

## Superdiffusion in self-reinforcing run-and-tumble model with rests

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(Received 8 October 2021; accepted 5 January 2022; published xxxxxxxxxx)

This paper introduces a run-and-tumble model with self-reinforcing directionality and rests. We derive a single governing hyperbolic partial differential equation for the probability density of random-walk position, from which we obtain the second moment in the long-time limit. We find the criteria for the transition between superdiffusion and diffusion caused by the addition of a rest state. The emergence of superdiffusion depends on both the parameter representing the strength of self-reinforcement and the ratio between mean running and resting times. The mean running time must be at least 2/3 of the mean resting time for superdiffusion to be possible. Monte Carlo simulations validate this theoretical result. This work demonstrates the possibility of extending the telegrapher's (or Cattaneo) equation by adding self-reinforcing directionality so that superdiffusion occurs even when rests are introduced.

DOI: [10.1103/PhysRevE.00.004100](https://doi.org/10.1103/PhysRevE.00.004100)

### I. INTRODUCTION

Persistent random walks with finite velocities are powerful models describing chemotaxis [1–5], organism movement and searching strategies [6–8], intracellular transport [9–11], and cell motility [12,13]. Stochastic cell movement plays a major role in embryonic morphogenesis, wound healing, and tumor cell proliferation [14]. The modeling of cell and bacteria migration toward a favorable environment is usually based on “velocity-jump” models describing self-propelled motion with the runs and tumbles. Finite velocities and inertial resistance to changes in direction make these random walks physically well motivated since random walkers in nature cannot instantaneously jump to different states. The collective behavior of cells and various organisms is another rapidly growing area of active matter research [15,16]. Various hyperbolic models involving nonlinear partial differential equations (PDEs) for the population densities have been used for analysis of spatiotemporal patterns describing the chemical and social interactions of organisms [17–21].

Models of cell motility have been predominantly concerned with Markovian random-walk models (see for example Refs. [13,22]). However, the analysis of random movement of metastatic cancer cells shows the anomalous superdiffusive dynamics of cell migration [23]. Over the past few years there have been several attempts to model anomalous transport involving superdiffusion [24–30]. Superdiffusion occurs as a

result of the power-law distributed running times with infinite second moment [25] or collective interaction between random walkers [31]. Such models are intrinsically non-Markovian involving nonlocal in time integral terms, making the inclusion of reactions, internal dynamics, chemical signals, and interparticle interactions cumbersome and unwieldy.

Recently, we introduced a persistent random-walk model with self-reinforcing directionality that generates superdiffusion from exponentially distributed runs, accurately modeling the statistics found in active intracellular transport [32]. Although this model involves strong memory, it can be formulated as a persistent random walk with space- and time-dependent coefficients, facilitating convenient implementations of reactions, chemotaxis, and interactions using the established methods within the persistent random-walk framework.

In Ref. [32], we considered a particle moving with velocity  $\pm v$  for exponentially distributed running times with rate  $\lambda$ . The key idea was to introduce conditional transition probabilities,  $q_+$  and  $q_-$ , involving self-reinforcing directionality. These conditional transition probabilities describe switching from one velocity state to the other dependent on the time that the particle has spent in the respective states such that  $q_{\pm} = wt^{\pm}/t + (1-w)t^{\mp}/t$ . In this case,  $t^+$  and  $t^-$  are the times that a particle has spent traveling in the positive and negative direction, respectively, and  $t = t^+ + t^-$ . The persistence probability  $w$  defines how much the random walk chooses to follow its past behavior. For example, if much time is spent moving in the positive direction ( $t^+ \rightarrow t$ ) and  $w = 1$ , then, the particle will choose to move in the positive direction with probability  $q_+ \rightarrow 1$ . To formulate the governing equations, we introduce  $p_+(x, t)$  and  $p_-(x, t)$ , which are the joint probability densities that the position of the particle is in the interval  $(x, x + dx)$  at time  $t$  and moving with positive and negative

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82 velocities, respectively. Then

$$\frac{\partial p_{\pm}}{\partial t} \pm v \frac{\partial p_{\pm}}{\partial x} = -\lambda(1 - q_{\pm})p_{\pm} + \lambda(1 - q_{\mp})p_{\mp}. \quad (1)$$

