Time-(ir)reversibility in active matter: from micro to macro

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Active matter encompasses systems whose individual constituents dissipate energy to exert propelling forces on their environment. This rapidly developing field harbors a dynamical phenomenology with no counterpart in passive systems. The extent to which this is rooted in the breaking of time-reversibility has recently triggered an important theoretical and experimental activity which is the focus of this review. Building on recent progress in the field, we disentangle the respective roles of the arrow of time and of the non-Boltzmann nature of steady-state fluctuations in single- and many-body active systems. We show that effective time-reversible descriptions of active systems may be found at all scales, and discuss how interactions, either between constituents or with external operators, may reveal the nonequilibrium nature of the microscopic source of energy. At a time when the engineering of active materials appears within our reach, this allows us to discuss to which extent methods stemming from equilibrium statistical mechanics may guide us in their design.

1 Introduction

Active matter describes systems whose fundamental constituents dissipate energy to exert self-propelling forces on the environment. From birds to bacteria, from cells to molecular motors, the biological world is filled with active entities. Indeed, active matter was initially strongly driven by its biophysical applications (Fig 1a-b). Since then, a wealth of synthetic active systems have been engineered in the lab, which now pave the way towards the engineering of synthetic active materials (Fig 1c-e). However, many fundamental questions need to be addressed before one may reach the level of complexity relevant for material design or to decipher the physical laws involved in biological processes, from morphogenesis to the large-scale organization of complex ecosystems.

In addition to its potential implications for biophysics and material design, the upsurge of interest in active matter also stems from its rich dynamical phenomenology, which is largely without counterpart in passive systems and has been extensively reviewed previously. This emerging physics stems from a microscopic nonequilibrium drive at the particle level that
leads to system-dependent violations of two hallmark features of thermal equilibrium: time-reversal symmetry (TRS) and Boltzmann statistics. For instance, the lack of TRS, when accompanied by the spontaneous emergence of macroscopic currents, is at the root of flocking behaviours, whether observed in groups of animals (Fig. 1b) or engineered in synthetic self-propelled colloids (Fig. 1d). Nothing prevents, however, the orientations of the birds within a flock to display an equilibrium-like statistics. Conversely, the emergence of self-assembled clusters in the absence of attractive forces shown in Fig. 1c transcends the constraints imposed by the Boltzmann weight. No manifest arrow of time is, however, observed in the corresponding motility-induced phase separation. The aim of this review is to disentangle the respective roles of the violations of TRS and of Boltzmann statistics in active matter and to discuss the vast literature which touches on these questions. At a time when the design of active materials has become a practical challenge, the existence of an effective TRS—and of its accompanying equilibrium toolbox—has become a central question.

This review is intended both for newcomers in the field of active matter as well as for condensed-matter and biophysics specialists. As such, it relies on general concepts of statistical mechanics and stochastic processes. We start by discussing the Langevin description of active particles in section 2 which we contrast with the Brownian dynamics of colloidal particles. We explain the meaning of TRS in this stochastic context and how TRS violations can be measured using the entropy production rate introduced in stochastic thermodynamics. We discuss the ambiguities that naturally emerge when characterizing the TRS of coarse-grained systems, which we loosely understand as integrating out some of the degrees of freedom. We illustrate this discussion...
by considering a free active particle whose position and orientation are recorded over time. TRS violation is demonstrated by a non-vanishing entropy production rate equal to the energy dissipated by the active force powering the motion. Measuring solely the particle position, however, restores TRS and leads to a vanishing entropy production rate.

We then turn in section 3 to the case of non-interacting active particles subjected to external potentials. We discuss how non-Boltzmann features emerge in this context. In particular, we compare the non-local dependency of the steady-state distribution on the external potential for different types of active particles. In addition, external potentials also lead to TRS violations, under the form of non-vanishing entropy production rates and steady-state currents. Conversely, we discuss the conditions under which an effective thermal equilibrium regime is recovered or a TRS is restored.

Finally, section 4 discusses the case of interacting active particles. We focus in particular on Motility-Induced Phase Separation (MIPS) whose macroscopic dynamics resembles an equilibrium phase separation despite a microscopic nonequilibrium drive at the particle level, which makes it interesting from a TRS perspective. We show how TRS violations can nevertheless be identified using field-theoretical methods and how they impact the construction of the phase diagram. We also discuss cases in which TRS is exactly restored at the macroscopic scale, either by considering specific classes of active systems endowed with tactic interactions or in the small-persistence-time limit.

2 TRS of a single active-particle: in and out of equilibrium

Sources and sinks of energy in active matter. Let us consider the simplest model of an active particle

\[ m\ddot{r} = -\gamma\dot{r} + f_p(t) - \nabla V(r) + \sqrt{2\gamma^2 D\eta(t)} \quad (1) \]

Here, \( r \) is the position of the particle, \(-\gamma\dot{r}\) a viscous damping term, \( f_p \) the self-propulsion force, \( V(r) \) an external potential, and \( \eta \) a Gaussian white noise that may represent thermal noise or other fluctuation sources. The self-propulsion force \( f_p \) is a defining feature of active matter: it is a time-dependent, non-conservative force, endowed with a particle-dependent stochastic dynamics, and powered by an irreversible consumption of energy. The presence of self-propulsion forces both drive active systems out of thermal equilibrium and distinguish active matter from other nonequilibrium systems, such as glasses or boundary driven fluids whose bulk dynamics is of equilibrium nature. The energy source powering \( f_p \) varies from system to system: it can be a local field, as in
Janus self-phoretic colloids or bacteria, or it can stem from a global external field, as for vibrated grains, Quincke rollers, or bi-electric colloids under AC fields. The dynamics of \( f_p \) can be equally diverse and can, for instance, include rotational diffusion or tumbles of its orientation, as well as fluctuations in its amplitude.

A natural question is whether one could subsume \( f_p(t) \) and \( \sqrt{2\gamma^2 D \eta(t)} \) into a single noise source \( \tilde{\eta}(t) \) and treat Eq. (1) as an effective equilibrium Langevin dynamics. The answer comes from thermodynamics: the main difference between passive and active particles lies in the injection of energy. For passive particles, the fluid is responsible both for the dissipation and the injection of energy (Fig. 2, left). The former results from the average force exerted by the fluid on the particle, \(-\gamma \dot{r}\), with a corresponding dissipated power \(-\gamma \dot{r}^2\). On the contrary, the latter stems from fluctuations of the fluid forces around their mean, \(\sqrt{2\gamma^2 D \eta(t)}\), which inject a mean power \(d\gamma^2 D/m\). When the fluid is at equilibrium, injection and dissipation of energy are related by the celebrated fluctuation-dissipation theorem through \(D = kT/\gamma\). For an active particle, on the contrary, most of the injection of energy comes from the self-propulsion force and it is thus physically disconnected from dissipation: \(\tilde{\eta}(t)\) would not satisfy a fluctuation-dissipation relation (See Fig. 2, right). Note that this discussion assumes that \(f_p\) is not a Gaussian white noise, otherwise it could indeed be absorbed in \(\eta(t)\) at the cost of a simple quantitative shift of the temperature. This observation is the motivation for most models of active particles considered in the literature that rely on variations of Eq. (1) with noises and drags not related by (generalized) Stokes-Einstein relations.

Since most active systems live at low Reynolds numbers, the overdamped limit of the Langevin dynamics is often assumed, although the role of inertia has recently attracted interest. Three standard models of active particles are described by the dynamical equation

\[
\dot{r} = \mathbf{v}_p - \mu \nabla V(r) + \sqrt{2D \eta(t)}
\]

(2)

where \(\mu = \gamma^{-1}\) is the particle mobility and \(\mathbf{v}_p = \mu f_p\) its self-propulsion velocity. For Active Brownian particles (ABPs) and Run-and-Tumble particles (RTPs), the magnitude of \(\mathbf{v}_p\) is constant, while its orientation undergoes either rotational diffusion or random, Poisson-distributed reorientation events. On the contrary, an Active Ornstein-Uhlenbeck particle (AOUP) has a self-propulsion velocity whose modulus fluctuates and is given by an Ornstein-Uhlenbeck process \(\dot{v}_p = -v_p/\tau + \sqrt{2D\tau^2}\xi\), with \(\xi\) a Gaussian white noise with unit amplitude. Using angular brackets to denote averages over the dynamics of the self-propulsion velocities, the temporal correlation of \(\langle \mathbf{v}_p(t)\mathbf{v}_p(0) \rangle\) can be equal in the three models. The physics of their self-propulsion, however, is quite different: the probability distribution of \(\mathbf{v}_p\) is Gaussian and peaked around 0 for
Figure 2: Colloidal dynamics resulting from interactions with fluid molecules (left). The mean resulting force is a drag $-\gamma v$, which dissipates energy by opposing motion, whereas fluctuations around it, described by the Gaussian white noise $\eta_{th}$, inject energy into the colloid’s dynamics. When the fluid is in equilibrium, injection and dissipation are related by the fluctuation-dissipation theorem. On the contrary, the propulsion of a bacterium (right), stems from the consumption of a separate energy source, which is disconnected from the dissipation. In the steady state, the energy balance between sources and sinks of energy is given by $\langle f_p \cdot \dot{r} \rangle + \frac{d\gamma D}{m} = \gamma \langle \dot{r}^2 \rangle$, which can be derived from Eq. (1) in $d$ space dimensions by computing the time derivative of $m\dot{r}^2/2$. The dissipation $w_p = \langle f_p \cdot \dot{r} \rangle$ measures the energy per unit time injected by the self-propulsion force into the system; it violates the equipartition $\frac{1}{2} m \langle \dot{r}^2 \rangle = \frac{1}{2} d\gamma D$ that would otherwise be satisfied for an equilibrated colloid. It is the microscopic signature of activity.
AOUPs, whereas it is uniform on a sphere of fixed radius for ABPs and RTPs.

Note that the discussion above for the translational degree of freedom $r$ can be extended to rotational ones. In particular, this leads to a class of particles called spinors, in which self-propulsion speed is replaced with a self torque or, more generally, the rotational noise and damping do not satisfy a Stokes-Einstein relation. These systems have been studied both at the theoretical [61, 107, 137, 200, 216] and experimental [22, 97, 162, 178] levels.

