Active particles in a tube: a generalized entropy potential approach

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We study the transport of self-propelled noninteracting active Brownian particles (ABPs) and run-and-tumble particles (RTPs) in long tubes of varying widths. Using a moment expansion, we construct a generalized Fick-Jacobs framework for the active particles when the tube width is large and slowly varying. We show that the variation of the particle density along the tube is well described by a one-dimensional generalized entropy potential. This potential resembles its passive counterpart, albeit with an effective temperature and an effective tube width that are renormalized by the activity. Our generalized entropy potential approach allows us to predict the steady-state density distribution along the tube as well as the mean escape time out of a spindle chamber. Finally, we show how to account for the emergence of spontaneous ratchet flows in asymmetric channel by including higher-order corrections neglected in the effective entropy potential approach.

The transport of active particles through long tubes plays a critical role in various biological and physical phenomena, particularly if the tube’s shape is irregular and its width changes [1, 2]. For example, channels with broken mirror symmetry perpendicular to their axes can create spontaneous directed transport of active particles, which is often referred to as ratchet transport or ratchet flow [3–7]. In terms of biological implications, during the infection of a human body by pathogens, microbes may migrate along the trachea, lymphangion, urinary tract, or blood vessels. The question of transport along tubes is also relevant to specific therapies, where engineered bacteria are transported along blood vessels to tumors, stimulating the immune system to kill cancer cells [8]. Although real systems often involve hydrodynamics and complex interactions, the study of simple active-particle transport along tubes already constitutes a rich and nontrivial starting point. Here we consider active Brownian particles (ABPs) and run-and-tumble particles (RTPs) [9, 10], which are commonly used to describe the motion of self-propelled colloids or microbes, such as bacteria [11–14].

The transport of passive particles in channels has been extensively studied [15–23]. In the seminal work of Jacobs [15], it was shown that the time evolution of the density of passive particles along a tube can be reduced to the Fick-Jacobs (FJ) equation. The latter describes the motion of particles in 2d or 3d tubes as an effective 1d motion along the tube, subject to an effective potential proportional to the local entropy of the particles, which is impacted by their motions in the transverse directions. The reduction of dimensions simplifies the analysis of phenomena such as first-passage problems and stochastic resonance in tubes [24, 25].

On the contrary, the question as to whether active particles moving in a long tube admit a similar framework has been little explored so far. Unlike passive particles, active particles accumulate near rigid walls [26–28] due to their persistent motion. As a result, the density of active particles along a tube is not proportional to the area of its cross-section and the implementation of a FJ approximation is thus harder than for passive systems. Corrections accounting for the boundary accumulation—which is proportional to the perimeter of the cross-section—indeed have to be included. We expect these corrections to be particularly significant when the particle persistence length is comparable to the width of the tube.

So far, only the limit of narrow tubes—whose widths are comparable to the particle size—has been discussed, in the presence of a strong translational diffusion [6]. These results show that a conservative potential cannot characterize the interplay between the particle activity and the boundaries, and that asymmetric channels can induce ratchet flows along the tube. What happens when the tube width increases remains to be explored.

A relevant example where larger tubes have to be considered is that of run-and-tumble bacteria \textit{Bacillus subtilis}. Indeed, the persistence length of these bacteria is of the order of 100 \textmu m [29] and they can move in vessels whose widths can be of the order of 40 ~ 200 \textmu m [21]. The bacterium size is typically a few \textmu m long [30] and thus significantly smaller than the vessel width. The translational diffusion of the bacterium is 3 orders of magnitude smaller than its effective large-scale diffusivity, showing thermal noise to be largely irrelevant to describe its large-scale transport [29, 30]. Note that blood vessels can have lengths that are vastly larger than the bacterium persistence length, which makes large-width long tubes particularly relevant for the transport of the bacterium. The transport of active particles in this regime has not been explored so far.

In this article, we thus focus on the case of channels with intermediate-to-large widths. We consider non-interacting ABPs and RTPs moving in two or three dimensions in long channels of length $L$, with rigid boundaries and varying width $w(x)$, where $\hat{x}$ is along the tube axis. By ‘long channels’, we refer to the case $L \gg \ell_p$, where $\ell_p$ is the persistence length of the active particles. We assume $w(x)$ is a slowly varying function such that $|w'(x)| \ll 1$, which implies that the variations in widths over a macroscopic length $L$ are negligible compared to $L$. In such a regime, large-scale currents of particles...
provoked by the inhomogeneity of confining walls are suppressed [31–33]. This allows us to treat the changes in width perturbatively and to calculate analytically the time evolution of the particle density and orientation fields along the tube. We show that, in the limit of slow-varying width, the particle density along the tube evolves in an effective entropy potential that we characterize, while the orientation along the tube axis has the same evolution as in a one-dimensional system in the absence of confinement. The particle activity controls the effective temperature of the system as well as the effective width entering the entropy potential. Our formalism first allows us to predict the steady-state density of particles along the tube as well as predict the mean-first-passage time of a particle escaping from a spindle channel. Finally, we show how a finite \( w(x) \) leads to a modified evolution for the particle orientation field along the tube, which allows us to quantitatively predict the ratchet flow in an asymmetric channel. Throughout the article, our analytic calculations are successfully compared with numerical simulations.

The article is organized as follows. In Sec. I, we review the FJ equation of passive particles and outline the procedures and prerequisites which are necessary for obtaining a FJ-like framework for active particles. In Sec. II, we derive the joint dynamics of the density and orientation field of the active particles along channels of varying widths, which leads to a generalized entropy potential in the limit of slow-varying width. We then show how the generalized entropy potential can be used to predict the steady-state density distribution of particles along the tube, how to generalize our algebra to 3d systems, and how to calculate the mean-first-passage time of a particle escaping from a spindle channel. In Sec. III, we discuss how higher-order corrections due to the variation of the channel width alter the dynamics of the orientation field. This then allows us to predict the ratchet flow of active particles in asymmetric tubes. Finally we close the article with a brief discussion on elongated and interacting particles in Sec. IV.

