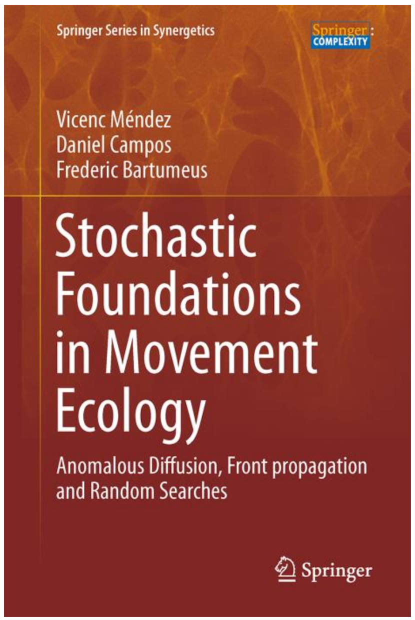
Advanced Study Group 2015:
Statistical Physics and Anomalous Dynamics of Foraging

MAX-PLANCK-GESELLSCHAFT



STOCHASTIC FOUNDATIONS IN MOVEMENT ECOLOGY:

Movement patterns and search efficiency

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MOVEMENT PATTERNS

1. Classical diffusion and Brownian motion
2. Persistent motion
3. CTRW and anomalous diffusion
    - Jump models
    - Velocity models
4. Multi-mode movement
    - Intermittent movement
    - Multiscale movement
    - Resetting and mortality mechanisms
5. Motion in two and three dimensions

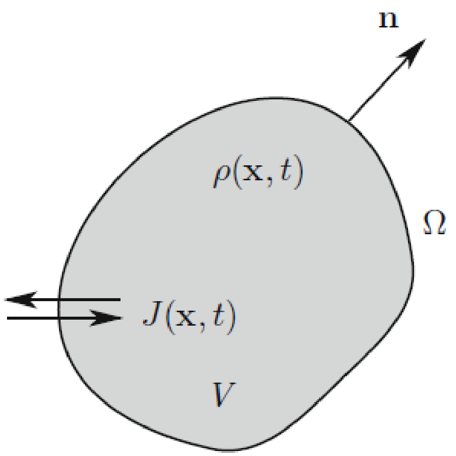
SEARCH EFFICIENCY
(MEAN FIRST-PASSAGE TIMES)

Macroscopic description

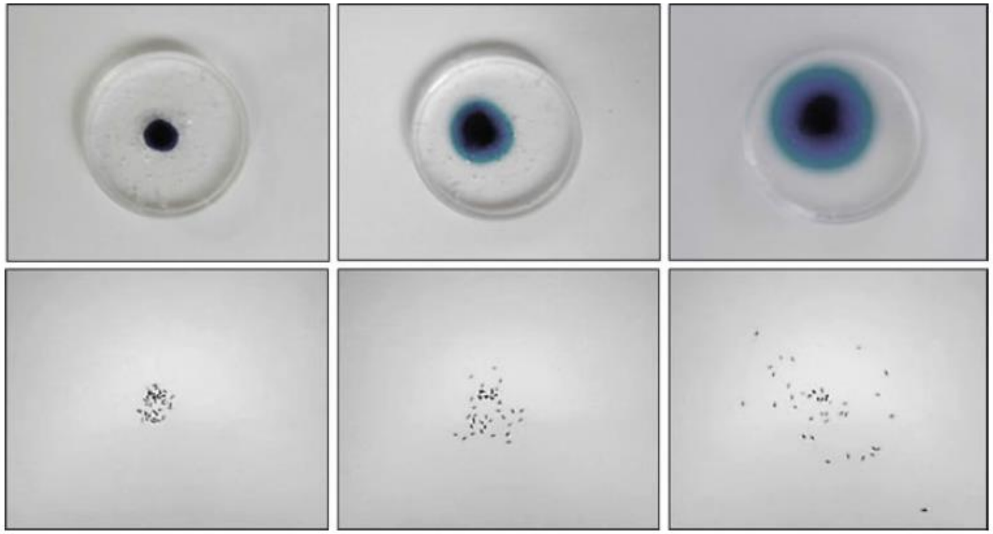
Mass balance: $$\frac{\partial \rho(\mathbf{x},t)}{\partial t} + \nabla \cdot \mathbf{J}(\mathbf{x},t) = 0$$

Constitutive equation: $$\mathbf{J}(\mathbf{x},t) = -D\nabla\rho(\mathbf{x},t)$$

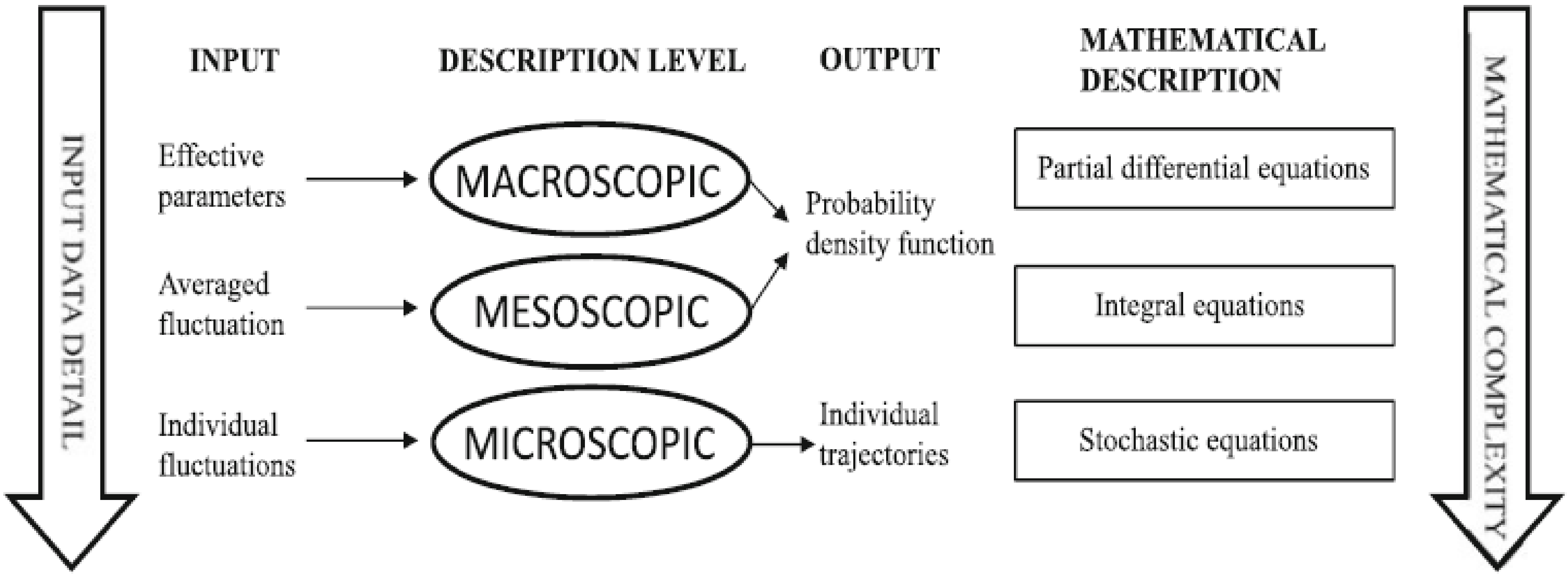
$$\Rightarrow \boxed{\frac{\partial \rho}{\partial t} = D\nabla^2\rho}$$



Biological analogy:



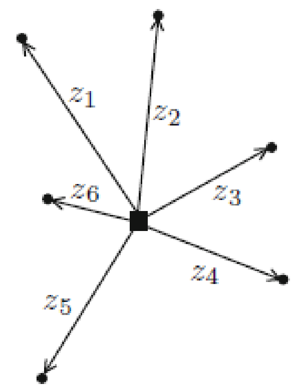
The three levels of description of stochastic processes

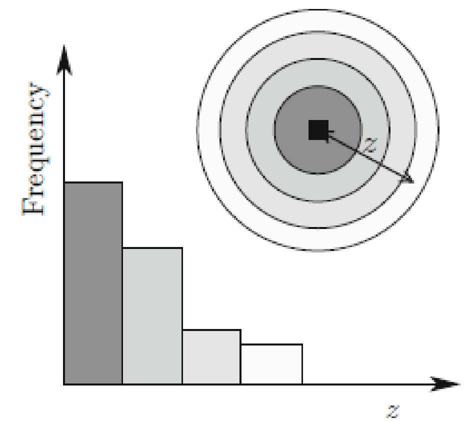


Mesoscopic description

$$\rho(x,t+\tau) = \int_{-\infty}^{\infty} \rho(x-z,t)\Phi(z)\mathrm{d}z$$

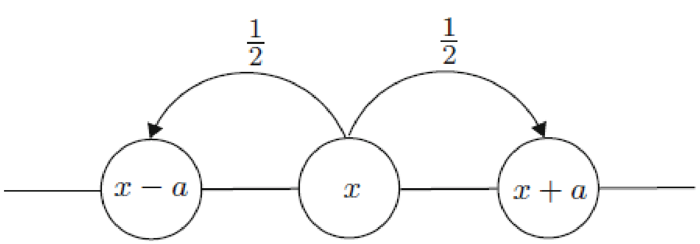
$$\rho(x,t) + \tau\frac{\partial\rho(x,t)}{\partial t} + \cdots = \rho(x,t)\int_{-\infty}^{\infty}\Phi(z)\mathrm{d}z - \frac{\partial\rho(x,t)}{\partial x}\int_{-\infty}^{\infty} z\Phi(z)\mathrm{d}z + \frac{\partial^2\rho(x,t)}{\partial x^2}\int_{-\infty}^{\infty}\frac{z^2}{2!}\Phi(z)\mathrm{d}z + \cdots$$





$$\Rightarrow \quad \frac{\partial\rho}{\partial t} = \frac{\partial^2\rho(x,t)}{\partial x^2}\int_{-\infty}^{\infty}\frac{z^2}{2\tau}\Phi(z)\mathrm{d}z + O(z^4/\tau) \qquad D \equiv \frac{1}{2\tau}\int_{-\infty}^{\infty} z^2\Phi(z)\mathrm{d}z = \frac{\langle z^2\rangle}{2\tau}$$

Isotropic random-walk



$$\frac{\partial\rho(x,t)}{\partial t} = \frac{1}{2\tau}\left[\rho(x+a,t) + \rho(x-a,t) - 2\rho(x,t)\right]$$

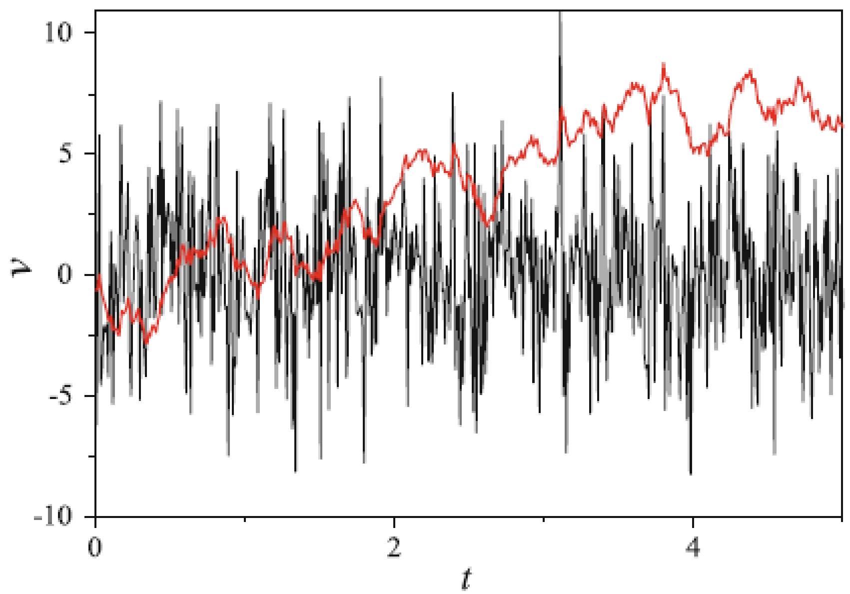
$$D \equiv a^2/2\tau$$

Microscopic description

A **Wiener process** $W(t)$ is a stationary process whose increments $W(t_2) - W(t_1)$ are independent Gaussian variables with zero mean and variance $|t_2 - t_1|$.

$$P(w_2, t_2 | w_1, t_1) = \frac{1}{\sigma\sqrt{2\pi(t_2 - t_1)}} \exp\left[-\frac{(w_2 - w_1)^2}{2(t_2 - t_1)\sigma^2}\right]$$

$$\begin{cases} \dfrac{\mathrm{d}x}{\mathrm{d}t} = v \\ m\dfrac{\mathrm{d}v}{\mathrm{d}t} = -\gamma v + \sigma\xi(t) \end{cases}$$



(Strong friction limit)

$$\gamma\frac{\mathrm{d}x}{\mathrm{d}t} = \sigma\xi(t)$$

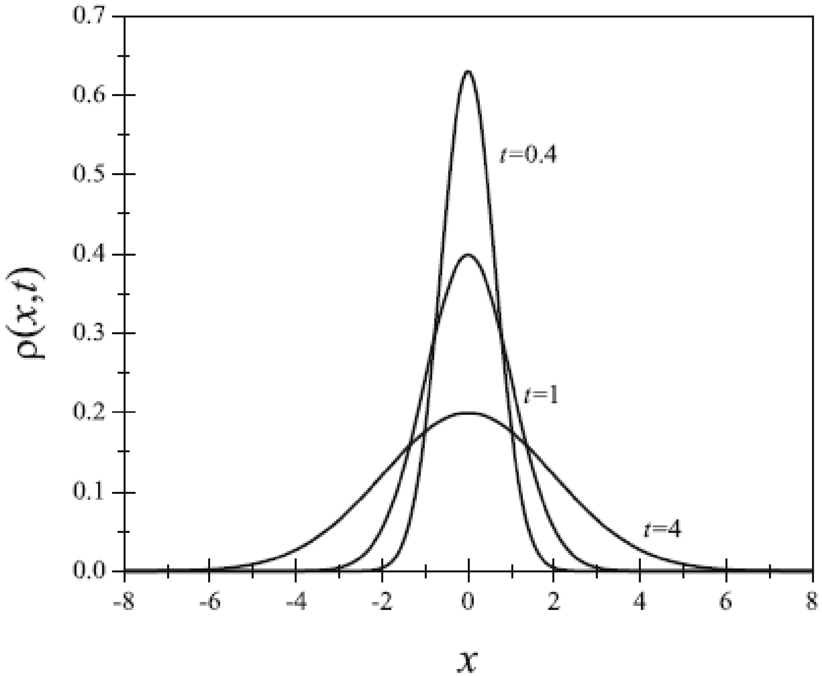
$$\Rightarrow \quad \frac{\partial\rho(x,t)}{\partial t} = \frac{\sigma^2}{2\gamma^2}\frac{\partial^2\rho(x,t)}{\partial x^2}$$

Fundamental properties

$$\rho(x,t) = \frac{1}{\sqrt{4\pi D t}} \int_{-\infty}^{\infty} g(y) e^{-\frac{(x-y)^2}{4Dt}} dy$$

$g(x) = \delta(x - x_0)$ ➡

$$\langle x^2(t) \rangle = x_0^2 + 2Dt$$



$$\lim_{a,\tau \to 0} v = \lim_{a,\tau \to 0} \frac{a}{\tau} = \lim_{a,\tau \to 0} \frac{a^2}{a\tau} = 2D \lim_{a,\tau \to 0} \frac{1}{a} = \infty$$!!!

