Charles University in Prague

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HABILITATION THESIS

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Řízení pohyblivé aktivní hmoty: dynamika a energetika

Steering motile active matter: dynamics and energetics

Department of Macromolecular Physics

Specialization: Theoretical Physics

Prague 2023

Contents

1 Introduction

Motile active matter is a vibrant multidisciplinary field that brings together physicists, biologists, and even social engineers. It uses tools from theoretical and experimental physics to understand the dynamics of self-propelling particles in various environments, interactions among them, and emergent behaviors in their large assemblies[4–7]. As shown in FIGURE 1.1, systems of interest range from self-propelled colloids[8–10], over motile cells, filaments, tissues and bacteria[11,12], flocking insects[13–15] and birds[16], and schools of fish[17] to the coordinate motion of ants[18] and the crowding of pedestrians[19].

Active matter systems at all scales share three characteristic features. First, they are driven out of equilibrium on the level of single particles, which irreversibly transform some fuel into a directed motion. The nonequilibrium state is thus sustained by the

Figure 1.1: Motile active matter. Examples of natural (top) and artificial (bottom) active matter systems across length scales. Except for the chemically propelled Janus particles[1], the optically steered symmetric active particles[2] (both bottom left), and the 'vibrobots'[3] (bottom middle), the sources are given inside the individual figures.

inflow of the fuel or food into the system, rather than, e.g., heating and cooling the walls as in a boundary-driven nonequilibrium system. The second important ingredient of active matter is that its effective dynamics can disobey standard thermodynamic limitations, such as the fluctuation-dissipation theorem, or even more universal symmetries, such as reciprocity. This is because the 'social' or 'feedback' interactions result from a complicated coarse-graining of the microscopic degrees of freedom far from thermodynamic equilibrium. The third characteristic feature of active matter is that the interactions often involve a time delay. Intuitively, these delays result from limited speeds of information transfer between and inside the individuals, decision-making, and body transformation of the individuals. Mathematically, the delays derive from the coarse-graining of time-local dynamics of the microscopic degrees of freedom.

The ultimate goal of the field of active matter is to provide an understanding of evolutionary mechanisms which led to the variety of behaviors observed in nature. A technical part of this task is to describe these behaviors theoretically by developing suitable generalizations of the tools of equilibrium statistical physics. A more practical objective is to create well-controlled (not necessarily artificial) counterparts of natural active particles, able to, e.g., perform medical tasks on the level of individual cells[20] or to form distributed collectively communicating sensorial networks on the macroscale[21].

This habilitation thesis is divided into two major parts summarizing the author's contributions to understanding the dynamics and energetics (or thermodynamics) of active matter. CHAPTER 2 investigates how to utilize the activity of single active particles or their ensembles to perform useful work or induce transport. CHAPTER 3 is devoted to the study of the effects of time-delayed interactions in active matter systems. Both these chapters are conceived as overviews of the corresponding parts of active matter research with a summary of the author's contributions, reprinted in the CHAPTER 7 of this thesis in the same order in which they appear in the text.

Most of the papers discussed in the thesis were written or conceived during the postdoctoral stay of the author in the group of Prof. Klaus Kroy at Uni. Leipzig. Therefore, up to a few exceptions, the presented work aims to describe overdamped active particles, such as bacteria or driven colloids, which are investigated experimentally in the group of Prof. Frank Cichos from Uni. Leipzig. The thesis contains only works where the author's contribution was significant. With a single exception, it does not contain the authors' contributions to the study of noise-induced coherence[22;23], maximum efficiency at fixed power[24–28], unstable stochastic systems[29–32], classical Brownian ratchets[29–32], optimal control of stochastic heat engines[33,34], and work fluctuations in small systems[35–46].

2 Active matter engines

Microscopic active particles such as artificial active colloids or bacteria have been employed to perform useful work in two conceptually different ways. The first one, exemplified in FIGURE 2.1a, aims to treat the system of active particles as a non-equilibrium heat bath and to transform the disordered energy from this bath into useful work via so-called active Brownian heat engines[47,51]. The second approach, depicted in FIGURE 2.1b-d, aims to harvest the energy of the active motion more directly by rectifying the

Figure 2.1: Extracting energy from active matter. Panel a) shows a colloidal particle confined by a harmonic potential in an active bath composed of living bacteria in water[47]. In this setup, energy is extracted from the active bath by varying in time the bath's activity (e.g., by reducing food content in the solvent) and the stiffness of the potential. The remaining panels show various ways to rectify (or directionalize) erratic motion of bacteria. In panel b), the bacteria are trapped between a cog wheel's asymmetric tooth to rotate it[48]. In panel c), a similar asymmetry of channel walls induces a directed (average) motion of bacteria[49]. Panel d) shows how to create a likewise directed motion of active particles by making the particle speed position-dependent instead of using potentials or walls[50].

direction of self-propulsion of otherwise randomly turning active Brownian particles via obstacles[48,49] or other ratchet-like mechanisms[50].

Of course, in both these cases, the energy of the autonomous motion of the active particles is transformed into work. Based on the mechanism underlying the autonomous motion, this energy conversion can be identified as heat-to-work conversion (for thermophoretically propelled swimmers) or as work-to-work conversion (for chemically propelled swimmers). The conceptual distinction between active heat engines and other engines is thus motivated rather theoretically than practically. The energy extracted from active matter systems can be identified as heat if one finds an equivalent setup with an equilibrium bath that would yield the same engine's performance. The temperature of the equilibrium bath can then be interpreted as the active system's effective temperature that allows attributing the energy flux from the active bath with a valid (second law) entropy production. The effective temperature then replaces thermodynamic temperature in standard upper bounds on the engine performance, such as the

Figure 2.2: Energy fluxes during energy extraction from active matter. An engine transforming the heat flux $\dot{q} = \dot{q}_{neq} + \dot{q}_{eq}$ from a non-equilibrium active matter system (neq) and perhaps also an equilibrium (eq) heat reservoir into usable power $\dot{w}$. The corresponding energy fluxes relevant for the engine's operation are depicted by arrows. The dashed arrow depicts the housekeeping heat flux, $\dot{q}_{hk}$, flowing from the active bath to the infinite equilibrium reservoir, which prevents the active bath from overheating. This energy flux and also $\dot{q}_{neq}$ are sustained by the energy influx $\dot{q}_{hk}+\dot{q}_{neq}$ into the non-equilibrium bath, which keeps it in a non-equilibrium "active" steady state. Template for the figure was taken from Ref.[51] (Publication 7.1).

Carnot's efficiency, which still limit active heat engines' performance. When an effective temperature does not exist, the active engines' efficiency is limited only by the trivial first law bound on the efficiency of work-to-work conversion, i.e., by one.

FIGURE 2.2 shows a diagram of energy fluxes involved in any energy extraction from an active matter system in a steady state. To stay active or, in other words, alive, the active matter system consumes per unit time the amount of energy $\dot{q}_{hk} + \dot{q}_{neq}$. If no energy is extracted from the active matter system, all this power has to be dissipated in a heat reservoir (or heat sink). Otherwise, the active matter system would overheat. Assuming that the power $\dot{q}_{neq}$ is extracted from the active matter system, the power delivered to the heat sink is $\dot{q}_{hk}$. In general, the engine dissipates a heat flux $\dot{q}_{eq}$ into the equilibrium reservoir and transforms into work only the rest of its energy influx $\dot{w} = \dot{q}_{neq} - \dot{q}_{eq}$. In majority of active matter engines, the energy influx $\dot{q}_{neq}$ depends just on the dynamics of the individual active particles, not on the type of their self-propelling mechanism. In particular, $\dot{q}_{neq}$ is usually independent of the efficiency with which the engines in the individual active particles transform the overall energy influx $\dot{q}_{hk} + \dot{q}_{neq}$ into their activity. Hence, it is reasonable to characterise the engine performance by the efficiency $\eta = \dot{w}/\dot{q}_{neq}$ of conversion of $\dot{q}_{neq}$ into the power $\dot{w}$, rather than the overall efficiency $\dot{w}/(\dot{q}_{neq} + \dot{q}_{hk})$ of the engine and active matter system. The latter efficiency is strongly system-dependent and usually tiny. For an active heat engine, η is in general limited by the Carnot's efficiency $\eta_C = 1 - T_c^{\text{eff}}/T_h^{\text{eff}}$ with largest and smallest values of the effective temperature T_c^{eff} and T_h^{eff} experienced by the engine. For an active engine, where an effective temperature cannot be defined, $\eta < 1$.

