Statistical Physics and Anomalous Dynamics of Foraging

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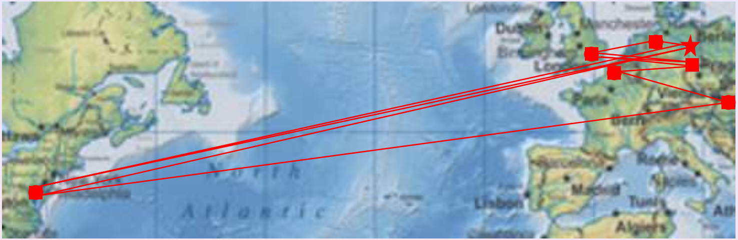
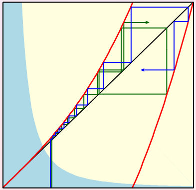
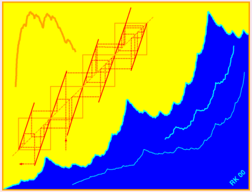
My own scientific foraging

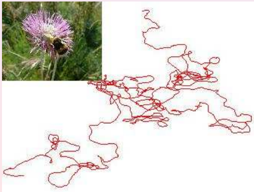




chaos

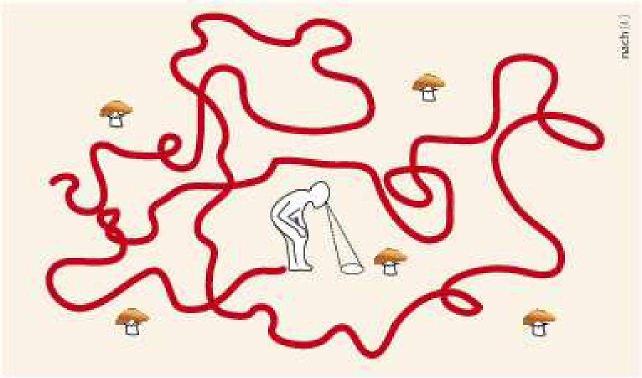


nonequ. stat. mech.



biology

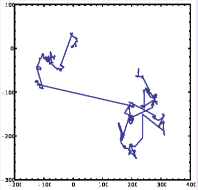
The problem

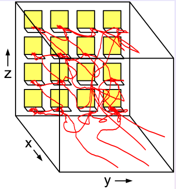


from: Chupeau et al., Nature Physics (2015)

News & Views in: RK, Physik Journal **14**, 22 (2015)

Outline of my talk





Theme of this talk:

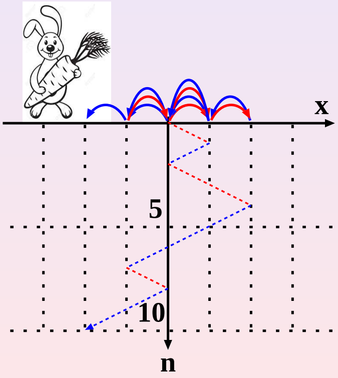
Understand the **search for food** of biological organisms in terms of **stochastic processes.**

Four parts (review and own work):

1. Lévy flight foraging hypothesis: overview
2. Biological data: analysis and interpretation
3. cell migration and bumblebee flights
4. simple stochastic models of foraging

A mathematical theory of random migration

Karl Pearson (1906):
model movements of biological organisms by a **random walk** in one dimension: position x_n at discrete time step n



$$x_{n+1} = x_n + \ell_n$$

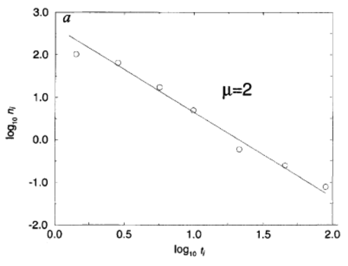
- *here:* steps of length $|\ell_n| = \ell$ to the left/right; sign determined by coin tossing
- Markov process: the steps are *uncorrelated*
- generates Gaussian distributions for x_n (central limit theorem)

Lévy flight search patterns of wandering albatrosses

famous paper by Viswanathan et al., Nature **381**, 413 (1996):

for albatrosses foraging in the South Atlantic the flight times were recorded

the histogram of flight times



was fitted by a Lévy distribution (power law $\sim t^{-\mu}$)

