Optimized Diffusion of Run-and-Tumble Particles in Crowded Environments

Thibault Bertrand,[1,*] Yongfeng Zhao,[2] Olivier Bénichou,[3] Julien Tailleur,[2] and Raphaël Voituriez[1,3,†]
[1]*Laboratoire Jean Perrin, UMR 8237 CNRS, Sorbonne Université, 75005 Paris, France*
[2]*Laboratoire Matière et Systèmes Complexes, UMR 7057 CNRS, Université Paris Diderot, 75205 Paris, France*
[3]*Laboratoire de Physique Théorique de la Matière Condensée, UMR 7600 CNRS, Sorbonne Université, 75005 Paris, France*

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We study the transport of self-propelled particles in dynamic complex environments. To obtain exact results, we introduce a model of run-and-tumble particles (RTPs) moving in discrete time on a d-dimensional cubic lattice in the presence of diffusing hard-core obstacles. We derive an explicit expression for the diffusivity of the RTP, which is exact in the limit of low density of fixed obstacles. To do so, we introduce a generalization of Kac's theorem on the mean return times of Markov processes, which we expect to be relevant for a large class of lattice gas problems. Our results show the diffusivity of RTPs to be nonmonotonic in the tumbling probability for low enough obstacle mobility. These results prove the potential for the optimization of the transport of RTPs in crowded and disordered environments with applications to motile artificial and biological systems.

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Run-and-tumble particles (RTPs) are a prototypical model of self-propelled particles (SPPs) at the colloidal scale, which belongs to the broader class of active matter systems [1,2]. In its simplest form, RTP trajectories consist of a sequence of randomly oriented "runs"—periods of persistent motion in a straight line at a constant speed—interrupted by instantaneous changes of direction, called "tumbles," occurring at random with a constant rate. This canonical model has played a pivotal role in the theoretical description of self-propelled biological entities such as bacteria [3–7], algae [8], eukaryotic cells [9], or larger-scale animals [10].

Whereas systems in thermal equilibrium display a time-reversal symmetry, this invariance is generically lost in active matter at the microscopic scale because of the continuous consumption of energy. Nevertheless, at a constant speed and tumbling rate, an isolated RTP performs a random walk with diffusive scaling at large enough time- and length scales which cannot be qualitatively distinguished from the equilibrium dynamics of Brownian colloids. Hence, it is only through their interactions with either other particles or the environment that RTPs display nonequilibrium features. Interactions between SPPs can indeed have spectacular consequences, which have attracted a growing interest over the past decade. For instance, dense active suspensions can display large-scale collective motion in settings where long-range order would be forbidden for equilibrium systems [11–14]. Another nonthermal collective effect is the propensity of active particles to cluster [15–17] or undergo phase separation [18–20] in the presence of purely repulsive interactions.

The interplay between active particles and their environment has also attracted a lot of interest [2]. Most motile biological systems such as bacteria or dendritic cells navigate disordered and complex natural environments such as soils, soft gels (e.g., mucus or agar), or tissues. Recent simulations have explored the dynamics of active particles in the presence of quenched disorder as well as active baths [21–25]. In confined geometries, active particles accumulate at the boundaries, at odds with the equilibrium Boltzmann distribution. This has been observed for a variety of systems from spherical and elongated particles in linear channels to bacteria in spherical cavities [26–31]. Such nontrivial interactions with obstacles can lead to effective trapping and thus have important consequences in the dynamics of SPPs in disordered environments. Indeed, active particles in the presence of static obstacles can display subdiffusive dynamics [32]. Trapping has been observed both in models [33–35] and in experiments of biological or synthetic microswimmers [36–38]. It was shown in numerical simulations of RTPs moving through arrays of obstacles that trapping can lead to the existence of an optimal activity level for drift through the system [39,40]. More recently, the presence of disordered obstacles was shown to destroy the emergence of large-scale correlations, preventing flocking and swarming [41]. Despite these various observations, the generic analysis of the dynamics of a single SPP in disordered environments remains mostly unexplored, and, in particular, analytical results are largely missing.

