpha_{3,i}\nu^\alpha_{3,j}(\nu^\alpha_{1,k}\nu^\alpha_{3,l} + \nu^\alpha_{1,l}\nu^\alpha_{3,k}) \\ &+ (\nu^\alpha_{1,i}\nu^\alpha_{3,j} + \nu^\alpha_{1,j}\nu^\alpha_{3,i})\nu^\alpha_{3,k}\nu^\alpha_{3,l}\big]\delta[\mathbf{x}-\mathbf{x}^\alpha(t)], \end{aligned} \tag{B22}$$

and

$$\begin{aligned} T^{(3)}_{ijkl}(\mathbf{x},t) \equiv \sum_\alpha &(\nu^\alpha_{1,i}\nu^\alpha_{3,j} + \nu^\alpha_{1,j}\nu^\alpha_{3,i})(\nu^\alpha_{1,k}\nu^\alpha_{3,l} + \nu^\alpha_{1,l}\nu^\alpha_{3,k}) \\ &\times \delta[\mathbf{x}-\mathbf{x}^\alpha(t)]. \end{aligned} \tag{B23}$$

These fourth-rank tensors can be decomposed, similar to what is done in Sec. B1, into totally symmetric traceless tensors, some of which are proportional to the alignment tensor $Q_{ij}(\mathbf{x},t)$, some to the biaxial tensor $B_{ij}(\mathbf{x},t)$, and some to the $Q^{(1)}_{ij}(\mathbf{x},t) = \nu^\alpha_{1,i}\nu^\alpha_{1,j} - (1/3)\delta_{ij}$. We will address these noise terms in a future publication. Here, we will concentrate on the isotropic part, i.e., term proportional to $\mathcal{L}_{ijkl} \equiv \delta_{ik}\delta_{jl} + \delta_{il}\delta_{jk} - \frac{2}{3}\delta_{ij}\delta_{kl}$ and to $\delta_{ij}\delta_{kl}$, which has the same structure as that of the thermal contributions. It is straightforward to see that only $T^{(1)}_{ijkl}(\mathbf{x},t)$ and $T^{(3)}_{ijkl}(\mathbf{x},t)$ contribute to the isotropic parts and we find

$$\begin{aligned} \langle \delta\sigma^A_{ij}(\mathbf{x},t)\,\delta\sigma^A_{kl}(\mathbf{x}',t')\rangle_s = {}& \frac{p_r p_t n_A(\mathbf{x},t)}{(p_r+p_t)^3}\,\delta(t-t')\,\delta(\mathbf{x}-\mathbf{x}') \\ &\times \left[\frac{W_r^2 + 3W_t^2}{15}\mathcal{L}_{ijkl} + \frac{W_r^2}{9}\delta_{ij}\delta_{kl}\right]. \end{aligned}$$

Thus, there is a well-defined transverse noise with strength $\Delta_\perp = n_A(\mathbf{x},t) p_r p_t (W_r^2 + 3W_t^2)/[15(p_r+p_t)^3]$ and a well-defined longitudinal noise with strength $\Delta_\parallel = n_A(\mathbf{x},t) p_r p_t W_r^2/[9(p_r+p_t)^3]$. For an estimate, we assume that $W_r \sim 10^{-17}$ J $\gg W_t$, $p_r \sim 10\ \mathrm{s}^{-1}$, $p_t \sim 0.1\ \mathrm{s}^{-1}$, and $\phi \sim 10^{-3}$, as in the experiments in Ref. [21]. We find $\Delta_\perp \sim 10^{-24}$ J s/m$^3$, which is 25% of the thermal contribution, which has a magnitude of $4 \times 10^{-24}$ J s/m$^3$. Thus, we conclude that in the dilute limit, the run-and-tumble dynamics of bacteria contributes but not so significantly to the noise temperature of the system.

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