- may be due to the food distribution on the ocean surface being scale invariant: **Lévy Environmental Hypothesis**

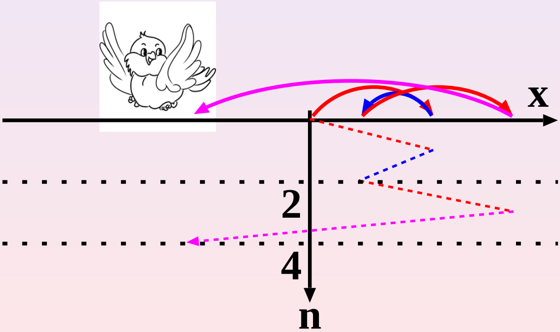
What are Lévy flights?

a random walk generating **Lévy flights**:

$x_{n+1} = x_n + \ell_n$ with ℓ_n drawn from a Lévy α-stable distribution

$$\rho(\ell_n) \sim |\ell_n|^{-1-\alpha} \; (|\ell_n| \gg 1) \,, \; 0 < \alpha < 2$$

P. Lévy (1925ff)



- fat tails: larger probability for long jumps than for a Gaussian!

Properties of Lévy flights in a nutshell

- a Markov process *(no memory)*
- which obeys a generalized central limit theorem if the Lévy distributions are α-stable (for $0 < \alpha \leq 2$)
  Gnedenko, Kolmogorov, 1949
- implying that both $\rho(\ell_n)$ and $\rho(x_n)$ are scale invariant and thus self-similar
- both $\rho(x_n)$ and $\rho(\ell_n)$ have **infinite variance**

$$\langle \ell_n^2 \rangle = \int_{-\infty}^{\infty} d\ell_n \, \rho(\ell_n) \ell_n^2 = \infty$$

- Lévy flights have **arbitrarily large velocities**, as $v_n = \ell_n / 1$

Lévy walks

cure the problem of infinite moments and velocities:

- a **Lévy walker** spends a time

  $$t_n = \ell_n / v \ , \ |v| = const.$$

  to complete a step; yields finite moments and finite velocities in contrast to Lévy flights

- Lévy walks generate anomalous (super) diffusion:

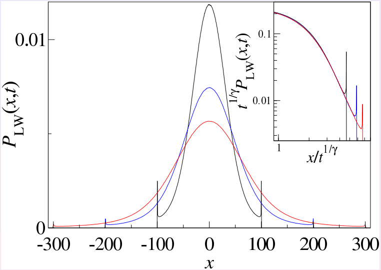
  $$\langle x^2 \rangle \sim t^\gamma \ (t \to \infty) \text{ with } \gamma > 1 \ ,$$

  see Shlesinger at al., Nature **363**, 31 (1993) for an outline;
  RK, Radons, Sokolov (Eds.), *Anomalous transport* (Wiley, 2008)

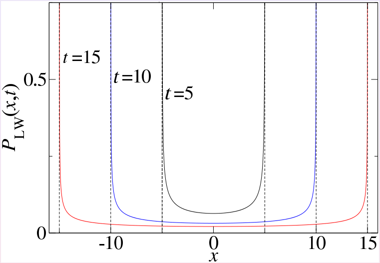
note: for the step length pdf $\rho(\ell_n) \sim |\ell_n|^{-1-\alpha}$ Continuous Time Random Walk Theory yields a specific relation $\gamma = \gamma(\alpha)$

Position distribution functions for Lévy walks

$1 < \alpha < 2$



$0 < \alpha < 1$



Zaburdaev et al., RMP **87**, 483 (2015)

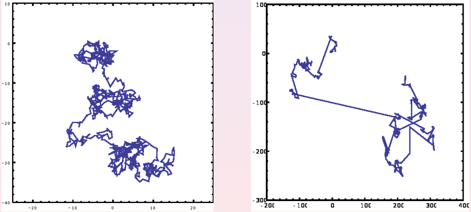
- power law tails
- truncation of densities due to finite velocities
- ballistic peaks

Optimizing the success of random searches

another paper by Viswanathan et al., Nature **401**, 911 (1999):

- question posed about *"best statistical strategy to adapt in order to search efficiently for randomly located objects"*
- random walk model leads to **Lévy flight hypothesis:**