In the rest of this section, I first briefly introduce periodically driven active heat engines and review our results for them in SECTION 2.1. Next, in SECTION 2.2, I highlight some of our general results, which hold both for active and standard periodically driven (heat) engines. Finally, in SECTION 2.3, I present our results on active ratchets that autonomously rectify the motion of active particles.

2.1 Active heat engines (Refs.[51–56])

As described above, the main theoretical difficulty in deciding whether an active engine can be treated as an active heat engine, and thus one can assess its performance using results valid for heat engines in contact with equilibrium heat reservoirs, is to determine if an effective temperature can describe the active bath. Motivated by the experimental realization of the 'Bacteria heat engine'[47], depicted in FIGURE 2.1a, and the claims made in this work that its efficiency can surpass the second law upper bound on the

efficiency of the corresponding thermodynamic (Stirling) cycle, which is conceptually an erroneous statement as that would mean that the engine investigated in this work is not a heat engine *, my colleagues and I wrote two papers[51,56] explaining when the effective temperature exists.

2.1.1 Effective temperature in overdamped active heat engines (Ref.[51])

In PUBLICATION 7.1[51] we have shown that effective temperature in general exists for engines described by Hamiltonian of the form

$$H = k(t)f(\mathbf{x}),\tag{2.1}$$

where $k(t)$ is an externally controlled parameter periodically varied in time, $\mathbf{x}$ denotes degrees of freedom of the engine, and f stands for a confining potential (such that the equilibrium partition function $\int d\mathbf{x} \exp(-\beta H)$ is finite for any positive inverse temperature β). The Hamiltonian describes the engine part of the compound bath-engine system; the existence of the effective temperature is, thus, in this case, independent of the details of the bath and the bath-engine coupling. Furthermore, this result is valid regardless of the details of the dynamics, which can thus be arbitrary, including non-Markovian, quantum, or other dynamics (even though the calculation of the effective temperature might sometimes be challenging). It thus proves that the efficiency analysis presented in Ref.[47] is unavoidably wrong not only conceptually but also numerically as the corresponding Hamiltonian $H = k(t)(x^2 + y^2)$ is of the form (2.1) and thus there certainly exists an effective temperature that allows limiting the efficiency of the engine below the ultimate second law bound. This illustrates how our result can serve as a simple sanity check of measured or calculated efficiencies of active heat engines.

To understand why an effective temperature can be always found for Hamiltonians of the form (2.1) but not for more general ones, e.g., containing also a kinetic energy $\mathbf{p}^2/2m$, it is enough to write down expressions for average heat and work fluxes

$$\dot{q}(t) = k(t)\dot{\sigma}_x(t) + \dot{\sigma}_p(t)/m \tag{2.2}$$
$$\dot{w}(t) = \dot{k}(t)\sigma_x(t), \tag{2.3}$$

where $\sigma_x(t) = \langle f(\mathbf{x})\rangle$ and $\sigma_p(t) = \langle \mathbf{p}^2\rangle/2$ ($\langle \bullet \rangle$ denotes the ensemble average). These

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*Similar claims of surpassing second law efficiencies by using non-equilibrium 'heat' reservoirs (such as various quantum squeezed baths[57]) fall into the very same category, pointing to authors' desire to sell their research well in high-impact journals rather than deep physics break troughs.

expressions follow from the first law[40] by identifying the changes of internal energy $U = \langle H \rangle = \langle k(t)f(\mathbf{x}) + \mathbf{p}^2/2m \rangle$ of the system related to the variation of the control parameter $k(t)$ as work, and the rest of $\dot{U}$ as heat. The work and heat fluxes are thus determined by the 'response' functions $\sigma_x(t)$ and $\sigma_p(t)$. A non-equilibrium bath can be prescribed an effective temperature $T_{\text{eff}}(t)$ if there is an equivalent setup with the same time-dependent Hamiltonian H and equilibrium heat bath at a time-dependent temperature $T_{\text{eff}}(t)$, which yields the same heat and work fluxes $\dot{w}$ and $\dot{q}$ (and thus the response functions $\sigma_x(t)$ and $\sigma_p(t)$) as the setup with non-equilibrium bath. In general, the response functions are functionals of the driving parameters determined by details of the engine and bath dynamics, and the time-dependent effective temperature has to be such that the functionals for the two setups agree numerically. It is reasonable to assume that finding such a mapping should always be possible when one needs to match a single functional, e.g., $\sigma_x(t)$. However, matching two or more functionals (such as when considering momentum degrees of freedom) by modifying the single effective temperature might not always be possible.

The simplest and most important situation demonstrating this conclusion is quasi-static driving. Then the distribution for $\{\mathbf{x}, \mathbf{p}\}$ at any time t has the Boltzmann form $p(\mathbf{x}, \mathbf{p}, t) = \frac{1}{Z} \exp\left(-\frac{k(t)f(\mathbf{x})}{k_{\text{B}}T_{\text{eff}}}\right) \exp\left(-\frac{\mathbf{p}^2}{2mk_{\text{B}}T_{\text{eff}}}\right)$ (Z stands for partition function and k_B the Boltzmann constant). The averages $\sigma_x(t)$ and $\sigma_p(t)$ then follow as integrals over $p(\mathbf{x}, \mathbf{p}, t)$. It is always possible to tune the effective temperature T_{eff} to match any given value of one of these averages. However, the resulting T_{eff} also automatically determines the other average. Thus, it is generally impossible to find an equilibrium setup that would match an arbitrary couple $\sigma_x(t)$ and $\sigma_p(t)$ resulting from the dynamics with a non-equilibrium bath that defies restrictions imposed by equilibrium dynamics, and similarly for more complicated settings. For an analysis when T_{eff} exists in settings with non-negligible momentum, see SUBSECTION 2.1.2.

In PUBLICATION 7.1[51] we have also shown how to calculate the time dependent effective temperature for the specific dynamics considered in Ref.[47] with arbitrary cycle duration and arbitrary protocols for the potential stiffness $k(t)$ and parameters of the active bath. Concretely, we considered dynamics described by the overdamped Langevin equation

$$\dot{x}(t) = -k(t)x(t)/\gamma + \eta(t), \tag{2.4}$$

where $-k(t)x(t) = -\partial H(x,t)/\partial x$ stands for the force exerted on the engine by the optical trap, γ is friction coefficient, and η denotes a zero-mean noise describing effects of the bacteria bath. For an equilibrium bath, the noise correlation function has to obey

the fluctuation dissipation relation and thus it reads $\langle \eta(t)\eta(t') \rangle = (2k_{\mathrm{B}}T_{\mathrm{eff}}(t)/\gamma)\delta(t-t')$. The relevant response function $\sigma_x(t) = \langle x^2 \rangle$ obeys the dynamical equation

$$\dot{\sigma}_x(t) = 2k(t)/\gamma\sigma_x(t) + 2\langle x(t)\eta(t) \rangle \tag{2.5}$$

for a general noise $\eta(t)$, which translates to

$$\dot{\sigma}_x(t) = 2k(t)/\gamma\sigma_x(t) + 2k_{\mathrm{B}}T_{\mathrm{eff}}(t)/\gamma \tag{2.6}$$

for the equilibrium bath. Comparing these two equations, one can conclude that the active bath can be in the general situation described by the effective temperature

$$T_{\mathrm{eff}}(t) = \gamma/k_{\mathrm{B}}\langle x(t)\eta(t) \rangle. \tag{2.7}$$

When the non-equilibrium noise is exponentially correlated, $T_{\mathrm{eff}}(t)$ can be calculated explicitly. Interestingly, it strongly depends on the stiffness of the potential, $k(t)$. This dependence on the dynamics of the engine must be considered when assessing limits on the engine's performance using known results. For example, the efficiency can reach Carnot's bound with the effective temperature only if the engine is driven quasi-statically and protocols for $k(t)$ and bath parameters are fine-tuned to yield constant $T_{\mathrm{eff}}(t)$ between the adiabatic strokes.