'Foraging' analogy:

How do we measure search efficiency?

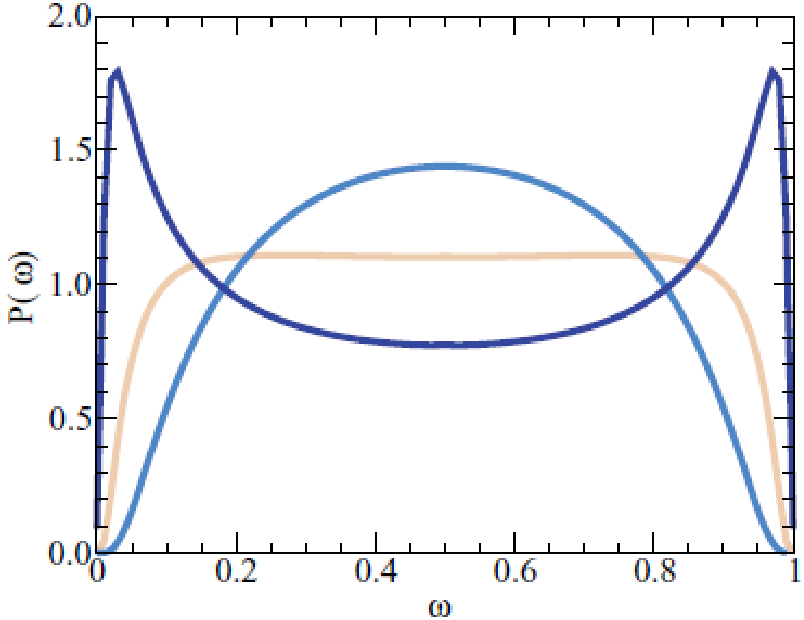
i) "Capture" rate: $k(t)$
ii) Mean volume $V(t)$ covered in time t (Wiener sausage)

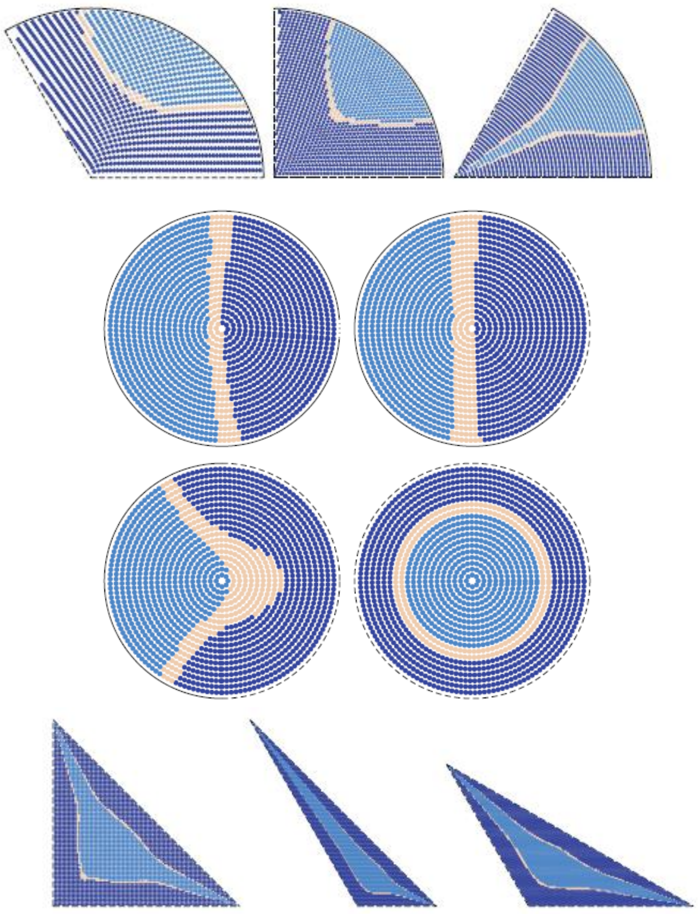
1D: $V(t) \sim t^{1/2}$ 2D (and higher): $V(t) \sim t$

iii) Time distribution to the next "capture": $f(t)$
iv) Survival probability up to time t_m: $S(t_m) = \int_{t_m}^{\infty} dt f(t) = exp[-\rho_B V(t)]$
v) Mean time to the next "capture": $\langle T \rangle = \int_0^{\infty} t f(t) dt = \int_0^{\infty} dt_m S(t_m)$
vi) Mean energy consumed to "capture": $\langle E \rangle = \int_o^{T} \dot{E}(v) dt \approx \dot{E}(\langle v \rangle) \langle T \rangle$
vii) …

Significance of the Mean First-Passage Time (mean time to "capture")

Uniformity index: $\omega \equiv \frac{T_1}{T_1+T_2}$





Mattos, Mejía-Monasterio, Metzler and Oshanin, PRE 86, 031143 (2012)

Method 1: Direct solution of the boundary condition problem

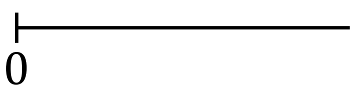
Semiinfinite media

General solution: $p(x,t) = \frac{1}{\sqrt{4\pi Dt}} e^{-(x-x_0)^2/4Dt}$

Image method for a target at $x=0$: $p(x,t) = \frac{1}{\sqrt{4\pi Dt}} \left[e^{-(x-x_0)^2/4Dt} - e^{-(x+x_0)^2/4Dt} \right] \approx$

$$\lim_{t\to\infty} p(x,t) \approx \frac{1}{\sqrt{4\pi Dt}} \frac{x x_0}{Dt} e^{-(x+x_0)^2/4Dt}$$

$$\to f(t) = +D \left. \frac{\partial p(x,t)}{\partial x} \right|_0 = \frac{x_0}{\sqrt{4\pi D t^3}} e^{-{x_0}^2/4Dt}$$



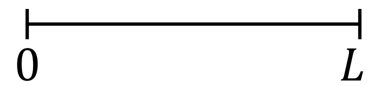
$\to \int_0^\infty dt f(t) = 1,$ but $\langle T \rangle$!!!!

$(f(t) \sim n^{-3/2} \sim t^{-3/2}$: Sparre-Andersen theorem)

Finite media

General solution (with $\rho_B = 0$): $p(x,t) = \sum_n \sum_i A_i \sin\left(\frac{i\pi x}{L}\right) e^{-(n\pi/L)^2 Dt}$

Two targets in $x = 0$ and $x = L$:



$$\lim_{t_m \to \infty} S(t_m) \sim e^{-(\pi/L)^2 D t_m}$$

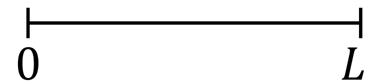
A closed expression is attainable in the Laplace space $\left(p(x,s) = \int_0^\infty dt e^{-st} p(x,t)\right)$

$$p(x,s) = \frac{\sinh\left(\sqrt{\frac{s}{D}}x_0\right)\sinh\left(\sqrt{\frac{s}{D}}(L-x_0)\right)}{\sqrt{sD}\sinh\left(\sqrt{\frac{s}{D}}L\right)}$$

$$\to f(s) = +D\frac{\partial p(x,s)}{\partial x}\bigg|_0 - D\frac{\partial p(x,s)}{\partial x}\bigg|_L = \frac{\sinh\left(\sqrt{\frac{s}{D}}x_0\right)\sinh\left(\sqrt{\frac{s}{D}}(L-x_0)\right)}{\sinh\left(\sqrt{\frac{s}{D}}L\right)} \qquad \left(f(t) \sim e^{-t/T^*}\right)$$

$$\to \langle T \rangle = \lim_{s \to 0} \frac{df(s)}{ds} = \frac{x_0(L-x_0)}{2D}$$

Method 2: Derivation of the MFPT evolution equation



$$\frac{\partial p(x,t)}{\partial t} = D\,\frac{\partial^2 p(x,t)}{\partial x^2}$$

$$\frac{\partial p(x_0,t_0)}{\partial t_0} = -D\,\frac{\partial^2 p(x_0,t_0)}{\partial {x_0}^2}$$ (backward equation: $p(x_0,t_0) = p(x_0,t_0|x,t)$)

$$\frac{\partial S(x_0,t_0)}{\partial t_0} = -D\,\frac{\partial^2 S(x_0,t_0)}{\partial {x_0}^2}$$ (survival probability: $S(x_0,t_0) = \int_0^L dx p(x_0,t_0)$)

$$-1 = D\,\frac{\partial^2 \langle T\rangle}{\partial {x_0}^2}$$ (using $\langle T\rangle = \int_0^\infty dt_0 S(x_0,t_0)$ as before)

For boundary conditions $\langle T\rangle_{x_0=0} = \langle T\rangle_{x_0=L} = 0$, we get again $\langle T\rangle = \frac{x_0(L-x_0)}{2D}$

Method 3: Renewal approximation

We assume one target located at $x = 0$ and introduce $q(t)$ as the rate at which target detection occurs for a free particle:

$$q(t; x_0) = f(t; x_0) + \int_0^t q(t - t'; 0) f(t'; x_0) dt$$

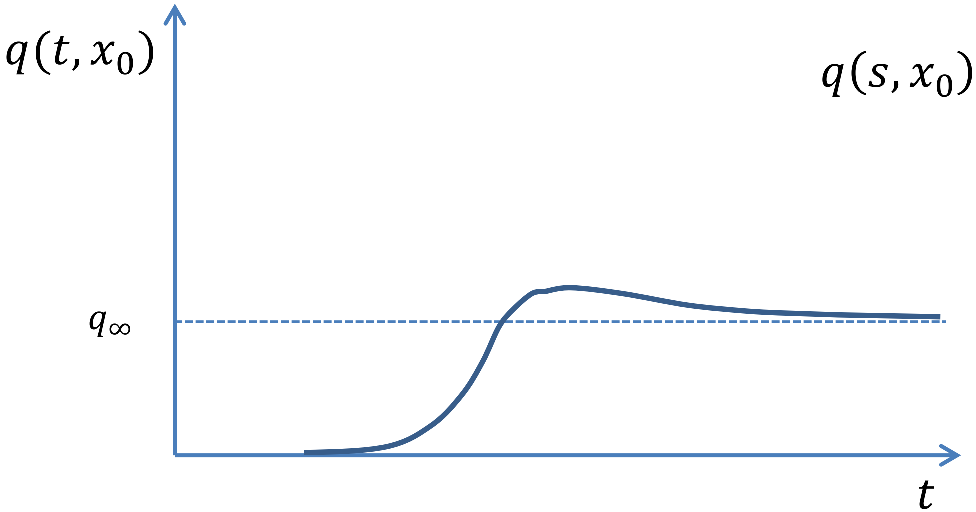
$$\Rightarrow \quad \boxed{f(s, x_0) = \frac{q(s, x_0)}{1 + q(s, 0)}}$$

Alternative derivation:

$q(t, x_0) = q_1(t, x_0) + q_2(t, x_0) + q_3(t, x_0) + \cdots = f(t, x_0) + f(t, x_0) * f(t, 0) + f(t, x_0) * f(t, 0) * f(t, 0) + \cdots$

$$q(s, x_0) = f(s, x_0) \sum_{i=0}^{\infty} f(s, 0) = \frac{f(s, x_0)}{1 - f(s, 0)} \quad \Rightarrow \quad \boxed{f(s, x_0) = \frac{q(s, x_0)}{1 + q(s, 0)}}$$

An essential advantage of this framework is that it allows a very general and intuitive understanding of the Mean First Detection Time (MFDT) in a finite media.



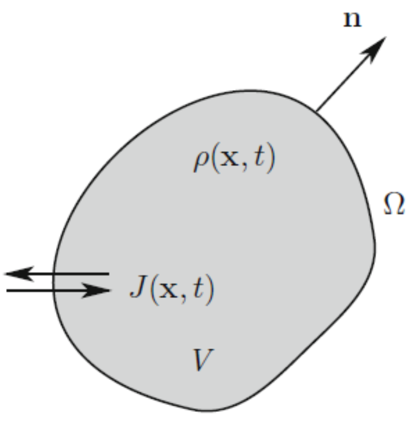
$$q(s,x_0) = q_\infty \frac{1}{s} + q_*(x_0)$$

$$\langle T\rangle = \int_0^\infty dt\, t f(t) = \lim_{s\to 0}\frac{df(s)}{ds} = \underbrace{\frac{1+q_*(0)}{q_\infty}}_{\text{Uniform initial condition}} - \frac{q_*(x_0)}{q_\infty} = \frac{q_*(0)-q_*(x_0)}{q_\infty} + \underbrace{\frac{1}{q_\infty}}_{x_0=0}$$

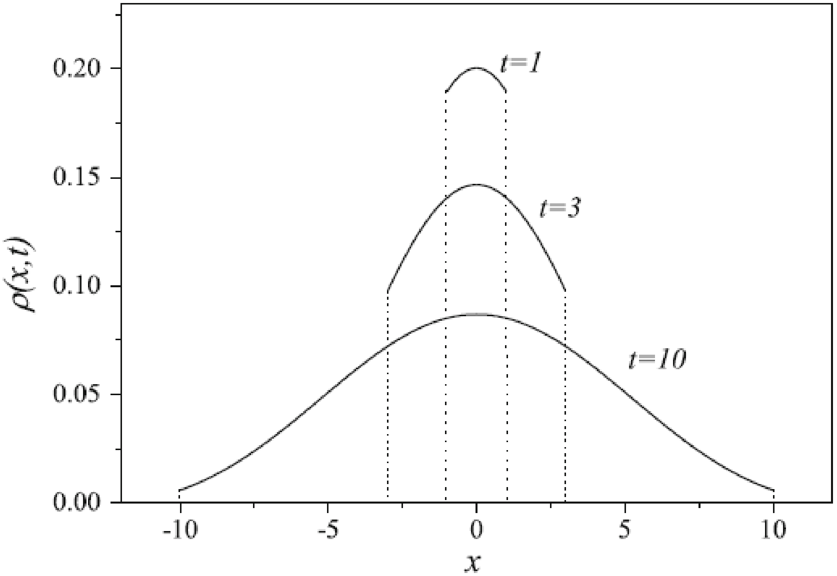
Macroscopic description

Mass balance: $$\frac{\partial \rho(\mathbf{x},t)}{\partial t} + \nabla \cdot \mathbf{J}(\mathbf{x},t) = 0$$

Constitutive equation: $$J(t+\tau) \approx J + \tau \frac{\partial J}{\partial t} = -D \frac{\partial \rho}{\partial x}$$



$$\boxed{\tau \frac{\partial^2 \rho}{\partial t^2} + \frac{\partial \rho}{\partial t} = D \frac{\partial^2 \rho}{\partial x^2}}$$



Mesoscopic description

It is convenient to separate particles moving to the right (ρ_+) or to the left (ρ_-):

$$\rho(x,t) = \rho_+(x,t) + \rho_-(x,t)$$
$$\rho_+(x,t+\tau) = p\rho_+(x-a,t) + q\rho_-(x-a,t)$$
$$\rho_-(x,t+\tau) = p\rho_-(x+a,t) + q\rho_+(x+a,t)$$