> Lévy flights provide an *optimal search strategy* for *sparse, randomly distributed, immobile, revisitable targets in unbounded domains*



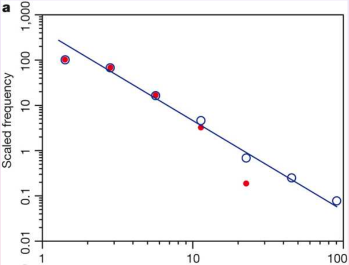
Brownian motion (left) vs. **Lévy flights** (right)

- yields the *second* **Lévy Foraging Hypothesis**

Revisiting Lévy flight search patterns

Edwards et al., Nature **449**, 1044 (2007):

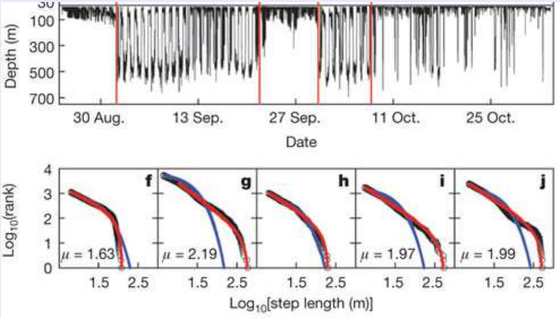
- Viswanathan et al. results revisited by correcting old data (Buchanan, Nature **453**, 714, 2008):



- **no Lévy flights:** new, more extensive data suggests (gamma distributed) stochastic process
- but claim that **truncated Lévy flights** fit yet new data Humphries et al., PNAS **109**, 7169 (2012)

Lévy Paradigm: Look for power law tails in pdfs

Humphries et al., Nature **465**, 1066 (2010): blue shark data



blue: exponential; red: truncated power law

- ⊖ velocity pdfs extracted, *not* the jump pdfs of Lévy walks
- ⊕ environment explains Lévy vs. Brownian movement
- ⊖ data averaged over day-night cycle, cf. oscillations

Summary: two different Lévy Flight Hypotheses

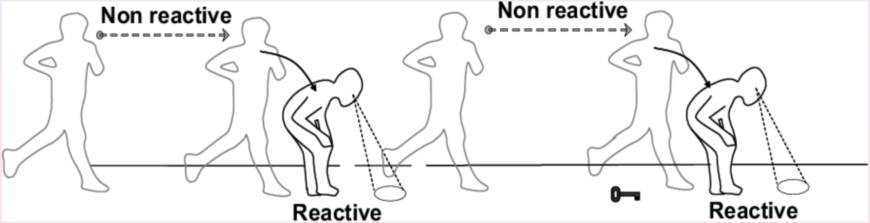
to be published

Bartumeus, Boyer, Chechkin, Giuggioli, RK, Pitchford, Watkins (tbp)

An alternative to Lévy flight search strategies

Bénichou et al., Rev. Mod. Phys. **83**, 81 (2011):

- for *non-revisitable targets* **intermittent** search strategies minimize the search time



- popular account of this work in Shlesinger, Nature **443**, 281 (2006): "How to hunt a submarine?"; cf. also protein binding on DNA

Beyond the Lévy Flight Foraging Hypothesis

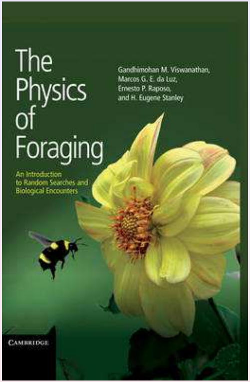
to be published

Bartumeus, Boyer, Chechkin, Giuggioli, RK, Pitchford, Watkins (tbp)

In search of a mathematical foraging theory

Summary:

- scale-free Lévy flight paradigm
- problems with the data analysis
- two Lévy Flight Hypotheses: **adaptive** and **emergent**
- intermittent search as an alternative
- need to go beyond the Lévy Flight Foraging Hypotheses



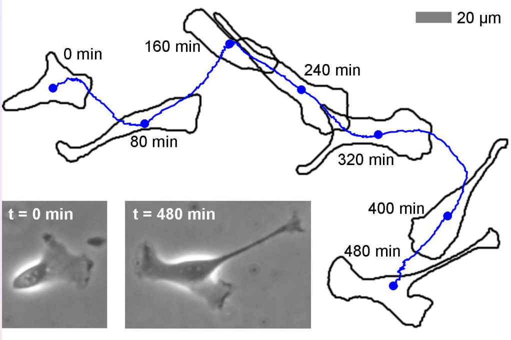
Ongoing discussions:

