

Strange diffusive dynamics: Beyond Brown & Einstein

—UP, 5th November 2021—

THE
PHILOSOPHICAL MAGAZINE
AND
ANNALS OF PHILOSOPHY.

[NEW SERIES.]

SEPTEMBER 1828.

XXVII. *A brief Account of Microscopical Observations made in the Months of June, July, and August, 1827, on the Particles contained in the Pollen of Plants; and on the general Existence of active Molecules in Organic and Inorganic Bodies.* By ROBERT BROWN, F.R.S., Hon. M.R.S.E. & R.I. Acad., V.P.L.S., Corresponding Member of the Royal Institutes of France and of the Netherlands, &c. &c.

[We have been favoured by the Author with permission to insert the following paper, which has just been printed for private distribution.—Ed.]

Rocks of all ages, including those in which organic remains have never been found, yielded the molecules in abundance. Their existence was ascertained in each of the constituent minerals of granite, a fragment of the Sphinx being one of the specimens examined.

My inquiry on this point was commenced in June 1827, and the first plant examined proved in some respects remarkably well adapted to the object in view.

This plant was *Clarkia pulchella*, of which the grains of pollen, taken from antheræ full grown, but before bursting, were filled with particles or granules of unusually large size, varying from nearly $\frac{1}{4000}$ th to about $\frac{1}{5000}$ th of an inch in length, and of a figure between cylindrical and oblong, perhaps slightly flattened, and having rounded and equal extremities. While examining the form of these particles immersed in water, I observed many of them very evidently in motion; their motion consisting not only of a change of place in the fluid, manifested by alterations in their relative positions, but also not unfrequently of a change of form in the particle itself; a contraction or curvature taking place repeatedly about the middle of one side, accompanied by a corresponding swelling or convexity on the opposite side of the particle. In a few instances the particle was seen to turn on its longer axis. These motions were such as to satisfy me, after frequently repeated observation, that they arose neither from currents in the fluid, nor from its gradual evaporation, but belonged to the particle itself.



Fluxes, random walks, & fluctuating forces . . .



Paul Langevin (1872-1946)

Albert Einstein (1879-1955)



Marian Smoluchowski
(1872-1917)



William Sutherland
(1859-1911)

Einstein's conditions on Brownian motion

Paul Lévy [Processus stochastiques & mouvement brownien (1948, 1965)]: «The stochastic process, that we will call linear Brownian motion, is a schematisation that well represents the properties of real Brownian motion, observable on a sufficiently small but not infinitely small scale, and which assumes that the same properties exist across the scales.»

Einstein's postulate: a stochastic process describes normal diffusion if

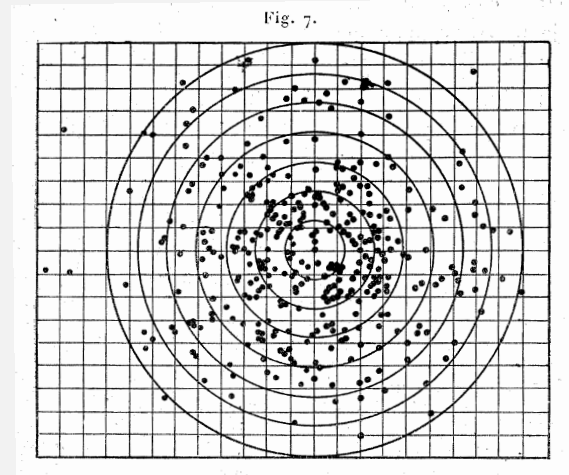
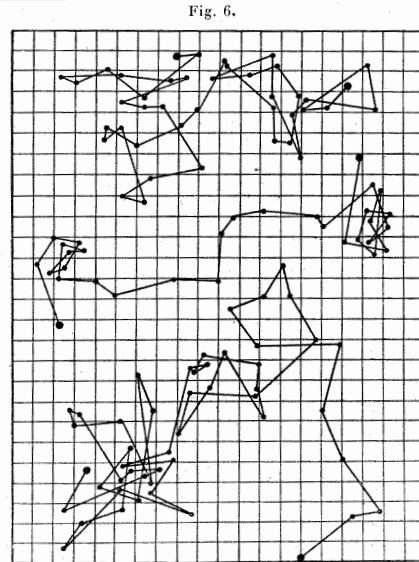
- (i) $\exists$ finite correlation time beyond which displacements are independent
- (ii) displacements are identically distributed
- (iii) displacements have a finite second moment

Main characteristics: linear mean squared displacement & Gaussian probability density

$$\langle \mathbf{r}^2(t) \rangle = 2dK_1t, \quad P(\mathbf{r}, t) = (4\pi K_1t)^{-d/2} \exp\left(-\frac{\mathbf{r}^2}{4K_1t}\right)$$

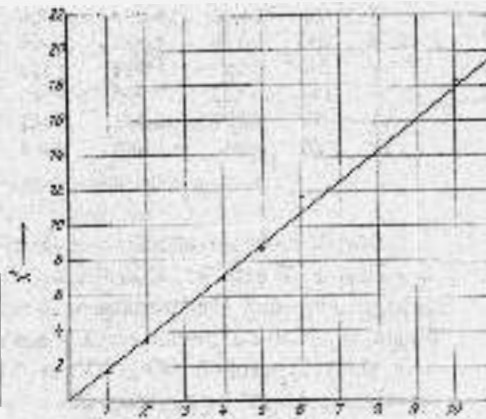
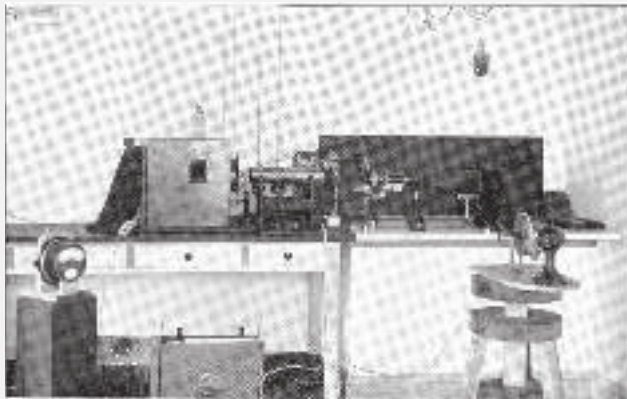
Violation of these conditions leads to anomalous diffusion with MSD $\langle \mathbf{r}^2(t) \rangle \simeq K_\alpha t^\alpha$ and/or non-Gaussian PDF

Les atomes: Brownian motion and Avogadro's number



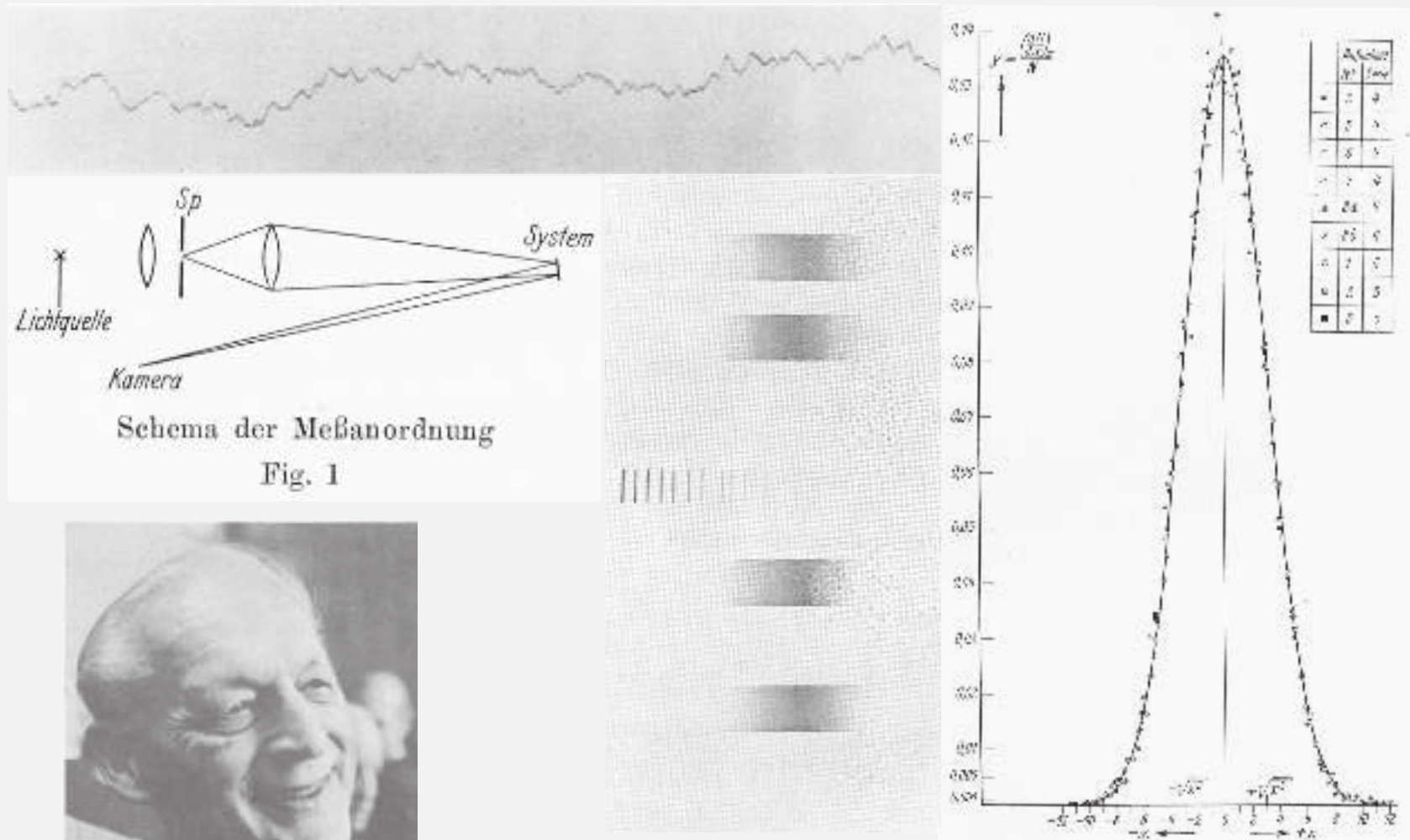
$\Delta t = 30 \text{ sec}$

$$K = \frac{k_B T}{m \eta} = \frac{(R/N_A) T}{m \eta}$$



J Perrin, Comptes Rendus (Paris) 146 (1908) 967: $N_A = 70.5 \times 10^{22}$; I Nordlund, Z Physik (1914): $N_A = 5.91 \times 10^{23}$ 5

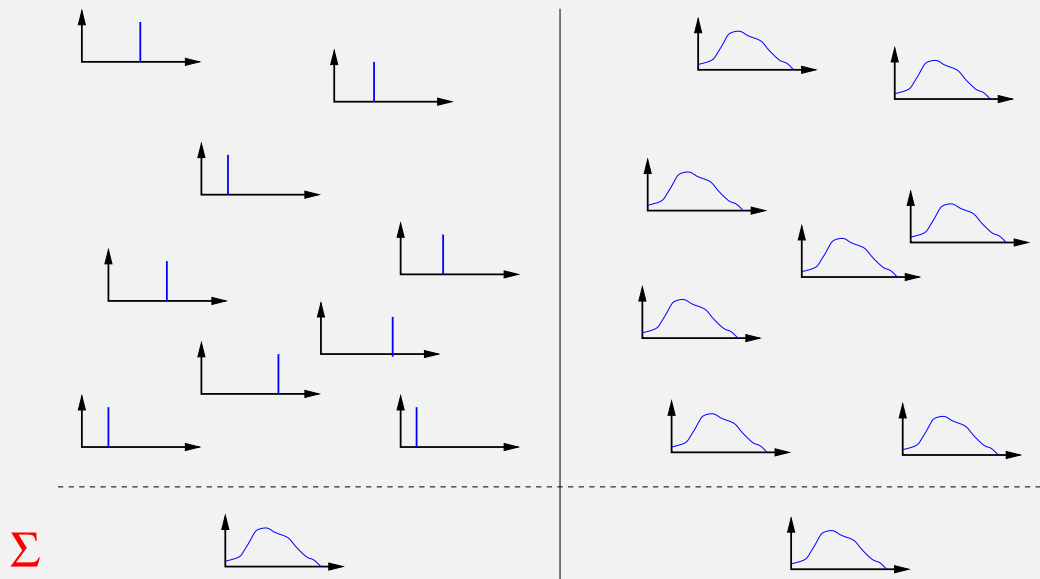
Kappler's diffusion measurements: mapping Boltzmann



E Kappler, Ann d Physik (1931): $N_A = 60.59 \times 10^{22} \pm 1\%$

$$P_{\text{eq}}(x) = \mathcal{N} \exp \left(-\frac{\theta x^2}{k_B T} \right)$$

Single molecular insight & information from fluctuations



Novel insights from single particle tracking (e.g., superresolution microscopy, supercomputing)

↪ Anomalous diffusion:

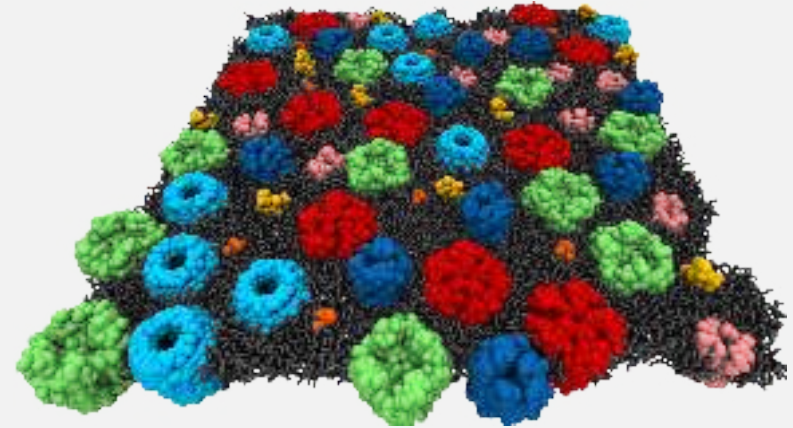
$$\langle \mathbf{r}^2(t) \rangle \simeq t^\alpha$$

(non)ergodicity, ageing, quenched/annealed disorder

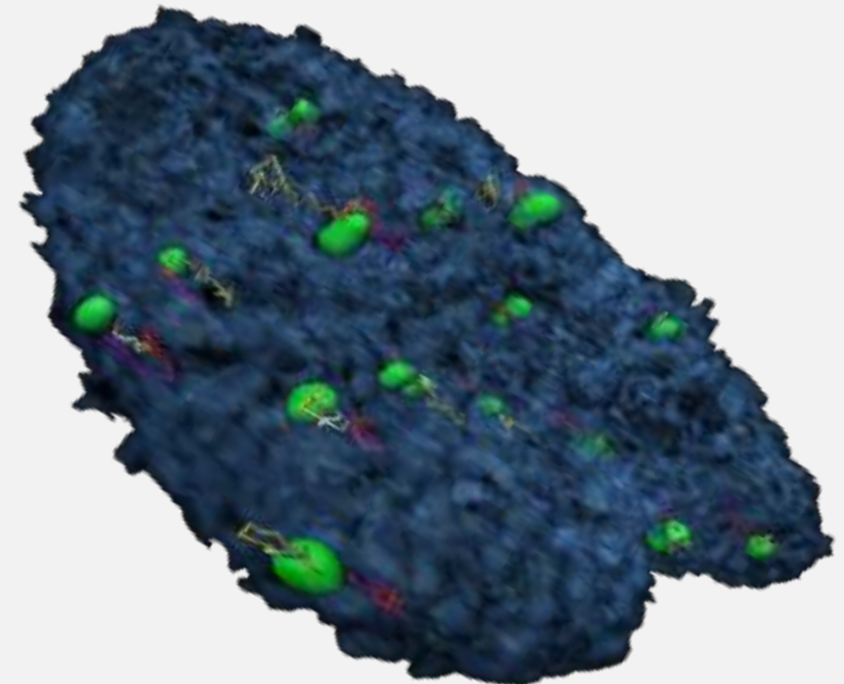
↪ Fluctuations are prominent:

