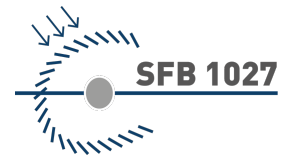




**Saarland  
University**



**ZBP**

## **Non-Markovian and Collective Search Strategies**

H. Rieger

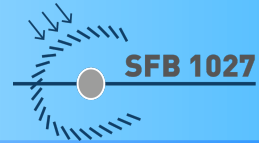
*Center for Biophysics & Physics Department  
Saarland University, Saarbrücken, Germany*



# Overview: The Target Problem in Nature



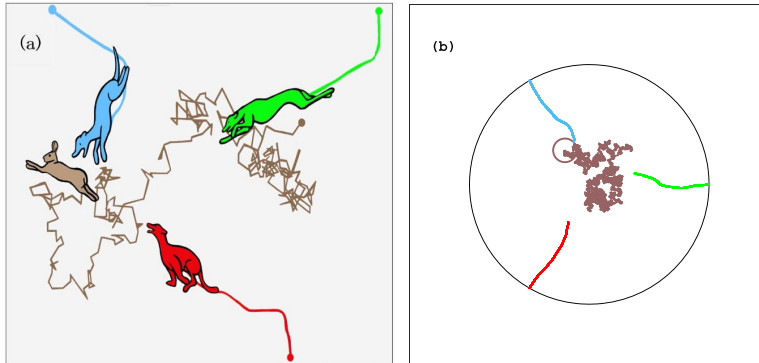
# The “target problem” in Nature



- Single searcher (stochastic), single target (immobile or stochastic) – typical FPT problem
- Group search: many searchers (stochastic), single target – independent / collective
- Group hunting: many searchers, single target – both with visibility
- Evasion strategies (predator-prey): single searcher, many targets – both with visibility
- Foraging: many searcher (communicating), many targets (immobile)



Hunters see target:



$$\frac{dX}{dt} = \sqrt{2D}\xi(t); \quad \frac{dY_n}{dt} = v_0 \frac{X - Y_n}{\|X - Y_n\|},$$

[Bernardi et al, PRL 128, 040601 (2022)]

+ Target sees hunter:

$$\frac{dX}{dt} = \sqrt{2D}\xi(t) + E, \quad E = \frac{v_c}{N} \sum_{n=1}^N g(r_n) \frac{X - Y_n}{\|X - Y_n\|}.$$

[Meng et al, NJP 25, 023033 (2023)]

Chasing a faster prey:

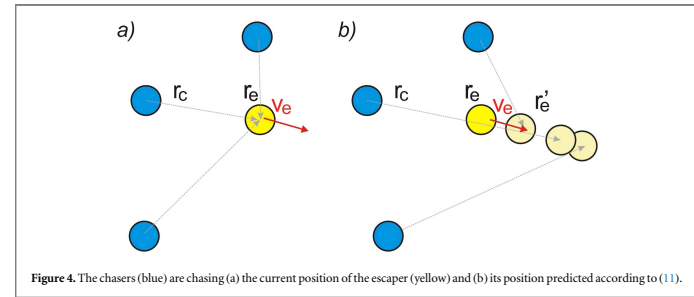


Figure 4. The chasers (blue) are chasing (a) the current position of the escaper (yellow) and (b) its position predicted according to (11).

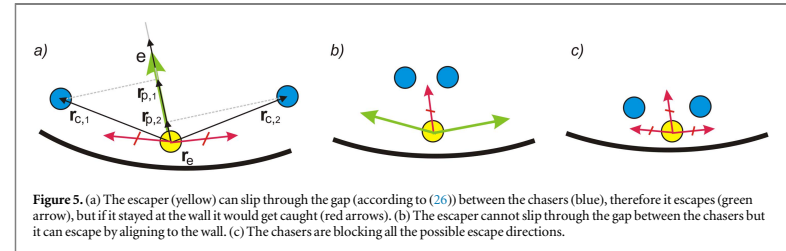


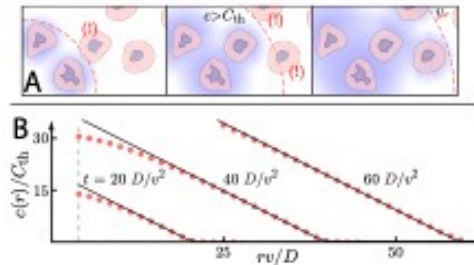
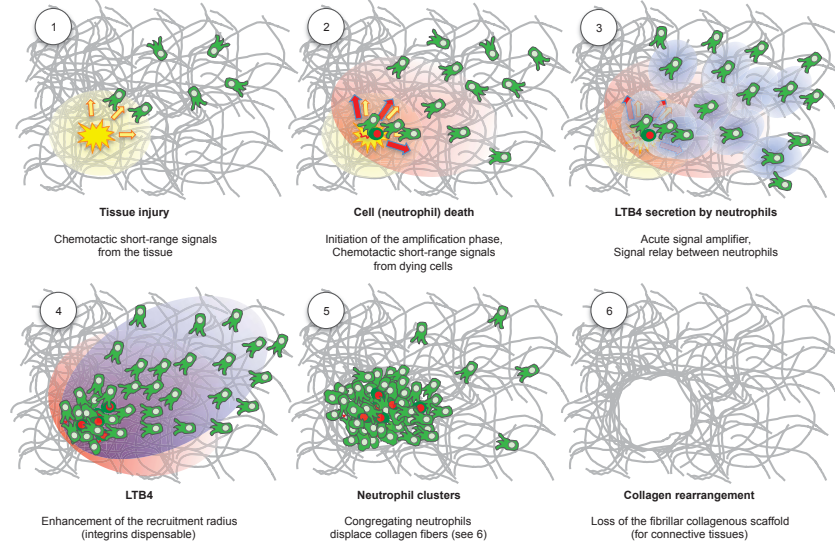
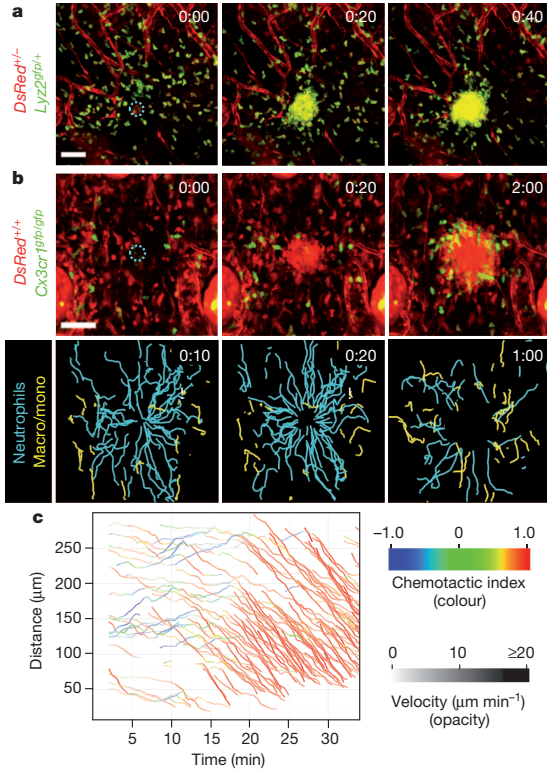
Figure 5. (a) The escaper (yellow) can slip through the gap (according to (26)) between the chasers (blue), therefore it escapes (green arrow), but if it stayed at the wall it would get caught (red arrows). (b) The escaper cannot slip through the gap between the chasers but it can escape by aligning to the wall. (c) The chasers are blocking all the possible escape directions.

etc.

[Janosov et al, NJP 19, 053003 (2017)]



# Neutrophil Swarming: Signaling Relay

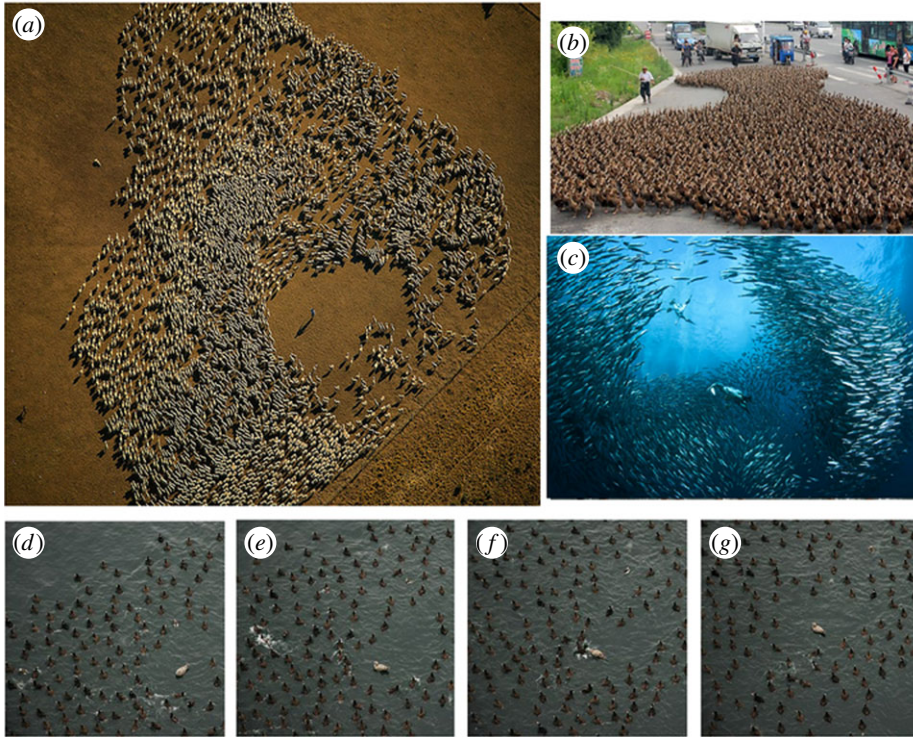


Models:

$$\frac{\partial c}{\partial t} = D \nabla^2 c + \rho \delta(z) \Theta[c - C_{th}]$$