• mussels: de Jager et al., Science (2011)

Applications:

• search algorithms for robots? Nurzaman et al. (2010)

Biological cell migration



Dieterich, RK et al., PNAS (2008)

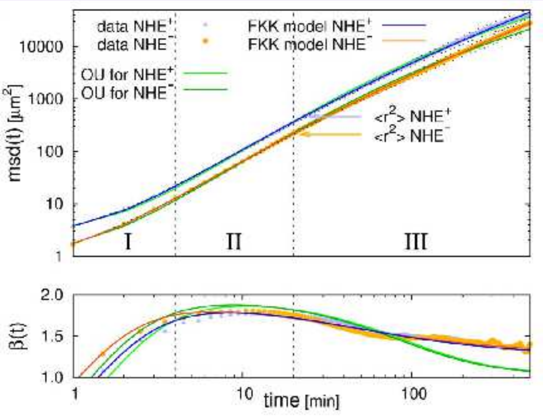
single MDCK-F (Madin-Darby canine kidney) cell crawling on a substrate: **Brownian motion?**

two cell types: wild (NHE^+) and NHE-deficient (NHE^-)

movie: NHE^+: t=210min, dt=3min

Mean square displacement

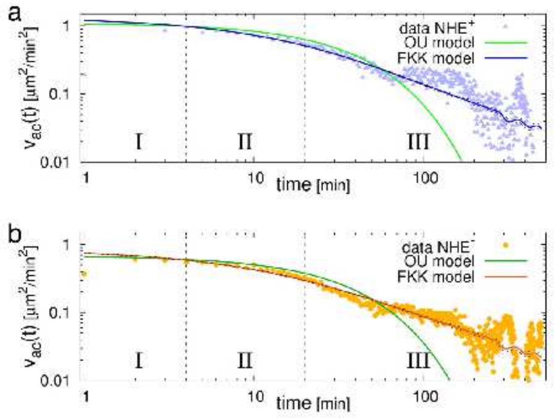
- $msd(t) := \langle [\mathbf{x}(t) - \mathbf{x}(0)]^2 \rangle \sim t^\beta$ with $\beta \to 2$ $(t \to 0)$ and $\beta \to 1$ $(t \to \infty)$ for Brownian motion; $\beta(t) = d \ln msd(t) / d \ln t$



anomalous diffusion if $\beta \neq 1$ $(t \to \infty)$; here: **superdiffusion**

Velocity autocorrelation function

- $v_{ac}(t) := \langle \mathbf{v}(t) \cdot \mathbf{v}(0) \rangle \sim \exp(-\kappa t)$ for Brownian motion
- fits with same parameter values as $msd(t)$



crossover from **stretched exponential to power law**

Position distribution function

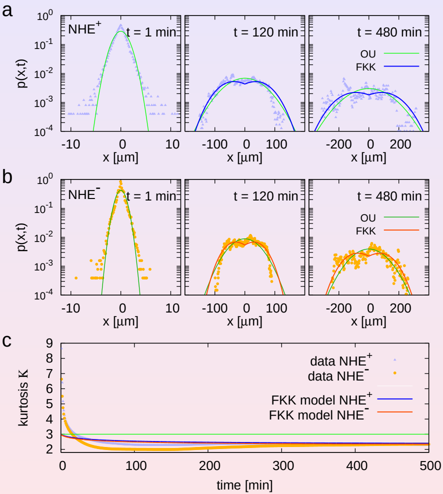
- $P(x,t) \rightarrow$ Gaussian $(t \rightarrow \infty)$ and kurtosis

$$\kappa(t) := \frac{\langle x^4(t) \rangle}{\langle x^2(t) \rangle^2} \rightarrow 3 \; (t \rightarrow \infty)$$

for Brownian motion (green lines, in 1d)