83 The advantage of this formulation is that  $q_{\pm}$  can be simply  
84 expressed as a function of space,  $x$ , and time,  $t$ . If one realizes  
85 that  $x = v(t_+ - t_-)$ , then

$$q_{\pm}(x, t) = \frac{1}{2} \left[ 1 \pm \frac{(2w - 1)(x - x_0)}{vt} \right]. \quad (2)$$

86 Expressing  $q_{\pm}$  in this way, we can write down (1) as a single  
87 hyperbolic PDE,

$$\frac{\partial^2 p}{\partial t^2} + \lambda \frac{\partial p}{\partial t} = v^2 \frac{\partial^2 p}{\partial x^2} - \frac{\lambda(2w - 1)}{t} \frac{\partial[(x - x_0)p]}{\partial x}. \quad (3)$$

88 This model has been shown to exhibit superdiffusion despite  
89 having exponentially distributed run times [32]. For values  
90 of  $w > 1/2$ , the conditional transition probabilities generates  
91 self-reinforcing directionality in (3) and for  $w > 3/4$ , super-  
92 diffusion. Research on reinforcement in random walks has  
93 been explored in jump processes [22]. The model represented  
94 in (3) is actually a continuous space and time generalization of  
95 the elephant random walk [33–39], which is discrete in space  
96 and time.

97 A limitation of (3) is that only active states were included  
98 in the model. In reality, most natural phenomena have rest  
99 states associated with passive movement, no movement, or  
100 even death. In particular, animals move by alternating between  
101 foraging and resting [40,41]. In modeling processes with rest  
102 states, the Lévy walk with rests [42–45] and persistent random  
103 walks with death [46] have been introduced.

104 The aim of this paper is to formulate the self-reinforcing  
105 velocity random walks with stochastic rests. Important ques-  
106 tions for this model are does superdiffusion still exist after  
107 introducing rests? and; if superdiffusion does exist, then what  
108 is the critical value of the ratio of mean running and resting  
109 time for which the phase transition from diffusion to superdif-  
110 fusion occurs?

111 In the first section, we formulate the self-reinforcing direc-  
112 tionality random walk with a rest state and derive the nonlocal  
113 hyperbolic governing partial differential equation for the PDF  
114 of particle position. In the second section, we find an analyt-  
115 ical expression for the second moment and the critical point  
116 where the transition from diffusion to superdiffusion occurs.  
117 Finally, we present the Monte Carlo simulations of the random  
118 walk with reinforcement, which confirms the existence of  
119 superdiffusion.

## 120 II. SELF-REINFORCING DIRECTIONALITY WITH RESTS

121 In this section, we introduce the self-reinforcing velocity  
122 random walk with transitions between moving states via an  
123 intermediate resting state with zero velocity. Consider a partic-  
124 cle that moves with constant speed  $v$  in the positive or negative  
125 direction for exponentially distributed running times with rate  
126  $\lambda$ . This movement is interrupted by rests with exponentially  
127 distributed resting times with rate  $\eta$ . Now we introduce three  
128 joint probability density functions,  $p_+(x, t)$ ,  $p_-(x, t)$ , and  
129  $p_0(x, t)$ . Here  $p_+(x, t)$  and  $p_-(x, t)$  are the same as the joint  
130 densities described in (1). Additionally,  $p_0(x, t)$  is the joint

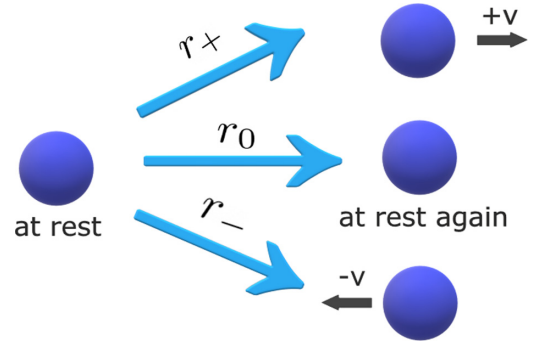


FIG. 1. A diagram showing the conditional transition probabilities,  $r_+$ ,  $r_-$ , and  $r_0$ , for the velocity random walk in (4). A particle at rest can switch to the positive velocity state, negative velocity state, or remain at rest.

probability density that a particle is in the interval  $(x, x + dx)$  at time  $t$  and has zero velocity. The governing equations for these probability densities are

$$\begin{aligned} \frac{\partial p_{\pm}}{\partial t} \pm v \frac{\partial p_{\pm}}{\partial x} &= -\lambda p_{\pm} + \eta r_{\pm} p_0, \\ \frac{\partial p_0}{\partial t} &= \lambda p_+ + \lambda p_- - \eta(1 - r_0)p_0. \end{aligned} \quad (4)$$