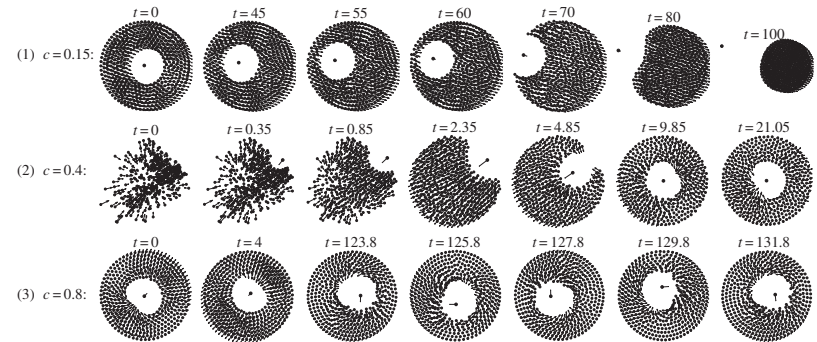
# Evasion strategies (predator-swarm interaction)



Model:

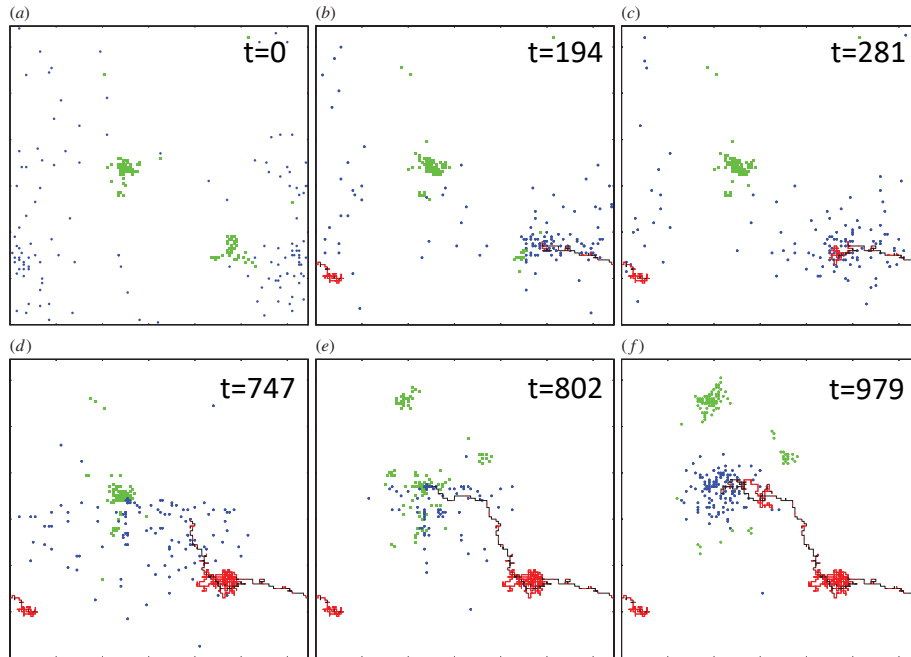
$$\frac{dx_j}{dt} = \frac{1}{N} \sum_{k=1, k \neq j}^N \left( \frac{x_j - x_k}{|x_j - x_k|^2} - a(x_j - x_k) \right) + b \frac{x_j - z}{|x_j - z|^2}$$

$$\frac{dz}{dt} = \frac{c}{N} \sum_{k=1}^N \frac{x_k - z}{|x_k - z|^p}$$





# Collective Foraging (by sharing information)



foragers: blue; targets: green; example trajectory: red

Continuum model::

$$\dot{\mathbf{r}}_i(t) = B_g \nabla g(\mathbf{r}_i) + B_C \nabla S(\mathbf{r}_i) + \eta_i(t),$$

$g(\mathbf{r})$  environmental quality function

$$S(\mathbf{r}_i) = \sum_{j=1, j \neq i}^N A(g(\mathbf{r}_j)) \frac{\exp\left(-\frac{(\mathbf{r}_i - \mathbf{r}_j)^2}{2\sigma^2}\right)}{2\pi\sigma^2}$$

$$A(g(\mathbf{r})) = \Theta(g(\mathbf{r}) - \bar{\kappa})$$

-> Application to Mongolian Gazelles

[Martinez-Garcia et al, PRL 110, 248106 (2013)]

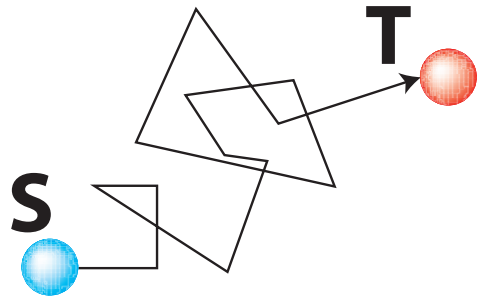


# Non-Markovian Search Strategies

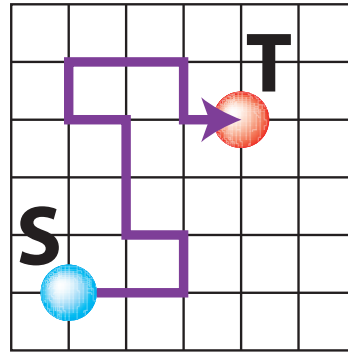




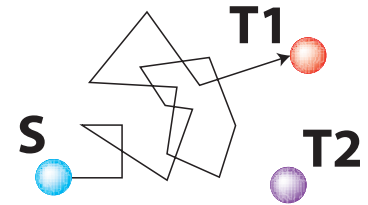
# First passage problems



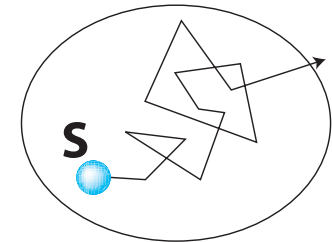
Scheme of a generic first-passage problem



Scheme of a discrete first-passage problem



Scheme of a two target first-passage problem



Scheme of a first-exit problem

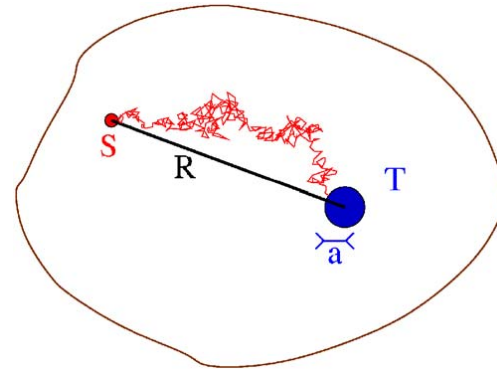
FPT( $t$ ) = probability density for the first-passage time, i.e the first time the random walker hits a target (start at position  $r_s$ , target at position  $r_t$ )



$$1d \quad \langle \mathbf{T}(\mathbf{r}_S) \rangle \sim \frac{L^2}{D}$$

$$2d \quad \langle \mathbf{T}(\mathbf{r}_S) \rangle = \frac{A}{2\pi D} \ln \frac{R}{a}$$

$$3d \quad \langle \mathbf{T}(\mathbf{r}_S) \rangle = \frac{V}{4\pi D} \left( \frac{1}{a} - \frac{1}{R} \right)$$



L, A, V system size (in 1,2,3d)

R initial searcher-target distance

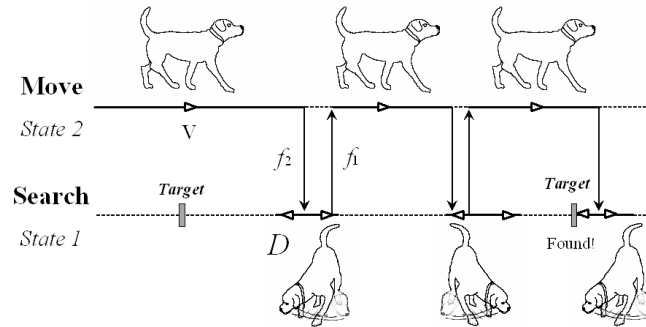
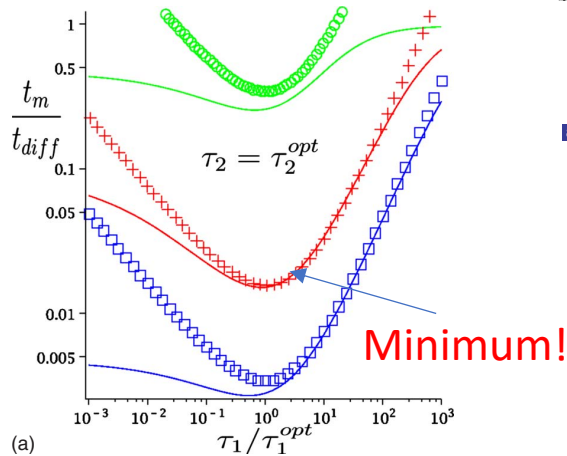
a target size