2.1.2 Effective temperature in underdamped active heat engines (Ref.[56])

In PUBLICATION 7.2[56], we studied the existence of effective temperature for engines with Hamiltonian of the form $H = k(t)x^n/n + p^2/2m$. We assumed that the dynamics is described by the system of Langevin equations

$$\dot{x}(t) \;\; = \;\; p(t)/m \tag{2.8}$$
$$\dot{p}(t) \;\; = \;\; -k(t)x(t)^n + F(t) + \eta(t), \tag{2.9}$$

where the 'friction' $F(t)$ stands for the systematic force exerted on the particle by the active bath and noise $\eta(t)$ for the stochastic component of that force. Since the bath is out of equilirbium, $F(t)$ and $\eta(t)$ are not interconnected by a fluctuation dissipation relation. It turns out that in this setting the existence of effective temperature can be proven for quasi-static drivings only. Under such conditions, the effective temperature consistently describing both the work and heat fluxes in Eqs. (2.2) and (2.3) exists if $\langle x(t)(F(t)+\eta(t)) \rangle = 0$, i.e., if the total force exerted by the bath at time t is independent

of the position $x(t)$ of the engine at the same time. This condition can be broken if the interaction between the engine and the active bath is strong enough to correlate the two subsystems. For example, if the engine is based on a colloidal particle trapped in the potential $k(t)x^n/n$ and the active particles in the bath interact with the colloid by a steric repulsion, slowly rotating active particles will accumulate close to the colloid, leading to nonzero $\langle x(t)(F(t)+\eta(t))\rangle$. This shows that when momentum is taken into account, the existence of the effective temperature depends not only on the engine Hamiltonian but also on the engine-bath coupling (cf the discussion in SUBSECTION 2.1.1).

2.1.3 Results (in)valid when effective temperature exists (Refs.[52,55])

As discussed above, when the active engine setup allows for describing the active bath by an effective temperature, its finite-time and quasi-static performance are limited by bounds for the corresponding heat engines with equilibrium reservoirs. While the quasi-static limitations on efficiency, such as Carnot's efficiency, are notorious, available limitations on the finite-time performance of heat engines are much less known. To give one specific example, when the active heat engine's dynamics obeys an overdamped Langevin equation, one can immediately write down limitations on the maximum efficiency of this engine for any fixed value of its output power using results of PUBLICATION 7.3[52].

Let $\delta P \equiv (P - P^*)/P^*$ denote the deviation from the maximum power P^* attainable in the given engine under the conditions that (i) the cycle with the effective temperature comprises two (effective) isotherms and two adiabats and (ii) the driving is slow (but not quasi-static) or the probability distributions for position at the ends of the isotherms are fixed (this somewhat awkward condition is discussed in PUBLICATION 7.6 introduced in SUBSECTION 2.2.2). Then our results in Ref.[52] shows that the maximum efficiency attainable by the engine for given δP obeys the inequalities

$$\frac{\eta_C}{2}\left(1+\sqrt{-\delta_P}\right) \leq \eta \leq \eta_C \frac{1+\sqrt{-\delta_P}}{2-(1-\sqrt{-\delta_P})\eta_C}\,, \tag{2.10}$$

where $\eta_C = 1 - T_c/T_h$ and T_c/T_h is the ratio of 'cold' and 'hot' effective temperatures. The main asset of active baths is that their hot effective temperature (achieved, e.g., by providing bacteria with a lot of food) can be very large without any danger of evaporating the lab, and thus η_C can be close to 1. Over the years, we have derived many similar results for various thermodynamic machines[24–28] all of which can find application also in the field of active heat engines (or refrigerators, etc.), but this thesis contains only PUBLICATION 7.3[52] as an example.

As a warning, I stress that the existence of effective temperature means that there is a setup with an equilibrium bath that has the same average thermodynamic performances as the given setup with an active bath, nothing more. When one studies other features of the active system, there is thus no guarantee of any further correspondence with the equilibrium system. For example, even though average work and heat for the equilibrium and active setups are equal, fluctuations of these quantities can be completely different. Such differences can be studied using Brownian dynamics simulations. Nevertheless, we have developed an alternative numerical method[55] (PUBLICATION 7.4) which can, in some cases, overperform these simulations, in particular, if one needs to determine with high accuracy higher moments of fluctuating thermodynamic fluxes. The method can be applied to systems with overdamped dynamics. It is based on approximating the real dynamics by a thermodynamically consistent hopping process in the discretized state space. It allows calculating the probability distribution to find the engine in a given state (position) and characteristic functions for arbitrary stochastic functionals of that position, such as work and heat. Details of this 'Matrix numerical method' are rather technical and I invite the interested reader to read more in the attached PUBLICATION 7.4[55].

2.2 General results (Refs.[53,54]):

There are some results obtained for standard heat engines, which are also valid for active engines even when the effective temperature does not exist. This generally holds for results obtained without assuming equilibrium concepts such as detailed balance or (equivalently) fluctuation-dissipation relation. Here, I present two examples of such results from our kitchen.

2.2.1 Quasi-static efficiency at finite power (Ref.[53])

PUBLICATION 7.5[53] shows that any cyclically driven microscopic engine can operate at maximum quasi-static efficiency and simultaneously deliver nonzero power with vanishing (or at least limited) fluctuations. For heat engines in contact with an equilibrium heat bath, this result shows that they can be operated with Carnot's efficiency while delivering finite, stable power. This can be interpreted as a Holy Grail of engineers, which was conjectured to be forbidden by recently discovered thermodynamic uncertainty relations[58] before our work was published. Nevertheless, we have shown that thermodynamic uncertainty relations only limit the performance of steady-state heat

engines, transforming a stationary heat flux from a hot to a cold reservoir into work.

The first main idea of our paper is that the work in cyclic heat engines (e.g., that in Eq. (2.3)) represents a different stochastic process than work in steady state heat engines[40,53]. Cyclic heat engines perform work when the engines' energy is decreased by externally modifying the potential. Variations in the engine's energy due to changes in its microstate are then related to heat interchanged with the bath. On the other hand, in steady-state heat engines, both heat and work are associated with the motion of particles in a fixed potential landscape, and thus both these quantities qualify as heat from the point of view of cyclic setups. The heat and work in cyclic engines have very different properties when the system is driven slowly. For very slow driving, the individual microstates are occupied according to the quasi-static probability density (Boltzmann distribution when the bath is in equilibrium), and the probability density for work per cycle is $\delta(w - W_{qs})$, where W_{qs} is the average quasi-static work. The work-type variables, in other words, self-average with increasing cycle time. According to the first law, heat plus work equals energy difference per cycle. With δ-distributed work, this implies that heat fluctuations are those of internal energy, and thus they do not vanish regardless of the driving speed[40,53].

With this insight, the only question remains whether one can drive a system quasi-statically in a finite time. For small systems, all relaxation times are under reasonable control. Thus one can make them very short (definitely shorter than overdamped timescales), for example, by increasing the stiffness in the potential (2.1). This is the second main idea of PUBLICATION 7.6[54], to which I refer for more details.

2.2.2 Maximum efficiency protocol for constrained driving (Ref.[54])

Our second general result on performance of cyclic engines is described in PUBLICATION 7.6[54], where we have derived maximum efficiency protocol for any heat engine described by the Hamiltonian of the form (2.1) under the experimentally relevant conditions that (i) the stiffness $k(t) \in [k_-, k_+]$, (ii) $T_{\text{eff}} \in [T_-, T_+]$, (iii) cycle time is arbitrary but fixed. Our derivation is based on the definition of heat flux (2.2) with $m = 0$, and thus it is completely independent of the details of engine or bath dynamics. Results of such generality are rare in the field of optimal finite-time control of (stochastic) heat engines. In fact, this is the only optimal protocol that is valid for arbitrary dynamics known to the author. All other optimal protocols described in the literature are derived based on standard functional optimization techniques, such as Euler-Lagrange formalism (see references in[54] for more details), which cannot be applied without prescribing the

dynamical equations.

Our derivation is based on the fact that, at second glance, the heat flux $\dot{q}(t) = k(t)\dot{\sigma}_x(t)$ resembles the Clausius equality $Q = TdS$ valid in equilibrium thermodynamics. In equilibrium thermodynamics, the most efficient cycle operating between temperatures T_- and T_+ is Carnot's cycle, which forms a rectangle in the $T-S$ diagram and has efficiency $\eta_C = 1 - T_-/T_+$. Hence, the most efficient cycle under our conditions must form a rectangle in the $k - \sigma_x$ diagram and has efficiency $\eta = 1 - k_-/k_+$. An important piece of the derivation is that the final formula for efficiency is independent of the system response σ_x (which cancels out between the nominator and denominator in the definition of efficiency). For power, this does not happen, and hence the piece-wise constant protocol for $k(t)$ is not always optimal. Nevertheless, one can prove that the piece-wise constant $k(t)$ maximizes power for slow enough driving and a small allowed range $k_+ - k_-$ for k. For more details, see PUBLICATION 7.6[54].