In this Letter, we introduce a minimal model of discrete time RTP moving on a d-dimensional cubic lattice in the presence of diffusing hard-core obstacles of density ρ, which model a potentially dynamic disordered environment. In particular, this generalizes to RTPs questions that have attracted a lot of attention for passively diffusing particles [42] and externally driven tracers [43–46]. We determine analytically numerous observables characterizing the dynamics: the mean free run time, defined as the mean time between consecutive collisions of the RTP with obstacles, the mean trapping time of the RTP by obstacles, and the large-scale diffusion coefficient of the RTP. This calculation is exact for fixed obstacles in the limit of low obstacle density $\rho \to 0$ and remains uniformly accurate in the tumble rate for finite values of ρ and mobile obstacles. Our analysis reveals the existence of a maximum of the diffusion coefficient of the RTP as a function of the tumbling rate, for a low enough mobility of obstacles. Our approach is based on a generalization of a theorem due to Kac on mean return times of Markov processes [47], which was already shown to have important applications in physics [48,49]. We show here that it implies the following exact result: For fixed obstacles, the mean free run time is given by $\langle \tau_r \rangle = 1/\rho$ and is *independent of the tumbling rate* of the RTP. In addition, in the case of moving obstacles, this result still holds for a proper choice of microscopic collision rules and is *independent of the diffusion coefficient of the obstacles*, provided that the time step of the obstacle dynamics is larger than that of the RTP. This strikingly simple result has the potential to find a variety of applications in general lattice gas problems.

Model and definitions—We consider a discrete time RTP on an infinite lattice in d dimensions surrounded by obstacles uniformly distributed with a density ρ as shown in Fig. 1. The RTP, of position $\boldsymbol{r}(t)$, is polarized in a given direction and, in the absence of interaction with obstacles,

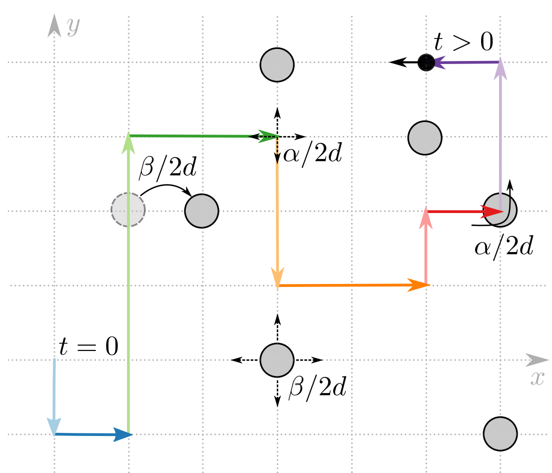

FIG. 1. *Example trajectory of a run-and-tumble particle* (*black*) on a 2D lattice among uniformly distributed obstacles (*gray*) at density ρ. At $t = 0$, the RTP starts from the origin and moves along the direction of its polarity (*black arrow*) in a sequence of linear runs (pictured here in different colors) punctuated by encounters with obstacles and tumbles. The obstacles have a probability of $\beta/2d$ to move in a given direction, and the RTP has a probability of $\alpha/2d$ to flip its polarity along a particular direction, potentially untrapping the RTP.