An immediate consequence of the absence of the Stokes-Einstein relation is that, in the presence of an external potential $V$, the stochastic dynamics of an active particle does not necessarily lead to a steady state given by a Boltzmann weight $P_{\text{eq}}(r) \propto \exp[-\beta V(r)]$. This leads to a host of interesting phenomena that we partly review in Section 3. Note, however, that while the Boltzmann weight may be the textbook definition of equilibrium statistical mechanics, a broader definition of equilibrium is based on dynamics; it equates with TRS in the steady state, under the form of a detailed-balance relation. We now discuss the origin of the latter and its rather subtle fate for active particles.

**Equilibrium & time-reversal symmetry.** The dynamics of a system is said to be time-reversal symmetric if observing a trajectory or its time-reversal are equally likely: $P[\{r(\tau), 0 \leq \tau \leq t\}] = P[\{r(t-\tau), 0 \leq \tau \leq t\}]$, which, using the definition of conditional probability, can equally be written as

$$P[\{r(\tau), 0 < \tau \leq t\}|r(0)]P_s(r(0)) = P[\{r(t-\tau), 0 < \tau \leq t\}|r(t)]P_s(r(t)).$$

(3)

Here $P_s(r)$ is the (stationary) probability to sample a configuration $r$ whereas $P[\{r(\tau), 0 \leq \tau \leq t\}|r(0)]$ is the probability of any trajectory $\{r(\tau)\}$ starting from $r(0)$. In the following, we restrict ourselves to Markovian dynamics for simplicity, even though the discussion can be generalized to non-Markovian processes. $P[\{r(\tau), 0 < \tau \leq t\}|r(0)]$ is then the average probability that a trajectory passing through $r(0)$ at 0 will follow $\{r(\tau)\}$. Microscopically, Eq. (3) is granted by the laws of classical mechanics and directly applies if $r$ describes both a colloidal particle and the surrounding fluid molecules. Mesoscopically, however, when $r$ solely describes the colloidal particle, Eq. (3) requires a statistical hypothesis on the distribution of the fluid degrees of freedom which have been coarse-grained out (See Box Microscopic vs statistical reversibility). In equilibrium, this is given by Boltzmann microcanonical hypothesis. For more general systems, coarse-graining out the fluid degrees of freedom need not lead to dynamics obeying a statistical time-reversal symmetry. A whole set of theoretical tools have thus been developed to test whether stochastic dynamics such as Eq. (1) or (2) satisfy TRS or not (See Box Identifying time-reversal symmetry breaking).
**Microscopic vs statistical reversibility.** Consider a colloidal particle embedded in an equilibrated fluid. When considering the full system, \{Fluid + Colloid\}, time-reversibility is given by Eq. (3), where \( r(s) \) describes the joint degrees of freedom of the colloid and of the fluid molecules. The time-reversibility of Hamilton’s equations of motion ensures that \( P\{r(\tau), 0 \leq \tau \leq t\} | r(0) = P\{r(t - \tau), 0 \leq \tau \leq t\} | r(t) \). This directly leads to \( P_s(r(0)) = P_s(r(t)) \): the probability is conserved along the trajectory, as guaranteed by Liouville theorem.

If \( r(s) \) now refers to the colloid only, then \( P\{r(\tau), 0 \leq \tau \leq t\} | r(0) \) is given by the measure of all initial conditions of the fluid molecules which are compatible with the trajectory of the colloid. Assuming microcanonical equilibrium, a scale separation between the fluid molecules and the colloid, and denoting by \( E(r) \) and \( E_{\text{tot}} \) the energies of the colloid and of the total system, the measure of these initial conditions is given by \( \Omega_{\text{traj}} / \Omega_{fl}[E_{\text{tot}} - E(r(0))] \). Here, \( \Omega_{fl}[E_{\text{tot}} - E(r(0))] \) is the phase-space volume of all fluid configurations at energy \( E_{\text{tot}} - E(r(0)) \) and \( \Omega_{\text{traj}} \) is that of the initial conditions compatible with the colloid trajectory. Conversely, the probability of the time-reversed trajectory is given by \( \Omega_{\text{traj}} / \Omega_{fl}[E_{\text{tot}} - E(r(t))] \), which now differs from that of the forward trajectories if the energy of the colloid has changed. The time-reversal condition (3) then simplifies into

\[
P_s(r(0)) \exp\left[E(r(0))/kT\right] = P_s(r(t)) \exp\left[E(r(t))/kT\right]
\]

where we have used that \( \Omega_{fl}(E_{\text{tot}} - E(r)) \propto \exp(-E(r)/kT) \) with \( T \) the temperature of the fluid, defined as \( T^{-1} = k \frac{\partial \log \Omega_{fl}}{\partial E} \bigg|_{E_{\text{tot}}} \). Equation (4) enforces the Boltzmann weight as a steady-state distribution for the colloidal particle.

Unlike the microscopic reversibility of Hamilton’s equations of motion, the statistical reversibility of the colloid’s dynamics requires a statistical hypothesis for the fluid molecules, which is here given by the microcanonical postulate. Another distribution for the fluid molecules would typically have led to a violation of Eq. (3); statistical irreversibility for the colloidal dynamics thus generically emerges from a microscopically reversible dynamics once the bath’s degrees of freedom have been coarse-grained out.

**Identifying time-reversal symmetry breaking.** The question of TRS and its breakdown arises in many different settings and formalisms, whether using Langevin dynamics or jump processes, for underdamped or overdamped dynamics, at the level of particles or fields. Its identification relies on an equally diverse set of tools\(^{74,199}\), which we illustrate for the simple setting of an
overdamped Brownian dynamics in the presence of a force field $F(r)$:

$$\dot{r} = \mu F(r) + \sqrt{2D}\eta ,$$  \hspace{1cm} (5)

where $\eta$ is a unit Gaussian white noise and $D$ and $\mu$ positive constants. For such Markovian dynamics, the TRS defined in Eq. (3) can be read at several levels.

- TRS amounts to an equality in the steady state of the joint two-time probability density $p(r_1,t; r_2,0) = p(r_2,t; r_1,0)$. This generalizes to any pairs of observables $A(r)$ and $B(r)$ where TRS implies $C_{AB}(t) = C_{BA}(t)$ with $C_{AB}(t) = \langle A(t)B(0) \rangle$. In experiments or simulations, measuring a non-vanishing $\Delta_{AB}(t) \equiv [C_{AB}(t) - C_{BA}(t)]/2$ offers a low-dimensional sufficient condition to prove a violation of TRS. $\Delta_{AB}(t)$ is the time anti-symmetric part of the correlation function $C_{AB}(t)$, an idea which can be generalized to other observables.

- The probability density $P(r,t)$ evolves according to a Fokker-Planck equation $\partial_t P = -HP$. TRS is equivalent to a symmetry of the Fokker-Planck operator: $H^\dagger = P_S^{-1} HP_S$, where $P_S$ is the stationary measure and $H^\dagger$ is the adjoint of $H$ (for the $L^2$ scalar product). In particular, this implies the existence of a basis in which $H$ becomes Hermitian and that it has a real spectrum. For overdamped Brownian dynamics with additive noise, this has been used to endow $H$ with a supersymmetric structure akin to that of Schrödinger’s equation.

- The Fokker-Planck equation can be read as a conservation equation for a probability current $J(r) = \mu F(r)P(r) - D\nabla P(r)$. TRS is equivalent to the vanishing of $J$ in the steady state. The experimental measurement of such a high dimensional object is difficult, but its projection on a finite set of relevant degrees of freedom has recently been used to sample TRS breakdown in biological systems.

- Another measure of TRS breakdown is obtained by computing:

$$\Sigma(0,t_f) = \int D[\{r(t)\}] P[\{r(t)\}] \hat{\Sigma}[\{r(t)\}] = \int D[\{r(t)\}] P[\{r(t)\}] \log \frac{P[\{r(t)\}]}{P[\{r(t_f - t)\}]} .$$  

Mathematically, $\Sigma$ is the Kullback-Leibler divergence between the probabilities of backward and forward paths and $\hat{\Sigma}$ can be seen as a ‘path-wise entropy production’. For dynamics (5), $\Sigma$ can be decomposed between the heat transferred to the thermal bath and the variation of the Gibbs-Shannon entropy of the measure $P(r,t)$.

The positivity of $\Sigma$ generalizes the second law of Thermodynamics to microscopic systems described by Langevin equations. In turn, the entropy production rate, defined as:

$$\sigma \equiv \lim_{t_f \to \infty} \frac{1}{t_f} \Sigma(0,t_f) ,$$  \hspace{1cm} (6)
is a direct measurement of the irreversibility of the dynamics\cite{101,103,113} that is commonly used in non-equilibrium statistical mechanics, even in the absence of any connection to Thermodynamics \cite{46,116}.

Of course, the four criteria discussed above are not independent from each other. For instance, for dynamics (5), the steady-state entropy production rate is connected to the probability current $J(r)$ defined above through:

$$\sigma = \frac{\mu}{D} \int d\mathbf{r} \frac{J^2(r)}{P_s(r)} .$$

From the knowledge of the dynamics, conditions can be derived for TRS to be violated. For dynamics (5), irreversibility requires the existence of a closed loop $C$ such that:

$$\oint_C \mathbf{F}(r) \cdot d\mathbf{r} \neq 0$$

This criterion generalizes the Kolmogorov criterion derived for Markov chains \cite{199}. Mathematically, $\mathbf{F}$ needs to contain a curl or a harmonic part \cite{91}. Conversely, TRS imposes a direct relation between the force field $\mathbf{F}$ and the steady-state probability: $\mu \mathbf{F} = D \nabla \log P_s$. All the discussion above generalizes—under more complex forms—to other dynamics, for instance involving variables which are odds under time-reversal symmetry \cite{74,199}.