2.3 Active ratchets (Refs.[50,59–61])

Qualitatively (and often even quantitatively), the motion of active Brownian particles such as bacteria or various active colloids is well described by the so-called active Brownian particle model. In two dimensions, it consists of the system of Langevin equations

$$\dot{x}(t) = v[x(t), y(t)]\cos[\theta(t)] + \sqrt{2D}\eta_x(t), \tag{2.11a}$$

$$\dot{y}(t) = v[x(t), y(t)]\sin[\theta(t)] + \sqrt{2D}\eta_y(t), \tag{2.11b}$$

$$\dot{\theta}(t) = \sqrt{2D_r}\eta_\theta(t), \tag{2.11c}$$

for position coordinates $x(t)$ and $y(t)$ and orientation $\theta(t)$ of the active particle, which determines its swimming direction. The formulae above assume that the particle's speed $v(x, y)$ can depend on its position. The mutually independent unbiased Gaussian white noises $\eta_i(t)$, $i = x, y, \theta$ of unit intensity ($\langle\eta_i(t)\eta_j(t')\rangle = \delta_{ij}\delta(t-t')$) represent translational and rotational Brownian motion of the active particle, and D and D_r denote the corresponding diffusion coefficients.

The most important ingredient of the model is that the particles move persistently until their reorient due to the rotational diffusion. The average reorientation time of the particles is given by $1/D_r$. Thus the average distance a particle travels until it changes its direction can be estimated as $v(x, y)/D_r$. Per the same time window, the particles' average displacement due to the transnational diffusion is $\sqrt{D/D_r}$. The ratio of these

two length scales, $v\sqrt{D/D_r}$, measures the importance of active motion over diffusion and is often referred to as the Péclet number.

If confined by walls (or even potentials), the active particles slide along walls due to their persistence until they get trapped for periods of duration $1/D_r$ in wedge-shaped regions, or pockets, such as in FIGURE 2.1. The particles can then propel freely movable objects in the active bath toward the pockets (FIGURE 2.1b). Alternatively, orienting fixed pockets in one direction renders a global current of the active Brownian particles in the opposite direction (FIGURE 2.1c).

One can ask whether active Brownian particles can render a macroscopic current by themselves without a necessity for confinement or other complications such as time-dependent activity[62]. We have positively answered this question in the series of papers studying the motion of active particles with space-dependent activity[50,59–61].

2.3.1 Active Brownian particles in activity landscapes (Refs.[59–61])

We started this program by studying the dynamics of active particles in spatially varying activity landscapes experimentally in PUBLICATION 7.7[60] and theoretically in PUBLICATION 7.8[61] for a simple one-dimensional setup and in PUBLICATION 7.9[59] for radially symmetric two-dimensional geometry. Our main findings are summarized using a piecewise constant active-passive activity landscape in FIGURE 2.3.

Due to their persistence, active Brownian particles accumulate at the active-passive interface, pointing from the active ($v(\mathbf{x}) > 0$) to the passive ($v(\mathbf{x}) = 0$) region. In the steady state, this accumulation can be described by a simple approximate model that reduces the complete Fokker-Planck equation for the probability density for position and orientation, $\tilde{\rho}(x, \theta)$, corresponding to Eqs. (2.11), to equations for position density $\rho(x) = \int d\theta \tilde{\rho}(x, \theta)$ and polarization $p(x) = \int d\theta \cos(\theta)\tilde{\rho}(x, \theta)$. Notably, the resulting approximate equations

$$\rho'(x) = p(x)v(x)/D, \tag{2.12a}$$

$$p''(x) = D/D_r p(x) + \rho(x)v'(x)/(2D), \tag{2.12b}$$

can be exactly mapped to equations for density and polarization in a model where the particle can have just two values of θ, so that it points either to the left or to the right. That the approximate model describes a related model exactly implies that results obtained by solving Eqs. (2.12) should be qualitatively correct regardless of the chosen parameter regime. For more details concerning the polarization and density patterns near active-passive interfaces, particularly for the properties of the corresponding decay

lengths, we refer to Refs.[59–61]. The results presented above can be used to construct an activity ratchet by imposing in the setup of FIGURE 2.3 instead of photon nudging boundaries periodic boundaries and letting the activity landscape travel from right to left. Such time-dependent ratchets have already been described in the literature[62].

2.3.2 Activity ratchet (Ref.[50])

In PUBLICATION 7.10[50], we show how the insights described above can be used to construct a ratchet just by a periodic spatial modulation of the particle activity. That such a ratchet can be constructed is nontrivial because, at long time scales, active Brownian particles usually behave like common (passive) ones, just with an increased diffusion co-

Figure 2.3: Density and polarization at active-passive interface. Panel a) shows the quasi-one-dimensional experimental setup with thermophoretically propelled Janus-type active particles sketched in panel c. When irradiated by a laser, these particles propel toward their polystyrene hemisphere. Naturally, the probability of finding the active particle is much larger in the passive than in the active region. Upon leaving the active-passive area, particles were steered back by photon nudging (they were irradiated by the laser only when pointing into the active-passive area with their polystyrene end). Panel b) shows the density in a) integrated over the y coordinate, and panel d) depicts the corresponding polarization (average orientation at a given position) of the active particle. Panel c) gives an intuitive explanation for the depletion of the active region and behavior of the polarization at the active-passive and passive-active interfaces. Symbols in b and d correspond to experimental data, dashed lines are analytical predictions, and solid lines were computed numerically using Ref.[55] (PUBLICATION 7.4). The figure is reprinted from Ref.[60] (PUBLICATION 7.7).

efficient $D + v^2/(2D_r)$ (and thus also correspondingly increased effective temperature). And one can show that Brownian particles traveling through a bath locally equilibrated at a spatially modulated temperature can only induce thermophoretic flows from 'hot to cold' but not a macroscopic transfer under spatially periodic conditions.

Furthermore, one-dimensional static activity landscapes can be proven to generally fail to produce a global current as follows: (i) Eq. (2.11a) implies that the current $j(x) = \langle \dot{x}(t) \rangle$ is proportional to the polarization. (ii) While activity landscapes can sort active particles according to their orientations, they can never reorient them and, hence, total orientation $\int dx\, p(x) = 0$. Physically, without external torques, polarization is a continuous function of position. Thus $p(x)$ must be zero at least at a single position to make the overall polarization vanish. (iii) In a steady state where the ratchet operates, the one-dimensional continuity condition $\partial j(x)/\partial x = 0$ implies that $j(x)$ is the same for all positions and, hence, it must vanish for all x.

Even though points (i) and (ii) also hold in two spatial dimensions, this argument does not apply here because the two-dimensional continuity condition $\partial j(x,y)/\partial x + \partial j(x,y)/\partial y = 0$ allows for nonzero global solutions with local zeros, corresponding to inevitable points of vanishing polarization. Around these points, the two-dimensional current forms vortices visible in FIGURE 2.1d. The piece-wise constant activity profile utilized in the ratchet depicted in this figure (and analyzed in Ref.[50]) consists of an asymmetric passive region surrounded by an active region, where the particles move with a constant nonzero speed. The easiest way to understand the ratchet's operation is to consider the y dimension as a 'periodic time modulation' of the piece-wise constant profile from the preceding section. An alternative explanation can be based on the fact that particles get polarized along the whole active-passive interface; however, those localized inside the wedge region can leave the passive region much harder than those on the tip side. This leads to an overall 'leakage' of particles oriented to the left along the two edges of the wedge-shaped passive domain and, thus, to a global current to the left. For more details concerning the performance of this ratchet, we refer to PUBLICATION 7.10[50].

3 Effects of time delay

To perform a useful task or to interact with a neighbor, both living and artificial agents must acquire and process information about their surroundings. This cannot be done instantaneously and thus response of active particles is always delayed after the stimuli (for delays of various animal specious to various stimuli, see TABLE 3.1). Consequently, effects of time delay have already been thoroughly investigated from an engineering point of view in control theory[73], which is a general framework for feedback systems with applications in life sciences, engineering, and sociology. The main insight is that time delays may induce oscillations, instabilities, and poor control performances, which should be familiar to everyone who experienced delayed hot water flow from a shower (see FIGURE 3.1). On the other hand, time delays are deliberately used in control theory to stabilize unstable periodic orbits in chaotic systems using, e.g., OGY or Pyragas control methods[74,75].

Even though active matter research shares some goals (and hence also issues) – such as precise control of interacting self-propelling particles – with control theory, physical theories of retarded active matter are scarce: As a notable exception, effects of time delay are well understood for traffic models[76]. Besides, time delay was studied with respect to stability and formation of dynamical patterns in the active Brownian dynamics model[77,78] and in several models of bird flocks, including the Vicsek model[79–82] and Cucker-Smale model[83]. All these studies suggest that moderate time delays foster order in the dynamics, while large delays induce disorder. The current interest of the active matter community in dynamics with time delay is mainly driven by the necessity to describe experiments involving feedback[2,84–86] and to adjust existing models to capture natural instances of retarded dynamics more accurately[13,80,87]. This has spurred the theoretical study of analytically tractable toy models capturing the main ingredients of experiments, and more detailed models to plan and analyze specific measurements and experiments.