makes one lattice step per unit time in this direction (run), until its polarity is reset randomly among the $2d$ possible directions on the lattice (tumble). We consider that these tumbling events happen at each time step with probability α, independently of the presence of obstacles. We assume that the obstacles perform symmetric nearest-neighbor random walks, with probability $\beta < 1$ to jump at each time step. We consider obstacles interacting via hard-core repulsion; i.e., each lattice site can contain at most one obstacle. The RTP is assumed to have hard-core interactions with obstacles; for the sake of simplicity, its size is, however, supposed negligible in front of the size of the obstacles. The RTP can therefore jump on a lattice site occupied by an obstacle but cannot cross it. This assumption, illustrated in Supplemental Material [50], renders the analytical calculations more tractable but does not fundamentally change the phenomenology, as shown in Ref. [50], where we analyzed the dynamics not allowing jumps of the RTP on occupied sites. We therefore consider the following interaction rule: When the RTP steps on a lattice site occupied by an obstacle, it cannot proceed and effectively gets trapped; the RTP is released by either (i) a tumble leading to a change of polarity or (ii) a step made by the obstacle in any direction. Our goal is to compute analytically the diffusion coefficient $\mathcal{D} = \lim_{t\to\infty} \langle r^2(t) \rangle/(2dt)$ as a function of the tumbling probability α, the jump probability of the obstacles β, and the obstacle density ρ, where $\langle \ldots \rangle$ represents an average over the trajectories. The dynamics starts with a Poisson distribution of obstacles, and we consider timescales much larger than $1/\alpha$ and $1/\rho$, so that a stationary state is reached.

First, we decompose the trajectory of the RTP in a sequence of linear runs $\boldsymbol{a}_i$, punctuated by either encounters with obstacles or tumbles in any direction:

$$\boldsymbol{r}(t) = \sum_{i=1}^{n(t)} \boldsymbol{a}_i \tag{1}$$

with the random variable $n(t)$ being the number of linear runs composing the trajectory up to a given time t. Hence, the RTP trajectory is a random sum of random variables, and the following exact asymptotics can be obtained by generalizing Wald's identity (see [50]):

$$\langle r^2(t) \rangle \underset{t\to\infty}{\sim} \langle n(t) \rangle \langle \boldsymbol{a}_i^2 \rangle + \sum_{\substack{i,j=1 \\ i\neq j}}^{\langle n(t) \rangle} \langle \boldsymbol{a}_i \cdot \boldsymbol{a}_j \rangle. \tag{2}$$

We now determine explicitly all terms involved in (2). It is useful to decompose a trajectory in successive phases of two types: (i) *mobile* phases of random duration τ_r, when the particle is freely moving on the lattice without interacting with obstacles, and (ii) *static* phases of random duration τ_s, when the particle is trapped by an obstacle. For a trajectory of length t, the average number of each of the mobile and static phases is given by $\mathcal{N}_s = t/(\langle \tau_s \rangle + \langle \tau_r \rangle)$.

We therefore deduce the mean number of runs performed until time t:

$$\langle n(t)\rangle \underset{t\to\infty}{\sim} \frac{t-\mathcal{N}_s\langle\tau_s\rangle}{\ell_p} = \frac{\langle\tau_r\rangle}{(\langle\tau_s\rangle+\langle\tau_r\rangle)\ell_p} t \equiv \bar{n}t, \quad (3)$$

where the first (persistence length $\ell_p \equiv \langle|\boldsymbol{a}_i|\rangle$) and second moments of the run length are given by

$$\ell_p = \frac{1}{1-(1-\rho)(1-\alpha)}, \qquad \langle \boldsymbol{a}_i^2\rangle = \frac{1+(1-\rho)(1-\alpha)}{[1-(1-\rho)(1-\alpha)]^2}. \quad (4)$$

In the case of moving obstacles, a trapped particle can be released by two competing independent mechanisms: tumbling of the RTP or stepping of the obstacle. Thus, the mean trapping time reads in the general case

$$\langle\tau_s\rangle = \frac{1}{1-(1-\alpha^*)(1-\beta^*)} - 1 \quad (5)$$

with probabilities $\alpha^* = \alpha(2d-1)/2d$ and $\beta^* = \beta(2d-1)/2d$.

