Optimal search: micro & macro scales

Ralf Metzler, U Potsdam & Tampereen teknillinen yliopisto

— MPIPKS, Dresden, 9th September 2015 —

Lévy foraging: on the watchout for sparse targets

Lévy foraging hypothesis: to avoid oversampling

Shlesinger & Klafter (1986): Lévy flights as efficient search mechanism

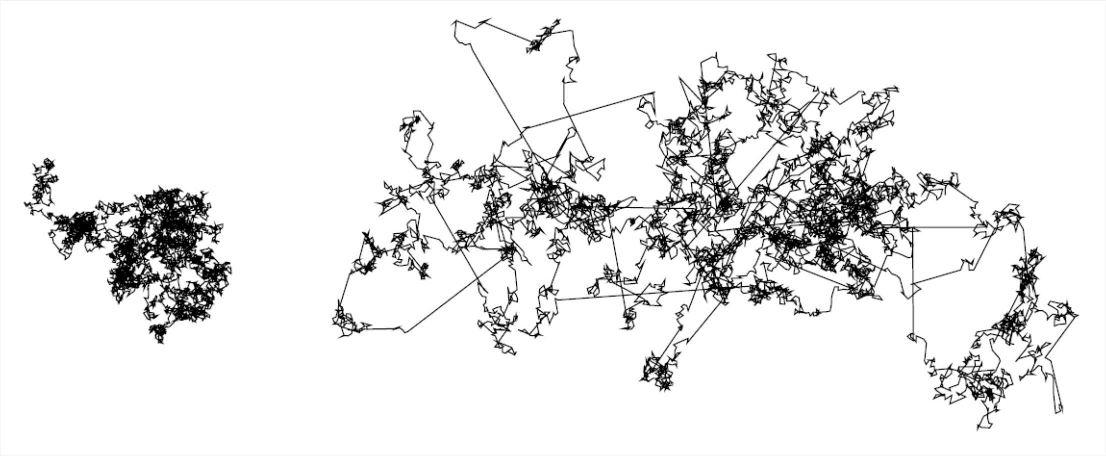
Lévy foraging hypothesis: *Superdiffusive motion governed by fat-tailed propagators optimise encounter rates under specific (but common) circumstances: hence some species must have evolved mechanisms that exploit these properties* [. . .].

Lévy flight (Mandelbrot): $\psi(t) = \tau^{-1} \exp(-t/\tau) \wedge$

$$\lambda(x) \simeq |x|^{-1-\alpha}, \quad 0 < \alpha < 2 \quad \curvearrowright \quad \langle x^2(t) \rangle \to \infty$$

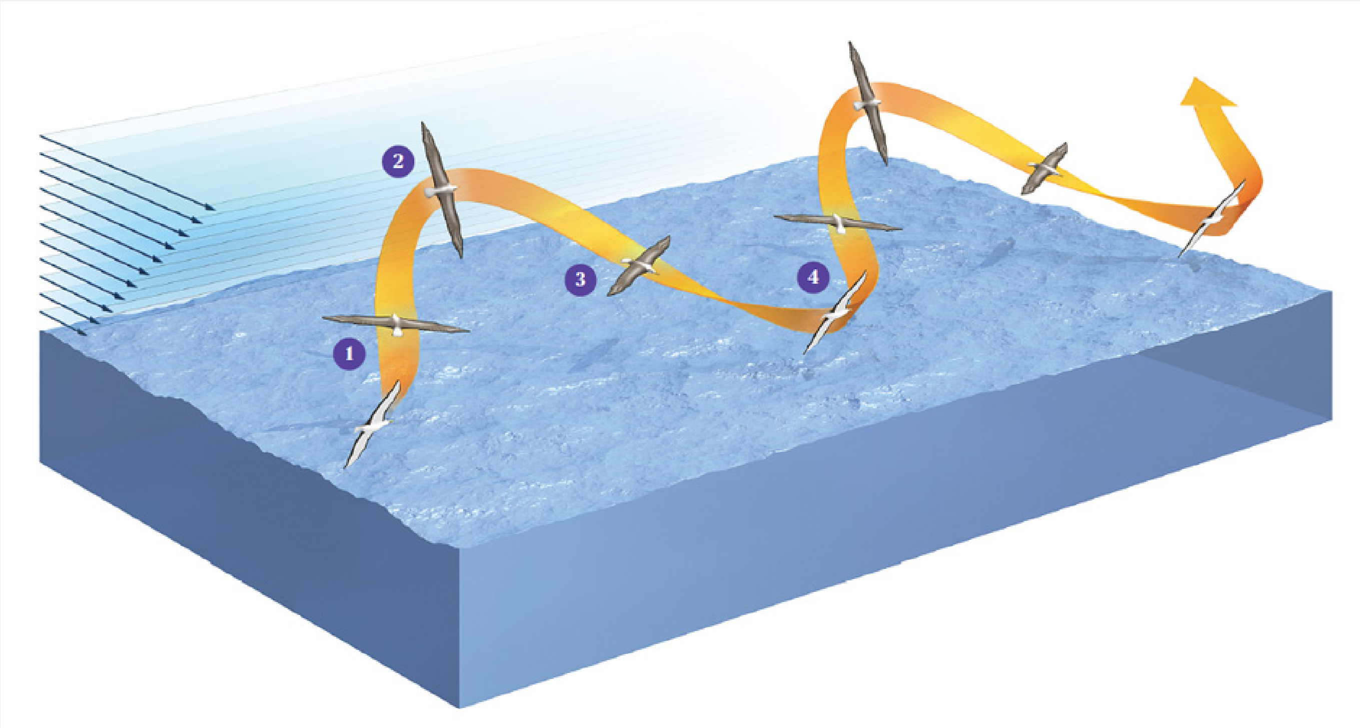
Lévy walk (Shlesinger, Klafter & Wong, JSP, 1982): spatiotemporal coupling

$$\psi(x,t) = \lambda(x)\delta(x - |v|t) \quad \curvearrowright \quad \langle x^2(t) \rangle \simeq t^{3-\alpha}$$



Viswanathan GE, da Luz MGE, Raposo EP, Stanley HE, The physics of foraging (CUP, 2011)

The good old albatross story: some do it



Dynamic soaring (unflapping flight)

Shear wind field >30 km/h:

[1] bird climbs into wind

[2] turns to leeward

[3] descends

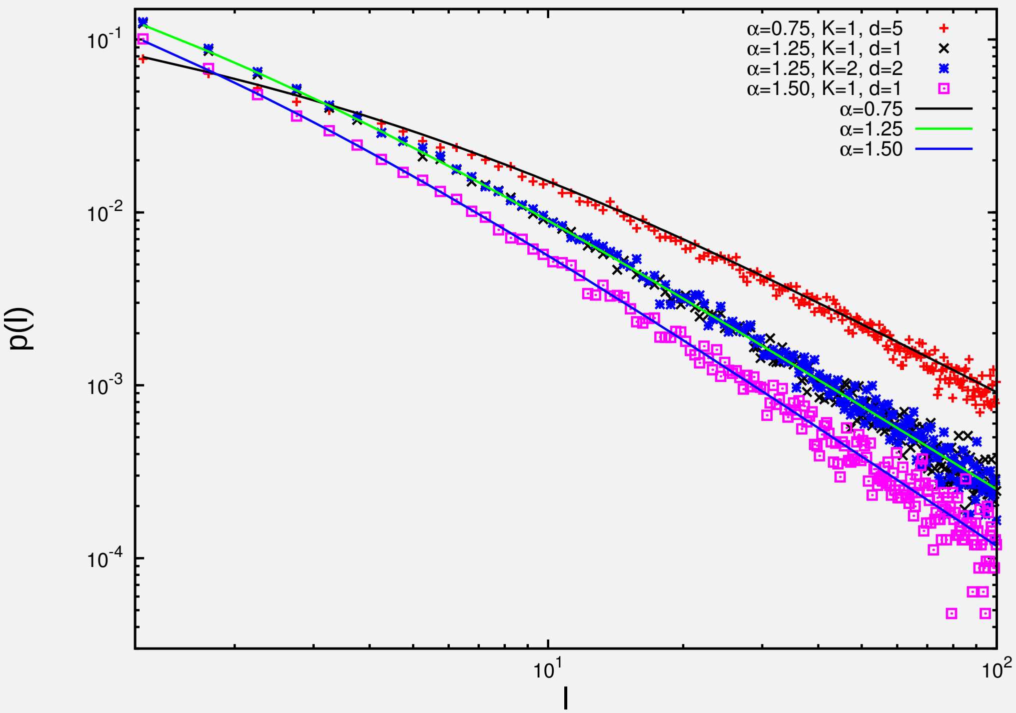
[4] again turns into wind

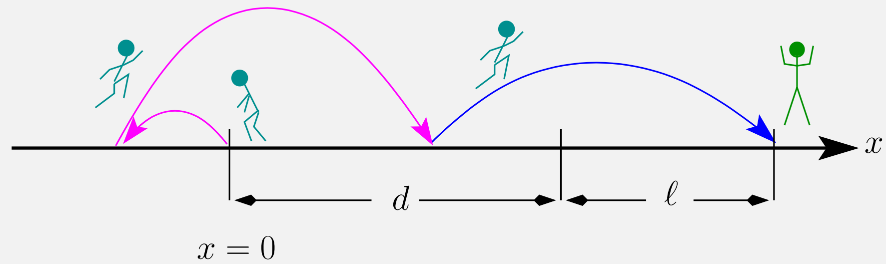
Viswanathan et al, Nature (1996, 1999): Lévy flight of albatross