In the rest of this section, I first briefly review stochastic delay differential equations, which describe the dynamics of feedback-driven active matter systems, and review our results for their solution in SECTION 3.1. Then, in SECTION 3.2, I review our results for

Animal	Stimulus/Response	Reaction Time [ms]	References
Human	auditory	$140 - 160$	[63]
	visual	$180 - 200$	[63]
	touch	~ 155	[63]
Fruit fly	roll perturbation	~ 5	[64]
	pitch perturbation	~ 12	[65]
	yaw perturbation	$10 - 25$	[66]
Starling	startling sound stimuli	$64 - 80$	[67]
	startling light stimuli	$38 - 76$	[67]
Teleost fish	startle response	$5 - 10$	[68,69]
Calanoida	stirring water	< 2.5	[70]
E. coli	chemical stimuli	$\sim 10^3 - 10^4$	[71]

Table 3.1: Typical reaction times measured between a stimulus and the corresponding discrete response strongly vary among species and the type of stimulus. Delay times comparable to the characteristic time scale of the stimulus may be expected to trigger qualitatively new effects in the dynamical response, similar to those analyzed in the present work. The table is taken from Ref.[72].

feedback-driven systems of active Brownian particles. Finally, in SECTION 3.3, I review our findings about the effects of time-delayed interactions in the Vicsek model.

Figure 3.1: Shower delay, a control problem from daily life. Due to the delayed hot water flow, we usually open the hot water tap too much and get burned once the hot water finally comes out of the shower. To reach a comfortable temperature, we regulate the faucet up and down and induce the oscillating behavior typical for delay systems. The figure was drawn by Daniel Geiss.

3.1 Equilibrium delay (Ref.[88])

The dynamics of most active matter systems considered in my work is strongly influenced by environmental noises such as thermal noise. Therefore they are described by stochastic delay differential equations[89]. These equations can be in general written in the form

$$\dot{\mathbf{x}}(t) = f[t, \mathbf{x}(t), \mathbf{x}(t - \tau)] + g[t, \mathbf{x}(t)]\boldsymbol{\xi}(t), \tag{3.1}$$

where τ stands for the delay time, $\mathbf{x}(t)$ describes the stochastic trajectory of the (possibly many-body) system, $f[t, x(t), x(t - \tau)]$ and $g[t, x(t)]$ are arbitrary real-valued functions, and $\boldsymbol{\xi}(t)$ represents the noise, which is usually but not necessarily Gaussian and white. For vanishing noise, stochastic delay differential equations become delay differential equations, which are notoriously difficult to treat analytically. In fact, up to a few exceptions such as Eq. (3.7) in SUBSECTION 3.2.1, exact solutions to them are known only if they are linear ($f[t, \mathbf{x}(t), \mathbf{x}(t - \tau)] = a + b\mathbf{x}(t) + c\mathbf{x}(t - \tau)$), where one can derive the Green's function for Eq. (3.1) using e.g., Laplace transform[90]. For the case when the noise is additive with constant intensity ($g[t, \mathbf{x}(t)] = g$), this result can then be used for the derivation of exact expressions for the probability distribution for $\mathbf{x}(t)$, $\rho_1(\mathbf{x}, t)$, and also for all higher joint probability distributions, e.g., $\rho_2(\mathbf{x}, t; \mathbf{x}', t')$, etc. However, when the dynamical equation is nonlinear, it is not even known how to write a closed Fokker-Planck equation for $\rho(\mathbf{x}, t)$. Instead, one obtains an infinite hierarchy of equations for ρ_n, $n = 1, 2, = \ldots$[91]. How to close this hierarchy is currently an open problem. In fact, to the best of our knowledge, no exact solutions to nonlinear stochastic delay differential equations have been known until recently, when we made a moderate breakthrough[88] by deriving a class of (to some extend) exactly solvable nonlinear stochastic delay differential equation by imposing fluctuation-dissipation relation in Eq. (3.1).

To be specific, in PUBLICATION 7.11[88], we consider stochastic delay differential equations (3.1) that can be written in the form of a system of Langevin equations (for simplicity in one dimension)

$$\dot{x}(t) = v(t), \tag{3.2}$$

$$m\dot{v}(t) = F(t, x(t)) + F_F(x(t), x(t - \tau)) + \eta(t), \tag{3.3}$$

where $F(t, x(t))$ is an arbitrary time-local external force, and the friction $F_F(x(t), x(t - \tau))$ and noise $\eta(t)$ obey the fluctuation dissipation relation. That is, we assume that the

friction can be written using a memory Kernel $\Gamma(t)$ as

$$F_F(x(t), x(t - \tau)) = -\int_{-\infty}^{t} dt' \Gamma(t - t')v(t'), \tag{3.4}$$

and the noise auto-correlation function fulfills the requirement

$$\langle \eta(t)\eta(t') \rangle = k_B T \Gamma(t - t'), \tag{3.5}$$

with some temperature T. To restrict the analysis to real-valued processes only, we, in addition, assume that the noise power spectrum is positive:

$$S(\omega) = \int_{-\infty}^{\infty} dt \, \langle \eta(t)\eta(0) \rangle \exp(i\omega t) > 0. \tag{3.6}$$

Under these conditions, the stochastic delay differential equation describes the dynamics of a particle dragged by the external force F through a non-Markovian but equilibrium bath. Hence, one can use all results valid under these conditions, such as fluctuation theorems, equilibrium linear response theory, etc. For example, when the external force is potential, $F(\mathbf{x}(t)) = -\nabla U(\mathbf{x}(t))$, the stationary probability distribution for $\{x(t), v(t)\}$ is given by the Boltzmann distribution $\rho(x, v) = \exp(-\beta H(x, v))/Z$, with the Hamiltonian $H(x, v) = U(x) + mv^2/2$, inverse temperature $\beta = 1/(k_B T)$, and partition function Z. In PUBLICATION 7.11[88], we detail two experimentally motivated examples of such processes. One potential issue that might constrain the practical applicability of our results is that the noise that fulfills the fluctuation-dissipation relation (3.5) is non-trivial and might be challenging to realize in experiments. Nevertheless, our numerical simulations suggest that this should be possible at least approximately.

Unfortunately, the described dynamical class involves only delay stochastic differential equations that are linear in the delayed position. Nonetheless, systems when the feedback is (at least approximately) linear in the time-delayed term are quite commonly used in practice. One example is the so-called feedback cooling[92,93]. Furthermore, I believe there is still untapped potential in using general results and symmetries of physics to derive solvable nonlinear stochastic delay differential equations. Currently, I am exploring ways to generalize these results.

3.2 Feedback driven active Brownian particles (Refs.[2,72,85,90,94])

Natural microswimmers such as bacteria represent rather complex biophysical systems[7]. To better understand their behavior, mimic their functionality, or eventually utilize

them to perform useful tasks, researchers nowadays intensely study experimentally and theoretically artificial microswimmers. These microswimmers are often spherical particles made from two hemispheres with different physical properties, called Janus particles after the homonymous two-faced Roman god. Typical examples are the catalytic microswimmers in FIGURE 1.1 and hot (or thermophoretic) microswimmers in FIGURE 2.3c. However, as discussed in SECTION 2.3, the Janus microswimmers swim ballistically until they are reoriented by rotational diffusion, significantly limiting the experimental control over their trajectories[95,96]. Therefore, my experimental colleagues developed[85,86]

Figure 3.2: Active particles with delayed attractive interactions. a) When the particles are further away (closer) than r_{eq} they swim towards (away from) each other with a constant speed v_{th}. Due to these two-body interactions, the particles form dynamical 'active molecules' in b). c) The interaction rule from a) with $r_{eq} = 0$ and one of the two particles fixed leads, for large enough delay times, to rotational motion of the active particle around the pinned one. d) Polar angles $\theta = \int_{t-\delta t}^{t} dt' \omega(t') = \psi(t) - \psi(t - \delta t)$ traveled by the active particle per one delay time as functions of time for a fixed swimming speed and different delays. Panels a) and b) are taken from Ref.[85] and panels c) and d) from Ref.[72].

a new type of symmetric thermophoretic microswimmers shown in Figure 3.2a. These particles are melamine resin spheres (radius 1 μm) covered by gold nanoparticles (radius 10 nm). If placed in water and irradiated by laser at their circumference, they swim with a constant speed proportional to the laser intensity in the direction of the vector connecting the laser focus with the particle center. The swimming direction can be controlled simply by changing the position of the laser focus.