- spatiotemporally fluctuating diffusivity
- strongly fluctuating reaction times

E Barkai, Y Garini & RM, Phys Today (2012)



Courtesy Matti Javanainen

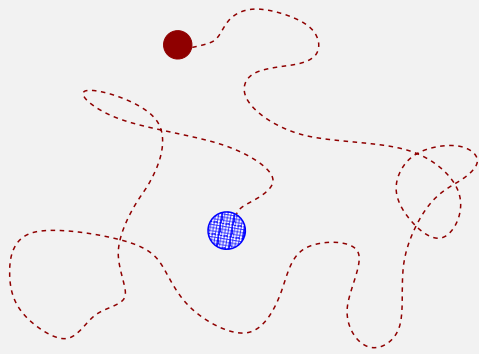


Courtesy Yuval Garini

Molecular reaction times: macro vs micro

Search rate for particle with diffusivity D_{3d} to find an immobile target of radius a (assuming immediate binding):

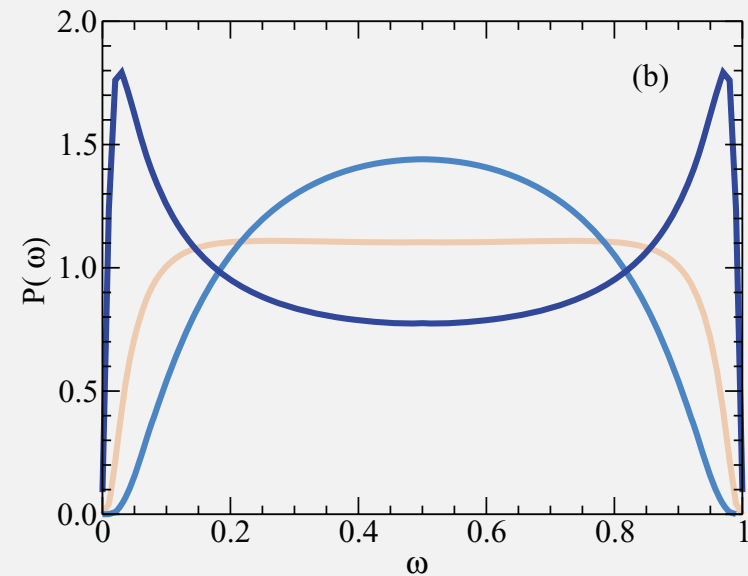
$$k_{\text{on}} = 4\pi D_{3d}a$$



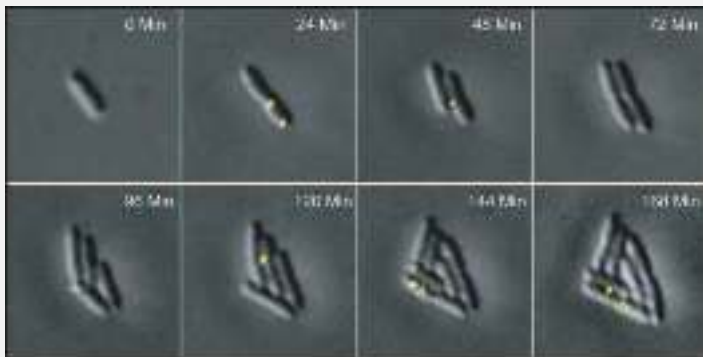
Uniformity index for two independent first-passage times τ_1, τ_2 :

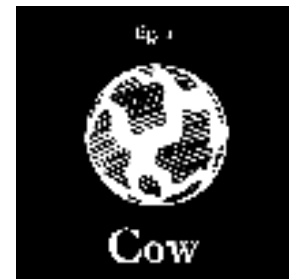
$$\omega = \frac{\tau_1}{\tau_1 + \tau_2}$$

$\leadsto \omega = 1/2$ means good reproducibility $\nwarrow$ many processes



Yu et al, Science (2006)



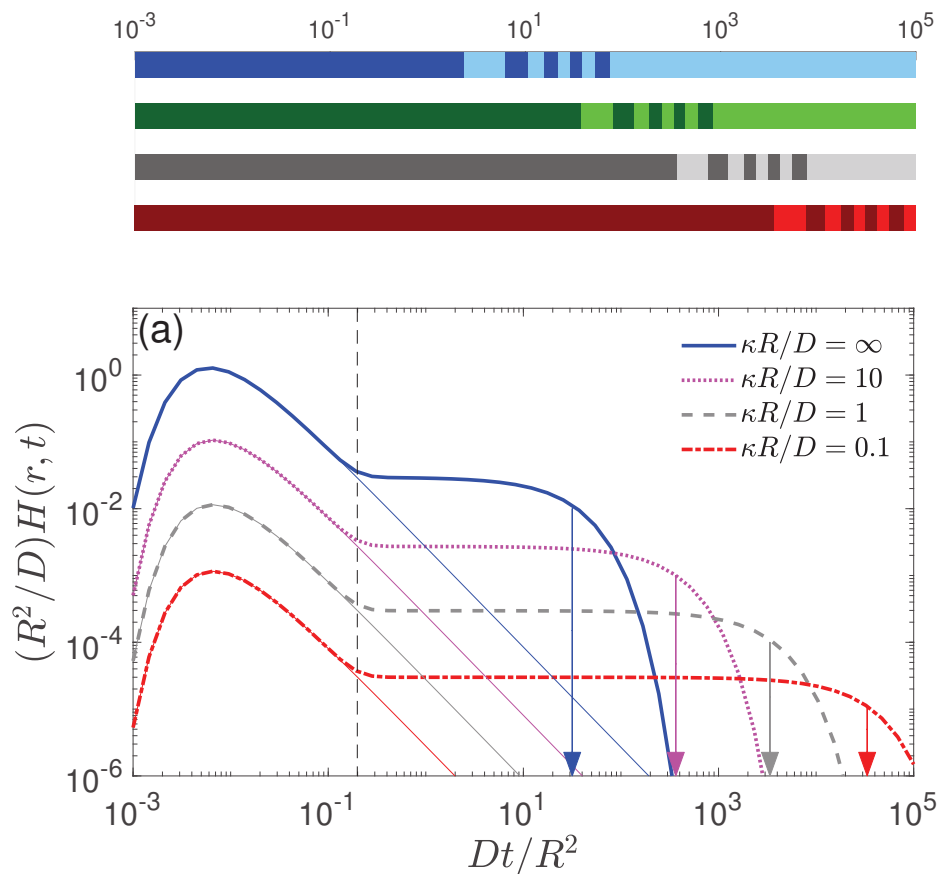


Strongly defocused (fluctuating) reaction times

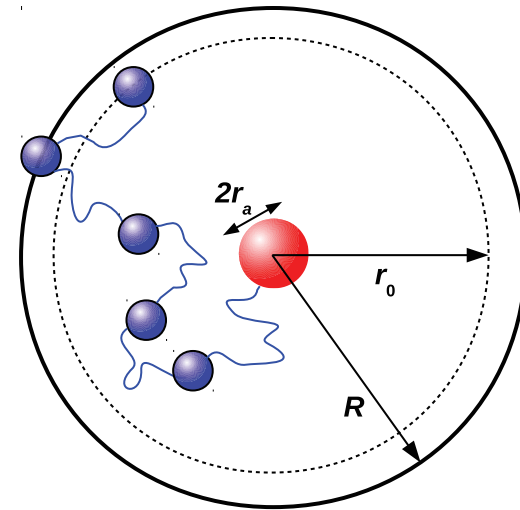
Geometry control: direct trajectories independent of outer boundary

Reaction control: finite reactivity requires multiple collisions

Full first passage time density:

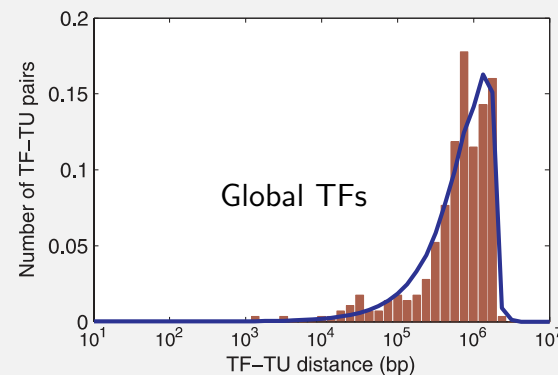
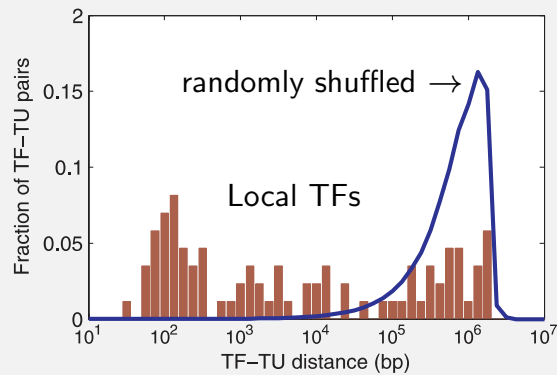
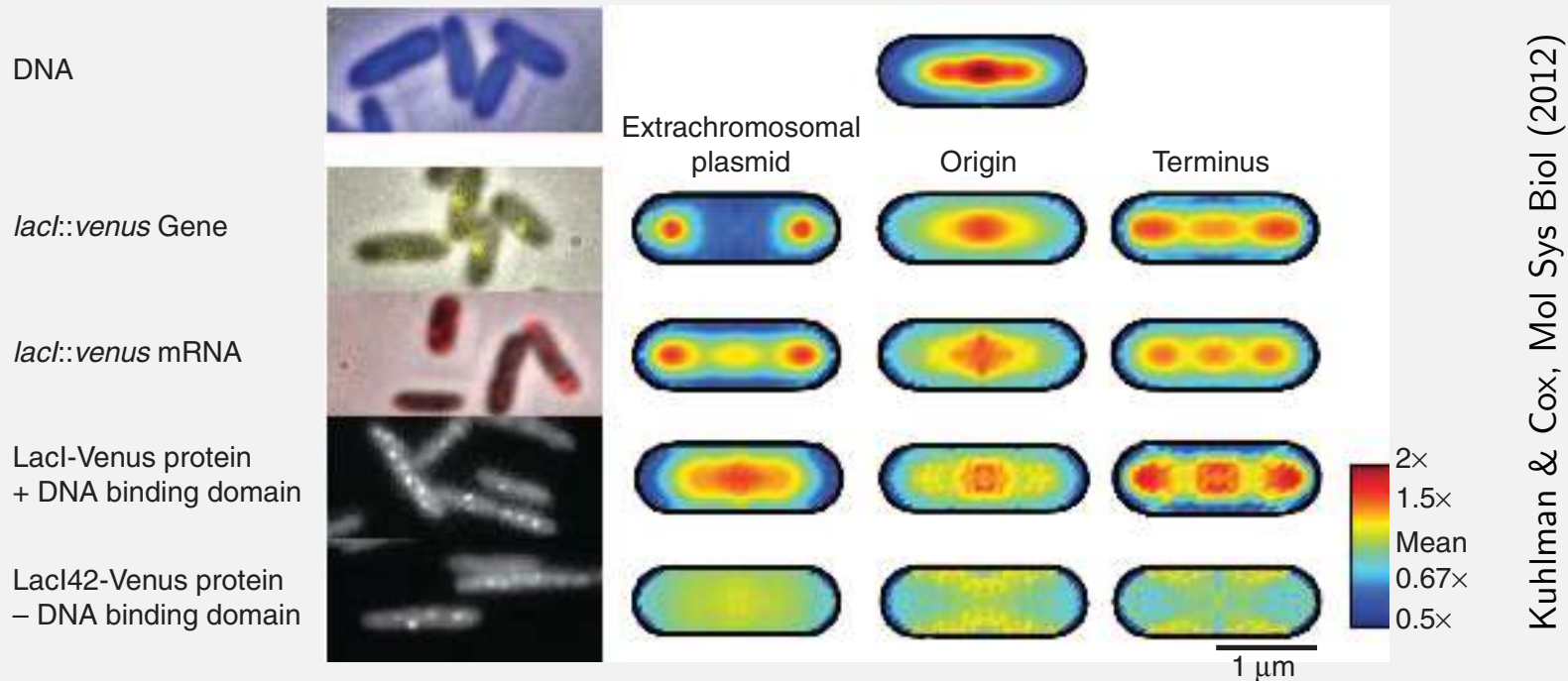


Direct vs indirect trajectories:



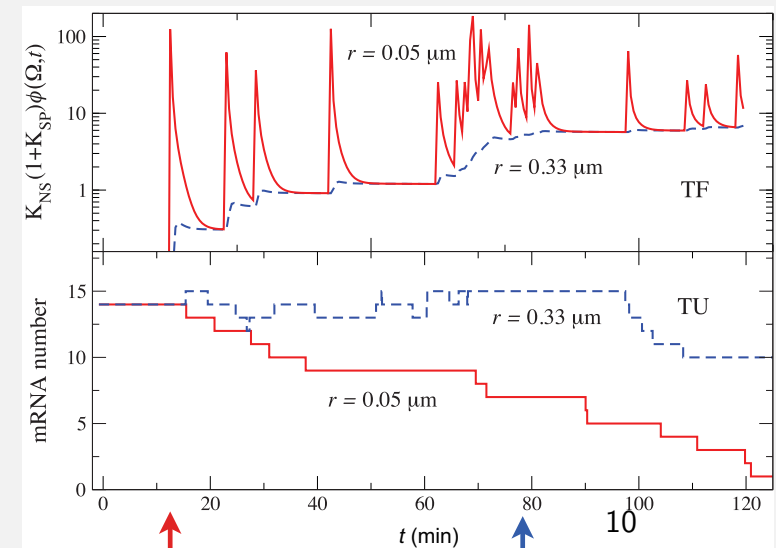
$$\langle t \rangle = \frac{(r_0 - r_a)(2R^3 - r_0 r_a [r_0 + r_a])}{6D r_0 r_a} + \frac{R^3 - r_a^3}{3\kappa r_a}$$

Inhomogeneous TF location, rapid search hypothesis

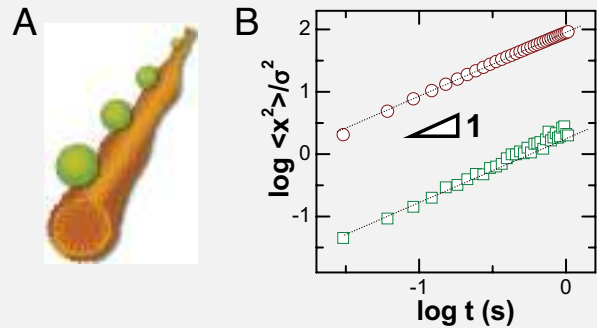


TF-TU gene-gene distance [G Kolesov . . . LA Mirny, PNAS (2007)]

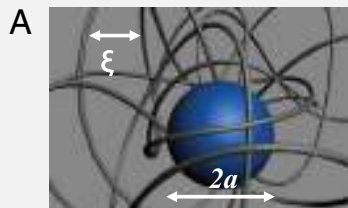
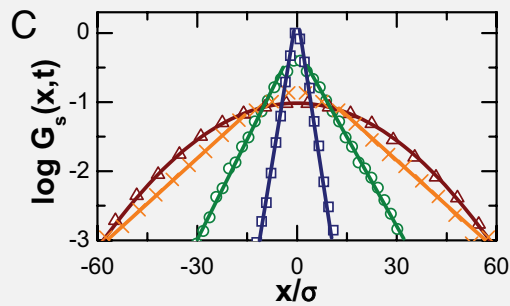
O Pulkkinen & RM, PRL (2013): Distance TF-TU matters $\rightarrow$