Edwards et al, Nature (2007): flawed data analysis

Humphries et al, PNAS (2012): single birds indeed Lévy fly

Overshooting the target: leapovers





$$\lambda(x) \simeq |x|^{-\alpha-1}$$

$$\wp_{\mathrm{fp}}(\tau) \sim \frac{d^{\alpha/2}}{\alpha\sqrt{\pi K^{(\alpha)}}\Gamma(\alpha/2)}\tau^{-3/2}$$ First passage: Sparre Andersen universality

$$\wp_l(\ell) = \frac{\sin(\pi\alpha/2)}{\pi}\frac{d^{\alpha/2}}{\ell^{\alpha/2}(d+\ell)} \curvearrowright \langle\ell\rangle \to \infty \ \forall\alpha$$ Leapover length

T Koren, MA Lomholt, AV Chechkin, J Klafter & RM, PRL (2007); AV Chechkin, RM, VY Gonchar & LV Tanatarov, JPA (2003)

Intermittent Lévy search process

Regularly spaced targets with density $1/L$ & periodic boundary conditions:

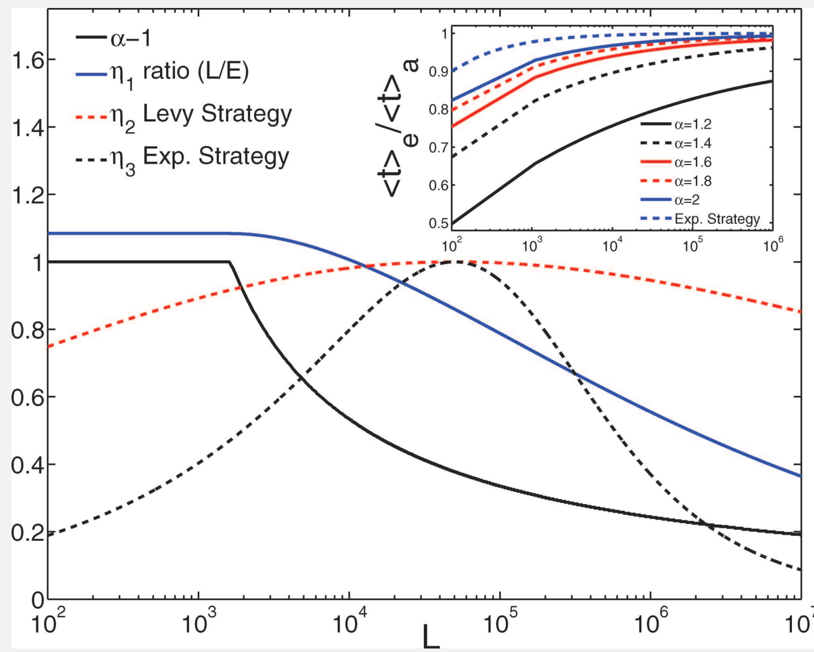
$$\frac{\partial P(x,t)}{\partial t} = \frac{1}{\tau_1}\int_{-L/2}^{L/2} dx' \int_0^\infty dt' W(x-x', t-t') P(x', t') - \frac{1}{\tau_1} P(x,t) + D\frac{\partial^2}{\partial x^2} - \wp_{\mathrm{fa}}\delta(x)$$

Transport kernel:

$$W(x,t) = \frac{\psi(t)}{2}\sum_{-\infty}^{\infty}\delta(|x+nL|-vt)$$

$$\psi(t) = 2v\lambda(vt)$$

$$\lambda(x) \simeq |x|^{-1-\alpha}$$



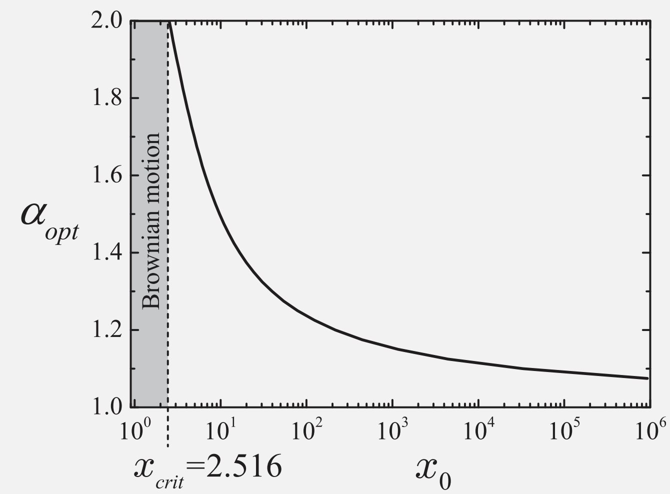
LFs stay close-to-optimal even for changing conditions $\Rightarrow$ *Plasticity of Lévy processes*

MA Lomholt, T Koren, RM & J Klafter, PNAS (2008)

Lévy flights do not always optimize random search

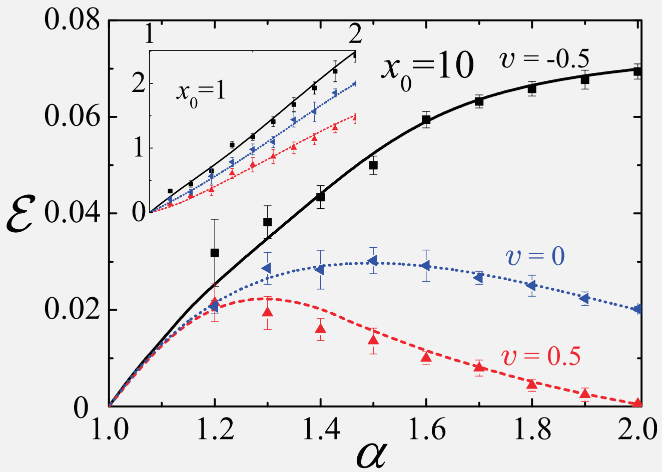
$$\frac{\partial P(x,t)}{\partial t} = \frac{\partial^\alpha P(x,t)}{\partial |x|^\alpha} - v\frac{\partial P(x,t)}{\partial x}$$

$$-\wp_{\rm fa}(t)\delta(x), \quad 1<\alpha<2$$

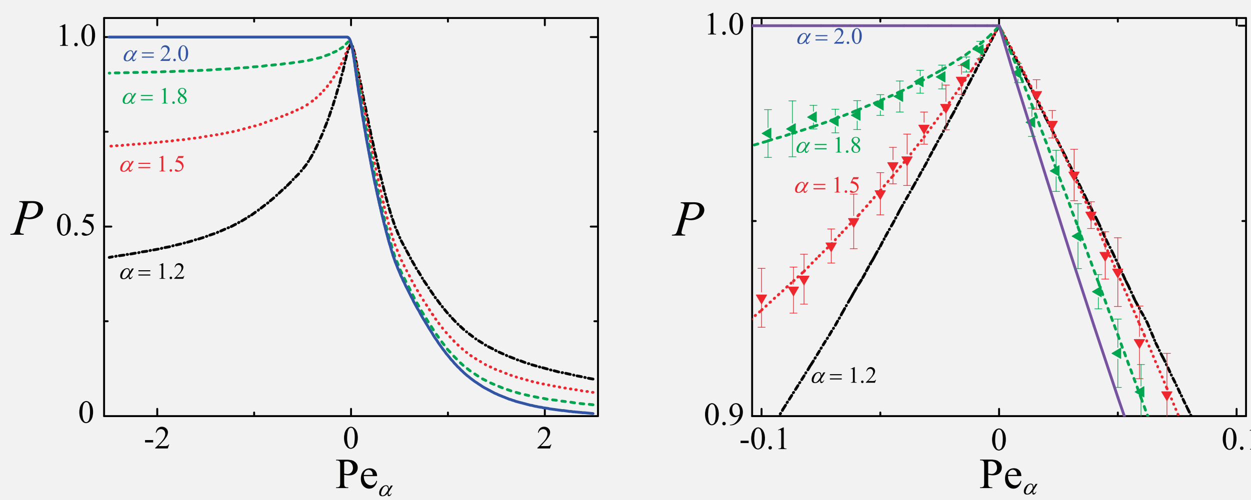


Search efficiency

$$\mathscr{E} = \left\langle \frac{1}{t} \right\rangle = \int_0^\infty \wp(s)ds$$



Search reliability $P = 1 - \mathscr{S}(\infty)$



VV Palyulin, AV Chechkin & R Metzler, PNAS (2014), JSTAT (2014)

Ultraweak ergodicity breaking of Lévy walks

$$\langle x^2(t)\rangle \sim \frac{2(\alpha-1)}{(3-\alpha)(2-\alpha)}t^{3-\alpha} \sim (\alpha-1)\overline{\delta^2(t)}, \;\; 1<\alpha<2$$

Time averaged MSD

$$\overline{\delta^2(\Delta)} = \frac{1}{T-\Delta}\int_0^{T-\Delta}\Big(x(t+\Delta)-x(t)\Big)^2 dt$$

$$\overline{\delta^2(\Delta)} \sim 2\left(\frac{(1+\Delta)^{3-\alpha}-1}{(3-\alpha)(2-\alpha)} - \frac{\Delta}{2-\alpha}\right) + \left(\frac{\alpha-1}{3}\left[\frac{\Delta}{T}\right]^3 - \alpha\left[\frac{\Delta}{T}\right]^2\right)T^{3-\alpha}$$

