

## Trail-Mediated Self-Interaction

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A number of microorganisms leave persistent trails while moving along surfaces. For single-cell organisms, the trail-mediated self-interaction will influence the dynamics. It has been discussed recently [Kranz *et al.* Phys. Rev. Lett. **117**, 038101 (2016)] that the self-interaction may localize the organism above a critical coupling  $\chi_c$  to the trail. Here we will derive a generalized active particle model capturing the key features of the self-interaction and analyze its behavior for smaller couplings  $\chi < \chi_c$ . We find that fluctuations in propulsion speed shift the localization transition to stronger couplings.

## I. INTRODUCTION

Motility or active motion of an organism is most useful if it can occur in response to external stimuli.<sup>1–3</sup> It has been recognized from the early days<sup>4</sup> that directed motion is already realized in both prokaryotic and eukaryotic single-celled microorganisms.<sup>5–7</sup> On the microbial scale, chemical signals and the corresponding response—chemotaxis—are the most widespread but by no means the only stimuli that are used as information.

Surface dwelling microorganisms like the bacteria from the species *Pseudomonas*, *Neisseria* and amoeboid slime molds are known to leave trails<sup>8,9</sup> of high molecular weight biopolymers like polysaccharides.<sup>10–12</sup> It is believed that these trails are used as a means of cell-cell communication in particular in the process of colony and spore formation.<sup>6,9,13–19</sup> The precise mechanisms, however, are still under active investigation.

Living organisms have intricate signal processing pathways, even on the microbial scale.<sup>20</sup> Therefore the response to a stimulus may be the result of a complicated control algorithm. On the other hand there is evolutionary value in robustness.<sup>21</sup> Simplicity often lends itself to robustness. In recent years there has been a growing recognition that mechanistic models that forgo the intracellular chemical signal processing may be able to explain surprisingly complicated behavior.<sup>22–26</sup> Here we follow this *active particle* approach and do not address the question of how much internal signal processing is involved in trail interaction.

Rapidly diffusing, small molecules such as cyclic adenosine monophosphate (cAMP) are also employed in cell-cell communication in the form of auto-chemotaxis.<sup>27,28</sup> This form of inter-microbial communication is relatively well understood both on the level of the intra-cellular signaling path-ways and on the level of collective effects. Most artificial active particles are auto-chemotactic in that they

create and are propelled by local chemical gradients.<sup>26,29</sup> All these systems are characterized by particles or organisms whose typical speed  $v_0$  or typical effective diffusivity  $D$  is much smaller than the diffusivity of the signaling molecules  $D_m \gg D, v_0 R$  not least because their size  $R$  is much bigger than molecular length scales. In effect, an organism's self-generated concentration field is to a lowest order approximation isotropic with respect to the organism itself even if the organism is in motion. Self-interaction of the organism with its own auto-chemotactic field due to direct coupling with the translational degrees of freedom has been studied in the past<sup>30</sup> and shown not to be strong enough to lead to trapping.<sup>31</sup>

The trail material, on the other hand, consists of entangled macromolecules<sup>32</sup> with a very low diffusivity  $D_m \ll D, v_0 R$ . A moving microorganism will therefore encounter an anisotropic distribution of its own trail. It obviously leaves a trail *behind* and not *all around*. As a consequence, the only observable dynamics is the effective dynamics that results from the interplay of the organism's propulsion mechanism and the trail-mediated self-interaction. We have recently shown that this self-interaction may profoundly alter the dynamics.<sup>33,34</sup> Here we will discuss this mechanism in more detail and on a more general basis.

We will start by specifying the model in Sec. II and derive the effective dynamics in Sec. III. Using this effective description we will analyze the orientational dynamics in Sec. IV and the translational diffusivity in Sec. V. We will briefly discuss the influence of speed fluctuations in Sec. VI before closing in Sec. VII.

## II. BARE DYNAMICS

In the following we will be exclusively concerned with the dynamics of a single microorganism on a pristine, essentially flat surface. The state of a microorganism at time  $t$  is fully described by its position  $\mathbf{r}(t)$ , its orientation  $\hat{\mathbf{n}}(t) = (\cos \varphi(t), \sin \varphi(t))$  and the trail it has left so far  $\tilde{\psi}(\mathbf{x}, t)$ . We assume active propulsion along the current