**TRS in active matter.** For equilibrium systems, TRS is ensured irrespectively of the degree of coarse graining and holds both for microscopic and coarse-grained mesoscopic descriptions. For active systems, on the contrary, this question is more subtle and the possible existence of TRS depends on the degrees of freedom which are being considered. This makes its characterization—in particular using an entropy production rate defined in the spirit of Eq. (6)—a somewhat ambiguous task, which has attracted a lot of interest both theoretically \cite{29,30,46,47,68,73,84,124,128,134,160,169,184} and experimentally \cite{16,65,66,78,79,131,159,205}.

To illustrate this, consider a zero-Reynolds swimmer at position $\mathbf{r}(t)$ moving through a fluid thanks to the displacement of some degrees of freedom $\mathbf{x}_i(t)$. (Think about the motion of a flagellum.) The solution of Stokes equation will lead to a flow $\mathbf{u}(t)$ and a self-propulsion speed $\mathbf{v}_p(t)$, which results from a propulsion force $\mathbf{f}(t)$ exerted on the fluid. (By Newton third law, $\mathbf{f}$ is equal and opposite to $\mathbf{f}_p$ in Eq. (1).) A recording of $\mathbf{r}(t)$ and $\mathbf{x}_i(t)$ of duration $t_f$ played backward is also a solution of Stokes equation. It would involve a force $-\mathbf{f}(t_f - t)$, a speed $-\mathbf{v}_p(t_f - t)$ and a flow $-\mathbf{u}(t_f - t)$. It is, however, distinguishable from the forward trajectory: our swimmer will swim
backward, a ‘pusher’ would become a ‘puller’. In probabilistic terms, the trajectory $r(t)$ given the displacements $x_i(t)$ is equally likely to occur as $r(t_f - t)$ given $x_i(t_f - t)$, even though they can be distinguished by the flow they generate.

The situation is reminiscent of the equilibrium Langevin dynamics of a passive charged particle at $r(t)$ in a magnetic field $B(t)$ created by electrons at positions $x_i(t)$, moving deterministically in a coil:

$$m \ddot{r} = -\gamma \dot{r} + q \dot{r} \times B(t) + \sqrt{2\gamma kT} \eta,$$

with $q$ the charge of the particle, $\gamma$ its damping coefficient, $m$ its mass, and $kT$ the temperature. The reverse trajectories $x_i(t_f - t)$ lead to a magnetic field $-B(t_f - t)$ so that $r(t_f - t)$ is equally likely to occur as $r(t)$ was in the presence of $B(t)$. Mathematically, the conditional probabilities of observing $r(t)$ given $x_i(t)$ and $r(t_f - t)$ given $x_i(t_f - t)$ are thus equal and the corresponding entropy production rate vanishes $\sigma = \lim_{t \to \infty} \frac{1}{t} \log \frac{P[r(t)] | \{x_i(t)\}}{P[r(t_f - t)] | \{x_i(t_f - t)\}} = 0$, consistently with thermodynamics. In a given experiment, however, it is not the conditional probability which is measured, but the joint probability of observing $r(t)$ and $x_i(t)$. When the electrons are driven by a fixed potential difference, for instance, they will not generate $x_i(t)$ and $x_i(t_f - t)$ with equal probability. The observation of $r(t)$ and $r(t_f - t)$ will thus not be equally likely: they do not inherit the underlying TRS dynamics (7) would have if the dynamics of $x_i(t)$ were time reversible.

This ‘induced’ irreversibility can be measured by comparing the occurrence frequency of $r(t)$ and $r(t_f - t)$ for the same field $B(t) = B_0$. The corresponding ‘Shannon’ entropy production rate is now finite, given by $\sigma = 2q^2 |B_0|^2 / (\gamma m)$. Note that this ‘entropy-production rate’ solely measures the irreversibility of the trajectories $r(t)$ in an experiment with a fixed magnetic field. In particular, it is not a measure of the creation of thermodynamic entropy in our magnetic system since the magnetic field has to be flipped under time-reversal. Equation (7) has also been used to describe the hair bundle of sensory cells. There, the term analogous to $B(t)$ has a different origin and does not flip under time reversal and thus leads to a non-vanishing thermodynamic entropy production rate. Whether a given definition of $\sigma$ can be connected to the thermodynamic entropy production rate or not depends on the physics of the system under study; it can always be connected to a measure of irreversibility in the sense described above, which is the perspective adopted in this review.

In active matter, the internal processes leading to $x_i(t)$ are often strongly irreversible. In living systems, they rely on an imbalance between the concentrations of ATP and ADP+P in the cells. For Janus self-diffusiophoretic colloids, it is the irreversible transmutation of hydrogen peroxyde into oxygen and water which powers self-propulsion. The observation of
Figure 3: Trajectories of a run-and-tumble particle experiencing translational noise. The noise-less trajectory is drawn as a dashed line and the direction of time is indicated by green arrows. One may record the position and orientation of the particle (a) or solely its position (b). The time-reversed trajectories of (a) and (b) are shown in (c) and (d). Their likeliness are clearly different since the noise has to fight self-propulsion in (c), but not necessarily in (d).

$r(t)$ and $r(t_f - t)$ thus need not occur with equal probabilities. (An interesting exception is when self-propulsion emerges from spontaneous symmetry breaking as in Quincke rollers\cite{31}.) It is this induced irreversibility that will be discussed in the rest of this article. Before turning to the corresponding computation of the entropy production rate, let us stress that the most irreversible process in active system is, generically, the one generating $x_i(t)$, and not the dynamics of $r(t)$. When trying to measure the energy dissipated in an active system, say using calorimetry, one would expect that this process strongly dominates all other sources of irreversibility. A large part of the irreversibility is thus lost if the irreversible process leading to the active force is not modelled\cite{47,147}. This is, in particular, the case of Eq. (1) in which the active force is an input of the problem whose origin is unspecified. The ‘dissipation’ measured through $w_p = \langle f_p \cdot \dot{r} \rangle$ thus cannot capture the full irreversibility of the system. As we show below, it is nevertheless an interesting object of study since it quantifies the violation of TRS encapsulated in the degrees of freedom $r(t)$ and $f_p(t)$.
Let us first show that, even at the level of dynamics \( \Pi \), the existence of TRS remains ambiguous and depends on which degrees of freedom are under study. We start by considering the situation depicted in Fig. 3, which compares the trajectory of a model run-and-tumble bacteria in two space dimensions with its time-reversed counterpart. The underlying stochastic dynamics is given by

\[
\dot{r}(t) = v_0u(\theta(t)) + \sqrt{2D}\eta(t)
\]  

(8)

where \( v_0 \) is a fixed self-propulsion speed and \( \theta(t) \) is fully randomized at rate \( \alpha \). The trajectory presented in Fig. 3a records the time evolution of both the particle position \( r(t) \) and its orientation \( \theta(t) \). Note that \( r(t) \) and \( \theta(t) \) uniquely characterize the realization of the noise through \( \sqrt{2D}\eta(t) = \dot{r}(t) - v_0u(\theta(t)) \). As detailed in Appendix A for the reversed trajectory \( r^R(t) = r(t_f - t) \), \( \dot{r}^R(t) = \theta(t_f - t) \) to be observed, the surrounding fluid molecules have to produce a different noise \( \eta^R(t) \) such that \( \sqrt{2D}\eta^R(t) = -\sqrt{2D}\eta(t_f - t) - 2v_0u(\theta(t_f - t)) \). This shows that time-reversed trajectories are obtained by making the noise \( \eta^R \) work against the active force to make the active particle retrace its steps. Using the Gaussian weights of these two noise realizations, their relative probability to occur can be computed, leading to a path-wise entropy production (See Box Identifying time-reversal symmetry breaking):

\[
\dot{\Sigma} [\{r(t), \theta(t)\}] = \frac{\mu}{D} \int_0^{t_f} dt \dot{r} \cdot f_p + \log \frac{P_0(r_0, \theta_0)}{P_f(r_f, \theta_f)},
\]

(9)

where \( P_f(r_f, \theta_f) \) is the probability of being at \( r_f = r(t_f) \) and \( \theta_f = \theta(t_f) \) given that the initial condition was sampled according to \( P_0 \). The right-hand side of Eq. (9) measures both the heat transferred to the bath, \( -\dot{Q} \equiv \int_0^{t_f} \dot{r} \cdot f_p dt \), and the change in the ‘stochastic’ Shannon entropy \( \dot{\Sigma} = \dot{\Sigma}_0 + \dot{\Sigma}_f \) between \( P_0 \) and \( P_f \) associated to the trajectory \( \{r(t), \theta(t)\} \)\(^{167}\). Taking the average over the forward path probability, and using the positivity of the Kullback-Leibler divergence, leads to a generalized second law \( \langle \dot{\Sigma} \rangle > \frac{\mu}{D} \langle \dot{Q} \rangle \). Alternatively, taking the limit \( t_f \to \infty \), leads to the steady-state entropy production rate

\[
\sigma = \lim_{t_f \to \infty} \frac{1}{t_f} \dot{\Sigma} = \frac{\mu \langle \dot{r} \cdot f_p \rangle}{D} = \frac{\mu w_p}{D},
\]

(10)

where we have used the ergodicity of the dynamics. The average dissipation of the active force \( w_p \) thus measures the irreversibility of the active dynamics \( \sigma \)\(^{34, 136}\). The latter stems from the velocity being aligned with the self-propulsion force, hence requiring an atypically strong noise to generate the time-reversed trajectories. Physically, the entropy production rate \( \sigma \) measures the (inverse) time scale over which the self-propulsion makes the trajectory irreversible: at short time scales, the translational diffusion due to Brownian motion dominates self-propulsion hence hiding the irreversible character of the dynamics; on longer time scales, translational diffusion plays a lesser
role in transport than self-propulsion, which makes the irreversibility stemming from the latter more apparent. Note that $\sigma$ diverges as $D$ goes to zero, so that the dynamics becomes strongly irreversible in this limit.