- *other solid lines:* fits from our model; parameter values as before

note: model needs to be amended to explain short-time distributions



crossover from peaked to broad **non-Gaussian distributions**

The model

- **Fractional Klein-Kramers equation** (Barkai, Silbey, 2000):

$$\frac{\partial P}{\partial t} = -\frac{\partial}{\partial x}[vP] + \frac{\partial^{1-\alpha}}{\partial t^{1-\alpha}}\kappa\left[\frac{\partial}{\partial v}v + v_{th}^2\frac{\partial^2}{\partial v^2}\right]P$$

with probability distribution $P = P(x, v, t)$, damping term κ, thermal velocity $v_{th}^2 = kT/m$ and Riemann-Liouville fractional derivative of order $1-\alpha$

for $\alpha = 1$ Langevin's theory of Brownian motion recovered

- **analytical solutions** for $msd(t)$ and $P(x, t)$ can be obtained in terms of special functions (Barkai, Silbey, 2000; Schneider, Wyss, 1989)

- model generates **anomalous dynamics** *different from Lévy walks*; no relation to Lévy hypothesis

What is a fractional derivative?

letter from Leibniz to L'Hôpital (1695): $\frac{d^{1/2}}{dx^{1/2}} = ?$

one way to proceed: we know that for integer m, n

$$\frac{d^m}{dx^m} x^n = \frac{n!}{(n-m)!} x^{n-m} = \frac{\Gamma(n+1)}{\Gamma(n-m+1)} x^{n-m};$$

assume that this also holds for $m = 1/2\ ,\ n = 1$

$$\Rightarrow \quad \boxed{\frac{d^{1/2}}{dx^{1/2}} x = \frac{2}{\sqrt{\pi}} x^{1/2}}$$

extension leads to the Riemann-Liouville fractional derivative

$$\frac{\partial^\gamma P}{\partial t^\gamma} := \begin{cases} \frac{\partial^m P}{\partial t^m} & , \quad \gamma = m \\ \frac{\partial^m}{\partial t^m} \left[\frac{1}{\Gamma(m-\gamma)} \int_0^t dt' \frac{P(t')}{(t-t')^{\gamma+1-m}} \right] & , \quad m-1 < \gamma < m \end{cases}$$

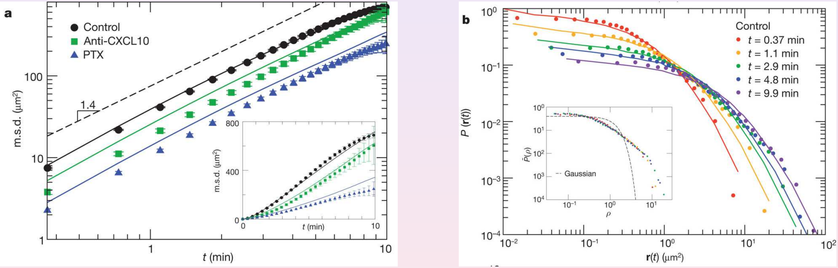
yields power laws in Fourier space $\frac{d^\gamma}{dx^\gamma} F(x) \leftrightarrow (ik)^\gamma \tilde{F}(k)$

$\exists$ well-developed mathematical theory of **fractional calculus**, see Sokolov, Klafter, Blumen, Phys. Today 2002 for a short intro

Generalized Lévy walks for migrating T cells

Harris et al., Nature **486**, 545 (2012):

• mean square displacement (for 3 different cell types) and position distribution function for T cells in vivo:



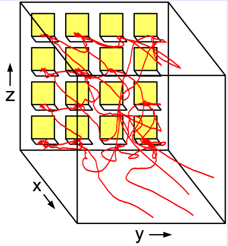
• T cell motility described by a generalized Lévy walk (Zumofen, Klafter, 1995)

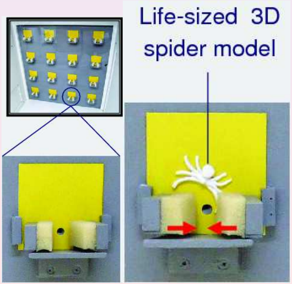
• search more efficient than Brownian motion

• pdf not Lévy: how does this fit to the Lévy paradigm?