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orientation  $\hat{\mathbf{n}}(t)$  with a mean speed  $v_0$  and small fluctuations on top, characterized by a translational diffusivity  $D_v$ ,

$$d\mathbf{r}(t) = \hat{\mathbf{n}}(t)(v_0 dt + \sqrt{2D_v} dW_t). \quad (1)$$

Here  $W_t$  denotes a Wiener process. Orientational persistence is observed to be limited in microorganisms such that the rotational diffusivity  $D_r^0$  should be substantial. It has been found that a torque is naturally generated by gradients of the trail field,  $\nabla\psi(\mathbf{x}, t)$ , perpendicular to the microorganism's instantaneous orientation. To be precise, the organism may not react to the *actual* trail field but only to the trail field it senses via some transfer function  $\Xi(\mathbf{x}, t)$  that may perform some spatial averaging and potentially some time integration. The orientation dynamics is therefore of the following form,

$$d\varphi(t) = \chi \nabla_{\perp}(t)(\Xi * \tilde{\psi})(\mathbf{r}(t), t) dt + \sqrt{2D_r^0} dZ_t, \quad (2)$$

where  $Z$  is a second, independent Wiener processes,<sup>35</sup>  $\chi$  characterizes the sensitivity of the microorganism to the trail and  $\nabla_{\perp}(t) := \hat{\mathbf{e}}_{\varphi}(t) \cdot \nabla$  where  $\hat{\mathbf{e}}_{\varphi}(t) \perp \hat{\mathbf{n}}(t)$ . The asterisk denotes a convolution in space and time and  $\Xi(\mathbf{x}, t)$  is normalized such that  $\int d^2x \int dt \Xi(\mathbf{x}, t) = 1$ . Along its trajectory  $\mathbf{r}(t) := \{\mathbf{r}(t')\}_{t' < t}$ , the microorganism deposits trail material with a constant rate  $k$  and distributed according to a compact profile  $\tilde{\Psi}(x^2)$  normalized such that  $\int \tilde{\Psi}(x^2) d^2x = 1$ ,

$$\tilde{\psi}(\mathbf{x}, t | \mathbf{r}(t)) = k \int_{-\infty}^t \tilde{\Psi}([\mathbf{x} - \mathbf{r}(t')]^2) dt'. \quad (3)$$

Equations. (1-3) constitute a set of stochastic integro-differential equations for the time evolution of a single crawling microorganism. We note that in order to understand the dynamics of the microorganism, we do not need the full trail field  $\tilde{\psi}(\mathbf{x}, t)$  but only what the organism senses  $\nabla_{\perp}\psi(t) := \nabla_{\perp}(t)(\Xi * \tilde{\psi})(\mathbf{r}(t), t)$ . We imagine a primarily mechanic response to the trail such that the transfer function is instantaneous on the time scales of the noise,  $\Xi(\mathbf{x}, t) \propto \delta(t)$ . Then it is sufficient to consider an effective profile  $\Psi := \Xi * \tilde{\Psi}$ , *i.e.*,

$$\nabla_{\perp}\psi(t) = k \nabla_{\perp}(t) \int_{-\infty}^t dt' \Psi([\mathbf{r}(t) - \mathbf{r}(t')]^2). \quad (4)$$

We may then expand the gradient as

$$\begin{aligned} \nabla_{\perp}(t) \Psi([\mathbf{r}(t) - \mathbf{r}(t')]^2) &= \\ &= 2\hat{\mathbf{e}}_{\varphi}(t) \cdot [\mathbf{r}(t) - \mathbf{r}(t')] \Psi'([\mathbf{r}(t) - \mathbf{r}(t')]^2), \end{aligned} \quad (5)$$

where the prime on  $\Psi$  denotes the derivative with respect to the argument.

### III. EFFECTIVE DYNAMICS

To make progress we have to make a number of assumptions. We need the trail profile to be sufficiently well

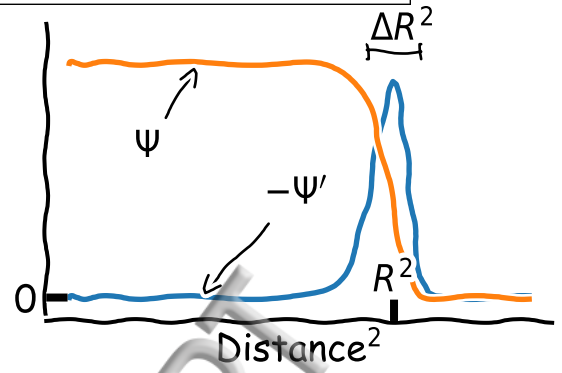


FIG. 1. Sketch of the trail profile (as sensed by the organism)  $\psi(r^2)$  and its (negative) derivative  $-\psi'(r^2)$  as a function of the squared distance from the trail's center. We assume well defined trail edges,  $\Delta R/R \ll 1$ , throughout.

defined (see Fig. 1) with a characteristic size  $R$  and a trail boundary of width  $\Delta R \ll R$ . Then we may approximate  $\Psi(x^2) \approx \Theta(R^2 - x^2)/\pi R^2$  where  $\Theta(x)$  is the Heaviside step-function. Likewise, we need the active propulsion speed to be sufficiently well defined, *i.e.*,  $D_v \ll v_0$ . Then the characteristic time to cross a trail  $\tau$  is narrowly distributed around  $R/v_0$ . We now assume *a priori* that trails are sufficiently straight that self crossings can be neglected. We will find below that the self-interaction renormalizes the rotational diffusivity  $D_r^0$  to an effective value  $D_r$ , *i.e.*, we assume  $D_r \langle \tau \rangle \ll 1$  where  $\langle \tau \rangle$  is the mean crossing time. If the trajectories are straight enough so that the organism only rarely crosses its own trail, we can safely ignore these self-crossings.