This improved experimental control allows steering the microswimmers with unprecedented precision, only hindered by the phenomenon that inevitably limits the accuracy of any feedback control, the delay of the feedback loop, i.e., the time required to measure the position, process the measurement in the computer, and change the laser focus. Even though the current (2023) variant of the experimental setup allows for short enough delays that hardly affect the dynamics, during the development of the experiment, we uncovered many surprising phenomena occurring for long enough delay times. In short, it turns out that trivial delayed interactions alone have the potential to underlie a large part of the complexity observed in motile active matter.

3.2.1 Active Brownian molecules (Refs.[85,90])

In Publication 7.12, we investigated the level of control achievable using the symmetric active particles by steering them to form active molecules in Figure 3.2b. We achieved that by implementing the simple rule depicted in Figure 3.2b. When the particles were farther than a fixed nonzero distance r_{eq}, we propelled them with a fixed speed v_{th} towards each other. And when they were closer than r_{eq}, we propelled them with the same speed away from each other. As a result the dynamics of the center of mass of the particles obeyed the nonlinear stochastic delay differential equation

$$\dot{r}(t) = -2v_{th}\,\text{sign}\,(r(t-\tau) - r_{eq}) + \sqrt{4D}\eta(t). \tag{3.7}$$

For vanishing delay, this equation describes an overdamped Brownian particle with unit friction coefficient diffusing in the absolute value potential $U(r) = 2v_{th}|r - r_{eq}|$. For nonzero delay, the particles are thus on average distant r_{eq} and their distance r exhibits exponentially decaying fluctuations following from the Boltzmann distribution $P(r) \propto \exp[U(r)/2D]$. Interestingly, the nonlinear delay differential equation obtained by neglecting the noise can be solved exactly by a triangle wave with amplitude $2v_{th}\tau$ and period 4τ. Due to the delay, the distance r is thus on average still given by r_{eq} but it oscillates around this value. Due to the noise, these oscillations have a finite correlation time, which can be predicted by an approximate solution of Eq. (3.7)[85].

Considering more than two particles, the first term on the right-hand side of Eq. (3.7) is given by the average of two-particle interactions, normalized to v_{th}. For zero delay, the equation describes the diffusion in a multi-dimensional absolute value potential, which insight can be used to determine the average structure of the resulting 'active molecules' in FIGURE 3.2b. Similarly, as for two particles, these molecules are highly dynamic. They oscillate due to the delay, and due to the noise, the individual particles in the molecules can even interchange their positions. For more details, I refer to videos supplementing Ref.[85] and to its full text in PUBLICATION 7.12.

Since the interactions used in the experiments are strongly nonlinear already for two particles, the theoretical analysis is limited to highly approximate calculations. To get more insights, we considered in PUBLICATION 7.13 a similar system with linear interactions, i.e., we considered a harmonic potential for vanishing delay instead of the absolute value potential. The main physical difference between this setup and the experimental setup of PUBLICATION 7.12 is that the latter assumes constant particle speeds while the 'harmonic potential' implies that the speed grows linearly with increasing interparticle distance. As a result, the dynamics can be reasonably linearized even for more than two particles, and the resulting approximated dynamical equations can be solved exactly. Interestingly, one can even obtain a reasonable analytical estimate for transition rates between different possible conformations of the molecules formed by the delayed harmonic interactions. However, this is only possible when neglecting that the usually used absorbing boundary condition is no longer valid for non-Markovian dynamics. As a result, the predicted transition rates are reasonably accurate for intermediate delays only. While this outperforms the usually employed short delay approximation[97], derivation of transition rates for non-Markovian dynamics still represents an interesting open problem.

The main qualitative difference between the 'constant-force' molecules of PUBLICATION 7.12[85] and 'harmonic' molecules of PUBLICATION 7.13[90] is that, due to the constant speed, the former are stable for arbitrarily long delay times. On the other hand, the oscillations in a harmonic potential get amplified for long delay times, leading to an exponential increase of inter-particle distances. Hence, the harmonic molecules exhibit both hallmark features of delay systems: instabilities and oscillations. Since the analysis in[90] is somewhat technical, I invite the interested reader to read more in the attached PUBLICATION 7.13.

3.2.2 Delay-induced chirality in systems of micro-swimmers (Refs.[72,94])

In PUBLICATION 7.14[72], we investigated what happens if the simple constant speed interaction from the previous subsection is used to propel the particles towards a fixed target particle. The situation is depicted in FIGURE 3.2c. The microswimmer detects the target's position vector $-\mathbf{r}(t)$ at time t and at time $t + \delta t$ swims in the direction $-\mathbf{r}(t)/|\mathbf{r}(t)|$ with a constant speed v_0 *. As depicted in the figure, this delayed attraction makes the particle rotate around the target for long enough delay times. Mathematically, the rotational motion of a single microswimmer is well described by the nonlinear stochastic delay differential equation

$$\dot{\phi}(t) = \omega_0 \sin[\phi(t) - \phi(t - \delta t)] + \sqrt{D/(2a^2)}\eta(t), \tag{3.8}$$

where $\phi(t)$ is the polar angle (see FIGURE 3.2c), D the transitional diffusion coefficient of the microswimmer, a its radius (the target particle is just a pinned, passive microswimmer), and $\omega_0 = v_0 \delta t/(2a)$. This equation describes a Kuramoto oscillator[98] trying to synchronize with its own past position. Assuming that, for $D = 0$, the system eventually converges into a state with constant angular velocity ω, one can use the formula $\phi(t) = \int_{-\infty}^{t} dt' \, \omega$ to rewrite Eq. (3.8) as $\omega = \omega_0 \sin(\omega \delta t)$ and find the stable solutions as functions of the control parameter $\omega_0 \delta t$ numerically. It turns out that, for $\omega_0 \delta t < 1$, the only stable solution is $\omega = 0$, while there are two stable rotating states differing in the sign of ω for $\omega_0 \delta t > 1$. For increasing delay (or, equivalently, swimming speed v_0), the system thus undergoes a normal supercritical pitchfork bifurcation[99]. Alternatively, approximating $\omega(t)\delta t$ by the delay angle $\theta(t) \equiv \int_{t-\delta t}^{t} dt' \, \omega(t')$, and expanding the sine in Eq. (3.8) up to the third order in the delay time δt (and neglecting the term $\dddot{\theta}(t)$, which makes the resulting approximate equation unstable[100]), one arrives at the Markovian Langevin equation, which describes the diffusion of an overdamped Brownian particle in a quartic potential. For $\omega_0 \delta t < 1$, the potential has a single minimum corresponding to the non-rotating state. And, for $\omega_0 \delta t > 1$, it has two symmetric minima corresponding to the two rotating states. In addition to this insight, the Markovian Langevin equations allow one to predict relaxation times to the stable rotating states and, using the Kramers' theory[101], the transition rates for changes between the two transiently-stable rotating states attained for $\omega_0 \delta t > 1$. This is the simplest version of the theory, which

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*I apologize that the notation throughout the text is not unified. For example, in more experimentally motivated papers, we denote delay as δt and in the theoretical ones as τ. I decided to reuse the notation employed in the attached publications in their commentary to help an interested reader to digest the publications more easily.

explains the behavior observed in experiments qualitatively. In PUBLICATION 7.14, we also developed a refined version of the above-described theory, which considers additional experimental details (most notably, another type of delay involved in the feedback loop). The refined theory gives even quantitative agreement with the experiments.

Interestingly, the single particle theory also fits the average angular velocity of multiple particles rotating around the target when each is attracted to the target by the same delayed attraction as the single particle. In addition, the individual particles interact sterically, hydrodynamically, and thermophoretically. Due to these interactions, the particles organize in concentric shells around the target, which rotate in the same direction for large delays, and can even counter-rotate for intermediate delays. While the corotation can be explained solely based on steric interactions, the counterrotation is caused by hydrodynamic coupling between the particles. Simply put, when the laser propels a particle, it also propels the water in the opposite direction. This backflow pushes particles in neighboring shells in opposite directions for intermediate delays. For more details, I refer to PUBLICATION 7.14[72].

As our current experimental setup is not capable of controlling more than 20 particles at once, we decided to study manybody systems with up to 200 particles using Brownian dynamics simulations. In the simulations, we took into account the steric repulsion between the particles but not the hydrodynamic coupling (taking into account hydrodynamics for such a large system represents a nontrivial numerical challenge). The results of these simulation, described in PUBLICATION 7.15[94], are quite surprising. While the average angular velocity of the system still qualitatively obeys the single particle theory described above, the detailed dynamics of the system experiences a series of dynamical phase transitions. These transitions are induced by shear stress caused by unequal angular velocities of the individual particle layers around the target particle. When $v_0 \delta t$ is increased, the system goes through the following dynamical phases:

1. stable, non-rotating crystallite.