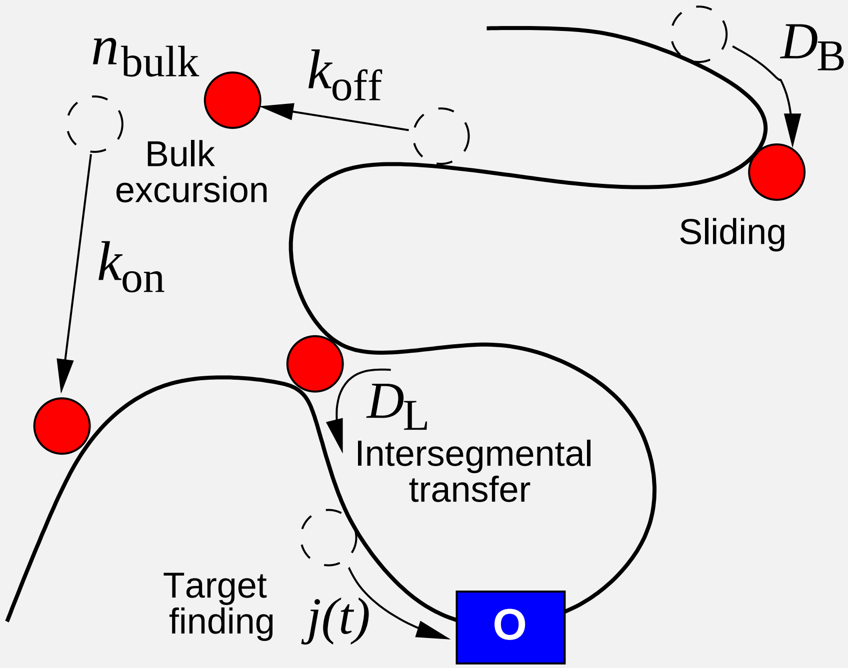
Linear response for constant external force f $(0<\alpha<2)$:

$$\langle x(t)\rangle \sim \beta f \begin{cases} \frac{1}{2}t^2, & 0<\alpha<1 \\ \frac{1}{2-\alpha}t^{3-\alpha}, & 1<\alpha<2 \end{cases} \qquad \langle x(t)\rangle = \frac{1}{2}\beta f\langle x^2(t)\rangle$$

A Godec & RM, PRL (2013), PRE (2013); D Froemberg & E Barkai, PRE (2013), EPJE (2013)

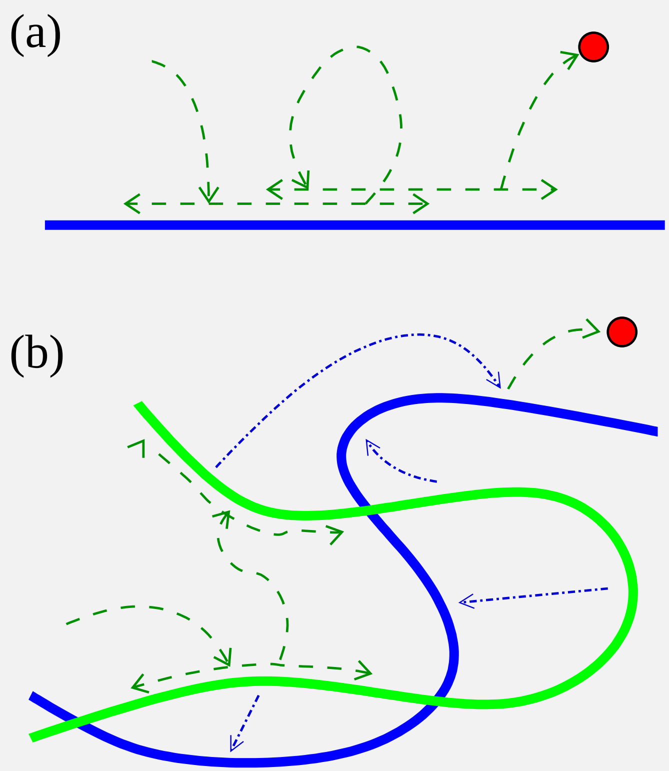
Optimal target search of proteins for binding site on DNA

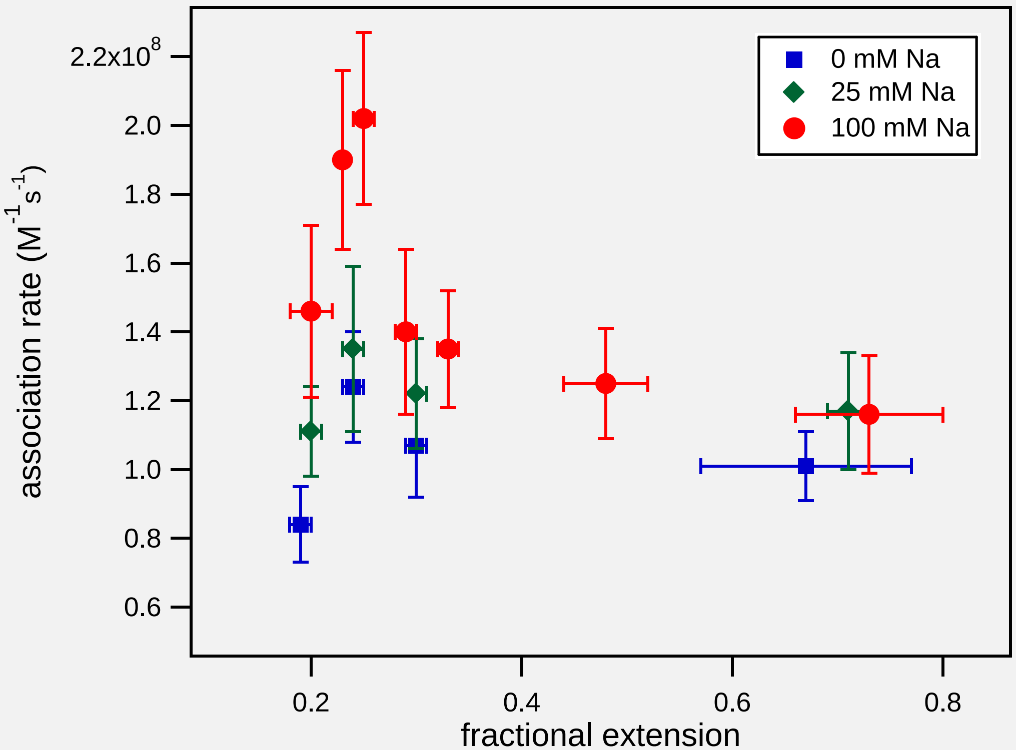
Lévy flight comp /w $\lambda(x) \simeq |x|^{-1-\alpha} \therefore \alpha = 1.2$ (3D SAW) $\wedge$ $\alpha = 0.5$ (3D RW)