I. THE FICK-JACOBS EQUATION

In this section, we first review the Fick-Jacobs equation and the concept of entropy potential for passive particles. Then we outline the assumptions and prerequisites which lead to a Fick-Jacobs-like framework for active particles.

A. Passive particles and the Fick-Jacobs equation

Consider passive Brownian particles with diffusion constant \( D \) moving in a long channel oriented along the \( x \)-axis, with no-flux boundary conditions along the \( d-1 \) other directions. We use arbitrary time and length units. For tubes with varying width, the sectional area \( A(x) \) of the channel is a function of the position \( x \) along the tube. The time evolution of the probability density function (PDF) \( P(x, t) \) of finding a particle at position \( x \) at time \( t \) satisfies the diffusion equation

\[
\partial_t P = D \Delta P .
\]

On the tube surface, the system is subject to a no-flux boundary conditions \( n \cdot \nabla P = 0 \), where \( n \) is the unit vector normal to the surface.

The density of particles along the tube can be found by considering the marginal distribution

\[
\rho(x, t) = \int_{S(x)} P(r, t) d^{d-1}r ,
\]

where \( S(x) \) refers to the tube section of area \( A(x) \). If \( A(x) \) is a slowly varying function of \( x \), the time evolution of \( \rho(x, t) \) can be closed by assuming that the transverse dynamics along \( S(x) \) relaxes on time scales that are much shorter than the relaxation time of \( \rho(x, t) \). The dynamics of \( \rho(x, t) \) is then described by the Fick-Jacobs equation [15, 16], which can be obtained by integrating the diffusion equation along all the spatial dimensions other than \( x \), leading to:

\[
\partial_t \rho = D \partial_{xx} \rho + \partial_x \left[ \rho \Gamma_{eqm}(x) \right] ,
\]

where \( \Gamma_{eqm}(x) \) is a 1d effective potential defined as

\[
\Gamma_{eqm}(x) = -D \log A(x)
\]

and referred to as an ‘entropy potential’. The physical intuition behind Eq. (3) is that particles spend more time in wider regions, where the entropy potential is smaller.

B. Generalized Fick-Jacobs framework for active particles

We now consider noninteracting ABPs in a long channel of length \( L \) in 2d with a slowly varying width. The top and bottom boundaries of the channel are described by \( y = w_1(x) \) and \( y = w_2(x) \), respectively. The width of the channel is then \( w(x) \equiv w_2(x) - w_1(x) \). Particles have constant speed \( v \) and persistence time \( \tau \), and experience a translational diffusion with diffusivity \( D \). We denote by \( u(\theta) \equiv (\cos \theta, \sin \theta) \) the orientation of the particle. The trajectory \( r(t), \theta(t) \) of a single particle is then given by the Itô-Langevin equation

\[
\dot{r} = v u(\theta) + \sqrt{2D} \dot{\xi}(t) , \quad \dot{\theta} = \sqrt{2\tau^{-1}} \eta(t) ,
\]

where \( \xi(t) \) and \( \eta(t) \) are zero-mean Gaussian white noises satisfying \( \langle \xi_i(t) \xi_j(t') \rangle = \delta_{ij} \delta(t-t'), \langle \eta(t) \eta(t') \rangle = \delta(t-t') \). The PDF \( \Phi(r, u; t) \) of finding an ABP at position \( r \) with orientation \( u \) then solves the Fokker-Planck (FP) equation:

\[
\partial_t \Phi = -\nabla \cdot (v \nabla \Phi) + D \Delta \Phi + \tau^{-1} \partial_{\theta \theta} \Phi .
\]

This is a continuity equation \( \partial_t \Phi = -\nabla \cdot \Gamma - \partial_{\theta} \Gamma^\theta \), from which we define the spatial flow of particles with orientation \( u \) as

\[
\Gamma \equiv v u(\theta) \Phi(r, u; t) - D \nabla \Phi
\]

and the angular flow as \( \Gamma^\theta = -(1/\tau) \partial_{\theta} \Phi \). The no-flux boundary condition at the walls then simply reads \( n \cdot \Gamma = 0 \), where \( n \) is the normal vector to the boundary at \( (x, w_{1,2}(x)) \).
Let us consider the marginal distribution
\[
\tilde{\Phi}(x, u) \equiv \int_{w_1(x)}^{w_2(x)} \Phi(x, y, u) dy .
\] (7)

From now on, we use the tilde notation to denote the 1d marginal of fields that describe their variation along the tube. Integrating Eq. (5) over \( y \) and using the no-flux boundary condition leads to the exact time evolution:
\[
\partial_t \tilde{\Phi} = - v \cos \theta \partial_x \tilde{\Phi} + (1/\tau) \partial_{\theta \theta} \tilde{\Phi} + D \partial_{xx} \tilde{\Phi} - D \partial_x [\Phi(x, w_2(x), u) w_2'(x) - \tilde{\Phi}(x, w_1(x), u) u_1'(x)] .
\] (8)

As for passive systems [15, 16], the key assumption toward an FJ equation is \( L \gg w(x) \), which implies that a local steady state is reached in the \( y \)-direction at any \( x \). To close the equation for \( \tilde{\Phi}(x, u) \) and obtain a generalized entropy potential, we need to establish a connection between the boundary values of the 2d PDF \( \Phi(x, w_{1,2}(x), u) \) and the marginal \( \tilde{\Phi}(x, u) \).

Specifically, if we can solve the boundary values \( \Phi(x, w_{1,2}(x), u) \) as
\[
\Phi(x, w_{1,2}(x), u) \simeq g(x, |u|) \tilde{\Phi}(x, u) ,
\] then we can define a potential through
\[
V'(x) = - D g(x, |u|) u'(x) ,
\]
and rewrite the second line of Eq. (8) as \( \partial_x [\tilde{\Phi}(x, u)V'(x)] \). This would lead to an effective entropy potential \( V(x) \).

However, an explicit analytic solution of Eq. (9) is out of reach and we thus follow an alternative route, based on the moment expansion of \( \tilde{\Phi} \), that we detail in Sec. II.