2. homogeneously rotating crystallite.

3. sheared or 'quaking' crystallite, where the outermost layers slide over (or lag behind) the inner layers.

4. ring phase, where the innermost layers are no longer in contact with the target particle.

5. a yin-yang phase, where the radial symmetry of the ring state is broken.

6. a blob phase, where the particles completely detach from the target and form a densely packed satellite orbiting around it while shaking from the shear stresses.

The shearing of the system is of slip and stick type observed in athermal granular materials, and thus it is accompanied by the formation of shear bands. For more details and for a detailed discussion of the individual dynamical phases, I refer to PUBLICATION 7.15[94]. A very good intuition about the behavior of this beautiful system can be obtained by watching videos of the individual phases, which can be found either in the paper's supplementary material or on YouTube [†].

3.2.3 Machine learning with micro-swimmers (Ref.[2])

One of the ultimate aims of active matter research is to develop autonomous, perhaps even self-learning, artificial microswimmers with applications, e.g., in engineering or medicine. Motivated by this goal and also with the vision that understanding the adaptation of artificial microswimmers to real-world conditions might bring new insights into evolutionary mechanisms at work in the development of bacteria and similar natural microswimmers, we have investigated in PUBLICATION 7.16[2] how our symmetric artificial microswimmers can learn to orient in real-world arenas by using reinforcement learning. To the best of our knowledge, our work represents the first experimental application of reinforcement learning to a real-world navigation problem in a noisy environment. Our setup is halfway to the goal of autonomous self-learning microswimmers because the brain that learns the optimal strategy is not inside the individual particles but in a computer operating the feedback loop.

In the experiment, the microswimmers are confined between two glass cover slides, and thus they effectively move in two dimensions. To implement the learning, we divided the plane into 7×7 equal squares shown in FIGURE 3.3a. Blue denotes the region through which the microswimmer can move to reach the green target state. When the swimmer entered the red absorbing boundary, it was returned back to its initial position at one of the blue states. To find the optimal policy to steer the swimmer from blue states to the target state using the set of allowed actions in FIGURE 3.3b, we implemented the reinforcement learning method called Q-learning[102]. In this method, one defines a Q-matrix where weight is given for performing the allowed actions in each blue state. Hence our matrix had $9 \times (5 \times 5 - 1)$ entries. The policy described by the Q-matrix imposes the action with the lowest weight in each state.

[†]One can either click the 'YouTube' above in the electronic version or use the link https://www.youtube.com/watch?v=1Gfgq7FvfaA&list=PLDwaP_kIyigWI4637AQH1upD4seyYOynw.

At the beginning of the learning, the Q-matrix is populated randomly, resulting in a random initial policy depicted in FIGURE 3.3c, left. During the learning, the Q-matrix is updated according to an algorithm, which gives a positive reward to actions leading the swimmer to the target and negative rewards to the actions which end up in one of the absorbing states (for more details, I refer to PUBLICATION 7.16[2]). The final policy obtained after the learning, depicted in FIGURE 3.3c, right, represents an optimal compromise between the fast approach to the target and staying in the blue arena in the noisy environment. We have tested that learning is more efficient if several microswimmers update the same Q-matrix.

My main job in this project was to explain why the optimal policy contains some unintuitive elements (e.g., those pointing to the left while the target is in the up di-

Figure 3.3: Reinforcement learning with artificial microswimmers. Panel a) shows the grid world where the swimmer learns to navigate using the set of allowed actions in b). The red squares in a) are absorbing states, and the green square is the target state. c) During the learning, the initial random policy (left) transforms into an optimal policy to reach the target as fast as possible (right). d) Due to the feedback loop delay between detecting the microswimmers' position and imposing the action and thermal noise, the real displacements Δr of the particle (blue circles) are symmetrically distributed along the desired displacement $v_\parallel \delta t e_\parallel$ ($v_\parallel$ is the particle swim speed, δt the time delay, and $e_\parallel$ unit vector in a desired direction). This leads to the optimal swim speed (or delay time) in e) to reach a target position without being absorbed by the boundary. Figures were taken from Ref.[2].

rection). Partially, this can be explained by a weak drift in the experimental sample. However, there is also a more fundamental reason for such a policy, which should be considered by any device or animal navigating with time delay in a noisy environment. Within the delay time between the decision where the particle should swim and taking the corresponding action, the swimmer performs Brownian motion (and it also perhaps moves due to the previous action). As a result, its relative position to the target at the time of actual implementation of the action is stochastic, resulting in the set of actual displacements depicted in FIGURE 3.3d, which are randomly distributed around the desired displacement. The corresponding error increases with the noise intensity D, delay time δt, and the swimming speed $v_\parallel$. As a consequence, there is an optimal speed that guarantees that the target is reached with maximum probability (see FIGURE 3.3e). Using a simple model detailed in Ref.[2], the optimal speed can be estimated as

$$v_\parallel^{opt} = \sqrt{\frac{2D}{\sinh \sigma_\theta^2 \delta t}},$$ (3.9)

where σ_θ^2 is the variance of the aiming error angle θ, depicted in FIGURE 3.3d. The variance depends on the previous action, noise intensity, and delay time, and in Ref.[2] we take it as a fit parameter.

The above formula also predicts an optimal delay time δt for a fixed swimming speed. Interestingly, this is in accord with the recent finding that the precision of reaching a target by the run-and-tumble bacteria also exhibits an optimum as a function of the run-and-tumble times[103,104], which play a similar role for the motion of bacteria as the single delay time δt in our experiments. For more details, I refer to PUBLICATION 7.16[2].

3.3 Delay Vicsek model (Refs.[80–82])

The Vicsek model[105] is one of the best-known toy models of active matter. Its original variant[106], is a simple generalization of the XY model (in two dimensions) and Heisenberg model (in three dimensions) in which the individual spins (agents) move in discrete time with a fixed speed v_0 in the direction of their orientation. At each time t, the spin of agent i assumes the value of the average spin of its neighbors closer than an interaction radius R at time $t-1$ modified by a noise (alignment interaction). For low noise intensities, the Vicsek model exhibits a global order (aligned spins) even in two dimensions, and hence it overcomes the equilibrium limitation imposed by the Mermin-Wagner theorem. For an intense noise, the spins are disordered. The nature of the transition between these two phases was long debated. The current consensus is that the transition is discontinuous

(or first order), with a microphase separation into dense bands (or sheets) of aligned spins and low-density bands of disorder traveling through the sample. The bands form only for large enough systems, where the crossover system size[107] increases with decreasing speed v_0. However, even at high speeds, microphase separation only occurs in simulations involving a significant number of particles. That is why understanding the true nature of the transition had to wait for sufficiently fast computers.

In fact, not only the original paper[106] reported that the transition is continuous (second order), as in the Heisenberg model. Nowadays, it seems to be clear that the transition looks second order whenever the density fluctuations in the simulation are not too large[15]. Since these fluctuations grow with the particle number N, the transition can be considered as smooth for small enough N (for fixed v_0). In this regime, the Vicsek model close to the transition exhibits a finite-size critical behavior[13,87] in the sense that a set of scaling functions and critical exponents describes susceptibility and space and time correlation functions[108,109].

Figure 3.4: Finite-size scaling in the delay Vicsek model. a) In the delay Vicsek model, each agent assumes at time $t + \tau$ average orientation of the particles, which were closer to it than R at time t. The agents move with constant speed v_0 in discrete time (time-step 1) in the direction of their orientation. The static critical exponents (b-d), the critical nearest neighbor distance (e), and the dynamical exponent z dramatically change with increasing delay from their values for the classical Vicsek model towards long-delay asymptotic values. The figures were taken from Ref.[80].

When comparing the predictions of the Vicsek model to data obtained for birds or insects, the finite size results in the region way below the crossover system size are of the main interest[13,87,110]. These comparisons show that the Vicsek model fails to predict the shape of time-correlation functions and scaling exponents found from experimental data for swarms of midgets[13,87], and also information spreading in bird flocks, e.g., when birds follow a leader or react to a local stimuli[110].

The authors of Refs.[13,15] argued that these failures of the Vicsek model follow from the fact that it completely neglects inertia in changing the orientation of the individual agents. Hence, they introduced an improved model called as inertia spin model, where the alignment interaction acts on the agent orientation indirectly by an additional 'spin' variable. The refined model's predictions nicely agree with the field observations[13,15,110]. Nevertheless, we see another important gap in the Vicsek model: it neglects time delay in the interactions. This is our main motivation for investigations of delay Vicsek model[80], where the alignment interaction is not based on the particle's neighbors at time $t-1$, but at time $t-1-\tau$ (see FIGURE 3.4a). Below, I present the results we have obtained for finite-size scaling (SUBSECTION 3.3.1) and information propagation (SUBSECTION 3.3.2) in the delay Vicsek model. I consider these results preliminary and am still actively working on their refinement.