Here the transition probabilities,  $r_+$ ,  $r_-$ , and  $r_0$ , describe three possible transitions that the particle can make from the rest state.  $r_+$  is the probability that the particle switches from the rest state to the moving state with positive velocity,  $v$ .  $r_-$  is the probability of switching from the rest state to the moving state with negative velocity  $-v$ .  $r_0$  is the probability that the resting particle remains at rest again after an exponentially distributed random time with rate  $\eta$  (see Fig. 1). Clearly,  $r_+ + r_- + r_0 = 1$ .

In this paper, we introduce self-reinforcing directionality through the conditional transition probabilities as follows:

$$r_{\pm} = w_1 \frac{t^{\pm}}{t} + w_2 \frac{t^{\mp}}{t} + w_3 \frac{t^0}{t}, \quad (5)$$

where  $t^+$ ,  $t^-$ , and  $t^0$  are the relative times that the particle has spent in the positive velocity, negative velocity, or resting state, respectively. The total time is  $t = t_+ + t_- + t_0$ . The weights,  $w_1$ ,  $w_2$ , and  $w_3$ , represent the amount of influence that each relative time has on the probability that a particle will transition to the corresponding state. Naturally, the weights are positive and  $w_1 + w_2 + w_3 = 1$ .

Why and how does (5) introduce self-reinforcing directionality into (4)? We demonstrate the effect on the conditional transition probabilities by considering weights  $w_1$  and  $w_2$ . For  $w_1 > w_2$ , the random walk reinforces its own past behavior by increasing the transition probability to the positive velocity state,  $r_+$ , when the time spent in that state,  $t^+$ , increases. The same can be said between  $r_-$  and  $t^-$ . In other words, the more the random walk spends time in either the positive or negative velocity state, the more likely a future transition into that state becomes. So the weights  $w_1$  and  $w_2$  perform an essential function in self-reinforcing directionality by either “punishing” or “rewarding” past choices and making future transitions to states dependent on time spent in the two active states. Now

165 we present a clear and effective method for simplifying (5) so  
166 that a single governing equation can be obtained.

167 We can rewrite (5) using  $t = t^+ + t^- + t^0$  and  $x = x_0 +$   
168  $v(t^+ - t^-)$  as

$$\begin{aligned} r_+(x, t) &= \frac{w_1 - w_2}{2} \frac{x - x_0}{vt} + \frac{w_1 + w_2}{2} + \Lambda \frac{t^0}{t} \\ r_-(x, t) &= -\frac{w_1 - w_2}{2} \frac{x - x_0}{vt} + \frac{w_1 + w_2}{2} + \Lambda \frac{t^0}{t} \\ r_0 &= 1 - r_+ - r_-, \end{aligned} \quad (6)$$

169 where  $\Lambda = -(w_1 + w_2)/2 + w_3$ .

170 In this paper, we introduce self-reinforcing directionality  
171 such that  $t_0$ , the time spent resting, does not explicitly con-  
172 tribute to the conditional transition probabilities  $r_+$  and  $r_-$ .  
173 To achieve this, we set  $\Lambda = 0$  and given  $w_1 + w_2 + w_3 =$   
174  $1$ , one finds that  $w_3 = 1/3$  and  $w_1 + w_2 = 2/3$  is a unique  
175 requirement. Self-reinforcement appears when  $w_1 > w_2$  and  
176 disappears for the symmetrical case when  $w_1 = w_2 = w_3 =$   
177  $1/3$ . Then the conditional transition probabilities in (6) can be  
178 written in terms of a self-reinforcing parameter,  $\alpha_0$ , as

$$r_{\pm} = \frac{1}{3} \pm \alpha_0 \frac{x - x_0}{2vt} \quad \text{and} \quad r_0 = \frac{1}{3}, \quad (7)$$

179 where

$$\alpha_0 = w_1 - w_2 \quad \text{and} \quad 0 < \alpha_0 < 2/3. \quad (8)$$

180 The formulation of self-reinforcement in this way presents  
181 a particularly powerful mechanism to introduce memory ef-  
182 fects and superdiffusion. It is clear that this mechanism is  
183 different to that used to generate superdiffusion in continuous  
184 time random walks or Lévy walks. Note that (7) is also valid  
185 for  $-2/3 < \alpha_0 \leq 0$ , for which the model exhibits behavior  
186 opposite to self-reinforcement. Using the definition of condi-  
187 tional transition probabilities in (7), we can formulate a single  
188 governing equation that enables various extensions, such as  
189 reactions, interactions, and chemotaxis, to be readily applied  
190 from the persistent random-walk framework. In our previous  
191 paper, we suggested a simple microscopic mechanism of self-  
192 reinforcement (see Sec. VII in Ref. [32]).

