NOVEL PROPERTIES AND EMERGENT COLLECTIVE PHENOMENA OF ACTIVE FLUIDS

A DISSERTATION

SUBMITTED TO THE FACULTY OF THE GRADUATE SCHOOL

OF THE UNIVERSITY OF MINNESOTA

BY

ZHENGYANG LIU

IN PARTIAL FULFILLMENT OF THE REQUIREMENTS

FOR THE DEGREE OF

DOCTOR OF PHILOSOPHY

ADVISOR: XIANG CHENG, PH.D.

DEC, 2020

Acknowledgements

Dedication

To my beloved family for supporting me over the years.

Abstract

Contents

List of Figures

Chapter 1

Introduction

- Chapter 1 briefly describe the history and significance of active fluid research.
- Chapter 2 presents the experimental techniques used in this theis.
- Chapter 3 talks about one of the emergent properties: reduced viscosity. Large portion of this chapter have been published in [1].
- Chapter 4 talks about another emergent property: giant number fluctuation. This work is under preparation for submission.
- Chapter 5 presents the study on the transition from disordered state to active turbulence in light-powered bacterial suspensions. This work is conducted with a close collaboration with Yi Peng and Xiang Cheng. Large portions of this chapter has been published in [2]. Yi Peng, Zhengyang Liu and Xiang Cheng conceived the experiment. Zhengyang Liu constructed the light-powered bacteria. Yi Peng performed the experiment. Zhengyang Liu and Yi Peng did the data analysis. All authors contribute to the model development and writing of the manuscript.
- Chapter 6 summarizes the contributions of this thesis and provides the outlook

on future research.

- Appendix A shows details of the construction of light-powered *E. coli*.
- Appendix B provides details of several particle tracking tools I developed.
- Appendix C shows details of photolithography.

1.1 Active Matter and Active Fluids

Active matter denotes a large group of active units which utilize ambient energy to achieve motions. Examples include flocking birds, schooling fish, herding beasts and even human crowds, down to actin filaments powered by motor proteins, bacteria and chemical reaction driven particles [3, 4, 5, 6, 7, 8, 9]. The concept roots from a broader class of matter: soft matter, which includes polymers, surfactants and colloidal grains and shares common properties such as complexity and flexibility [10]. Like soft matter, active matter is also complex and flexible. What makes them more complex is the self-propulsion of each individual constituent, which endows them with more intrguing and counter-intuitive properties, challenging our understandings [11].

Active fluids, sometimes referred to as active gels, are suspensions of active agents such as cells, particles and biological macromolecules that are capable of utilizing chemical energy to sustain their self-propulsion. They are a subset of active matter, and the "fluids" in the name suggests the important role of the viscous hydrodynamic interaction and stress, in contrast to dry active matter [6]. The first glimmering of active fluids dates back to 1969, when Finlayson and Scriven found that motion could spontaneously set in a previously still material without the intervention of outside forces, due to composition-dependent stress [12]. However, the study on active fluids did not bloom, until 26 year later, when the seminal paper on modeling collective flocks came out [13]. From then on, physicists are getting unprecedentedly intereted in biological phenomena, leading to the emergence of a new field of study - active fluids.

Early accomplishments in the research of active fluids include two successful theoretical predictions on the abnormal rheology and the spontaneous active turbulence [14, 15], which were then demonstrated in quite a few experiments [16, 17, 18, 19, 20, 21]. From these beginnings, the field has been enjoying a vibrant interplay between experiment and theory, and more complex environment and geometrical constraints have been investigated [22]. As of now, the study of active fluids has provided us with a good qualitative understanding of some biological processes, such as how active turbulence enhances nutrient transport.

There are two promising directions in active fluids. One is to get quantitative understanding of the novel properties. These works will not only provide more accurate predictions on new systems, but also guide the engineering of artificial robots that can perform tasks in complex environment, such as drug delivery. Another direction is to invite chemistry and biology to collaborate on this highly interdisciplinary subject. A complete understanding of the behavior and properties of living systems will require the knowledge of biochemical signaling, which opens the door of an ambitious mission: elucidating tissue dynamics and developmental biology [6, 23]. The works that are to be described in Sec. 2, 3 and **??** are along the first direction: seeking more quantitative understanding of rheology and active turbulence of active fluids.

1.2 Novel Properties

Active fluids exhibit novel properties such as reduced viscosity and enhanced diffusion [4]. The reduced viscosity is induced by the force excerted by the swimming mechanisms of the active agents, such as bacteria and algae [27]. And the enhanced diffusion is attributed to the interaction - steric collision or hydrodynamic perturbation - between