Foraging bumblebees: the experiment

- tracking of **bumblebee flights** in the lab: foraging in an artificial carpet of **flowers with or without spiders**
- **no test** of the Lévy hypothesis but work inspired by the *paradigm*





safe and **dangerous** flowers

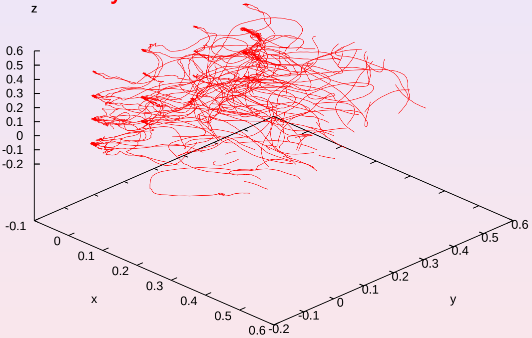
three experimental stages:

1. spider-free foraging
2. foraging under predation risk
3. memory test 1 day later

Ings, Chittka (2008)

Bumblebee experiment: two main questions

1. What type of motion do the bumblebees perform in terms of stochastic dynamics?

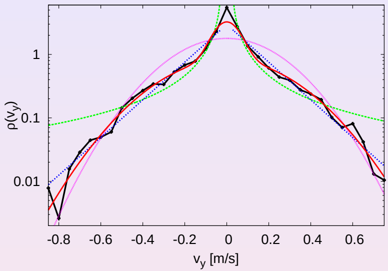


2. Are there changes of the dynamics under variation of the environmental conditions?

Flight velocity distributions

experimental **probability density** (pdf) of bumblebee v_y**-velocities** without spiders (bold black)

best fit: mixture of 2 Gaussians, cp. to exponential, power law, single Gaussian

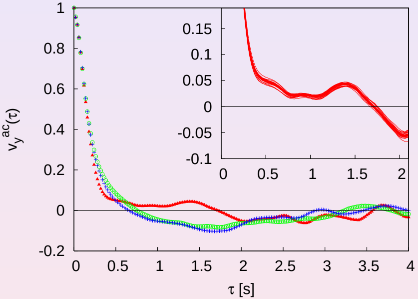


biological explanation: models spatially different flight modes near the flower vs. far away, cf. intermittent dynamics

big surprise: no difference in pdf's between different stages under variation of environmental conditions!

Velocity autocorrelation function || to the wall

$$V_y^{AC}(\tau) = \frac{\langle (v_y(t)-\mu)(v_y(t+\tau)-\mu)\rangle}{\sigma^2}$$



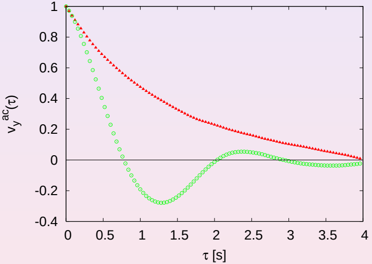
3 stages: spider-free, predation thread, memory test

all changes are in the flight correlations, *not* in the pdfs

model: Langevin equation

$$\frac{dv_y}{dt}(t) = -\eta v_y(t) - \frac{\partial U}{\partial y}(y(t)) + \xi(t)$$

η: friction, ξ: Gauss. white noise



result: velocity correlations with repulsive interaction U

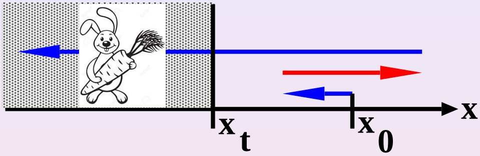
bumblebee - spider off / on

Lenz, RK et al., PRL (2012)

Searching for a single target

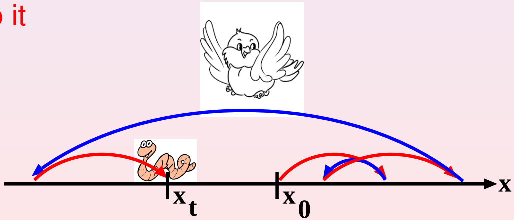
two basic types of foraging (James et al., 2010):

1. **cruise forager:** detects a target while moving



first passage problem

2. **saltaltory forager:** only detects a target when landing on it / next to it



first arrival problem

First passage and first arrival: solutions

1. **Brownian motion:**

$$\varrho_{FP}(t) \sim t^{-3/2} \sim \varrho_{FA}(t)$$

Sparre-Andersen Theorem (1954)