The situation is completely different if one tries to characterize the TRS breaking for the trajectory shown in Figs. 3b&d. There, only the position of the particle is measured and its original and final orientations are unknown. If the system is endowed with periodic boundary conditions, the steady state distribution is an isotropic, uniform distribution so that it is equally likely to find trajectories with $\theta(t)$ or the flipped orientation $\tilde{\theta}(t) = \pi - \theta(t)$. The entropy production thus vanishes since the time reversed of any trajectory with $\theta(t)$ can be realized with the same probability by a trajectory starting from the final position $r(t_f)$ with a flipped orientation $\tilde{\theta}(t_f)$. Note that this symmetry resembles that of underdamped Langevin equations in which the time-reversal symmetry in configuration space emerges from a symmetry in phase-space upon flipping the velocities under time reversal. This parallel between active particles and underdamped passive ones has been exploited to reveal a similar symmetry of the evolution operator of AOUPs\textsuperscript{36,68,124}. Note that this TRS in position space is independent of the value of $D$ and holds even for $D = 0$.

Finally, we comment on the fact that whether or not one observes TRS in active systems depends on what can be measured. Consider for example Quincke colloidal particles\textsuperscript{31}. These particles acquire self-propulsion through the spontaneous breaking of a symmetry: their polarity stems from an asymmetric charge distribution on their surface. For an isolated particle, measuring this asymmetry or the flow of the surrounding fluid are required to distinguish a forward trajectory from a time-reversed one. In sum, in a dilute, uniform active system, the observation of a breakdown of TRS depend on the degrees of freedom which are considered. Describing the energy source\textsuperscript{47,147}, or considering the inertia of these typically overdamped systems\textsuperscript{169}, will lead to different characterization of the irreversibility of the dynamics. This strongly differs from equilibrium dynamics, in which TRS holds irrespective of the degree of coarse-graining.

The situation changes drastically when active particles are interacting with their surrounding. While an ambiguity regarding the status of TRS may remain for isolated active particles in the steady state, their interactions with external potentials or with other particles typically reveal their non-equilibrium nature, as we discuss in Sections 3 and 4.
3 Non-interacting active particles in the presence of obstacles and external potentials

Consider a system in equilibrium in which a small obstacle is introduced. The corresponding perturbation $\delta V(r)$ leads to a localized perturbation of the Boltzmann weight $P_{eq}(r) \propto \exp[-\beta(V(r) + \delta V(r))]$. In that sense, the perturbation remains local. Furthermore, TRS is maintained so that even systems with asymmetric obstacles cannot harbor steady currents. Both features are challenged in active systems, whose fate in the presence of obstacles and external potentials have attracted a lot of interest\(^\text{112,118,125,123,157,159,64,188,99,100,121,138,173,186,203}^\) both for fundamental reasons, in that they probe the relationship between active and passive dynamics, but also for practical ones. External potentials and confinements are indeed the toolbox used to engineer and probe active systems, from optical & acoustic tweezers\(^\text{189}^\) to centrifuges\(^\text{164}^\) and arrays of obstacles\(^\text{72}^\). In addition to a wealth of experimental works\(^\text{50,54,76,77,142,172}^\), these questions have been addressed at the theoretical level by considering the overdamped dynamics

$$\dot{r} = v_p - \mu \nabla V(r)$$

(11)

where the self-propulsion $v_p$ evolves either through tumbles\(^\text{4,166,185}^\), rotational diffusion\(^\text{173,203}^\), or as an Ornstein-Uhlenbeck process\(^\text{68,183}^\). In all cases, one can define a persistence time $\tau$, a typical self-propulsion speed $v_0$, a persistence length $\ell_p = v_0 \tau$, and a large-scale diffusivity $D_{eff} \propto \ell_p^2/\tau$. In the limit $\tau \to 0$ keeping $D_{eff}$ constant, the dynamics becomes equivalent to a passive one and leads to a Boltzmann distribution with an effective temperature $T_{eff} \equiv D_{eff}/\mu$. As the persistence time increases, active systems both develop non-Boltzmann features and exhibit TRS violations. We first review below the $\tau = 0$ limit before discussing the nonequilibrium static and dynamic features that develop as $\tau$ increases.

The $\tau = 0$ limit and the universal effective equilibrium regime. For AOUPs, the equilibrium behaviour stems from the fact that the Gaussian process $v_p$ becomes, as $\tau \to 0$, a white noise: $\langle v_{p,\alpha}(t)v_{p,\beta}(0)\rangle = \delta_{\alpha,\beta}D/\tau \exp(-|t-t'|/\tau) \longrightarrow 2D\delta(t-t')$. The dynamics is thus equivalent to a passive one with a temperature $T_{eff} = D/\mu$. The effective equilibrium regime also exists for ABPs and RTPs, despite their non-Gaussian nature. This has been established in any dimension\(^\text{39,173}^\) and we detail it here for RTPs in $d = 1$. In the presence of a confining potential $V(x)$, the steady-state distribution is given by\(^\text{175,199}^\):

$$P(x) = \frac{v_0^2P_0}{v_0^2 - \mu^2 V'(x)^2} \exp\left[ -\frac{\mu}{\tau} \int_0^x dx' \frac{V''(x')}{v_0^2 - \mu^2 V'(x')^2} \right],$$

(12)

where $\tau^{-1}$ is the tumbling rate. Note that Eq. (12) exhibits, in general, a non-Boltzmann form: the forces experienced by the particle (that do not stem from the bath) are not proportional to $\nabla \log P$.\[\text{Page 14}\]
Next, consider the $\tau \to 0$ limit, keeping $T_{\text{eff}} = \frac{v_0^2 \tau}{\mu}$ finite. This implies a large $v_0$ limit, so that $v_0 \gg \mu V'(x)$ for smooth potentials, which allows one to expand (12) into

$$P(x) = P_0 \exp[-V(x)/T_{\text{eff}}].$$

(13)

For confining potentials, even if the condition $v_0 \gg \mu V'(x)$ cannot hold everywhere, the approximation (13) can be shown to be self-consistent if $\mu V''(x_0) \tau \ll 1$, where $x_0$ is the minimum of the potential, see Appendix B. These criteria generalize to $v_0 \gg \mu |\nabla V|$ and $\mu \tau \Delta V \ll 1$ in higher dimensions. 

This effective equilibrium regime was demonstrated theoretically for sedimenting RTPs, ABPs, and AOUPs, whose sedimentation profiles have been computed theoretically and lead to Eq. (13) in the small $\tau$ limit. Experimentally, the effective equilibrium regime has been measured for sedimenting self-propelled diffusiophoretic colloids. For ABPs, RTPs and AOUPs in harmonic traps, the effective equilibrium regimes have also been studied theoretically and measured in experiments. Probing effective equilibrium regimes in more general experimental settings remains an open challenge.

**Departure from the $\tau = 0$ limit: non-Boltzmann distributions.** Non-thermal effects have naturally been the focus of the community and the departure from the $\tau = 0$ limit is particularly relevant from that perspective. Despite a universal $\tau = 0$ regime, different models of self-propelled particles have been shown to lead to different behaviours, both from a static and a dynamic perspective, as soon as $\tau \neq 0$. General expressions for arbitrary potentials have been obtained for a single RTP in one dimension to any order in $\tau$, see Eq. (12). For AOUPs, many different approaches have been developed. Some are based on calculating the steady-state directly using either path integrals or perturbative approaches. Others rely on effective equilibrium approximations of the dynamics. As a result, the steady-state distribution for $N$ interacting AOUPs has been obtained to order $\tau$ in any dimension. For a single AOUP, it has been obtained explicitly up to order $\tau^2$ using a perturbative expansion that can be extended to higher orders. We use these results below to illustrate and contrast the departure of the steady-state distribution from its $\tau = 0$ limit for both RTPs and AOUPs.

In both cases, the steady-state distribution in the presence of a confining potential $V(x)$ can be written, in one dimension, as in Eq. (13), albeit with $V(x)$ replaced by an effective potential.
\( V_{\text{eff}}(x) \), which can be computed perturbatively. For an AOUP, one finds

\[
V_{\text{eff}}(x) = V(x) - \tau \left( T_{\text{eff}} V''(x) - \frac{V'(x)^2}{2} \right) - 2 \tau^2 \left( \frac{T_{\text{eff}}^2 V^{(4)}(x)}{2} + \int_x^\infty \frac{V'(y)^2 V^{(3)}(y) dy}{2} - T_{\text{eff}} V'(x) V^{(3)}(x) - T_{\text{eff}} \frac{V''(x)}{4} \right) + O(\tau^3) .
\]

(14)

A number of interesting features can already be noted in this perturbative expansion. First, a purely repulsive potential \( V(x) \) may lead to an effective potential with attractive parts, due to the term \(-\tau T_{\text{eff}} V''(x)\). While derived perturbatively, this gives a heuristic explanation for the accumulation of active particles close to walls, which is a trademark of active particles. Second, an important difference between passive and active systems can be observed at order \( \tau^2 \) in Eq. (14): The steady-state distribution \( P(x) \) is a non-local functional of \( V \) for active particles. Consider a dilute system. In thermal equilibrium, a perturbation of the potential \( \delta V \) localized at \( y \) does not impact \( P(x \neq y) \propto e^{-\beta [V(x) + \delta V(x)]} = e^{-\beta V(x)} \), up to an overall normalization. In the active case, Eq. (14) reveals a completely different behaviour: \( P(x \neq y) \) now depends on \( V(y) \) for arbitrary large values of \( |x - y| \), as exemplified in Appendix C. This is a simple heuristic explanation of remarkable experiments conducted on swimming bacteria that show an array of asymmetric obstacles to act as a pump when placed in the middle of a microfluidic cavity. (See Fig. 4).

The derivation of the steady-state distribution of a single RTP can also be carried out using Eq. (12), yielding

\[
V_{\text{eff}}(x) = V(x) - \frac{\mu \tau}{T_{\text{eff}}} \left( (V'(x))^2 + \frac{1}{T_{\text{eff}}} \int_x^\infty dy (V'(y))^3 \right) + O(\tau^2) .
\]

(15)

Again, both the emergence of effective attractive interactions out of repulsive potentials and the non-locality of \( P(x) \) emerge as \( \tau \) departs from 0. Contrary to AOUPs, however, both effects are already present at order \( \tau \), hence highlighting the non-universality of the departure from the \( \tau = 0 \) equilibrium limit across models.