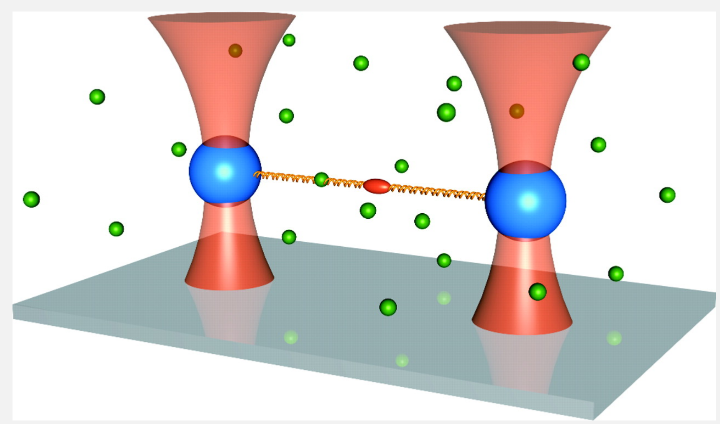


Lévy stable jump lengths at varying salt conditions: bulk not necessary

Probing how DNA conformation optimises search





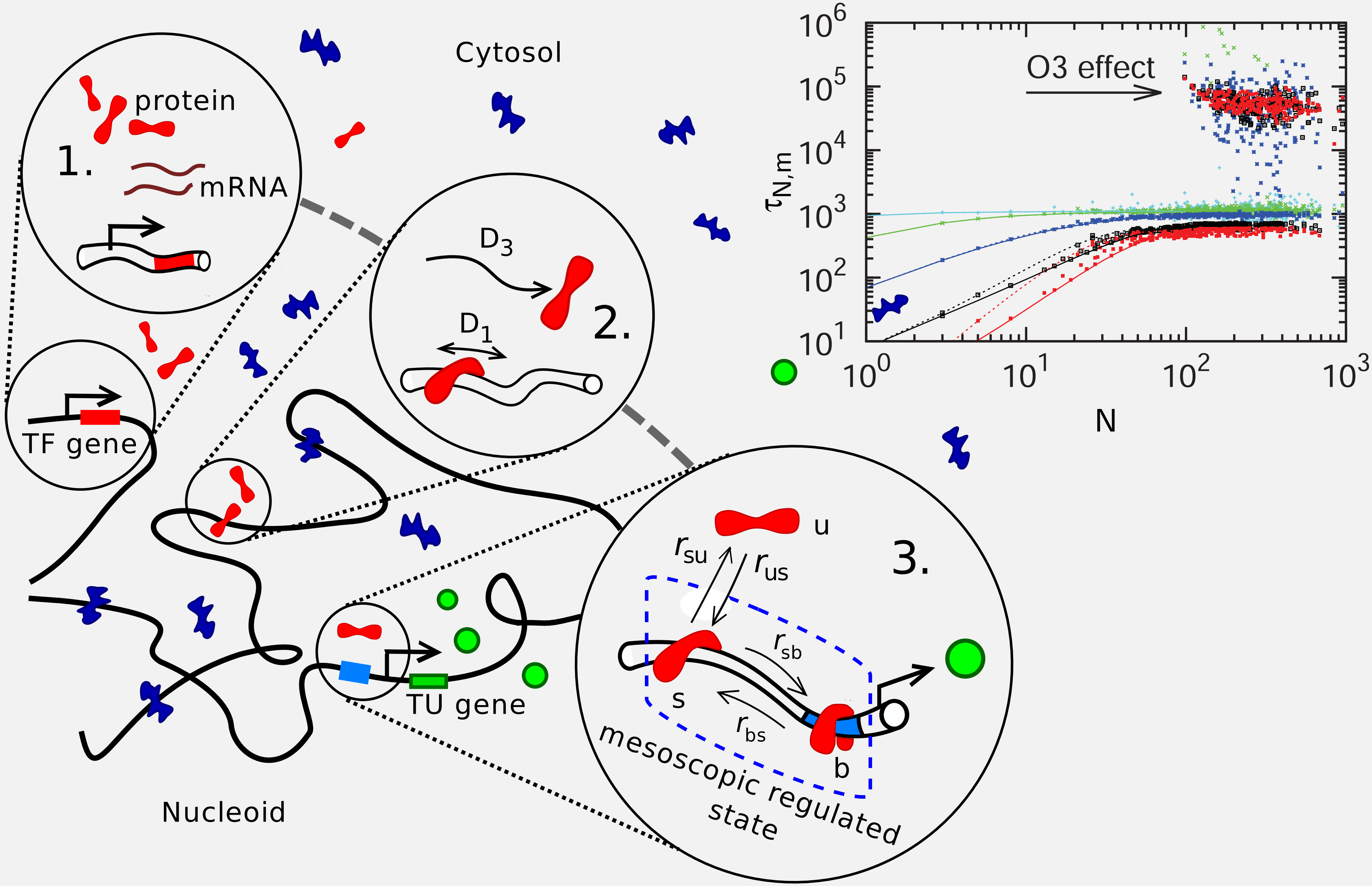


pCco5 plasmid DNA: 6538bp $\approx 2.2\mu$m $\approx 45\ell_p$

[comp λ DNA 48.5kbp]

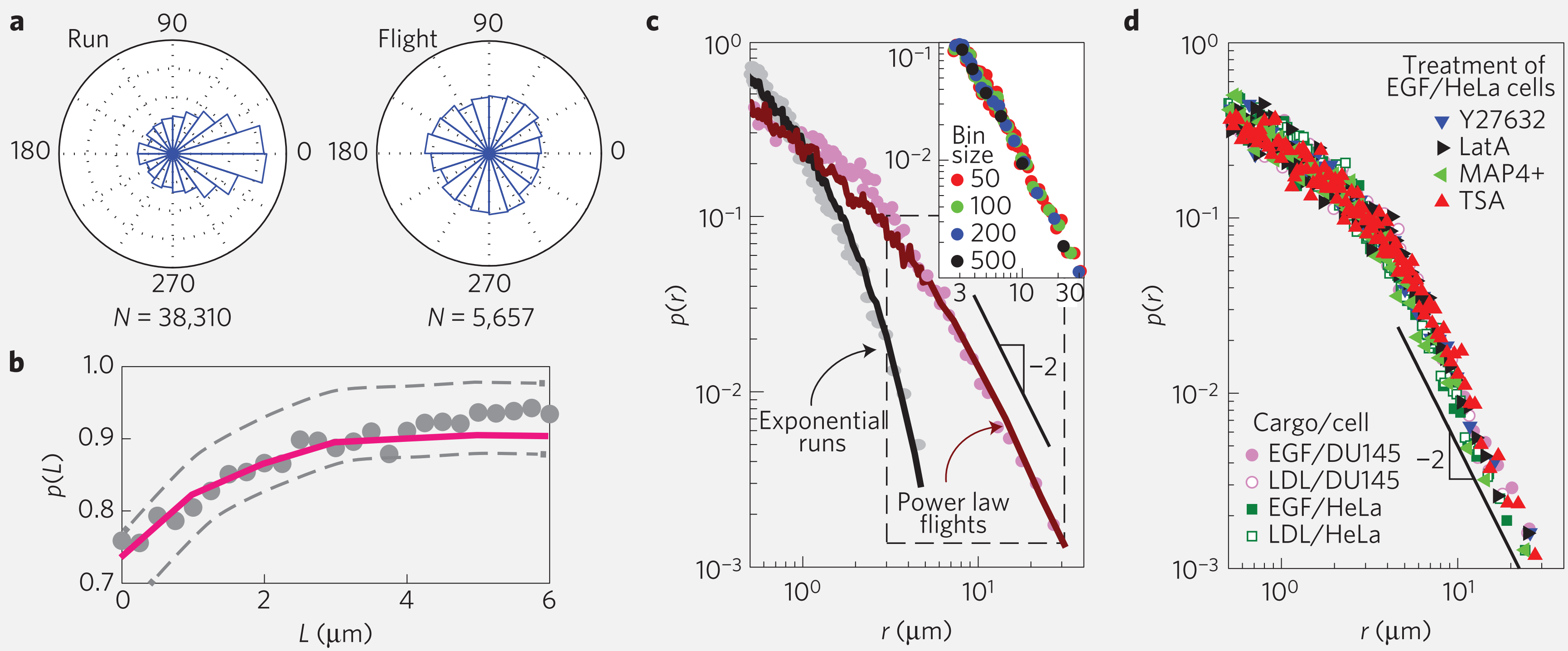
B van den Broek, MA Lomholt, S-M Kalisch, RM & GJL Wuite, PNAS (2008)

Intra/intercellular signalling is diffusion controlled



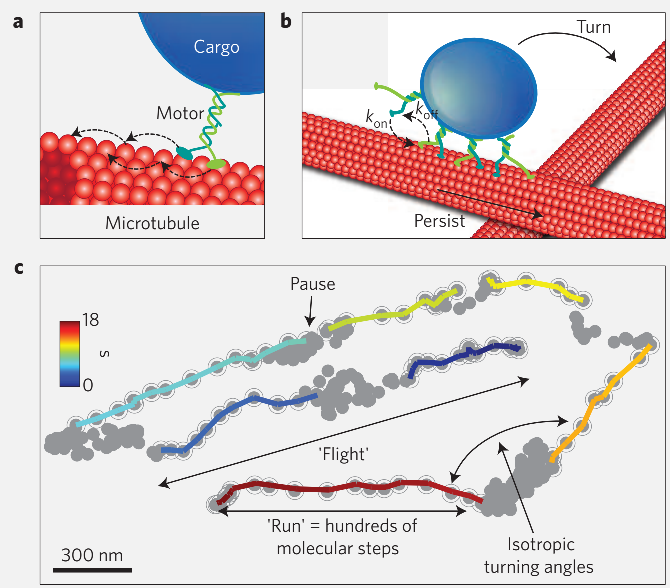
O Pulkkinen & RM, PRL (2013); M Bauer & RM, PLoS ONE (2013); Sci Rep (2015)

Lévy walks of molecular motors in living cells



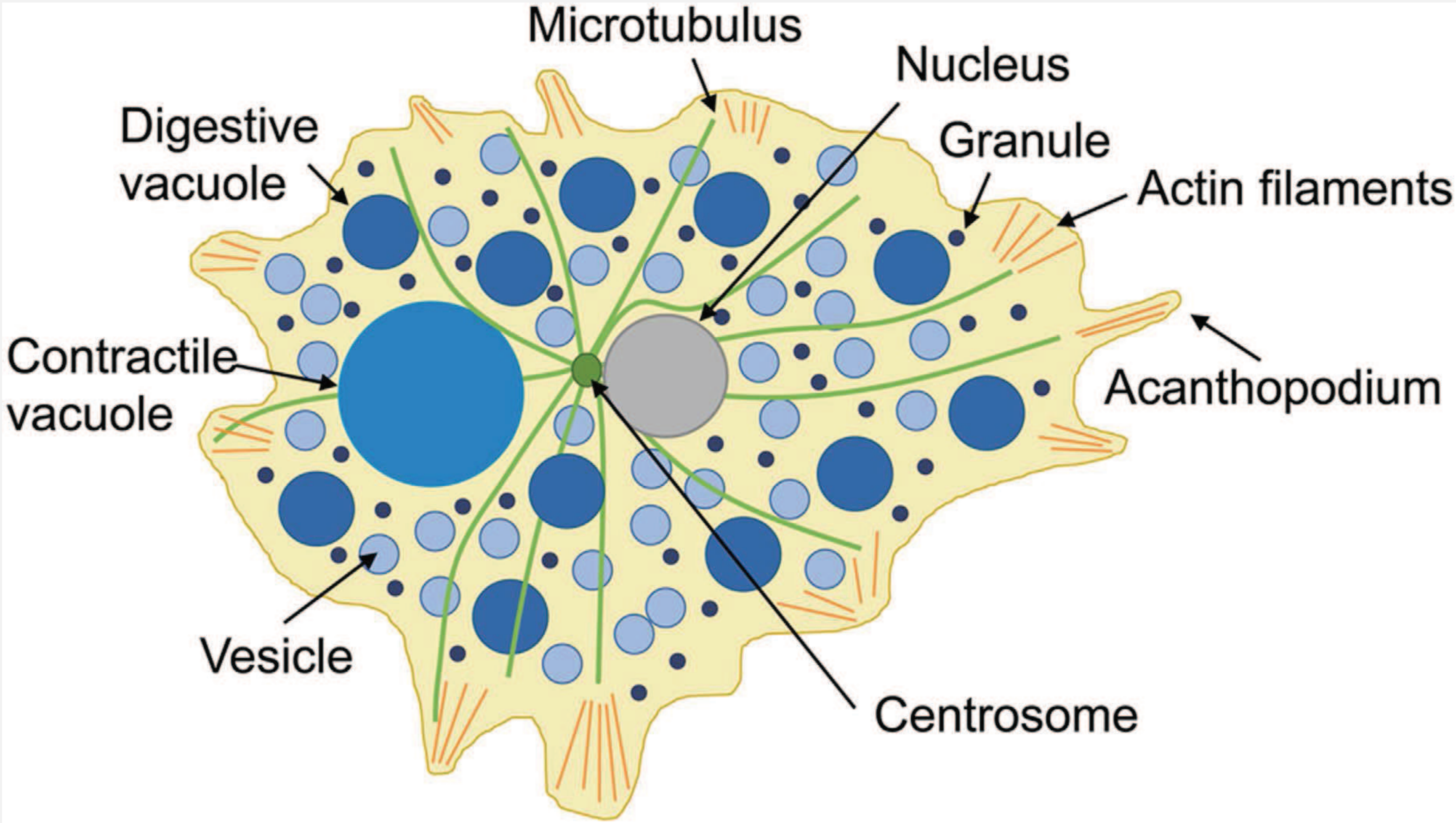
Run: motor motion on microtubule for $1/k_{\text{off}}$