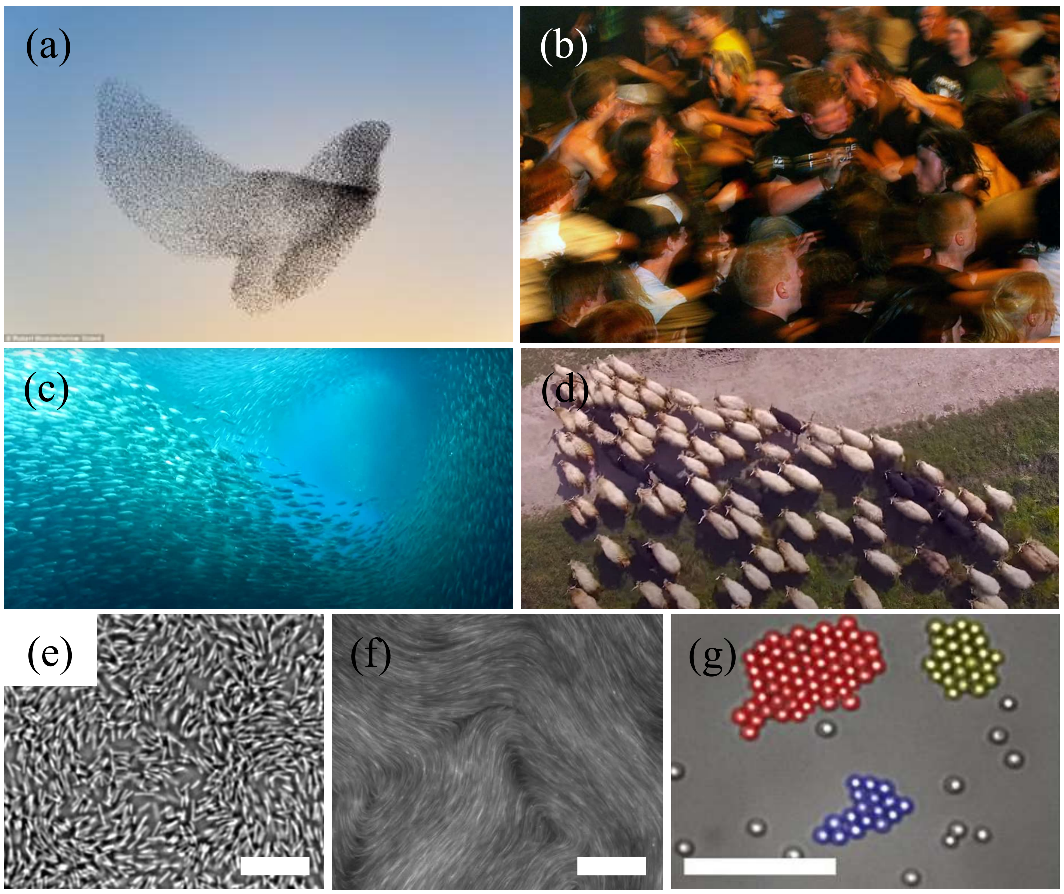

Figure 1.1: **Examples of living matters and active fluids.** (a) Flocking birds, (b) people in a mosh pit at heavy metal converts, (c) schooling fish, (d) herding sheeps, (e) swarming bacteria (f) microtubule and (g) clustering active Janus particles. Scalebars in (e) and (g) are 10 µm. Scalebar in (f) is 200 µm. Images courtesy of Robert Wolstenhome (a), Ulrike Biets (b) [24], biographic (c, d), DeCamp (f) [25] and Palacci (g) [26].

tracer particles and swimmers [28, 29, 30, 31, 32, 33, 34, 35, 36]. In this section, the existing works regarding rheology and diffusion in active fluids are reviewed, and motivations for investigating the rheology of bacterial suspensions under confinement (Chap. 2) will be discussed.

1.2.1 Rheology

Viscosity of a fluid can be understood as its resistence to flow. When flowing, fluid elements move relative to others, resulting in energy dissipation due to friction. The more energy is required, the more "viscous" the fluid is known to be. A suspension of passive particles is always more viscous than its suspending fluid, a fact that was first formulated by Einstein in 1906 [37]. Recently, the study of active fluids revealed that active particles modify the viscosity of their suspending fluids in a different and interesting way.

In 2004, Hatwalne et al. predicted that micro-swimmers, depending on their self-propelling mechanisms, can modify the suspension viscosity in different ways [14]. Most common micro-swimmers, such as unicellular microorganisms, can be classified into two types: pushers and pullers, based on the far field flow they generate. Fig. 1.2b illustrates the most common pushers and pullers in nature: bacterium and algae. If one puts a elongated rod-like bacterium in a simple shear flow, as illustrated in Fig. 1.2a, the preferred orientation of the bacterium is along the extensile flow [38]. Such an orientation makes the flow generate by the swimming bacterium coincide with the imposed shear flow, and thus compensating the viscous dissipation of energy, which effectively reduces the viscosity. In contrast, in the case of puller swimmers, such an orientation makes opposites the directions of swimming induced flow and imposed shear flow, which enhances the visocity.

Their prediction was confirmed by numerical solutions of the theory [39, 40] and experiments [19, 20, 21]. Cates et al. reached at the same conclusions as Hatwalne et al. did: while contractile gels exhibit a divergence of apparent viscosity, extensile gels show a zero-viscosity phase. Giomi et al., on top of these results, emphasized the important role of particle shape. They showed, in their numerical study, an rheological equivalence between rod-like pusher swimmers and disk-like puller swimmers (see Fig. 1.2c). In particular, they predicted a thickening effect of spherical puller swimmers (corresponds to the 0 shape parameter in Fig. 1.2c). This prediction was later on challenged by another theory in the framework of swim stress, which predicts a viscosity reduction of a spherical pusher swimmer suspension [41]. Due to the difficulty of synthesizing large amount of artificial swimmers, this debate has not been resolved yet. However, with the rapid development of synthesizing techniques [26, 42], it is getting more promising that we will resolve it, and formulate a more complete understanding on how active swimmers modify the rheology.

Experimental confirmation of these predictions posed challenges on traditional rheometries due to the tiny shear stress that is required to be measured. As a result, new rheometries are needed [43]. In 2009, Sokolov and Aranson came up with an innovative way of measuring the such tiny stress [19]. By moving a probe in a suspension of *Bacillus subtilis* bacteria, a pusher type swimmer, they generated a large vortex. By studying the decay of the vortex, they got a measure of the viscosity. For the first time, they experimentally confirmed that pusher swimmers reduced the viscosity (see their results in Fig. 1.2d). In 2013, Gachelin et al. adopted a microfluidic viscometer to measure the viscosity of suspensions of *Escherichia coli* bacteria, another pusher type swimmer [20]. They confirmed again the viscosity reduction. A more remarkable finding is the non-newtonian behavior: the viscosity was reduced at low shear rate, but was enhanced at high shear rate. This observation suggested that it is the competation between bacterium intrinsic shear rate and the impose flow shear rate that determines how the viscosity is modified. In 2015, Lopez et al. published arguably the most important experimental work on the rheology of active fluids, which showed that the apparent viscosity of an *E. coli* suspension can be reduced to zero if the swimming activity is sufficiently high [21]. The authors modified an old-fashioned Couette concentric cylinders, where the outer cylinder was set to rotate at a fixed rate and the torque on the inner cylinder was measured. The high sensitivity was achieved by using a string that was highly sensitive to torque to hang the inner cylinder, so that a stress, as small as that generated by bacterial suspensions, can be detected (see their rheometer and results in Fig. 1.2e-f). The authors termed their zero-viscosity suspensions "superfluids".

Despite the great progress on the rheology of active fluids made so far, their remained complexity that are not readily understood. Confinement, or more generally boundary conditions or geometry, is one of the leading factors that contribute to this complexity. The behavior of active particles can be altered greatly by confinement. In 2005, Voituriez et al. showed theoretically that a spontaneous flow transition from a homogeneous immobile state could happen in active polar gel under confinement [44]. Such spontaneous flow transition was confirmed in both numerical and experimental studies [45, 46, 47]. The complexity introduced by geometry was also manifested by the experiments where single bacterial vortex was stabilized by confinement [48, 49, 50] and where asymmetric gears were powered by swimming bacteria [51, 52]. The effect of confinement on the rheology of active fluids was first studied theoretically based a kinetic theory [53] and a generalized Navier-Stokes model [54]. In this thesis, I will present the first experimental study on active fluid rheology using bacterial suspensions (Chap. 2). The fact that our experimental results agreed with neither theory manifested the complexity and the lack of understanding of active fluids. Together with the experimental results, we provided a heuristic model that qualitatively captured the rheological properties and hope to stimulate further theoretical studies on this matter.

