

shake your hips

an active particle with a fluctuating propulsion force

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preprint: <https://arxiv.org/abs/2102.11758>

Applied Math Seminar
Courant Institute, NYU (online) 5 March 2021



Langevin equations for the 2D active Brownian particle (ABP) model:

$$\begin{aligned}\dot{\mathbf{x}} &= (U_{\text{swim}} + \sqrt{2D_{\parallel}} \dot{w}_{\parallel}) \mathbf{p}_{\parallel}(\phi) + \sqrt{2D_{\perp}} \mathbf{p}_{\perp}(\phi) \dot{w}_{\perp}, \\ \dot{\phi} &= \Omega + \sqrt{2D_{\text{r}}} \dot{w}_{\text{r}}.\end{aligned}$$

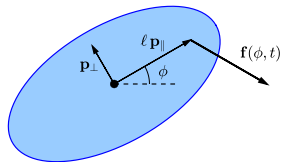
- translational noises $\sqrt{2D_{\parallel}} \dot{w}_{\parallel}$ and $\sqrt{2D_{\perp}} \dot{w}_{\perp}$ are respectively along (\mathbf{p}_{\parallel}) and perpendicular (\mathbf{p}_{\perp}) to the direction of swimming
- the rotational noise $\sqrt{2D_{\text{r}}} \dot{w}_{\text{r}}$ affects the swimming direction
- $w_i(t)$ are independent standard Wiener processes.

[Peruani & Morelli (2007); van Teeffelen & Löwen (2008); Baskaran & Marchetti (2008); Romanczuk & Schimansky-Geier (2011); Romanczuk *et al.* (2012); Kurzthaler *et al.* (2016); Kurzthaler & Franosch (2017); Ai *et al.* (2013); Solon *et al.* (2015); Zöttl & Stark (2016); Wagner *et al.* (2017); Redner *et al.* (2013); Stenhammar *et al.* (2014); Chen & Thiffeault (2021)]

A particle with a fluctuating force



How do we derive the ABP model?
Easy enough (it seems).



Particle subjected to a fluctuating force (e.g. flagellum)

$$\mathbf{f}(\phi, t) = (F_{\parallel} + \sqrt{2E_{\parallel}} \dot{w}_{\parallel}) \mathbf{p}_{\parallel}(\phi) + (F_{\perp} + \sqrt{2E_{\perp}} \dot{w}_{\perp}) \mathbf{p}_{\perp}(\phi)$$

acting at the point $\ell \mathbf{p}_{\parallel}$ with respect to the **center of reaction** [Happel & Brenner (1983)] satisfies

$$m \dot{\mathbf{u}} = -\mathbb{K} \cdot \mathbf{u} + \mathbf{f}, \quad I \dot{\omega} = -\sigma_{\tau} \omega + \tau,$$

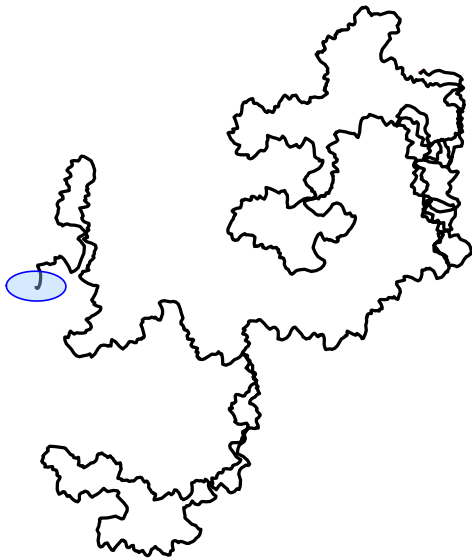
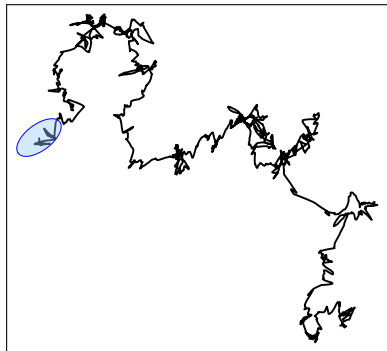
where $\mathbb{K} = \mathbb{Q} \cdot \text{diag}(\sigma_{\parallel}, \sigma_{\perp}) \cdot \mathbb{Q}^{\top}$ is the **resistance matrix**, with $\mathbb{Q}(\phi)$ a 2×2 rotation matrix.

The force exerts a **torque** $\tau(t) = \ell (F_{\perp} + \sqrt{2E_{\perp}} \dot{w}_{\perp})$.