Flight: consecutive runs persisting in direction



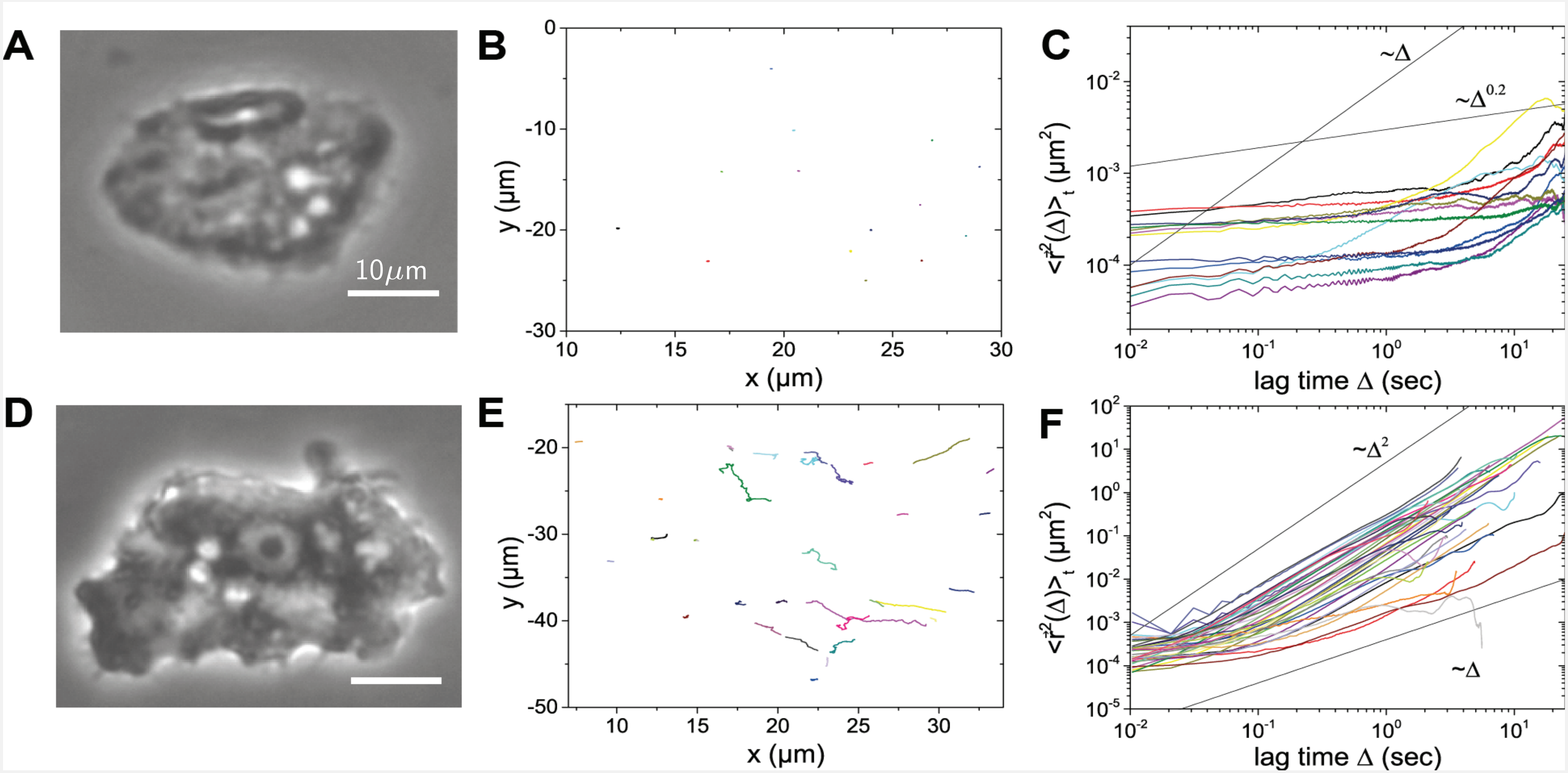
K Chen, B Wang & S Granick, Nat Mat (2015)

Superdiffusion in supercrowded castellani: mixing



JF Reverey, J-H Jeon, H Bao, M Leippe, RM & C Selhuber-Unkel, Sci Rep (2015)

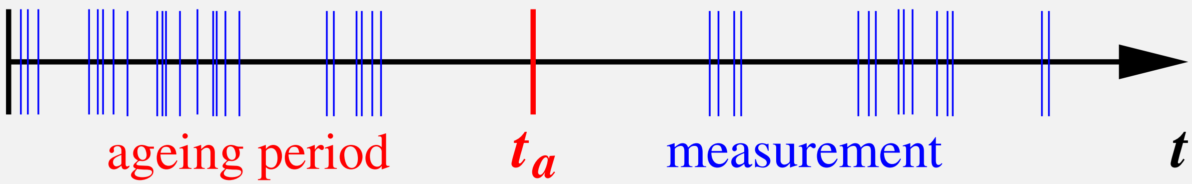
Superdiffusion in living Acanthamoeba castellani



Blebbistatin treated cells: A-C right after treatment; D-F 1 h after treatment

JF Reverey, J-H Jeon, H Bao, M Leippe, RM & C Selhuber-Unkel, Sci Rep (2015)

Ageing effects in single trajectory time averages: $\psi(\tau) \simeq \tau^{-1-\alpha}$

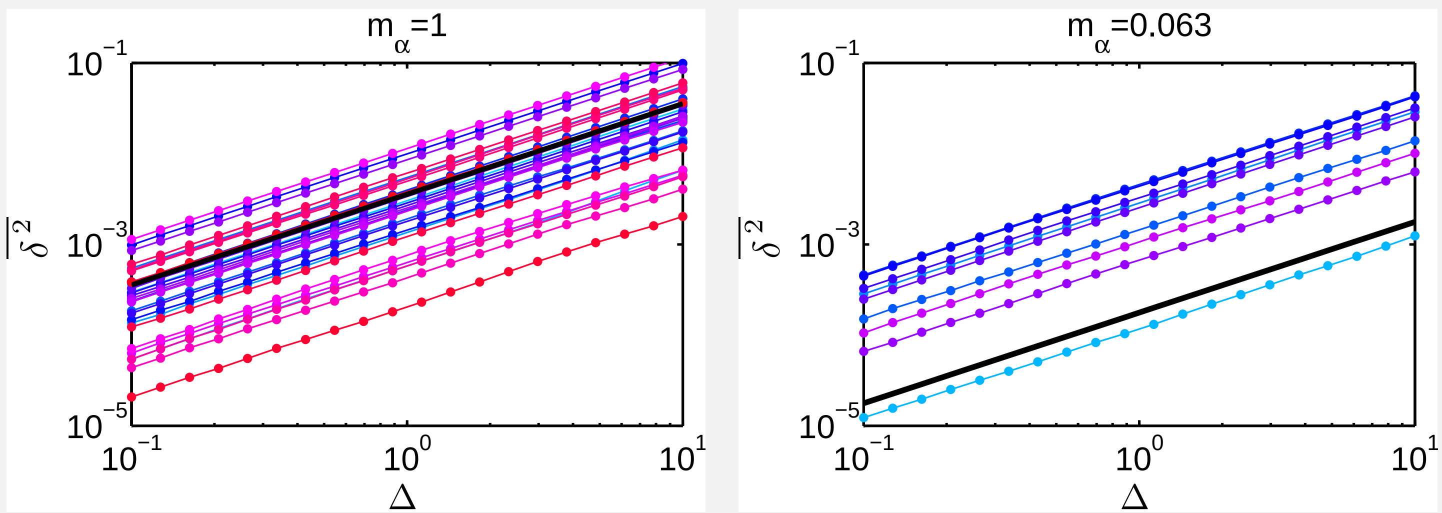


Ageing mean squared displacement ($\Lambda(z) = (1+z)^\alpha - z^\alpha$)

$$\left\langle \overline{\delta^2(\Delta)} \right\rangle_a = \frac{\Lambda_\alpha(t_a/T)}{\Gamma(1+\alpha)} \frac{g(\Delta)}{T^{1-\alpha}} \quad \not\Leftrightarrow \quad \langle x^2(t) \rangle_a \simeq \begin{cases} t^\alpha, & t_a \ll t \\ t_a^{\alpha-1} t, & t_a \gg t \end{cases}$$