In the following we will adopt units such that  $R = v_0 = 1$  and  $k = \pi$ . With the above assumptions, Eq. (1-3) reduce to

$$d\mathbf{r}(t) = \hat{\mathbf{n}}(t)(dt + \sqrt{2D_v} dW_t) \quad (6)$$

$$d\varphi(t) = \chi \nabla_{\perp}\psi(t) dt + \sqrt{2D_r^0} dZ_t \quad (7)$$

$$\nabla_{\perp}\psi(t) = \hat{\mathbf{e}}_{\varphi}(t) \cdot \int_{-\infty}^t dt' \mathbf{r}_{tt'} \delta(1 - r_{tt'}) \quad (8)$$

where  $\mathbf{r}_{tt'} \equiv \mathbf{r}(t) - \mathbf{r}(t')$ .

Due to the Dirac delta in Eq. (8) and our assumption that self-crossings are negligible, we only need to integrate over a time interval of order unity. To this end, we iterate the equations of motion (6,7) to lowest order and find

$$\begin{aligned} \mathbf{r}(t) - \mathbf{r}(t-t') &= \hat{\mathbf{n}}(t)t' + \sqrt{2D_v}\hat{\mathbf{n}}(t)W_{-t'} \\ &+ \hat{\mathbf{e}}_{\varphi}(t) \int_t^{t-t'} du \int_t^u \times \\ &\times [\chi \nabla_{\perp}\psi(w) dw + \sqrt{2D_r^0} dZ_w] \\ &+ 2\sqrt{D_v D_r^0} \hat{\mathbf{e}}_{\varphi}(t) \int_t^{t-t'} Z_u dW_u, \end{aligned} \quad (9)$$

where we have used that  $\hat{\mathbf{e}}_{\varphi}(w) \approx \hat{\mathbf{e}}_{\varphi}(t)$  to lowest order. In the following we are going to drop the last term in Eq. (9)

because it contains the product of the small parameters  $D_v, D_r^0 \ll 1$ .

The first term in Eq. (9) turns the Dirac delta in Eq. (8) into a first passage time problem of a one-dimensional Brownian motion with unit drift,  $t + \sqrt{2D_v}W_t$ , on the positive half line with a reflecting boundary at 0, *i.e.*,

$$\int_{-\infty}^t dt' r_{tt'} \delta(1 - r_{tt'}) = \mathbf{r}(t) - \mathbf{r}(t - \tau), \quad (10)$$

where  $\tau$  is a random variable, the first passage time. The characterization of the first passage time distribution  $p(\tau)$  is a non-trivial task that we are not going to pursue here but note that for  $D_v \rightarrow 0$ ,  $p(\tau) \rightarrow \delta(\tau - 1)$ .

Making use of Eqs. (9) and (10) in Eq. (8) we find a closed equation for  $\nabla_{\perp}\psi(t)$ ,

$$\nabla_{\perp}\psi(t) = \int_t^{t-\tau} du \int_t^u [\chi \nabla_{\perp}\psi(w) dw + \sqrt{2D_r^0} dZ_w]. \quad (11)$$

Once we have a solution of Eq. (11) we can use it in Eqs. (6, 7) to analyze the effective dynamics of a microorganism under trail-mediated self-interaction.

Let us start by considering a different representation of Eq. (11),

$$\nabla_{\perp}\psi(t) = \int_0^{\tau} (\tau - w) [\chi \nabla_{\perp}\psi(t - w) dw + \sqrt{2D_r^0} dZ_{t-w}], \quad (12)$$

to investigate the mean gradient

$$\langle \nabla_{\perp}\psi(t) \rangle_Z = \chi \int_0^{\tau} dw (\tau - w) \langle \nabla_{\perp}\psi(t - w) \rangle_Z. \quad (13)$$

This is solved by the ansatz  $\langle \nabla_{\perp}\psi(t) \rangle_Z \sim e^{\alpha t}$  given the rate  $\alpha$  solves the equation  $\lambda_{\tau}(\alpha) = 0$  where [cf. Eq. (A5)]

$$\lambda_{\tau}(\alpha) = 1 - \frac{\chi}{\alpha} \left[ \tau + \frac{1}{\alpha} (e^{-\alpha\tau} - 1) \right]. \quad (14)$$

For vanishing speed fluctuations,  $D_v \rightarrow 0$ ,  $\tau \equiv 1$ , and we recover the behavior of Ref. 33, *i.e.*, the average gradient relaxes to zero,  $\alpha < 0$ , for weak coupling to the trail,  $\chi < 2$ , whereas it grows exponentially above the critical value  $\chi_c = 2$ . For a discussion of the localization transition that occurs for  $\chi > \chi_c$  we refer to Ref. 33.