3.3.1 Finite-size scaling in delay Vicsek model (Ref.[80])

In PUBLICATION 7.17[80], we report on our study of finite size scaling in the delay Vicsek model. In the study, we fixed noise intensity, particle speed v_0, and interaction radius R and considered various particle numbers N ranging from 64 to 2048 particles. We simulated the delay Vicsek model in a cube with edge L and periodic boundary conditions. Keeping in mind that our results were obtained for a specific set of parameters is important because it is known that scaling exponents in the Vicsek model are, in general, parameter dependent.

For each N, we varied L to obtain the susceptibility χ of the system as a function of the nearest neighbor distance between the particles, r_1. Afterward, we computed the static critical exponents γ and ν and the asymptotic nearest neighbor distance r_C by the best data collapse of the resulting curves by shifting and rescaling the x and y axis as $(r_1 - r_C)N^{1/3\nu}$ and $\chi N^{-\gamma/3\nu}$. We have repeated this procedure for delay times τ ranging from 0 to $v_0\tau/R \sim 1$. The resulting delay dependences of the critical exponents and r_C are given in FIGURE 3.4b-e. With increasing delay time, all the parameters converge from their standard-Vicsek-model values to long delay plateau values. An analytical

argument given in the supplementary information to[80] shows that, for long delays, the delay Vicsek model dynamics depends just on the combination $v_0\tau$. Thus, while the precise form of the delay dependence of the static critical parameters γ, ν, and r_C varies with the particle speed, they should converge to the same plateau values as in FIGURE 3.4 for arbitrary nonzero v_0. I am now working on a numerical check of these results. Unfortunately, the numerical simulations, mainly calculating susceptibilities and other correlation functions, are incredibly time-consuming.

The most interesting observations from the static finite size scaling are the unprecedentedly large values of the critical exponents γ and ν for intermediate and long delays and the maximum found in the asymptotic nearest neighbor distance r_C. While we still haven't understood the meaning of the large scaling exponents, the maximum in r_C reflects the known[79,82,83] effect of stabilization of the flocking phase by short delays. Delayed reactions enhance the system's stability against random perturbations. On the other hand, too long delays prevent the agents from efficiently following their neighbors. The maximum in r_C results from a compromise between these two tendencies.

For each set N, v_0, R, noise intensity, and delay time τ, the susceptibility exhibits a maximum that marks the system size (or, equivalently, the nearest neighbor distance r_1) corresponding to the order-disorder transition. For the parameters at the transition, we have calculated space and time-correlation functions. For each τ, the correlation functions for different N can again be collapsed to a single master curve by rescaling time as $t/\tau_R = t/\xi^z$, where τ_R and ξ are the correlation time and length, and z is the dynamical exponent. The resulting dependence of z on the delay time is given in FIGURE 3.4f. For $\tau = 0$, $z = 2$ as in the standard Vicsek model with a small v_0 and in the Heisenberg model. With increasing delay time, z converges to ~ 1, which is the value reported for natural swarms in Ref.[13], and which is also close to the prediction from the inertia spin model[15]. Besides, the shapes of time correlation functions obtained from the delay Vicsek model are also similar to those found for natural swarms and the inertia spin model (for details, see PUBLICATION 7.17[80]). According to our analysis, time delay thus represents another way to explain the dynamical scaling observed in natural swarms. However, this work is still in progress.

3.3.2 Information propagation in delay Vicsek model (Refs.[81,82])

When we found that the delay Vicsek model is capable of reproducing dynamical scaling and time correlations observed in natural swarms, we focused on the study of information propagation in the model in a similar fashion as it was done for natural bird flocks[110].

Even without delay, the study of information propagation in motile systems such as the Vicsek model is a complicated task, in particular when the source of information is moving, which is quite a generic situation in flocks following a leader bird. Therefore, we have started our investigation in PUBLICATION 7.18[81] with a simple lattice model, where a scalar field at a given site assumes at discrete time $t + 1$ average value of itself and its neighbors at time t. At first glance, the model can be classified as a lattice variant of the Vicsek model with zero speed of the agents and a vanishing noise. However, it turns out that its different continuum limits converge to the spin-wave approximations of either the inertia spin model (when lattice constant is kept proportional to time step) or the Vicsek model (when lattice constant squared is kept proportional to time step).

Using the lattice model, we studied two types of local information sources called firm and lax leaders. Firm leaders are meant to describe a leader particle deliberately trying to influence the whole system and correspond to fixing the field's value at the origin during the whole evolution of the system. Lax leader describes the spreading of a random fluctuation through the system and corresponds to setting the field's initial value at the origin to a given value and letting the system evolve freely for $t > 0$. It turns out that a reasonable definition of signal speed is (distance from the leader)/(the time when the field changes most rapidly at that distance). Using this definition, we found that the information spreading in the lattice model is approximately diffusive for both types of perturbation, i.e., the distance traveled by the signal is proportional to $\sqrt{t}$. Interestingly, this result is obtained regardless of the fact the information spreading in the inertia spin model is predicted to be linear[110].

Next, we considered the Vicsek model with very weak noise and the two types of perturbations from the lattice model, which, however, traveled through the system at the same speed as the other agents. For low speeds, the information spreads in the same way as in the lattice model. However, the information spreading is no longer purely conductive for larger speeds. As a result, the information spreads diffusively in the direction opposite to the leaders heading and approximately ballistically (distance traveled proportional to t) in the direction of the leader.

In PUBLICATION 7.19[82], we performed an analogous analysis of information spreading in the delay Vicsek model, together with the analysis of the ability of the system to follow a moving leader. Concerning the latter, we found in accord with the results described in the previous SUBSECTION 3.3.1 that delays foster the stability of the aligned state of the system against random perturbations but hinder the system's ability to follow a leader. Concerning information propagation, we found that the information spreading in the direction opposite to the leader's motion is still diffusive. However, for

a fixed low (but nonzero) speed of the agents, the information spreading in the leader's direction is diffusive for short delays but becomes increasingly linear as the delay is increased. Furthermore, the delay introduces oscillations into the dispersion relations. Again, I consider these results preliminary, and we are working intensely to improve our understanding of information spreading in Vicsek and related models.

Finally, in Ref.[82], we have also studied linear response in the delay Vicsek model. Out of thermal equilibrium, it lacks its general properties as a response is no longer bound to be given by equilibrium (or stationary) correlation functions, and we indeed have not found such a general relation. Our analysis further suggests that the response in the Vicsek model to a torque applied to a subgroup of agents is linear only in the parameter regime when the average polarization of the system is approximately conserved. For more details, I refer to PUBLICATION 7.19[82].

4 Final Remarks

This thesis summarizes some of the advances in our understanding of the dynamics and thermodynamics of active matter, focusing on energy extraction from active self-propulsion and the effects of time-delayed interactions. These results represent tiny contributions to the knowledge acquired over the past years in this dynamic field. And even our results leave more loose ends than answers. For example, we have just started with investigations of the importance of delay in active matter systems. More importantly, most of our current models are rather based on observed phenomenology than on some deeper (bio)physical principles. Hence one of the natural topics for future investigation is to derive more reliable models of interparticle interactions by using a bottom-up approach based on the capabilities of the individuals in question. For example, our preliminary works show that the Vicsek model can be (approximately) derived by considering agents moving with a fixed speed and trying to maximize their local orientational correlations with their neighbors. Similarly, other types of agents combined with other local target functions might result in new models more suitable to a given situation than our present models. Besides continuing the study of the influence of delay on the dynamics of experimental Brownian active matter systems, studying such a bottom-up approach to the derivation of active matter systems is my main goal for the forthcoming years.

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6 List of discussed Papers

The following papers are discussed in this habilitation thesis. The best five of these papers, according to my personal taste, are marked with an asterisk (*).

1. Holubec, V., Steffenoni, S., Falasco, G. & Kroy, K. Active Brownian heat engines. *Physical Review Research* **2.** `https://journals.aps.org/prresearch/abstract/10.1103/PhysRevResearch.2.043262` (2020).

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12. Khadka, U., Holubec, V., Yang, H. & Cichos, F. Active particles bound by information flows. *Nature Communications* **9.** `https://www.nature.com/articles/s41467-018-06445-1` (2018).

13. Geiss, D., Kroy, K. & Holubec, V. Brownian molecules formed by delayed harmonic interactions. *New Journal of Physics* **21,** 093014. `https://dx.doi.org/10.1088/1367-2630/ab3d76` (2019).

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