A sample trajectory



*standard ABP with
independent rotational noise:*



$U_{\text{swim}} = 1$, $\Omega = 0$, $m = I = .05$,
 $\sigma_{\parallel} = 0.5$, $\sigma_{\perp} = E_{\perp} = \sigma_r = \ell = 1$,
 $E_{\parallel} = 0$.

play movie

Particle with a fluctuating force: standard SDE form

We rewrite the system in the standard SDE form **drift**+noise:

$$\frac{d\hat{\mathbf{x}}}{dt} = \hat{\mathbf{u}}, \quad \frac{d\hat{\mathbf{u}}}{dt} = \hat{\mathbb{B}} \cdot (\hat{\mathbf{U}} - \hat{\mathbf{u}}) + \hat{\Sigma}(\hat{\mathbf{x}}) \cdot \dot{\mathbf{w}}$$

where

$$\hat{\mathbf{x}} = (\mathbf{x}, \phi), \quad \hat{\mathbf{u}} = (\mathbf{u}, \omega), \quad \dot{\mathbf{w}} = (\dot{w}_{\parallel}, \dot{w}_{\perp})$$

$$\hat{\mathbb{B}} = \text{diag}(\mathbb{K}/m, \sigma_{\text{r}}/I), \quad \hat{\mathbf{U}} = (\mathbf{U}_{\text{swim}}, \Omega) = (\mathbb{K}^{-1} \cdot \mathbf{F}, \ell F_{\perp}/\sigma_{\text{r}}),$$

$$\hat{\Sigma} = \begin{pmatrix} (\sqrt{2E_{\parallel}}/m) \mathbf{p}_{\parallel} & (\sqrt{2E_{\perp}}/m) \mathbf{p}_{\perp} \\ 0 & \sqrt{2E_{\perp}} \ell/I \end{pmatrix}.$$

The third components of vectors and matrices **wearing a hat** pertain to angular quantities. (“grand”)

Overdamped limit (dubious)



Typically, in the **overdamped limit** (small mass, or large drag) the term $d\hat{\mathbf{u}}/dt$ is neglected,

$$\frac{d\hat{\mathbf{x}}}{dt} = \hat{\mathbf{u}}, \quad \cancel{\frac{d\hat{\mathbf{u}}}{dt}} = \hat{\mathbb{B}} \cdot (\hat{\mathbf{U}} - \hat{\mathbf{u}}) + \hat{\Sigma} \cdot \dot{\mathbf{w}}$$

resulting in

$$\frac{d\hat{\mathbf{x}}}{dt} = \hat{\mathbf{U}} + (\hat{\mathbb{B}}^{-1} \cdot \hat{\Sigma}) \cdot \dot{\mathbf{w}}.$$

Close to the standard ABP model, except that **here there are only two** $(\dot{w}_{\parallel}, \dot{w}_{\perp})$ rather than **three** $(\dot{w}_{\parallel}, \dot{w}_{\perp}, \dot{w}_r)$ independent noises:

The rotational noise is **correlated to the translational noise**, since the former is caused by the torque of the latter. **We will see the consequences of this correlation later.**

Overdamped limit (better)



But first note that taking the overdamped limit in this way is suspicious, since the original noise is additive:

$$\frac{d\hat{\mathbf{x}}}{dt} = \hat{\mathbf{u}}, \quad \frac{d\hat{\mathbf{u}}}{dt} = \hat{\mathbb{B}} \cdot (\hat{\mathbf{U}} - \hat{\mathbf{u}}) + \hat{\Sigma}(\hat{\mathbf{x}}) \cdot \dot{\mathbf{w}}$$

in the sense that there is no **Itô vs Stratonovich ambiguity** in interpretation, whereas

$$\frac{d\hat{\mathbf{x}}}{dt} = \hat{\mathbf{U}} + \hat{\mathbb{B}}^{-1} \cdot \hat{\Sigma}(\hat{\mathbf{x}}) \cdot \dot{\mathbf{w}}.$$

has a multiplicative noise.

[Kupferman *et al.* (2004); Lau & Lubensky (2007); Farago (2017)]

Care is thus required in taking the overdamped limit...

$$\frac{d\hat{\mathbf{x}}}{dt} = \hat{\mathbf{u}}, \quad \frac{d\hat{\mathbf{u}}}{dt} = \hat{\mathbb{B}} \cdot (\hat{\mathbf{U}} - \hat{\mathbf{u}}) + \hat{\Sigma}(\hat{\mathbf{x}}) \cdot \dot{\mathbf{w}}$$

Safer approach: we take the overdamped limit of the **Fokker–Planck equation** for the probability density $p(\hat{\mathbf{x}}, \hat{\mathbf{u}}, t)$ corresponding to our SDE [Kupferman *et al.* (2004); Bo & Celani (2013); Pavliotis (2014); Hottovy *et al.* (2014)]:

$$\varepsilon^2 \partial_t p + \varepsilon \nabla_{\hat{\mathbf{x}}} \cdot (\hat{\mathbf{u}} p) + \varepsilon \nabla_{\hat{\mathbf{u}}} \cdot (\hat{\mathbb{B}} \cdot \hat{\mathbf{U}} p) = \mathcal{L}p$$

where $\varepsilon \rightarrow 0$ is the **overdamped limit**, and

$$\mathcal{L}p := \nabla_{\hat{\mathbf{u}}} \cdot (\hat{\mathbb{B}} \cdot \hat{\mathbf{u}} p) + \nabla_{\hat{\mathbf{u}}} \otimes \nabla_{\hat{\mathbf{u}}} : (\hat{\mathbb{E}} p)$$

with $\hat{\mathbb{E}} := \frac{1}{2} \hat{\Sigma} \cdot \hat{\Sigma}^\top$.