Mean run time: Generalized Kac's theorem—We now determine the mean free running time $\langle\tau_r\rangle$. In the case of fixed obstacles, it can be exactly defined as the mean return time to the set $\mathcal{O}$ of all obstacles. Remarkably, this quantity can be determined exactly by adapting Kac's theorem [47] (see [50] for details). For that purpose, we introduce the auxiliary process $\tilde{\boldsymbol{r}}(t)$. It is identical to $\boldsymbol{r}(t)$ in mobile phases, but the durations of all its static phases are set to 1: Upon each trapping event by an obstacle, the auxiliary process is released in the same direction as the original process $\boldsymbol{r}(t)$ would be but after a single time step. The mean running time is then identical for both processes $\boldsymbol{r}(t)$ and $\tilde{\boldsymbol{r}}(t)$; for the process $\tilde{\boldsymbol{r}}(t)$, which has a uniform stationary distribution, the Kac theorem takes a simple form and yields $\langle\tau_r\rangle = 1/P_{\mathrm{stat}}(\mathcal{O})$, where $P_{\mathrm{stat}}(\mathcal{O})$ is the stationary probability of $\mathcal{O}$ for the auxiliary process. We therefore find the simple expression

$$\langle\tau_r\rangle = \frac{1}{P_{\mathrm{stat}}(\mathcal{O})} = \frac{1}{\rho}, \quad (6)$$

which is strikingly independent of the tumbling probability α and echoes results obtained on continuous space and time processes in confined domains [49,51]. Interestingly, this result can be generalized to the case of moving obstacles. To this end, we encode the dynamics of the full system of N obstacles of positions $\mathbf{r}_i(t)(1\le i\le N)$ and the auxiliary process $\tilde{\boldsymbol{r}}(t)$ in a $d(N+1)$ tuple $\mathbf{x}(t)$. The process $\mathbf{x}(t)$ performs a symmetric random walk on the hypercubic lattice of dimension $d(N+1)$, which is, however, not of the nearest-neighbor type, because several particles can move in a given time step. Defining $\mathcal{T} = \{\mathbf{x}, \exists i, \mathbf{r}_i = \mathbf{r}\}$ as the set of trapped configuration, $\langle\tau_r\rangle$ can be defined as the mean return time of the process $\mathbf{x}(t)$ to the set $\mathcal{T}$ and as such verifies $\langle\tau_r\rangle = 1/P_{\mathrm{stat}}(\mathcal{T})$ in virtue of the Kac theorem. Here $P_{\mathrm{stat}}(\mathcal{T})$ can depend on the specific choice of microscopic collision rules between the RTP and obstacles. However, it can be generically written $P_{\mathrm{stat}}(\mathcal{T}) = C\rho$, where the constant C is of the order of 1 and can be exactly set to 1 for a proper choice of microscopic rule [52]. Here, we retain our initial choice, more relevant to real motile systems, and show in Ref. [50] a very good agreement between our predictions and the results of numerical simulations. This shows finally that, up to a redefinition of microscopic interaction rules, the general expression (6) still holds for moving particles, showing that the mean free running time is universally set by the density of obstacles only, independently of both the tumbling probability of the RTP and the dynamics of obstacles parametrized by β. This result, key to the derivation below, has potential applications to many other lattice gas models.

Long time correlations—As opposed to the classical RT dynamics in free space, obstacles induce nontrivial correlations $\langle\boldsymbol{a}_i\cdot\boldsymbol{a}_j\rangle$ that remain to be determined to compute the diffusion coefficient of the RTP [see Eq. (2)]. A first approximation to the diffusion coefficient can be obtained by neglecting these correlations, yielding $\mathcal{D}_0 \equiv \bar{n}\langle\boldsymbol{a}_i^2\rangle/(2d)$, where $\bar{n}$ and $\langle a_i^2\rangle$ are determined exactly by Eqs. (3) and (4). As shown in Fig. 2(b), $\mathcal{D}_0$ is already a qualitatively satisfactory approximation. Nevertheless, this approximation fails in the case of mobile obstacles, and a more thorough treatment of the correlations is already necessary to obtain exact expressions even in the limit of low density of fixed obstacles. We thus treat exactly the case of fixed obstacles ($\beta = 0$) to the lowest order in ρ. The correlations can be qualitatively understood in the case of adjacent runs. If $\boldsymbol{a}_i$ ends by a trapping event, then clearly $\langle\boldsymbol{a}_i\cdot\boldsymbol{a}_{i+1}\rangle < 0$, because the obstacle forbids the run $\boldsymbol{a}_{i+1}$ to keep the direction of $\boldsymbol{a}_i$; alternatively, if $\boldsymbol{a}_i$ ends by a tumble, one still finds $\langle\boldsymbol{a}_i\cdot\boldsymbol{a}_{i+1}\rangle < 0$, because particles are less likely to encounter obstacles upon retracing their steps.