D diffusion constant



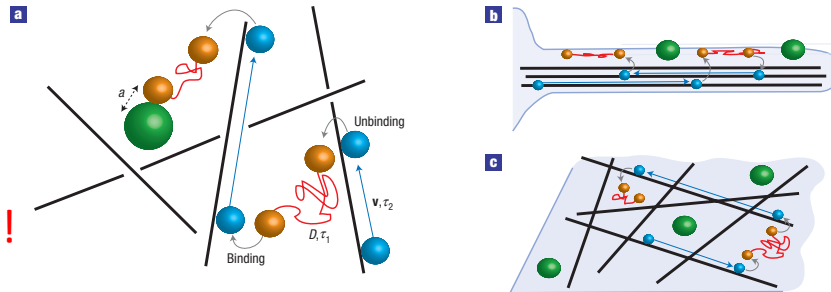
A **search strategy** is simply one **parameter set** for the of a stochastic process / random walk under consideration

Example:  
**Intermittent search**



Walker / searcher alternates stochastically between ballistic and diffusive behavior

[Bénichou et al, PRL 2005]



[Loverdo et al, Nat.Phys. 2008]



## Example: Persistent Walk

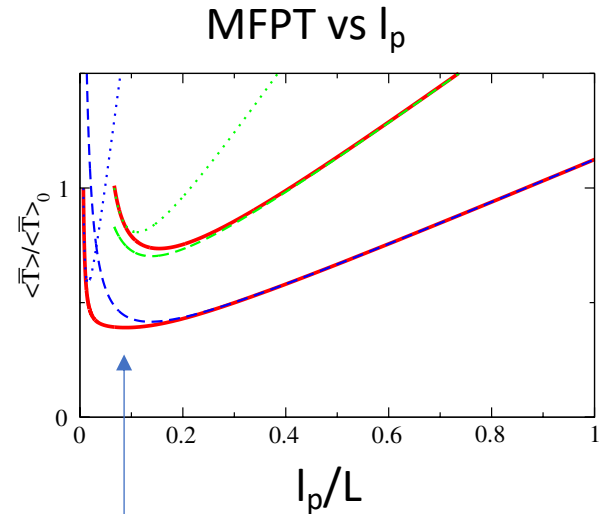
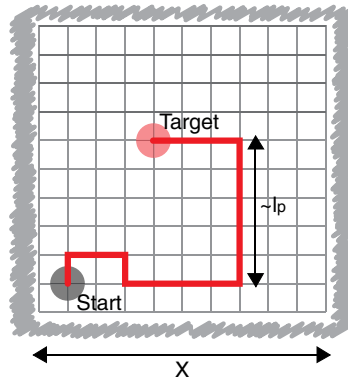
Probability

$$p_1 \text{ forward} = p_3 + \varepsilon$$

$$p_2 \text{ backward} = p_3 - \delta \quad (\delta=0)$$

$p_3$  orthogonal

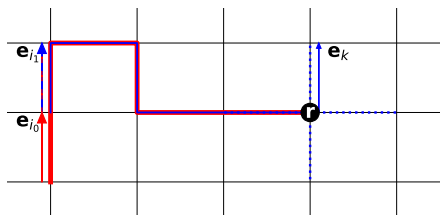
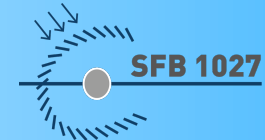
$$\Rightarrow \text{persistence length } l_p \sim 1/(1 - \varepsilon)$$



Minimum!



# Non-Markovian random walks with n-step memory



Conditional transition probabilities:  $p(\mathbf{e}_k | \mathbf{e}_{i_0}, \dots, \mathbf{e}_{i_{n-1}})$

$T_n(\mathbf{r}, \mathbf{r}_T; \mathbf{e}_{i_0}, \dots, \mathbf{e}_{i_{n-1}})$  = average **first passage time** to reach the target at position  $\mathbf{r}_T$  with **n last directions**  $\{\mathbf{e}_{i_0}, \dots, \mathbf{e}_{i_{n-1}}\}$

Backward equation for  $T_n$ :  $T_n(\mathbf{r}, \mathbf{r}_T; \mathbf{e}_{i_0}, \dots, \mathbf{e}_{i_{n-1}}) = 1 + \sum_k p(\mathbf{e}_k | \mathbf{e}_{i_0}, \dots, \mathbf{e}_{i_{n-1}}) T_n(\mathbf{r} + \mathbf{e}_k, \mathbf{r}_T; \mathbf{e}_{i_1}, \dots, \mathbf{e}_{i_{n-1}}, \mathbf{e}_k)$

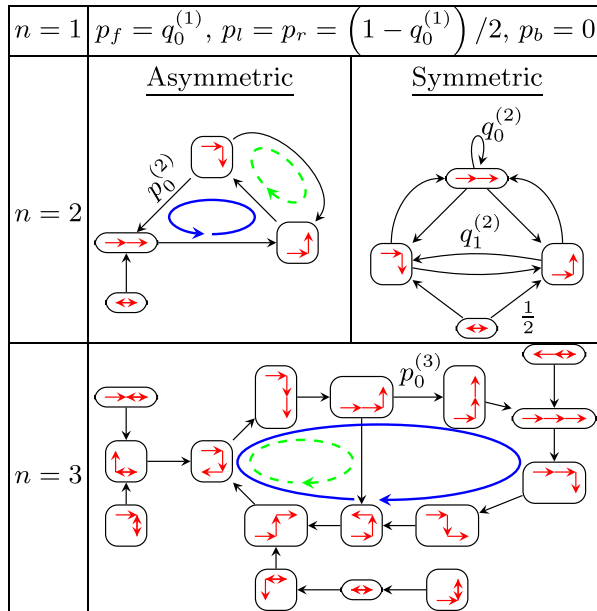
Solution:  $\tilde{t}_{n\alpha}(\mathbf{q}, \mathbf{r}_T) = T_n(\mathbf{q}, \mathbf{r}_T; s_{n\alpha})$

$$\tilde{\mathbf{t}}_n(\mathbf{q}, \mathbf{r}_T) = V[\delta(\mathbf{q}) - e^{-i\mathbf{q}\cdot\mathbf{r}_T}][\mathbb{I} - \mathbf{P}_n \mathbf{E}_n(\mathbf{q})]^{-1} \mathbf{u}_n.$$

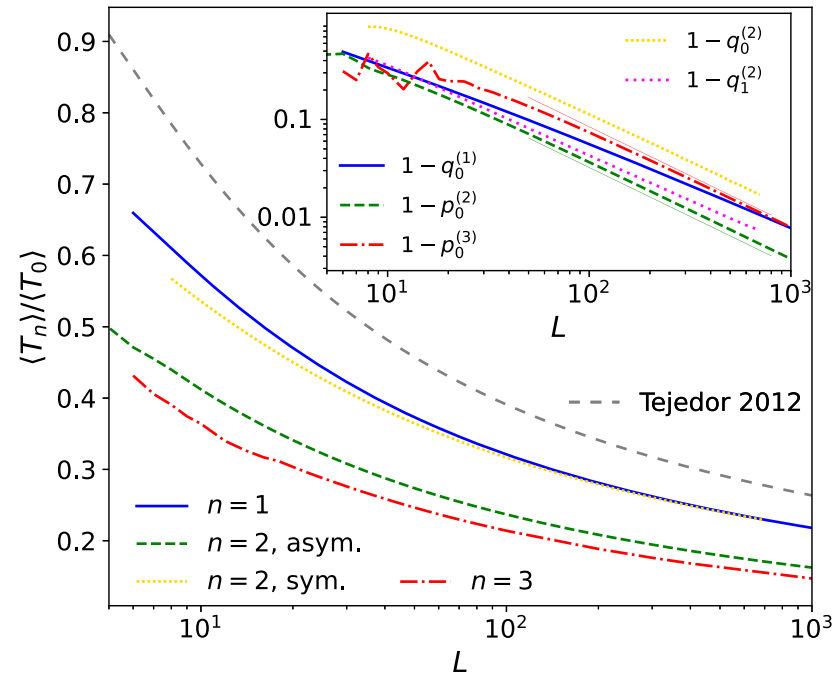
$$\langle \mathbf{t}_n \rangle = \sum_{\mathbf{q} \neq 0} [\mathbb{I} - \mathbf{P}_n \mathbf{E}_n(\mathbf{q})]^{-1} \mathbf{u}_n.$$



# Optimal search strategies with n-step memory



Optimal search strategies on a 2d square lattice for  $n = 1, 2, 3$



The corresponding MFPT normalized by the MFPT for a blind random walk



Philosophy:

try to avoid sites already visited!