Now we proceed order-by-order with an expansion $p = p_0 + \varepsilon p_1 + \dots$.

At leading order we have

$$\mathcal{L}p_0 = 0, \quad \text{with solution} \quad p_0 = P(\hat{\mathbf{x}}, t) \varphi(\hat{\mathbf{x}}, \hat{\mathbf{u}})$$

where P is yet to be determined and $\varphi(\hat{\mathbf{x}}, \hat{\mathbf{u}})$ is the invariant density for an Ornstein–Uhlenbeck process [Risken (1996)]:

$$\varphi = (2\pi)^{-3} (\det \hat{\mathbf{A}})^{-1/2} \exp\left(-\frac{1}{2} \hat{\mathbf{u}} \cdot \hat{\mathbf{A}}^{-1} \cdot \hat{\mathbf{u}}\right).$$

Here the symmetric positive-definite matrix $\hat{\mathbf{A}}(\hat{\mathbf{x}})$ is the unique solution to the [continuous-time Lyapunov](#) (Sylvester) equation

$$\boxed{\hat{\mathbf{B}} \cdot \hat{\mathbf{A}} + \hat{\mathbf{A}} \cdot \hat{\mathbf{B}}^T = 2\hat{\mathbf{E}}.}$$

For us $\hat{\mathbf{B}} = \hat{\mathbf{B}}^T$. When $\hat{\mathbf{B}}$ commutes with $\hat{\mathbf{E}}$, as occurs for [thermal fluctuations](#), the solution is $\hat{\mathbf{A}} = \hat{\mathbf{E}} \cdot \hat{\mathbf{B}}^{-1}$; **this is not the case here.**

$$\hat{\mathbf{B}} \cdot \hat{\mathbf{A}} + \hat{\mathbf{A}} \cdot \hat{\mathbf{B}}^T = 2\hat{\mathbf{E}}$$

The solution of this matrix problem is implemented as `LyapunovSolve` in Mathematica, `sylvester` in Matlab, and `solve_continuous_lyapunov` in Python.

We find

$$\hat{\mathbf{A}} = \hat{\mathbf{Q}} \cdot \begin{pmatrix} \frac{E_{\parallel}}{m\sigma_{\parallel}} & 0 & 0 \\ 0 & \frac{E_{\perp}}{m\sigma_{\perp}} & \frac{2E_{\perp}\ell}{m\sigma_r + I\sigma_{\perp}} \\ 0 & \frac{2E_{\perp}\ell}{m\sigma_r + I\sigma_{\perp}} & \frac{E_{\perp}\ell^2}{I\sigma_r} \end{pmatrix} \cdot \hat{\mathbf{Q}}^T$$

where $\hat{\mathbf{Q}}(\phi) = \text{diag}(\mathbf{Q}, 1)$ is a 3×3 rotation matrix about the third axis.

$$\mathcal{L}p_1 = \nabla_{\hat{\mathbf{x}}} \cdot (\hat{\mathbf{u}} \varphi P) - \hat{\mathbf{u}} \cdot \hat{\mathbb{A}}^{-1} \cdot \hat{\mathbb{B}} \cdot \hat{\mathbb{U}} \varphi P.$$

The solution can be written in two pieces $p_1 = p_1^{(1)} + p_1^{(2)}$, with

$$p_1^{(1)} = (\nabla_{\hat{\mathbf{x}}} P - \hat{\mathbb{U}} \cdot \hat{\mathbb{B}}^\top \cdot \hat{\mathbb{A}}^{-1} P) \cdot \hat{\chi}^{(1)}$$

$$p_1^{(2)} = -\frac{1}{2} P \nabla_{\hat{\mathbf{x}}} \hat{\mathbb{A}}^{-1} : \hat{\chi}^{(2)},$$

where $\hat{\chi}^{(1)}$ and $\hat{\chi}^{(2)}$ satisfy

$$\mathcal{L}\hat{\chi}^{(1)} = \hat{\mathbf{u}} \varphi, \quad \mathcal{L}\hat{\chi}^{(2)} = \hat{\mathbf{u}} \hat{\mathbf{u}} \hat{\mathbf{u}} \varphi.$$

It is easy to solve for $\hat{\chi}^{(1)} = -\hat{\mathbb{A}} \cdot \hat{\mathbb{B}}^{-\top} \cdot \hat{\mathbb{A}}^{-1} \cdot \hat{\mathbf{u}} \varphi$;

$\hat{\chi}^{(2)}$ is harder to solve for in general.