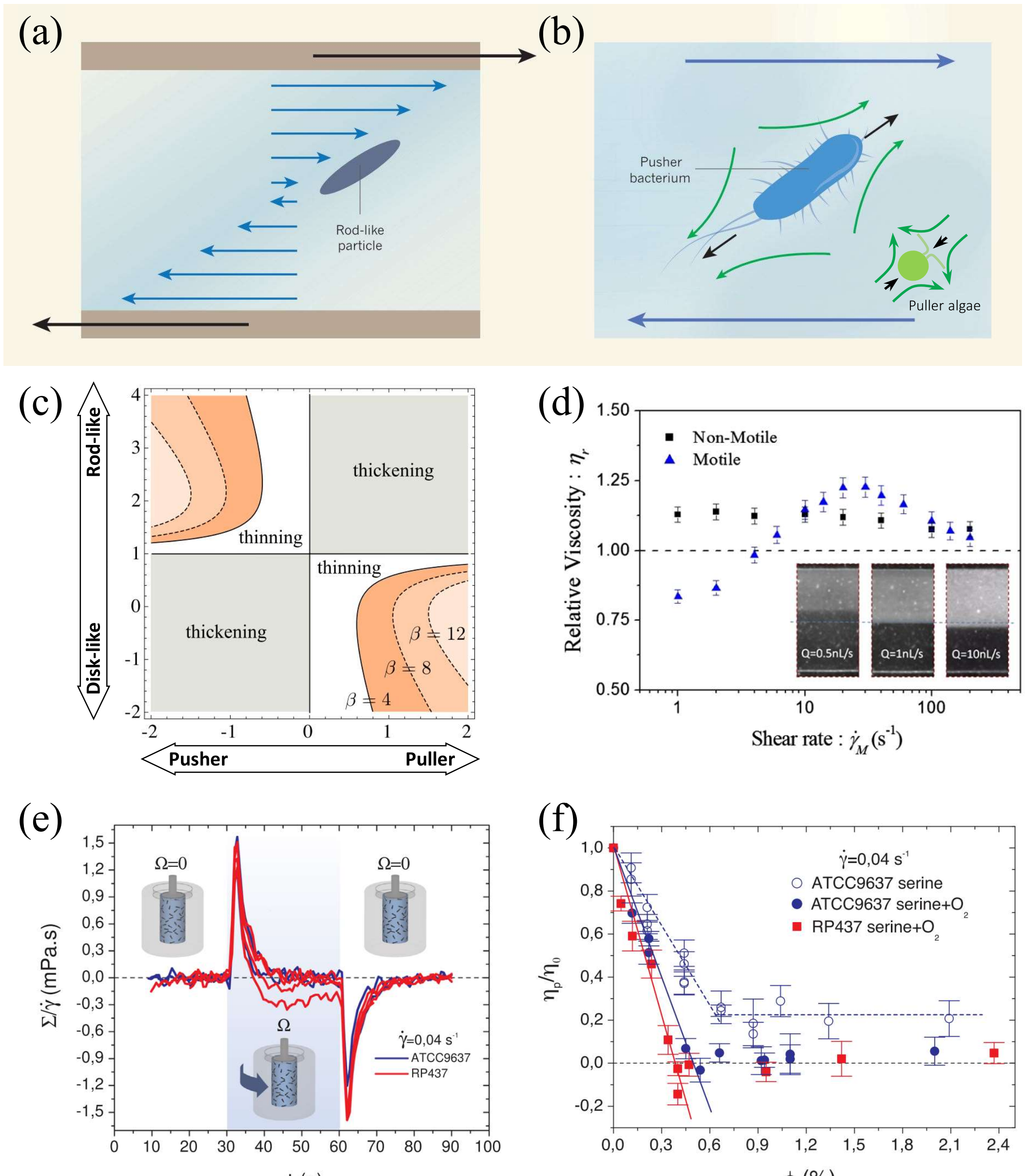

Figure 1.2: **Rheology of active fluids.** (a) The preferred orientation of the bacterium is along the extensile flow. (b) The most common pushers and pullers in nature: bacterium and algae, and their corresponding far field flow. (c) Rheological effect phase diagram of swimmer shape and swimming mechanism. (d) Non-Newtonian behavior of *E. coli* suspensions. (e) Stress response of *E. coli* suspensions in a modified Couette concentric cylinder rheometer. (f) Viscosity of *E. coli* suspensions at various volume fractions. Image courtesy of Marchetti (a, b) [43], Giomi (c) [40], Gachelin (d) [20] and Lopez (e, f) [21].

1.2.2 Diffusion

The diffusion of passive particles in active fluids, such as nutrients and signaling molecules, are significantly enhanced. Such enhancement has been shown to have great biological and ecological importance [28, 36, 31], as well as to provide a useful tool of probing novel properties of active fluids [55]. Unlike the study of rheology, which was initiated by theoretical prediction, the study of enhanced diffusion started from an experiment.

In 2000, Wu and Libchaber studied the diffusion of spherical polystyrene particles in a bath of actively swimming *E. coli* [28] (see Fig. 1.3a for their experimental system). They characterized the diffusion of the tracer particles by measuring their means squared displacement (MSD) (see Fig. 1.3b for typical MSD data), and reported two findings: 1) the MSD exhibits a superdiffusive regime at short time, which is followed by a diffusive regime at longer time; 2) the effective temperature, backed up from effective diffusion coefficient using Stokes-Einstein equation, is several order of magnitude larger than room temperature. Their qualitative findings were confirmed by computational [56, 57], theoretical [58] and other experimental studies [59, 33, 60, 36, 32]. A remarkable progress towards quantitative understanding was made by Mino et al., who experimentally identified that the enhancement of diffusivity is proportional to the "activity flux" (defined as concentration multiplied by the mean velocity of swimmers). This model was further developed to capture the experimental result more accurately and to account for more complex conditions [61, 62, 31].