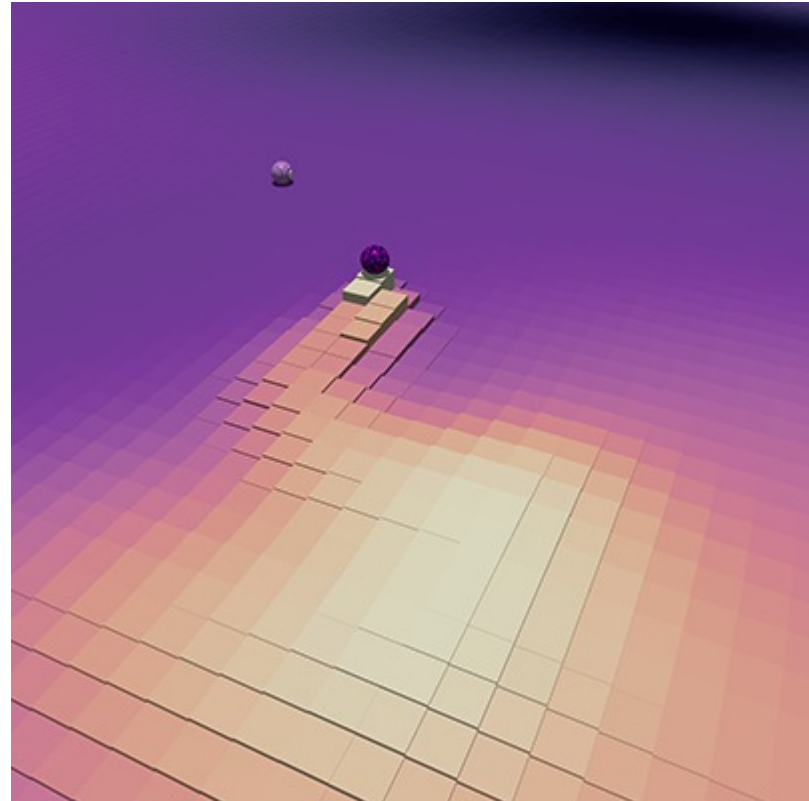
Searcher releases chemo-repulsive  
diffusive cue  $c_i$

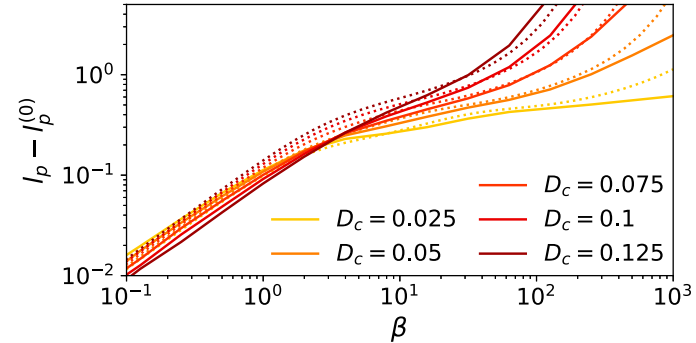
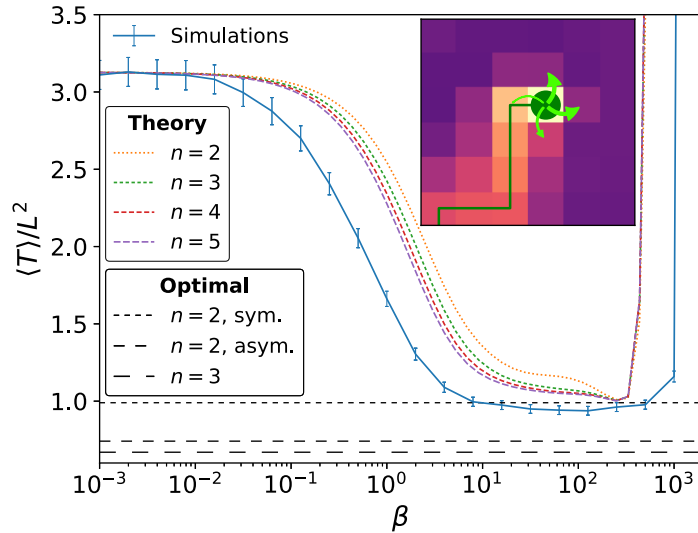
Transition probabilities:

$$p_{i \rightarrow j} = \left[ 1 + \sum_{k \neq j} \exp[-\beta(c_k - c_j)] \right]^{-1}$$

$\beta \rightarrow 0$ : conventional random walk

$\beta \rightarrow \infty$ : jump to site with lowest  $c_i$





Persistence length of the auto-chemotactic searcher as function of  $\beta$  and

MFPT of the auto-chemotactic searcher as function of  $\beta$  and comparison with prediction for n-step memory

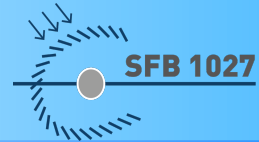




# **Collective Search: Chemotactic Walker**



# N searcher / M targets



Consider confined 2d space, area A:

N independent, non-communicating random walkers, 1 target:

$$\text{FPT}_1(t) \sim e^{-t/\tau} \Rightarrow \text{MFPT}_1 \sim \tau \Rightarrow \text{MFPT}_N \sim \tau/N$$

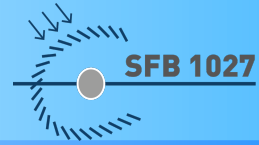
1 random walker, M randomly distributed targets:

$$\text{MFPT}_{\text{first target}} \sim 1/M^\beta, \text{ with } \beta \sim 1.$$

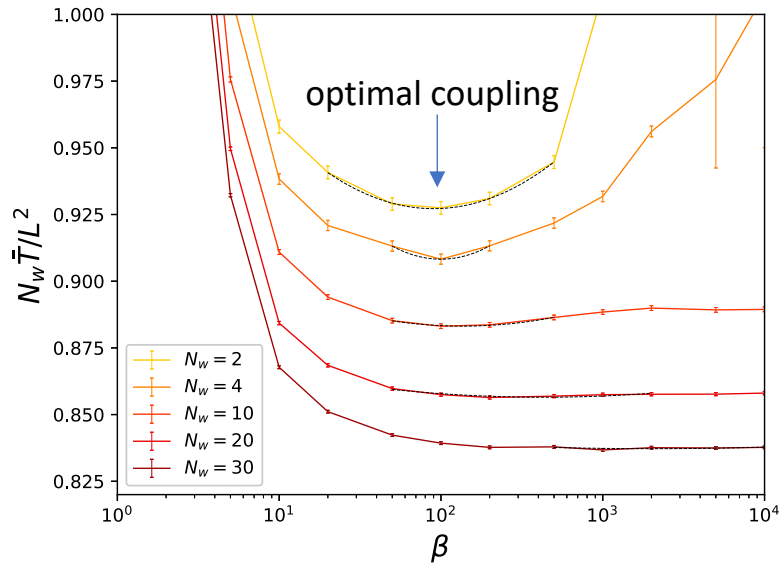
$$\text{MFPT}_{\text{all targets}} \sim \text{cover time}(A) \text{ for } M/A \rightarrow 1.$$



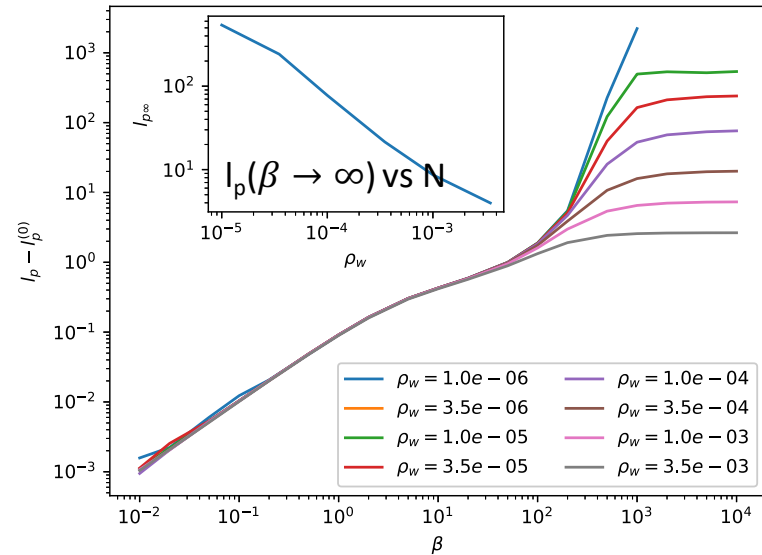
# N chemotactic searchers, 1 target



Optimal coupling  $\beta$  to chemotactic field  $c$



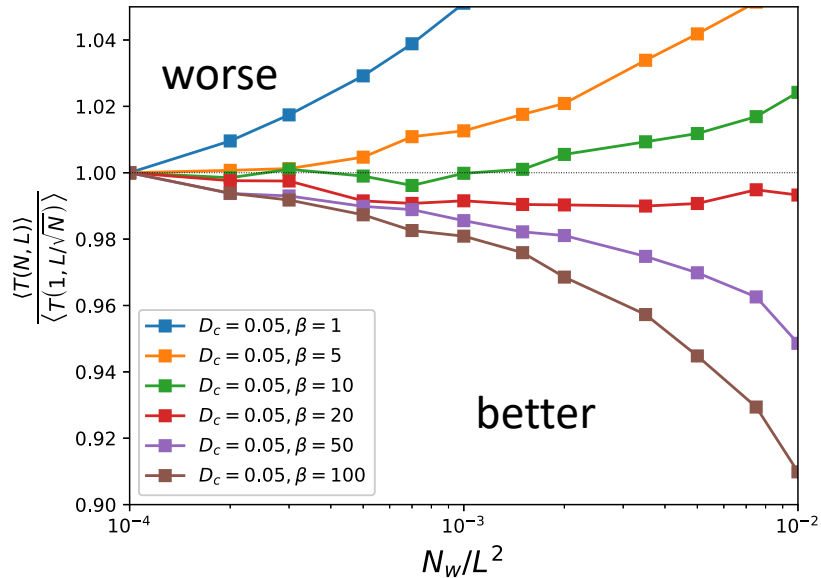
Persistence length vs. coupling  $\beta$