However, we shall not need its precise expression in our derivation.

Order ε^2 (the last one)



$$\mathcal{L}p_2 = \nabla_{\hat{\mathbf{x}}} \cdot (\hat{\mathbf{u}} p_1) + \nabla_{\hat{\mathbf{u}}} \cdot (\hat{\mathbb{B}} \cdot \hat{\mathbf{U}} p_1) + \partial_t p_0,$$

to which we need only apply a **solvability condition** by integrating over $\hat{\mathbf{u}}$ (denoted by angle brackets):

$$\partial_t P = -\nabla_{\hat{\mathbf{x}}} \cdot \langle \hat{\mathbf{u}} p_1 \rangle.$$

There is a trick based on the **adjoint of \mathcal{L}** that can be used to evaluate the averages

$$\begin{aligned}\langle \hat{\mathbf{u}} \hat{\chi}^{(1)} \rangle &= -\hat{\mathbb{B}}^{-1} \cdot \langle \hat{\mathbf{u}} \hat{\mathbf{u}} \varphi \rangle = -\hat{\mathbb{B}}^{-1} \cdot \hat{\mathbb{A}} \\ \langle \hat{\mathbf{u}} \hat{\chi}^{(2)} \rangle &= -\hat{\mathbb{B}}^{-1} \cdot \langle \hat{\mathbf{u}} \hat{\mathbf{u}} \hat{\mathbf{u}} \hat{\mathbf{u}} \varphi \rangle\end{aligned}$$

where the fourth moment for the Gaussian φ

$$\langle \hat{\mathbf{u}} \hat{\mathbf{u}} \hat{\mathbf{u}} \hat{\mathbf{u}} \varphi \rangle_{ijkl} = \hat{A}_{ij} \hat{A}_{kl} + \hat{A}_{ik} \hat{A}_{jl} + \hat{A}_{il} \hat{A}_{jk}.$$

We have thus evaluated the required average $\langle \hat{\mathbf{u}} \hat{\chi}^{(2)} \rangle$ **without needing to solve for $\hat{\chi}^{(2)}$** .

The overdamped Fokker–Planck equation



After a lengthy but straightforward calculation we find

$$\partial_t P + \nabla_{\mathbf{x}} \cdot ((\mathbf{U}_{\text{swim}} + \mathbf{V}_{\text{noise}})P) + \partial_\phi(\Omega P) = \nabla_{\hat{\mathbf{x}}} \otimes \nabla_{\hat{\mathbf{x}}} : (\hat{\mathbb{D}} P)$$

where the **noise-induced drift** [Grassia *et al.* (1995); Lau & Lubensky (2007); Hottovy *et al.* (2012a,b, 2014); Volpe & Wehr (2016); Farago (2017)] is

$$\mathbf{V}_{\text{noise}} = \frac{2\ell E_\perp (\sigma_\parallel^{-1} - \sigma_\perp^{-1})}{\sigma_r (1 + I\sigma_\perp/m\sigma_r)} \mathbf{p}_\parallel$$

and the translational-rotational **grand diffusion tensor** is

$$\hat{\mathbb{D}} = \hat{\mathbb{Q}} \cdot \begin{pmatrix} D_\parallel & 0 & 0 \\ 0 & D_\perp & \sqrt{D_\perp D_r} \\ 0 & \sqrt{D_\perp D_r} & D_r \end{pmatrix} \cdot \hat{\mathbb{Q}}^\top$$

with $D_\parallel = E_\parallel/\sigma_\parallel^2$, $D_\perp = E_\perp/\sigma_\perp^2$, and $D_r = E_\perp \ell^2/\sigma_r^2$.



$$\mathbf{V}_{\text{noise}} = \frac{2\ell E_{\perp}(\sigma_{\parallel}^{-1} - \sigma_{\perp}^{-1})}{\sigma_r(1 + I\sigma_{\perp}/m\sigma_r)} \mathbf{p}_{\parallel}$$

$\mathbf{V}_{\text{noise}} \neq \mathbf{0}$ implies that **the particle appears to swim at a constant speed**, even for $\mathbf{U}_{\text{swim}} = \mathbf{0}$ (no net propulsion), and even for **small mass**.

$\mathbf{V}_{\text{noise}}$ is only present when the fluctuating force **exerts a torque**; it is an inertial effect that **vanishes for isotropic particles** ($\sigma_{\parallel} = \sigma_{\perp}$).

Péclet numbers based on the **advective time** $a/|\mathbf{V}_{\text{noise}}|$ and **diffusive times** a^2/D_{\perp} and $1/D_r$, with a the particle size:

$$\text{Pe}_{\perp} = \frac{|\mathbf{V}_{\text{noise}}|a}{D_{\perp}} \sim \frac{\ell}{a}, \quad \text{Pe}_r = \frac{|\mathbf{V}_{\text{noise}}|}{D_r a} \sim \frac{a}{\ell}.$$

Pe_{\perp} is not large, but also not necessarily small. Pe_r is a dimensionless correlation length that **diverges as $\ell \rightarrow 0$** , since the **rotational diffusivity D_r then vanishes**.