So we obtain a Markovian embedding that can be treated in analogy to the diffusion case:

$$\tau\frac{\partial\rho_+(x,t)}{\partial t} + O(\tau^2) = -a\frac{\partial\rho_+(x,t)}{\partial x} + O(a^2) - \lambda\tau\rho_+(x,t) + \lambda\tau a\frac{\partial\rho_+(x,t)}{\partial x} + \lambda\tau\rho_-(x,t) - \lambda\tau a\frac{\partial\rho_-(x,t)}{\partial x}$$

$$\tau\frac{\partial\rho_-(x,t)}{\partial t} + O(\tau^2) = +a\frac{\partial\rho_-(x,t)}{\partial x} + O(a^2) - \lambda\tau\rho_-(x,t) - \lambda\tau a\frac{\partial\rho_-(x,t)}{\partial x} + \lambda\tau\rho_+(x,t) + \lambda\tau a\frac{\partial\rho_+(x,t)}{\partial x}$$

$$\Rightarrow \quad \frac{\partial\rho_+}{\partial t} + v\frac{\partial\rho_+}{\partial x} = \lambda(\rho_- - \rho_+)$$
$$\frac{\partial\rho_-}{\partial t} - v\frac{\partial\rho_-}{\partial x} = -\lambda(\rho_- - \rho_+)$$

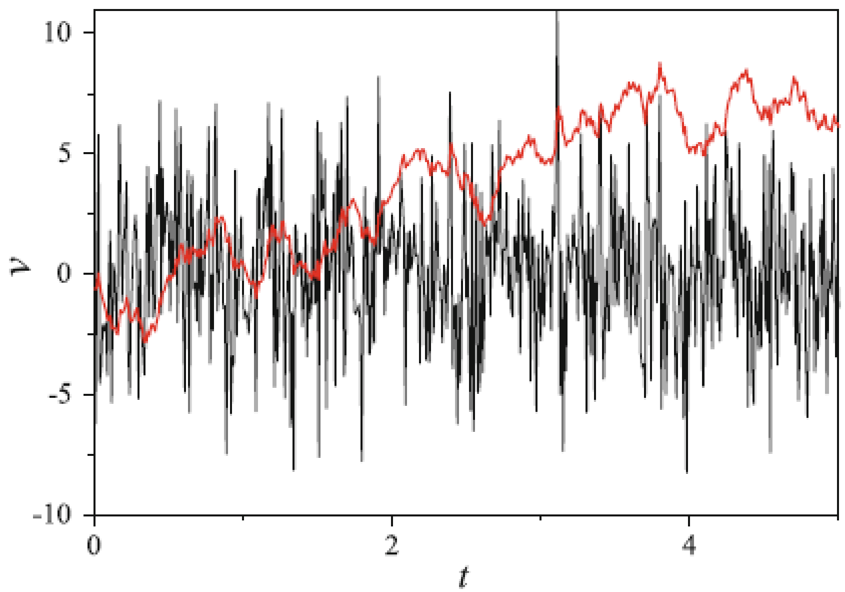
$$\Rightarrow \quad \boxed{\tau\frac{\partial^2\rho}{\partial t^2} + \frac{\partial\rho}{\partial t} = D\frac{\partial^2\rho}{\partial x^2}}$$

Microscopic description

An **Ornstein-Uhlenbeck process** is defined as a stationary, Gaussian and Markovian process whose increments are independent and follow a Gaussian distribntion.

$$\frac{\mathrm{d}x}{\mathrm{d}t} = v$$
$$\frac{\mathrm{d}v}{\mathrm{d}t} = -\gamma v + \sigma \xi(t)$$

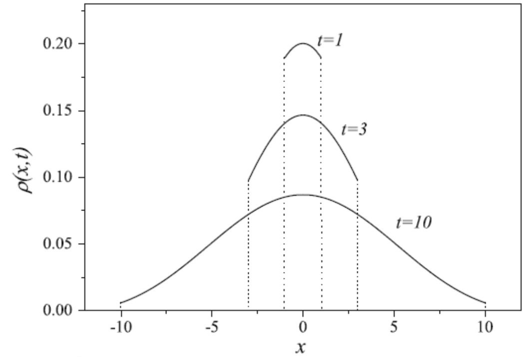
$$\Rightarrow \quad \frac{\partial P(x,v,t)}{\partial t} = -v \frac{\partial P(x,v,t)}{\partial x} + \frac{\partial}{\partial v}[\gamma v P(x,v,t)] + \frac{\sigma^2}{2}\frac{\partial^2 P(x,v,t)}{\partial v^2}$$



Fundamental properties

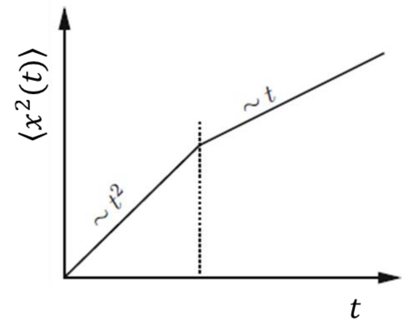
Telegrapher's equation

$$\rho(x,t) = \begin{cases} \frac{e^{-t/2\tau}}{2}\left\{\delta(x-vt)+\delta(x+vt)+\frac{1}{2v\tau}\left[I_0(z)+\frac{t}{2\tau z}I_1(z)\right]\right\} & \text{for } |x|<vt \\ 0 \quad \text{for } |x|\geq vt \end{cases}$$



$$\langle x^2(t)\rangle = x_0^2 + 2D\tau\left(\frac{t}{\tau}+e^{-t/\tau}-1\right)$$

$$\left(\langle x^2(t)\rangle = \begin{cases} v^2t^2, & t \ll \tau \\ 2Dt, & t \gg \tau \end{cases}\right)$$



Ornstein-Uhlenbeck process

$$P(v,t) = \frac{1}{\sqrt{2\pi\sigma_v^2}}e^{-\frac{(v-\langle v\rangle)^2}{2\sigma_v^2}}$$

$$\sigma_v^2 \equiv \langle v^2\rangle - \langle v\rangle^2$$

$$\langle x^2\rangle = \frac{\sigma^2}{\gamma^2}\left[t-\frac{2}{\gamma}\left(1-e^{-\gamma t}\right)+\frac{1}{2\gamma}\left(1-e^{-2\gamma t}\right)\right]+\left[x_0+\frac{v_0}{\gamma}\left(1-e^{-\gamma t}\right)\right]^2$$

$$\langle v^2\rangle = v_0^2e^{-2\gamma t}+\frac{\sigma^2}{2\gamma}\left(1-e^{-2\gamma t}\right)$$

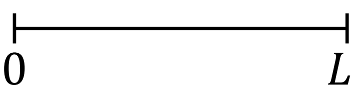
Method 1: Direct solution of the boundary condition problem

$$\frac{\partial \rho_+}{\partial t} + v\frac{\partial \rho_+}{\partial x} = \lambda(\rho_- - \rho_+)$$
$$\frac{\partial \rho_-}{\partial t} - v\frac{\partial \rho_-}{\partial x} = -\lambda(\rho_- - \rho_+)$$

$$J = \rho_+ - \rho_- \quad \Longrightarrow \quad \rho = \rho_+ + \rho_-$$

$$s\rho(x,t) = -v\frac{\partial J(x,t)}{\partial x}$$
$$sJ(x,t) = -v\frac{\partial \rho(x,t)}{\partial x} - 2\lambda J(x,t)$$

$$\rho_+(0,t) = 0$$
$$\rho_-(L,t) = 0$$



$$\Rightarrow \quad \rho(x,s) = \begin{cases} A_1(s,x_0)\left[e^{\frac{\beta s x}{v}} + \frac{1-\sqrt{\beta}}{1+\sqrt{\beta}}e^{-\frac{\beta s x}{v}}\right]; & x < x_0 \\ A_2(s,x_0)\left[e^{\frac{\beta s x}{v}} + \frac{1+\sqrt{\beta}}{1-\sqrt{\beta}}e^{-\frac{\beta s(2L-x)}{v}}\right]; & x > x_0 \end{cases}$$

$$\beta \equiv \frac{s+2\lambda}{s}$$

$$f(s,x_0) = v\rho_+(L,s) + v\rho_-(0,s) \quad \Rightarrow \quad \boxed{\langle T\rangle = \lim_{s\to 0}\frac{df(s,x_0)}{ds} = \frac{\lambda x_0(L-x_0)}{v^2} + \frac{L}{2v}}$$

Masoliver, Porrà and Weiss. PRA 45, 2222 (1992)

Method 2: Derivation of the MFPT evolution equation

$$\frac{\partial \rho_+}{\partial t} + v\frac{\partial \rho_+}{\partial x} = \lambda(\rho_- - \rho_+)$$
$$\frac{\partial \rho_-}{\partial t} - v\frac{\partial \rho_-}{\partial x} = -\lambda(\rho_- - \rho_+)$$

$\Rightarrow$

$$-1 = v\frac{\mathrm{d}T_+(x')}{\mathrm{d}x'} + \lambda\left[T_-(x') - T_+(x')\right]$$
$$-1 = -v\frac{\mathrm{d}T_-(x')}{\mathrm{d}x'} + \lambda\left[T_+(x') - T_-(x')\right]$$

$$J = T_+ - T_-$$
$$T = T_+ + T_-$$

$\Rightarrow$

$$0 = v\frac{\mathrm{d}T(x')}{\mathrm{d}x'} - 2\lambda J(x')$$
$$-2 = v\frac{\mathrm{d}J(x')}{\mathrm{d}x'}$$

$$T_+(L) = 0$$
$$T_-(0) = 0$$

$\Rightarrow$

$$\boxed{\langle T\rangle = \frac{\lambda x_0(L - x_0)}{v^2} + \frac{L}{2v}}$$

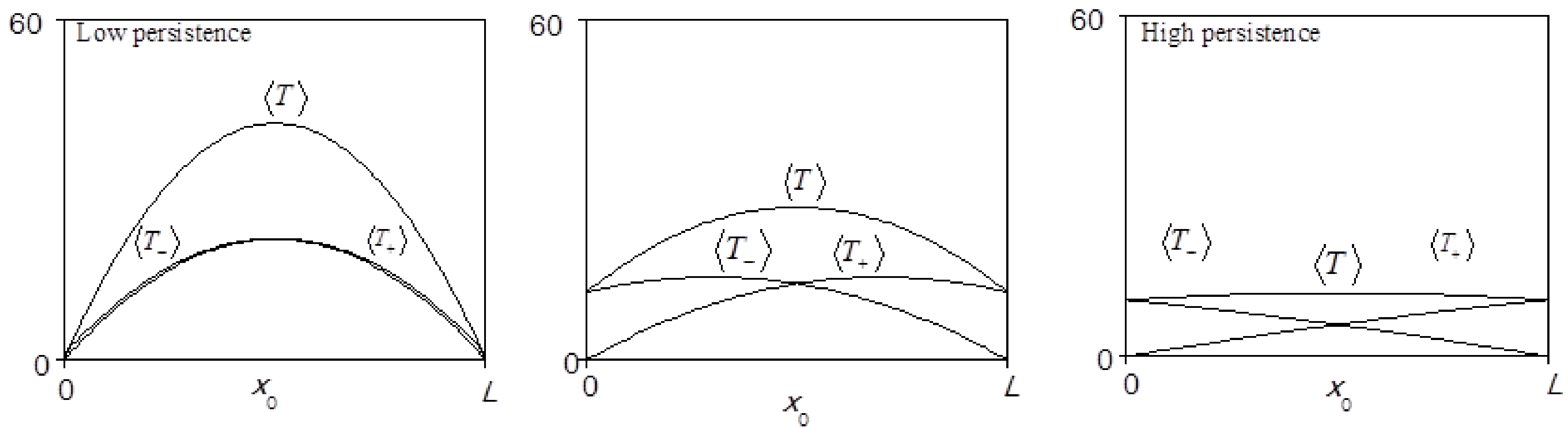
Weiss. J. Stat. Phys. 37, 325 (1984)

2. PERSISTENT MOTION

$$\langle T_+ \rangle = \frac{\lambda x_0 (L - x_0)}{2v^2} + \frac{L - x_0}{2v}$$

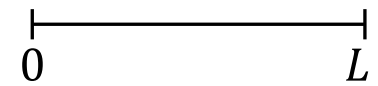
$$\langle T \rangle = \frac{\lambda x_0 (L - x_0)}{v^2} + \frac{L}{2v}$$

$$\langle T_- \rangle = \frac{\lambda x_0 (L - x_0)}{2v^2} + \frac{x_0}{2v}$$



Fluctuating forces

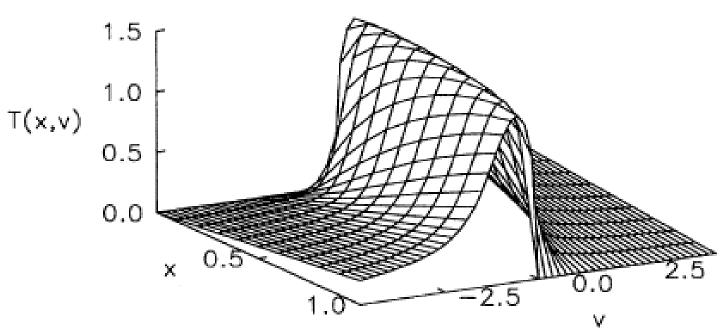
$$\ddot{X}(t) = \xi(t) \qquad \langle \xi(t)\xi(t') \rangle = D\delta(t - t')$$



$$\frac{\partial \rho(x,v,t)}{\partial t} = \frac{D}{2}\frac{\partial^2 \rho(x,v,t)}{\partial v^2} - v\frac{\partial \rho(x,v,t)}{\partial x}$$

$$-1 = \frac{D}{2}\frac{\partial^2 T}{\partial {v_0}^2} + v\frac{\partial T}{\partial x_0} \qquad T(L,v) = 0 \quad \text{if } v \geq 0, \quad T(0,v) = 0 \quad \text{if } v \leq 0$$

$$\Rightarrow \quad T(x,v) = \left(\frac{2L^2}{D}\right)^{1/3}\left[A\left(\frac{x}{L}, (2/LD)^{1/3}|v|\right)\Theta(-v) + A\left(1 - \frac{x}{L}, (2/LD)^{1/3}|v|\right)\Theta(v)\right]$$



$$T(x,0) = N\left(\frac{2L^2}{D}\right)^{1/3}\left(\frac{x}{L}\right)^{1/6}\left(1 - \frac{x}{L}\right)^{1/6} \times \left[F\left(1, -\frac{1}{3}; \frac{7}{6}; \frac{x}{L}\right) + F\left(1, -\frac{1}{3}; \frac{7}{6}; 1 - \frac{x}{L}\right)\right]$$

Masoliver and Porrà. PRL 75, 189 (1995)