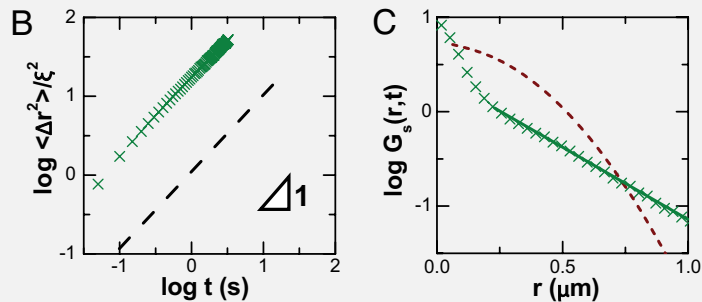
Brownian yet non-Gaussian diffusion in soft & bio-matter



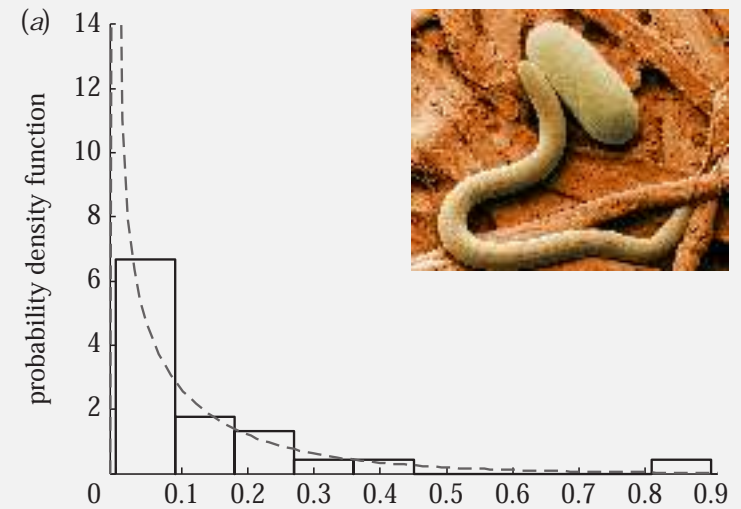
Colloidal beads on nanotubes



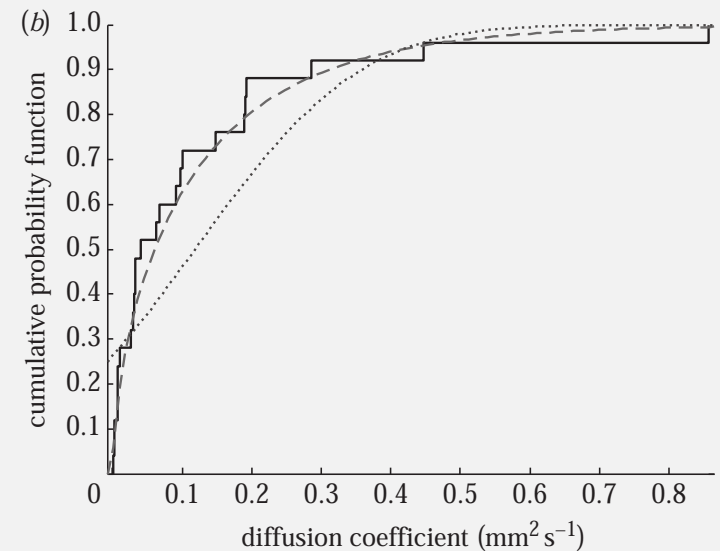
Nanospheres in entangled actin



Wang et al, PNAS (2009); Nature Mat (2012)



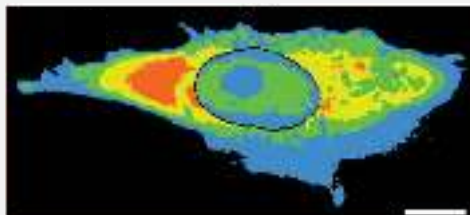
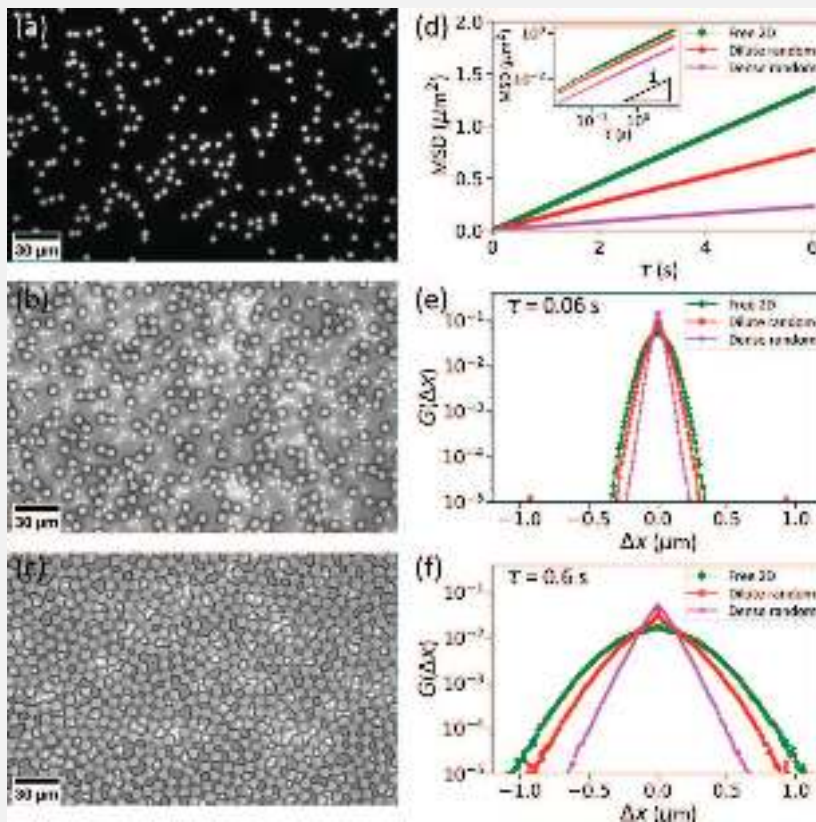
Motion of *Phasmarhabditis* nematodes



S Hapca, JW Crawford & IM Young, Interface (2009) 11

Fickian yet non-Gaussian diffusion in micropillar matrix

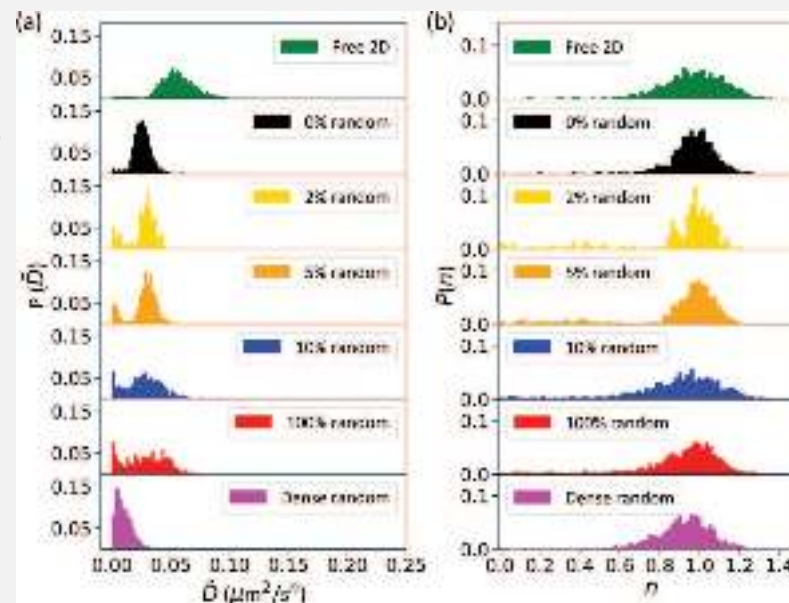
← Increasing density



[Kühn et al, PLoS ONE (2011)]

I Chakraborty & Y Roichman, PRR (2020)

Apparent diffusivity



Anomalous diffusion exponent

Increasing disorder →

Superstatistics for non-Gaussian displacement PDFs

Superstatistical approach: patches of different diffusivities/mobilities or particles with different diffusivities (sizes/shapes) [$G(x, t|D)$ Gaussian Green's function for given D]:

$$P(x, t) = \int_0^\infty G(x, t|D)p(D)dD$$

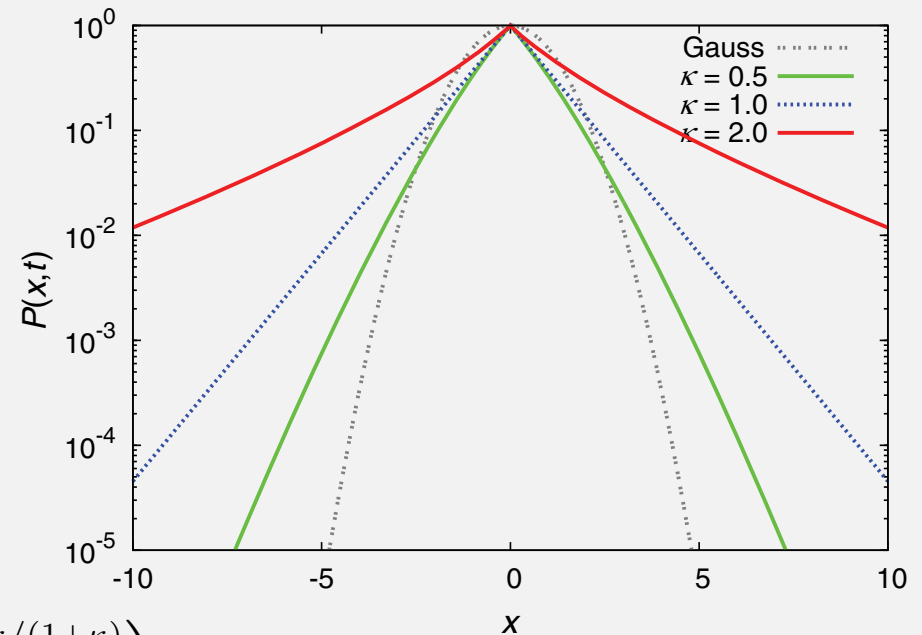
- $p(D) \propto \exp(-D/D^*) \rightsquigarrow$

$$P(x, t) = (4D^*t)^{-1/2} \exp\left(-\frac{|x|}{[D^*t]^{1/2}}\right)$$

- $p(D) \propto \exp(-[D/D^*]^\kappa) \rightsquigarrow$

$$P(x, t) \simeq \frac{|x|^{(1-\kappa)/(1+\kappa)}}{(D^*t)^{1/(1+\kappa)}}$$

$$\times \exp\left(-a(\kappa) \left[\frac{x^2}{4D^*t}\right]^{\kappa/(1+\kappa)}\right)$$



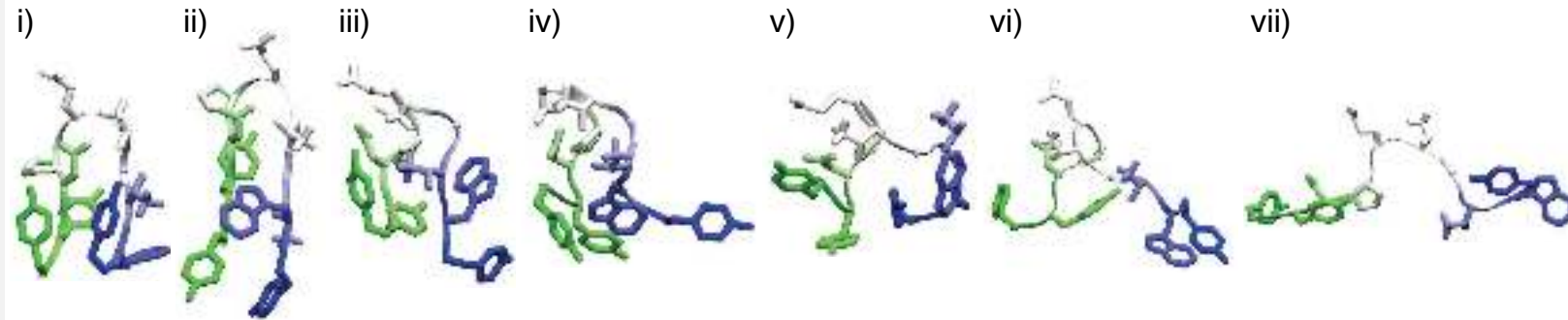
NB1: Superstatistics is closely related to (generalised) grey Brownian motion

[E.g., A Mura, MS Taqqu & F Mainardi, Physica (2008)]

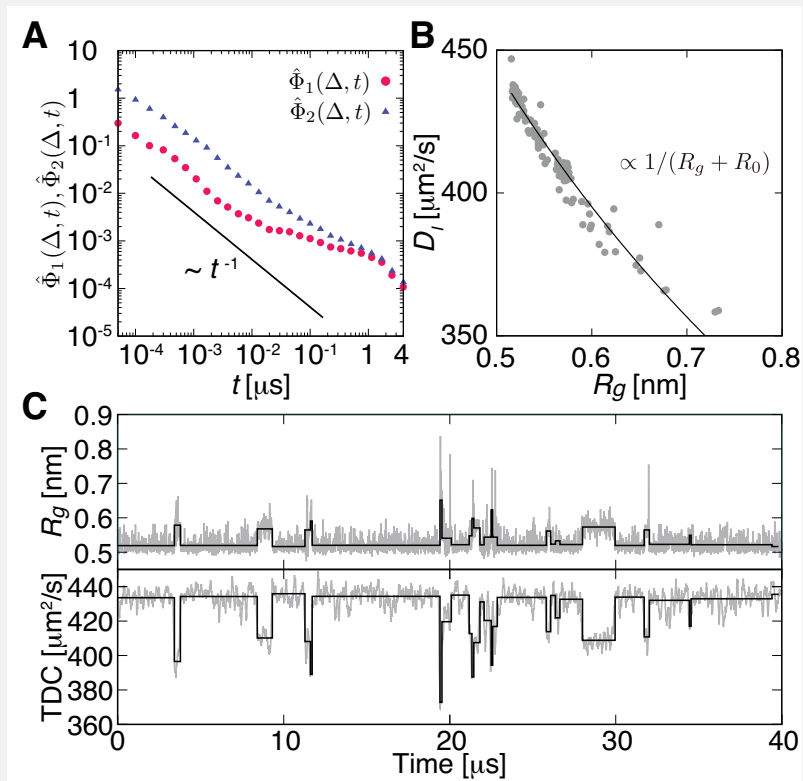
NB2: $p(D)$ is static $\rightsquigarrow P(x, t)$ has fixed shape $\blacktriangledown$ observed cross-over

NB3: $\exists$ also long history of superstatistics in turbulence

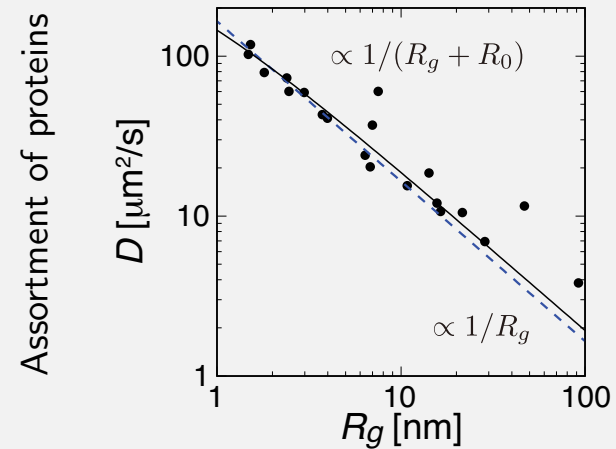
Instantaneous diffusivity of shape-fluctuating proteins