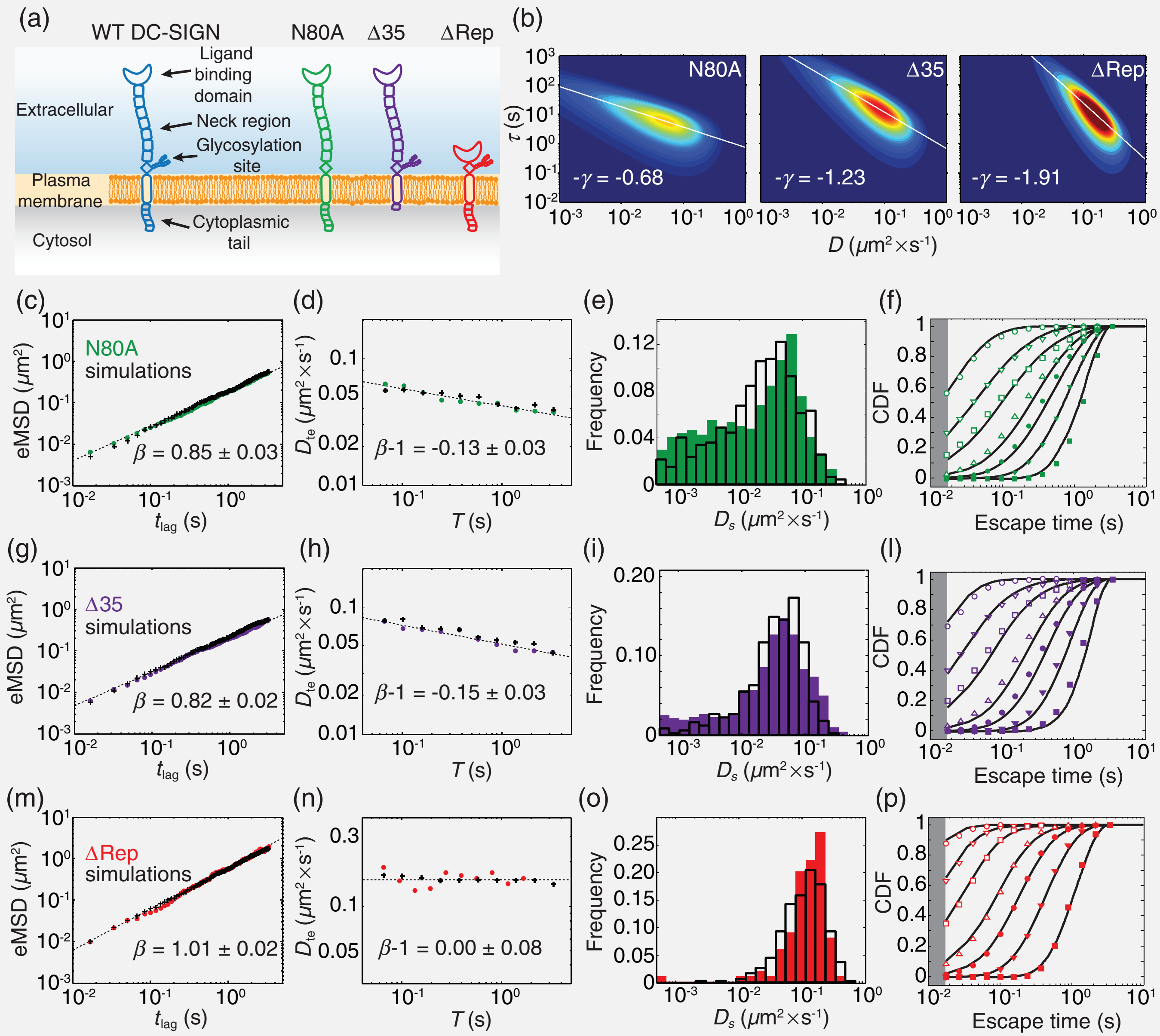
Probability to make at least one step during $[t_a, t_a + T]$: *population splitting*

$$m_\alpha(T/t_a) \simeq (T/t_a)^{1-\alpha}, \quad T \ll t_a$$



J Schulz, E Barkai & RM, PRL (2013), PRX (2014)

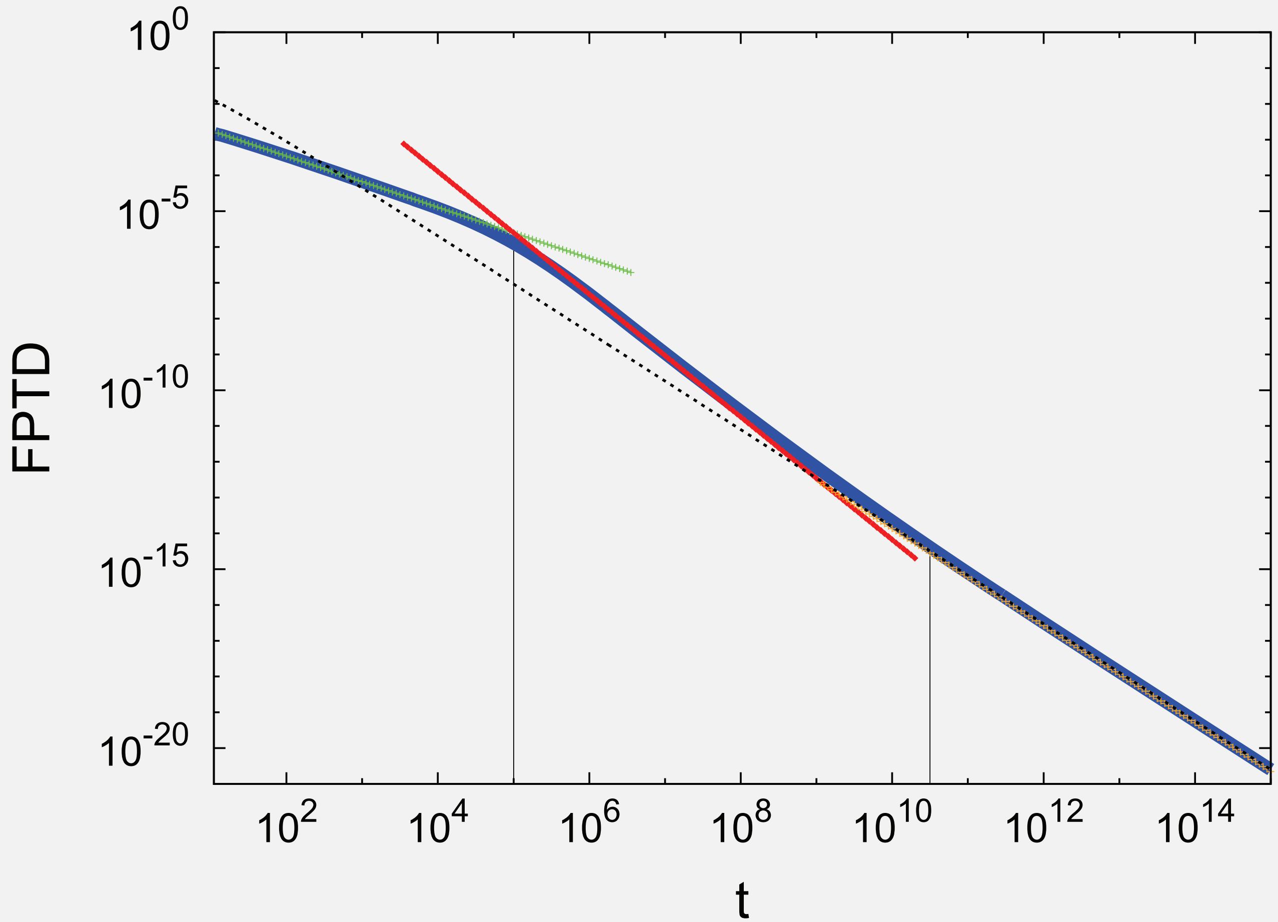
Ageing in the motion of membrane embedded proteins



C Manzo et al, PRX (2015)