2. PERSISTENT MOTION

Alternative in semiinfinite media

$$\ddot{X}(t) = \xi(t)$$

$$Q(x_0, v_0; t) = \int_{-\infty}^{\infty} \mathrm{d}v \int_0^{\infty} \mathrm{d}x \; P(x, v; x_0, v_0; t) \qquad \frac{\mathrm{d}}{\mathrm{d}t} Q(x_0, v_0; t) = \int_{-\infty}^{\infty} \mathrm{d}v \; vP(0, v; x_0, v_0; t)$$

$$P_0(0, v_1; 0, v_0; t_1) = \int_0^{t_1} \mathrm{d}t \int_0^{\infty} \mathrm{d}v \; vP_0(0, v_1; 0, -v; t_1 - t) P(0, -v; 0, v_0; t)$$

$$\begin{aligned} \tilde{P}_0(x, v; x_0, v_0; s) = \int_0^{\infty} \mathrm{d}F \; F^{-1/3} & \\ \times [\theta(x - x_0) \mathrm{e}^{-F(x-x_0)} \mathrm{Ai}(-F^{1/3} v + F^{-2/3} s) \mathrm{Ai}(-F^{1/3} v_0 + F^{-2/3} s) & \\ + \theta(x_0 - x) \mathrm{e}^{-F(x_0-x)} \mathrm{Ai}(F^{1/3} v + F^{-2/3} s) \mathrm{Ai}(F^{1/3} v_0 + F^{-2/3} s)]. & \end{aligned}$$

$$Q(x_0, v_0; t) = \frac{3^{4/3} \Gamma(1/4)}{2\pi^{3/2}} \left(\frac{{x_0}^{2/3}}{t} \right)^{1/4} U(-1/6, 2/3, {v_0}^3 / 9{x_0}^2) \sim t^{-1/4}$$

Burkhardt. J. Stat. Mech. P07004 (2007)

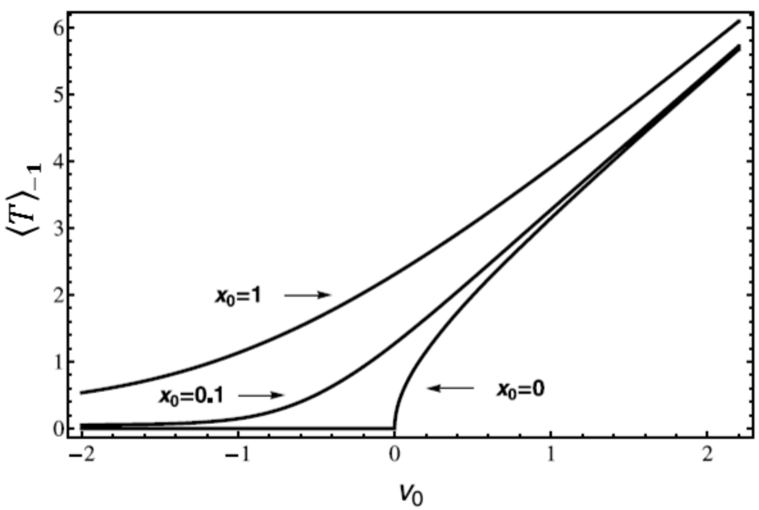
Fluctuating and constant forces

$$\frac{dv}{dt} = \gamma + \xi(t)$$

$$P_\gamma(x, v; x_0, v_0; t) = \exp\left[\frac{1}{2}\gamma(v - v_0) - \frac{\gamma}{4}t\right] P_0(x, v; x_0, v_0; t)$$

$$Q_1(x_0, v_0; \infty) = 1 - \frac{e^{-v_0/2}}{\sqrt{2\pi}} \int_0^\infty dF\, F^{-7/6} \exp\left(-\frac{1}{12F} - Fx_0\right) \mathrm{Ai}\left(F^{1/3} v_0 + \frac{1}{4}F^{-2/3}\right)$$

$$\begin{aligned} T_{-1}(x_0, v_0) = {} & \frac{1}{8}\sqrt{\frac{3}{\pi}} \int_0^\infty dt\, t^{-3/2} (6x_0 + 2v_0 t + t^2) \exp\left[-\frac{3}{4}\left(\frac{x_0 + v_0 t}{t^{3/2}} - \frac{1}{2}t^{1/2}\right)^2\right] \\ & - \frac{e^{v_0/2}}{2\pi} \int_0^\infty dF\, F^{-7/6} \exp\left(-\frac{1}{12F} - Fx_0\right) \mathrm{Ai}\left(F^{1/3} v_0 + \frac{1}{4}F^{-2/3}\right) \\ & \times \left[\sqrt{6\pi} - \frac{\pi}{\sqrt{F}} \exp\left(\frac{1}{6F}\right) \mathrm{erfc}\left(\frac{1}{\sqrt{6F}}\right)\right] \end{aligned}$$

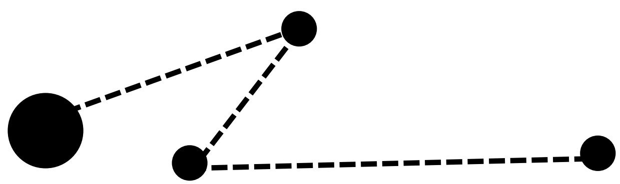


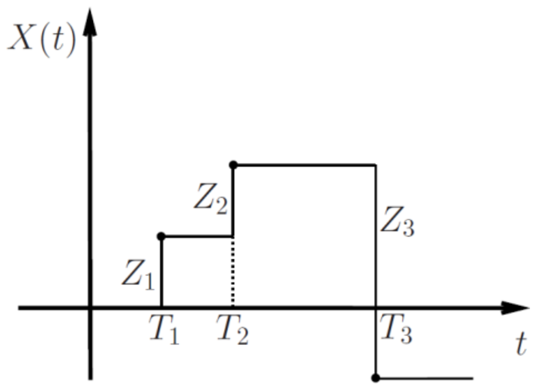
Burkhardt. J. Stat. Phys. 133, 217 (2008)

CTRW: Jump model

We define the position of the particle after n jumps as: $X_n = \sum_{i=1}^{n} Z_i$

…and the time it takes to perform these n jumps as: $T_n = \sum_{i=1}^{n} \Theta_i$





…where Z_i and Θ_i each are iid random variables distributed, respectively, according to

$\phi(x)$: Jump-length probability distribution function (*dispersal kernel*)

$\varphi(t)$: Waiting-time probability distribution function

Probability density of staying (ρ) and arriving (j):

Random jumps: $$\rho_n(k) = \rho_0(k)\Phi(k)^n$$

Random waiting times: $$P_n(s) = \phi(s)\varphi(s)^n = \varphi(s)^n \frac{1-\varphi(s)}{s}$$

$$\rho(k,s) = \sum_{n=0}^{\infty} \rho_n(k) P_n(s) = \rho(k,0)\frac{1-\varphi(s)}{s}\sum_{n=0}^{\infty}[\Phi(k)\varphi(s)]^n$$

$$= \rho(k,0)\frac{1-\varphi(s)}{s}\frac{1}{1-\Phi(k)\varphi(s)}$$ (Montroll-Weiss equation)

$$\rho(x,t) = \overbrace{\rho(x,0)\phi(t)}^{\text{stay}} + \overbrace{\int_0^t j(x,t-u)\phi(u)\mathrm{d}u}^{\text{arrival}}$$

$$j(k,s) = \rho(k,0)\frac{1}{1-\Phi(k)\varphi(s)}$$

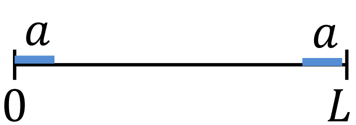
Example: exponential waiting times and jumps

$$\begin{cases} \varphi(t) = \lambda e^{-\lambda t} \\ \phi(x) = \dfrac{\beta}{2} e^{-\beta |x|} \end{cases}$$

Diffusive asymptotic limit: $\lim_{t\to\infty} \langle X^2 \rangle = 2 \dfrac{\langle Z^2 \rangle}{2d\langle \Theta \rangle}\, t$

$$j_L(x,s) = \sum_{m=-\infty}^{\infty} j(x+Lm,s) = \frac{\beta}{2}\left(\sqrt{\frac{s+\lambda}{s}} + \sqrt{\frac{s}{s+\lambda}}\right) \underbrace{\frac{\exp\left(-\sqrt{\frac{s}{s+\lambda}}\beta x\right) + \exp\left(-\sqrt{\frac{s}{s+\lambda}}\beta (L-x)\right)}{1-\exp\left(-\sqrt{\frac{s}{s+\lambda}}\beta L\right)}}_{I(s,x)}$$

First-passage:



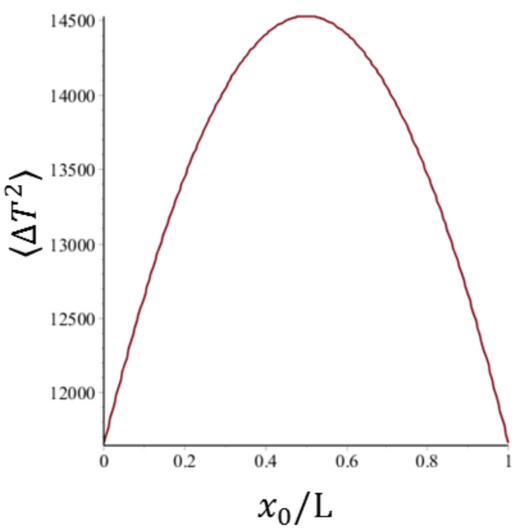
$$q(t,x_0) = \int_0^a j_L(x,t)\,dx + \int_{L-a}^{L} j_L(x,t)\,dx = \frac{\lambda}{s} \sinh\left(\sqrt{\frac{s}{s+\lambda}}\beta a\right) I(s,x_0)$$

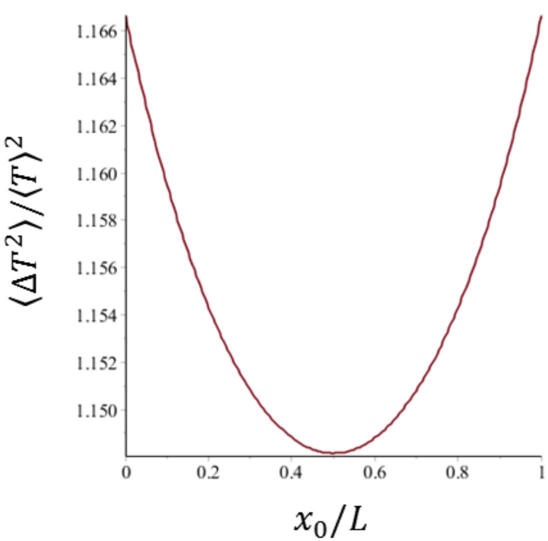
$$q_\infty = \frac{2a\lambda}{L} \qquad q_*(s,x_0) = \frac{a\beta^2\left(L^2 - 6Lx_0 + 6{x_0}^2 + 2a^2\right)}{6L}$$

$$\langle T \rangle = \left(\frac{q_*(0)}{q_\infty} - \frac{q_*(x_0)}{q_\infty} \right) + \frac{1}{q_\infty} = \frac{\beta^2 x_0 (L - x_0)}{2\lambda} + \frac{L}{2a\lambda}$$

$$\langle \Delta T^2 \rangle = \langle T^2 \rangle - \langle T \rangle^2 = \lim_{s \to 0} \frac{d^2 f(s, x_0)}{ds^2} = \cdots = \frac{1 + q_*(s,0) + q_*(s,x_0)}{q_\infty} \langle T \rangle$$

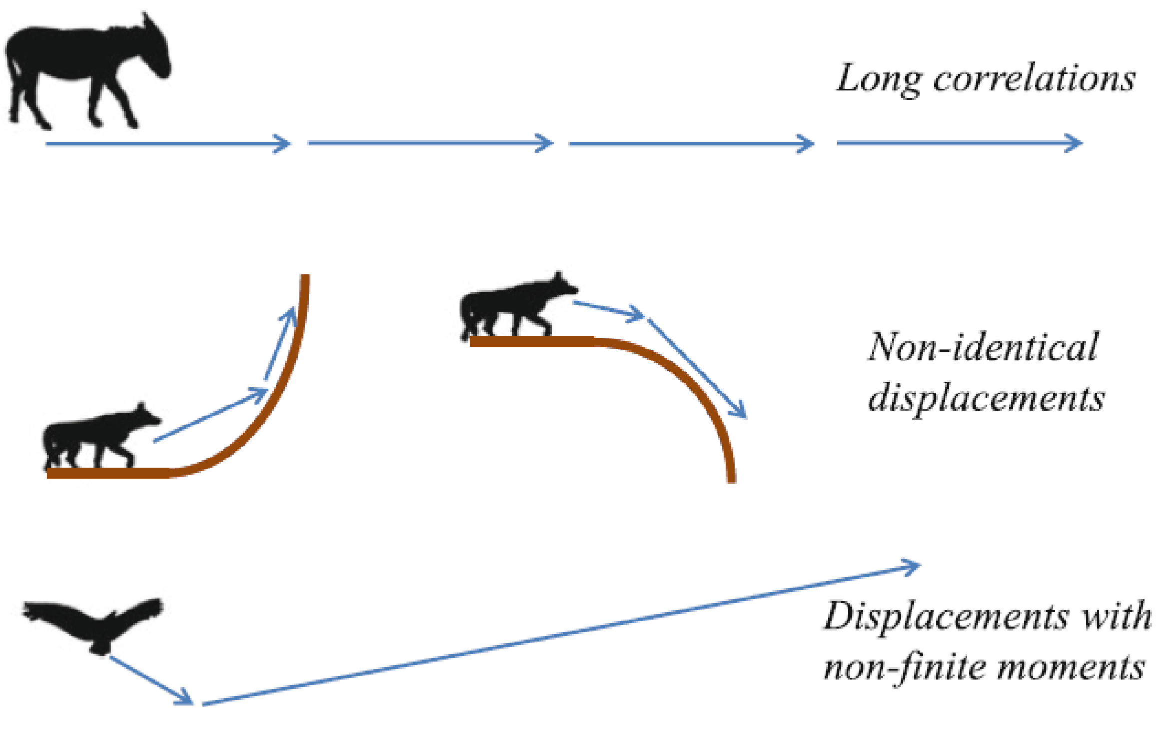
$$= \langle T \rangle^2 + \frac{\beta^2}{6\lambda} (L^2 + 2a^2) \langle T \rangle$$





Anomalous diffusion

$$\langle x^2 \rangle \sim t^{\gamma}$$



Fractional Brownian Motion

$$\frac{\mathrm{d}x}{\mathrm{d}t} = \sqrt{2D}\,\xi(t)$$

Heterogeneous diffusion

$$\frac{\partial \rho}{\partial t} = \nabla \cdot (D_0 x^{\theta} \nabla \rho)$$

Lévy noise/fluctuations

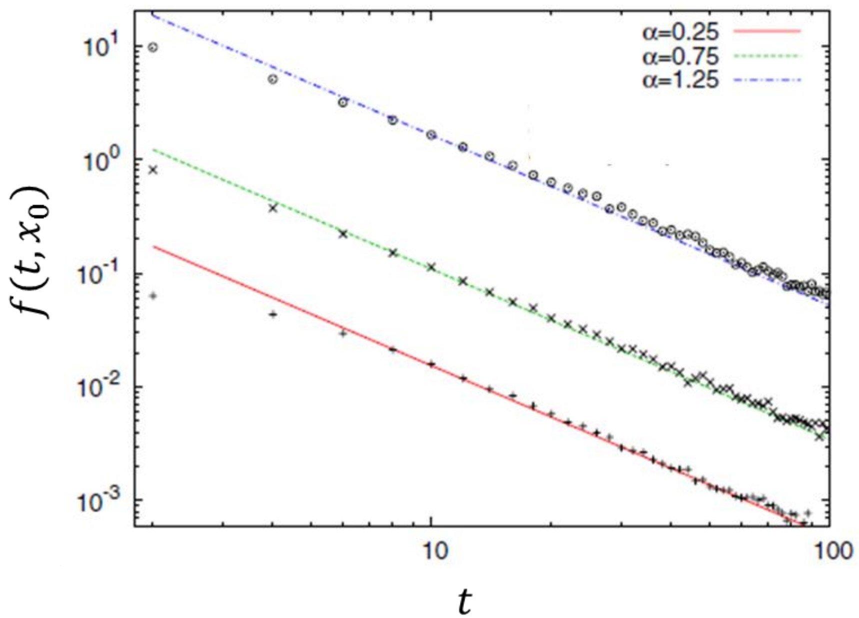
$$\frac{\mathrm{d}x}{\mathrm{d}t} = \sqrt{2D}\,\xi(t)$$