193 Now we will derive the single governing equation. From  
194 combining (4), we obtain three equations,

$$\begin{aligned} \frac{\partial p}{\partial t} &= -\frac{\partial J}{\partial x}, \quad \frac{\partial p_0}{\partial t} = \lambda p - \gamma p_0, \quad \text{and} \\ \frac{\partial J}{\partial t} &= -v^2 \frac{\partial p}{\partial x} + v^2 \frac{\partial p_0}{\partial x} - \lambda J + v\eta(r_+ - r_-)p_0, \end{aligned} \quad (9)$$

195 where  $p(x, t) = p_+(x, t) + p_-(x, t) + p_0(x, t)$  so that  $p(x, t)$   
196 is the probability density of finding the particle in the interval  
197  $(x, x + dx)$  at time  $t$  regardless of the particle's velocity state.  
198 Furthermore,  $\int_{-\infty}^{\infty} p(x, t) dx = 1$ . In addition,  $J = vp_+ - vp_-$   
199 and

$$\gamma = \lambda + (1 - r_0)\eta = \lambda + \frac{2}{3}\eta. \quad (10)$$

200 The initial conditions are

$$\begin{aligned} p(x, 0) &= \delta(x - x_0), \quad p_0(x, 0) = 0 \quad \text{and} \\ J(x, 0) &= v(2u - 1)\delta(x - x_0), \end{aligned} \quad (11)$$

201 where  $u$  is the probability that the particle begins with positive  
202 velocity and  $(1 - u)$  to begin with negative velocity. Solving

the second equation in (9) with the initial condition  $p_0(x, 0) =$   
0, one can also write  $p_0(x, t)$  in terms of  $p(x, t)$  as

$$p_0(x, t) = \lambda \int_0^t e^{-\gamma(t-t')} p(x, t') dt'. \quad (12)$$

Combining (9), (12), and (7), a single equation can be  
found for  $p$  as

$$\begin{aligned} \frac{\partial^2 p}{\partial t^2} + \lambda \frac{\partial p}{\partial t} - v^2 \frac{\partial^2 p}{\partial x^2} + \lambda v^2 \int_0^t e^{-\gamma(t-t')} \frac{\partial^2 p(x, t')}{\partial x^2} dt' \\ + \frac{\lambda \alpha_0 \eta}{t} \frac{\partial}{\partial x} \left[ (x - x_0) \int_0^t e^{-\gamma(t-t')} p(x, t') dt' \right] = 0. \end{aligned} \quad (13)$$

Now the crucial question is does the intermediate rest state  
destroy superdiffusion seen in the self-reinforcing direction-  
ality random-walk model? To answer this, we perform moment  
analysis.

If the parameter  $\eta \rightarrow \infty$ , then the average rest time, which  
is  $1/\eta$ , approaches 0. The fourth term in (13) approaches 0  
because  $\gamma$  defined in (10)  $\rightarrow \infty$ . However, the last term in  
(13) does not approach 0 because  $(1 - r_0)\eta e^{-\gamma(t-t')} \rightarrow \delta(t -$   
 $t')$  as  $\eta \rightarrow \infty$ . So in this case, (13) becomes the same as the  
governing equation in the case of no rests, which can be found  
in (10) in Ref. [32].