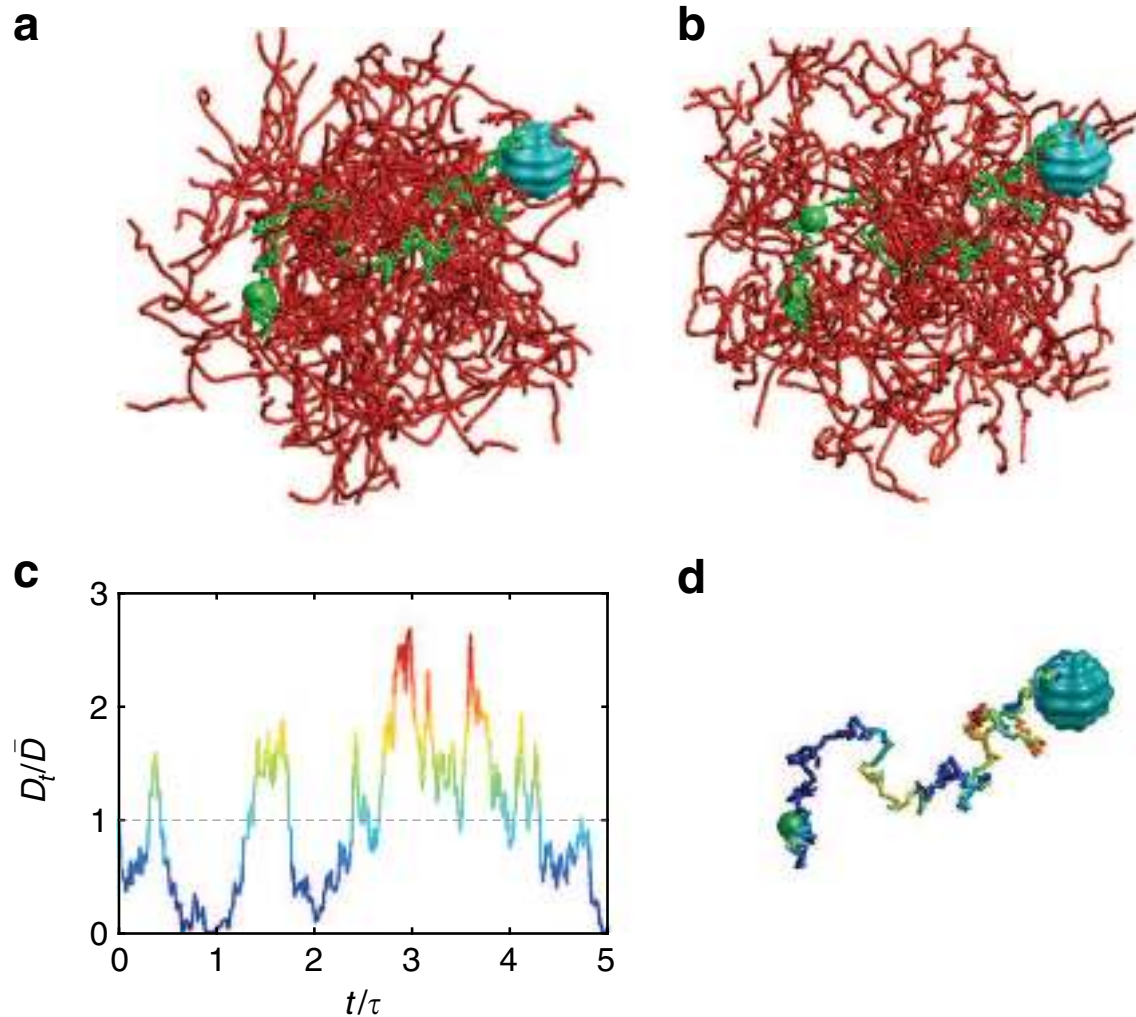
Instantaneous Einstein-Stokes-type relation (for different pressure & temperature):



$$D \propto \frac{1}{R_g + R_0}, \quad R_0 \approx 0.3\text{nm}$$



"Annealed" diffusing-diffusivity in rearranging heterogeneous environment



Fickian, non-Gaussian diffusion with diffusing diffusivity

MV Chubinsky & G Slater, PRL (2014): diffusing diffusivity

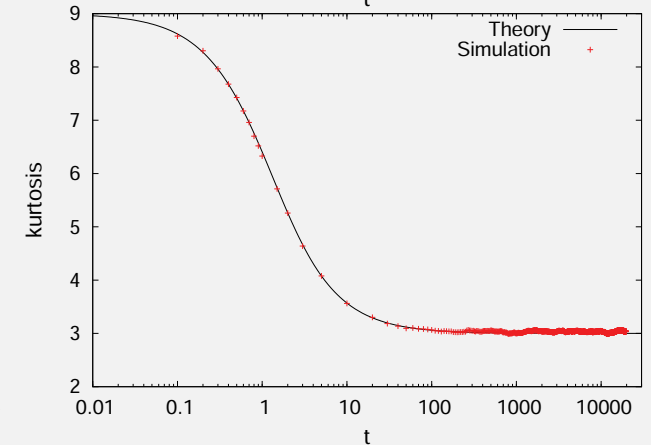
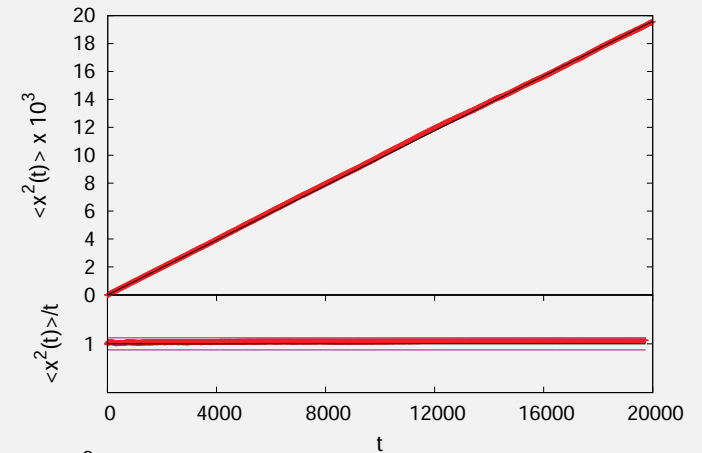
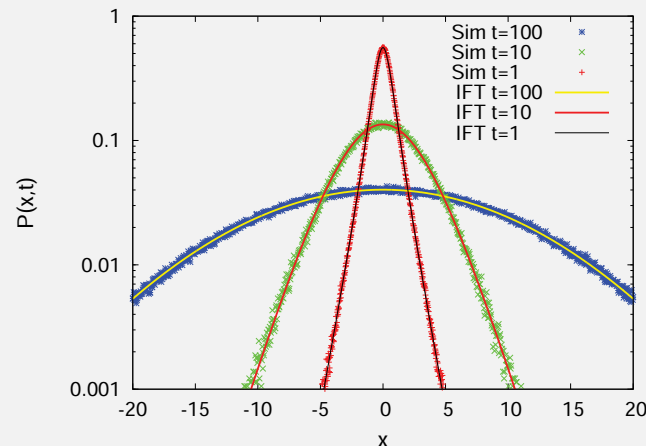
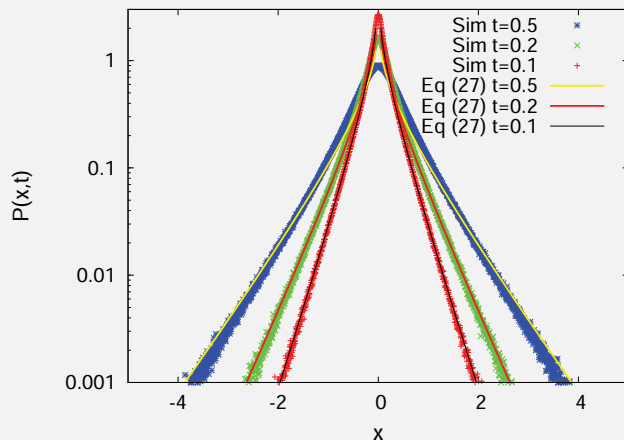
[see also R Jain & KL Sebastian, JPC B (2016)]

Our minimal model for diffusing diffusivity:

$$\dot{x}(t) = \sqrt{2D(t)}\xi(t)$$

$$D(t) = y^2(t)$$

$$\dot{y}(t) = -\tau^{-1}y + \sigma\eta(t)$$



Generalised γ distribution & non-equilibrium diffusivity initial conditions: V Sposini, AV Chechkin, G Pagnini, F Seno & RM, NJP (2018)

AV Chechkin, F Seno, RM & IM Sokolov, PRX (2017)

Random-diffusivity models for non-Gaussian diffusion

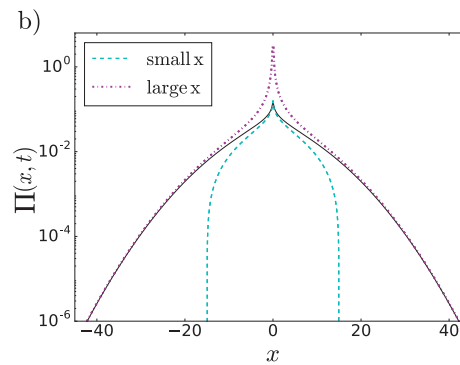
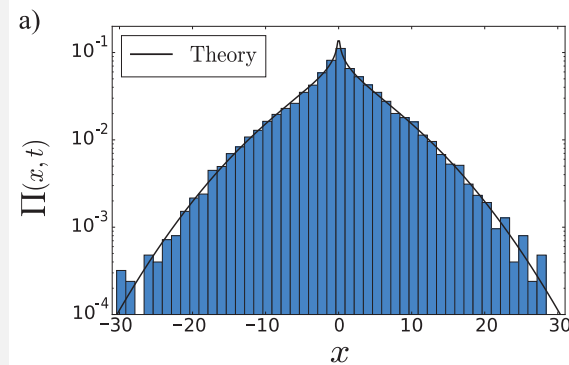
1 Multimerisation of tracer [F Baldovin, F Seno & E Orlandini, Frontiers (2019); M Hidalgo-Soria & E Barkai, PRE (2020)]

2 Two-state model [A Sabri, X Xu, D Krapf & M Weiss, PRL (2020)]

3 Extreme value statistic of tails for small # jumps [E Barkai & S Burov, PRL (2020)]

4 Compartmentalisation model with partial reflectivity [J Ślęzak & S Burov, Sci Rep (2021)]

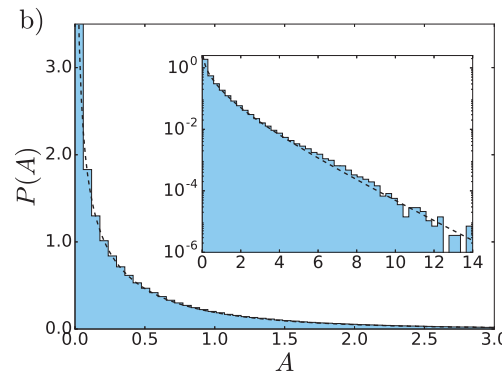
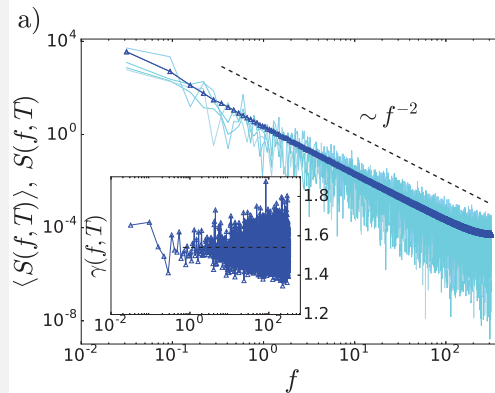
5 Jump processes & functionals of Brownian motion [V Sposini, D Grebenkov, RM, G Oshanin & F Seno, NJP (2020)]



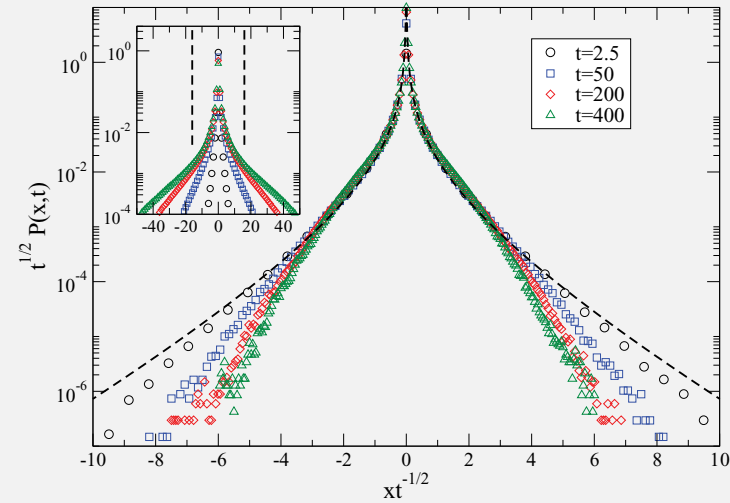
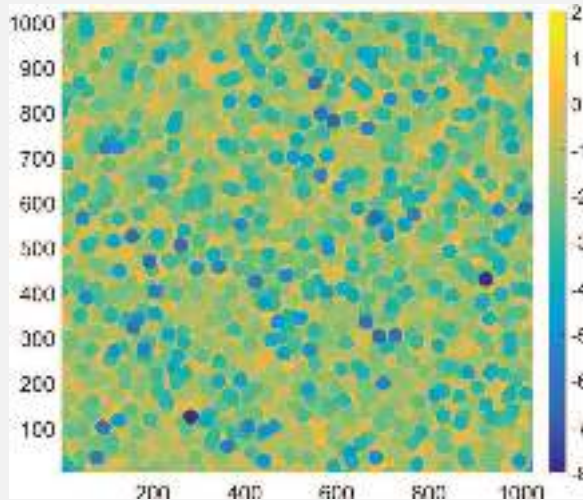
$$\dot{x}_t = \sqrt{2D_0\Psi_t}\xi_t \quad \therefore$$

Rectified BM: $\Psi_t\Theta(B_t)$:

$$P(x, t) = \frac{\exp(-x^2/[8D_0t])}{2\sqrt{\pi^3D_0t}} \times K_0\left(\frac{x^2}{8D_0t}\right)$$

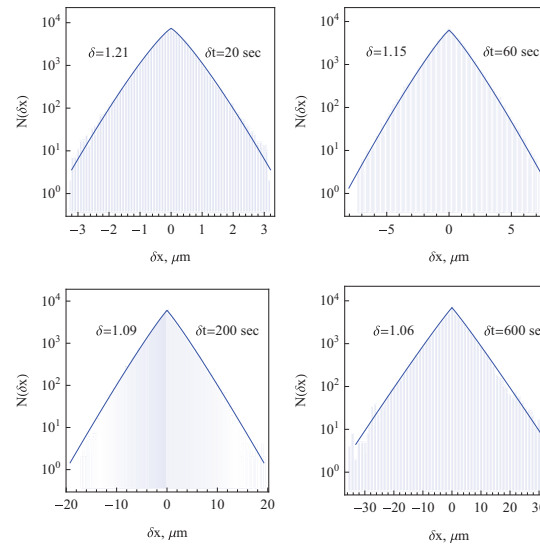
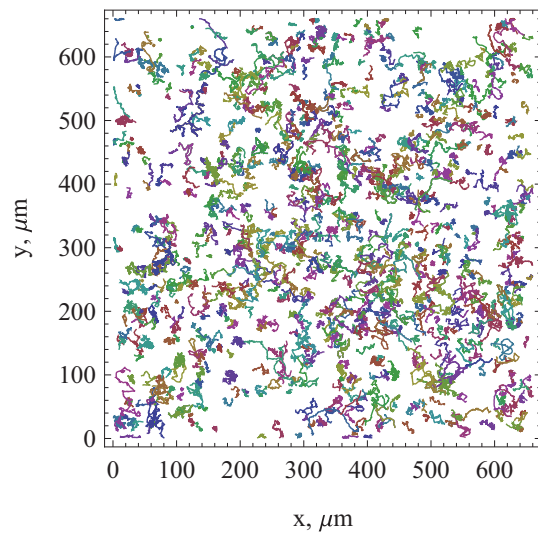


Non-Gaussian diffusion in quenched landscape models



L Luo & M Yi, PRE (2018,2019); see also EB Postnikov, A Chechkin & IM Sokolov, NJP (2020)