Example: exponential waiting times and power-law jumps (LÉVY FLIGHTS)

$$\begin{cases} \varphi(t) = \lambda e^{-\lambda t} \\ \phi(x) = H(|x| - \epsilon)\, [H(x) + H(-x)]\, \frac{\alpha \epsilon^{\alpha}}{2|x|^{1+\alpha}} \end{cases}$$

0

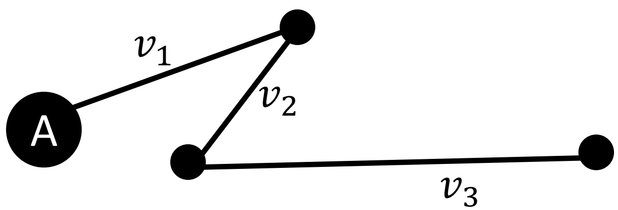
$$\Rightarrow \quad f(t, x_0) \sim \frac{{x_0}^{\alpha/2}}{\Gamma(\frac{\alpha}{2})\sqrt{2\pi\alpha c \Gamma(1-\alpha)\cos(\pi\alpha/2)}}\, t^{-3/2}$$

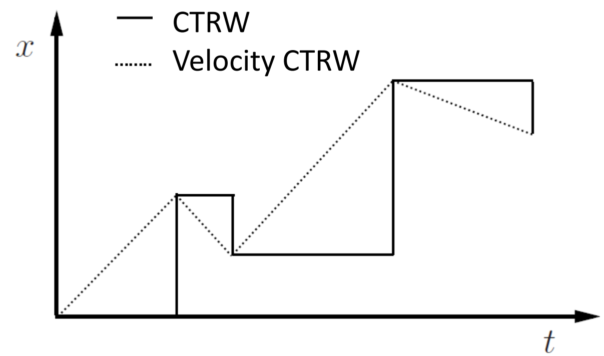


Koren, Lomholt, Chechkin, Klafter and Metzler, PRL 99, 160602 (2007)

CTRW: Velocity model

We use the same definition as before $X_n = \sum_{i=1}^{n} Z_i$ $T_n = \sum_{i=1}^{n} \Theta_i$





…where now $\varphi(t)$ and $\phi(x)$ are not independent, but coupled through a velocity distribution $h(v)$ in the form

$$\Psi(x,t) = \varphi(t) \int_{-\infty}^{\infty} dv\, \delta(x - vt) h(v)$$

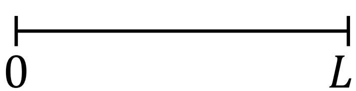
$$\phi(x) = \int_{0}^{\infty} dt\ \varphi(t) \int_{-\infty}^{\infty} dv\, \delta(x - vt) h(v)$$

Example: exponential flights with constant speed

$$\begin{cases} \varphi(t) = \lambda e^{-\lambda t} \\ \phi(x) = \dfrac{\delta(x - vt) + \delta(x + vt)}{2} \, \lambda e^{-\lambda t} \end{cases}$$

$$\Rightarrow \quad \rho_L(x,s) = \frac{1}{2v}\sqrt{\frac{s+\lambda}{s}} \underbrace{\frac{\exp\left(-\sqrt{s(s+\lambda)}x_0/v\right) + \exp\left(-\sqrt{s(s+\lambda)}(L - x_0)/v\right)}{1 - \exp\left(-\sqrt{s(s+\lambda)}L/v\right)}}_{H(s,x)}$$

First-passage:



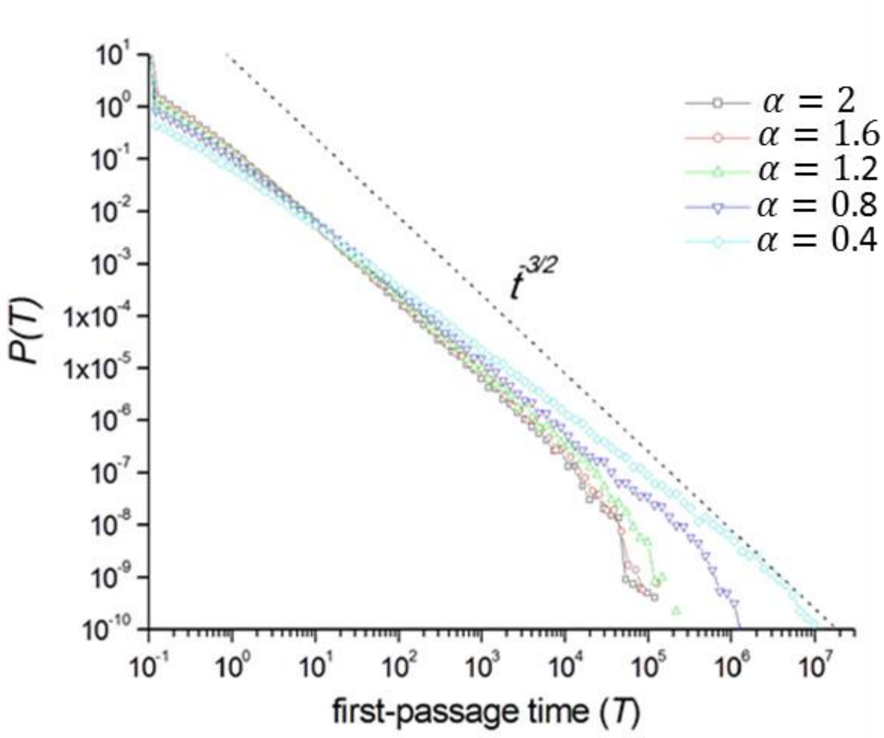
$$q(t,x_0) = \int_{-\infty}^{0} v\rho_L(0,v,t)dv + \int_{0}^{\infty} v\rho_L(L,v,t)dv = \frac{1}{2}\sqrt{\frac{s+\lambda}{s}} H(s,x_0)$$

$$q_\infty = \frac{v}{L} \qquad q_*(s,x_0) = \frac{\lambda\left(L^2 - 6Lx_0 + 6{x_0}^2\right)}{12vL}$$

$$\Rightarrow \quad \langle T \rangle = \lim_{s \to 0}\left(\frac{q_*(s,0)}{q_\infty} - \frac{q_*(s,x_0)}{q_\infty}\right) + \frac{1}{q_\infty} = \frac{\lambda x_0(L - x_0)}{2v^2} + \frac{L}{2v}$$

Example: power-law flights with constant speed (LÉVY WALKS)

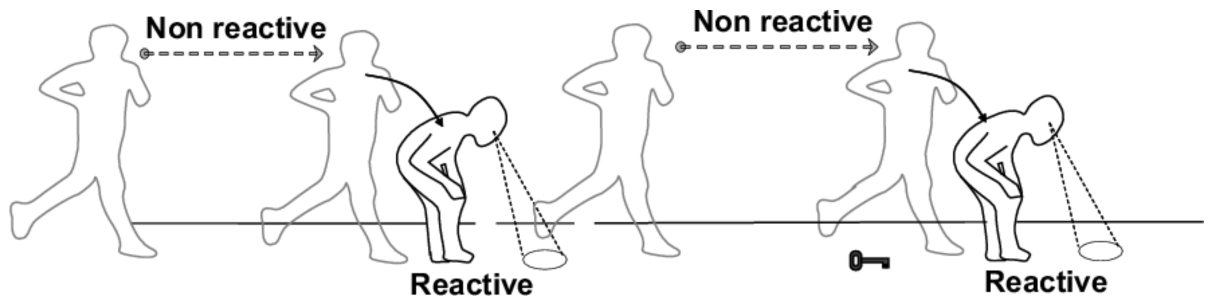
$$
\begin{cases}
\varphi(t) = H(t-\epsilon)\,\frac{\alpha\epsilon^{\alpha}}{t^{1+\alpha}} \\
\phi(x) = \frac{\delta(x-vt)+\delta(x+vt)}{2} H(t-\epsilon)\,\frac{\alpha\epsilon^{\alpha}}{t^{1+\alpha}}
\end{cases}
$$



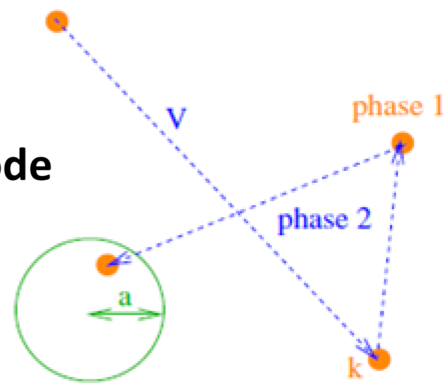
$$
f(t,x_0) \sim \begin{cases} t^{-3/2}\,; & 1 \le \alpha \le 2 \\ t^{-1-\alpha/2}\,; & 0 \le \alpha \le 1 \end{cases}
$$

Korabel and Barkai, J.Stat.Mech. P05022 (2011)
Dybiec and Gudowska-Nowak. EPL 88, 10003 (2009)

Intermittent movement



Static mode



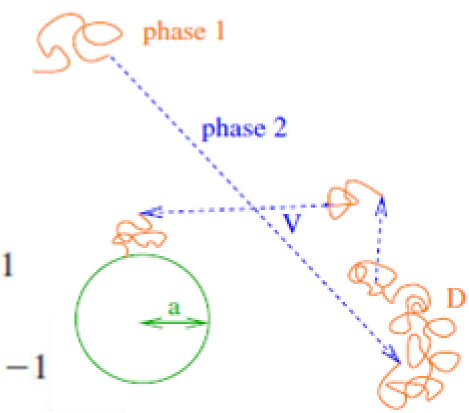
$$V\frac{dt_2^+}{dx}+\frac{1}{\tau_2}(t_1-t_2^+)=-1$$

$$-V\frac{dt_2^-}{dx}+\frac{1}{\tau_2}(t_1-t_2^-)=-1$$

$$\frac{1}{\tau_1}\left(\frac{t_2^+ + t_2^-}{2}-t_1\right)=-1$$

$$\frac{1}{\tau_1}t_2-\left(\frac{1}{\tau_1}+k\right)t_1=-1.$$

Diffusive mode



$$V\frac{dt_2^+}{dx}+\frac{1}{\tau_2}(t_1-t_2^+)=-1$$

$$-V\frac{dt_2^-}{dx}+\frac{1}{\tau_2}(t_1-t_2^-)=-1$$

$$D\frac{d^2t_1}{dx^2}+\frac{1}{\tau_1}\left(\frac{t_2^+}{2}+\frac{t_2^-}{2}-t_1\right)=-1,$$

$$V\frac{dt_2^+}{dx}-\frac{1}{\tau_2}t_2^+=-1 \qquad -V\frac{dt_2^-}{dx}-\frac{1}{\tau_2}t_2^-=-1$$

Bénichou, Loverdo, Moreau and Voituriez. Rev. Mod. Phys. 83, 81 (2011)

For a 1D size domain b:

Static mode

$$t_m = (\tau_1 + \tau_2)\left[\frac{b^2}{3V^2\tau_2^2} + \left(\frac{1}{k\tau_1} + 1\right)\frac{b}{a}\right]$$

$$\tau_1^{\mathrm{opt}} = \sqrt{\frac{a}{Vk}}\left(\frac{b}{12a}\right)^{1/4}$$

$$\tau_2^{\mathrm{opt}} = \frac{a}{V}\sqrt{\frac{b}{3a}}$$

Diffusive mode

$\underline{bD^2 \ll a^3V^2}$

$$\tau_1^{\mathrm{opt}} = \frac{1}{2}\sqrt[3]{\frac{2b^2D}{9V^4}}$$

$$\tau_2^{\mathrm{opt}} = \sqrt[3]{\frac{2b^2D}{9V^4}},$$

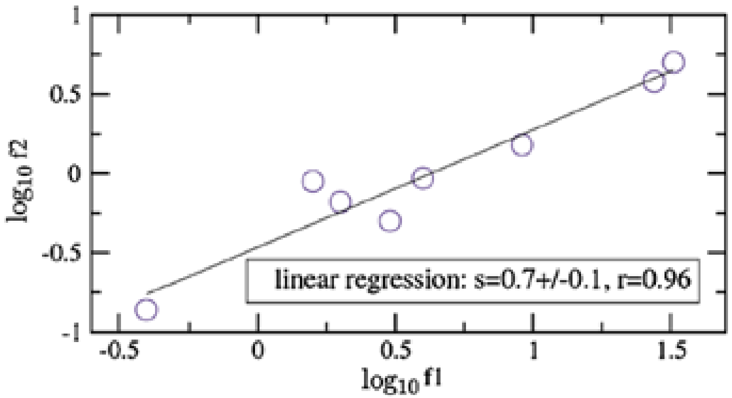
$$t_m^{\mathrm{opt}} \simeq \sqrt[3]{\frac{3^5}{2^4}\frac{b^4}{DV^2}}$$

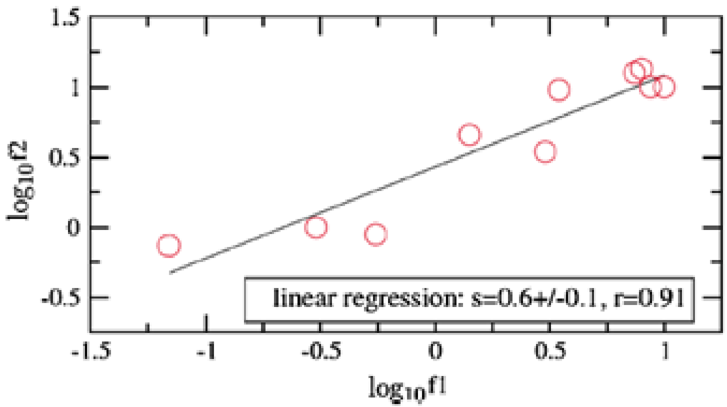
$\underline{bD^2 \gg a^3V^2}$

$$\tau_1^{\mathrm{opt}} = \frac{Db}{48V^2a},$$

$$\tau_2^{\mathrm{opt}} = \frac{a}{V}\sqrt{\frac{b}{3a}},$$

$$t_m^{\mathrm{opt}} \simeq \frac{2a}{V\sqrt{3}}\left(\frac{b}{a}\right)^{3/2}$$





Bénichou, Loverdo, Moreau and Voituriez. Rev. Mod. Phys. 83, 81 (2011)