Although a lot of progress has been made on understanding diffusion isotropic particles (spheres) in an active bath, how anisotropic particles diffuse remained largely unexplored. Yet, the diffusion of anisotropic particles has both fundamental and application significance. On the one hand, it was shown that the Brownian motion (i.e. in a passive bath) of anisotropic particles exhibited a subtle interplay between orientational and translational motions [63]. Previous studies preferred to consider an active bath equivalent to a high temperature passive bath [28], and it was shown to be a good equivalence for isotropic particles. A fundamentally interesting question to ask is: does active bath also alters the interplay between orientational and translational motions? The answer is yes, and we will see that this interplay is specific to swimming mechanisms. On the other hand, few particles or molecules in nature are perfectly isotropic. Generalizing the enhanced diffusion to anisotropic particles will have significant impact on applying this knowledge on real world problems. In 2016, Peng et al. studied the diffusion of polystyrene ellipsoids in a quasi-2D free-standing soap film of *E. coli* bath (see setup schematic in Fig. 1.3c) [29]. In contrast to the pure Brownian motion, where ellipsoids preferred to diffuse along their major axes [63], they found that an active bath forced the ellipsoids to move primarily along the minor axes (see Fig. 1.3d-e for a comparison). This phenomenon was explained by considering the far-field dipole flow of a single *E. coli* bacterium. An interesting prediction naturally arises: in a bath of puller swimmers, whose far-field flow is opposite to that of pushers, the diffusion of ellisoidal tracers should be primarily along the major axes. This prediction was later on proved experimentally by Yang et al. [34] in a green algae *C. reinhardtii* bath and I was involved in this work. Due to the fact that my contribution was relatively small to this work, I will not provide more details about it in my thesis. However, readers interested are encouraged to find out more in our original paper [34].

1.3 Collective Motion and Giant Number Fluctuations

Collective motion is defined as an emergent directed movement in a large number of animals or particles, which are capable of moving on their own. In the seminal paper by Reynolds published in 1987, he tried to use a simulation approach - rather than scripting the paths beforehand - to generate vivid motions of animals in computer graphics [64]. This idea has soon evoked enormous research interest of physicists because a seemingly

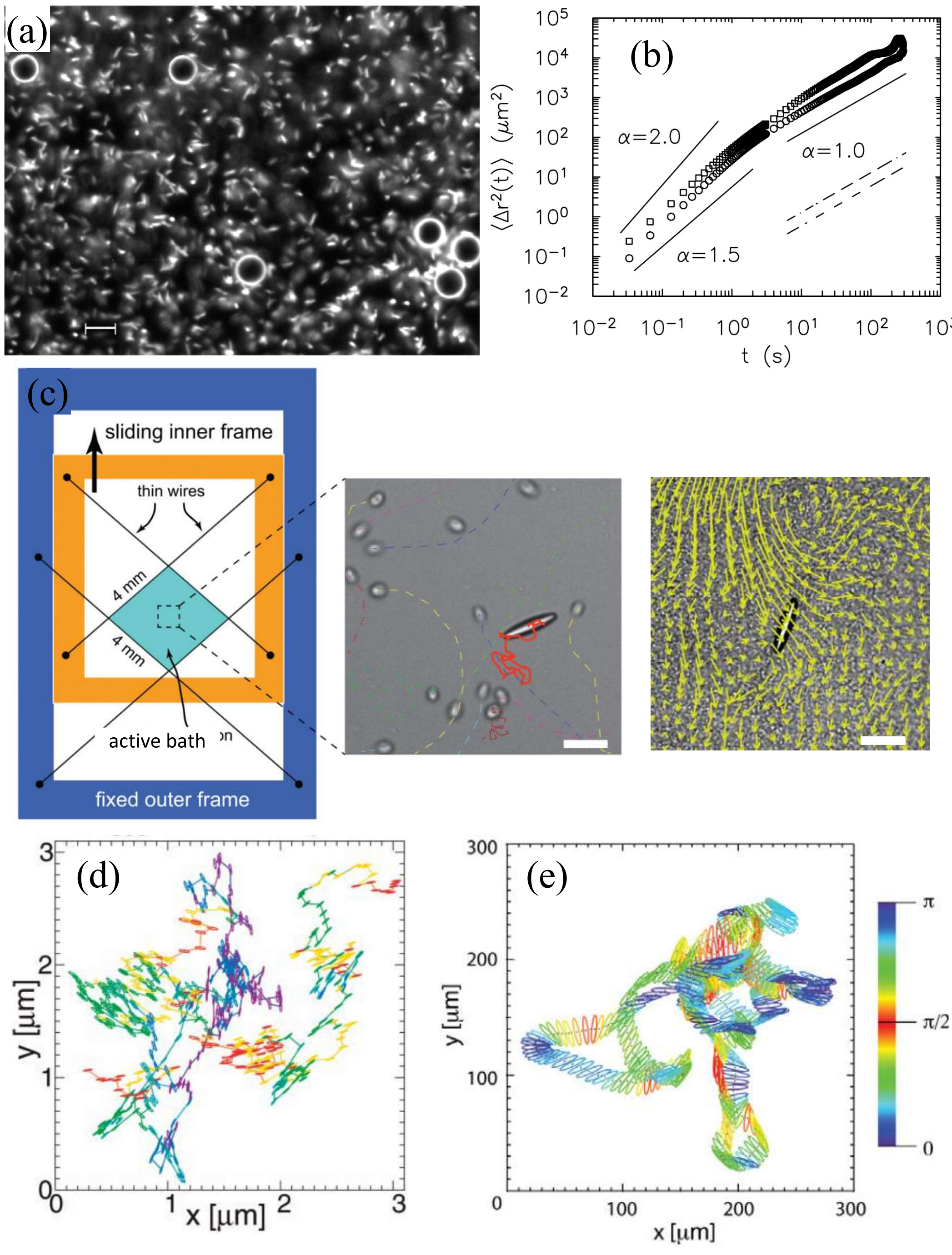

Figure 1.3: **Diffusion of passive tracers in an active bath.** (a) 10 μm diameter PS particles suspended in a bath of E. coli (b) Mean squared displacement (MSD) of tracer paticles as a function of lag time. (c) Free-standing film setup adopted by Peng et al. and Yang et al. (left)[29, 34]. A microscopic image of ellipsoidal PS particle suspending in *C. reinhardtii* (middle) and *E. coli* (right) baths. Scale bar: 20 μm. (d) and (e) present both the translational and orientational trajectories of ellipsoids diffusion in water and *E. coli* bath, respectively. Image courtesy Wu (a, b) [28], Yang (c) [34], Han (d) [63] and Peng (e) [29].

universal animal behavior was found in animals across different length scales: large animals as birds and fish, all the way down to insects or even microorganisms.

In this section, we first review recent progresses on understanding the collective motions in various living and non-living systems. Our research on "imaging the emergence of active turbulence" will be motivated (detailed in Chap. ??). Then, I will describe an important consequence of the collective phenomena: giant number fluctuations, and I will motivate our research on "giant number fluctuations in 3-dimensional bacterial suspensions" (detailed in Chap. 3).