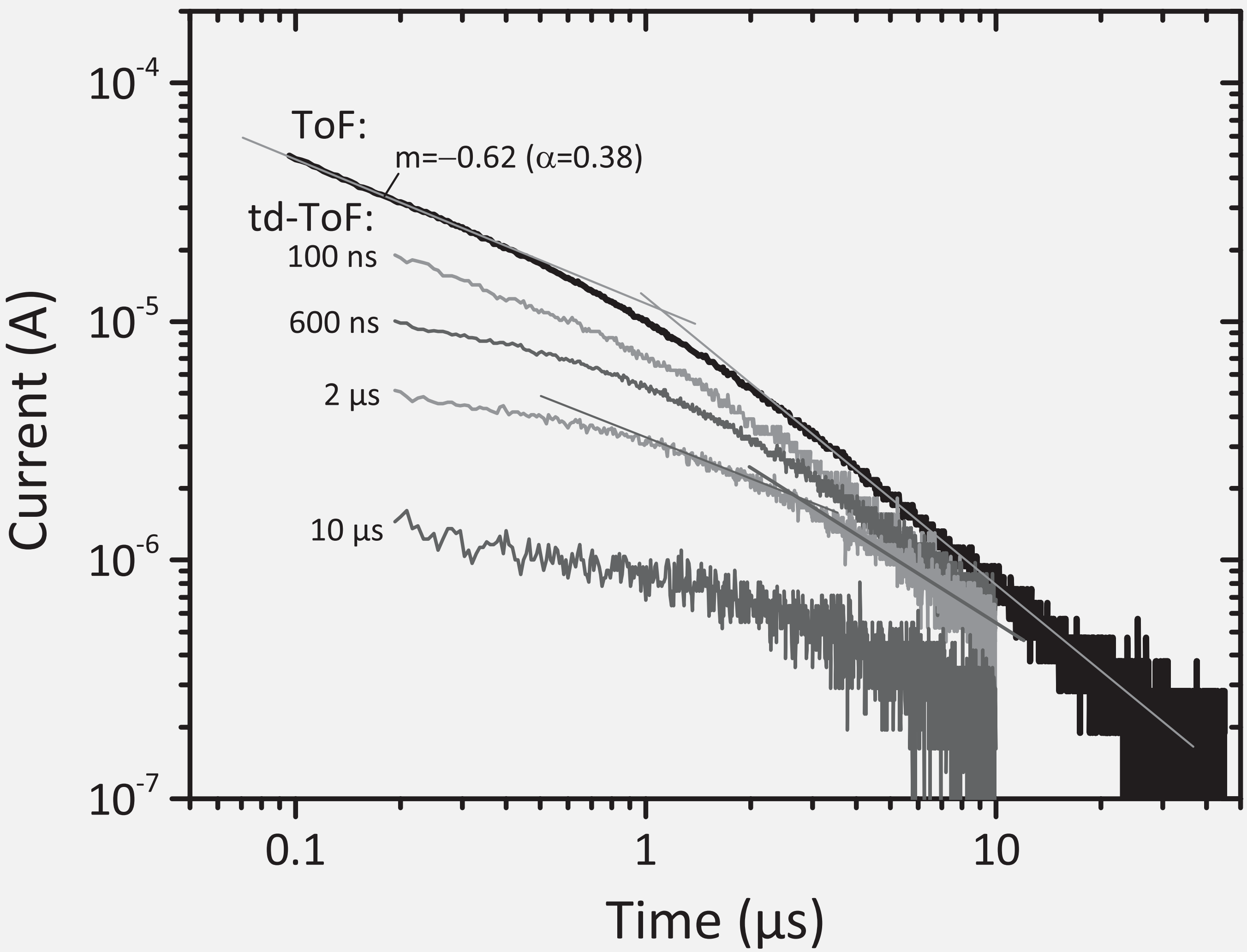
Ageing induces crossovers in the first passage dynamics

$$\wp_a(t_a,t) \simeq \begin{cases} t_a^{\alpha-1}t^{-\alpha}, & t_a \gg t \\ t_a^{\alpha}t^{-1-\alpha}, & t_a \ll t \ll t_a^2 \\ x_0 K_\alpha^{-1/2} t^{-1-\alpha/2}, & t_a^2 \ll t \end{cases}$$



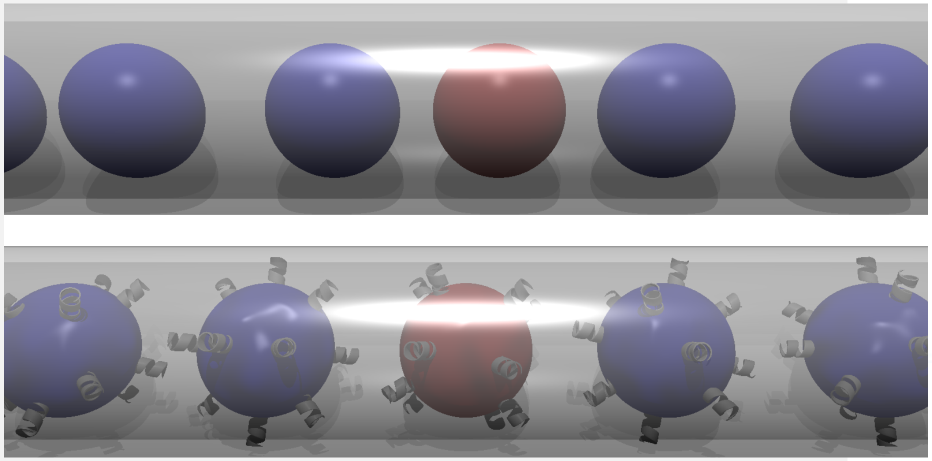
H Krüsemann, A Godec & RM, PRE (2014); J Phys A (2015)

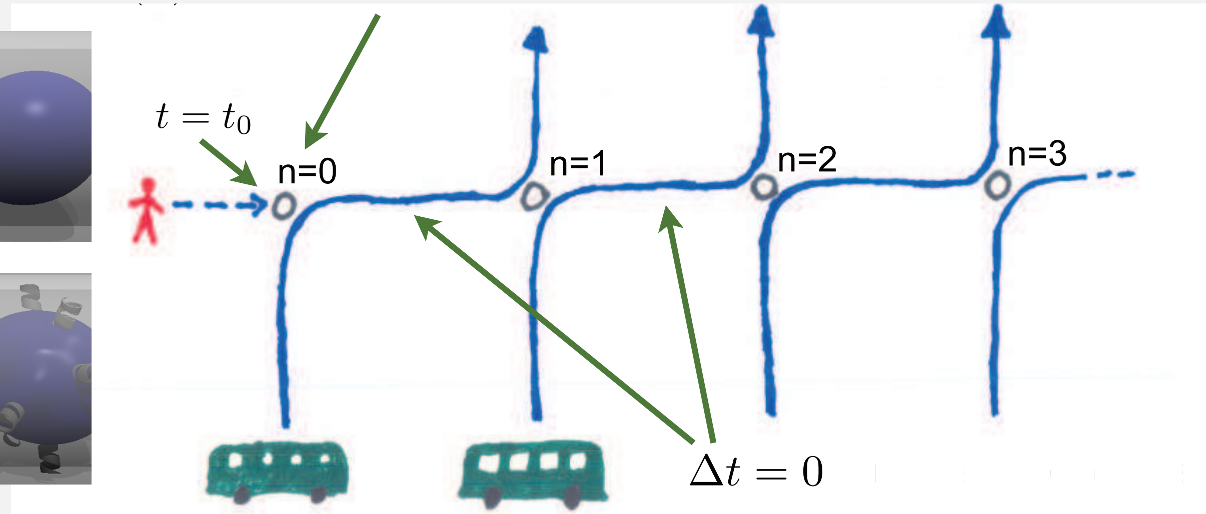
Ageing charge carrier motion in polymeric semiconductors



M Schubert, . . . & D Neher, Phys Rev B (2013)

Ultraslow dynamics in ageing many-particle systems



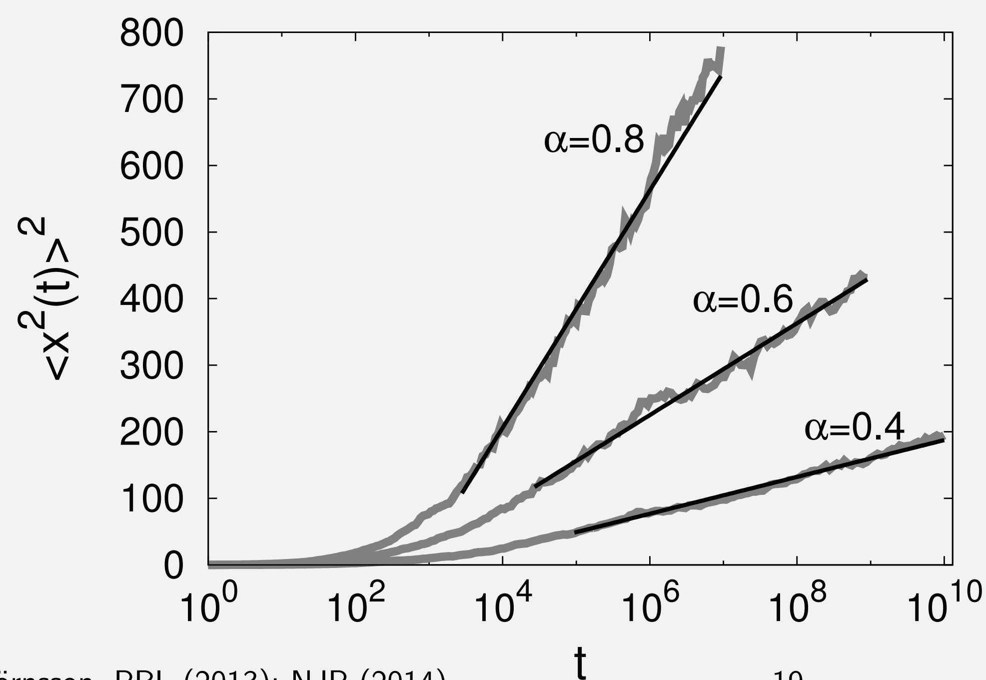


Brownian particles: Harris' law $\langle x^2(t)\rangle \simeq t^{1/2}$

Functionalised particles moving /w $\psi(t) \simeq t^{-1-\alpha}$
$\curvearrowright$ scaling argument: $n \to \log t$:

$$\left\langle x^2(t)\right\rangle \simeq \log^{1/2}\left(\frac{t}{t_0}\right)$$

WEB: $\overline{\delta^2(\Delta)} \simeq (\Delta/T)\log^{1/2} T$



[LP Sanders,] MA Lomholt, L Lizana, [K Fogelmark,] RM & T Ambjörnsson, PRL (2013); NJP (2014)