Increasing non-Gaussianity in moving amoeba cells

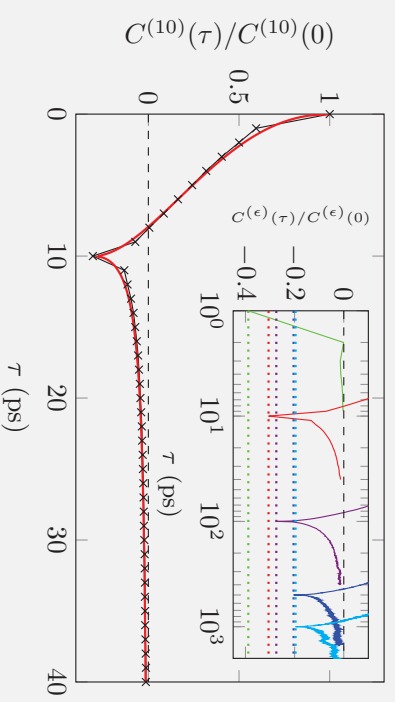
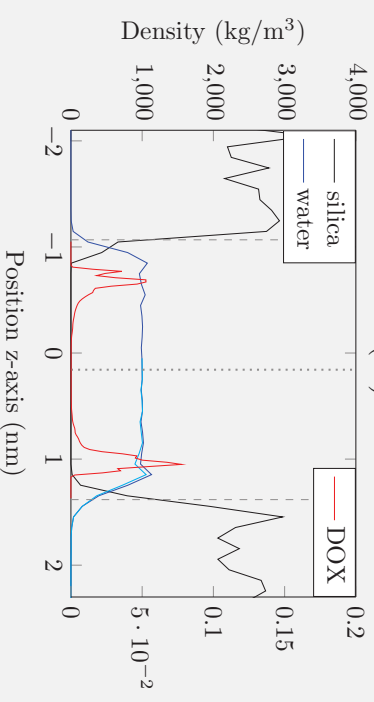
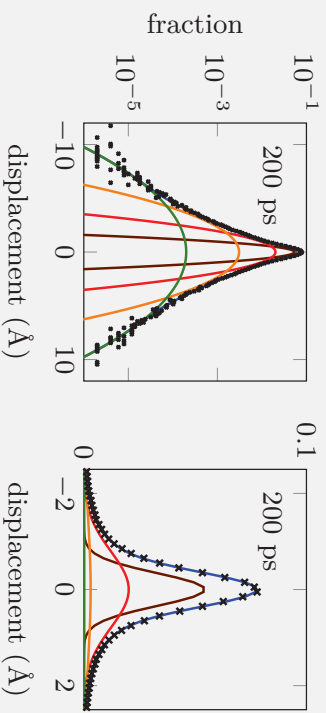
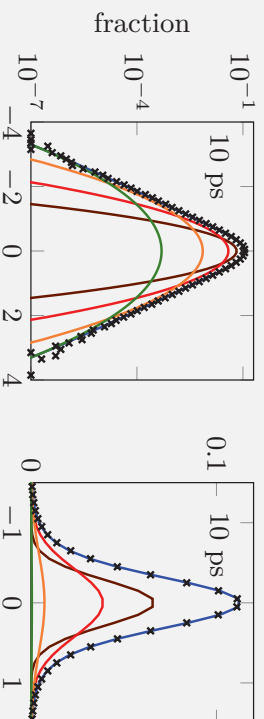
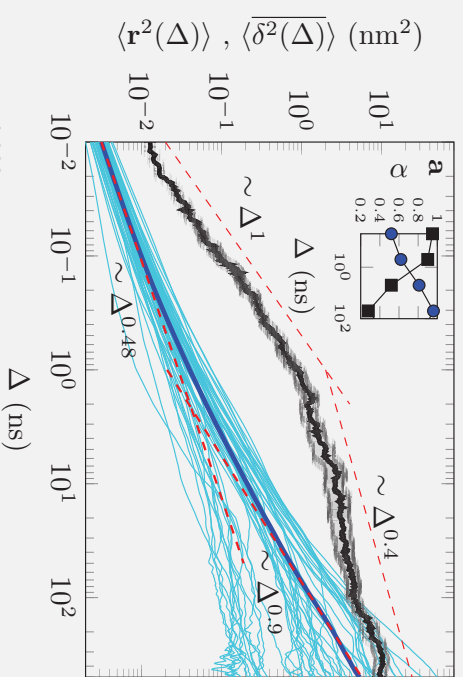
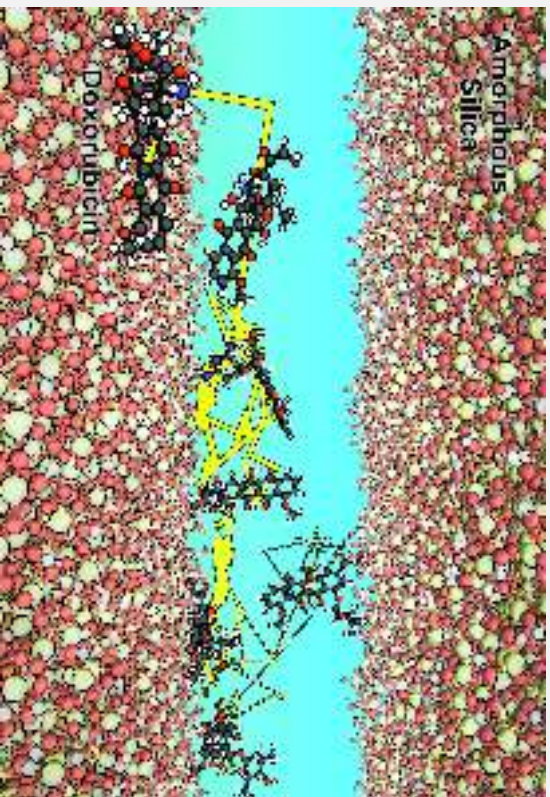


AG Cherstvy, O Nagel, C Beta & RM, PCCP (2018)

CE Wagner et al, Biomacromol (2017)



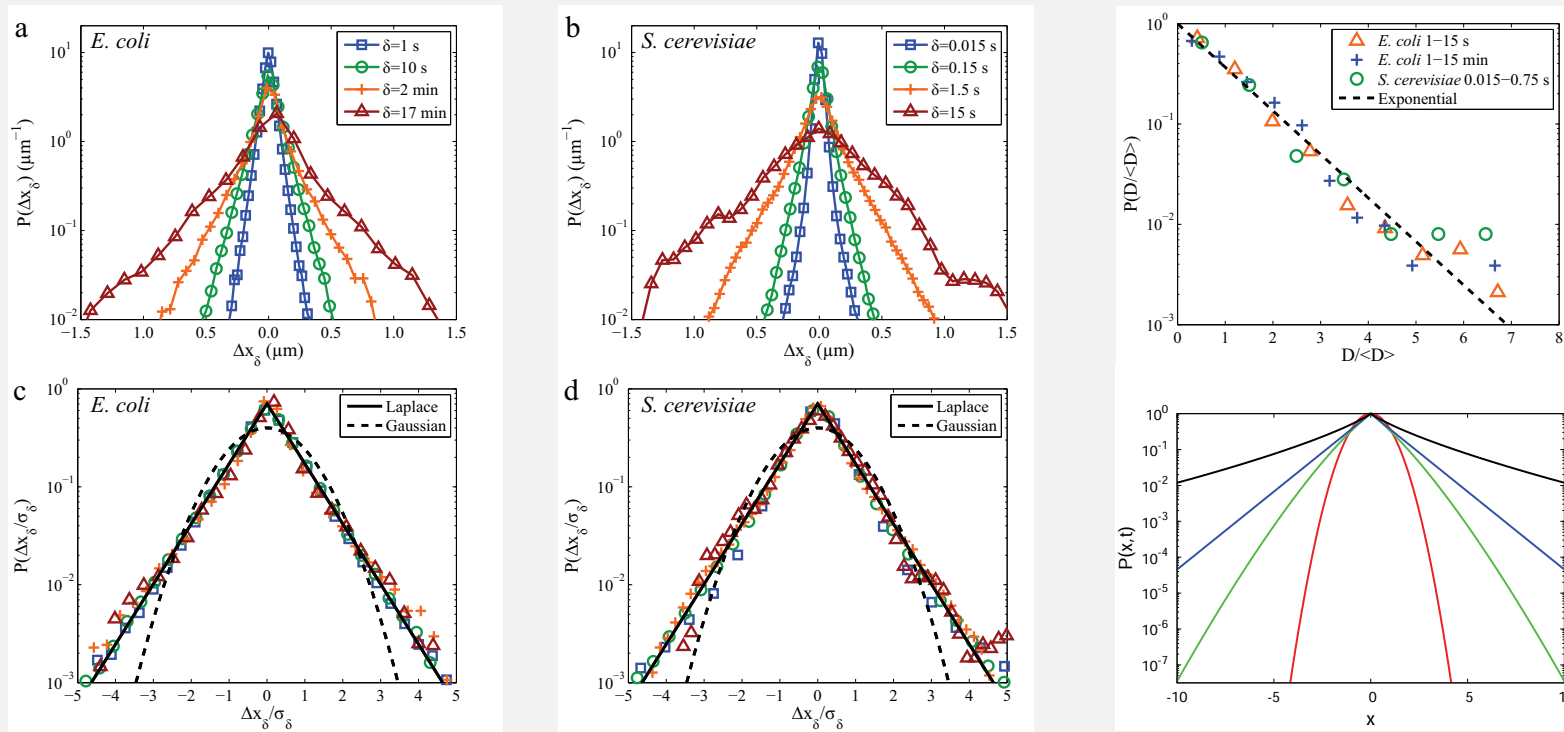
Doxorubicin drug molecule diffusion in silica nanochannels



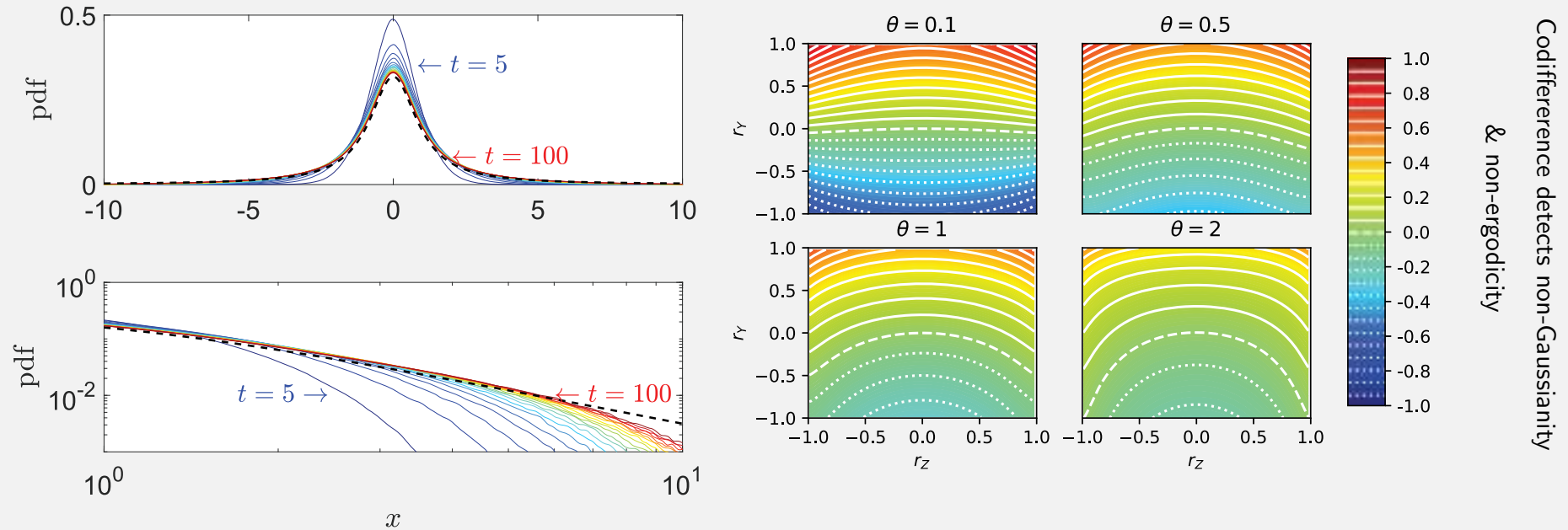
Non-Gaussian diffusion in viscoelastic systems

Passive motion of submicron tracers in the cytoplasm of living cells & crowded media is viscoelastic [L Oddershede & RM, PRL (2011); JH Jeon, N Leijnse, L Oddershede & RM, NJP (2013)]

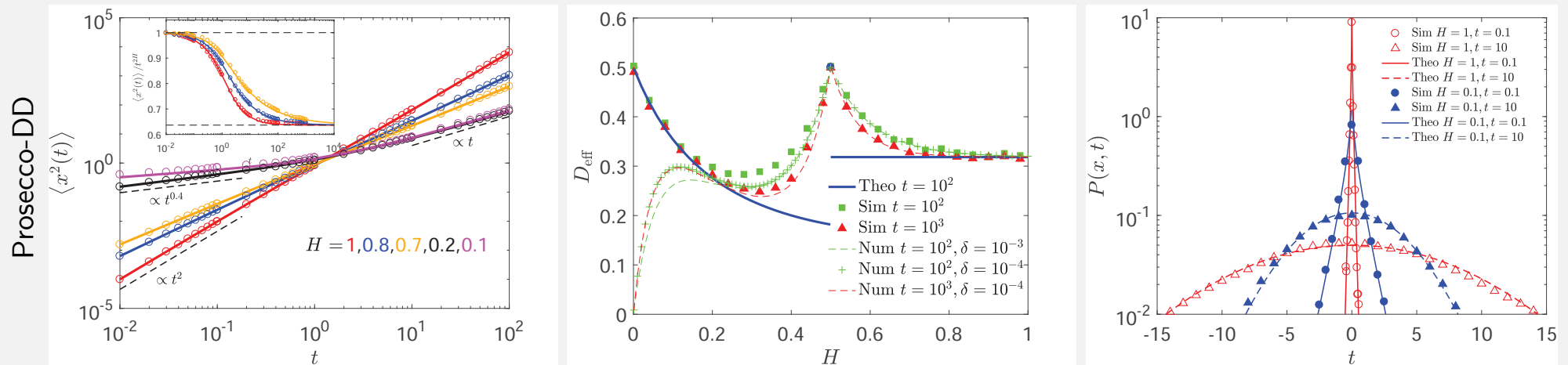
RNA-protein particles in *E.coli* & *S.cerevisiae* perform exponential anomalous diffusion:



Non-Gaussian dynamics in the presence of correlated noise

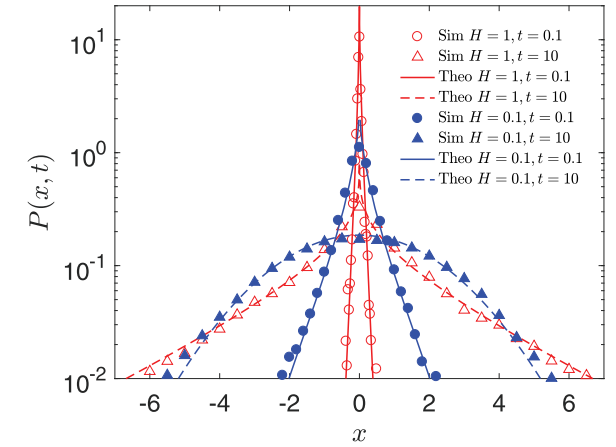
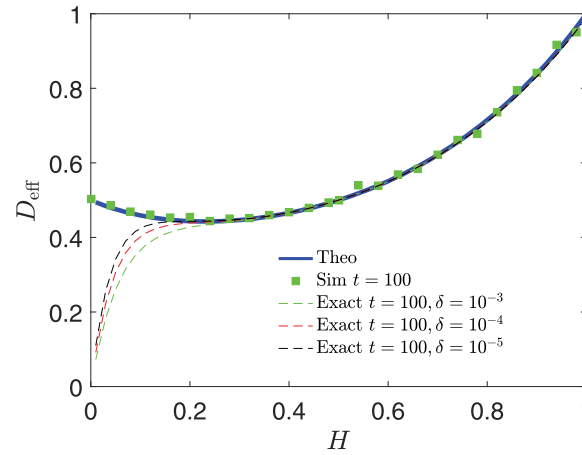
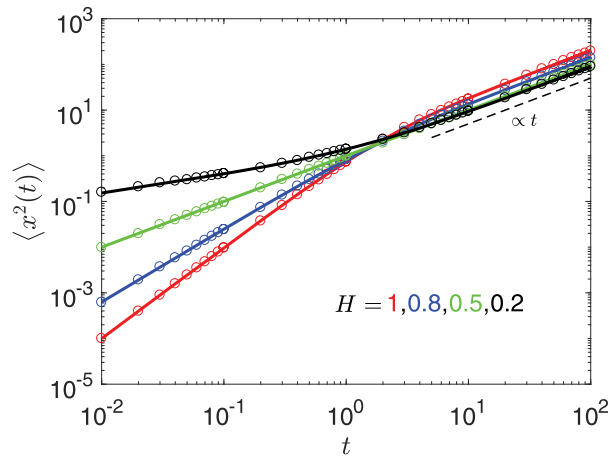