Much less is known in higher dimensions, where exact results and controlled perturbative expansions are harder to get. The far-field perturbations due to localized objects have been characterized and the steady-state distributions of AOUPs can be obtained perturbatively. Interestingly, both the effective attractions and the non-local corrections to the density field remain present. The perturbation to the density field induced by an asymmetric obstacle now decays as a dimension-dependent power-law of the distance to the object. These results on the impact of an asymmetric object have also been extended to active particles experiencing pairwise interactions. By contrast, in the passive case, a perturbation of the density field on the scale of the correlation...
Figure 4: (a) & (b) Microfluidic chamber in which run-and-tumble bacteria or colloidal particles can be inserted. An array of asymmetric obstacles split the cavity into two regions (a). While colloidal particles would lead to a uniform density away from the obstacles, bacteria accumulate in one side of the system (b), as shown by their fluorescence signal. Inset of (a): The non-Boltzmann distribution solely stems from the interaction between particles and walls. Replacing the aligning torques experienced by the bacteria upon encountering a wall (solid blue line) by a specular reflection (dashed blue line) of their orientation would lead to a time-reversal symmetric dynamics and a uniform density. The arrow of time can be read in the bacterial dynamics (solid blue line) by comparing the occurrence probability of forward and backward trajectories. The former requires no tumble to occur during a time $\tau$ whereas the latter requires a tumble to return to the original position. (c) Steady-state density profiles (green) generated by an asymmetric obstacle (grey) placed at the center of the system. Closed boundary conditions (bottom) lead to a density difference in the two compartments whereas periodic boundary conditions (top) lead to a linear profile away from the obstacle and a non-zero current.
length is expected. Away from criticality, these are short-range effects and hence much weaker than those found in active systems. Finally, these power-law corrections to the density field have striking consequences in the presence of a disordered potential, as exemplified by the suppression of the motility-induced phase separation.

To illustrate the discussion above, we now come back to the examples of sedimenting and trapped active particles whose effective equilibrium regimes were discussed before. In the case of sedimenting active particles, the sedimentation profiles remain given by the Boltzmann weight in their distal region even when the condition $v_0 \gg \mu \nabla V$ does not hold: $\rho(z) \propto \exp(-\delta mg z/\lambda)$ where $\delta mg$ is the effective weight of the particles and $\lambda$ is a system-dependent constant that differs for AOUPs, ABPs and RTPs. For AOUPs, $\lambda$ is always equal to $T_{\text{eff}}$ even outside the small $\tau$ regime. By contrast, $\lambda$ explicitly depends on $\delta mg$ for ABPs and RTPs, and leads to a gravitational collapse, $\lambda = 0$, when the sedimentation speed $\mu \nabla V$ equals the self-propulsion one. Next, we turn to the harmonic confinement of active particles. First, results on AOUPs suggest that, as for sedimentation, the equilibrium phenomenology survives: the steady state remains a Gaussian, albeit with a potential-dependent effective temperature and the entropy production vanishes. This is in stark contrast with ABPs and RTPs for which a trapping force $F(r) = -kr$ leads to a finite horizon $r_{\text{max}} = v_0/(\mu k)$. The Gaussian behaviour in the small $\tau$ limit is replaced by a sharp density accumulation at $r = r_{\text{max}}$ in the opposite limit. It is interesting to note that AOUPs, which are praised for their simplicity, miss, in this case, an important feature of active dynamics.

**Departure from the $\tau = 0$ limit: the emergence of non-equilibrium dynamical features.** As discussed in the Box *Identifying time-reversal symmetry breaking*, the departure from thermal equilibrium is not only signaled by a non-Boltzmann distribution but, most importantly, by the emergence of novel dynamical features resulting from the breakdown of TRS. This can already be seen at the non-interacting level in the presence of external potentials for large enough persistence times. Some of these nonequilibrium dynamical features have recently attracted a lot of attention and are discussed below.

1. **Steady-state currents.** One of the most important results in non-equilibrium statistical mechanics is the generic emergence of steady-state currents resulting from the interplay between the breakdown of TRS and the lack of spatial symmetries. From Brownian ratchets to molecular motors, this has been exemplified first by considering non-equilibrium dynamics in the presence of asymmetric potentials. These results extend...
to active particles, whose isotropic motions are also rectified in the presence of asymmetric potentials, leading to the emergence of steady-state currents. Analytically, the current has been computed for AOUPs and RTPs in one dimension in the presence of a periodic, asymmetric potential. Perturbatively in $\tau$, the currents scale as $\tau^2$ and $\tau$ for AOUPs and RTPs, respectively. This highlights, once again, the difference between these models as they depart from the effective equilibrium regime. Mathematically, it can be traced back to the order in $\tau$ at which the non-local terms appear in Eqs (14) and (15).

These results can easily be generalized to a single localized obstacle in the presence of periodic boundary conditions. In one space dimension, the current then decays as the inverse system size and a linear density profile is observed away from the obstacle (See Fig 4(c)). These results generalize to higher dimensions where asymmetric obstacles also generate currents. In the case of localized obstacles, the currents are long ranged and decay with the distance $r$ to the object as a dimension-dependent power-law: $|J| \propto r^{-d}$.

The presence of a current signals a non-zero mean force exerted by the obstacle on the active fluid. By Newton’s third law, a current implies a net force exerted by the fluid on the object. This explains, for instance, why an asymmetric gear immersed in a bacterial bath exhibits a persistent biased rotating motion in the steady state. From a mechanical balance perspective, relevant in these overdamped systems, a non-zero mean current implies a non-zero drag, which has to be balanced by a net force from the object, whence relating currents and forces in active systems.

The generic emergence of currents outside equilibrium when spatial symmetries are broken displays interesting exceptions. In active systems, for instance, currents are absent if, instead of using asymmetric potentials, one enforces an asymmetric spatial modulation of the self-propulsion speed, despite non-homogeneous steady-state density profiles. The currents are, somewhat counter-intuitively, restored upon the addition of pairwise forces.

2. **Entropy production.** The computation of the entropy production rate for a non-interacting run-and-tumble particle presented in section 2 can be generalized to the case of an external force $\mathbf{F}$: $\dot{\mathbf{r}} = \mu \mathbf{f}_p + \mu \mathbf{F} + \sqrt{2D} \mathbf{\eta}$. When computing the entropy production in the full $(r, f_p)$ space, one then finds $D \sigma/\mu = \langle \dot{\mathbf{r}} \cdot \mathbf{f}_p \rangle + \langle \dot{\mathbf{r}} \cdot \mathbf{F} \rangle$. For a conservative force $\mathbf{F} = -\nabla V(r)$, this reduces to $\sigma = \frac{\mu}{D} \langle \dot{\mathbf{r}} \cdot \mathbf{f}_p \rangle = \frac{\mu}{D} w_p$. The absence of $V$ in this second formula does not imply
an entropy production rate independent of the potential: the dissipation $w_p$ indeed depends on $V(r)$ through the precise form of the steady-state distribution.

Integrating out $f_p$ to compute the entropy production rate $\dot{\sigma}$ in $r$-space is, however, not as easy as in the absence of external force and there is no general expression for $\dot{\sigma}$. We simply know that coarse-graining these mesoscopic stochastic dynamics can only lower their entropy production rate so that $\dot{\sigma} \leq \sigma$ (see, e.g., 150). Progress has been made when the active noise is a Gaussian process, as is for instance the case for AOUPs. There, the computation has been carried out for $N$ interacting particles in $d$ dimensions, in the presence of forces stemming from a potential $V$, leading to $68, 82, 128, 129\sigma = \frac{D}{2}\tau \langle (\dot{r} \cdot \nabla)^3 V(r) \rangle$. This expression simplifies in the small persistence time limit to give $\sigma = \frac{D}{2}\tau \langle \sum_{i,j,k} (\nabla_i \nabla_j \nabla_k V)^2 \rangle$. It is remarkable that, to order $\tau$, AOUPs are time-reversal symmetric, despite their steady-state distribution already being different from the Boltzmann weight.

3. **Activated events, non-Arhenius law and Onsager-Machlup symmetry.** In equilibrium, an important consequence of TRS is the celebrated Onsager-Machlup symmetry 112, 140 which states that, in a macroscopic system (or in a small-noise limit), the most likely path to realize a rare excursion follows the time-reversal of the most likely relaxation from this rare event into the most probable state. This has important consequences, for instance, for reaction-rate theory where it implies that, in the small noise limit, transitions between states are realized by following steepest-gradient ascent and descent in a free energy landscape. This symmetry breaks down out of equilibrium, an effect that has attracted a lot of interest 20, 21, 187 and may lead to non-equilibrium dynamical phase transitions 11, 24, 25, 33. Apart from recent results on nucleation pathways in MIPS 105, 154, 156, reaction-rate theory remains largely uncharted territory for active matter. Interesting differences with equilibrium dynamics have already been observed at the level of first-passage time computations 5, 30, 211. In the low-noise regime, Arhenius law is, for instance, not valid 210 and the barrier crossing is controlled by a combination of force balance and potential differences.

4. **Linear response** studies the reaction of systems to small perturbations. For Markov processes, even out of equilibrium, the Agarwal formula generically predicts the response of an observable $A$ to the perturbation of the system by a field $B$ from the knowledge of steady-state correlations 1, 14, 151. This formula also requires the knowledge of the steady-state distribution and it only reduces to the celebrated fluctuation-dissipation theorem (FDT) when the steady state is given by a Boltzmann weight. Experimentally, the FDT allows the characterization, at the microscopic scale, of passive systems using microrheological, mechanical measurements.
A first approach to linear response in active systems relied on measurements of ‘violations’ of the equilibrium FDT, or lack thereof. This first allows identifying regimes in which an ‘effective temperature’ can be defined \cite{27,45,85,104,108,110,133,173,182,183,204}. Then, the breakdown of FDT can also be used to identify the time scales over which activity drives biological systems out of equilibrium, both in vitro \cite{131} and in vivo \cite{26,65,67,84,159,205}. An alternative approach is to start from a microscopic model of active systems and explicitly construct its linear response \cite{114}. This has, in particular, been carried out using perturbative expansions \cite{41,68,129} or Markovian approximations \cite{37,49} and might pave the way towards a systematic microrheology of active systems.