More quantitatively, an exact computation confirms this analysis and yields (see [50] for details)

$$\langle\boldsymbol{a}_i\cdot\boldsymbol{a}_{i+1}\rangle = \frac{\alpha}{\alpha+\rho}\frac{\mathcal{C}_+-\mathcal{C}_-}{2d} - \frac{\rho}{\alpha+\rho}\frac{\mathcal{C}_-}{2d-1} \quad (7)$$

with the contribution to positive correlations $\mathcal{C}_+ = \ell_p^2$ and to negative correlations $\mathcal{C}_- = [1+(1-\rho)(1-\alpha)]/\{[1-(1-\rho)(1-\alpha)][1-(1-\rho)(1-\alpha)^2]\}$. This analysis shows, in particular, that both contributions of trapping and tumble events yield contributions of the order of $\mathcal{O}(\rho)$ for $\rho\to 0$. The exact determination of all correlations $\langle\boldsymbol{a}_i\cdot\boldsymbol{a}_j\rangle$ seems out of reach by the direct enumeration techniques used for $j = i+1$; we therefore focus on the small density limit $\rho\to 0$ and write

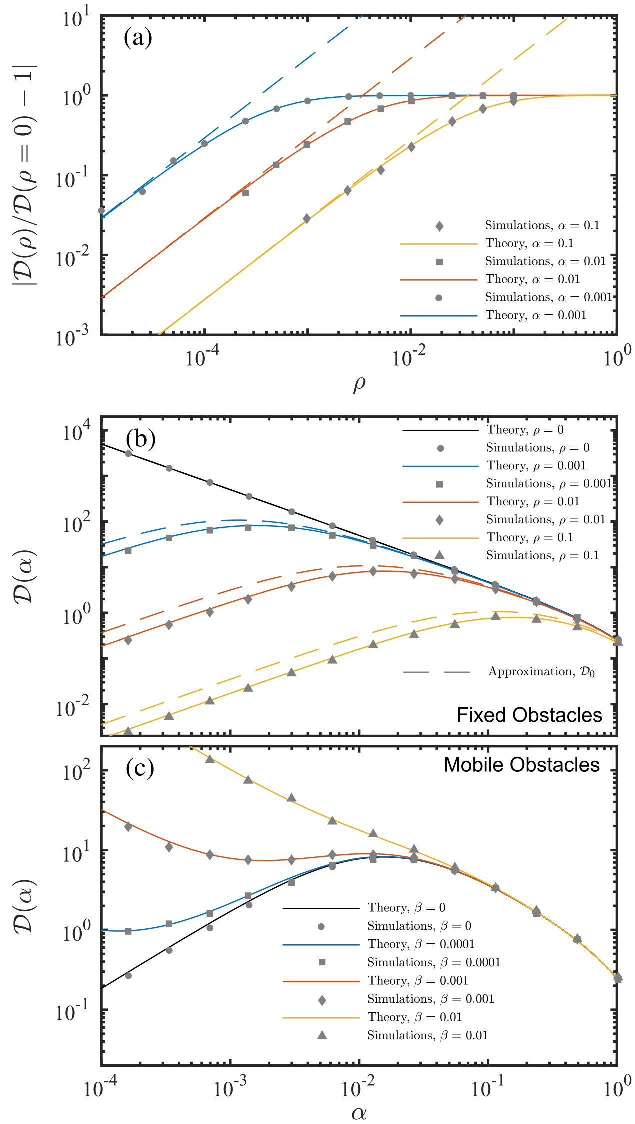

FIG. 2. *Diffusivity of a run-and-tumble particle*–(a) Diffusion coefficients for fixed obstacles relative to the free diffusion coefficient $\mathcal{D}(\rho = 0) = (2 - \alpha)/\alpha$ at various tumbling rates α as a function of the obstacle density ρ; dashed lines show the linear expansion in ρ. Diffusion coefficients for (b) fixed obstacles at various obstacle densities ρ and (c) mobile obstacles at various obstacle mobilities β and density $\rho = 0.01$ as a function of the tumbling probability α. In both cases, the symbols are results of numerical simulations, and the solid lines are given by Eq. (11). In (b), dashed lines show $\mathcal{D}_0$, our approximation where correlations between runs are neglected.

$$\langle \boldsymbol{a}_i \cdot \boldsymbol{a}_{i+k} \rangle \underset{\rho \to 0}{=} g(\alpha, k) \frac{\rho}{\alpha} + o(\rho), \tag{8}$$