Viscoelastic diffusing-diffusivity model

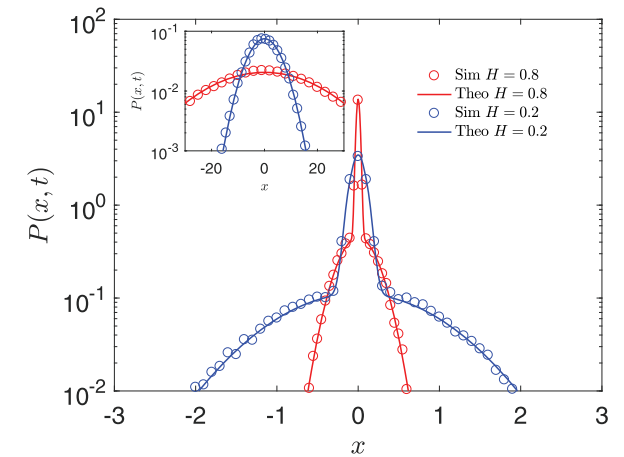
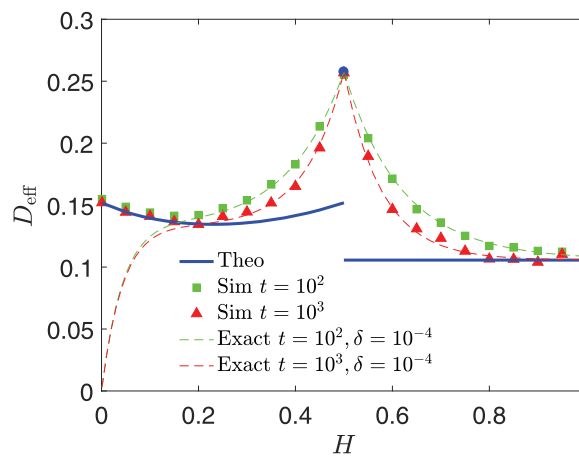
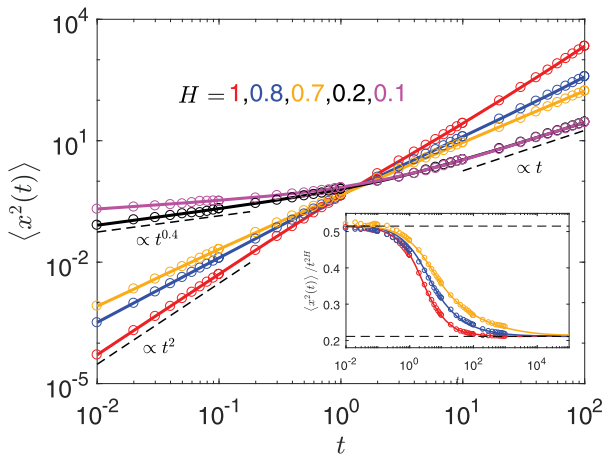


Viscoelastic diffusing-diffusivity model

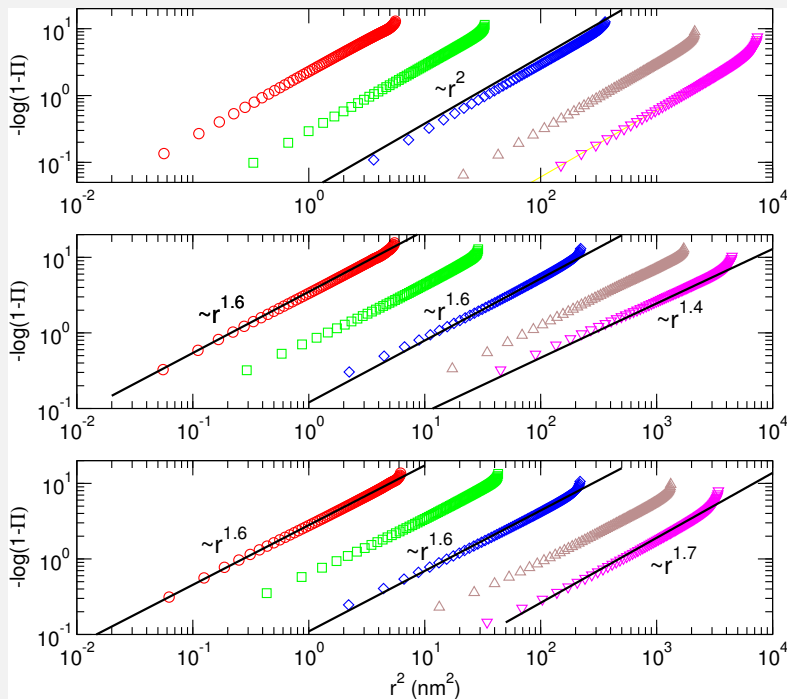
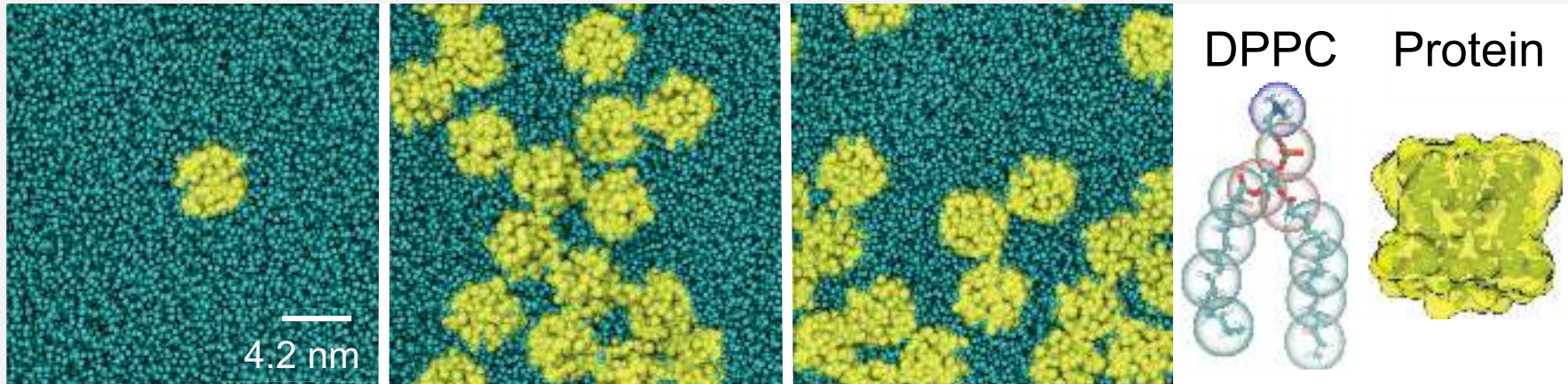
Tyagi model



Switching model



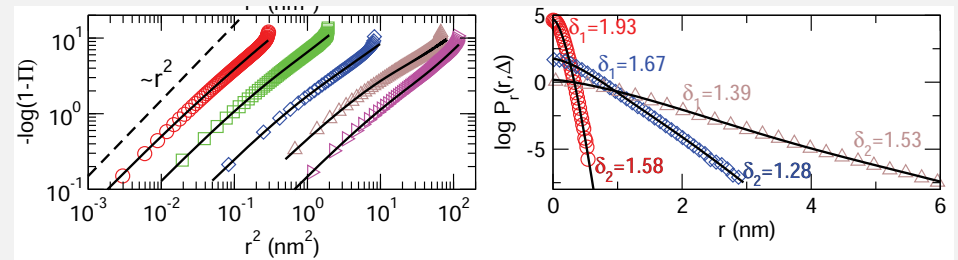
Crowding in membranes: non-Gaussian lipid/protein diffusion



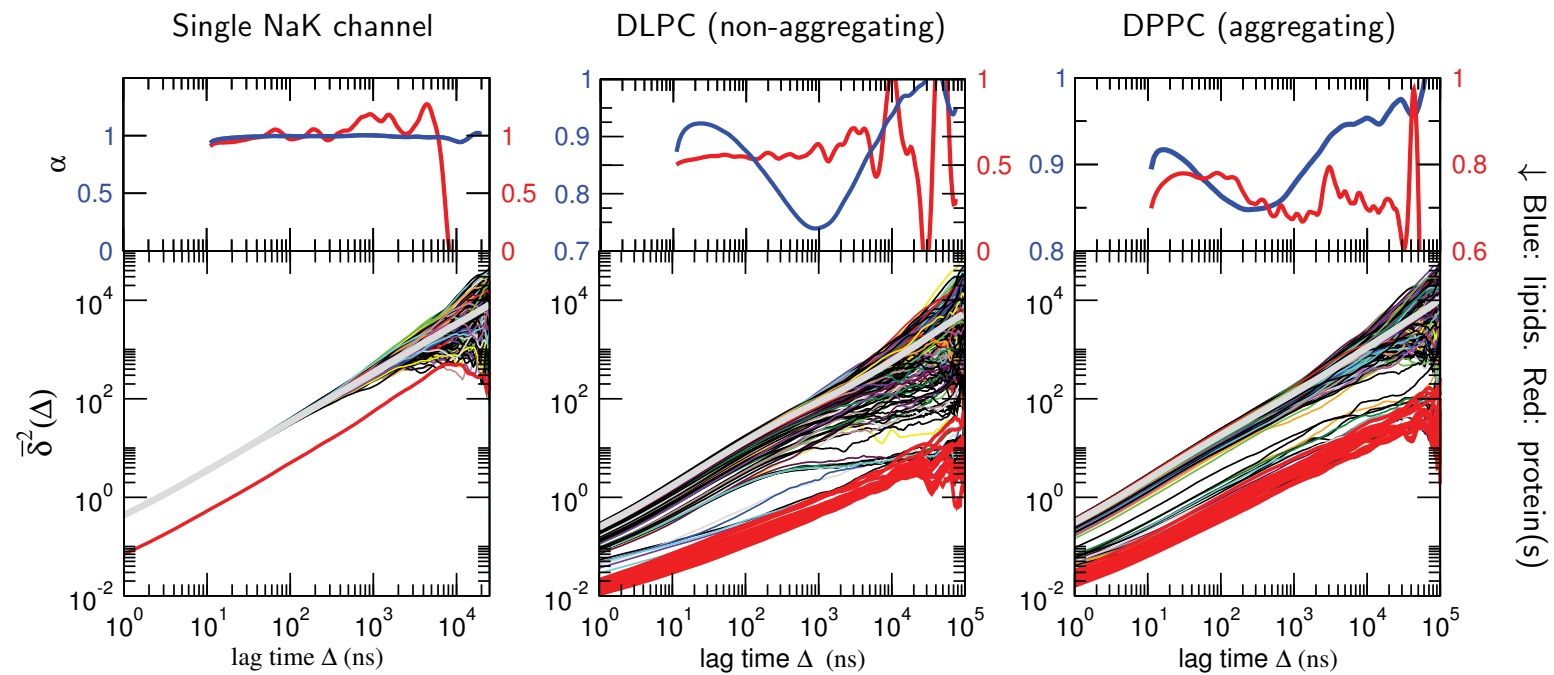
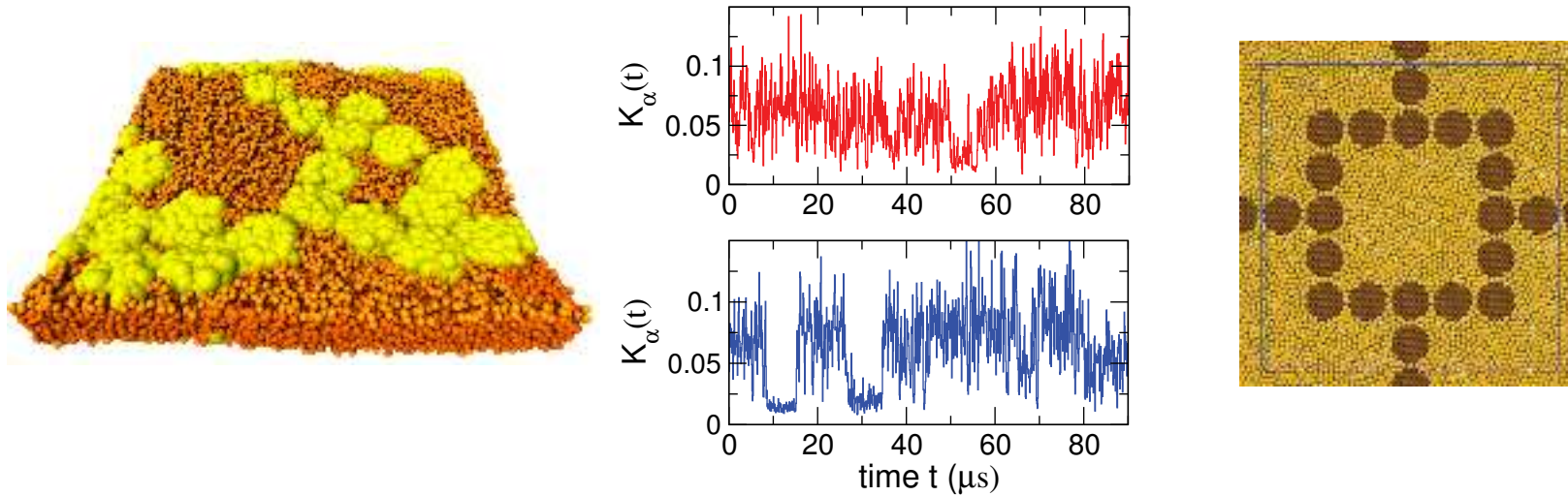
Dilute membrane: $P(r, t)$ Gauss

Crowded membrane ($\delta \approx 1.3 \dots 1.7$):

$$P(r, t) \propto \exp \left(- \left[\frac{r}{ct^{\alpha/2}} \right]^\delta \right)$$