### III. MOMENT CALCULATIONS AND SUPERDIFFUSION

To find an analytical expression for the second moment  
 $\mu_2(t) = \int_{-\infty}^{\infty} x^2 p(x, t) dx$ , we use (13) with the assumption  
that  $x_0 = 0$ . Then

$$\begin{aligned} \frac{d^2 \mu_2(t)}{dt^2} + \lambda \frac{d\mu_2(t)}{dt} - \frac{2\lambda \alpha_0 \eta}{t} \int_0^t e^{-\gamma(t-t')} \mu_2(t') dt' \\ = 2v^2 \left( 1 - \frac{\lambda}{\gamma} \right) + \frac{2v^2 \lambda}{\gamma} e^{-\gamma t}. \end{aligned} \quad (14)$$

Now using the initial conditions (11), we obtain the initial  
conditions for the second moment,

$$\mu_2(0) = 0 \quad \text{and} \quad \frac{d\mu_2(0)}{dt} = 0. \quad (15)$$

Using the Laplace transform of (14) and (15), the equation for  
 $\hat{\mu}_2(s) = \int_0^{\infty} \mu_2(t) e^{-st} dt$  is

$$\begin{aligned} \frac{d\hat{\mu}_2}{ds} + \frac{2s + \lambda + 2\lambda \alpha_0 \eta (s + \gamma)^{-1}}{s(s + \lambda)} \hat{\mu}_2 \\ = -\frac{2v^2}{s^3(s + \lambda)} \left( 1 - \frac{\lambda}{\gamma} \right) - \frac{2v^2 \lambda}{\gamma s(s + \gamma)^2 (s + \lambda)}. \end{aligned} \quad (16)$$

Now let us look at the long-time limit ( $s \rightarrow 0$ ) for (16),  
then

$$\frac{d\hat{\mu}_2}{ds} + \frac{1 + \frac{2\alpha_0 \eta}{\gamma}}{s} \hat{\mu}_2 \approx -\frac{2v^2}{s^3 \lambda} \left( 1 - \frac{\lambda}{\gamma} \right) - \frac{2v^2}{s \gamma^3}. \quad (17)$$

When neglecting the rest state,  $\eta \rightarrow \infty$  or  $\gamma = \lambda + (1 -$   
 $r_0)\eta \rightarrow \infty$ , then (17) becomes

$$\frac{d\hat{\mu}_2}{ds} + \frac{1 + 2\alpha_0}{s} \hat{\mu}_2 \approx -\frac{2v^2}{s^3 \lambda}. \quad (18)$$

The homogeneous solution for (18) is  $\hat{\mu}_2(s) = C_2 s^{-2\alpha_0 - 1}$   
where  $C_2$  is a constant, which gives  $\mu_2(t) \sim t^{2\alpha_0}$  taking the

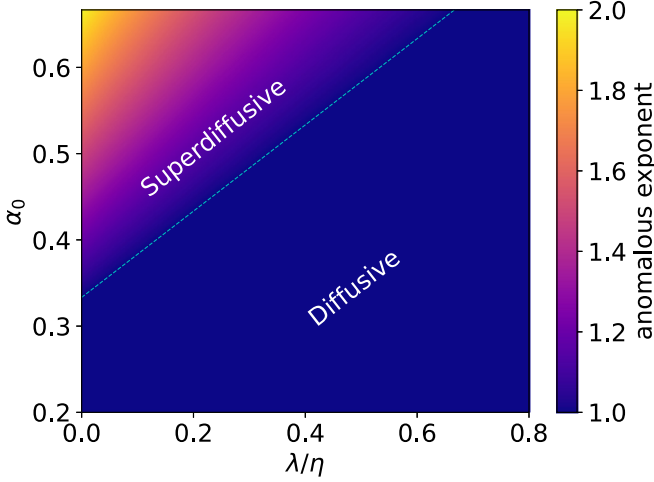


FIG. 2. A diagram showing where the diffusive and superdiffusive regimes are found for varying values of  $\alpha_0$  and  $\lambda/\eta$ . The cyan dashed line shows  $\alpha_0 = \lambda/2\eta + 1/3$ . The anomalous exponent is defined in (25).

inverse. This shows that  $2\alpha_0$  is the anomalous exponent. Analogously, from (17) we obtain

$$\hat{\mu}_2(s) \sim C_2 s^{-\frac{2\alpha_0\eta}{\gamma}-1}, \quad (19)$$

which gives

$$\mu_2(t) \sim C_2 t^{\frac{2\alpha_0\eta}{\gamma}}. \quad (20)$$

This shows that even with rests, self-reinforcing directionality is enough to generate superdiffusion (see Fig. 2). The first moment,  $\mu_1(t) = \int_{-\infty}^{\infty} x p(x, t) dx$ , can be found in a similar way as

$$\mu_1(t) \sim C_1 t^{\frac{\alpha_0\eta}{\gamma}}, \quad (21)$$

where  $C_1$  is a constant.