1.3.1 Collective Motion

The research on collective motion dates back to the 1980s, when flocking birds, schooling fish, herding beasts and even human crowds (Fig. 1.1a-d) were regarded as an orientationally ordered phase of living matter, in analogy with ferromagnetic spins [64, 13, 65, 66, 67, 24]. Besides macroscopic systems mentioned above, smaller and more laboratory accessible model systems have joined this family and have been studied extensively. As examples, actin filaments and bacteria exhibit turbulence-like swirling patterns, and synthetic active colloids form dynamic clusters (Fig. 1.1e-g) [68, 17, 69, 26, 70, 71, 72].

While being fascinated by the patterns formed by collectively moving animals or particles, researchers are trying to come up with rules, models and theories to explain and predict this process. There is a vast literature trying to understand collective motions in different systems from various approaches. To get an idea of how extensively it has been studied, Ref [64] by Reynolds has been cited more than 10,000 times so far. I will briefly review the attempts to model collective motion, which are most relevant to our research that will be detailed in the following chapters. A more comprehensive review on the studies of collective motions can be found in the review paper by Vicsek [5]. In 1987, Reynolds came up with arguably the first set of rules to capture the features of collective motions, based on a simple self-propelled particle model. Three rules were set into the system: seperation, alignment and cohesion, as illustrated in Fig. 1.4a-c, where the blue and green triangles in are the actively moving particles in his simulation, called "boids" [64]. In 1995, Vicsek modified Reynolds' model by replacing the separation and cohesion rule with a random perturbation in the velocity of each particle, while keeping the alignment rule, which dictates one particle to always point to the same direction as its neighbors [13]. Due to the simpler and more robust rules compared to Reynolds' model, Vicsek's model was able to simulate huge flocks. In later studies, the Vicsek Model has become a standard model where properties of collective motions are explored [73, 74, 75, 76, 77]. Despite the success of discrete and finite system simulation in understanding 2D collective motions, it was challenging to study long range, long time and higher dimensional dynamics using such approach. In 1995, Toner and Tu wrote down a continuum equation of motion for a "large universality class of models" such as the Vicsek Model based on symmetry and conservation arguments [78]. In 2002, Simha and Ramaswamy made the first attempt to address hydrodynamic effect in self-propelled particle suspensions [15]. Within the framework of liquid crystal physics, they formulated an equation of motion with hydrodynamic terms to account for the "flow-alignment" phenomenon [79]. The inclusion of hydrodynamic effects turned out to be very important, because it directly accounted for phenomena in bacterial suspensions, the largest group of prokaryotic organisms and the most studied model active system. Their theory captures several aspects of bacterial suspensions well, including the emergence of active turbulence and giant number fluctuations as a consequence of bend instability (illustrated in Fig. 1.4d). In 2008, Saintillan and Shelly adapted kinetic theories, which were previously used to study polymers, to study the suspensions of self-propelled particles [80, 81]. Their theory generalized the predictions by Simha and Ramaswamy on the instability, and made interesting investigation on the nonlinear effects, such as pattern formation and efficient fluid mixing. Fig. 1.4e shows one instance of their simulation on the evolution of fluid mixing driven by active pusher swimmers.

Two types of

The existence of hydrodynamic interactions distincts

To test the prediction of the kinetic theory by Saintillan and Shelly, we perform experiment

1.3.2 Giant Number Fluctuations

Large scale inhomogeneity

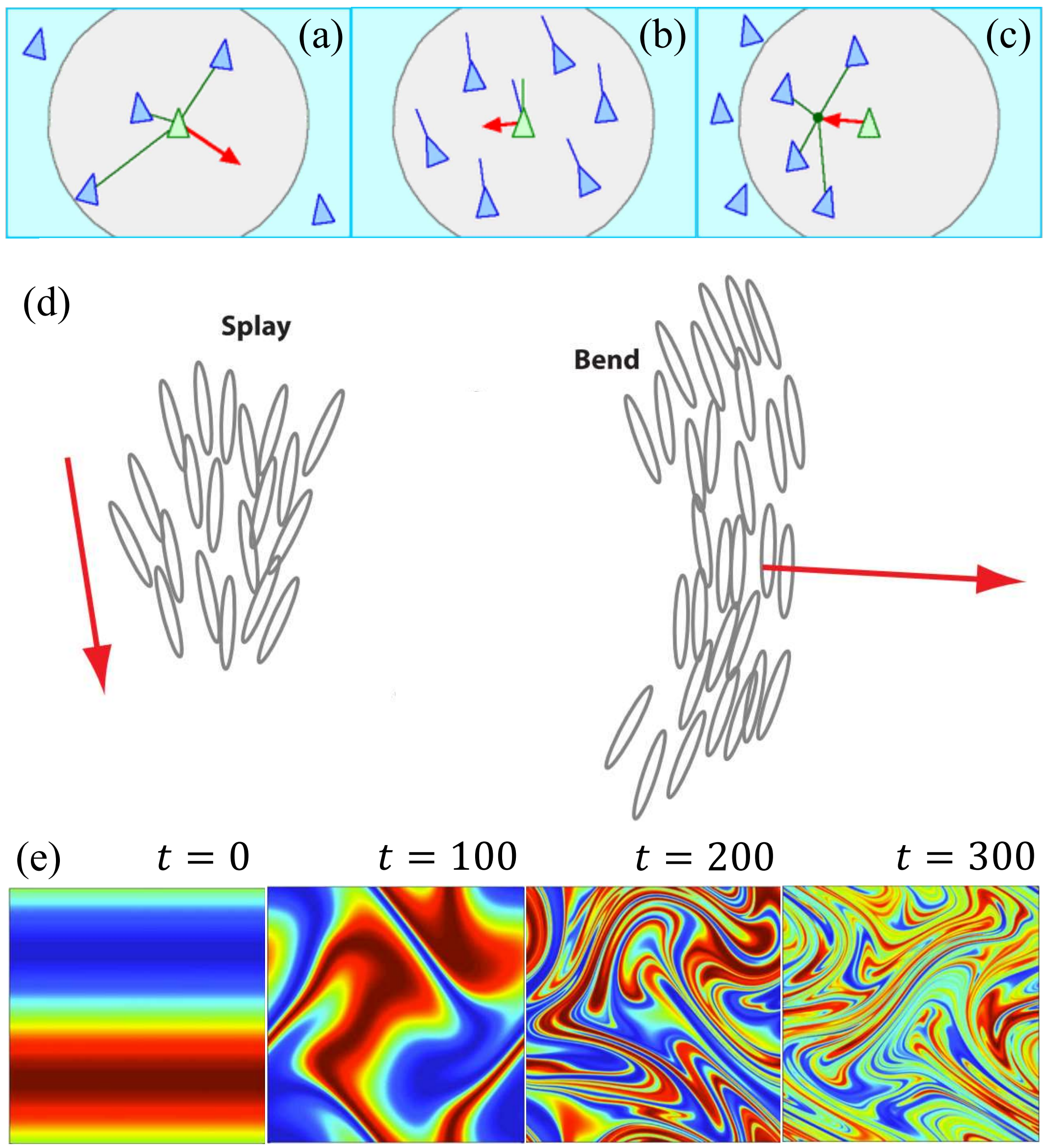

Figure 1.4: **Illustrations of existing models and theories of collective motions.** (a)-(c) Reynolds' "boids" model obeying the rules of separation (a), alignment (b) and cohesion (c). (d) Nematic self-propelled particle model, displaying splay (left) and bend (right) instability. (e) Simulation of efficient fluid mixing driven by active pusher swimmers. Image courtesy of Reynolds (a-c) [64], Ramaswamy (d) [4] and Saintillan (e) [81].