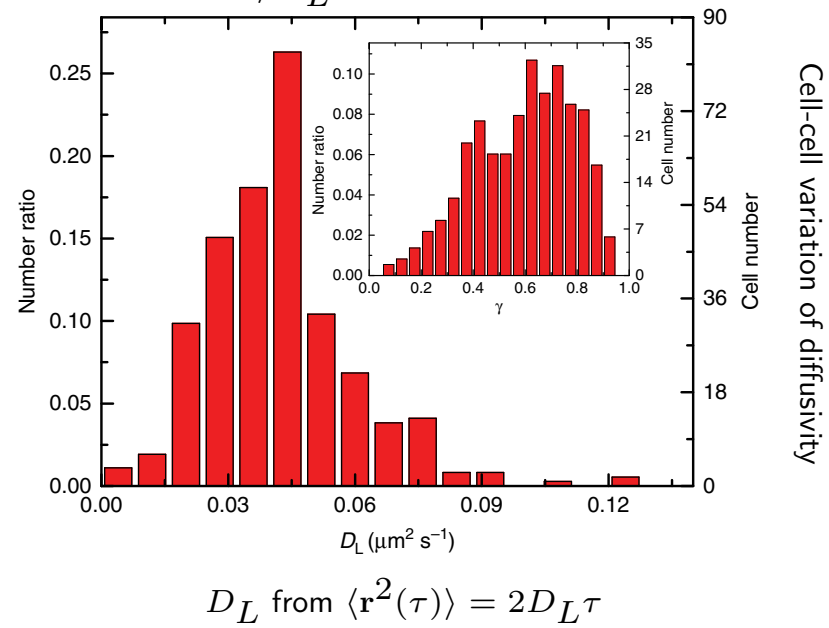
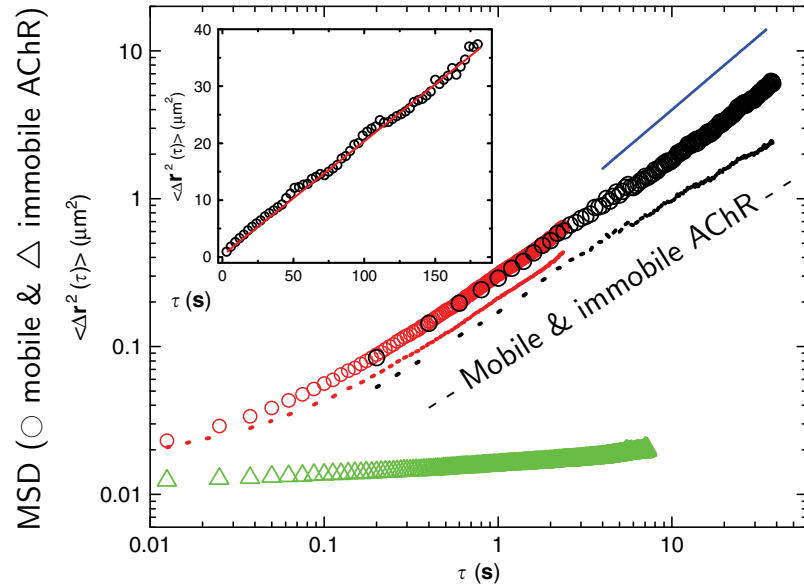
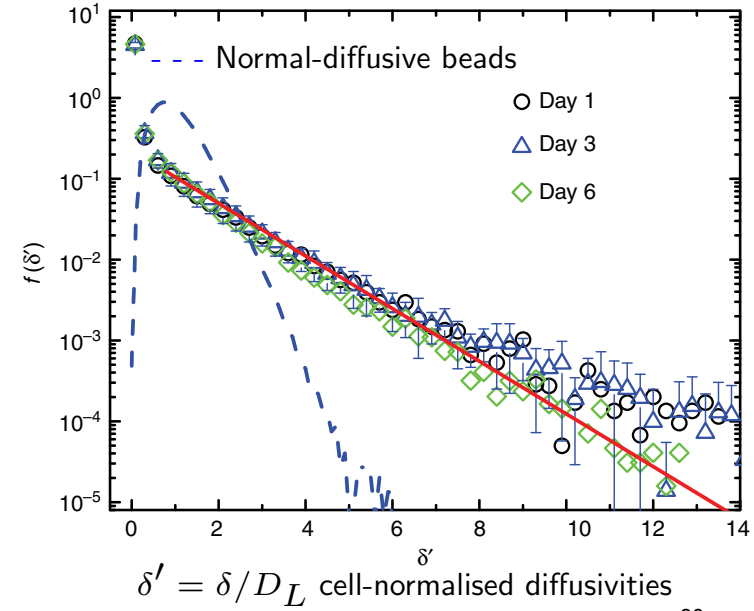
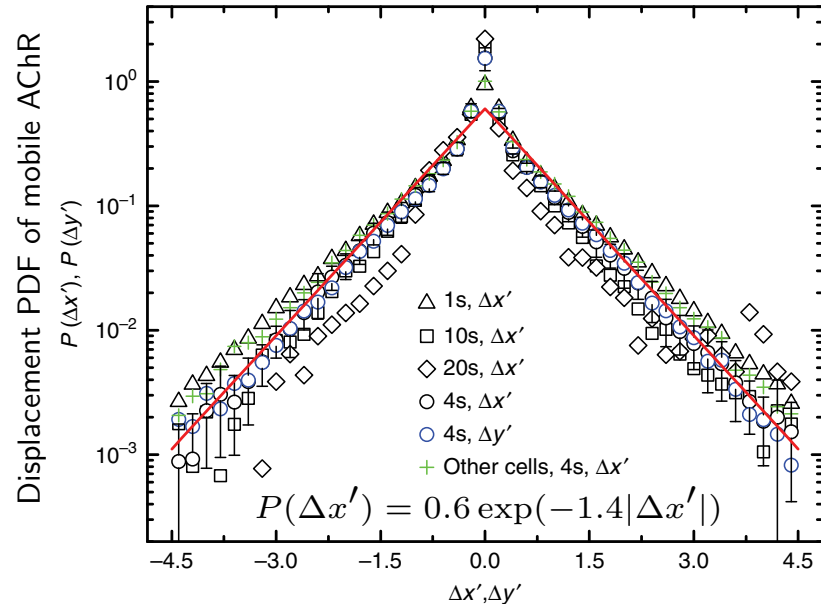


Intermittent lipid diffusion in protein-crowded membranes

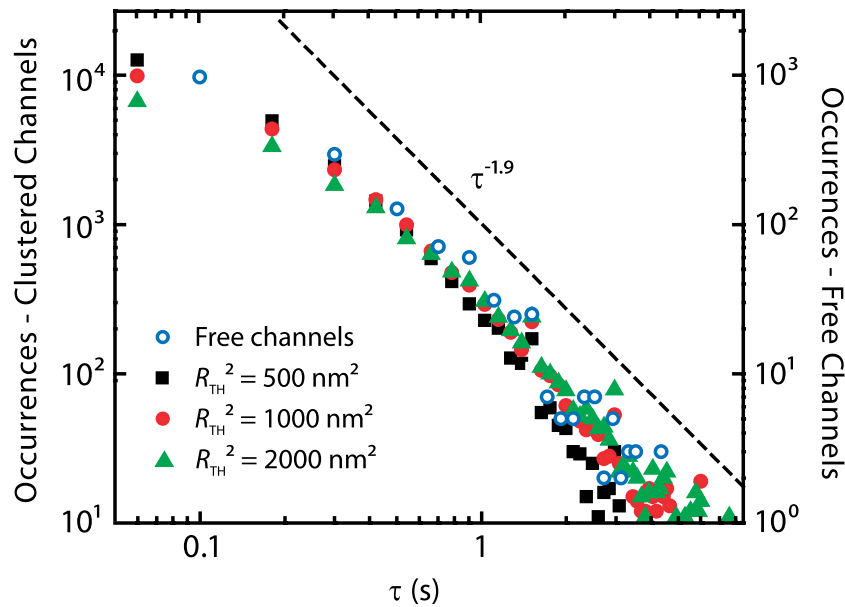
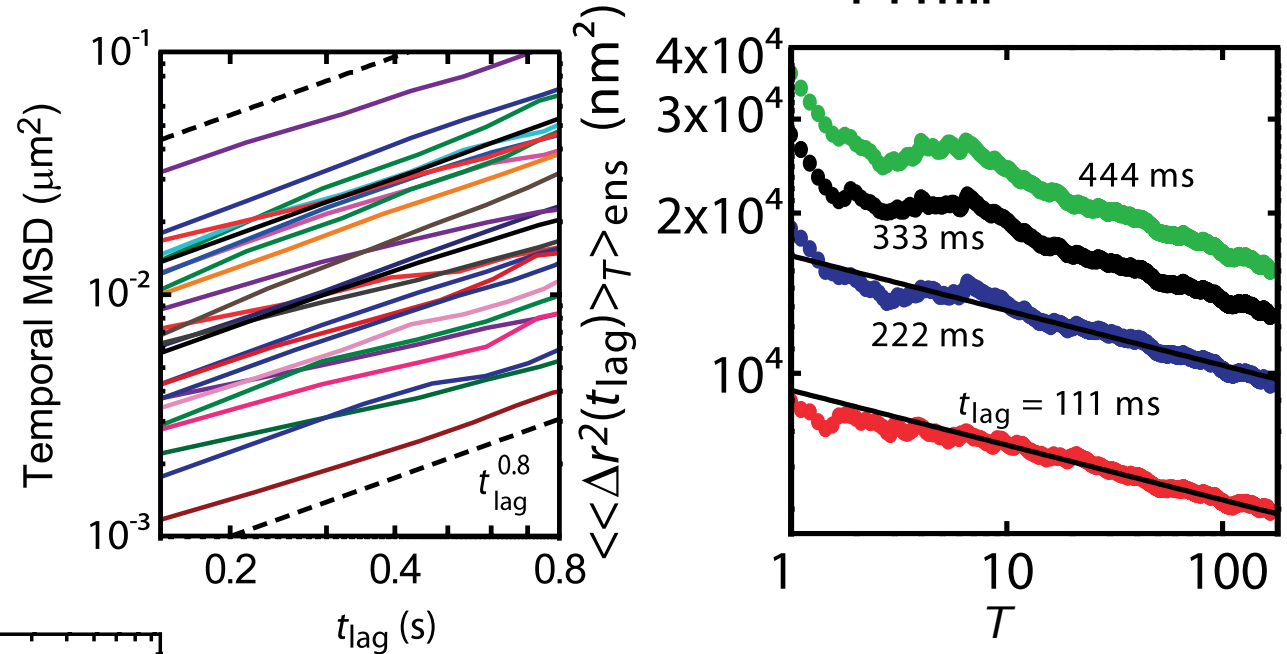
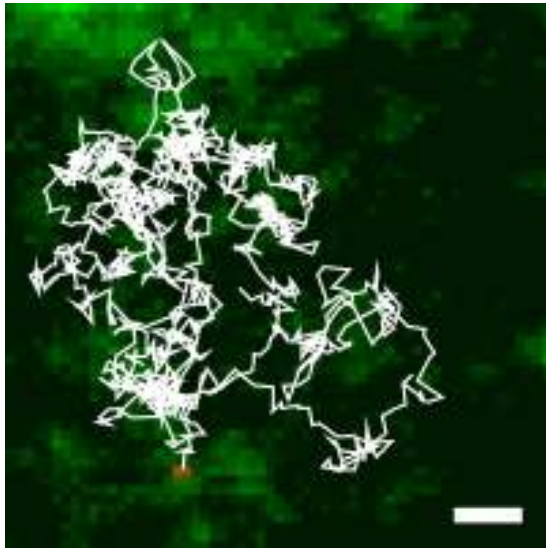


J-H Jeon, M Javanainen, H Martinez-Seara, RM & I Vattulainen, PRX (2016); compare Faraday Disc (2013)

Non-Gaussianity of acetylcholine receptors in *Xenopus* cells



CTRW-like motion of Ka channels in plasma membrane



$$\psi(\tau) \simeq \tau^{-1-\alpha} \text{ scale free}$$

$$\overline{\delta^2(\Delta)} \text{ apparently random}$$

$$\Delta/T^{1-\alpha} \simeq \overline{\delta^2(\Delta)} \neq \langle \mathbf{r}^2(\Delta) \rangle \simeq \Delta^\alpha$$

$$P(\mathbf{r}, t) \simeq \exp(-\beta r^{1/[1-\alpha/2]})$$

Time averaged MSD & weak ergodicity breaking (WEB)

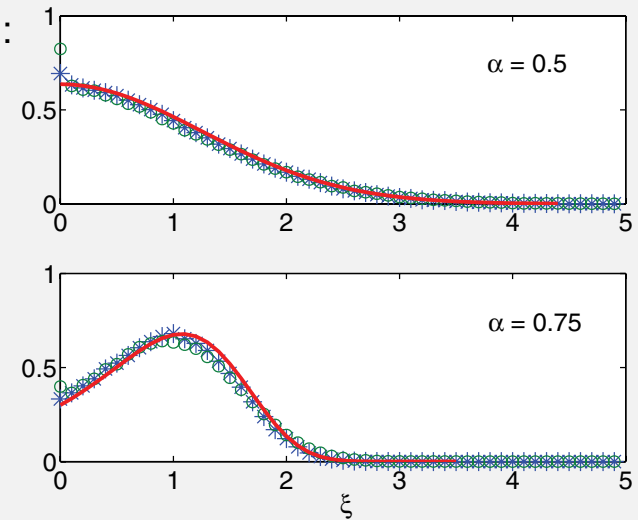
Time averaged MSD $\simeq \Delta$ is pseudo-Brownian and ageing ($\langle x^2(t) \rangle \simeq K_\alpha t^\alpha$):

$$\langle \overline{\delta^2(\Delta)} \rangle \sim \frac{1}{N} \sum_i^N \overline{\delta_i^2(\Delta)} \sim \frac{2dK_\alpha}{\Gamma(1+\alpha)} \frac{\Delta}{T^{1-\alpha}} \quad \therefore \quad K_\alpha \equiv \frac{\langle \delta \mathbf{r}^2 \rangle}{2\tau^\alpha}$$

Amplitude distribution $\overline{\delta^2}$ of trajectories ($\xi \equiv \overline{\delta^2} / \langle \overline{\delta^2} \rangle$):

$$\phi_\alpha(\xi) \sim \frac{\Gamma^{1/\alpha}(1+\alpha)}{\alpha \xi^{1+1/\alpha}} L_\alpha^+ \left(\frac{\Gamma^{1/\alpha}(1+\alpha)}{\xi^{1/\alpha}} \right)$$

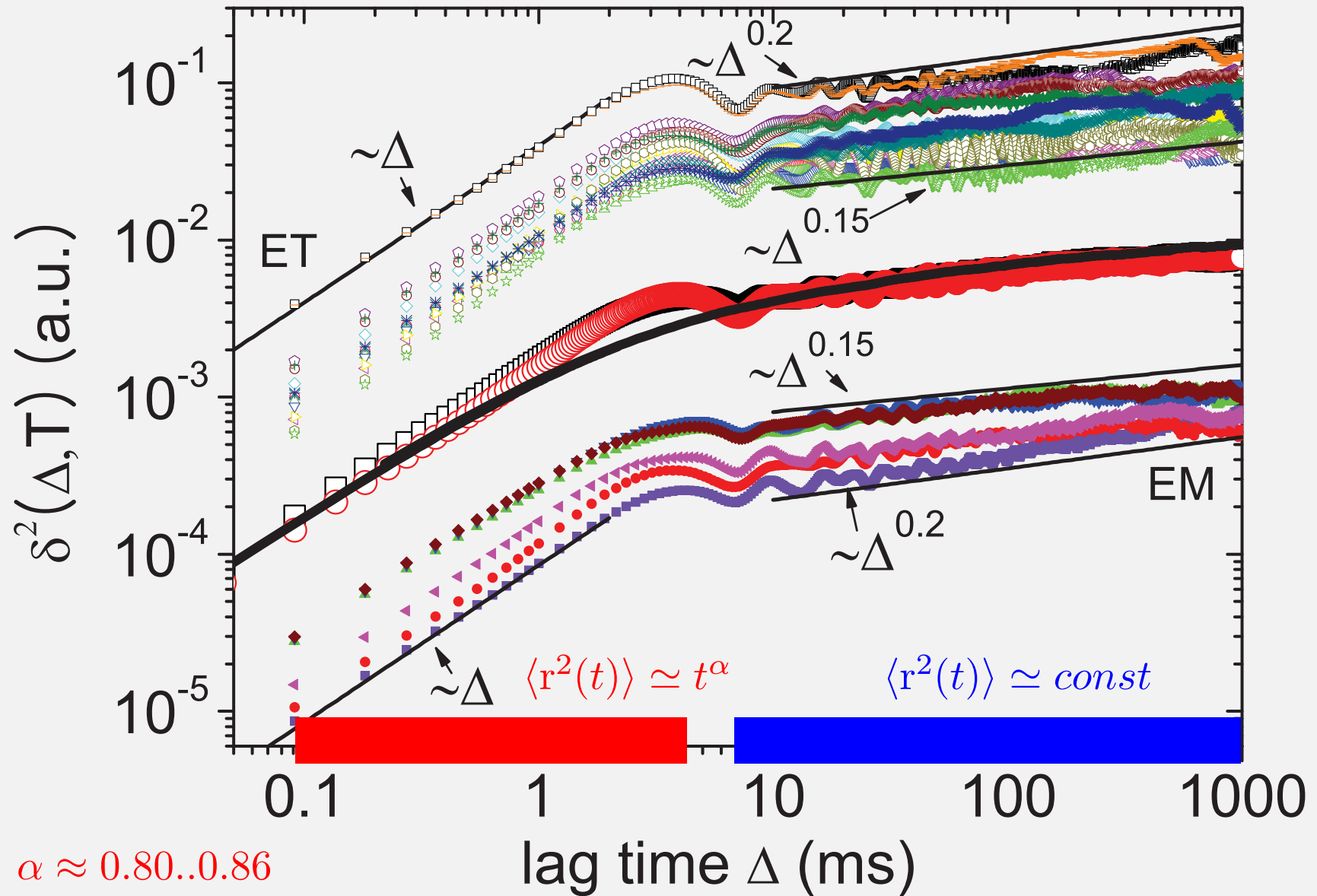
$$\phi_{1/2}(\xi) = \frac{2}{\pi} \exp \left(-\frac{\xi^2}{\pi} \right); \quad \phi_1(\xi) = \delta(\xi - 1)$$