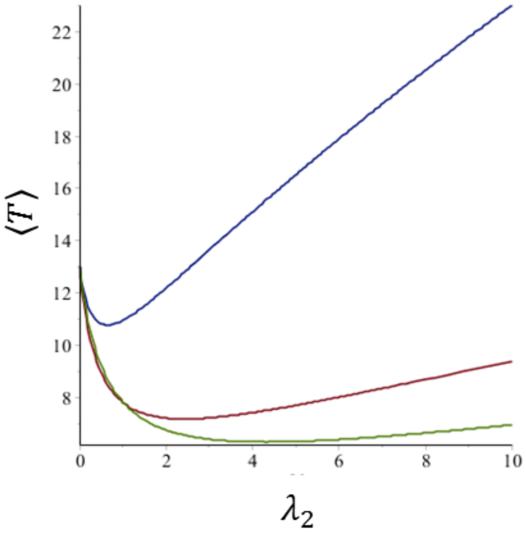
Intermittent movement

1D Diffusive mode

$$\frac{\partial \rho_1(x,t)}{\partial t} = D\frac{\partial^2 \rho_1(x,t)}{\partial x^2} - \lambda_1\rho_1(x,t) + \lambda_2\rho_2(x,t) + \lambda_2\rho_3(x,t)$$

$$\frac{\partial \rho_2(x,t)}{\partial t} = v\frac{\partial \rho_2(x,t)}{\partial x} + \frac{\lambda_1}{2}\rho_1(x,t) - \lambda_2\rho_2(x,t)$$

$$\frac{\partial \rho_3(x,t)}{\partial t} = -v\frac{\partial \rho_3(x,t)}{\partial x} + \frac{\lambda_1}{2}\rho_1(x,t) - \lambda_2\rho_3(x,t)$$



$$q(t,x_0) = \int_{-\infty}^{0} v\rho_1(0,v,t)dv + \int_{0}^{\infty} v\rho_1(L,v,t)dv$$

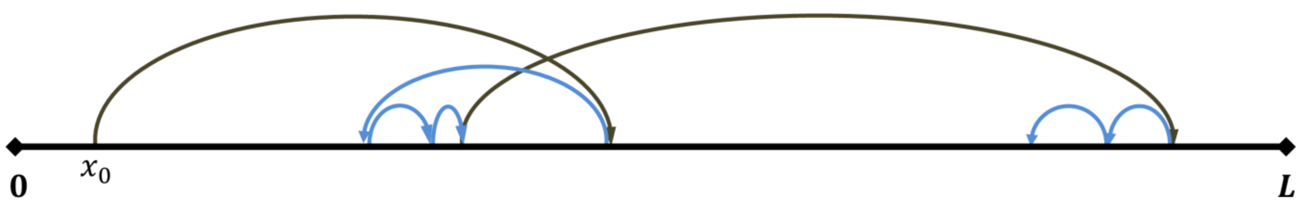
$$q_\infty = \frac{\lambda_2}{\lambda_1+\lambda_2}\frac{v}{L}$$

$$q_*(x_0) = \frac{w{\lambda_2}^2 x_0(L-x_0)}{2L(w\lambda_1+{\lambda_2}^2)} + \frac{\lambda_1 w^2\left(1-e^{-\beta L}-e^{-\beta x_0}-e^{-\beta(L-x_0)}\right)}{2(w\lambda_1+{\lambda_2}^2)^{3/2}(1-e^{-\beta L})}$$

$$(\lambda_2)_{opt} \sim \sqrt{(\lambda_1)_{opt}}$$

2-scale (CTRW) movement

$$\begin{cases} \varphi(t) = w_1 \lambda_1 e^{-\lambda_1 t} + (1 - w_1)\lambda_2 e^{-\lambda_2 t} \\ \phi(x) = \dfrac{\delta(x - vt) + \delta(x + vt)}{2}\varphi(t) \end{cases}$$



We use a Markovian embedding by dividing into modes (like in the telegraph equation)

$$q_i(t;\rho_0) = f_i(t;\rho_0) + \sum_{k=1}^{n} \int_0^t f_k(t - t';\rho_0) q_i(t';\rho_k) dt'$$

$$f(t;\rho_0) = \sum_{i=1}^{n} f_i(t;\rho_0) \quad \Rightarrow \quad \langle T \rangle = \lim_{s \to 0} \sum_{i=1}^{n} \frac{df_i(s;\rho_0)}{ds}$$

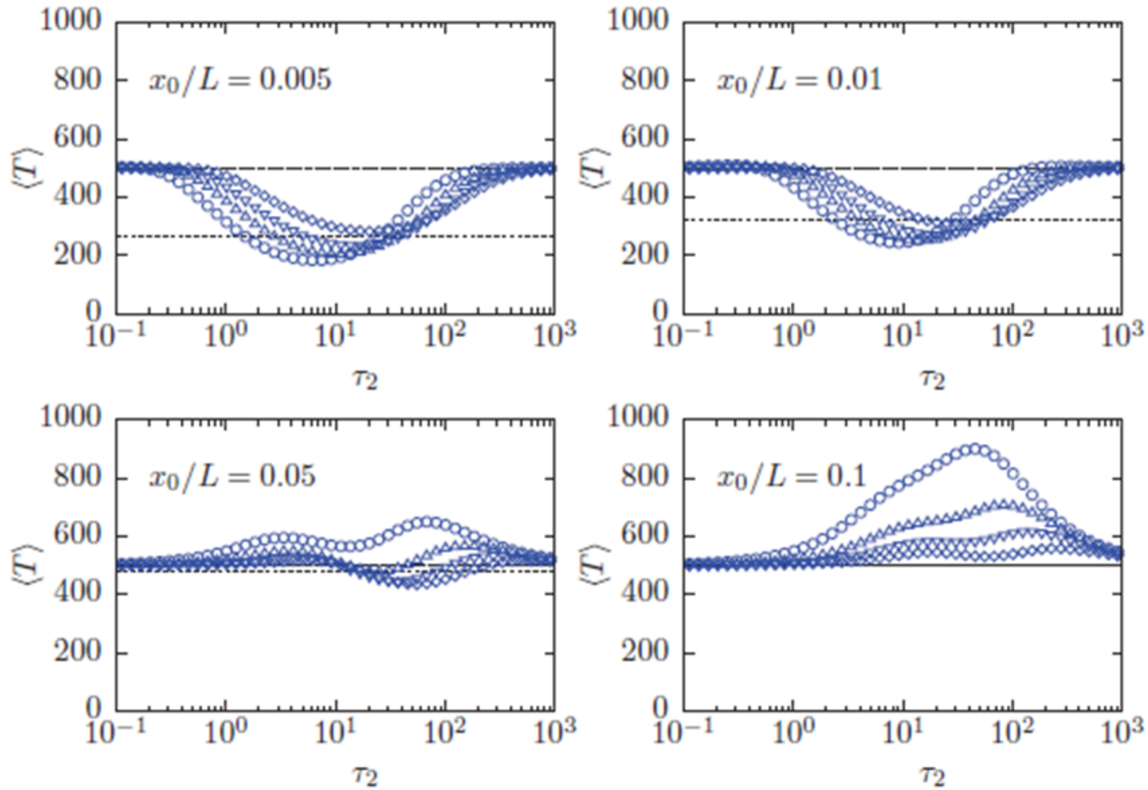
Campos, Bartumeus, Raposo and Méndez, PRE (in press)

4. MULTI-MODE MOVEMENT

$$\langle T\rangle = \frac{L}{2v} + \frac{1-w}{w\lambda_2}\left(1 - \frac{1+\frac{Lw\lambda_2}{2v}}{1+\sqrt{w}}\, exp\left[-\frac{\sqrt{w}x_0\lambda_2}{v}\right]\right)$$

$$\left(\frac{x_0}{L}\right)_{cr} = 0.105$$

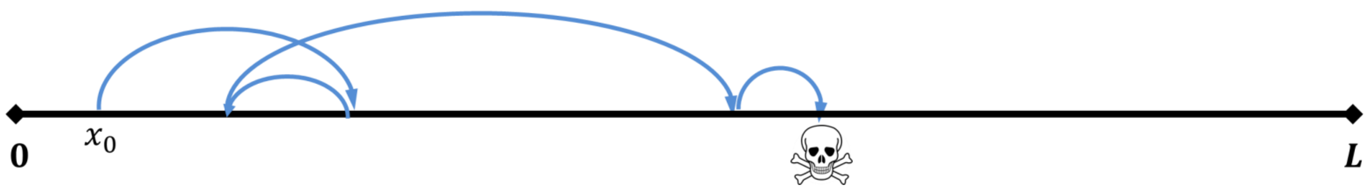
$$(\lambda_2)_{opt} \approx \frac{v}{x_0} \qquad w_{opt} \approx \frac{2x_0}{L}$$



Campos, Bartumeus, Raposo and Méndez, PRE (in press)

Random-walks with mortality

$$\begin{cases} \varphi(t) = \lambda e^{-\lambda t} \qquad \varphi_m(t) = \omega e^{-\omega t} \\ \phi(x) = \dfrac{\delta(x - vt) + \delta(x + vt)}{2} \, \lambda e^{-\lambda t} \end{cases}$$



$$q^*(x_{tg},t|x_0) = f^*(x_{tg},t|x_0) + \int_0^t q^*(x_{tg},t|x_{tg},t') f^*(x_{tg},t'|x_0)\, dt' \qquad f^*(x_{tg},s|x_0) = \frac{q(x_{tg},s+\omega_m|x_0)}{1+q(x_{tg},s+\omega_m|x_{tg})} = f(x_{tg},s+\omega_m|x_0)$$

$$S_\infty^* = 1 - \int_0^\infty f^*(x_{tg},t|x_0)dt = 1 - \lim_{s\to 0} f^*(x_{tg},s|x_0),$$

Semiinfinite media

$$1 - S_\infty^* = \begin{cases} \frac{\alpha_\omega(\omega_m)}{\alpha_\omega(\omega_m)+\omega_m}\, e^{-\alpha_\omega(\omega_m)|x_{tg}-x_0|/v_f}, & x_0 \neq x_{tg} \\ \frac{\alpha_\omega(\omega_m)-\omega_m}{\alpha_\omega(\omega_m)+\omega_m}, & x_0 = x_{tg}. \end{cases}$$

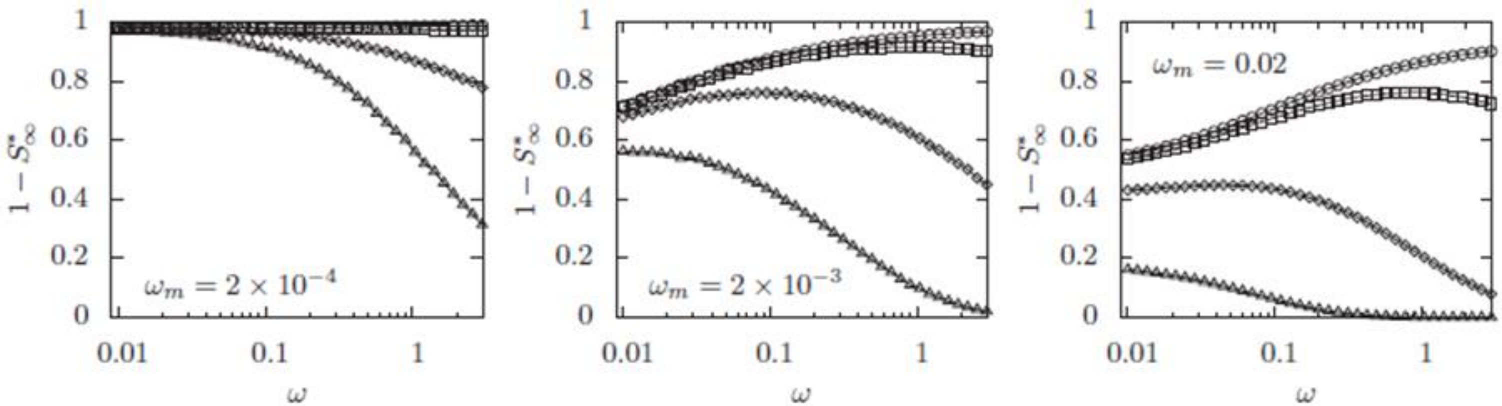
Finite media

$$S_\infty^* = \begin{cases} 1 - \frac{\alpha_\omega(\omega_m)}{\omega_m\beta_L^- + \alpha_\omega(\omega_m)\beta_L^+}\left(e^{-\alpha_\omega(\omega_m)|x_{tg}-x_0|/v_f} + e^{-\alpha_\omega(\omega_m)(L-|x_{tg}-x_0|)/v_f}\right), & x_0 \neq x_{tg} \\ \frac{2\omega_m\beta_L^-}{\omega_m\beta_L^- + \alpha_\omega(\omega_m)\beta_L^+}, & x_0 = x_{tg}, \end{cases}$$

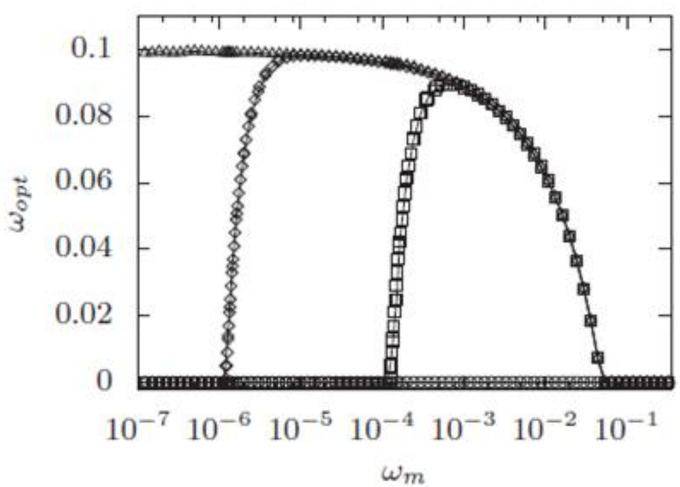
Campos, Abad, Méndez, Yuste and Lindenberg, PRE 91, 052115 (2015)