For significant fluctuations,  $D_v > 0$ , we need to analyze the ensemble average,  $\lambda(\alpha) := \int_0^{\infty} d\tau p(\tau) \lambda_{\tau}(\alpha)$ , over the unknown first passage time distribution  $p(\tau)$ . For the time being we assume that we may approximate  $\lambda(\alpha) \approx \lambda_{\langle\tau\rangle}(\alpha)$ , *i.e.*, by replacing the random variable  $\tau$  by its mean which is known exactly,<sup>36</sup>

$$\langle \tau \rangle = 1 + D_v (e^{-1/D_v} - 1) \simeq 1 - D_v. \quad (15)$$

From  $\lambda_{\langle\tau\rangle}(\alpha)$  we find a critical coupling strength  $\chi_c = 2/(1 - D_v)^2$  which is shifted to larger values for increasing speed fluctuations.

For  $\chi < \chi_c$ ,  $\nabla_{\perp}\psi(t)$  represents a stochastic process with zero mean and Eq. (11) can be solved in the Fourier domain<sup>37</sup> (cf. Sec. A)

$$\widetilde{\nabla_{\perp}\psi}(\omega) = \frac{\sqrt{2D_r^0}}{\chi} \times [\lambda_{\tau}^{-1}(i\omega) - 1] i\omega \tilde{Z}_{\omega}. \quad (16)$$

Note that by the Wiener representation theorem,  $i\omega \tilde{Z}_{\omega} \sim \mathcal{N}(0, 1)$  are iid normal random variables. In other words  $\nabla_{\perp}\psi(t)$  is essentially filtered white noise. In particular,

$$\tilde{\varphi}(\omega) = \sqrt{2D_r^0} \lambda_{\tau}^{-1}(i\omega) \tilde{Z}_{\omega} \quad (17)$$

is a stationary Gaussian process for  $\chi < \chi_c$ . This implies that the joint probability,

$$\begin{aligned} P(\varphi_1 - \varphi_2, t) &= P(\varphi_1, \varphi_2, t', t' + t) \\ &= \frac{1}{\sqrt{2\pi\delta\varphi^2(t)}} e^{-(\varphi_1 - \varphi_2)^2 / 2\delta\varphi^2(t)}, \end{aligned} \quad (18)$$

is fully specified by the angular mean square displacement

$$\delta\varphi^2(t) = \langle [\varphi(t' + t) - \varphi(t')]^2 \rangle. \quad (19)$$

#### IV. THE ANGULAR MEAN SQUARE DISPLACEMENT

Using Eq. (17) we find

$$|s|^2 \widehat{\delta\varphi^2}(s) = 2D_r^0 \int_0^{\infty} d\tau p(\tau) |\lambda_{\tau}(s)|^{-2}, \quad (20)$$

where  $\hat{f}(s) = \text{LT}[f](s) = \int_0^{\infty} dt f(t) e^{-st}$  is the Laplace transform of  $f(t)$ ,  $s = \sigma + i\omega \in \mathbb{C}$ . To make progress and derive the results discussed in Ref. 33, we will again use the mean first passage time approximation,

$$|s|^2 \widehat{\delta\varphi^2}(s) = 2D_r^0 |\lambda_{\langle\tau\rangle}(s)|^{-2} \quad (21)$$

and will analyze  $\lambda_{\langle\tau\rangle}^{-1}(s)$ , cf. Eq. (14).

In order to understand the angular mean square displacement in the time domain, we need to know the analytical structure of  $\lambda_{\langle\tau\rangle}^{-1}(s)$ . Due to the oscillating factor  $e^{-i\omega}$  there are infinitely many poles in the complex plain and an analytical inverse Laplace transform is not tractable. We may, however, consider the asymptotic limits  $t \rightarrow \infty$  and  $t \rightarrow 0$ . Note that, apart from the trivial scale factor  $D_r^0$ , the only control parameters that affect  $\delta\varphi^2(t)$  is the coupling strength  $\chi$  and the speed fluctuations  $D_v$ .