There are two new effects compared to standard ABP:

- The noise-induced drift $\mathbf{V}_{\text{noise}}$ (for $\sigma_{\parallel} \neq \sigma_{\perp}$);
- The coupling terms $\sqrt{D_{\perp} D_{\text{r}}}$ in the grand diffusion tensor $\hat{\mathbb{D}}$.

One way to see their repercussion is to compute the **long-time effective diffusivity** of the active particle.

Recall the overdamped Fokker–Planck equation for $P(\hat{\mathbf{x}}, t)$ is

$$\partial_t P + W_i \partial_{x_i} P + \Omega \partial_{\phi} P = \partial_{x_i} \partial_{x_j} (D_{ij} P) + 2 \partial_{x_i} \partial_{\phi} (\hat{D}_{i3} P) + \partial_{\phi}^2 (D_{\text{r}} P)$$

where $\mathbf{W} = \mathbf{U}_{\text{swim}} + \mathbf{V}_{\text{noise}} = W \mathbf{p}_{\parallel}$ is the total drift, and indices are summed over 1, 2.



To find the effective diffusivity, we focus on **large scales** $\delta^{-1} \sim \ell^{-1}$ and **long times** δ^{-2} , with δ a **small parameter**.

We let

$$\partial_t \rightarrow \partial_t + \delta^2 \partial_T, \quad \partial_{\mathbf{x}} \rightarrow \partial_{\mathbf{x}} + \delta \partial_{\mathbf{X}}$$

and expand

$$P = \mathcal{P}(\mathbf{X}, T) + \delta P_1(\phi; \mathbf{X}, T) + \delta^2 P_2(\phi; \mathbf{X}, T) + \dots,$$

where we anticipated the functional dependencies to abridge the derivation.

Just kidding! I won't subject you to another asymptotic expansion.



Cut to the chase: at order δ^2 we have the solvability condition

$$\begin{aligned}\partial_T \mathcal{P} &= \langle W_i (W_j - 2\partial_\phi \widehat{D}_{j3}) / D_r + D_{ij} \rangle \partial_{X_i} \partial_{X_j} \mathcal{P} \\ &=: D_{\text{eff}} \nabla_{\mathbf{X}}^2 \mathcal{P} \quad (\text{isotropic})\end{aligned}$$

where angle brackets are repurposed for angular averaging, and the **effective diffusivity** is (recall: $W = U_{\text{swim}} + V_{\text{noise}}$)

$$\begin{aligned}D_{\text{eff}} &= \frac{1}{2}(D_{\parallel} + D_{\perp}) + \widetilde{D} \\ \widetilde{D} &:= \frac{W D_r}{2(D_r^2 + \Omega^2)} \left(W + \frac{2E_{\perp} \ell}{\sigma_{\perp} \sigma_r} \right).\end{aligned}$$

Compare to \widetilde{D} for the standard ABP model,

$$\frac{U_{\text{swim}}^2 D_r}{2(D_r^2 + \Omega^2)}$$

[Howse *et al.* (2007); Peruani & Morelli (2007); Lindner & Nicola (2008); Golestanian (2009); Fodor *et al.* (2016); Caprini & Marconi (2021)].

Effective diffusivity for wiggler (non-swimmer)



The new diffusivity \tilde{D} combines contributions from the **propulsion** U_{swim} , the **noise-induced drift** V_{noise} , and from the coupling terms in \hat{D} .

To best see these new effects, we set $U_{\text{swim}} = \Omega = D_{\parallel} = 0$: the particle is “**shaking its hips**” but would be a non-swimmer if not for the noise-induced drift.

A **wiggler**? But maybe the field has enough cute names.

[Similar to a “treadmiller” or reciprocal swimmer that doesn’t strictly swim, but only diffuses; see Crowdy & Or (2010); Lauga (2011); Obuse & Thiffeault (2012).)]

For the wiggler:

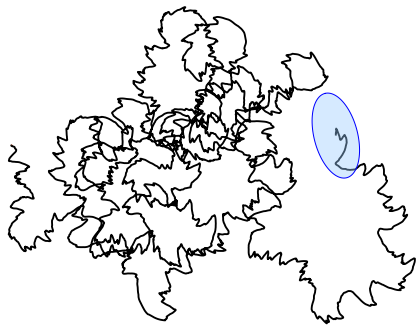
$$\tilde{D}_0 = \frac{2D_{\perp}(1 + I\sigma_{\parallel}/m\sigma_r)}{(1 + I\sigma_{\perp}/m\sigma_r)^2} \frac{\sigma_{\perp}}{\sigma_{\parallel}} \left(\frac{\sigma_{\perp}}{\sigma_{\parallel}} - 1 \right).$$

Negative for particles with $\sigma_{\perp} < \sigma_{\parallel}$ (oblate), so that it hinders diffusion.