2. **Lévy flights:**

$\varrho_{FP}(t) \sim t^{-3/2}$ (Chechkin et al., 2003; numerics only)
$\varrho_{FA}(t) = 0 \ (0 < \alpha \leq 1)$; $\varrho_{FA}(t) \sim t^{-2+1/\alpha} \ (1 < \alpha < 2)$

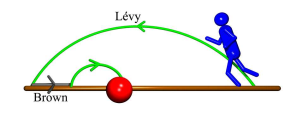
Palyulin et al. (2014)

3. **Lévy walks:**

$\varrho_{FP}(t) \sim t^{-1-\alpha/2} \ (0 < \alpha \leq 1)$; $\varrho_{FP}(t) \sim t^{-3/2} \ (1 < \alpha < 2)$
(numerics: Korabel, Barkai (2011); analytically: Artuso et al., 2014)
$\varrho_{FA}(t)$: the same as for Lévy flights, cf. simulations

Blackburn, RK et al. (2016)

Combined Lévy-Brownian motion search

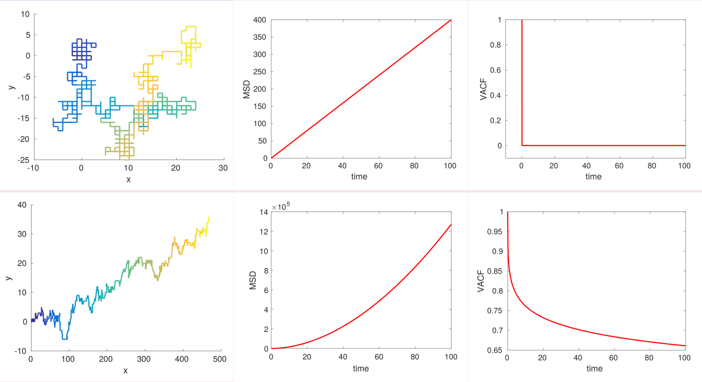


- intermittency modeled by the fractional diffusion equation
$$\frac{\partial f(x,t)}{\partial t} = K_\alpha \frac{\partial^\alpha f(x,t)}{\partial |x|^\alpha} + K_B \frac{\partial^2 f(x,t)}{\partial x^2}$$
with Riesz fract. derivative $\sim -|k|^\alpha f(k,t)$ in Fourier space
- define search reliability by cumulative probability P of reaching a target: $P = \lim_{s\to 0} \int_0^\infty \varrho_{FA}(t) \exp(-st) dt$
- **result:** Brownian motion regularizes Lévy search, $0 < P < 1$ for $0 < \alpha \leq 1$
- calculate search efficiency defined by
$$\varepsilon = \langle \text{visited \# targets}/\text{\# steps} \rangle \simeq \langle 1/t \rangle = \int_0^\infty \varrho_{FA}(s) ds$$

Palyulin, RK et al., JPA (2016); EPJB (2017)

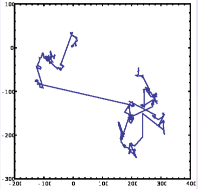
From anomalous single particles to collective motion

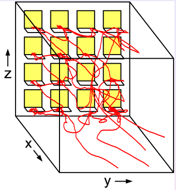
construct cellular automaton models for time-correlated (anomalous) random walks:



Nava-Sedeno, Hatzikirou, RK, Deutsch, Sci.Rep., in print

Summary





- Be careful with (power law) paradigms for data analysis.
- A profound biological embedding is needed to better understand foraging.
- Much work to be done to test other types of anomalous stochastic processes for modeling foraging problems.

Acknowledgements

• **Lévy Flight Hypothesis:** *Advanced Study Group* on Statistical physics and anomalous dynamics of foraging, MPIPKS Dresden (2015); F.Bartumeus (Blanes), D.Boyer (UNAM), A.V.Chechkin (Kharkov), L.Giuggioli (Bristol), *convenor:* RK (London), J.Pitchford (York)
http://www.mpipks-dresden.mpg.de/~asg_2015

• **cell migration:** P.Dieterich (TU Dresden), R.Preuss (Garching), A.Schwab (U.Münster)

• **bumblebee flights:** F.Lenz, T.Ings, L.Chittka (all QMUL), A.V.Chechkin (Kharkov)

Literature:

RK, *Search for food of birds, fish and insects*, book chapter (Springer, 2018); available on my homepage