C. Active particles with homogeneous confinement

To make this article self-content, we first briefly review the calculations of the steady-state density and polarization profiles of ABPs in a channel with no-flux flat boundaries presented in Ref. [28]. (For AOPUs, one can refer to Ref. [34].) The solutions will serve as ansatz of density and polarization profiles in channels of varying widths. Other references that assume a vanishing thermal translational noise [35–37] are beyond the scope of this article. This channel is invariant by translation along the \( x \)-axis and \( w \) is constant. The boundaries are located at \( y = 0 \) and \( w \) (Fig. 1a).

In this section, we characterize the steady-state density and polarization across the channel. We introduce the single-particle probability density \( \rho(r) \equiv \langle \delta(r - r(t)) \rangle \), the average orientation field \( m(r) \equiv \langle u(t) \delta(r - r(t)) \rangle \), and the average nematic tensor field \( Q(r) \equiv \langle (u(t)u(t) - 1/2) \delta(r - r(t)) \rangle \), where \( \langle \cdot \rangle \) denotes ensemble averages with respect to \( \Phi \). We note that these fields are single-particle observables. For \( N \) non-interacting particles, replacing \( r(t), u(t) \) by \( r_i(t), u_i(t) \) and summing over \( i \) would lead to the standard number-density, orientation, and nematic-order fields. The dynamics of these fields are given by [9, 10].

\[
\partial_t \rho = - v \nabla \cdot m + D \Delta \rho , \quad \partial_t m = -(v/2) \nabla \rho - v \nabla \cdot Q - \mathbf{m}/\tau + D \Delta \mathbf{m} .
\] (10) (11)

Note that the dynamic equations have the same form for RTPs with tumbling rate \( \tau^{-1} \) [9, 10].

In homogeneous channels with translational symmetry along \( x \), the steady-state profiles \( \rho, m, \) and \( Q \) are only functions of \( y \). The boundary conditions now read

\[
v m_y = D \rho'(y) , \quad v (\rho/2 + Q_{yy}) = D m_y' \]

at \( y = 0 \) and \( w \). In the steady state, the translational symmetry of the system along \( x \) implies that \( m_y = 0 \) and \( Q_{yy} = 0 \). To close the equations, we assume \( Q = 0 \). We note that such a truncation was argued to be valid for a Péclet number \( Pe \equiv v l_p / D < 100 \) [38]. Here, we find that this approximation leads to satisfying predictions for the number of particles accumulated near boundaries even for \( Pe \sim 10^4 \) (see Fig. 1b).

In the steady state, the ABPs accumulate near the confining walls at \( y = 0 \) and \( y = w \), forming a boundary layer with a characteristic thickness
\[
\ell_b \equiv D / \sqrt{(D_a + D)/\tau} ,
\] (13)
where \( D_a \equiv v^2 \tau/2 \) is the active contribution of the effective diffusion constant. If \( w \gg \ell_b \), the two boundary layers are far apart, and the density profile near the homogeneous wall at \( y = 0 \) reads
\[
\rho_{hm}(y) \simeq \rho_b \left( \frac{D_a}{D} e^{-y/\ell_b} + 1 \right) ,
\] (14)
where \( \rho_b \) is the bulk density at \( y = w/2 \). Then, the polarization profile satisfies
\[
m_{hm}(y) = m_y(y) = \frac{D p_h'(y)}{v} = - \frac{D_a \rho_b}{v \ell_b} e^{-y/\ell_b} .
\] (15)

FIG. 1. The steady-state density profile of active Brownian particles inside tubes of constant width. (a): An illustration of an ABP moving in a homogeneous tube of width \( w \). We impose periodic boundary condition in the \( x \)-direction. The walls are located at \( y = 0 \) and \( y = w \). (b): The density profile of particles near the wall localized at \( y = 0 \), normalized by the bulk density \( \rho_b \), for different values of \( \tau \). Symbols represent simulation data and solid lines represent the theoretical prediction given by Eq. (14). The inset shows the same data using a log scale for the \( y \)-axis. Parameters: \( w = 10^3 \), \( v = 1 \), \( D = 0.1 \).
This result has been obtained in Refs. [26, 28]. The density of ‘excess’ particles (per unit length) accumulated near the boundary can then be estimated as \( \rho_{\text{b}} \int_0^\infty dy D_a e^{-y/\ell_b}/D = \rho_{\text{b}} D_a \ell_b / D. \)

Hence, truncating at the second order in the moment expansion of \( \Phi \), the density profile \( \rho_{\text{hm}}(y) \) near a hard boundary decreases exponentially towards the bulk density \( \rho_{\text{b}} \) over a characteristic length \( \ell_b \). We test the approximation in agent-based simulations in Fig. 1b. Because of translational symmetry along the \( x \) direction, we only simulate the \( y \)-component of Eq. (4) using Euler time-stepping. To implement the no-flux boundary condition, we follow Ref. [28] and use a potential-free algorithm: If a particle moves out of the confined region after a time step, we place it back at its position at the beginning of the time step, while still allowing its orientation to evolve. The numerical results show a slightly slower decay in the bulk than the one predicted by Eq. (14), which is due to a nonzero value of \( \nabla \cdot Q \). A better estimate can be obtained by truncating at a higher-order in the moment expansion of \( \Phi \), which allows identifying more exponential components to account for a slower decay. Overall, for our purpose with \( w \gg \ell_b \), Eq. (14) provides a reasonable estimation of \( \rho_{\text{hm}}(y) \), even when the persistent length of the particle \( \ell_p \equiv v \tau \) is comparable to \( w \).