Chapter 2

Rheology of Bacterial Suspensions under Confinement*

2.1 Introduction

2.2 Methods

2.3 Results

2.4 Discussion and Conclusion

*Reproduced in part with permission from (Zhengyang Liu, Kechun Zhang and Xiang Cheng, "Rheology of bacterial suspensions under confinement", *Rheologica Acta*, Springer).

Chapter 3

Giant Number Fluctuations in 3-Dimensional Space

3.1 Introduction

3.2 Methods

3.3 Results

3.4 Discussion and Conclusion

Bibliography

[1] Zhengyang Liu, Kechun Zhang, and Xiang Cheng. Rheology of bacterial suspensions under confinement. *Rheologica Acta*, 58(8), 2019.

[2] Yi Peng, Zhengyang Liu, and Xiang Cheng. Imaging the emergence of bacterial turbulence using light-powered Escherichia coli. *arXiv e-prints*, page arXiv:2003.12399, March 2020, 2003.12399.

[3] John Toner, Yuhai Tu, and Sriram Ramaswamy. Hydrodynamics and phases of flocks. *Annals of Physics*, 318(1 SPEC. ISS.):170–244, 2005.

[4] Sriram Ramaswamy. The Mechanics and Statistics of Active Matter. *Annual Review of Condensed Matter Physics*, 1(1):323–345, 2010, 1004.1933.

[5] Tamás Vicsek and Anna Zafeiris. Collective motion. *Physics Reports*, 517(3-4):71–140, 2012, 1010.5017.

[6] M. C. Marchetti, J. F. Joanny, S. Ramaswamy, T. B. Liverpool, J. Prost, Madan Rao, and R. Aditi Simha. Hydrodynamics of soft active matter. *Reviews of Modern Physics*, 85(3):1143–1189, 2013, 1207.2929.

[7] David Saintillan and Michael J. Shelley. Active suspensions and their nonlinear models. *Comptes Rendus Physique*, 14(6):497–517, 2013.

[8] Clemens Bechinger, Roberto Di Leonardo, Hartmut Löwen, Charles Reichhardt, Giorgio Volpe, and Giovanni Volpe. Active particles in complex and crowded environments. *Reviews of Modern Physics*, 88(4), 2016, 1602.00081.

[9] F. Jülicher, K. Kruse, J. Prost, and J. F. Joanny. Active behavior of the Cytoskeleton. *Physics Reports*, 449(1-3):3–28, 2007.

[10] P. G. De Gennes. Soft matter. *Science*, 256(5056):495–497, 1992.

[11] Sharon C. Glotzer. Editorial: Soft Matters. *Physical Review Letters*, 114(5):5–6, 2015.

[12] B. A. Finlayson and L. E. Scriven. Convective instability by active stress. *Proceedings of the Royal Society of London. Series A, Mathematical and Physical Sciences*, 310(1501):183–219, 1969.

[13] Tamás Vicsek, András Czirók, Eshel Ben-Jacob, Inon Cohen, and Ofer Shochet. Novel type of phase transition in a system of self-driven particles. *Phys. Rev. Lett.*, 75:1226–1229, Aug 1995.

[14] Yashodhan Hatwalne, Sriram Ramaswamy, Madan Rao, and R. Aditi Simha. Rheology of Active-Particle Suspensions. *Physical Review Letters*, 92(11):1–4, 2004, 0308529.

[15] R. Aditi Simha and Sriram Ramaswamy. Hydrodynamic fluctuations and instabilities in ordered suspensions of self-propelled particles. *Physical review letters*, 89(5):058101, 2002, 0108301.

[16] Christopher Dombrowski, Luis Cisneros, Sunita Chatkaew, Raymond E. Goldstein, and John O. Kessler. Self-concentration and large-scale coherence in bacterial dynamics. *Physical Review Letters*, 93(9):2–5, 2004.

[17] Henricus H. Wensink, Jörn Dunkel, Sebastian Heidenreich, Knut Drescher, Raymond E. Goldstein, Hartmut Löwen, and Julia M. Yeomans. Meso-scale turbulence in living fluids. *Proceedings of the National Academy of Sciences of the United States of America*, 109(36):14308–14313, 2012.

[18] Salima Rafaï, Levan Jibuti, and Philippe Peyla. Effective viscosity of microswimmer suspensions. *Physical Review Letters*, 104(9):1–4, 2010, 0909.4193.

[19] Andrey Sokolov and Igor S. Aranson. Reduction of viscosity in suspension of swimming bacteria. *Physical Review Letters*, 103(14):2–5, 2009.

[20] Jérémie Gachelin, Gastón Miño, Hélène Berthet, Anke Lindner, Annie Rousselet, and Éric Clément. Non-newtonian viscosity of escherichia coli suspensions. *Physical Review Letters*, 110(26):1–5, 2013, 1210.2102.

[21] Héctor Matías López, Jérémie Gachelin, Carine Douarche, Harold Auradou, and Eric Clément. Turning Bacteria Suspensions into Superfluids. *Physical Review Letters*, 115(2):1–5, 2015, 1503.05511.

[22] Sriram Ramaswamy. Active fluids. *Nature Reviews Physics*, 1(11):640–642, 2019.

[23] A. I. Curatolo, N. Zhou, Y. Zhao, C. Liu, A. Daerr, J. Tailleur, and J. Huang. Cooperative pattern formation in multi-component bacterial systems through reciprocal motility regulation. *Nature Physics*, 2020.

[24] Jesse L. Silverberg, Matthew Bierbaum, James P. Sethna, and Itai Cohen. Collective motion of humans in mosh and circle pits at heavy metal concerts. *Physical Review Letters*, 110(22):1–5, 2013.