4 TRS in the presence of interactions in active systems

One of the most striking features of active systems is the wealth of dynamical phenomena it exhibits that are without counterparts in equilibrium. From the emergence of travelling waves in colloidal rollers \cite{31} to the collective migration of cell monolayers \cite{150}, a trademark of active systems is the emergence of macroscopic steady-state currents (See Fig. 1). This is a clear TRS-breaking, non-equilibrium feature that allows to immediately distinguish active from passive systems in many situations. Mechanistically, as exemplified by the physics of flocking \cite{194,201}, this naturally emerges in phase transitions whose order parameters are coupled to the particle orientations. Estimating the entropy production rate in these strongly irreversible systems is an open problem, on which progress has been made recently using field-theoretical descriptions of flocking models \cite{29}. Note that, while the global phenomenology of a model can be strongly out of equilibrium some of its features may retain an equilibrium nature, as was for instance suggested for angular correlations between birds in starling flocks \cite{132}. Identifying the degrees of freedom that contribute to TRS violations is thus also an open challenge \cite{16,78,129,134}.

Microscopically, the breakdown of TRS emerges from very simple interactions between particles, even without relying on alignment. Indeed, mutual hard-core exclusion suffices to make active dynamics irreversible \cite{122} (See Box Violation of TRS resulting from hard-core interactions for a simple example). A natural question is then whether TRS survives in some classes of interacting active-matter systems. We discuss below two such instances. First, we consider MIPS in which TRS is partially restored by coarse-graining in certain classes of systems. We then discuss under which conditions coarse-graining may restore TRS exactly, considering in particular tactic systems. Finally, we turn to the small-persistence-time regime in which an exact TRS is recovered for interacting AOUPs despite a non-Boltzmann distribution.
Violation of TRS resulting from hard-core interactions. Consider the following one-dimensional lattice model of run-and-tumble particles \cite{122,179,191}: the particles hop to the right and to the left at rate $p$ on empty sites, respectively. In addition, particles change direction at a rate $\alpha$.

Consider the sequence of configuration $C_1$ to $C_4$:

$C_1$ $+$ $-$ $+$ $-$ $-$ $-$ $+$ $-$ $+$ $-$ $-$ $-$ $-$ $-$ $-$ $-$ $-$ $-$ $-$ $-$ $-$ $-$ $-$ $-$ $-$ $-$ $-$ $-$ $-$ $-$ $-$ $-$ $-$ $-$ $-$ $-$ $-$ $-$ $-$ $-$ $-$ $-$ $-$ $-$ $-$ $-$ $-$ $-$ $-$ $-$ $-$ $-$ $-$ $-$ $-$ $-$ $-$ $-$ $-$ $-$ $-$ $-$ $-$ $-$ $-$ $-$ $-$ $-$ $-$ $-$ $-$ $-$ $-$ $-$ $-$ $-$ $-$ $-$ $-$ $-$ $-$ $-$ $-$ $-$ $-$ $-$ $-$ $-$ $-$ $-$ $-$ $-$ $-$ $-$ $-$ $-$ $-$ $-$ $-$ $-$ $-$ $-$ $-$ $-$ $-$ $-$ $-$ $-$ $-$ $-$ $-$ $-$ $-$ $-$ $-$ $-$ $-$ $-$ $-$ $-$ $-$ $-$ $-$ $-$ $-$ $-$ $-$ $-$ $-$ $-$ $-$ $-$ $-$ $-$ $-$ $-$ $-$ $-$ $-$ $-$ $-$ $-$ $-$ $-$ $-$ $-$ $-$ $-$ $-$ $-$ $-$ $-$ $-$ $-$ $-$ $-$ $-$ $-$ $-$ $-$ $-$ $-$ $-$ $-$ $-$ $-$ $-$ $-$ $-$ $-$ $-$ $-$ $-$ $-$ $-$ $-$ $-$ $-$ $-$ $-$ $-$ $-$ $-$ $-$ $-$ $-$ $-$ $-$ $-$ $-$ $-$ $-$ $-$ $-$ $-$ $-$ $-$ $-$ $-$ $-$ $-$ $-$ $-$ $-$ $-$ $-$ $-$ $-$ $-$ $-$ $-$ $-$ $-$ $-$ $-$ $-$ $-$ $-$ $-$ $-$ $-$ $-$ $-$ $-$ $-$ $-$ $-$ $-$ $-$ $-$ $-$ $-$ $-$ $-$ $-$ $-$ $-$ $-$ $-$ $-$ $-$ $-$ $-$ $-$ $-$ $-$ $-$ $-$ $-$ $-$ $-$ $-$ $-$ $-$ $-$ $-$ $-$ $-$ $-$ $-$ $-$ $-$ $-$ $-$ $-$ $-$ $-$ $-$ $-$ $-$ $-$ $-$ $-$ $-$ $-$ $-$ $-$ $-$ $-$ $-$ $-$ $-$ $-$ $-$ $-$ $-$ $-$ $-$ $-$ $-$ $-$ $-$ $-$ $-$ $-$ $-$ $-$ $-$ $-$ $-$ $-$ $-$ $-$ $-$ $-$ $-$ $-$ $-$ $-$ $-$ $-$ $-$ $-$ $-$ $-$ $-$ $-$ $-$ $-$ $-$ $-$ $-$ $-$ $-$ $-$ $-$ $-$ $-$ $-$ $-$ $-$ $-$ $-$ $-$ $-$ $-$ $-$ $-$ $-$ $-$ $-$ $-$ $-$ $-$ $-$ $-$ $-$ $-$ $-$ $-$ $-$ $-$ $-$ $-$ $-$ $-$ $-$ $-$ $-$ $-$ $-$ $-$ $-$ $-$ $-$ $-$ $-$ $-$ $-$ $-$ $-$ $-$ $-$ $-$ $-$ $-$ $-$ $-$ $-$ $-$ $-$ $-$ $-$ $-$ $-$ $-$ $-$ $-$ $-$ $-$ $-$ $-$ $-$ $-$ $-$ $-$ $-$ $-$ $-$ $-$ $-$ $-$ $-$ $-$ $-$ $-$ $-$ $-$ $-$ $-$ $-$ $-$ $-$ $-$ $-$ $-$ $-$ $-$ $-$ $-$ $-$ $-$ $-$ $-$ $-$ $-$ $-$ $-$ $-$ $-$ $-$ $-$ $-$ $-$ $-$ $-$ $-$ $-$ $-$ $-$ $-$ $-$ $-$ $-$ $-$ $-$ $-$ $-$ $-$ $-$ $-$ $-$ $-$ $-$ $-$ $-$ $-$ $-$ $-$ $-$ $-$ $-$ $-$ $-$ $-$ $-$ $-$ $-$ $-$ $-$ $-$ $-$ $-$ $-$ $-$ $-$ $-$ $-$ $-$ $-$ $-$ $-$ $-$ $-$ $-$ $-$ $-$ $-$ $-$ $-$ $-$ $-$ $-$ $-$ $-$ $-$ $-$ $-$ $-$ $-$ $-$ $-$ $-$ $-$ $-$ $-$ $-$ $-$ $-$ $-$ $-$ $-$ $-$ $-$ $-$ $-$ $-$ $-$ $-$ $-$ $-$ $-$ $-$ $-$ $-$ $-$ $-$ $-$ $-$ $-$ $-$ $-$ $-$ $-$ $-$ $-$ $-$ $-$ $-$ $-$ $-$ $-$ $-$ $-$ $-$ $-$ $-$ $-$ $-$ $-$ $-$ $-$ $-$ $-$ $-$ $-$ $-$ $-$ $-$ $-$ $-$ $-$ $-$ $-$ $-$ $-$ $-$ $-$ $-$ $-$ $-$ $-$ $-$ $-$ $-$ $-$ $-$ $-$ $-$ $-$ $-$ $-$ $-$ $-$ $-$ $-$ $-$ $-$ $-$ $-$ $-$ $-$ $-$ $-$ $-$ $-$ $-$ $-$ $-$ $-$ $-$ $-$ $-
rate. All in all, it is thus the interaction between the particles which generates the violation of TRS, as first explained in [122].

**TRS and effective equilibrium descriptions of MIPS.** Consider an equilibrium system comprising Brownian particles interacting via a pairwise potential made of a hard core and a soft attractive tail. The steady state of the system is found by balancing entropy, which favors disordered attractive configurations, with energy. At moderate densities, the latter favors cohesion thanks to the attractive part of the potential. As the temperature is lowered, energy wins over entropy and a gas-to-liquid phase transition is observed. When the total number of particles is conserved, this leads to phase coexistence. Now, make the particle active. A natural way to preserve phase separation is to make self-propulsion weak enough that it does not overcome the attractive interactions. Interestingly, however, the largest part of the phase diagram exhibiting liquid-gas coexistence is not found at small self-propulsion speeds but at large ones [152], and it is observed even in the absence of any attractive tail [63, 153] (See Fig. 5). A cohesive phase may thus emerge out of purely repulsive pairwise forces in active systems. This phase-separated state cannot be accounted for using the Boltzmann weight and is a trademark of active particles. It results from a motility-induced phase separation [40] through which particles whose self propulsion is hindered at high density separate between a dense, almost arrested, phase and a dilute active gas.

Despite its non-Boltzmann nature, the dynamics of such a phase-separated system at the macroscopic scale, however, does not reveal any clear breakdown of TRS at first sight, and the difference with an equilibrium phase separation is hard to pinpoint. Therefore, many ideas based on equilibrium theories have been proposed to account for MIPS [144, 145, 176, 177, 180, 185, 188]. Below we first focus on large-scale TRS violations in MIPS before discussing when and how a generalization of equilibrium approaches may be used to describe MIPS and other phase transitions.