II. THE FICK-JACOBS FRAMEWORK IN THE LIMIT OF TUBES WITH SLOW-VARYING WIDTH

A. The generalized entropy potential

We now turn to non-interacting ABPs/RTPs in a long channel of length \( L \) in 2d with a varying width. First, we consider the exact dynamics of the 1d marginal density field \( \rho(x,t) \equiv \int \rho(x,y,t) dy \) and of the corresponding marginal for the orientation field along the tube \( m_1(x,t) \equiv \int m(x,y,t) dy \):

\[
\partial_t \tilde{\rho} = -v \partial_x \tilde{m}_1 + D \partial_{xx} \tilde{\rho} - D \partial_x [\rho(x,w_2)w_2(x) - \rho(x,w_1)w_1(x)], \tag{16}
\]

\[
\partial_t \tilde{m}_1 = -\frac{v}{2} \partial_x (\tilde{\rho} + \tilde{m}_2) - \frac{\tilde{m}_1}{\tau} + D \partial_{xx} \tilde{m}_1 - D \partial_x [m(x,w_2)w_2(x) - m(x,w_1)w_1(x)], \tag{17}
\]

where \( \rho(x,y) \) and \( m(x,y) \) are defined as in Sec. 1C, and we have introduced the second marginal \( \tilde{m}_2 \equiv \int Q_{xx} dy. \) Next, in order to close Eqs (16)-(17), we employ an approximation to establish relations between the boundary and bulk values.

We assume that the width of the tube changes slowly, so that \( |w'(x)| \ll 1 \), leading to width variations over the tube length \( L \) that are much smaller that \( L \). This allows us to assume that the channel is locally flat and parallel to the \( x \)-axis, so that particles at position \( x \) obey the same local PDF \( \Phi(x,y,u) \) as \( \Phi_{\text{hm}}(y,u) \) in a tube of constant width \( w_{\text{hm}} = w(x) \) (Fig. 1a). If \( w_{\text{hm}} \gg \ell_b \), the two boundary layers are far away from each other, and they effectively decouple so that the local density profile near each boundary wall is given by Eq. (14). Then

\[
\rho(x,w_{1,2}(x)) \simeq \rho_{\text{hm}}(0) = \rho_b \left( \frac{D_a}{D} + 1 \right). \tag{18}
\]

The integrated density \( \tilde{\rho} \) is then the sum of a bulk contribution, \( \rho_{\text{b}} w(x) \), and of contributions due to the two boundary layers, \( \int_0^\infty \rho_{\text{hm}}(y) dy \). Direct calculations lead to

\[
\tilde{\rho} \simeq \rho_b (w(x) + 2D_a \ell_b / D). \tag{19}
\]

Eliminating \( \rho_b \) from Eqs. (20) and (19) then yields

\[
\rho(x,w_{1,2}(x)) \simeq \frac{D_{\text{eff}} \tilde{\rho}}{Dw(x) + 2D_a \ell_b}, \tag{20}
\]

where \( D_{\text{eff}} = D_a + D \) is the effective diffusion constant of ABPs/RTPs. Substituting Eq. (20) into the second line of Eq. (16) finally leads to

\[
- D \partial_x [\rho(x,w_2)w_2(x) - \rho(x,w_1)w_1(x)] \simeq -D \partial_x \left[ \frac{D_{\text{eff}} w'(x)}{dw(x) + 2D_a \ell_b} \tilde{\rho} \right] = \partial_x [\tilde{\rho} V'(x)], \tag{21}
\]

where we have introduced the effective potential

\[
V(x) \equiv -D_{\text{eff}} \log[2D_a \ell_b / D + w(x)]. \tag{21}
\]

The boundary-value problem in the dynamics of \( \tilde{\rho} \) is then solved, and its dynamics is given by

\[
\partial_t \tilde{\rho} = -v \partial_x \tilde{m}_1 + D \partial_{xx} \tilde{\rho} + \partial_x [\tilde{\rho} V'(x)]. \tag{22}
\]

Under the assumption of slow-varying width, the boundary values \( m(x,w_{1,2}(x)) = 0 \) because \( m(x,w_{1,2}(x)) = 0 \) in channels of
constant width, and the second line in Eq. (17) vanishes. The boundary-value problem in the dynamics of \( \tilde{m}_1 \) is automatically solved without the emergence of an effective potential,

\[
\partial_t \tilde{m}_1 = -(v/2) \partial_x (\tilde{\rho} + \tilde{m}_2) - \tilde{m}_1/\tau + D \partial_{xx} \tilde{m}_1 , \tag{23}
\]

so that the dynamics of \( m_1 \) is independent of the confinement. In line with the dynamics of \( \tilde{m}_1 \) is the moment expansion by assuming \( \tilde{m}_2 = 0 \) to close Eqs. (22) and (23). From now on and consider the following dynamics:

\[
\begin{align*}
\partial_t \tilde{\rho} &= -v_0 \partial_x (\rho + \tilde{m}_2) + \partial_x [\rho V'(x)] , \\
\partial_t \tilde{m}_1 &= -(v/2) \partial_x \tilde{\rho} - \tilde{m}_1/\tau + D \partial_{xx} \tilde{m}_1 , \tag{24}
\end{align*}
\]

which are the first central result of this article.

The closure \( \tilde{m}_2 = 0 \) can be justified by considering the relaxation time of the moments \( \tilde{m}_n = \int \Phi(x,y,u,t) \cos(n\theta) d\theta dy. \) Since the density field is a conserved field, its relaxation time diverges as \( \tau \rightarrow \infty. \) Similarly, \( \tilde{m}_n \) has a relaxation time of order \( \tau/n^2 [10]. \) Thus, at large times, the moments of order \( n \geq 1 \) are fast modes enslaved to \( \tilde{\rho}. \) The dynamics of \( \tilde{\rho} \) is modulated by the change in tube width, which are assumed to be small. This allows us to expand all observables in derivatives of \( \tilde{\rho}. \) Since \( \tilde{m}_n \) are of the order of \( \partial^0 \tilde{\rho} \), keeping only the moments up to order \( \partial^0 \tilde{\rho} \) leads to the truncation \( \tilde{m}_2 = 0 \) in Eqs. (24) and (25).