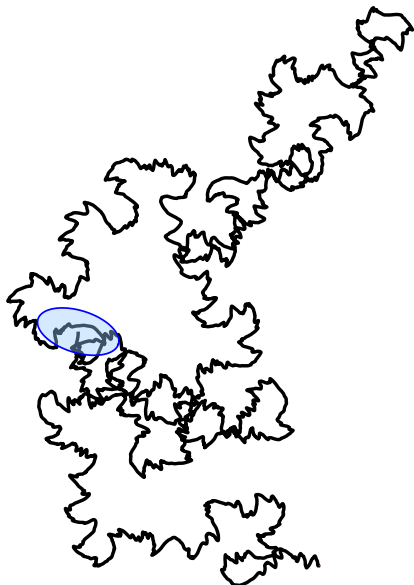
Prolate wiggler trajectories



A prolate wiggler ($\sigma_{\parallel} < \sigma_{\perp}$) has an **enhanced** diffusivity compared to a passive particle. [Possibly related to an effect observed by Lauga (2011)].



play movie



Wiggler ($\mathbf{U}_{\text{swim}} = \Omega = 0$); $m = I = .05$, $\sigma_{\parallel} = 0.5$, $\sigma_{\perp} = E_{\perp} = \sigma_r = \ell = 1$, $E_{\parallel} = 0$.

Oblate wiggler trajectories



An oblate wiggler ($\sigma_{\parallel} > \sigma_{\perp}$) has a **reduced** diffusivity compared to a passive particle.

Similar reduced diffusivity observed for ABP with $\Omega \neq 0$, due to “over-rotating.” [See also the flipping rod of Takagi *et al.* (2013)].

play movie



Wiggler ($\mathbf{U}_{\text{swim}} = \Omega = 0$); $m = I = .05$, $\sigma_{\parallel} = 2$, $\sigma_{\perp} = E_{\perp} = \sigma_r = \ell = 1$, $E_{\parallel} = 0$.

D_{eff} for the wiggler: The neutral wiggler



With $U_{\text{swim}} = D_{\parallel} = 0$, the effective diffusivity is

$$D_{\text{eff}0} = \tilde{D}_0 + \frac{1}{2}D_{\perp} = D_{\perp} \frac{(\sigma_{\parallel} - 2\sigma_{\perp} - I\sigma_{\parallel}\sigma_{\perp}/m\sigma_r)^2}{2\sigma_{\parallel}^2(1 + I\sigma_{\perp}/m\sigma_r)^2} \geq 0.$$

$D_{\text{eff}0}$ attains a minimum of zero for

$$\sigma_{\perp} = \sigma_{\parallel}/(2 + I\sigma_{\parallel}/m\sigma_r) < \sigma_{\parallel} \quad (\text{oblate}).$$

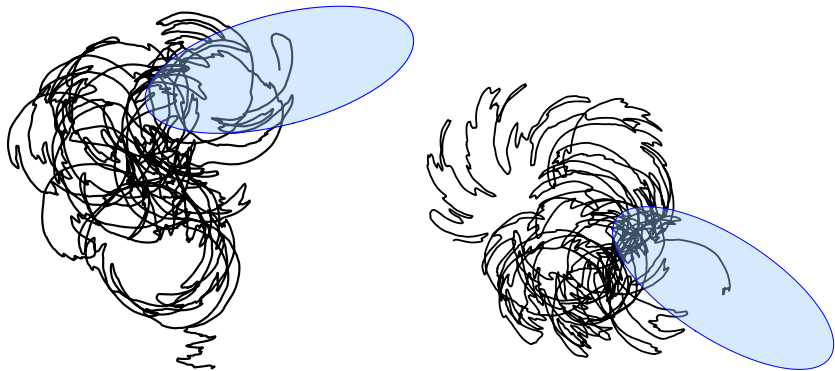
A particle satisfying this relation is a **neutral active particle** that can only diffuse via D_{\parallel} and thermal noise.

Note that swimmers are rarely oblate, but perhaps synthetic active particles can be manufactured this way.

The neutral wiggler



Indeed, we can see that a neutral wiggler is going nowhere, though it may “diffuse” on very long timescales:



Wiggler ($U_{\text{swim}} = \Omega = 0$).