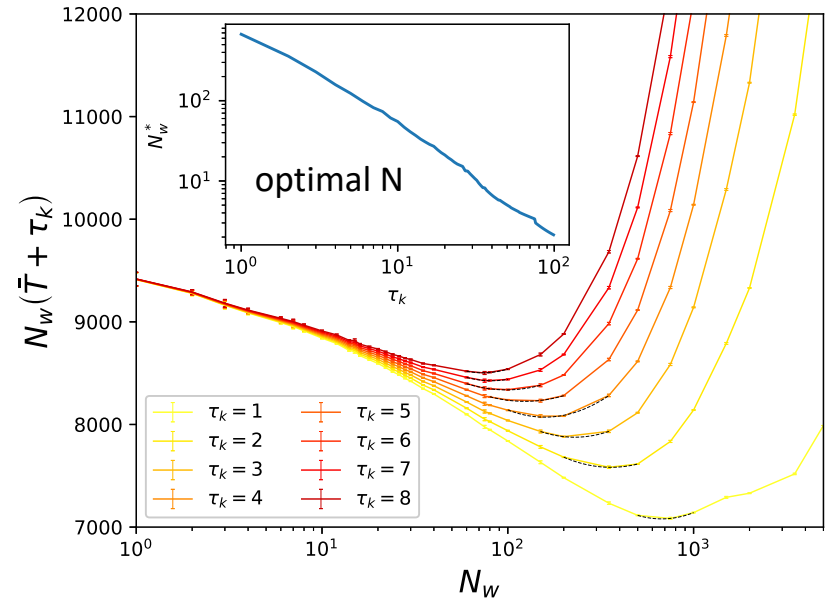


# N chemotactic searchers, 1 target

Compare MFPT( $N, L^2$ ) (N searcher in area  $L^2$ )  
with MFPT( $1, L^2/N$ ) (1 searcher in area  $L^2/N$ )



Cost for N-walker search:  
 $N * \text{MFPT} + N * \tau_k$ ,  $\tau_k = \text{cost for 1 searcher}$





# Optimal Searcher Number in a Costly Search

Total search cost:

$$\mathcal{K} = J_T \bar{T} + J_N \bar{\mathcal{T}} + K_N \bar{N}$$

$\bar{T}$  mean search time (MFPT)

$\bar{\mathcal{T}}$  sum of the times spent by all searchers

$\bar{N}$  number of searcher created

$J_T$  target cost rate

$J_N$  searcher support cost

$K_N$  searcher creation cost

$$\gamma = J_N/J_T, \quad \beta = K_N/J_T$$

searchers introduced at  $t_1, t_2, \dots, t_n, \dots$

Independent searcher result:

$$\mathcal{K} = \sum_{n=1}^{\infty} \left[ (1 + n\gamma) \int_{t_n}^{t_{n+1}} S_n(t) dt + \kappa S_n(t_n) \right]$$

$$S_n(t) = \prod_{k=1}^n s(t - t_k)$$

$s(t)$  survival probability  $s(t) = \int_t^{\infty} \rho(t) dt$

$\rho(t)$  FPT distribution

Exponential survival probability

$N_{\text{opt}}$  searcher must be introduced all at once

Algebraic survival probability

$N_{\text{opt}}$  searcher must be introduced in fixed time intervals



# **Collective Search: Chemotactic ABPs**



# N **active** Brownian particles (**ABPs**), M targets

## **ABPs:**

Disk-like particles with radius  $a$

Motion with velocity  $v_0$  along  $\mathbf{e}_i = \begin{pmatrix} \cos \varphi_i \\ \sin \varphi_i \end{pmatrix}$

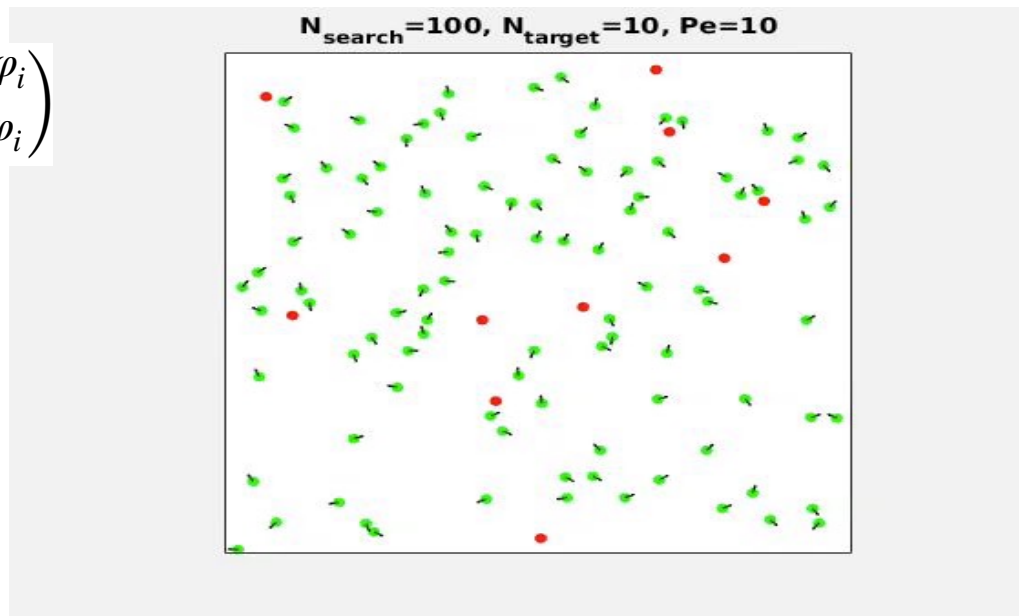
Position:  $\dot{\mathbf{r}}_i(t) = V_0 \mathbf{e}_i(t) + \frac{1}{\gamma_t} \sum_{j \neq i} \mathbf{f}_{ji}$

excluded volume

Orientation:

$$\dot{\varphi}_i(t) = \sqrt{2D_r} \eta_i(t)$$

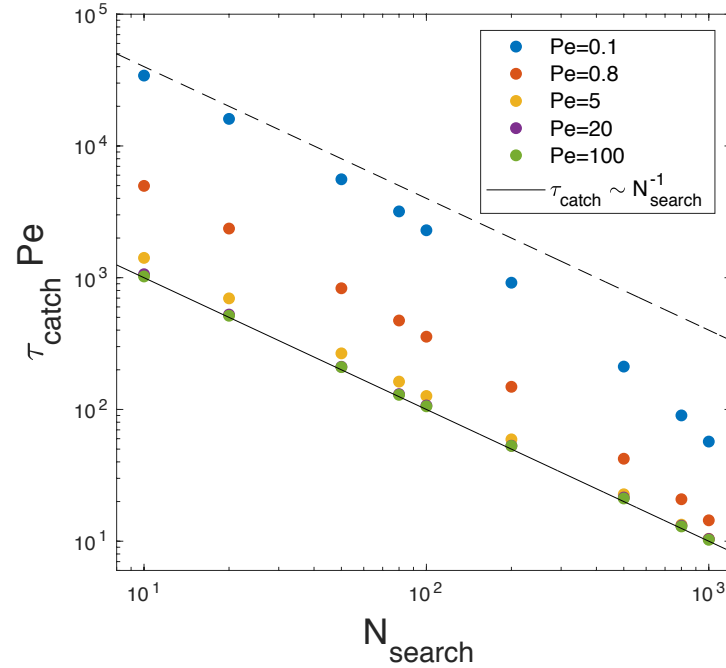
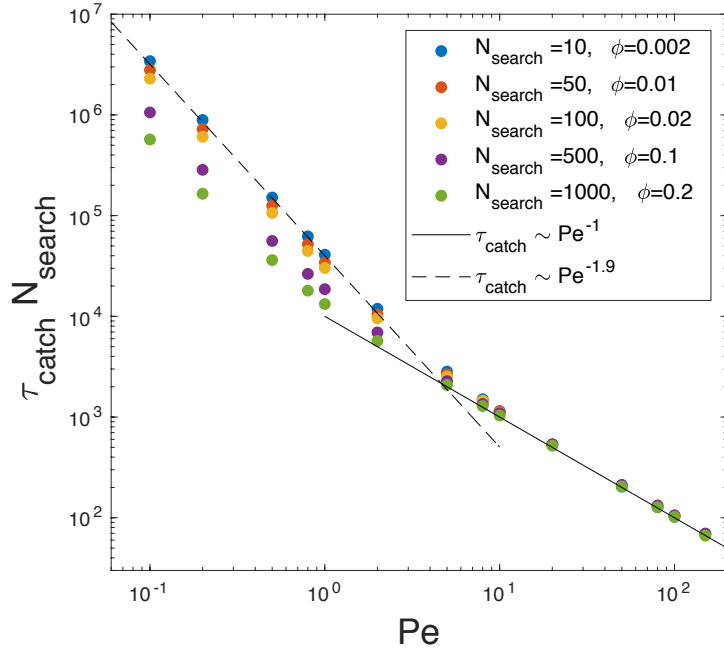
Gaussian white noise