[25] Stephen J. DeCamp, Gabriel S. Redner, Aparna Baskaran, Michael F. Hagan, and Zvonimir Dogic. Orientational order of motile defects in active nematics. *Nature Materials*, 14(11):1110–1115, 2015, 1501.06228.

[26] Jeremie Palacci, Stefano Sacanna, Asher Preska Steinberg, David J Pine, and Paul M Chaikin. Colloidal Surfers. *Science*, 339(February):936–939, 2013.

[27] David Saintillan. Rheology of Active Fluids. *Annual Review of Fluid Mechanics*, 50(1):563–592, 2018.

[28] Xiao-Lun Wu and Albert Libchaber. Particle diffusion in a quasi-two-dimensional bacterial bath. *Phys. Rev. Lett.*, 84:3017–3020, Mar 2000.

[29] Yi Peng, Lipeng Lai, Yi Shu Tai, Kechun Zhang, Xinliang Xu, and Xiang Cheng. Diffusion of ellipsoids in bacterial suspensions. *Physical Review Letters*, 116(6):1–5, 2016, 1509.05893.

[30] Avi Caspi, Rony Granek, and Michael Elbaum. Enhanced Diffusion in Active Intracellular Transport. *Physical Review Letters*, 85(26):5655–5658, 2000.

[31] Alexander Morozov and Davide Marenduzzo. Enhanced diffusion of tracer particles in dilute bacterial suspensions. *Soft Matter*, 10(16):2748–2758, 2014.

[32] Alison E. Patteson, Arvind Gopinath, Prashant K. Purohit, and Paulo E. Arratia. Particle diffusion in active fluids is non-monotonic in size. *Soft Matter*, 12(8):2365–2372, 2016, 1505.05803.

[33] Kyriacos C. Leptos, Jeffrey S. Guasto, J. P. Gollub, Adriana I. Pesci, and Raymond E. Goldstein. Dynamics of Enhanced Tracer Diffusion in Suspensions of Swimming Eukaryotic Microorganisms. *Physical Review Letters*, 103(19):1–4, 2009.

[34] O. Yang, Y. Peng, Z. Liu, C. Tang, X. Xu, and X. Cheng. Dynamics of ellipsoidal tracers in swimming algal suspensions. *Physical Review E*, 94(4), 2016.

[35] Chantal Valeriani, Martin Li, John Novosel, Jochen Arlt, and Davide Marenduzzo. Colloids in a bacterial bath: Simulations and experiments. *Soft Matter*, 7(11):5228–5238, 2011, 1109.4111.

[36] Hüseyin Kurtuldu, Jeffrey S. Guasto, Karl A. Johnson, and J. P. Gollub. Enhancement of biomixing by swimming algal cells in two-dimensional films. *Proceedings of the National Academy of Sciences of the United States of America*, 108(26):10391–10395, 2011.

[37] A. Einstein. Eine neue bestimmung der moleküldimensionen. *Annalen der Physik*, 324(2):289–306, 1906, https://onlinelibrary.wiley.com/doi/pdf/10.1002/andp.19063240204.

[38] Dieter Forster. Microscopic theory of flow alignment in nematic liquid crystals. *Physical Review Letters*, 32(21):1161–1164, 1974.

[39] M. E. Cates, S. M. Fielding, D. Marenduzzo, E. Orlandini, and J. M. Yeomans. Shearing active gels close to the isotropic-nematic transition. *Physical Review Letters*, 101(6):1–4, 2008, 0805.1925.

[40] Luca Giomi, Tanniemola B. Liverpool, and M. Cristina Marchetti. Sheared active fluids: Thickening, thinning, and vanishing viscosity. *Physical Review E - Statistical, Nonlinear, and Soft Matter Physics*, 81(5):1–9, 2010, 1002.0517.

[41] S. C. Takatori and J. F. Brady. Superfluid Behavior of Active Suspensions from Diffusive Stretching. *Physical Review Letters*, 118(1):1–5, 2017.

[42] Antoine Bricard, Jean Baptiste Caussin, Nicolas Desreumaux, Olivier Dauchot, and Denis Bartolo. Emergence of macroscopic directed motion in populations of motile colloids. *Nature*, 503(7474):95–98, 2013, 1311.2017.

[43] M. Cristina Marchetti. Soft matter: Frictionless fluids from bacterial teamwork. *Nature*, 525(7567):37–39, 2015.

[44] R. Voituriez, J. F. Joanny, and J. Prost. Spontaneous flow transition in active polar gels. *Europhysics Letters*, 70(3):404–410, 2005, 0503022.

[45] Miha Ravnik and Julia M. Yeomans. Confined active nematic flow in cylindrical capillaries. *Physical Review Letters*, 110(2):1–5, 2013, 1212.3174.

[46] H. Wioland, E. Lushi, and R. E. Goldstein. Directed collective motion of bacteria under channel confinement. *New Journal of Physics*, 18(7), 2016, 1603.01143.

[47] Kun Ta Wu, Jean Bernard Hishamunda, Daniel T.N. Chen, Stephen J. DeCamp, Ya Wen Chang, Alberto Fernández-Nieves, Seth Fraden, and Zvonimir Dogic. Transition from turbulent to coherent flows in confined three-dimensional active fluids. *Science*, 355(6331), 2017, 1705.02030.

[48] Francis G. Woodhouse and Raymond E. Goldstein. Spontaneous circulation of confined active suspensions. *Physical Review Letters*, 109(16), 2012, 1207.5349.

[49] Hugo Wioland, Francis G. Woodhouse, Jörn Dunkel, John O. Kessler, and Raymond E. Goldstein. Confinement stabilizes a bacterial suspension into a spiral vortex. *Physical Review Letters*, 110(26):1–5, 2013, 1304.2875.

[50] Enkeleida Lushi, Hugo Wioland, and Raymond E. Goldstein. Fluid flows created by swimming bacteria drive self-organization in confined suspensions. *Proceedings*

of the National Academy of Sciences of the United States of America, 111(27):9733–9738, 2014, 1407.3633.

[51] Andrey Sokolov, Mario M. Apodaca, Bartosz A. Grzybowski, and Igor S. Aranson. Swimming bacteria power microscopic gears. *Proceedings of the National Academy of Sciences of the United States of America*, 107(3):969–974, 2010.

[52] Alex E. Hamby, Dhruv K. Vig, Sasha Safonova, and Charles W. Wolgemuth. Swimming bacteria power microspin cycles. *Science Advances*, 4(12), 2018.

[53] Roberto Alonso-Matilla, Barath Ezhilan, and David Saintillan. Microfluidic rheology of active particle suspensions: Kinetic theory. *Biomicrofluidics*, 10(4):18–26, 2016.