Parameter values: $m = I = .05$, $\sigma_{\parallel} = 0.5$, $\sigma_{\perp} = 0.2$, $E_{\perp} = \sigma_{\tau} = \ell = 1$, $E_{\parallel} = 0$.

play movie



Another striking feature of \tilde{D}_0 is that it is independent of ℓ , the position where the torque is applied:

$$\tilde{D}_0 = \frac{2D_{\perp}(1 + I\sigma_{\parallel}/m\sigma_r)}{(1 + I\sigma_{\perp}/m\sigma_r)^2} \frac{\sigma_{\perp}}{\sigma_{\parallel}} \left(\frac{\sigma_{\perp}}{\sigma_{\parallel}} - 1 \right).$$

This is a paradox: for $\ell = 0$, we have $\mathbf{V}_{\text{noise}} = 0$ and $\hat{D}_{i3} = 0$, so **none of the effects mentioned here occur!**

The resolution is that there is a **transient** of duration

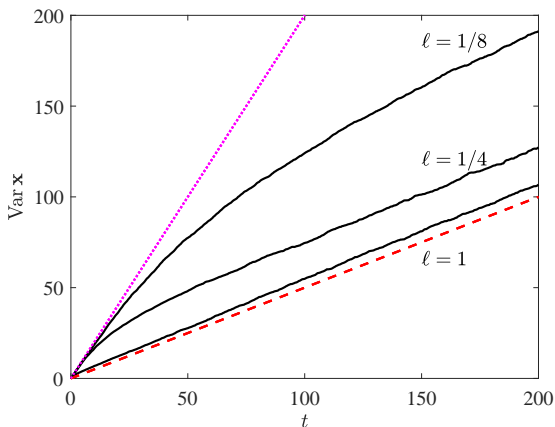
$$D_r^{-1} = \sigma_r^2/E_{\perp}\ell^2 \sim \delta^{-2}$$

before the long-time form of D_{eff} applies, and this transient becomes **infinite as $\ell \rightarrow 0$** .

D_{eff} for the wiggler as $\ell \rightarrow 0$



This transient can be seen in the simulations of the full inertial equations:



5 000 oblate wigglers ($\mathbf{U}_{\text{swim}} = \Omega = 0$). **Upper dotted line:** $4 \times \frac{1}{2}(D_{\parallel} + D_{\perp})t$; **Bottom dashed line:** $4D_{\text{eff}}t$. As ℓ becomes smaller, there is a longer transient before the behavior begins to follow D_{eff} . Parameter values: $m = I = .05$, $\sigma_{\parallel} = 2$, $E_{\perp} = \sigma_{\perp} = \sigma_r = 1$, $E_{\parallel} = 0$.



$$\tilde{D}_0 = \frac{2D_{\perp}(1 + I\sigma_{\parallel}/m\sigma_r)}{(1 + I\sigma_{\perp}/m\sigma_r)^2} \frac{\sigma_{\perp}}{\sigma_{\parallel}} \left(\frac{\sigma_{\perp}}{\sigma_{\parallel}} - 1 \right).$$

It is important to note that the ratio \tilde{D}_0/D_{\perp} is **rarely negligible**: all the dimensionless ratios appearing on the right are typically of **order one**.

The **transient time scale** D_r^{-1} can be estimated by a^2/D_{\perp} , where a is the particle size; if D_r^{-1} is very long, then D_{\perp} was likely negligible to begin with.



So why haven't these types of corrections been observed?

- Many authors **simulate the ABP model directly**, since the inertial equations are expensive to solve due to the small step size required, in which case the new effects are ruled out.
- **Particle anisotropy** is seldom considered.
- Experimentally, diffusivities are measured directly from the distributions of displacements, and so any connection between the rotational and translational diffusivities is typically lost. One approach might be to **measure the covariance matrix $\hat{\mathbf{A}}$ directly**.
- Harder to observe if the swimmers are **relatively fast**.



- Arbitrary **three-dimensional** active particles, with the force not necessarily applied on an axis of symmetry. (Mostly done; quite messy. Is this why is the **third Euler angle** is rarely if ever considered?)
- There are several other possible extensions, such as the inclusion of **multiple forces and torques** acting on the body.
- Consequences to
 - swim pressure [Takatori *et al.* (2014); Takatori & Brady (2014)]
 - run-and-tumble dynamics [Subramanian & Koch (2009); Cates & Tailleur (2013)]
 - non-Newtonian swimming [Datt & Elfring (2019)]
 - velocity-dependent friction [Erdmann *et al.* (2000)]
 - and particle interactions [Fodor *et al.* (2016); Marath & Wettlaufer (2019)]?
- See preprint <https://arxiv.org/abs/2102.11758>.

