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The statistical physics of active matter: From self-catalytic colloids to living cells

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ABSTRACT

These lecture notes are designed to provide a brief introduction into the phenomenology of active matter and to present some of the analytical tools used to rationalize the emergent behavior of active systems. Such systems are made of interacting agents able to extract energy stored in the environment to produce sustained directed motion. The local conversion of energy into mechanical work drives the system far from equilibrium, yielding new dynamics and phases. The emerging phenomena can be classified depending on the symmetry of the active particles and on the type of microscopic interactions. We focus here on steric and aligning interactions, as well as interactions driven by shape changes. The models that we present are all inspired by experimental realizations of either synthetic, biomimetic or living systems. Based on minimal ingredients, they are meant to bring a simple and synthetic understanding of the complex phenomenology of active matter.

1. Introduction

Active matter consists of systems made of a large number of interacting constituents able to convert some source of energy stored in the environment into directed motion [1–3]. In contrast with driven systems, for which the departure from equilibrium is controlled by an external field or through boundary conditions, the breakdown of time reversal symmetry, characteristic of nonequilibrium dynamics, occurs at the level of individual components. The drive is local and sustained, being independent for each active agent. The large scale behavior emerges from collective self-organization, leading to novel phenomena such as nonequilibrium phase transitions and collective directed motion.

Examples of interacting self-propelled agents can be found at different scales. Bacteria and self-catalytic colloids are canonical examples of active particles at the micro-scale, with typical self-propulsion speed of the order of 10 μm/s [4–6]. Tracers in living cells, reflecting the intracellular activity of molecular motors and cytoskeletal filaments, also follow an active dynamics [7–10]. A living cell in itself can be regarded as an active "particle", with size of about 10 μm and speed of the order of 10 μm/h. Assembly of such cells in epithelial tissues exhibit collective migration that underlies development and organ formation [11–13]. At larger scales, groups of animals such as bird flocks, fish schools, or even a human crowd can be modeled as interacting self-propelled agents [14].

As a novel class of nonequilibrium systems, active matter has been at the center of various studies during the past decades. The modeling of active systems merges tools from statistical mechanics, soft matter and hydrodynamics. One of the main goal is to explore and classify the various emergent phases, and to understand how phase transitions are controlled by

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the microscopic interactions [2]. Identifying generic properties of such phases allows one to classify the spontaneous self-organization depending on the type of active components. As an example, the orientational order depend on the shape and symmetry of the microscopic agents: (i) ferromagnetic-like order is observed when the particles are polar, namely when they have distinct head and tail [15,16]; (ii) nematic order is reported for apolar particles with head–tail symmetry [17,18]; (iii) no orientational order appears when particles are spherical in shape, yet other surprising collective behaviors emerges due to the self-propulsion [3,19,20]. The role of the surrounding medium allows for another classification. We focus here on the case where the medium is regarded as an inert substrate only providing some passive friction, so that the momentum of the particles is not conserved.

The lecture notes are organized as follows. After a brief review of the dynamics of a passive Brownian particle in an equilibrium thermal bath, Section 2 presents generic minimal models that have emerged as paradigm for the phenomenological modeling of collections of self-propelled particles. We first describe noninteracting particles by discussing the properties of both the free motion and the density profile under confinement. Section 3 is dedicated to interacting agents. We first discuss strategies that can be employed to obtain an effective hydrodynamic theory. We present separately the treatment of steric and alignment interactions, revealing respectively the possibility of a phase separation even when interactions are purely repulsive, and the emergence of collective directed motion in ordered states. Finally, we discuss how particle models have recently been adapted to describe dense epithelial tissues by merging the Vertex Model that describes cells as irregular polygons that tile the plane with active matter ideas to develop a model of motile cells where the behavior is tuned by cellular shape. We conclude with a brief discussion and outlook.

2. A single active particle: a first insight into the phenomenology of active matter

2.1. Passive Brownian particle

In the early twentieth century, the experiment by Jean Perrin was one of the first attempts to extract quantitative information from the random trajectories of colloidal grains suspended in water [21]. Perrin noticed that the instantaneous velocity of the grains could not be quantified properly due to the discontinuities in their trajectories. This finding motivated the phenomenological description proposed by Paul Langevin [22]. He postulated that the effect of the solvent on the colloids could be separated into two contributions: a mean drag force $-\zeta\mathbf{v}$ opposed to the displacement, where ζ denotes the friction coefficient, and a random force $(2B)^{1/2}\boldsymbol{\xi}$ describing the effect of collisions by solvents atoms that drive the colloid motion. Assuming that the colloid has a mass m and is subject to a potential U, the dynamics follows from Newton's second law,

$$m\dot{\mathbf{v}} = -\nabla U - \zeta\mathbf{v} + (2B)^{1/2}\boldsymbol{\xi}. \tag{1}$$

This is the seminal Langevin equation, in its underdamped version, describing the dynamics of a passive Brownian particle (PBP). The random force is taken as a Gaussian white noise with correlations $\left\langle \xi_\alpha(t)\xi_\beta(0)\right\rangle = \delta_{\alpha\beta}\delta(t)$. The Langevin equation allows one to predict the time evolution of a number of observables. In the absence of potential, the average velocity squared is given by

$$\left\langle [\mathbf{v}(t)]^2\right\rangle = d\frac{B}{m\zeta}\left(1-\mathrm{e}^{-2|t|/\tau_\mathrm{m}}\right), \tag{2}$$

where we have introduced the inertial time scale $\tau_\mathrm{m} = m/\zeta$, and d denotes the spatial dimension. We have assumed that the initial velocity is zero. At large times, the equipartition theorem relates the velocity fluctuations to the solvent temperature as $\left\langle \mathbf{v}^2\right\rangle = d(T/m)$, where we have set the Boltzmann constant to unity. The amplitude of the noise is then fixed by $B = \zeta T$. In the absence of potential, the mean-square displacement (MSD) $\left\langle \Delta\mathbf{r}^2(t)\right\rangle = \left\langle [\mathbf{r}(t)-\mathbf{r}(0)]^2\right\rangle$ can be obtained from Eq. (1) as

$$\left\langle \Delta\mathbf{r}^2(t)\right\rangle = 2d\frac{T}{\zeta}\left[|t| - \tau_\mathrm{m}\left(1-\mathrm{e}^{-|t|/\tau_\mathrm{m}}\right)\right] = \begin{cases} d\dfrac{T}{\zeta}\dfrac{t^2}{\tau_\mathrm{m}} & \text{for } t \ll \tau_\mathrm{m}, \\ 2d\dfrac{T}{\zeta}|t| & \text{for } t \gg \tau_\mathrm{m}. \end{cases} \tag{3}$$

The particle's motion is ballistic at short times and diffusive at large times. The translational diffusion coefficient $D_\mathrm{t} = \lim_{t\to\infty}\left\langle \Delta\mathbf{r}^2(t)\right\rangle/2dt$ can be expressed in terms of the temperature and the friction coefficient via the Einstein relation: $D_\mathrm{t} = T/\zeta$. The diffusion coefficient is also related to the velocity autocorrelation through the Green–Kubo formula,

$$D_\mathrm{t} = \frac{1}{d}\int_0^\infty \langle \mathbf{v}(t)\cdot\mathbf{v}(0)\rangle\,\mathrm{d}t. \tag{4}$$

This can be regarded as a simplified statement of the fluctuation–dissipation theorem which connects the amplitude of fluctuations with the relaxation of the system [23]. It formally expresses the fact that the random force and the damping force originate from the same microscopic processes, namely the collision between the colloid and the surrounding solvent particles.

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