[54] Jonasz Słomka and Jörn Dunkel. Geometry-dependent viscosity reduction in sheared active fluids. *Physical Review Fluids*, 2(4):9–12, 2017, 1608.01757.

[55] Todd M. Squires and Thomas G. Mason. Fluid mechanics of microrheology. *Annual Review of Fluid Mechanics*, 42:413–438, 2010.

[56] Patrick T. Underhill, Juan P. Hernandez-Ortiz, and Michael D. Graham. Diffusion and spatial correlations in suspensions of swimming particles. *Physical Review Letters*, 100(24):1–4, 2008, 0805.3784.

[57] Zhi Lin, Jean Luc Thiffeault, and Stephen Childress. Stirring by squirmers. *Journal of Fluid Mechanics*, 669:167–177, 2011, 1007.1740.

[58] Ramin Golestanian. Anomalous diffusion of symmetric and asymmetric active colloids. *Physical Review Letters*, 102(18):1–4, 2009, 0904.3044.

[59] D. T.N. Chen, A. W.C. Lau, L. A. Hough, M. F. Islam, M. Goulian, T. C. Lubensky, and A. G. Yodh. Fluctuations and rheology in active bacterial suspensions. *Physical Review Letters*, 99(14):1–4, 2007, 0709.1465.

[60] Gastón Miño, Thomas E. Mallouk, Thierry Darnige, Mauricio Hoyos, Jeremi Dauchet, Jocelyn Dunstan, Rodrigo Soto, Yang Wang, Annie Rousselet, and Eric Clement. Enhanced diffusion due to active swimmers at a solid surface. *Physical Review Letters*, 106(4):1–4, 2011, 1012.4624.

[61] G. L. Miño, J. Dunstan, A. Rousselet, E. Clément, and R. Soto. Induced diffusion of tracers in a bacterial suspension: Theory and experiments. *Journal of Fluid Mechanics*, 729:423–444, 2013, 1210.7704.

[62] T. V. Kasyap, Donald L. Koch, and Mingming Wu. Hydrodynamic tracer diffusion in suspensions of swimming bacteria. *Physics of Fluids*, 26(8), 2014.

[63] Y. Han, A. M. Alsayed, M. Nobili, J. Zhang, T. C. Lubensky, and A. G. Yodh. Brownian motion of an ellipsoid. *Optics InfoBase Conference Papers*, (October):626–631, 2006.

[64] Craig W Reynolds. Flocks-Hers-and-Schools. 21(July):25–34, 1987.

[65] Vijay Narayan, Sriram Ramaswamy, and Narayanan Menon. Long-Lived Giant Number Fluctuations. *Science*, 317(July):105–108, 2007, 0612020.

[66] Ashley J.W. Ward, David J.T. Sumpter, Iain D. Couzin, Paul J.B. Hart, and Jens Krause. Quorum decision-making facilitates information transfer in fish shoals. *Proceedings of the National Academy of Sciences of the United States of America*, 105(19):6948–6953, 2008.

[67] M. Ballerini, N. Cabibbo, R. Candelier, A. Cavagna, E. Cisbani, I. Giardina, V. Lecomte, A. Orlandi, G. Parisi, A. Procaccini, M. Viale, and V. Zdravkovic. Interaction ruling animal collective behavior depends on topological rather than metric distance: Evidence from a field study. *Proceedings of the National Academy of Sciences of the United States of America*, 105(4):1232–1237, 2008.

[68] Jörn Dunkel, Sebastian Heidenreich, Knut Drescher, Henricus H. Wensink, Markus Bär, and Raymond E. Goldstein. Fluid dynamics of bacterial turbulence. *Physical Review Letters*, 110(22):1–5, 2013, 1302.5277.

[69] Ivo Buttinoni, Julian Bialké, Felix Kümmel, Hartmut Löwen, Clemens Bechinger, and Thomas Speck. Dynamical clustering and phase separation in suspensions of self-propelled colloidal particles. *Physical Review Letters*, 110(23):1–5, 2013, 1305.4185.

[70] Tim Sanchez, Daniel T.N. Chen, Stephen J. Decamp, Michael Heymann, and Zvonimir Dogic. Spontaneous motion in hierarchically assembled active matter. *Nature*, 491(7424):431–434, 2012.

[71] Volker Schaller, Christoph Weber, Christine Semmrich, Erwin Frey, and Andreas R. Bausch. Polar patterns of driven filaments. *Nature*, 467(7311):73–77, 2010.

[72] Andrey Sokolov, Igor S. Aranson, John O. Kessler, and Raymond E. Goldstein. Concentration dependence of the collective dynamics of swimming bacteria. *Physical Review Letters*, 98(15):1–4, 2007, 1101.3387.

[73] Guillaume Grégoire and Hugues Chaté. Onset of Collective and Cohesive Motion. *Physical Review Letters*, 92(2):4, 2004, 0401208.

[74] Hugues Chaté, Francesco Ginelli, Guillaume Grégoire, and Franck Raynaud. Collective motion of self-propelled particles interacting without cohesion. *Physical Review E - Statistical, Nonlinear, and Soft Matter Physics*, 77(4):1–15, 2008, 0712.2062.

[75] Francesco Ginelli, Fernando Peruani, Markus Bär, and Hugues Chaté. Large-scale collective properties of self-propelled rods. *Physical Review Letters*, 104(18):1–4, 2010, 0911.1924.

[76] Sandrine Ngo, Anton Peshkov, Igor S. Aranson, Eric Bertin, Francesco Ginelli, and Hugues Chaté. Large-scale chaos and fluctuations in active nematics. *Physical Review Letters*, 113(3):1–6, 2014, 1312.1076.

[77] Benoît Mahault, Francesco Ginelli, and Hugues Chaté. Quantitative Assessment of the Toner and Tu Theory of Polar Flocks. *Physical Review Letters*, 123(21):1–6, 2019, 1908.03794.

[78] John Toner and Yuhai Tu. Long-range order in a two-dimensional dynamical XY model: How birds fly together. *Physical Review Letters*, 75(23):4326–4329, 1995, 9506001.

[79] Dieter Forster. *Hydrodynamic Fluctuations, Broken Symmetry, and Correlation Functions*. 1975.

[80] David Saintillan and Michael J. Shelley. Instabilities and pattern formation in active particle suspensions: Kinetic theory and continuum simulations. *Physical Review Letters*, 100(17):1–4, 2008.

[81] David Saintillan and Michael J. Shelley. Hydrodynamic fluctuations and instabilities in ordered suspensions of self-propelled particles. *Physics of Fluids*, 20(12):123304, 2008, 0108301.