##### A. Short-Time Asymptotics

Expanding  $\lambda_{\langle\tau\rangle}(\sigma)$  in powers of  $\sigma^{-1}$  we find

$$\begin{aligned} \lambda_{\langle\tau\rangle}(\sigma) &= 1 - \chi(1 - D_v)\sigma^{-1} + \chi\sigma^{-2} \\ &\quad + O(\sigma^{-2}e^{-1/\sigma^{-1}}). \end{aligned} \quad (22)$$

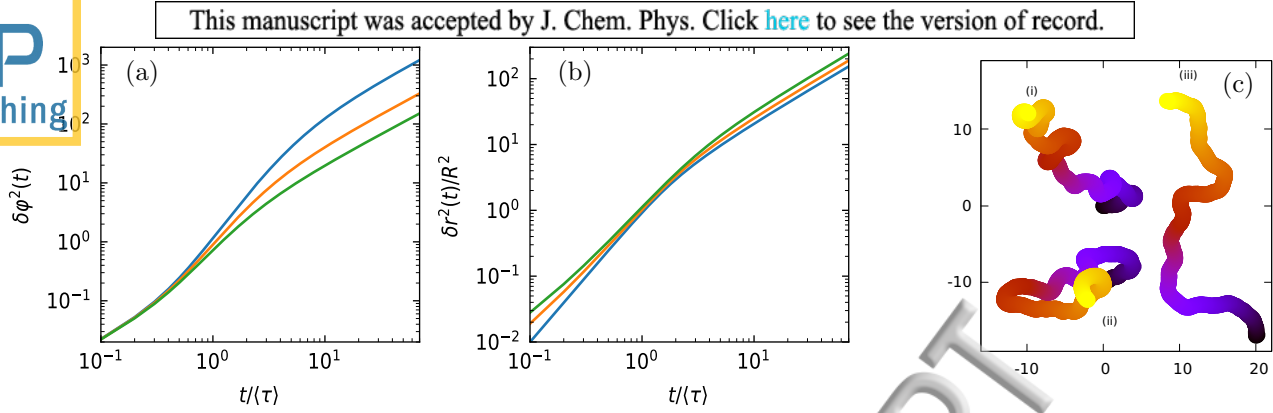


FIG. 2. Influence of the speed fluctuations  $D_v$  on the effective dynamics for strong coupling to the trail  $\chi = 1.8$ . (a,b) Angular mean square displacement  $\delta\varphi^2(t)$  and translational mean square displacement  $\delta r^2(t)/R^2$  as a function of time  $t$  normalized by the mean crossing time  $\langle\tau\rangle$  for three different magnitudes of the speed fluctuations  $D_v/v_0R = 0$  (blue), 0.05 (yellow), 0.1 (green) and a common value of the orientational diffusivity  $D_r^0\langle\tau\rangle = 0.1$ . (c) Sample trajectories  $r(t)$  for the three different  $D_v/v_0R = 0$  (i), 0.05 (ii), and 0.1 (iii) color coded as a function of time for a total duration  $50\langle\tau\rangle$  and  $D_r^0\langle\tau\rangle = 0.01$ . See Sec. C for details on the numerics.

The first three terms are dominant as long as  $e^{-1/\sigma^{-1}} \ll 1$ , *i.e.*, as long as  $\sigma^{-1} \ll 1$ , or upon reinstating units, for times  $t \ll \langle\tau\rangle$ . Then we have

$$|\lambda_{\langle\tau\rangle}(\sigma \rightarrow \infty)|^{-2} \simeq 1 + 2(1 - D_v)\chi\sigma^{-1} - 2\chi(1 + \chi/\chi_c)\sigma^{-2}, \quad (23)$$

and in the time domain

$$\delta\varphi^2(t \rightarrow 0)/2D_r^0 \simeq t + \chi(1 - D_v)t^2 - \frac{1}{3}\chi(1 + \chi/\chi_c)t^3. \quad (24)$$

In other words, the angular mean square displacement starts with the bare diffusivity  $D_r^0$  before the self-interaction becomes visible on times of the order  $1/\chi(1 - D_v)$ .

## B. Long-Time Asymptotics

Expanding  $\lambda_{\langle\tau\rangle}(\sigma)$  in powers of  $\sigma$  we find

$$\lambda_{\langle\tau\rangle}(\sigma) = 1 - \chi/\chi_c + \frac{\chi}{3\chi_c}(1 - D_v)\sigma + O(\sigma^2). \quad (25)$$

This shows that  $\delta\varphi^2(t \rightarrow \infty) = 2D_r t$  will asymptotically always be diffusive with a renormalized diffusivity<sup>38</sup>

$$D_r/D_r^0 = |\lambda_{\langle\tau\rangle}(0)|^{-2} = 1 + \frac{\chi}{\chi_c} \times \frac{2 - \chi/\chi_c}{(1 - \chi/\chi_c)^2} \quad (26)$$

which diverges for  $\chi \rightarrow \chi_c$ .

The validity of the long time asymptotics is bounded by the radius of convergence of the Taylor expansion, Eq. (25). The latter is determined by the location of the pole of  $\lambda_{\langle\tau\rangle}^{-1}(s)$  closest to the origin of the complex plane. In Sec. B we show that Eq. (25) holds for  $|s| < 3(\chi_c/\chi - 1)/\langle\tau\rangle$ , *i.e.*, for times

$$t/\langle\tau\rangle \gg t^* := \frac{\chi/\chi_c}{1 - \chi/\chi_c}. \quad (27)$$

The onset of the asymptotic regime,  $t^*$ , diverges with the rotational diffusivity as  $\chi \rightarrow \chi_c$ .