Péclet number:  $\text{Pe} = \frac{V_0}{D_r a} = \frac{\text{persistence length}}{\text{particle radius}}$



# How long does it take (for ABPs) to catch **all** targets?



$$Pe = \frac{V_0}{D_r a} = \frac{\text{persistence length}}{\text{particle radius}}$$

*Diffusive motion:  $Pe \ll 1$*   
*Ballistic motion:  $Pe \gg 1$*





Position:

$$\dot{\mathbf{r}}_i(t) = V_0 \mathbf{e}_i(t) + \frac{1}{\gamma_t} \sum_{j \neq i} \mathbf{f}_{ji} \quad \text{with} \quad \mathbf{e}_i = \begin{pmatrix} \cos \varphi_i \\ \sin \varphi_i \end{pmatrix}$$

Orientation:

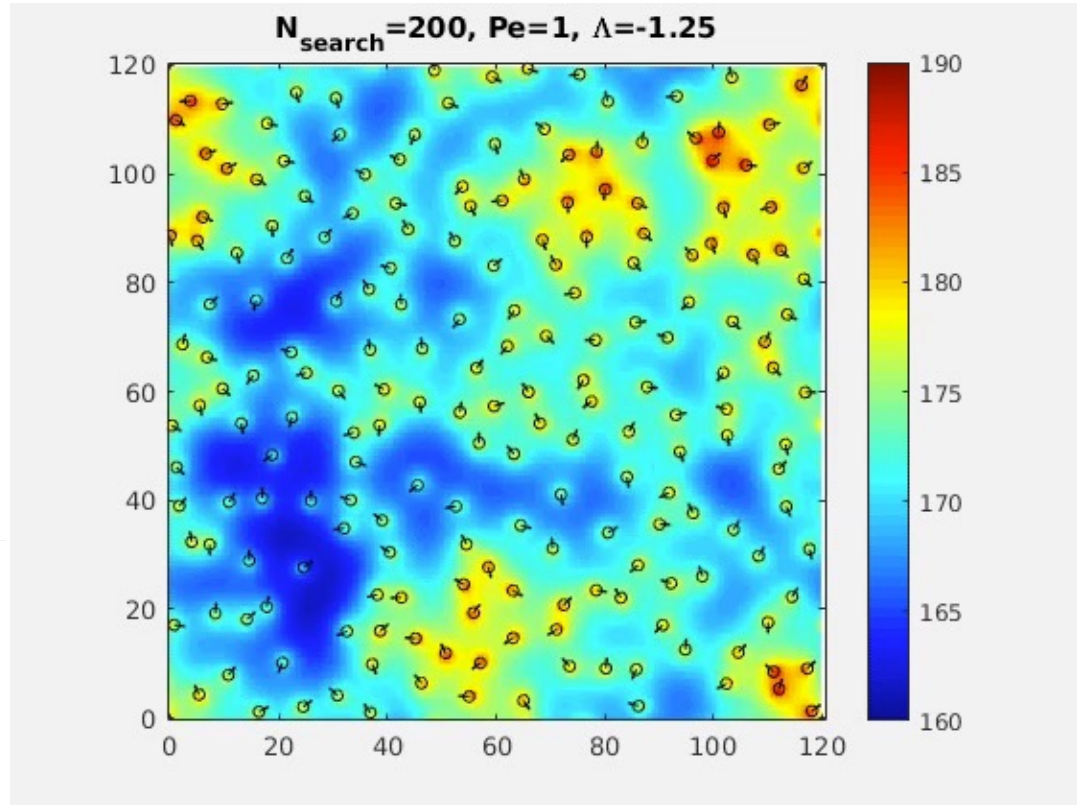
$$\dot{\varphi}_i(t) = \frac{1}{\gamma_r} \mathbf{e}_i(t) \times \kappa \nabla c(\mathbf{r}_i(t), t) + \sqrt{2D_r} \eta_i(t)$$

$\kappa < 0$  align antiparallel to the gradient (chemorepulsion)

$\kappa > 0$  align parallel to the gradient (chemoattraction)

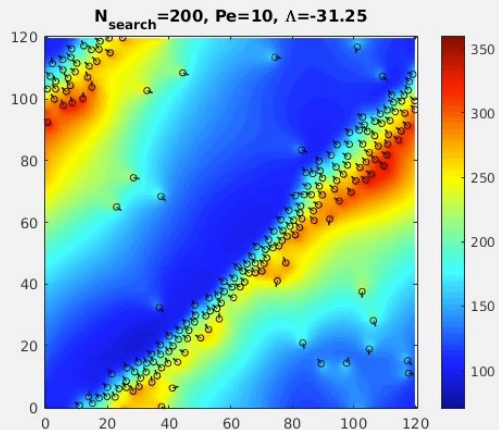
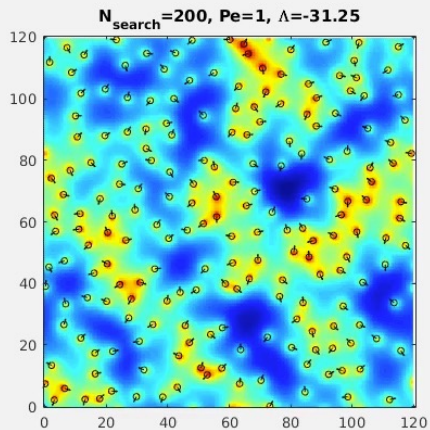
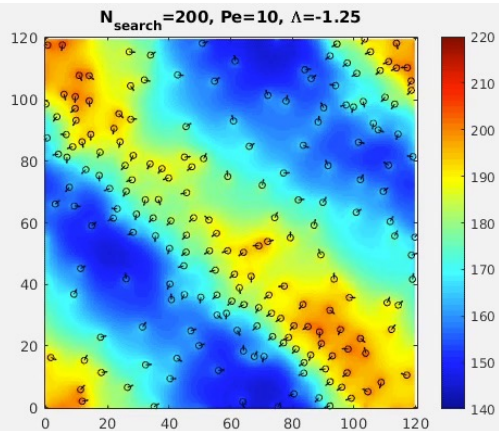
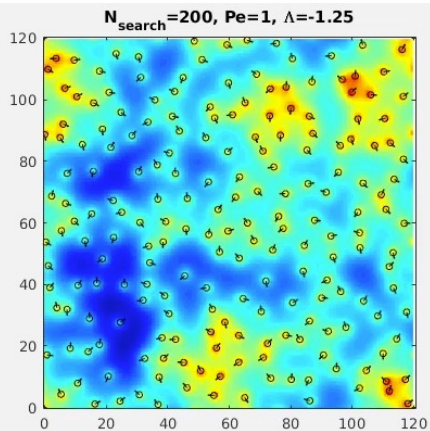
Chemical field

$$\frac{\partial}{\partial t} c(\mathbf{r}, t) = D \nabla^2 c - kc + h \sum_{i=1}^N \delta[\mathbf{r} - \mathbf{r}_i(t)]$$



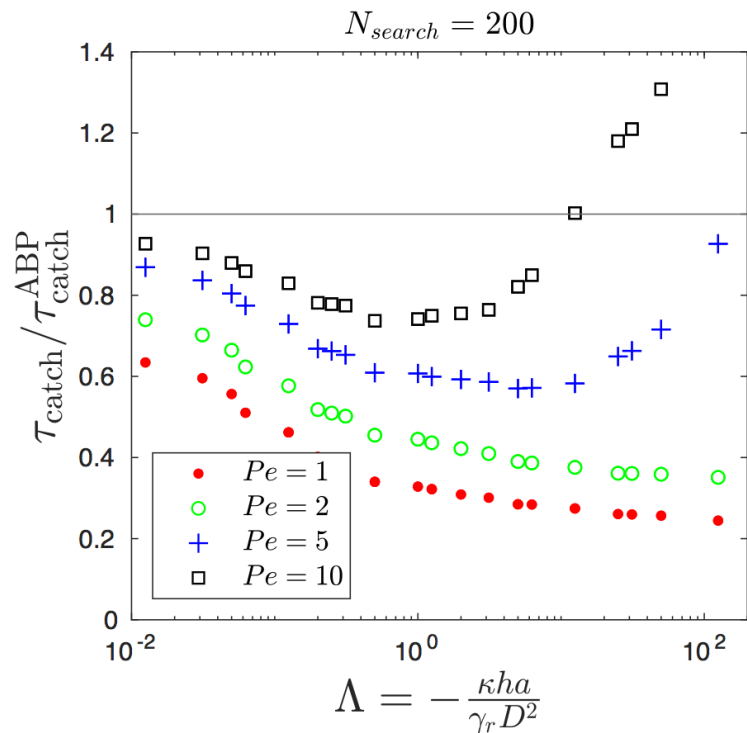
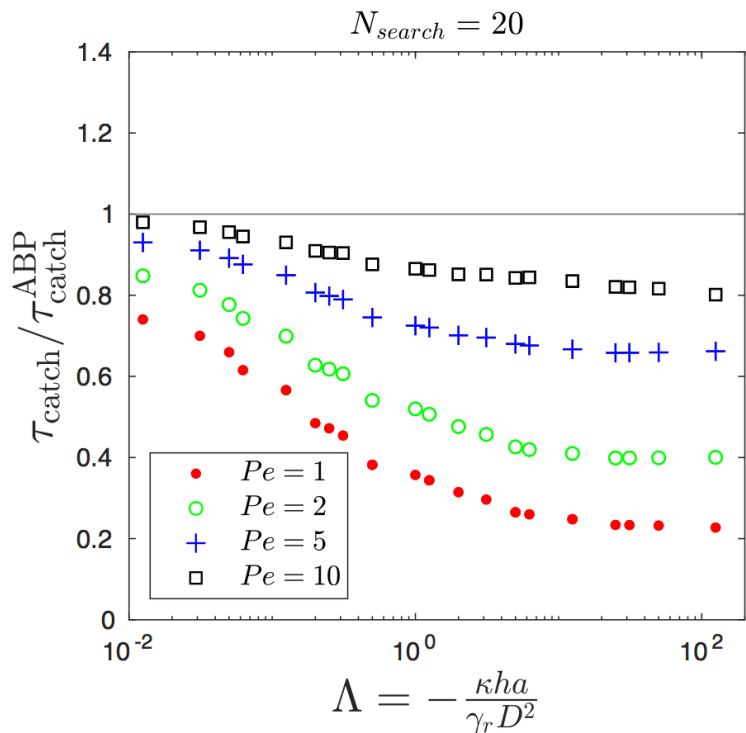