In the following sections, we confirm superdiffusion through Monte Carlo simulations for both the second moment and the variance  $\text{Var}[x(t)] = \mu_2(t) - [\mu_1(t)]^2$  (see Figs. 3 and 4). The Monte Carlo simulation results in Figs. 4 show that  $C_1 \neq C_2$  (and further that  $C_2 > C_1^2$ ) such that the variance is nonzero and follows the same time dependence as the second moment. Now let us consider for what parameter values superdiffusion is achieved.

For superdiffusion, the anomalous exponent in (20) must satisfy the condition

$$1 < \frac{2\alpha_0}{\frac{\lambda}{\eta} + \frac{2}{3}} < 2, \quad (22)$$

where (10) has been used to simplify the expression. Evidently, superdiffusion only depends on two parameters: the self-reinforcement parameter,  $\alpha_0$ , and the ratio between run and rest rates,  $\lambda/\eta$ . Rearranging, (22) becomes

$$\frac{1}{3} + \frac{1}{2} \frac{\lambda}{\eta} < \alpha_0 < \frac{2}{3} + \frac{\lambda}{\eta}. \quad (23)$$

The left inequality gives  $1/3 < \alpha_0$ , which in conjunction with (8) means that  $1/3 < \alpha_0 < 2/3$  is needed for superdiffusion.

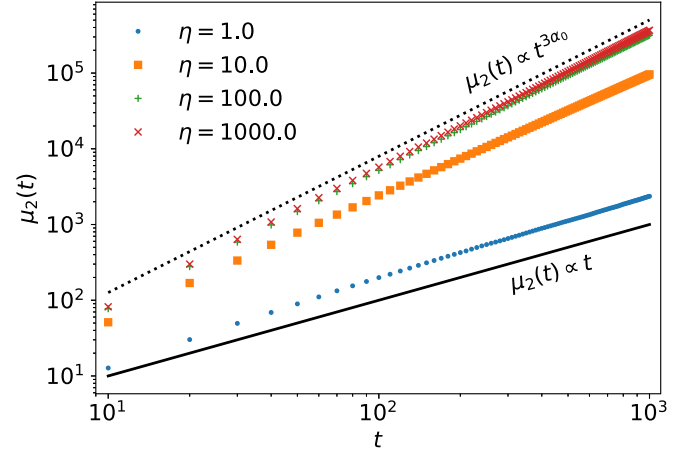


FIG. 3. Mean-squared displacements for the random-walk simulation with varying  $\eta$ . The parameters for the simulation were  $\alpha_0 = 0.6 < 2/3$ ,  $r_0 = 1/3$ ,  $\lambda = 1$ ,  $\nu = 1$  and the number of particles  $N = 10^4$ . The solid black line shows diffusion  $\mu_2(t) \sim t$  and dashed black line shows the predicted superdiffusion from (20) and (22):  $\mu_2(t) \sim t^{3\alpha_0}$  as  $\lambda/\eta \rightarrow 0$  ( $\eta \rightarrow \infty$ ).

Then considering (8) again, we find the limits  $0 \leq \lambda/\eta < 2/3$  are necessary for superdiffusion.

It follows from (20) that in the superdiffusive regime, the second moment

$$\mu_2(t) \sim t^\sigma, \quad (24)$$

where the anomalous diffusion exponent [17,44,47] is

$$\sigma = \frac{3\alpha_0}{1 + \frac{3}{2} \frac{\lambda}{\eta}} \quad (25)$$

with the bounds  $1/3 < \alpha_0 < 2/3$  and  $0 \leq \lambda/\eta < 2/3$ . The phase diagram showing different parameter values and the corresponding superdiffusive or diffusive states can be seen in Fig. 2.