In summary, under the assumption of a slow-varying \( w(x) \), the dynamics of the particle density along the tube is equivalent to that of self-propelled particles experiencing a generalized entropy potential \( V(x) \) given by Eq. (21), while the polarization field evolves as if in a free space. Note that the effective potential found for the active particles differs from the passive one in two respects: First, the passive diffusivity \( D \) entering \( \tilde{V}_{\text{eff}} \) has to be replaced by \( D_{\text{eff}}; \) Second, the area \( A(x) \) is replaced by \( w(x) + 2D_a \ell_b / D. \) This is a signature of the accumulation of active particles near boundaries—the number of excess particles accumulated near both boundaries is \( 2n_{\text{bd}} \equiv 2D_a \ell_b / D. \) This ‘buffer’ of active particles lower the impact of the variations of the tube width on the dynamics of \( \rho(x,t) \). This can be understood as follows. Since the width of the boundary layer scales as \( \ell_b \sim D_a^{-1/2} \) at large \( D_a \), we find that \( n_{\text{bd}} \sim D_a^{3/2}. \) In this limit, this thin boundary layer thus contributes significantly to the total density. The particles then spend most of the time near the boundaries. The number of particles absorbed by the boundary is independent of the width of the 2D channel, so that the particles have less time to sample the change in the channel width.

In Fig. 2b, we compare the dynamics given by Eqs. (24) and (25) with the result of agent-based simulations. Starting from an initially density such that \( \rho(x,0) \) is a constant, we simulate ABPs in a spindle channel whose width varies according to \( w(x) = A(1 - \cos(2\pi x/L)) + 2C_0 \) and impose no-flux boundary conditions. The initial position \( \rho(x,t) \) and orientation \( \theta \) of the particle are random. We then measure \( \rho(x,t) \) in simulations (circles) at different times, and compare it with the numerical solutions (solid curves) of Eqs. (24) and (25). We use a semi-spectral method and 4th order Adams–Bashforth time-stepping to solve the partial differential equations. To highlight the importance of the boundary layer to \( V(x) \), we compare our simulations with those of a fully passive dynamics Eq. (2) with \( D \) replaced by \( D_{\text{eff}} \) (dashed curves). Clearly, our generalized potential Eq. (21) captures better the dynamics of ABPs.

Note that, in this section, we truncated the moment expansion by setting \( m_{n \geq 2} = 0 \). In principle, we can continue the moment expansion and calculate the dynamics of \( \tilde{m}_2 \). We expect that a boundary term of the form \( 2D \partial_x [Q_{xx}(x,w_2)w_2'(x) - Q_{xx}(x,w_1)w_1'(x)] \) will appear in the evolution equation, yielding an entropy potential for \( \tilde{m}_2 \) that will be generically distinct from that entering the dynamics of \( \tilde{\rho}. \) To continue this procedure for higher order moments \( \tilde{m}_n \) with \( n > 2 \) would require computing the steady-state moments in channels of constant width, which is beyond the scope of this article.

### B. Steady-state density profiles in the diffusive limit

We now consider the steady state of Eqs. (24) and (25). The steady state of Eq. (25) imposes

\[
\tilde{m}_1 = -(v/2) \partial_x \tilde{\rho} + D \tau \partial_{xx} \tilde{m}_1 .
\]

Substituting this into Eq. (24) then leads to

\[
\left( \frac{v^2}{2} + D \right) \partial_{xx} \tilde{\rho} + \partial_x [\tilde{\rho} V'(x)] - vD \tau \partial^3_x \tilde{m}_1 = 0 .
\]

Since \( \partial^3_x \tilde{m}_1 \sim \partial^4_x \tilde{\rho} \), we neglect this term in the limit of large \( L \) and slow-varying \( w(x) \). In periodic tubes, \( w(0) = w(L) \) and the density of active particles along the tube has the form of a Boltzmann weight with an effective temperature \( T_{\text{eff}} \).

\[
\tilde{\rho}_B(x) \propto \exp(-V(x)/D_{\text{eff}}) = 2n_{\text{bd}} + w(x) . \tag{26}
\]

This prediction can be compared by agent-based simulations with both channels of symmetric (Fig. 3a) and asymmetric (Fig. 3c) shapes. Compared to the passive predictions, the 1D density profiles are flattened by the existence of boundary layers. We note that the approximation does not hold at position where \( \rho(x) \) is not small.

### C. Generalization to 3d tubes

Our construction of the effective potential can also be applied to the case of 3D tubes. We consider tubes along the \( x \) direction without loss of generality. We note that a large curvature of the boundary in the \( yz \) plane can also induce particle accumulations, and the full solution of the density profile near the curved wall can be nontrivial [31]. Suppose the radius of the boundaries of cross-sections is larger than \( \ell_b \) such that the boundary is locally flat. Then the density profile near the boundary can be approximated again by Eq. (14). The integration of the density profile in a cross-section in the \( yz \) plane
can be estimated as the sum of contributions from bulk and the boundary. We have \( \dot{\rho}(x) \approx \rho_b[A(x) + n_{bd}P(x)] \), where \( A(x) \) is the area of the cross-section of the tube along the \( yz \) plane at \( x \), and \( P(x) \) is the perimeter of the cross-section. Following the same procedures as in Sec. II, we have

\[
V(x) = -D_{\text{eff}} \log [n_{bd}P(x) + A(x)].
\]

Note that \( n_{bd} = D_a \xi_b / D \) and \( D_a = v^2 \tau / d \) in \( d \)-dimensional space.

The steady-state marginal density along the tube can then be estimated from Eq. (27) and compared with simulations of RTPs in a 3d tube with rotational symmetry along the \( x \) axis (Fig. 4a). Note that the estimation is valid only for sufficiently large \( C_0 \) to ensure that the curvature of the tube is negligible. Otherwise, the accumulation of particles along a curved boundary will further flatten the density profile (Fig. 4b). The agreement in Fig. 4a also indicates that our previous analysis, detailed for ABPs, directly applies to RTPs. This is expected since ABPs and RTPs with the same values of \( v_0 \) and \( \tau \) share the same dynamics for \( \rho \) and \( m \).