For  $\chi \rightarrow \chi_c$  we write  $\chi = \chi_c(1 - \delta\chi)$ . Assuming the smallest pole  $\sigma = O(\delta\chi)$  to be confirmed below we expand to lowest order

$$\lambda_{\langle\tau\rangle}(\sigma) = \delta\chi + \frac{1}{3}(1 - D_v)\sigma + O(\delta\chi^2, \sigma^2, \sigma\delta\chi). \quad (28)$$

Close to the critical coupling strength we therefore find

$$|\lambda_{\langle\tau\rangle}(\sigma)|^{-2} \simeq \frac{9}{(1 - D_v)^2\sigma^2} \times \frac{1}{[1 + 3\delta\chi/(1 - D_v)\sigma]^2}, \quad (29)$$

*i.e.*, a superballistic behavior

$$\delta\varphi^2(t) = \frac{3}{2}\chi_c D_r^0 t^3 \quad (30)$$

in a diverging time window  $\langle\tau\rangle \ll t \ll 1/3\delta\chi$ .

## V. THE TRANSLATIONAL MEAN SQUARE DISPLACEMENT

The velocity autocorrelation function  $C(t) := \langle \dot{\mathbf{r}}(t+t') \cdot \dot{\mathbf{r}}(t') \rangle = 2D_v\delta(t) + C_{nn}(t)$  where  $C_{nn}(t) := \langle \hat{\mathbf{n}}(t+t') \cdot \hat{\mathbf{n}}(t') \rangle$  can be determined explicitly with the help of Eq. (18),<sup>39</sup>

$$C_{nn}(t) = \int_{-\infty}^{\infty} d\varphi P(\varphi, t) \cos \varphi = e^{-\delta\varphi^2(t)/2}. \quad (31)$$

The asymptotic translational diffusivity is then given by a Green-Kubo integral

$$D/D^0 = D_r^0 \int_0^{\infty} dt \left[ 2D_v\delta(t) + e^{-\delta\varphi^2(t)/2} \right], \quad (32)$$

where  $D^0 = 1/D_r^0$  is the diffusivity for  $\chi = D_v = 0$ .<sup>39</sup>

The (translational) mean square displacement  $\delta r^2(t) := \langle [\mathbf{r}(t) - \mathbf{r}(0)]^2 \rangle$ ,

$$\delta r^2(t) = 2 \int_0^t du \int_0^u dw C(w) \quad (33)$$

$$= 2D_v t + 2 \int_0^t dw (t-w) e^{-\delta\varphi^2(w)/2} \quad (34)$$

cannot be given in closed form. However, the form of Eq. (33) indicates, that it will be dominated by the small angle behavior,  $\delta\varphi^2(t) < 1$ , of the angular mean square displacement.

In the following we will derive analytic expressions for the diffusivity  $D$  in certain limiting cases.

### A. Short Persistence Regime

For parameters such that  $\delta\varphi^2(\langle\tau\rangle) \gg 1$ , we may use the short time expansion, Eq. (24). With this, the condition reads  $2D_r^0 \gg 1/[1 + \chi(1 - D_v)]$  which shows that this regime applies for small coupling strength  $\chi$  and large intrinsic rotational diffusivity  $D_r^0$ . Given this is fulfilled, we have

$$D/D_0 = D_v/D_0 + D_r^0 \int_0^\infty dt e^{-D_r^0[t + \chi(1 - D_v)t^2]} \quad (35)$$

$$= \sqrt{\pi/\kappa} \operatorname{erfc}(1/\sqrt{\kappa}) e^{1/\kappa} + D_v/D_0 \quad (36)$$

$$= 1 + D_v/D_0 - \kappa/2 + 3\kappa^2/4 + O(\kappa^3), \quad (37)$$

where  $\kappa := 4\chi(1 - D_v)/D_r^0 \ll 1$  is a kind of Peclet number relating the ‘‘convective’’ rate  $\chi$  to the diffusive rate  $D_r^0$ .

### B. Long Persistence Regime

The opposite limit is given by an angular mean square displacement which reaches the value one well into the asymptotic regime,  $\delta\varphi^2(t^*) \ll 1$ . A condition which may be estimated as  $D_r/(1 - \chi/\chi_c) \ll 1$ . Then we may approximate  $\delta\varphi(t) = 2D_r t$  for all relevant times and directly find

$$D/D^0 = D_r^0/D_r, \text{ or, equivalently, } D = 1/D_r. \quad (38)$$

In other words for very persistent trails, *i.e.*, small intrinsic directional noise  $D_r^0$  and/or small coupling strength  $\chi \ll \chi_c$ , the asymptotic translational diffusivity is inversely proportional to the asymptotic rotational diffusivity. Higher order terms are given in Ref. 33.