**Large-scale TRS violations in MIPS.** We now focus on the MIPS observed in systems with quorum-sensing interactions, i.e. when the speed of a particle explicitly depends on the local density of particles around it [17, 102, 185]:

\[ \dot{r}_i = v(r_i, [\rho])u_i, \quad \rho(r) \equiv \sum_i \delta(r - r_i), \] (18)
where \( u_i \) undergoes either rotational diffusion or instantaneous Poisson-distributed tumbles. A common form for \( v(r, \rho) \) is then
\[
v(r, \rho) = f[\tilde{\rho}(r, t)], \quad \tilde{\rho}(r, t) \equiv \int dr \rho(r) K(r_i - r),
\]
(19)
where \( K \) is a kernel which can stem from integrating out the signal used by the particles to communicate\(^{[141]}\), and \( f \) determines how the particles react to their peers. Equations (18) and (19), together with \( K(r) = \delta(r) \) and \( f \) a linearly decaying function, have been proposed as a toy model for systems with pairwise repulsive forces\(^{[23, 191]}\), even though the latter offer a richer phenomenology such as hexatic order\(^{[9, 55, 94]}\) or bubbly phases\(^{[170, 193]}\).

A glimpse into the large-scale behaviour of this system can be obtained using a diffusive approximation on Eq. (18), which leads to the fluctuating hydrodynamics\(^{[120, 173, 176]}\)
\[
\dot{\rho} = \nabla \cdot [\rho D \nabla \mu + \sqrt{2 \rho D} \Lambda] \quad \text{with} \quad D = \frac{v^2 \tau}{d} \quad \text{and} \quad \mu = \log \rho + \log f(\tilde{\rho}),
\]
(20)
where \( \Lambda \) is a Gaussian white-noise field of zero mean and correlations \( \langle \Lambda_\alpha(r, t) \Lambda_\beta(r', t') \rangle = \delta_{\alpha\beta} \delta(r - r') \delta(t - t') \) and \( d \) is the number of space dimensions. By analogy to the equilibrium model \( B \), we refer to \( \mu \) as a chemical potential. The dynamics (20) satisfies TRS if and only if \( \mu(r) \) is a gradient of a free-energy functional\(^{[173]}\). This holds when a generalization of the Schwarz equality to functional derivatives is obeyed:
\[
\frac{\delta \mu(r, \rho)}{\delta \rho(r')} = \frac{\delta \mu(r', \rho)}{\delta \rho(r)},
\]
(21)
where the equality is understood as between distributions\(^{[141]}\).

For a generic \( f(\tilde{\rho}) \), Eq. (21) is not satisfied and the dynamics (20) does not obey TRS. An interesting exception is when \( K(r) = \delta(r) \); \( v \) is then a local function of the density and Eq. (20) satisfies an exact TRS\(^{[135]}\). For more general kernels, a free-energy functional is only found for \( f(\tilde{\rho}) = v_0 \exp(-\lambda \tilde{\rho}) \)\(^{[83]}\). When this is not the case, it is interesting to see which features of the dynamics are directly responsible for breaking TRS. To do this, we can expand \( \mu \) to second order in gradients:
\[
\mu[r] = \log \rho + \log f(\rho) - \kappa \Delta \rho \quad \text{where} \quad \kappa(\rho) = -\ell^2 \frac{f'(\rho)}{f(\rho)},
\]
(22)
and \( \ell^2 = \int dr K(r) r^2 \) is a measure of the interaction range\(^{[176]}\). The entropy production rate can then be computed using methods akin to those presented in\(^{[134]}\) as:
\[
\sigma = -\lim_{t \to \infty} \frac{1}{2t} \int_0^t ds \int dr \dot{\rho}(r, t) \kappa[\rho(r, t)] \Delta \rho + \mathcal{O}(\nabla^4) \simeq \frac{1}{2} \int dr \langle \dot{\rho}(r) \kappa[\rho(r)] \Delta \rho \rangle,
\]
(23)

where the last equality stems from ergodicity. A few comments are in order. First, a completely local approximation to $\mu$, that neglects all gradient terms, leads to a vanishing entropy production rate. This is consistent with the apparent macroscopic similarity between MIPS and an equilibrium liquid-gas separation. Then, taking gradients into account, TRS is broken and Eq. (23) offers a spatial decomposition of the entropy production rate. It suggests that the latter is most pronounced in inhomogeneous regions, namely next to interfaces between coexisting phases. Figure 5 shows a measure of $\sigma$ in a simplified version of the field-theory (20) undergoing MIPS, which is commonly referred to as active model B. The entropy production rate is indeed peaked at the interface between the gas and liquid phases, a result that was confirmed using microscopic simulations of AOUPs [29]. This role of interfaces in TRS breakdown also has consequences for static properties, as exemplified by the construction of the phase diagram which we now discuss.

**Phase diagram and generalized thermodynamics of MIPS.** A natural question is whether the dynamical differences between MIPS and an equilibrium phase separation also affect the static properties, and in particular the density profiles connecting coexisting phases which, as we discuss below, determine the phase diagram. The simplest way of answering this question is to take a mean-field approximation. In a homogeneous system, we can use a local approximation of $\mu$, defined in Eq. (20), to obtain the Landau free energy $F = \int d\mathbf{r} \phi(\rho(\mathbf{r}))$, where $\phi(\rho) = \rho(\log \rho - 1) + F(\rho)$ with $F'(\rho) = \ln f(\rho)$. The linear stability of a homogeneous phase at density $\rho_0$ is then lost whenever $\phi''(\rho_0) < 0$, i.e. $\rho_0 f'(\rho_0) < -f(\rho_0)$. This defines a spinodal region within which the system is linearly unstable to MIPS [25]. At this level, there is no difference with an equilibrium mean-field theory. To account for the resulting phase-separated state, it is necessary to consider inhomogeneous profiles.

To do so, we again use the leading-order gradient expansion of $\mu$ given by Eq. (22). At this level, the mapping to equilibrium is violated and equation (21) is not satisfied. (Again, an exception occurs for $f(\tilde{\rho}) = v_0 \exp(-\lambda \tilde{\rho})$.) The attempts [180, 185, 188] to build the phase diagram using common-tangent constructions on $\Phi(\mathbf{r})$ are thus bound to fail [174, 189]. Somewhat surprisingly, if $\mu(\mathbf{r})$ cannot be written as the functional derivative of a free energy with respect to $\rho(\mathbf{r})$, a gradient form can be found upon a change of variable $\rho \to R(\rho)$, where $R'(\rho) = 1/\kappa(\rho)$. Then, $\mu(\mathbf{r}) = \nabla_\mathbf{r} \delta \mathcal{H} / \delta R(\mathbf{r})$, where $\mathcal{H} = \int d\mathbf{r} [\Phi(R) + \frac{\kappa}{2R^2}(\nabla R)^2]$ and $\Phi'(R) = \log \rho(R) + \log f(\rho(R))$. This allows identifying $\mu$ and a generalized pressure $P \equiv R^2 \delta \mathcal{H} / \delta R - \Phi$ as state variables, which are equal in coexisting phases [176, 177]. Equivalently, a common-tangent construction on $\Phi(R)$ can be used to construct the coexisting densities. Despite its mean-field nature, this construction was shown to
give precise estimates of the phase diagram for microscopic models of quorum-sensing active particles undergoing MIPS, without any fitting parameters\cite{176,177} (See Fig 5). Note that the agreement does not extend up to the putative critical point close to which the mean-field theory is expected to break-down in a Ginzburg interval (which is not numerically resolved). Furthermore, at large propulsion speeds, domain walls become so sharp that higher-order gradients cannot be neglected leading to quantitative differences with the predictions of \cite{22}.

**Tactic dynamics.** In the case of MIPS, the strong TRS violations exhibited at the single-particle level ($\sigma$ is infinite in the absence of translational diffusion) are thus partially erased upon coarse-graining. TRS violations, occuring mostly at interfaces, survive because condition \cite{21} is generically not satisfied. A natural question is then whether there exist active systems whose fluctuating hydrodynamics satisfy the integrability condition \cite{21}. This question was answered for tactic dynamics, in which particles move according to Eq. \cite{8} and whose orientations $u_i$ perform tumbles at rate $\alpha$ and diffuse with rotational diffusivity $\Gamma$. Taxis is implemented by coupling self-propulsion with the gradient of a field $c(r)$ through\cite{120,141,163}

\[
\dot{v}_p = v_0 - v_1 u_i \cdot \nabla c \quad \alpha = \alpha_0 + \alpha_1 u_i \cdot \nabla c \quad \Gamma = \Gamma_0 + \Gamma_1 u_i \cdot \nabla c \quad (24)
\]

The field $c(r)$ can be either externally imposed or, more interestingly, can be a functional of the particle density. Under the hypothesis that the large-scale diffusive scaling of non-interacting active particles survives the addition of interactions, the fluctuating hydrodynamics of this model can be constructed and Eq. \cite{21} can be satisfied in a number of non-trivial cases\cite{141}. In particular, when $c(r)$ is a diffusive signalling field produced by the particles, this system models swimming bacteria interacting via chemotaxis. The integrability of the large-scale dynamics then reveals a mapping between bacteria interacting both via chemotractant and chemorepellent and Brownian colloids interacting via attractive and repulsive forces. While the model violates TRS at the microscopic scale, the latter is restored upon coarse-graining and the rich phase diagram of this system can be accounted for exactly using equilibrium theories. Note that the fate of TRS at the fluctuating hydrodynamic level in active systems is an open, non-trivial question. For instance, another model of tactic dynamics defined as $\dot{r}_i = v_1 \nabla c + v_2(u(\theta) \cdot \nabla)\nabla c$ was shown to lead to a violation of TRS at the coarse-grained level\cite{120}. The results of\cite{141} thus establish a non-trivial embedding of equilibrium physics in active matter systems, but slight perturbations, albeit leading to minor modifications of large-scale behaviours, may trigger TRS violations.