# Chemorepulsion



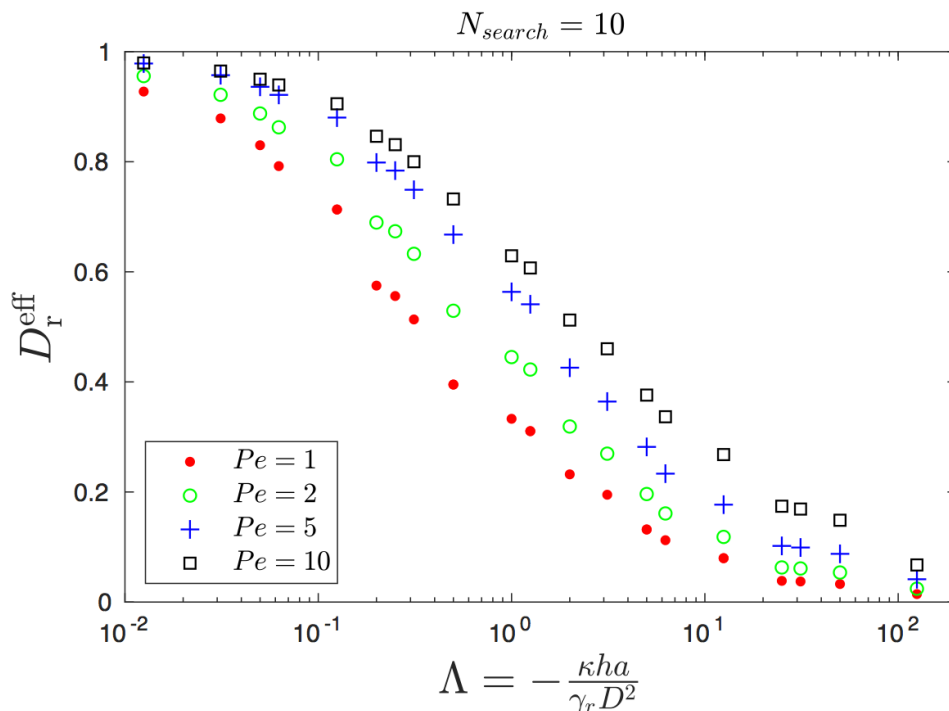


# Repulsive chemotactic particles search faster





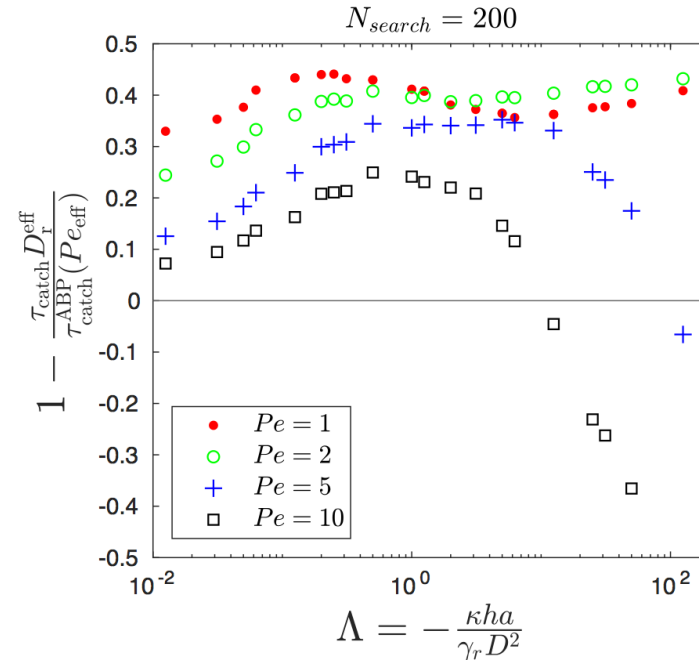
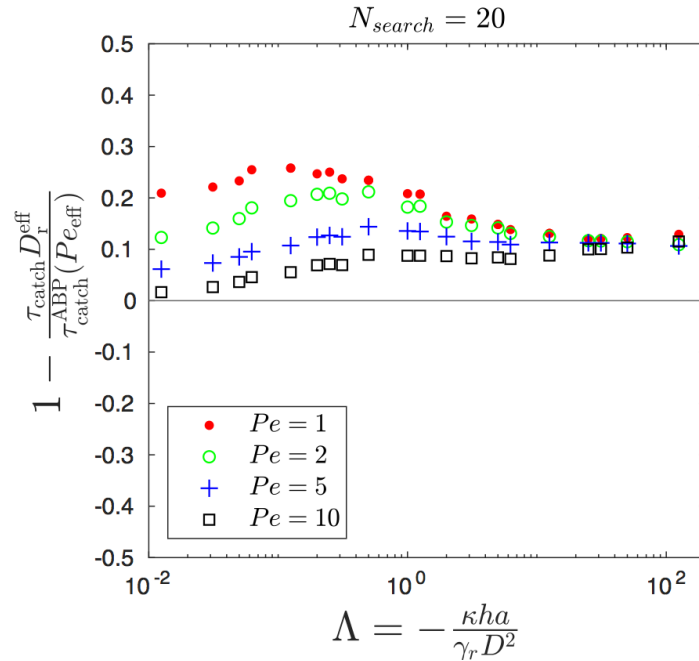
# Chemo-repulsion leads to persistent motion



$$\langle \mathbf{e}(t) \cdot \mathbf{e}(0) \rangle \sim \exp(-D_r^{\text{eff}} t) \Rightarrow Pe_{\text{eff}} = \frac{V_0}{D_r^{\text{eff}} a}$$



# Collective effects? Yes!



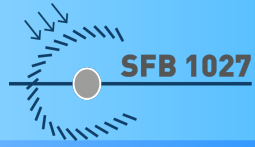
CTP's outperform ABP's if  $\tau_{\text{catch}} D_r^{\text{eff}} < \tau_{\text{catch}}^{\text{ABP}}(Pe_{\text{eff}})$



Thank you for your attention!

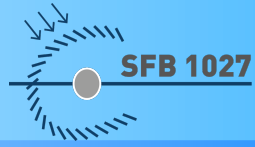


# Title





# Title







$$\text{MFPT} = \langle T \rangle = \int_0^{\infty} dt \text{FPT}(t)$$

**Markovian processes:**  $P(r_{n+1}, t_{n+1} | r_n, t_n; \dots; r_1, t_1) = P(r_{n+1}, t_{n+1} | r_n, t_n)$  for all  $t_{n+1} > t_n > \dots > t_1$

**Renewal equation:**  $P(\mathbf{r}_T, t | \mathbf{r}_S) = \delta_{t,0} \delta_{\mathbf{r}_T, \mathbf{r}_S} + \int_0^t \text{FPT}(t') P(\mathbf{r}_T, t - t' | \mathbf{r}_T) dt'$

**Def.:**  $H(\mathbf{r}_T | \mathbf{r}_S) = \int_0^{\infty} (P(\mathbf{r}_T, t | \mathbf{r}_S) - P_{\text{stat}}(\mathbf{r}_T)) dt$

-> Express MFPT  
in terms of P:

$$\langle \mathbf{T} \rangle = \frac{H(\mathbf{r}_T | \mathbf{r}_T) - H(\mathbf{r}_T | \mathbf{r}_S)}{P_{\text{stat}}(\mathbf{r}_T)}$$




PHYSICAL REVIEW LETTERS **127**, 070601 (2021)