FIG. 3. Steady-state density profiles of ABPs along a corrugated 2d channel. (a,b): Density profiles in symmetric channels with \( w_{1,2}(x) = \pm[A(1 - \cos(2\pi x/L))/2 + C_0] \). (c,d): Asymmetric channel with \( w_{1,2} = \pm[A(1 - \cos(2\pi x/L))]^3 /2 + C_0 \) (e) and the corresponding density profile of ABPs (d). In all panels, circles represent the simulation data. Solid lines are the theoretical estimation obtained by Eq. (26). Dashed lines are obtained using the passive counterpart Eq. (3).

FIG. 4. The 1d density profile of RTPs along a corrugated 3d tube. The cross sections in \( yz \) plane is circular of radius \( R(x) = R_0[1 - \cos(2\pi x/L)] /2 + C_0 \). \( C_0 = 500 \) (a) and 50 (b). Circles represent data from agent-based simulations. The theoretical estimation of the density profile is obtained by \( \exp(-V(x)/D_{\text{eff}}) \). The solid lines are calculated using the \( V(x) \) in Eq. (27), while the dashed lines are using the passive counterpart Eq. (3). \( L = 8 \times 10^3 \), \( R_0 = 100 \), \( v = 5 \), \( \tau = 100 \), \( D = 0.1 \).

D. Mean-escape time of an active particle from a spindle chamber

With the generalized entropy potential (21), one can calculate the mean-first-passage time (MFT) of one particle escaping from a spindle chamber (Fig. 3a). The mean-first-passage time \( t_{\text{MFP}} \) of a particle starting from the middle of the spindle \( x = L/2 \) with random orientation and reaching one of the necks at \( x = 0 \) or \( L \) is given by Kramer’s seminal work \([39, 40]\)

\[
t_{\text{MFP}} \sim \frac{\pi}{2\sqrt{V''(L/2)V''(0)}} \exp \frac{V(0) - V(L/2)}{D_{\text{eff}}}.
\]

For passive particles, substituting Eq. (3) leads to \( t_{\text{MFP}} \propto 1/D \).

The \( 1/D \) scaling of \( t_{\text{MFP}} \) for passive particles can be checked in simulations (Fig. 5a). \( t_{\text{MFP}} \) for active particles, however, does not follow the \( 1/D_{\text{eff}} \) scaling because the activity contributes to both the effective diffusion constant and the effective width of the channel. \( t_{\text{MFP}} \) first decreases with \( D_{\text{eff}} \), similar to passive particles, and then increases after an optimal \( D_{\text{eff}} \) (Fig. 5b-d). Unlike passive particles, ABPs have finite moving speed, and the time for ABPs to travel \( L/2 \) is bounded by \( L/(2v) \). For larger \( D_{\text{eff}} \), the time for ABPs to stay near the boundary increases with \( \tau \), which explains the increase of escape time for ABPs from the channel. Note that Eq. (28) with the effective potential Eq. (21) qualitatively describe the transition away from the passive regime. At large \( \tau \) the condition that \( w \gg \ell_p \) cannot be held and Eq. (21) fails. Thus, quantitative agreement in the large \( D_{\text{eff}} \) limit cannot be expected.

III. EMERGENCE OF RATCHET FLOW: BEYOND THE SLOW-VARYING WIDTH APPROXIMATION

The presence of spatial anisotropy in non-equilibrium systems often lead to the emergence of spontaneous current \([41]\),
a phenomenon referred to as ratchet current. This phenomenon has attracted a lot of interest [3-7] but there is no general principle to predict the amplitude of ratchet currents and their dependence on the details of the systems. Active particles moving in channels with broken parity symmetry constitute a setup with ratchet currents [4-6]. We show an example of ratchet flows of active particles in an asymmetric tube in Fig. 6a.

Before detailing the underlying mechanism, we stress that ratchet currents emerge only in systems with broken detailed balance. The Boltzmann-like steady state given by Eq. (26) obeys detailed balance so that no macroscopic currents survive with the approximation considered so far. This indicates that ratchet currents do not survive in the $L \to \infty$ limit with vanishing $w'(x)$. To observe a non-zero current, we thus have to work to higher order. In this section we discuss how corrections can be introduced into our formalism to account for finite $w'(x)$, and how these corrections lead to the emergence of a ratchet flow.

### A. The generalized entropy potential for the polarization field

To account for a non-vanishing $w'(x)$, we assume that the wall at position $x$ is locally flat, but tilted with a slope of $w'_{1,2}(x)$ (See Fig. 7a). In the limit of wide channels, $w \gg \ell_b$, the boundary layers near the top and bottom walls decouple and we can assume a local translational symmetry along the tangential direction of the boundaries. Then, at the boundary, $\mathbf{m}$ is locally normal to the boundary with a magnitude given by $|m_{hm}(h)|$ in Eq. (15), where $h$ is the distance from the wall. Locally, $m_x(x,y)$ is $\mathbf{m}$ projected on the $x$-axis. From Fig. 7a we have

$$m_x(x, w_2(x)) = -|m_{hm}(0)| \sin \arctan w_2'(x) \approx -|m_{hm}(0)| w_2'(x) = -D_0 \rho_b w_2'(x)/(v \ell_b),$$

and similarly $m_x(x, w_1(x)) \approx D_0 \rho_b w_1'(x)/(v \ell_b)$. This approximation can be justified in Fig. 7b, where we plot $m_x(x, y)/w'(x)$ at different position $x$ of ABPs in a spindle channel in the steady state of an agent-based simulation. The simulation data shown as circles are compared with $|m_{hm}(y)|$ shown as a solid line. In the bulk $\mathbf{m} \approx 0$, and only the two nonzero boundary layers contribute to $\tilde{m}_1$ through:

$$\tilde{m}_1 \approx (w_1'(x) - w_2'(x)) \int_0^\infty dy \frac{|m_{hm}(y)|}{w'(x)} = -D_0 \rho_b w'(x)/v.$$

Thus, eliminating $\rho_0$ in Eqs. (29) and (30) gives

$$m_x(x, w_1(x)) = -\tilde{m}_1 w_1'(x)/[w'(x)\ell_b],$$
$$m_x(x, w_2(x)) = \tilde{m}_1 w_2'(x)/[w'(x)\ell_b].$$

The second line of Eq. (17) now reads

$$-D \partial_x \left( \tilde{m}_1 \frac{w_1'^2(x) + w_2'^2(x)}{w'(x)\ell_b} \right) = \partial_x \left[ \tilde{m}_1 V'_m(x) \right],$$
Eqs. (33) and (34). To do so, we consider periodic tubes with potential cannot describe the 1d dynamics of 2d ABPs. The solid line represents shifted profile \( \tilde{m}_m \) given by Eq. (15) with \( y \rightarrow y - w_1(x) \). Inset shows the magnitude of \( m_m \) in linear scale. We use a symmetric channel with \( A = 50, L = 800 \).