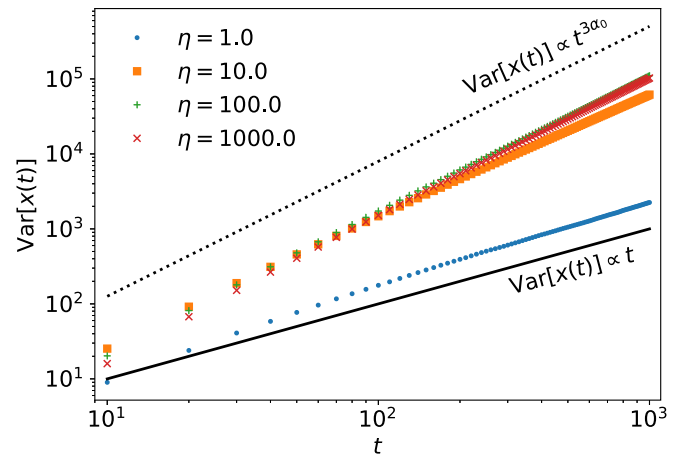


FIG. 4. The variance for the random-walk simulation with varying  $\eta$ . The parameters for this simulation were exactly the same as in Fig. 3. The solid and dashed black lines are also exactly the same, showing a constant multiplicative difference between the second moment and the variance

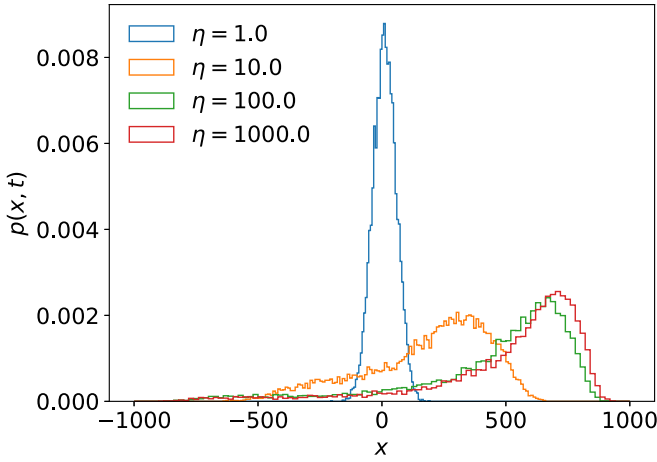


FIG. 5. PDF of particle positions at  $t = 1000$  for the random-walk simulation with varying  $\eta$ . Identical simulation data from Fig. 3 was used. The parameters for the simulation were  $\alpha_0 = 0.6$ ,  $r_0 = 1/3$ ,  $\lambda = 1$ , and  $\nu = 1$  and the number of particles  $N = 10^4$ .

It is particularly interesting to note that there is a smooth transition from diffusion to superdiffusion dependent on the ratio between running and resting rates,  $\lambda/\eta$ , in addition to the self-reinforcing parameter,  $\alpha_0$ . In modeling various different transport phenomena with this self-reinforcing random walk with rests, we expect the dependence of the diffusion-superdiffusion transition on  $\lambda/\eta$  to be especially useful as there is a clear physical meaning to why superdiffusion emerges from a random walk with rests. For example, modeling transport mediated by multiple types of motor proteins will involve heterogeneous values of  $\lambda$  and  $\eta$  and may elucidate why some motor protein transport is more superdiffusive than others.

#### IV. MONTE CARLO SIMULATIONS

In this section, we validate the theoretical result in (20) and show the displacement PDFs as we vary  $\eta$ . The numerical simulations for a single random walk corresponding to Eq. (4) were performed as follows:

(1) Initialize variables for current simulation time  $T_c = 0$ , particle position  $X_c = 0$  and current particle state  $S_c = 1$ . In this case, there are only three possible values for  $S_c = 0$  or  $\pm 1$  corresponding to the rest, positive velocity and negative velocity states, respectively. For simplicity, we assume the random walk starts in the positive velocity state.

(2) Initialize the constants of the simulation:  $\lambda$ ,  $\eta$ ,  $\nu$ ,  $\alpha_0$ ,  $r_0$ , and  $t_{\text{end}}$ , the end time of simulation.

(3) If  $S_c = 0$ , then generate a random number  $\Delta T = -\ln(U)/\eta$ , where  $U \in [0, 1)$  is a uniformly distributed random number. If  $S_c = \pm 1$ , then generate a random number  $\Delta T = -\ln(U)/\lambda$ . We emphasize that  $\Delta T$  has exponential distribution with the density  $\frac{d}{dt}\text{Prob}[\Delta T < t] = \eta \exp(-\eta t)$  for the rest state or  $\lambda \exp(-\lambda t)$  for the moving states.

(4) Increment the current simulation time  $T_c = T_c + \Delta T$  and the particle position  $X_c = X_c + \nu S_c \Delta T$ .