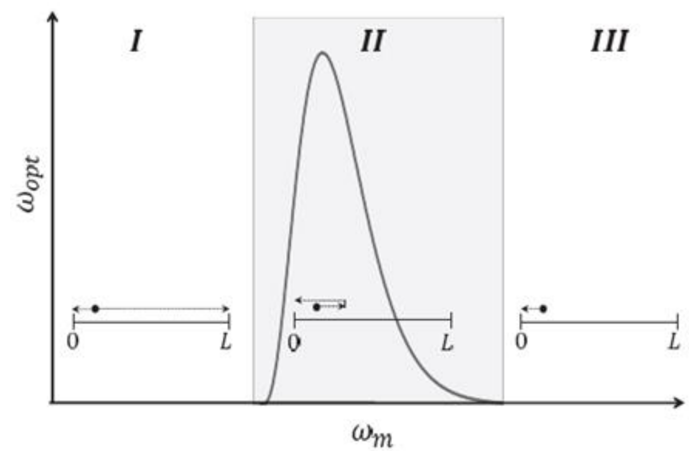
$$S_\infty = \frac{2\omega_m\left[1 - e^{-\alpha_m L/v}\right]}{\omega_m\left[1 - e^{-\alpha_m L/v}\right] + \alpha_m\left[1 + e^{-\alpha_m L/v}\right]}$$

$$\alpha_m \equiv \sqrt{\omega_m(\omega + \omega_m)}$$



Optimal motion scales emerge for intermediate values of the mortality

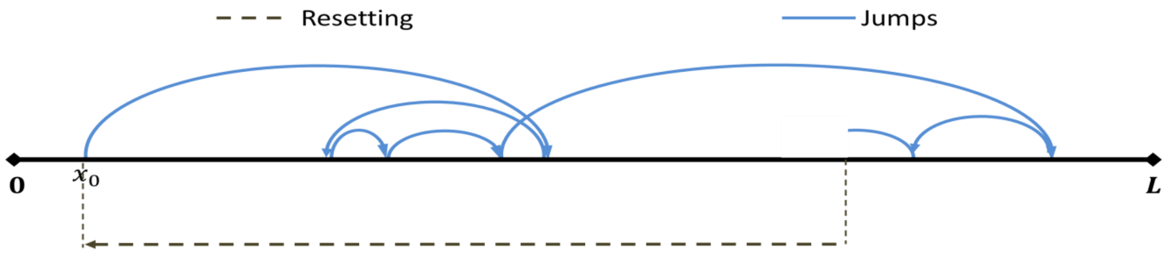




Campos, Abad, Méndez, Yuste and Lindenberg, PRE 91, 052115 (2015)

Random walk with resetting

$$\begin{cases} \varphi(t) = \lambda e^{-\lambda t} \qquad \varphi_m(t) = \omega e^{-\omega t} \\ \phi(x) = \dfrac{\delta(x-vt)+\delta(x+vt)}{2}\,\lambda e^{-\lambda t} \end{cases}$$



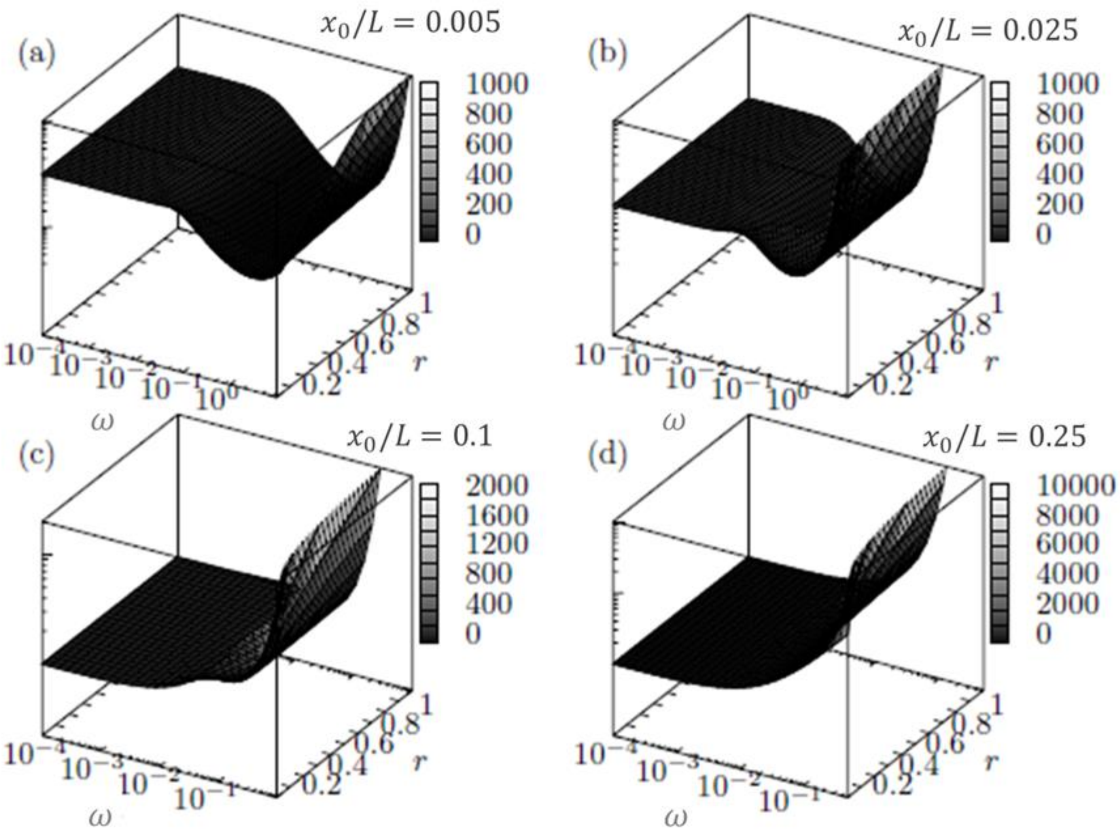
$$\begin{aligned} P(x,t;x_0,x_0^*) &= P_m(x,t;x_0) + P_m(x,t;x_0^*) * \varphi(t) \\ &+ P_m(x,t;x_0^*) * \varphi(t) * \varphi(t) + \ldots \end{aligned}$$

$$P(x,s;x_0,x_0^*) = P_m(x,s;x_0) + \frac{P_m(x,s;x_0^*)\varphi(s)}{1-\varphi(s)}$$

Campos and Méndez. arXiv:1509.05641

$$\langle T \rangle = \frac{1}{\omega_m}\left(\frac{\left(1+\frac{\omega_m}{\alpha_m}\right)\left(1-e^{-\alpha_m L/v}\right)}{e^{-\alpha_m x_0/v}+e^{-\alpha_m L/v}} - 1\right)$$

$$\alpha_m \equiv \sqrt{\omega_m(\lambda+\omega_m)}$$



$$\left(\frac{x_0}{L}\right)_{cr} = 0.115$$

$$(\omega_m)_{opt} = \frac{0.768v}{x_0}$$

Diffusion with resetting

$$(\omega_m)_{opt} = 2.538D/{x_0}^2$$

Lévy flights with resetting

Optimal Lévy exponent: 1/4

Campos and Méndez. arXiv:1509.05641
Evans and Majumdar. PRL 106, 160601 (2011)
Kusmierz et al. PRL 113, 220602 (2014)

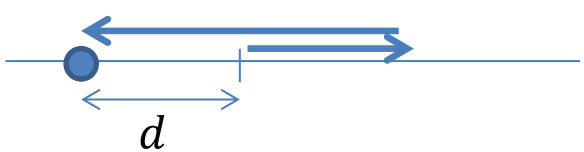
Conclusion

A necessary condition for the emergence of optimal search efficiency (which involves a nontrivial exploration-exploitation tradeoff) is the existence of two scales involved in motion (either movement scales, mortality, resetting, ...). More scales are convenient as long as uncertainty increases.

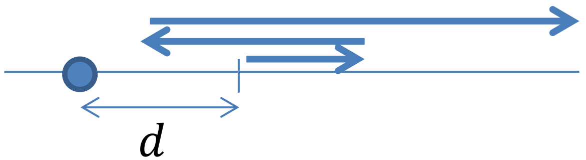
Analogy with optimal deterministic searches:

For the 1-dimensional case, the optimal (deterministic) search strategy is:

Distance known: $\langle T\rangle = 2d/v$



Distance unknown: $\langle T\rangle = 9d/v$



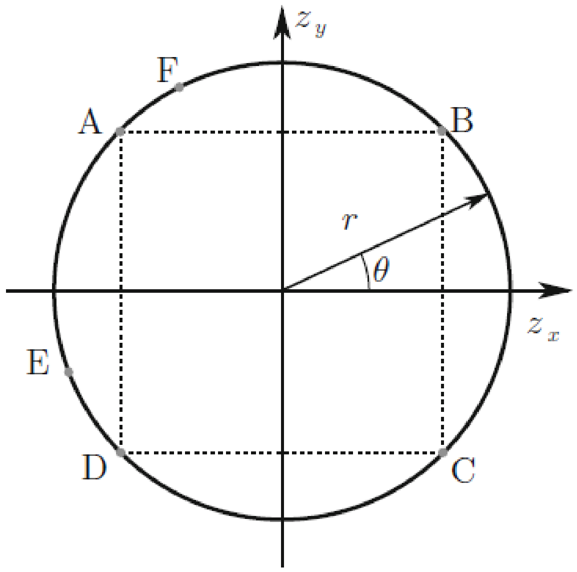
Baeza-Yates, Culberson and Rawlins. Inform. Comput. 106, 234 (1993)

Classical diffusion

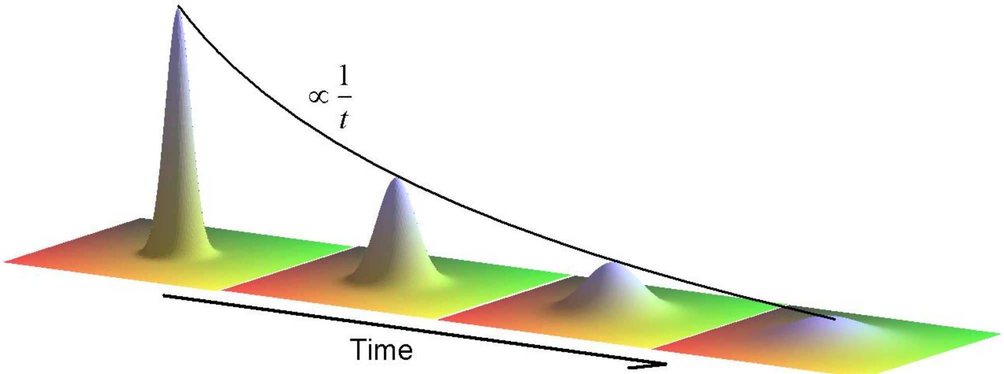
$$\frac{\partial\rho(r,t)}{\partial t} = D\frac{\partial^2\rho(r,t)}{\partial r^2}$$

$$D \equiv \frac{\langle r^2\rangle}{4\tau} \equiv \frac{1}{4\tau}\int_{-\infty}^{\infty} \mathrm{d}z_x \int_{-\infty}^{\infty} \mathrm{d}z_y r^2 \Phi(r) =$$

$$= \frac{1}{4\tau}\int_0^{2\pi} \mathrm{d}\theta \int_0^{\infty} r^2\Phi(r) r\,\mathrm{d}r = \frac{\pi}{2\tau}\int_0^{\infty} r^3\Phi(r)\mathrm{d}r$$



$$\rho(r,t) = \frac{e^{-r^2/4Dt}}{4\pi Dt}$$



Persistent motion (2D extensions of the Ornstein-Uhlenbeck process)

Case 1: independent Cartesian coordinates

$$\frac{\mathrm{d}x}{\mathrm{d}t} = v_x, \quad \frac{\mathrm{d}y}{\mathrm{d}t} = v_y$$
$$\frac{\mathrm{d}v_x}{\mathrm{d}t} = -\gamma v_x + \sigma \xi_x(t), \quad \frac{\mathrm{d}v_y}{\mathrm{d}t} = -\gamma v_y + \sigma \xi_y(t)$$

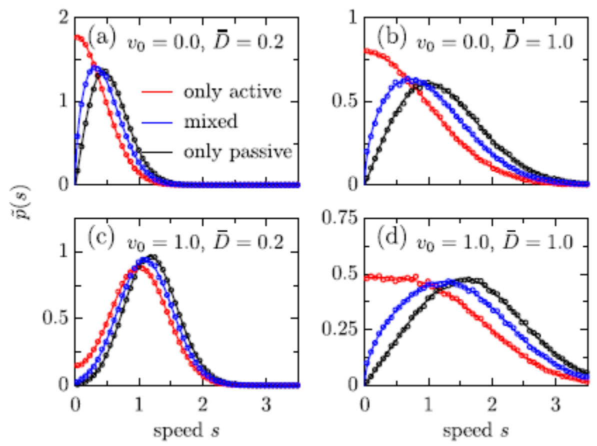
$$\langle x^2(t) + y^2(t) \rangle = \frac{\sigma^2}{\gamma^3}\left(2\gamma t - 1 + \mathrm{e}^{-2\gamma t}\right)$$ (Fürth's formula)

$$\langle \mathbf{v}(t)\mathbf{v}(0) \rangle = \langle v_x(t) v_x(0) \rangle + \langle v_y(t) v_y(0) \rangle = 2v_0^2 \mathrm{e}^{-\gamma t}$$

Case 2: Isotropic fluctuations

$$\frac{\mathrm{d}v}{\mathrm{d}t} = -\gamma(v - v_s) + \sigma \xi_\theta(t)$$
$$\frac{\mathrm{d}\theta}{\mathrm{d}t} = \frac{\sigma}{v}\xi_\perp(t)$$

$$\tilde{p}(s) \sim s^{D/D+D_v}\left[e^{-A(s-v_0)^2} + e^{-A(s+v_0)^2}\right]$$

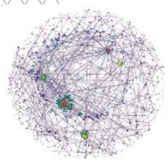


Romanczuk and Schimansky-Geier. PRL 106, 230601 (2011)

MFPT in higher dimensions: Renewal approach

Fractal media: 

$$\rho(r,t) \sim t^{-d_f/d_w} f\left(\frac{r}{t^{1/d_w}}\right)$$

Scale-free networks: 

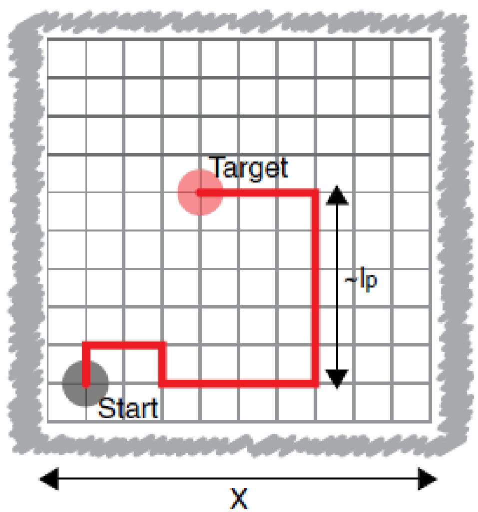
$$\rho(r,t) \sim t^{-d_B/d_w} f\left(\frac{r}{t^{1/d_w}}\right)$$

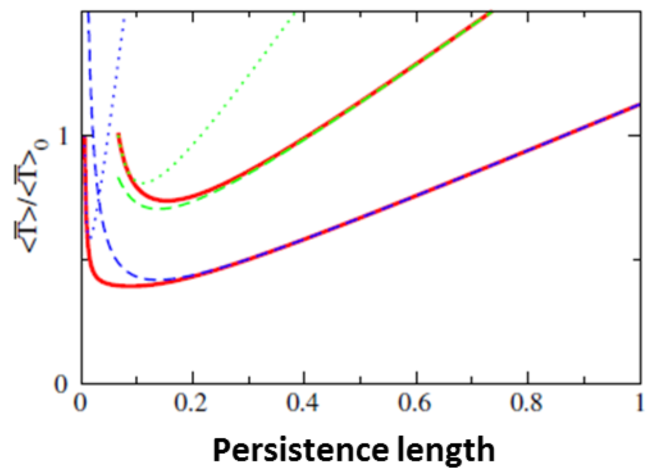
$$\langle \mathrm{T} \rangle \sim \begin{cases} N(A - B r^{d_w - d_f}) & \text{for } d_w < d_f \\ N(A + B \ln r) & \text{for } d_w = d_f \\ N(A + B r^{d_w - d_f}) & \text{for } d_w > d_f \end{cases}$$