We note that the effective potential (21) entering the dynamics of \( \tilde{m}_1 \) has a slope of \( \frac{1}{2v} \). The numerical justification of the assumption. Circles represent measured polarization profile at different \( x \) from agent-based simulations, scaled by the local tangential slope of the boundary \( w_1(x) \).

The effective dynamics of \( \tilde{m}_1 \) has parity symmetry, leading to \( \tilde{I}(x) = \tilde{I}(\pm 1 \rightarrow x) \). The periodic boundary condition holds, and \( \tilde{I}(x) \) depends both on \( w(x) \) and on the slopes of the two boundaries separately. If the channel is symmetric such that \( w_2(x) = -w_1(x) = w'(x)/2 \), the effective potential simplifies into

\[
V_m(x) = -\frac{D}{2\ell_b} \int \frac{w_1'^2(x) + w_2'^2(x)}{w'(x)} dx
\]

We note that the effective potential (21) entering the dynamics of \( \tilde{m}_1 \) is unaltered in the presence of tilted flat boundaries. Assuming that the wall is located at \( y = 0 \), without loss of generality, the density profile along \( y \) in Fig. 7a is given by the rescaling

\[
y \rightarrow y \cos \arctan w_1'(x) \sim y - y[w_1'(x)]^2/2
\]

in \( \rho_{m_0}(y) \). The correction term scales as \( [w_1'(x)]^2/2 \), which can be neglected at order \( [w'(x)] \). Then, under the same closure as in Sec. II, \( \tilde{m}_2 = 0 \), we obtain an FJ-like set of equations for the density and orientation fields along the tube, valid up to order \( w'(x) \),

\[
\partial_t \tilde{\rho} = -v \partial_x \tilde{m}_1 + D \partial_{xx} \tilde{\rho} + \frac{1}{\tau} \partial_x [\tilde{\rho} V'(x)] , \\
\partial_t \tilde{m}_1 = -\frac{v}{2} \partial_x \tilde{\rho} - \tilde{m}_1/\tau + D \partial_{xx} \tilde{m}_1 + \partial_x [\tilde{m}_1 V_m'(x)] .
\]

We note that \( V_m(x) \neq V(x) \) so that a single conservative potential cannot describe the 1d dynamics of 2d ABPs.

B. Ratchet flows of ABPs along 2d corrugated channels

We now estimate the strength of the ratchet flow from Eqs. (33) and (34). To do so, we consider periodic tubes with \( w(0) = w(L) \), such that \( \tilde{\rho}(0) = \tilde{\rho}(L) \) and \( \tilde{m}_1(0) = \tilde{m}_1(L) \). In the steady state, \( \partial_t \tilde{\rho} = \partial_t \tilde{m}_1 = 0 \). Eq. (33) can be integrated once to obtain the flux of the particles \( \tilde{J} \) as

\[
\tilde{J} = v \tilde{m}_1(x) - D \tilde{\rho}'(x) - \tilde{\rho}(x) V'(x) .
\]

We note that \( \tilde{J} \) does not depend on \( x \) in the steady state. Integrating Eq. (35) along the channel then leads to

\[
\tilde{J} L = J_{tot}[\tilde{\rho}] = - \int_0^L \tilde{\rho}(x) V'(x) dx .
\]

The last equality comes from the periodic boundary conditions and the fact that, in the steady-state, \( \tilde{m}_1 \) can be written as a total derivative according to Eq. (17). Note that \( J_{tot}[\tilde{\rho}] = 0 \) whenever \( \tilde{\rho} \) is a local function of \( V(x) \). This applies, in particular, to effective Boltzmann weights \( \tilde{\rho}_s = \exp(-V(x)/D_{\text{eff}}) \).

We now compute the steady-state density \( \tilde{\rho}_s \) and the flux \( \tilde{J} \) from Eqs. (33) and (34). The steady state of Eq. (33) gives

\[
\tilde{m}_1(x) = \frac{D}{v} \tilde{\rho}''(x) + \frac{1}{v} \partial_x [\tilde{\rho}(x) V'(x)] .
\]

Substituting it into Eq. (34), in the steady state we have

\[
\tilde{m}_1 = \frac{\tau}{1 - \tau V''_m} \left[ D \partial_{xx} \tilde{m}_1 + \tilde{m}_1 V''_m(x) - \frac{v}{2} \partial_x \tilde{\rho} \right]
\]

\[
= \frac{\tau}{1 - \tau V''_m} \left[ (V'_m + D \partial_x) \left( \frac{D}{v} \tilde{\rho}'' + \frac{1}{2} \partial_x (\tilde{\rho} V') \right) - \frac{v \tilde{\rho}''}{2} \right]
\]

\[
\simeq \frac{\tau}{1 - \tau V''_m} \left[ \frac{V'_m \partial_x (\tilde{\rho} V')}{v} + \frac{D \partial_x (\tilde{\rho} V')}{v} - \frac{v \tilde{\rho}''}{2} \right] .
\]