### C. Critical Regime

Close to the critical coupling strength,  $\chi \rightarrow \chi_c$ , we use Eq. (30), to make the ansatz

$$\delta\varphi^2(t)/2D_r^0 = t\Theta(\langle\tau\rangle - t) + 3\chi_c t^3 \Theta(t - \langle\tau\rangle)/4, \quad (39)$$

patching together the short time, bare diffusion  $2D_r^0 t$ , and the intermediate time, superballistic behavior,  $\propto t^3$ . The asymptotic diffusion is irrelevant here because  $\delta\varphi^2(t) \gg 1$  before it sets in. Using this ansatz in Eq. (32), we find

$$D/D^0 = D_v/D^0 + D_r^0 \int_0^{\langle\tau\rangle} dt e^{-D_r^0 t} + D_r^0 \int_{\langle\tau\rangle}^\infty dt e^{-3D_r^0 \chi_c t^3/4}. \quad (40)$$

The second integral can be expressed in terms of the generalized exponential integral  $E_n(x)$ ,

$$D/D^0 = 1 + D_v/D^0 - e^{-D_r^0 \langle\tau\rangle} + \frac{1}{3} D_r^0 \langle\tau\rangle E_{2/3}(3D_r^0 \langle\tau\rangle/4). \quad (41)$$

Consistent with our assumption  $D_r^0 \langle\tau\rangle \ll 1$  we need to expand this to yield

$$D/D^0 \simeq \Gamma(4/3)(D_r^0 \langle\tau\rangle)^{2/3} - (\sqrt[3]{3/2} \langle\tau\rangle - 1)D_r^0, \quad (42)$$

where  $\Gamma(x)$  is the Euler Gamma-function. Note that for a perfectly persistent organism,  $D_r^0 \rightarrow 0$ , the translational diffusivity will obviously diverge  $D \sim (D_r^0 \langle\tau\rangle)^{-1/3}$ .

## VI. THE EFFECT OF SPEED FLUCTUATIONS

Nonzero speed fluctuations  $D_v > 0$  have multiple effects as can be seen by the examples in Fig. 2. For the angular mean square displacement, the influence lies mostly in the distance to the critical point  $\chi_c$ . At vanishing fluctuations,  $D_v = 0$ , the chosen coupling strength  $\chi = 1.8$  is close to the critical value  $\chi_c = 2$  and the trajectories already begin to violate the assumptions of the derivation by turning quickly. For increasing fluctuations  $D_v$ , the critical value  $\chi_c = 2/(1 - D_v)^2$  shifts to higher values. In effect, both the intermediate regime of the angular mean square displacement as well as the asymptotic diffusivity  $D_r$  decrease and the trajectories become straighter.

For the translational mean square displacement  $\delta r^2(t)$ , the effects are less drastic but can be seen in both the short and the long time limit. For short times, the ballistic regime,  $\delta r^2(t) \propto t^2$  is replaced by diffusive behavior,  $\delta r^2(t) = D_v t$ . At intermediate times, the directed motion prevails if the short time diffusivity is small enough as it has been discussed by Peruani and Morelli<sup>40</sup>. For long times the straighter trails enhance translational diffusivity for increasing fluctuations  $D_v$  but rather mildly so because the differences in  $\delta\varphi^2(t)$  mostly occur at large displacements  $\delta\varphi^2(t) \gg 1$ .

## VII. CONCLUSION

We have started by motivating a model of a self-propelled particle (the microorganism) on a two-dimensional

plane that interacts with its own trail, cf. Eqs (1–3). A simplified version of this model has been introduced by us before.<sup>43</sup> Here we argued that in reality the microorganism will not interact with the trail,  $\tilde{\psi}$ , itself but with its observation of the trail,  $\psi$ . Given that  $\psi$  has well defined edges,  $\Delta R/R \ll 1$ , that the trails are reasonably straight,  $D_r \langle \tau \rangle \ll 1$  and the propulsion speed  $v_0$  is well defined,  $D_v/Rv_0 \ll 1$ , we showed how to decouple the equation for the trail's gradient, Eq. (11), from the equation of motion of the particle, Eqs. (6,7).

Analyzing the effective trail gradient, Eq. (11), we showed that it fails to regress to a zero mean beyond a critical coupling strength

$$\frac{k\chi_c}{\pi v_0^2 R} = \frac{2}{(1 - D_v/v_0 R)^2} \geq 2. \quad (43)$$

However for  $\chi < \chi_c$ , both the effective trail gradient, Eq. (16), as well as the orientation, Eq. (17), turn out to be filtered white noise. The filter function  $\lambda_\tau^{-1}(i\omega)$ , Eq. (14), therefore, is crucial for the dynamics. In essence we derived generalized expressions for the effective angular [Eq. (26)] and translational diffusivity [Eqs. (37, 38, 42)], special cases of which have been presented in Ref. 33.