Ageing effects in other processes

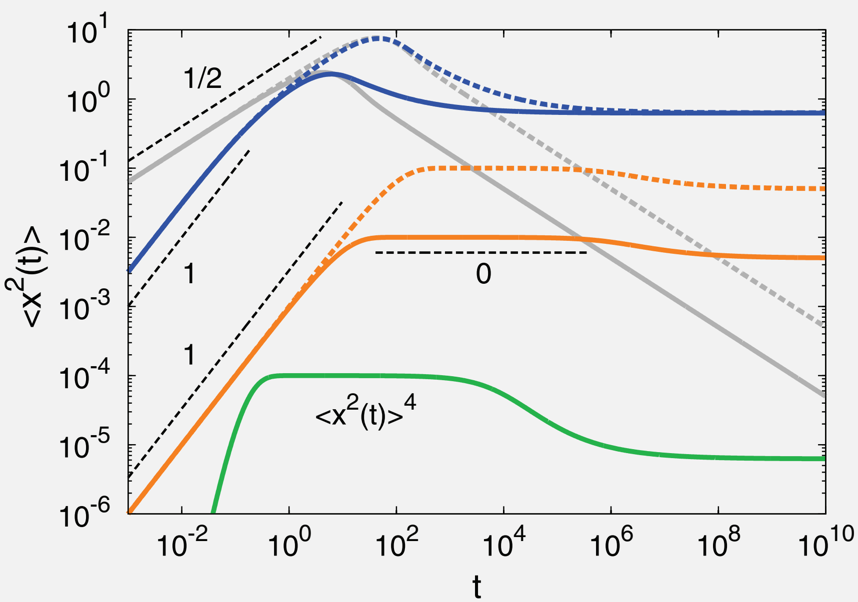
Transient ageing in fractional Brownian and Langevin equation motion: J Kursawe, JHP Schulz & RM, PRE (2013)

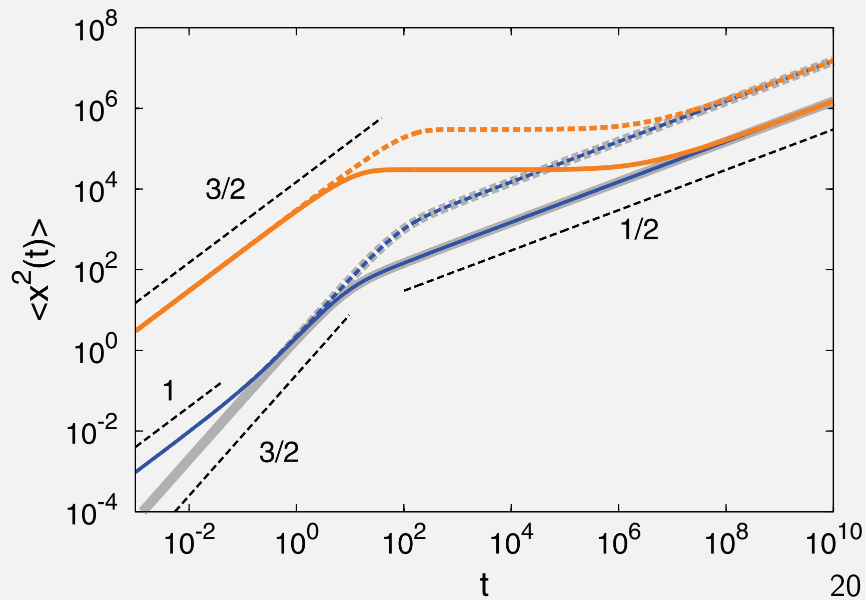
Ageing in heterogeneous diffusion processes: AG Cherstvy, AV Chechkin & RM, JPA (2014)

Ageing in generalised diffusion processes: AG Cherstvy & RM, JSTAT (2014)

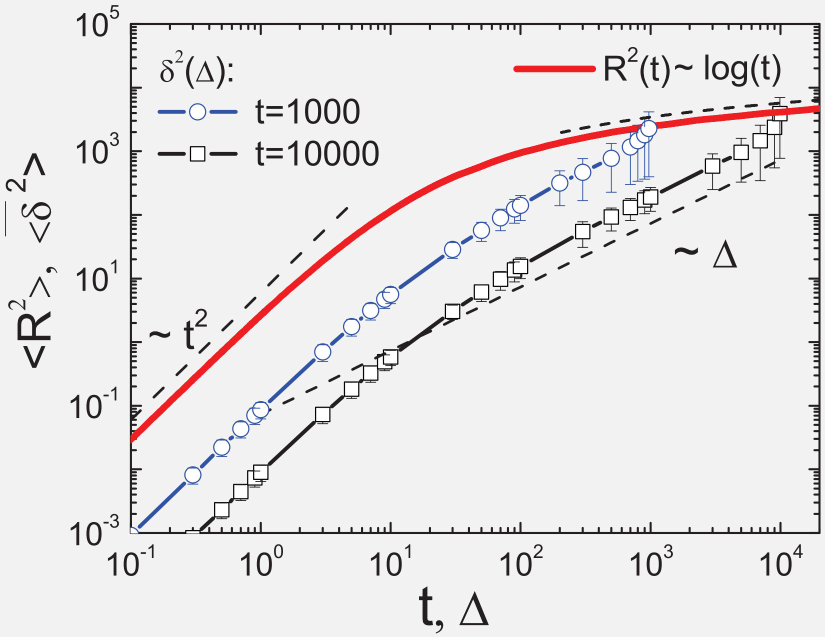
Ageing Scaled Brownian Motion: H Safdari, AV Chechkin, G Jafari & RM, PRE (2015)

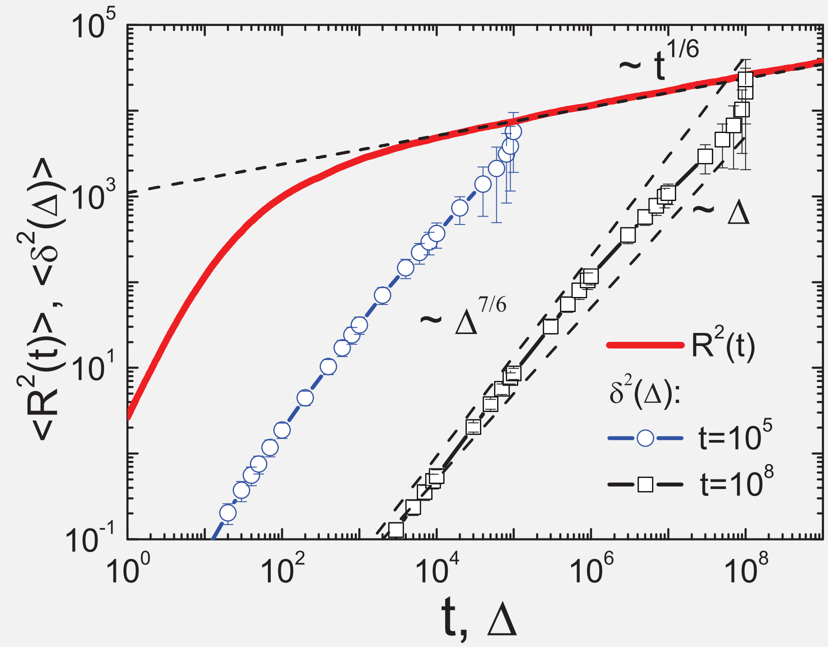
General result: same ageing depression Λ_α as CTRW
Strong ageing: TAMSD converges to EAMSD





WEB in granular gas & SBM as mean field theory





Haff's law: $\mathscr{T}(t) = \mathscr{T}_0/(1 + t/\tau_0)^2$

$$\langle \mathbf{r}^2(t) \rangle \sim 6 D_0 \tau_0 \log(1 + t/\tau_0)$$

$$\left\langle \overline{\delta^2(\Delta)} \right\rangle \sim 6 D_0 \tau_0 \Delta / T$$

A Bodrova, AV Chechkin, AG Cherstvy & RM, NJP (2015); PCCP (2015)

Abb. 140. Erlegter Albatroß mit 2,80 Meter Spannweite.
In der Mitte Kapitänlt. Siburg und Oberlt. Löwisch.

∑ummary

- I Lévy processes are observed within experimental resolution on both macro & micro scales
- II For sparse targets different formulations are optimal for Cauchy flights ($\alpha = 1$)
- III Scale-free processes work well even for non-optimal conditions
- IIII In presence of external bias (wind, water current) LFs perform significantly worse than Brownian search (overshooting phenomenon)
- IIIII Ageing occurs in anomalous diffusion systems & gives rise to modified system response

RM, J-H Jeon, AG Cherstvy & E Barkai, PCCP (2014)

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