From (37) to (38), we keep only terms up to the order \( v \). Substituting Eq. (38) into (35) yields a first-order non-homogeneous linear ordinary differential equation of \( \tilde{\rho} \). Its solution is given by the sum of the general solution \( \rho_{m_0}(x) \) of the complementary equation with \( \tilde{J} = 0 \) and a particular solution with \( \tilde{J} \neq 0 \). \( c \) is a constant real number that is set by the total number of active particles. We choose \( c = \tilde{\rho}_{ss}(0) \) for simplicity. First, \( \rho_{h}(x) \) is given by:

\[
\rho_{h}(x) = \exp[-I(x)] ,
\]

\[
I(x) \equiv \int_l^x V'(l) - \tau [V'_m(l) V'(l)]' - D \tau V'''(l) dl ,
\]

\[
\tilde{D}(x) = D_{\text{eff}} - \tau V'_m(x) V'(x) - D \tau [V''_m(x) + V''(x)] .
\]

We note that if \( w(x) \) has parity symmetry, \( V' \) and \( V''_m \) are odd functions, leading to \( I(L) = 0 = \tilde{I}(0) \). The periodic boundary condition holds, and \( \tilde{J} = 0 \) is the proper solution of Eq. (35). Thus no spontaneous currents appear in channels with parity symmetry. We note that if \( V_m = 0 \) and if terms of order \( w''(x) \) are neglected, \( \tilde{D} \to D_{\text{eff}} \) and \( I(x) \to V(x)/D_{\text{eff}} \). \( \rho_{h}(x) \) then reduces to the Boltzmann weight Eq. (26) with no spontaneous currents as well.
If \( w(x) \) does not have parity symmetry in \( x \), \( I(0) \neq I(L) \), and \( h(0) \neq h(L) \). Thus the periodic boundary condition requires \( \tilde{J} \neq 0 \). The full solution of Eq. (35) with non-zero \( \tilde{J} \) reads

\[
\tilde{\rho}_{xs}(x) = \rho_h(x) \left[ \tilde{\rho}_{xs}(0) - \tilde{\rho}_{xs}(L) \right] \int_0^x \frac{1 - \tau V_m''(s)}{D(s)} ds. 
\]

From the periodic boundary condition \( \tilde{\rho}_{xs}(0) = \tilde{\rho}_{xs}(L) \), we can solve

\[
\tilde{J} = \frac{\tilde{\rho}_{xs}(0) - \rho_h(L) - 1}{\rho_h(L)} \left[ \int_0^L \frac{1 - \tau V_m''(s)}{D(s)} ds \right]^{-1}. 
\]

We note again that a non-local functional dependence of \( w(x) \) in Eq. (40) is necessary to give a non-zero \( \tilde{J} \).

Finally, we check the theoreric prediction of \( \tilde{J} \) in agent-based simulations (Fig. 6). In the simulations, we use asymmetric tubes with \( w(x) = A(1 - \cos(2\pi x/L)^N)) + 2C_0 \). With increasing \( N \), the maximum of \( w(x) \) increases, and the strength of the ratchet current \( J_{\text{tot}} \) increases, which we measure from simulations as \( J_{\text{tot}} = \langle \dot{x}(t) \rangle_t \). We find the analytical prediction \( JL \) with \( J \) given by Eq. (42) gives predictions of order-of-magnitude agreements with measurements from simulations. We note that neglecting \( V_m \) in Eq. (42) leads to no ratchet flow. We also note that, given \( \tilde{\rho}_{xs}(x) \) measured from simulations, the value of \( J_{\text{tot}}[\tilde{\rho}_{xs}] \) using the generalized entropy potential given in Eq. (21) also agrees with the measurements in simulations.

IV. DISCUSSION

In this article, we extended the Fick-Jacobs equation from passive particles to active particles in a wide tube \( w(x) \gg \ell_b \) with slow varying width \( |w'(x)| \ll 1 \). Under such assumptions, the local translational symmetry along the boundary can be recovered and the boundary layers decouple. Contributions to the integration of the probability density of particles from the bulk and boundaries can be separated. We considered different levels of approximations. With the assumption of locally homogeneous boundaries, we constructed a generalized entropy potential \( V'(x) \) Eq. (21) in which the 1d density of active particles \( \tilde{\rho} \) evolves. The approximation of locally flat and horizontal boundaries captures well the dynamics in large spatial-temporal scales in a long tube. The steady state predicts the density profiles better than that from the passive entropy potential using an effective temperature given by the large-scale diffusivity of the active particles. Using the Kramers’ law, we can predict the mean-first-passage time with the generalized effective potential Eq. (21). The analysis for ABPs automatically holds for RTPs, because ABPs and RTPs share the same dynamics of the density and polarization fields \( \tilde{m}_1, \tilde{m}_2 \). The analysis can be extended to higher dimensions as well. Note that the calculations require a finite \( D \), which ensures a continuous density profile near the boundary and a nonzero \( \ell_b \).

We then worked beyond the assumption of vanishing \( w'(x) \) and allowed the boundary to be tilted. This led to a correction term in the dynamics of the orientation field \( \tilde{m}_1 \), which amounts to a drift term stemming from a different entropy potential \( V_m(x) \). While the improvement in the prediction of the density profiles is not significant at large scales, this term enables us to predict the spontaneous ratchet flow observed in simulations of active particles in asymmetric channels. We note that \( V'(x) \neq V_m(x) \) so that the problem does not reduce to 1d dynamics of ABPs in a single conservative potential.

Note that further analytical progress could be made by truncating at higher order moments and by considering the curvature of the boundaries. This would require calculating the probability density near a curved boundary \( \tilde{m}_1 \). How to account for the deviation from the local steady state in the y-direction at finite \( w'(x) \) remains at this stage a challenging question.

Then, in this work, dilute spherical particles are considered. Elongated active particles can align with rigid boundaries and accumulate as well \[43\]. The probability of particles leaving the boundaries then decreases with a larger aspect ratio, and the number of accumulated particles increases with the length of the particle in the dilute limit \[43\]. A larger boundary accumulation is expected to further flatten the density profile \( \tilde{\rho} \) of elongated particles. For dense systems, the interactions between particles will also impact the boundary layer close to the wall.

Finally, we note that the experimental setup considered here could be easily engineered for many type of synthetic active particles ranging from Quincke rollers \[44\] to phoretic Janus colloids \[45\].

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