Condamin, Bénichou, Tejedor, Voituriez and Klafter. Nature 450, 77 (2007)

Persistent searchers (in discrete media):

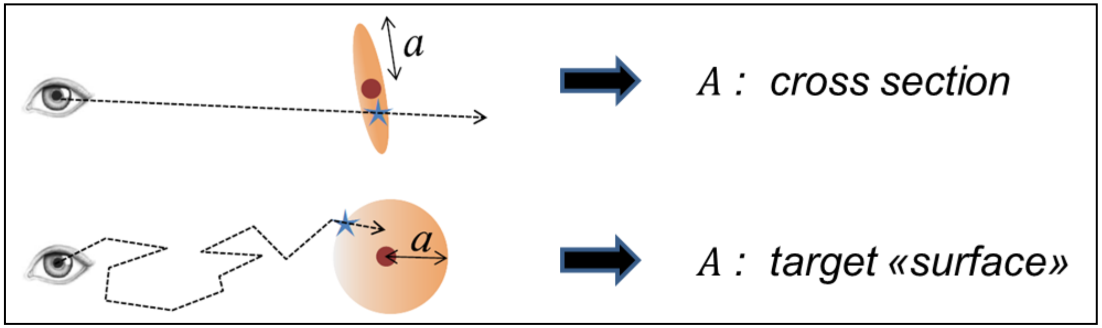
$$\langle T \rangle = A_d L^2 + B_d V$$

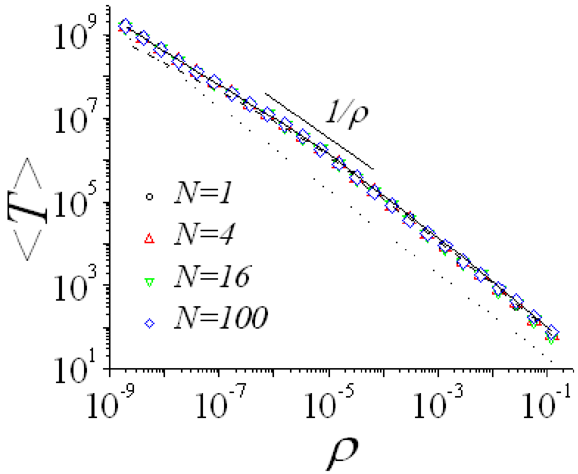


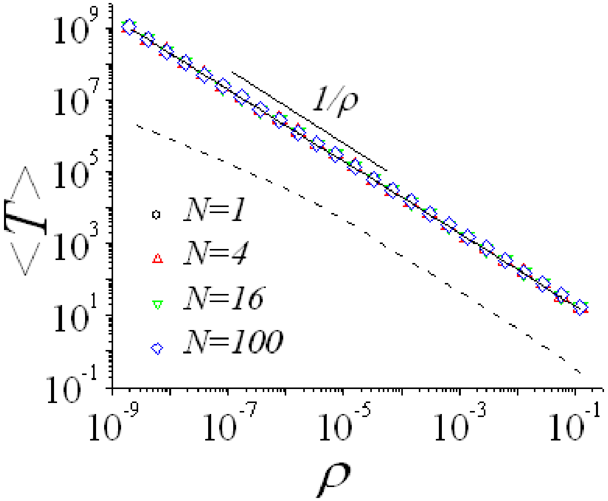


Tejedor, Voituriez and Bénichou. PRL 108, 088103 (2011)

MFPT in higher dimensions: CTRW







$$\langle T\rangle = \frac{L^2}{v^2} g_d(x_0) + \frac{L^d}{Av\alpha(v)} = \frac{L^2}{v^2} g_d(x_0) + \frac{1}{\rho}\frac{1}{Av\alpha(v)}$$

Campos, Bartumeus and Méndez. PRE 88, 022101 (2013)

Anomalous diffusion in 2D and 3D (?)

It is very usual to find that analysis of experimental trajectories of living organisms (cells are a typical example) often yield clear signatures of anomalous diffusion (e.g. Mean square displacement and velocity correlations).

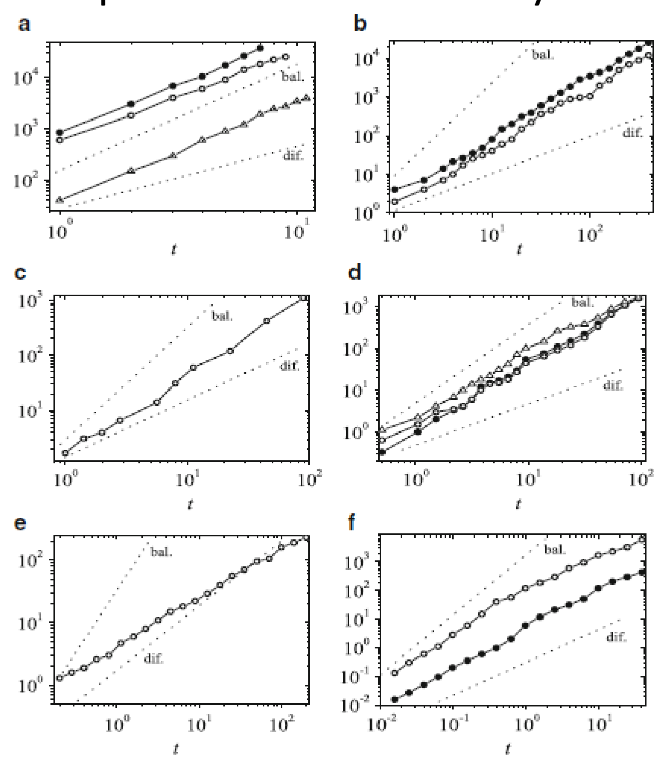


Fig. 7.4 Mean square displacement of cells; *dotted lines* indicate diffusive ($\langle x^2 \rangle \sim t$) and ballistic ($\langle x^2 \rangle \sim t^2$) scaling. (**a**) Cells of amoebas *Tetramitus rostatus* (*full circles*), *Naegleria gruberi* (*open circles*) and *Acanthamoeba castellanii* (*triangles*) (Data extracted from [39]). (**b**) Epithelial Madin-Darby canine kidney cells of wild-type (*full circles*) and NHE-deficient (*open circles*) (Data extracted from [20]). (**c**) neuN human mammary epithelial cells (Data extracted from [52]). (**d**) MCF-10A human mammary cells expressing pBABE (*full circles*), neuN (*open circles*) and neuT (*triangles*) (Data extracted from [51]). (**e**) Strain AX4 of *Dictyostelium discoideum* cells (Data extracted from [40]). (**f**) Strain AX2 of *Dictyostelium discoideum* cells at the vegetative state (*full circles*) and after 5.5 h starving (*open circles*) (Data extracted from [64])

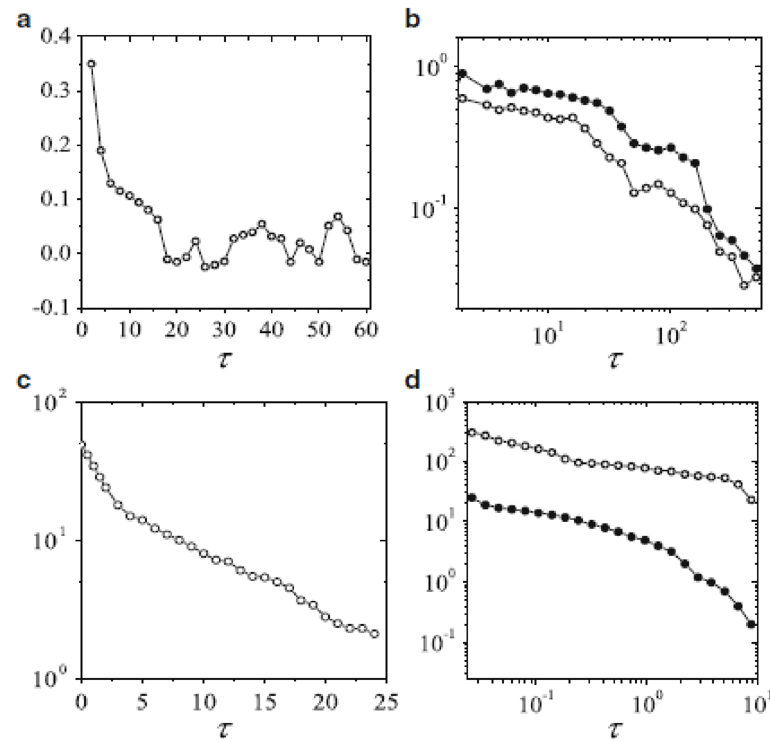
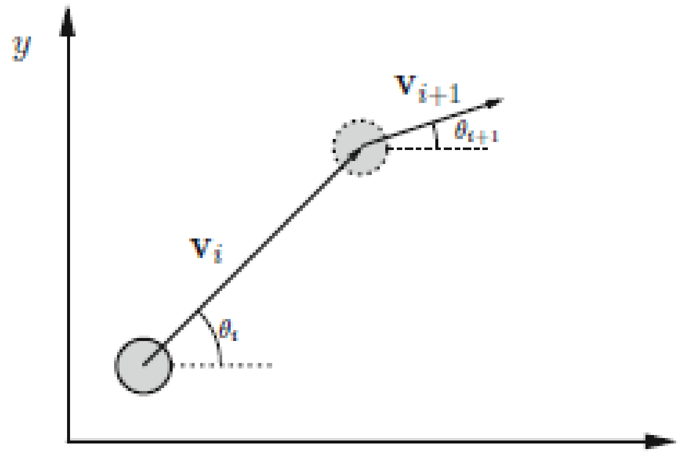


Fig. 7.3 Velocity cell correlations $\langle v(t)v(t+\tau) \rangle$. (**a**) Hydra cells migrating in endodermal aggregates (Data extracted from [67]). (**b**) Epithelial Madin-Darby canine kidney cells of wild-type (*full circles*) and NHE-deficient (*open circles*) (Data extracted from [20]). (**c**) Strain AX4 of *Dictyostelium discoideum* cells (Data extracted from [58]). (**d**) Strain AX2 of *Dictyostelium discoideum* cells at the vegetative state (*full circles*) and after 5.5 h starving (*open circles*) (Data extracted from [64])

Illustrative example: Two.dimensional CTRW



$$j_1(\mathbf{r},t,\theta)=\rho_1(\mathbf{r},0,\theta)\delta(t)+\int_{-\infty}^{\infty}\int_0^{2\pi}\int_0^t j_2(\mathbf{r}-\mathbf{e}_\theta v\tau,\theta-\alpha,t-\tau)p(\alpha)h(v)\varphi_2(\tau)\mathrm{d}\tau\mathrm{d}\alpha\mathrm{d}v$$

$$j_2(\mathbf{r},t,\theta)=\rho_2(\mathbf{r},0,\theta)\delta(t)+\int_0^t j_1(\mathbf{r},t-\tau,\theta)\varphi_1(\tau)\mathrm{d}\tau$$

$$\rho_1(\mathbf{r},t,\theta)=\rho_1(\mathbf{r},0,\theta)\phi_1(t)+\int_0^t j_1(\mathbf{r},t-\tau,\theta)\phi_1(\tau)\mathrm{d}\tau$$

$$\rho_2(\mathbf{r},t,\theta)=\int_{-\infty}^{\infty}\int_0^t j_2(\mathbf{r}-\mathbf{e}_\theta v\tau,t-\tau,\theta)h(v)\phi_2(\tau)\mathrm{d}\tau\mathrm{d}v$$

Campos, Méndez and Llopis. J. Theor. Biol. 267, 526 (2010)

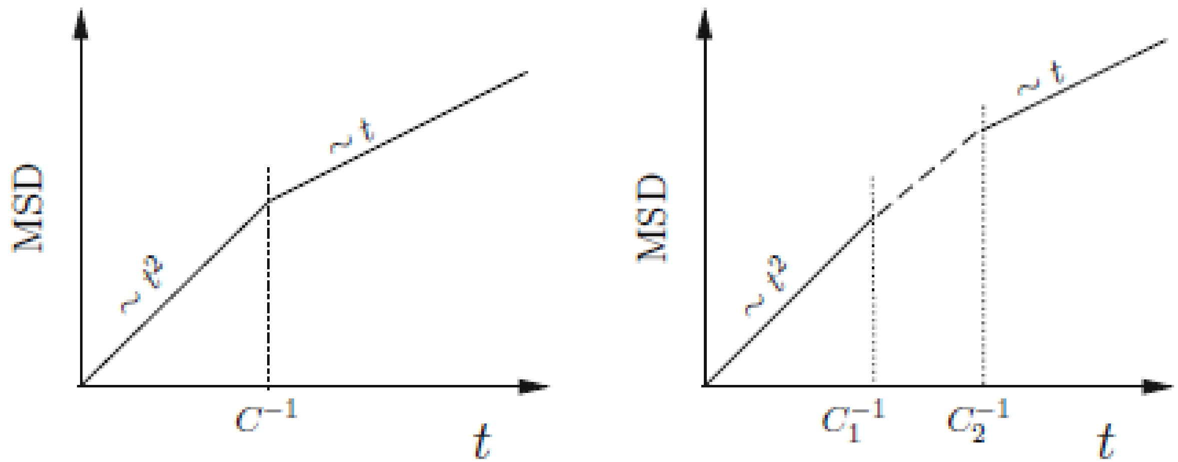
Approximation 1: Fluctuating speed and instantaneous turns

$$\langle x^2(t) + y^2(t)\rangle = 2\frac{\langle v^2\rangle - \langle v\rangle^2}{\lambda^2}\left(\lambda t - 1 + e^{-\lambda t}\right) + 2\frac{\langle v\rangle^2}{\lambda D}\left(D\lambda t - 1 + e^{-D\lambda t}\right)$$ (2 scales)

Approximation 2: Constant speed and exponential turning times (reorientations)

$$\frac{\partial \rho_1}{\partial t} = \lambda_1 D \frac{\partial^2 \rho_2}{\partial \theta^2} + \lambda_1 \rho_2 - \lambda_2 \rho_1$$
$$\frac{\partial \rho_2}{\partial t} = -v_s \mathbf{e}_\theta \nabla \rho_2 - \lambda_1 \rho_2 + \lambda_2 \rho_1$$

➡ $$\langle x^2(t) + y^2(t)\rangle = 2v_s^2\left[c_0(t) + c_1(t)e^{-\mu_1 t} + \sum_{k=2}^{5} c_k e^{-\mu_k t}\right]$$ (5 scales !!)



Campos, Méndez and Llopis. J. Theor. Biol. 267, 526 (2010)

OPEN QUESTIONS

MOVEMENT PATTERNS

1. Classical diffusion and Brownian motion
   Most results known
2. Persistent motion
   Langevin description: almost everything to be done
3. CTRW and anomalous diffusion
   MFPT of Lévy walks
4. Multi-mode movement
   Links between information use and internal/external scales
5. Motion in two and three dimensions
   Almost everything to be done (and revised)

SEARCH EFFICIENCY
(MEAN FIRST-PASSAGE TIMES)