**Small $\tau$ regime.** Finally, let us mention that the equilibrium regime recovered in the $\tau \to 0$ limit while keeping $kT_{\text{eff}} = v_0^2/\mu$ constant discussed for the single-particle case survives under the addition of pairwise forces. The departure from this limiting case has been studied analytically
Figure 5: (a) Phase diagram of ABPs interacting via a Lennard-Jones potential. For vanishing self-propulsion $v_0$, the system is effectively in equilibrium and undergoes a traditional liquid-gas phase separation. The phase-separated (blue) region survives at small $v_0$ until the self-propulsion is strong enough to overcome attractive interactions, hence vaporising the liquid phase. A reentrance into a phase-separated (orange) region is observed at larger $v_0$. The latter stems from a motility-induced phase separation and would also be observed in the absence of the attractive tail of the pair potential. Symbols correspond to binodals measured in simulations of self-propelled particles interacting via a Lennard-Jones potential. The phase-separated regions are estimated numerically up to unresolved critical regions using a methodology described in Appendix D. (b) & (c) Simulations of a scalar field-theory undergoing motility-induced phase separation. The order parameter $\Phi(x, y)$ shown in panel (b) distinguishes a liquid phase ($\Phi = 1$) from a gas one ($\Phi = -1$). The entropy production rate can be decomposed spatially as $\sigma = \int d^2r \dot{\sigma}(r)$. The plot of $\dot{\sigma}(r)$ in panel (c) shows the interface to contribute most to the TRS violations measured by $\sigma$. Adapted from [134]. (d) Phase diagrams of microscopic models of quorum-sensing active particles (symbols). Equating the generalized pressures $P$ and chemical potentials $\mu$ in coexisting phases lead to a theoretical prediction (red line) in quantitative agreement with microscopic simulations. An equilibrium construction based on a local approximation of $\mu$ (black solid line) is quantitatively incorrect. Adapted from [176].
for AOUPs, both using Markovian approximations and an explicit small-\( \tau \) expansion. To linear order in \( \tau \), the system satisfies detailed balance with a non-Boltzmann form. Casting \( \ln P \) into an effective potential, pairwise repulsive forces lead to effective attractive interactions. While the latter do not allow to quantitatively account for MIPS, they qualitatively capture how self-propulsion turns repulsive forces into attractive ones. Finally, note that \emph{bona fide} equilibrium systems can be studied under the perturbation of a small self-propulsion velocity, which allows studying the fate of thermodynamical concepts like surface tension or chemical potential in weakly active systems. The same applies to equilibrium phases, like the hexatic phase observed in 2D melting, which has been shown to survive activity.

5 Perspectives

Most active-matter models such as Eq. (1) aim at modelling the effective dynamics of self-propelled particles and not the irreversible consumption of energy powering the propulsion force. As such, they are unable to account for all the dissipative processes occurring in the system, hence rendering the theoretical assessment of its full irreversibility a somewhat hopeless endeavour. This highlights an important property of nonequilibrium systems: irreversibility depends on the degrees of freedom under study and on the scale of their description. This raises the question of the scale at which dissipation is maximal. It also opens up the possibility that equilibrium statistics prove relevant to describe specific scales or observables. Effective-equilibrium descriptions have indeed proven successful in qualitatively accounting for part of active matter phenomenology such as the motility-induced phase separation. On the contrary, time is now ripe for the identification of TRS-violating emerging behaviours and for the quantification of entropy-production rates in active pattern-forming systems. In turn, the connection between entropy production rates and more directly accessible observables such as steady-state currents remains an open challenge at the coarse-grained scale. These questions are particularly relevant in the biophysical context that gave birth to the field of active matter: cells are constantly dissipating energy to exert biological functions; assessing which of them genuinely rely on nonequilibrium processes is a fascinating open challenge.

Beyond the violation of TRS observed in active systems, we have reviewed their most salient non-Boltzmann features. That the steady-state distributions are not captured by the Boltzmann weight indeed allows for phenomenologies unmatched in passive systems, but it also impairs our ability to design smart active materials. An important challenge facing the community is then to develop alternatives to equilibrium thermodynamics that would grant us the same level of intuition.
and control over active systems as we have over passive ones. Natural starting points are then the various limits in which effective equilibrium concepts can be proven relevant. From the small-but-non-zero persistence-time limit, to emerging TRS restored by coarse-graining, to the identification of state functions, we have reviewed cases in which efforts were rewarded. Beyond these cases, this calls for an extensive exploration of the fate of thermodynamic state variables (entropy, chemical potentials, etc.). At the local level, inferring effective interactions by means of rapidly developing learning algorithms seems a promising avenue[133][44][195].

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A Entropy production

The forward trajectory \( r(t) \) and \( \theta(t) \) uniquely characterize the realization of the noise through

\[
\eta(t) = \frac{\dot{r}(t) - v_0 u(\theta(t))}{\sqrt{2D}} \tag{25}
\]

For the reversed trajectory \( r^r(t) = r(t_f - t), \theta^r(t) = \theta(t_f - t) \) to be observed, the surrounding fluid molecules have to produce a different noise

\[
\eta^r(t) = \frac{\dot{r}^r(t) - v_0 u(\theta^r(t))}{\sqrt{2D}} = \frac{-\dot{r}(t_f - t) - v_0 u(\theta(t_f - t))}{\sqrt{2D}} = -\eta(t_f - t) - \frac{2v_0 u(\theta(t_f - t))}{\sqrt{2D}} \tag{26}
\]

To characterize the irreversibility of the process it is useful to note that the probability of a trajectory is given by its Onsager-Machlup form\[140][210]

\[
P[\{r(t), \theta(t)\}] = Z^{-1} P[\{\theta(t)\}|\theta_0] \exp \left[ -\frac{1}{4D} \int_0^{t_f} dt [\dot{r}(t) - v_0 u(\theta)]^2 \right] P_0(r_0, \theta_0) \tag{27}
\]

where \( P[\{\theta(t)\}|\theta_0] \) is the probability of the realization of \( \theta(t) \) starting from \( \theta_0 \), \( P_0 \) is the probability of the initial condition, and \( Z^{-1} \) is a normalization. Note that, for fully randomizing tumbles, \( P[\{\theta(t_f - t)\}|\theta_f] = P[\{\theta(t)\}|\theta_0] \). Taking the logarithm of the ratio between forward and backward trajectories yield the corresponding ‘path-wise entropy production’\[167]\:

\[
\hat{\Sigma}[\{r(t), \theta(t)\}] \equiv \log \frac{P[\{r(t), \theta(t)\}]}{P[\{r(t_f - t), \theta(t_f - t)\}]} = \frac{\mu}{D} \int_0^{t_f} dt \dot{r} \cdot f_p + \log \frac{P_0(r_0, \theta_0)}{P_f(r_f, \theta_f)} \tag{28}
\]
where \( P_f(r_f, \theta_f) \) is the probability of being at \( r_f \equiv r(t_f) \) and \( \theta_f \equiv \theta(t_f) \) given that the initial condition was sampled according to \( P_0 \).

### B Self-consistency of the effective temperature regime

Let us consider the self-consistency of Eq. (13) in the presence of a confining potential. Close to the minimum \( x_0 \) of the potential, the condition \( v_0 \gg \mu V'(x) \) trivially holds. Let us expand the distribution (13) around \( x_0 \). It is then given by a locally Gaussian distribution

\[
P(x) \sim \exp \left[ -\frac{V''(x_0)(x-x_0)^2}{2T_{\text{eff}}} \right]
\]

This predicts a typical displacement \( x_t \sim \sqrt{T_{\text{eff}}/V''(x_0)} \) which in turn leads to a typical force that scales as \( V'(x_t) \sim \sqrt{\frac{\tau v_0^2 V''(x_0)}{\mu}} \), where we have used \( T_{\text{eff}} = v_0^2 \tau / \mu \). The condition \( v_0 \gg \mu V'(x) \) then becomes \( \mu V''(x_0) \tau \ll 1 \): the typical time between two tumbles has to be much shorter than the relaxation time inside the potential well.

### C Non-locality of the steady-state distribution

Consider the effective potential given in Eq. (14). Its non-local nature becomes apparent if one adds a localized perturbation \( \delta V(x) = \epsilon \delta(x-y) \), centered around \( y \), to the potential \( V(x) \). The effective potential \( V_{\text{eff}}(x) \) then picks up a contribution due to \( \delta V \), because of the term \( \int \delta V'(y)^2 \delta V^{(3)}(y) dy \). To linear order in \( \epsilon \), it reads

\[
\delta V_{\text{eff}}(x) = \frac{\epsilon \tau^2}{2} \left[ (V'(y)^2)^{(3)} + 2V''(y)V^{(3)}(y) + 2V'(y)V^{(4)}(y) \right] \Theta(x-y) ,
\]

which adds a global step to the density profile at \( x = y \).

### D Self-propelled ABPs interacting via a Lennard-Jones potential

We consider \( N \) active Brownian particles evolving in two space dimensions under the dynamics:

\[
\dot{r}_i = v_0 u(\theta_i) - \sum_j \nabla V(r_i - r_j) + \sqrt{2D_r} \eta_i , \quad \dot{\theta}_i = \sqrt{2D_\theta} \xi_i
\]

where \( \eta_i \) and \( \xi_i \) are independant Gaussian white noises, and \( V \) is the Lennard-Jones potential

\[
V(r) = 4\varepsilon \left( \frac{\sigma_{12}}{r^{12}} - \frac{\sigma_6}{r^6} \right) .
\]
Interactions between particles are truncated at $|r| = 2.7\sigma$ and we used periodic boundary conditions. Figure 5a was obtained using $\sigma = 0.37$, $T = 0.4$ and $D_r = 2$. The phase-separated regions were found by running simulations for $\rho_0 = 2.5\sigma^2$ ($v_0 < 8$) and $\rho_0 = 4\sigma^2$ ($v_0 > 8$) in systems of line sizes $L = 80$ up to $t = 2000$, where $\rho_0$ is the rescaled number density $\rho_0 \equiv N\sigma^2/L^2$. The symbols correspond to estimates of the coexisting densities. The latter were obtained from the local maxima of histograms of the density field, constructed using bins of linear size 4.

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