- Ai, B., Chen, Q., He, Y., Li, F., & Zheng, W. (2013). *Phys. Rev. E*, **88**, 062129.
- Baskaran, A. & Marchetti, M. (2008). *Phys. Rev. E*, **77**, 011920.
- Bo, S. & Celani, A. (2013). *Phys. Rev. E*, **88** (6).
- Caprini, L. & Marconi, U. M. B. (2021). *The Journal of Chemical Physics*, **154** (2), 024902.
- Cates, M. E. & Tailleur, J. (2013). *Europhys. Lett.* **101**, 20010.
- Chen, H. & Thiffeault, J.-L. (2021). *J. Fluid Mech.* . <http://arxiv.org/abs/2006.07714>, in press.
- Crowdy, D. G. & Or, Y. (2010). *Phys. Rev. E*, **81**, 036313.
- Datt, C. & Elfring, G. J. (2019). *Phys. Rev. Lett.* **123** (15).
- Erdmann, U., Ebeling, W., Schimansky-Geier, L., & Schweitzer, F. (2000). *Eur. Phys. J. B*, **15** (1), 105–113.
- Farago, O. (2017). *Phys. Rev. E*, **96** (4).
- Fodor, E., Nardini, C., Cates, M. E., Tailleur, J., Visco, P., & van Wijland, F. (2016). *Phys. Rev. Lett.* **117** (3).
- Golestanian, R. (2009). *Physical Review Letters*, **102** (18).
- Grassia, P. S., Hinch, E. J., & Nitsche, L. C. (1995). *J. Fluid Mech.* **282**, 373–403.
- Happel, J. & Brenner, H. (1983). *Low Reynolds number hydrodynamics*. The Hague, Netherlands: Martinus Nijhoff (Kluwer).



- Hottovy, S., McDaniel, A., Volpe, G., & Wehr, J. (2014). *Comm. Math. Phys.* **336** (3), 1259–1283.
- Hottovy, S., Volpe, G., & Wehr, J. (2012a). *J. Stat. Phys.* **146** (4), 762–773.
- Hottovy, S., Volpe, G., & Wehr, J. (2012b). *Europhys. Lett.* **99**, 60002.
- Howse, J. R., Jones, R. A. L., Ryan, A. J., Gough, T., Vafabakhsh, R., & Golestanian, R. (2007). *Physical Review Letters*, **99** (4).
- Kupferman, R., Pavliotis, G. A., & Stuart, A. M. (2004). *Phys. Rev. E*, **70** (3).
- Kurzthaler, C. & Franosch, T. (2017). *Soft Matter*, **13**, 6396–6406.
- Kurzthaler, C., Leitmann, S., & Franosch, T. (2016). *Sci. Rep.* **6**, 36702.
- Lau, A. W. C. & Lubensky, T. C. (2007). *Phys. Rev. E*, **76**, 0111123.
- Lauga, E. (2011). *Phys. Rev. Lett.* **106** (17).
- Lindner, B. & Nicola, E. M. (2008). *The European Physical Journal Special Topics*, **157** (1), 43–52.
- Marath, N. K. & Wettlaufer, J. S. (2019). *J. Chem. Phys.* **151** (2), 024107.
- Obuse, K. & Thiffeault, J.-L. (2012). In: *IMA Volume on Natural Locomotion in Fluids and on Surfaces: Swimming, Flying, and Sliding*, (Childress, S., Hosoi, A., Schultz, W. W., & Wang, J., eds) The IMA Volumes in Mathematics and its Applications pp. 197–206. Springer New York.

- Pavliotis, G. A. (2014). *Stochastic Processes and Applications*. Berlin: Springer.
- Peruani, F. & Morelli, L. G. (2007). *Phys. Rev. Lett.* **99** (1).
- Redner, G. S., Hagan, M. F., & Baskaran, A. (2013). *Phys. Rev. Lett.* **110**, 055701.
- Risken, H. (1996). *The Fokker–Planck Equation: Methods of Solution and Applications*. Berlin: Springer, second edition.
- Romanczuk, P., Bär, M., Ebeling, W., Lindner, B., & Schimansky-Geier, L. (2012). *The European Physical Journal Special Topics*, **202** (1), 1–162.
- Romanczuk, P. & Schimansky-Geier, L. (2011). *Phys. Rev. Lett.* **106** (23).
- Solon, A. P., Fily, Y., Baskaran, A., Cates, M. E., Kafri, Y., Kardar, M., & Tailleur, J. (2015). *Nat. Phys.* **11**, 673–678.
- Stenhammar, J., Marenduzzo, D., Allen, R., & Cates, M. E. (2014). *Soft Matter*, **10**, 1489–1499.
- Subramanian, G. & Koch, D. L. (2009). *J. Fluid Mech.* **632**, 359–400.
- Takagi, D., Braunschweig, A. B., Zhang, J., & Shelley, M. J. (2013). *Phys. Rev. Lett.* **110** (3).
- Takatori, S. C. & Brady, J. F. (2014). *Soft Matter*, **10** (47), 9433–9445.
- Takatori, S. C., Yan, W., & Brady, J. F. (2014). *Phys. Rev. Lett.* **113**, 028103.
- van Teeffelen, S. & Löwen, H. (2008). *Phys. Rev. E*, **78**, 020101.
- Volpe, G. & Wehr, J. (2016). *Reports on Progress in Physics*, **79** (5), 053901.
- Wagner, C., Hagan, M. F., & Baskaran, A. (2017). *J. Stat. Mech.: Theory Exp.*, 043203.
- Zöttl, A. & Stark, H. (2016). *J. Phys.: Condens. Matter*, **28**, 253001.