Editors' Suggestion

## Optimal Non-Markovian Search Strategies with $n$ -Step Memory

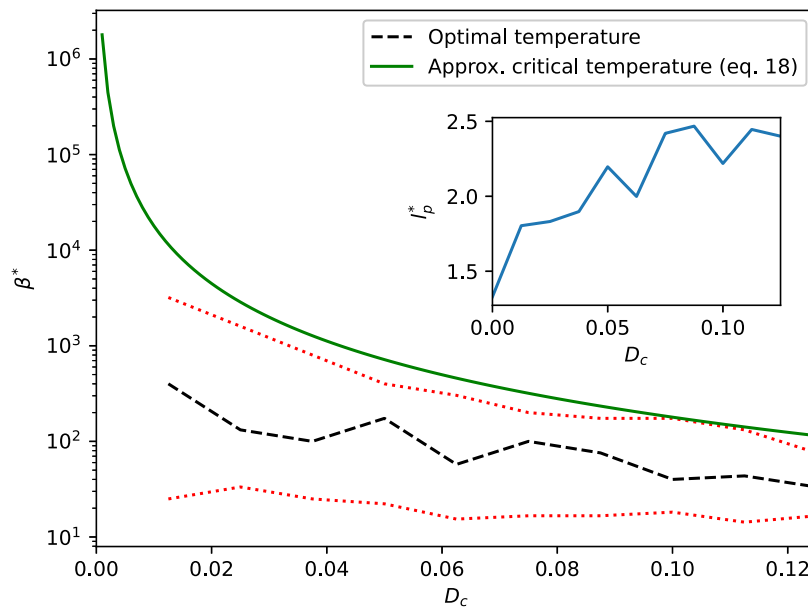
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Stochastic search processes are ubiquitous in nature and are expected to become more efficient when equipped with a memory, where the searcher has been before. A natural realization of a search process with long-lasting memory is a migrating cell that is repelled from the diffusive chemotactic signal that it secretes on its way, denoted as an autochemotactic searcher. To analyze the efficiency of this class of non-Markovian search processes, we present a general formalism that allows one to compute the mean first-passage time (MFPT) for a given set of conditional transition probabilities for non-Markovian random walks on a lattice. We show that the optimal choice of the  $n$ -step transition probabilities decreases the MFPT systematically and substantially with an increasing number of steps. It turns out that the optimal search strategies can be reduced to simple cycles defined by a small parameter set and that mirror-asymmetric walks are more efficient. For the autochemotactic searcher, we show that an optimal coupling between the searcher and the chemical reduces the MFPT to 1/3 of the one for a Markovian random walk.

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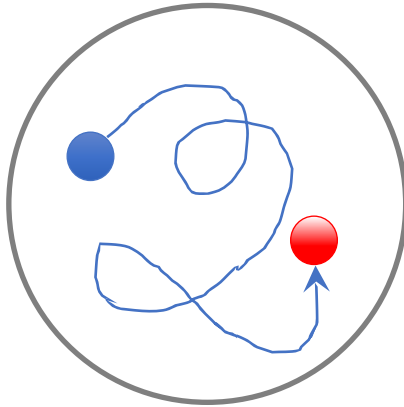
$$l_p \simeq 2 + \frac{e^{\beta D_c^2}}{2}$$

$$\beta^* = D_c^{-2} \ln(2l_p^* - 4)$$

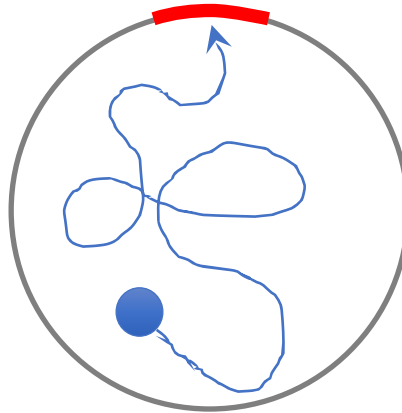
Figure 3: Optimal inverse temperature range  $\beta^*$  as a function of  $D_c$  (black dashed line) with error range (red dotted line), together with equation (10) for  $l_p^* = 5$ . The inset shows the value of the persistence length at the optimal point  $(\beta^*, D_c)$ .



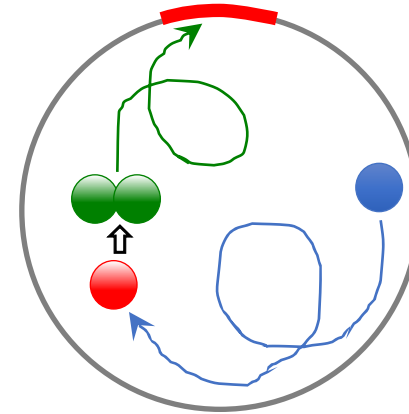
Reaction Kinetics



Narrow Escape Problem



Reaction-Escape

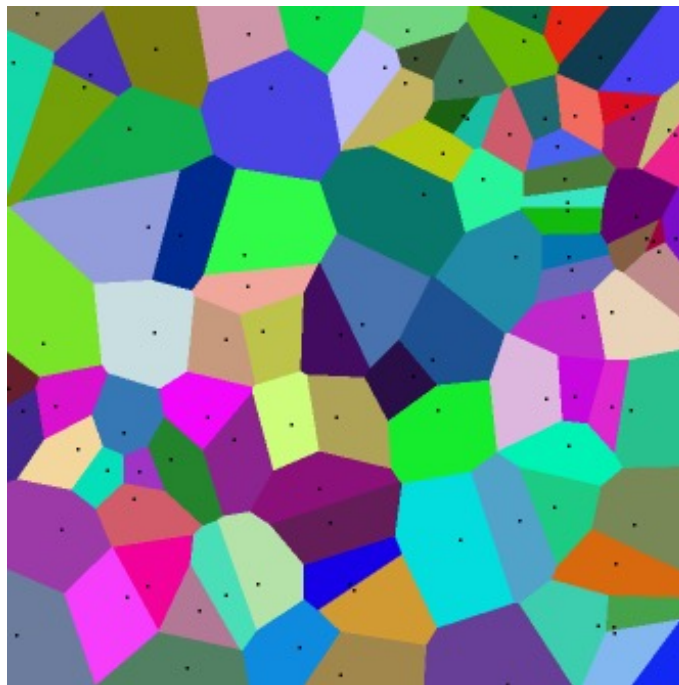


**Mean First Passage Time (MFPT)**

depends on geometrical and motility parameters



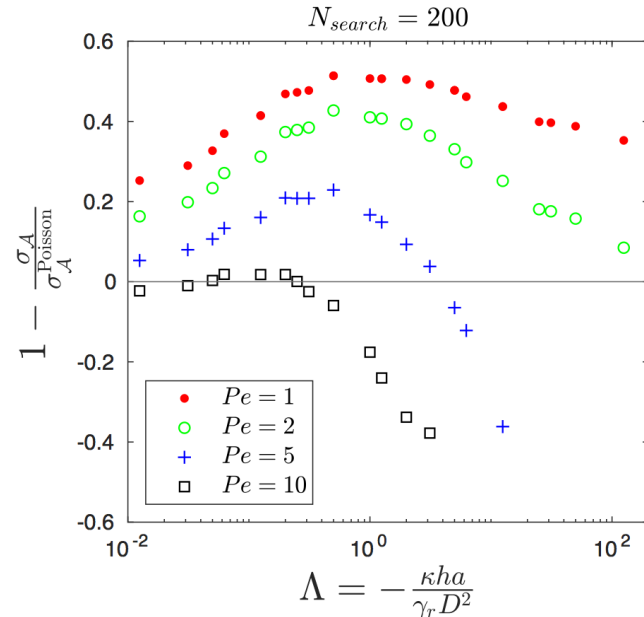
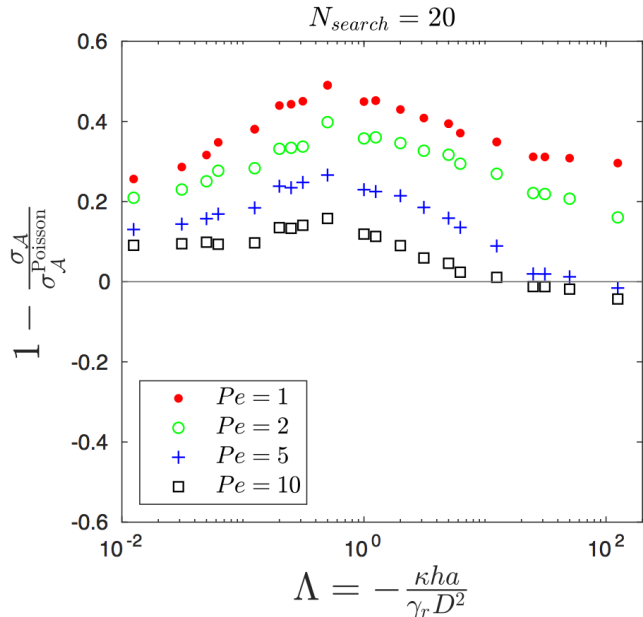
# Are the search areas uniformly distributed ?



$\sigma_{\mathcal{A}}^{\text{Poisson}} \approx 0.5292$  is the standard deviation  
of the normalized areas  $\mathcal{A} = A/\langle A \rangle$   
of Poisson Voronoi cells.



# Spatial order correlates with search efficiency



Ordered if  $\sigma_{\mathcal{A}} < \sigma_{\mathcal{A}}^{\text{Poisson}}$

Clustered if  $\sigma_{\mathcal{A}} > \sigma_{\mathcal{A}}^{\text{Poisson}}$