where a generalization of the argument given above for $k = 1$ shows that $\forall k$, $g(\alpha, k) \neq 0$. The only two length scales entering this problem are $1/\rho$ and $1/\alpha$; for all k, $g(\alpha, k)$ has the dimension of a length squared. In the limit of low density, the only relevant length scale left is $1/\alpha$, and a dimensional analysis yields (taking α small) $g(\alpha, k) \underset{\alpha \to 0}{\sim} -\xi_k/\alpha^2$, where ξ_k is a lattice-dependent dimensionless number; for $k = 1$, Eq. (7) yields the exact value $\xi_1 = 11/24$.

Finally, the correction to the diffusion coefficient reads

$$\frac{\mathcal{D} - \mathcal{D}_0}{\bar{n}/2d} \underset{\rho, \alpha \to 0}{\sim} -\frac{2\rho}{\alpha^3} \sum_{k=1}^{\infty} \xi_k. \tag{9}$$

This result is exact to linear order in ρ in the limit $\alpha \to 0$. It involves dimensionless constants ξ_k, which are found numerically to satisfy $\xi_k \approx \xi_1 \Gamma^{k-1}$, with $\Gamma \approx 0.22$. We show in Fig. 2(a) a perfect agreement between our numerical simulations and Eq. (9).

We now aim at obtaining an approximate solution uniformly accurate in α; to this end, we need to go beyond the linear order in ρ/α and therefore consider nonvanishing correlations $\langle \boldsymbol{a}_i \cdot \boldsymbol{a}_{i+1} \rangle$. We also generalize our argument here to mobile obstacles, for which the nearest-neighbor correlations need to be amended. Indeed, two independent mechanisms can now release the RTP when trapped by an obstacle, yielding correlations of a different nature: (i) a tumble of the RTP, as in the case of fixed obstacles, or (ii) a step made by the obstacle away from the course of the RTP. The latter induces large correlations in the limit $\alpha \to 0$ which must be taken into account to quantitatively describe the RTP dynamics. Taking these events into account yields

$$\langle \boldsymbol{a}_i \cdot \boldsymbol{a}_{i+1} \rangle = \frac{\alpha}{\alpha + \rho} \frac{\mathcal{C}_+ - \mathcal{C}_-}{2d} + \frac{\rho}{\alpha + \rho} \left(\frac{\beta^*}{\alpha^* + \beta^*} \mathcal{C}_+ - \frac{\alpha^*}{\alpha^* + \beta^*} \frac{\mathcal{C}_-}{2d - 1} \right) \equiv \gamma \ell_p^2, \tag{10}$$