(5) If  $S_c = \pm 1$ , then set  $S_c = 0$ . If  $S_c = 0$ , then generate a uniformly distributed random number,  $V \in [0, 1)$  and cal-

culate  $R_{\pm} = r_0 \pm \alpha_0 X_c / (2\nu T_c)$ . For  $0 \leq V < R_+$ , set  $S_c = 1$ . For  $R_+ \leq V < R_+ + R_-$  set  $S_c = -1$ . Otherwise, set  $S_c = 0$ .

(6) Iterate steps 3 to 5 until  $T_c \geq t_{\text{end}}$ .

The numerical simulations in this paper were performed using Python3, taking advantage of the “Numba” package for JIT compilation and the “multiprocessing” package for CPU parallelization. These packages were used to significantly improve simulation execution times.

Figures 3 and 4 show the emergence of superdiffusion and excellent correspondence with (20). Figure 5 shows the behavior of the PDF as the value of  $\eta$  is varied. Clearly, when the rests become negligible in the asymptotic limit  $\lambda/\eta \rightarrow 0$  ( $\eta \rightarrow \infty$ ), the drift of particles caused by self-reinforced directionality dominates. This clearly shows that particles engage in self-reinforcing directionality as rest states become less time-consuming and particles choose to move in the same direction as their past history.

#### V. SUMMARY AND CONCLUSIONS

In this paper, we have formulated a run-and-tumble model with self-reinforcing directionality and rests. The system of PDEs (4) has been reduced to a single, nonlocal equation for the total probability density (13). From this single governing equation, we demonstrated the emergence of superdiffusion by deriving the second moment for the long-time limit. This emergence depends on two parameters: the self-reinforcement of particles,  $\alpha_0$ , and the ratio between running and resting rates,  $\lambda/\eta$ . We find that at the critical point,  $\lambda/\eta = 2/3$ , superdiffusion emerges and remains for  $\lambda/\eta < 2/3$ . In other words, the mean running time must be at least  $2/3$  of the mean resting time for superdiffusion to occur in this model. Interestingly, we find that even a rest state cannot completely destroy the superdiffusion generated by self-reinforcement. Further, we present the method for Monte Carlo simulation of these random walks and show that the second moment corresponds with theoretical predictions. This superdiffusive model involving rests has potential application modeling the trapping of intracellular vesicles in actin-rich regions of neurons. This resting behavior is thought to act as functional reservoirs and help maintain the flow of presynaptic vesicles in the neurons of *Caenorhabditis elegans* [48].

Since our model describes an anomalous random walk with strong memory, it would be interesting to explore its ergodic properties considering both the Khinchin and fluctuation-dissipation theorems [47,49–52]. We expect ergodicity breaking for our model as is the case for the discrete random walk with global memory [53,54]. A natural extension of resting times distributed with constant rate  $\eta$  is to introduce a rest state that is non-Markovian with a residence time-dependent rate [55,56]. Recently, we considered the case with Mittag-Leffler distributed rest times for which the mean residence time in the rest state was divergent [57]. This dominates self-reinforcing directionality in the long-time limit and generates subdiffusion. It is also interesting to consider the case when the velocities alternate at nonexponentially distributed random times [58] or driven by random trials [59]. Furthermore, this new framework opens new avenues to include interactions of particles

359 by density-dependent rates,  $\lambda(p)$  and  $\eta(p)$ , and velocity,  
 360  $v(p)$ , leading to aggregation and pattern formation in active  
 361 matter [16].

### ACKNOWLEDGMENTS

362 S.F. is thankful for the support and hospitality of the  
 363 Ural Mathematical Center at the Ural Federal University,  
 364 Ekaterinburg. S.F. also acknowledges financial support from  
 365 **RSF** Project No. 20-61-46013. D.H. acknowledges the sup-  
 366 port from **Wellcome Trust** Grant No. 215189/Z/19/Z, the  
 367

**Medical Research Council**, as part of United Kingdom  
 Research and Innovation (also known as UK Research  
 and Innovation) [MC/UP/1201/21] and Churchill College,  
 University of Cambridge. A.O.I. acknowledges financial  
 support from the Ministry of Science and Higher Educa-  
 tion of the **Russian Federation** (Ural Mathematical Center  
 Project No. 075-02-2021-1387). D.H. and M.A.A.S ac-  
 knowledge financial support from **FAPESP/SPRINT** Grant  
 No. 18/15308-4. M.A.A.S acknowledges the Brazilian gov-  
 ernment's research funding agency CNPq (process no.  
 312667/2018-3).

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