The effect of the self-interaction becomes apparent on a timescale  $t/\langle \tau \rangle \sim 1/\chi$  which indicates the start of an intermediate regime displaying angular superdiffusion that extends to times  $t/\langle \tau \rangle \sim \chi/\chi_c(1 - \chi/\chi_c)$  beyond which the dynamics is effectively diffusive again. The onset of the asymptotic regime diverges for  $\chi \rightarrow \chi_c$ . The translational dynamics is unaffected by the asymptotic behavior of the angular motion due to the exponential suppression in Eq. (31). Consequently, the translational diffusivity remains finite at the critical coupling  $\chi \rightarrow \chi_c$ , Eq. (42). A detailed analysis of the localized phase  $\chi > \chi_c$  requires a new approach that includes the effect of frequent self-crossings neglected here and is left to future work.

We note that trail-mediated self-interactions have been recently studied in the context of aggregation and collective motion of myxobacteria, where experiments revealed that the collective motion of the wild type of *Myxococcus Xanthus* is organized in a network structure made out of trails, in contrast with signaling-deficient mutants of the species.<sup>41,42</sup> These results have been rationalized theoretically using a phenomenological agent-based model with implemented trail-following rules.<sup>43</sup> It will be interesting to extend our study to mechanistically study the case of myxobacteria by incorporating both positional and orientational coupling to the trail and making predictions about the collective behaviour as has been performed for the case of *Pseudomonas aeruginosa*.<sup>33,34</sup> We also note that the self-trapping reported here is somehow reminiscent of the milling patterns that appear in a similar cognitive flocking model of animals.<sup>44</sup>

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## Appendix A: Solving Eq. (11)

To this end we start from yet another representation of Eq. (11),

$$\nabla_\perp \psi(t) = \sqrt{2D_r^0} \int_0^\tau du (Z_t - Z_{t-u}) + \chi \int_0^\tau du \int_{t-u}^t dw \nabla_\perp \psi(w). \quad (A1)$$

Employing the Fourier representation, we find for the first term

$$\int_0^\tau du (Z_t - Z_{t-u}) = \int_{-\infty}^\infty d\omega \tilde{Z}_\omega e^{i\omega t} \int_0^\tau du (1 - e^{-i\omega u}) \quad (A2)$$

and for the second term

$$\int_0^\tau du \int_{t-u}^t dw \nabla_\perp \psi(w) = \int_{-\infty}^\infty d\omega \int_0^\tau du \int_{t-u}^t dw \widetilde{\nabla_\perp \psi}(\omega) e^{i\omega w}. \quad (A3)$$

Upon performing the  $w$ -integral this yields

$$\int_0^\tau du \int_{t-u}^t dw \nabla_\perp \psi(w) = \int_{-\infty}^\infty d\omega \frac{\widetilde{\nabla_\perp \psi}(\omega)}{i\omega} e^{i\omega t} \int_0^\tau du (1 - e^{-i\omega u}). \quad (A4)$$

Together with

$$\int_0^\tau du (1 - e^{-i\omega u}) = \tau + \frac{1}{i\omega} (e^{-i\omega\tau} - 1) \quad (A5)$$

this implies that Eq. (11) in the Fourier domain reads

$$\widetilde{\nabla_\perp \psi}(\omega) = \frac{1 - \lambda_\tau(i\omega)}{\chi} \left( \chi \widetilde{\nabla_\perp \psi}(\omega) + \sqrt{2D_r^0} i\omega \tilde{Z}_\omega \right) \quad (A6)$$

which can easily be solved for  $\widetilde{\nabla_\perp \psi}(\omega)$  to yield Eq. (16).

## Appendix B: Poles near the Origin

For  $\chi < \chi_c$  we can rule out a pole at the origin. Then we may rewrite the condition  $\lambda_{\langle \tau \rangle}(s) = 0$  as

$$s^2 - \chi \langle \tau \rangle s - \chi (e^{-s\langle \tau \rangle} - 1) = 0, \quad (B1)$$

and to third order in  $s$

$$\frac{1}{6}\chi\langle\tau\rangle^3s^3 + (1 - \chi\langle\tau\rangle^2/2)s^2 = 0. \quad (\text{B2})$$

This is solved by  $s^* = -3(\chi_c/\chi - 1)/\langle\tau\rangle$ .

### Appendix C: Details of the Numerics

We determined  $\delta\varphi^2(t)$  using a numerical inverse Laplace transformation of Eq. (21) by the method of Abate and Valkó<sup>45</sup> implemented in Python with the help of the multi-precision library `mpmath`.<sup>46</sup> The translational mean square displacement  $\delta r^2(t)$ , we determined by numerical integration of Eq. (33) using SciPy's<sup>47</sup> `quad` method.

For the trajectories we used SciPy's inverse fast Fourier transform `ifft` to determine  $\varphi(t)$  from Eq. (17) and then Euler integration of Eq. (6).

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