which yields the exact Eq. (7) in the limit of fixed obstacles, $\beta \to 0$. In order to cover the regime of large correlations, we next assume that correlations are induced by interactions between successive runs only; classical results [53] then yield $\langle \boldsymbol{a}_i \cdot \boldsymbol{a}_j \rangle = \gamma^{|i-j|} \ell_p^2$. We have checked numerically that these correlations decay exponentially (see [50]). After summation, we obtain finally

$$\mathcal{D} \underset{\rho \to 0}{\sim} \frac{\bar{n}}{2d} \left[\langle \boldsymbol{a}_i^2 \rangle + \frac{2\gamma}{1 - \gamma} \ell_p^2 \right], \tag{11}$$

where $\bar{n}$, $\langle \boldsymbol{a}_i^2 \rangle$, ℓ_p, and γ are defined explicitly in Eqs. (3), (4), and (10). This explicit expression, though approximate, provides a uniformly accurate determination of the diffusion coefficient as we show below; it is, in addition, consistent with the exact limit $(\alpha, \beta, \rho \to 0)$ defined above.

Optimized diffusivity of the RTP—In Fig. 2, we show our theoretical predictions for the diffusion coefficient in the case of static and mobile obstacles along with the results of simulations. We observe a very good agreement between the theory and simulations. For fixed obstacles ($\beta = 0$), the diffusion coefficient is nonmonotonic in the tumbling probability α. Qualitatively, this behavior can be understood as follows: (i) In the limit of high tumbling probability $\alpha \sim 1$, the RTP tumbles at each time step; decreasing α then increases the long time diffusion coefficient by increasing the persistence length; (ii) in the limit of low tumbling probability $\alpha \to 0$, the RTP proceeds mainly in long straight runs, interrupted by trapping events whose duration τ_s diverges for $\alpha \to 0$ leading to a vanishing diffusion coefficient. The analysis of Eq. (11) shows that the optimal tumbling probability satisfies $\alpha_m \propto \rho$; in turn, the optimal diffusion coefficient is found to scale as $\mathcal{D}_m \propto 1/\rho$.

In the case of mobile obstacles, the nonmonotonicity in the diffusion coefficient is preserved only for low enough obstacle mobility $\beta \leq \beta_c \propto \rho$. While the diffusion coefficient in the limit of high tumbling probability is independent of the obstacle mobility in the regime $\rho \to 0$, not surprisingly, it shows a strong dependence on β at low tumbling probability. It is interesting to note that no matter the obstacle mobility the RTP diffusion coefficient always monotonically increases for a low enough decreasing tumbling probability ($\alpha \lesssim \beta$), showing that, in these cases, the important unlocking mechanism is obstacle mobility.

Discussion—Using a minimal model of RTPs in crowded environments, we have shown that such active particles display a nonmonotonic diffusivity as a function of the tumbling probability for static and mobile obstacles. Our analytical prediction is exact in the limit of low obstacle density for fixed obstacles. Its derivation is based on the generalization of a theorem by Kac, a strikingly simple result expected to find a variety of applications in general lattice gas problems. While derived for a particular model for which analytical progress was tractable, our results qualitatively extend far beyond this case. First, we show in Ref. [50] that they extend to other microscopic types of obstacles. Then, a similar behavior has been previously observed in a mean-field model of bacterial diffusion in porous media [54]; our result is also reminiscent of the negative differential mobility observed in Refs. [40,44] for active tracer particles. Furthermore, our results, which are exact in the low density limit, extend qualitatively to moderate to high densities of relevance to experimental settings and, in particular, to the diffusion of bacteria in soft agar gels [54,55]. Finally, while the derivation of the results reported in this Letter is specific to RTPs on a lattice, the underlying mechanisms are not, and we expect similarly rich behaviors for the diffusivities of other active particles, on a lattice or in continuous space. This could potentially lead to an optimization of the diffusion coefficient of active particles with respect to their reorientation dynamics and, as such, to an enhancement of their transport properties or exploration efficiency in crowded environments.

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*thibault.bertrand@upmc.fr
†voiturie@lptmc.jussieu.fr

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