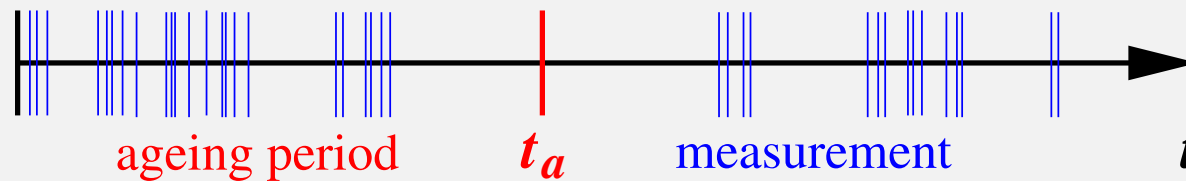
Confinement does not effect a plateau ($\langle x^2(t) \rangle \simeq \text{const}(T)$):

$$\langle \overline{\delta^2(\Delta)} \rangle \sim \left(\langle x^2 \rangle_B - \langle x \rangle_B^2 \right) \frac{2 \sin(\pi\alpha)}{(1-\alpha)\alpha\pi} \left(\frac{\Delta}{T} \right)^{1-\alpha}; \quad \frac{1}{(K_\alpha \lambda_1)^{1/\alpha}} \ll \Delta \ll T$$

Granule subdiffusion in harmonic optical tweezer potential



Ageing effects in single trajectory time averages

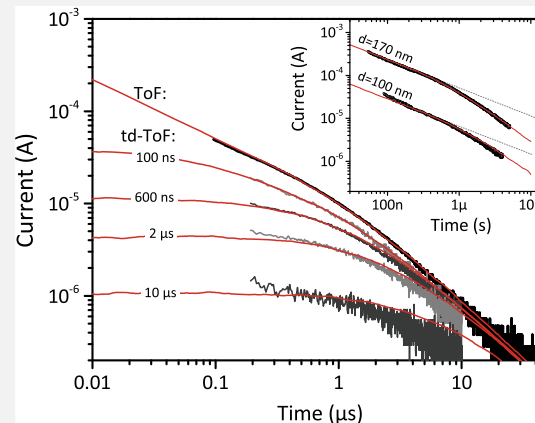
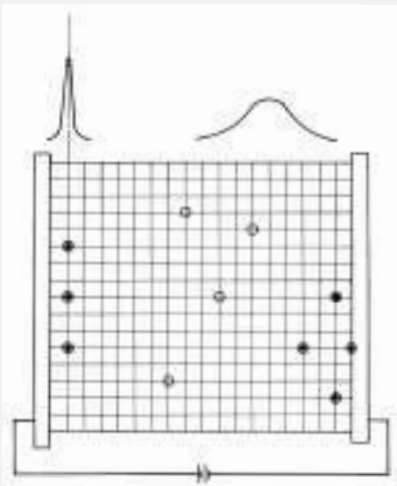


Ageing mean squared displacement ($\Lambda(z) = (1 + z)^\alpha - z^\alpha$)

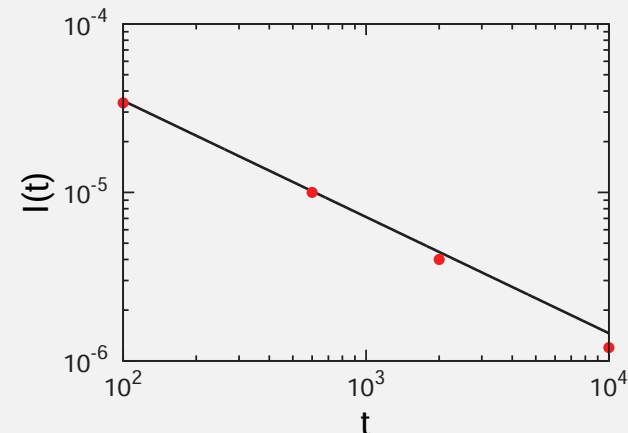
$$\langle \overline{\delta^2(\Delta)} \rangle_a = \frac{\Lambda_\alpha(t_a/T) g(\Delta)}{\Gamma(1 + \alpha) T^{1-\alpha}} \Leftrightarrow \langle x^2(t) \rangle_a \simeq \begin{cases} t^\alpha, & t_a \ll t \\ t_a^{\alpha-1} t, & t_a \gg t \end{cases}$$

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

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



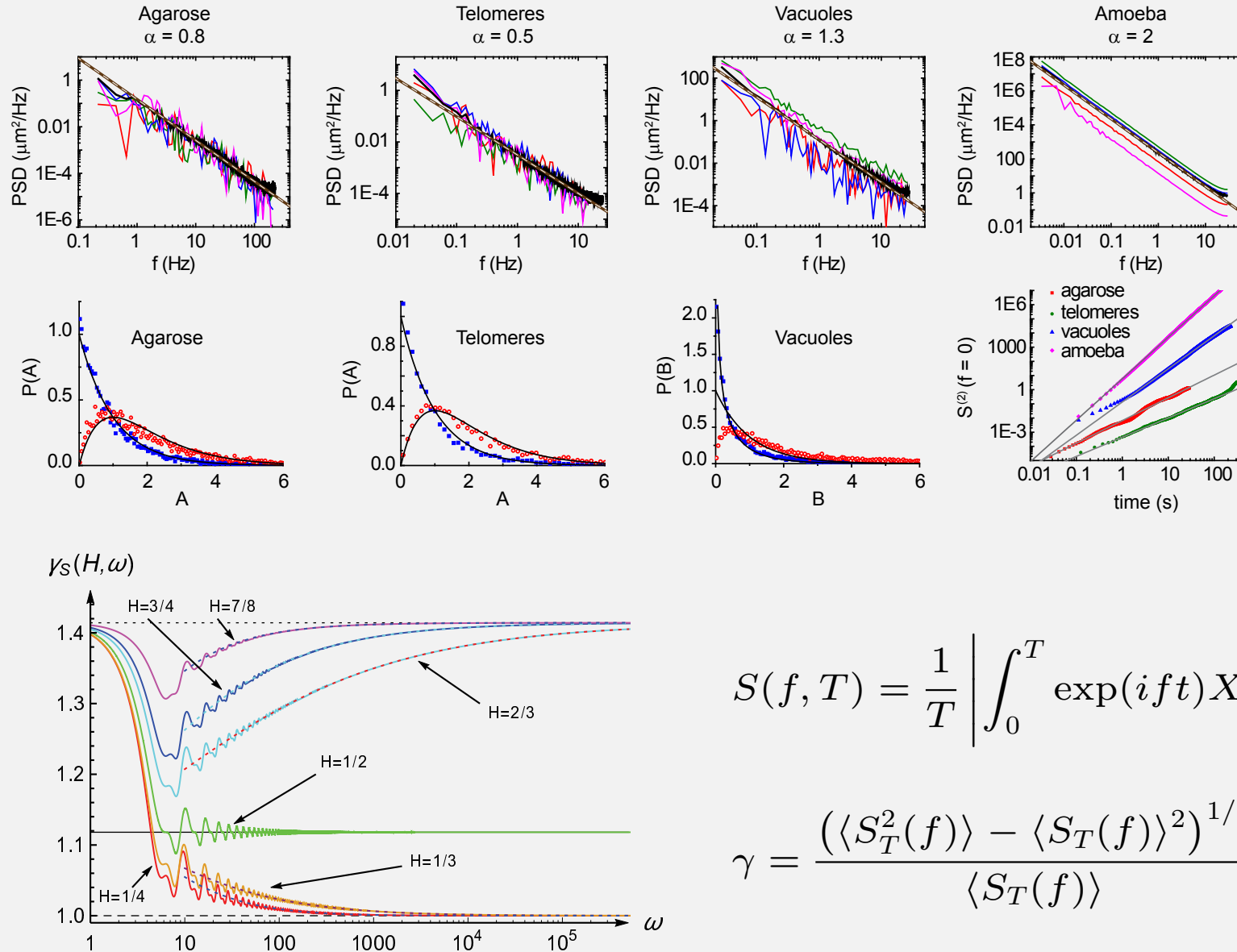
M Schubert, . . . & D Neher,
Phys Rev B (2013)



H Krüsemann, R Schwarzl & RM,
Transp Porous Media (2016), PRE (2015)

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

Power spectral density of a single FBM trajectory



$$S(f, T) = \frac{1}{T} \left| \int_0^T \exp(i f t) X_t dt \right|^2$$

$$\gamma = \frac{(\langle S_T^2(f) \rangle - \langle S_T(f) \rangle^2)^{1/2}}{\langle S_T(f) \rangle}$$

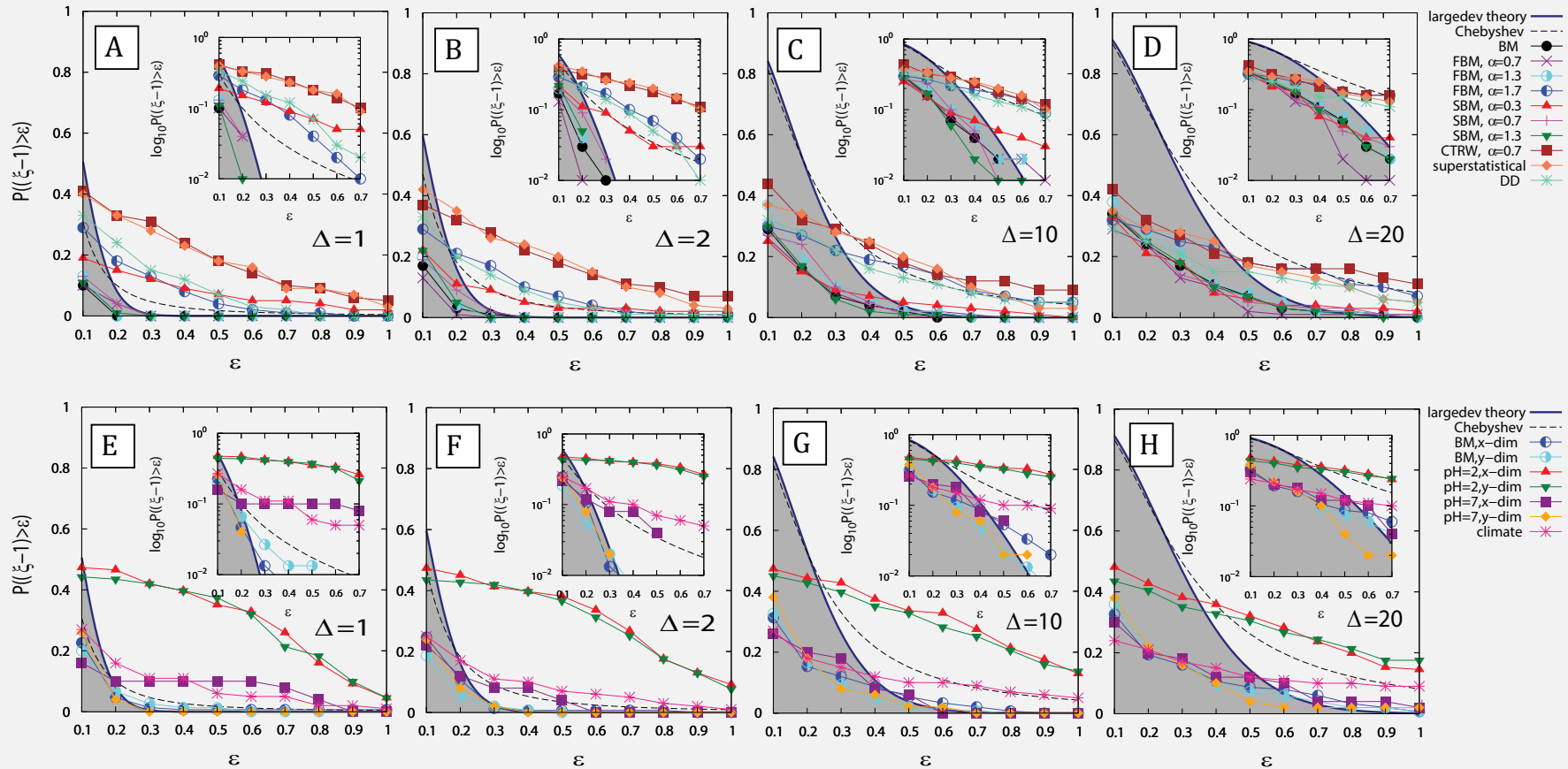
Large-deviation statistics for TAMSD

Chebyshev's inequality for Brownian motion $X(1), X(2), \dots, X(N)$, given deviation ε :

$$P((\xi - 1) \geq \varepsilon) \leq \frac{4\Delta}{4\Delta + 3N\varepsilon^2}, \quad \xi = \frac{\overline{\delta^2(\Delta)}}{\langle \delta^2(\Delta) \rangle}, \quad \langle \xi \rangle = 1$$

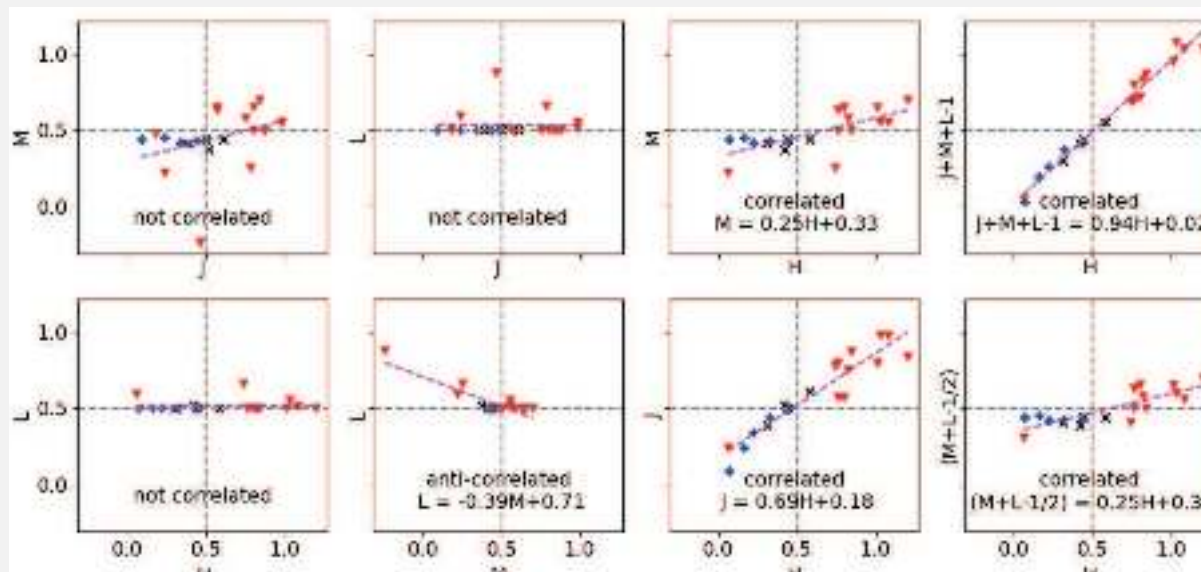
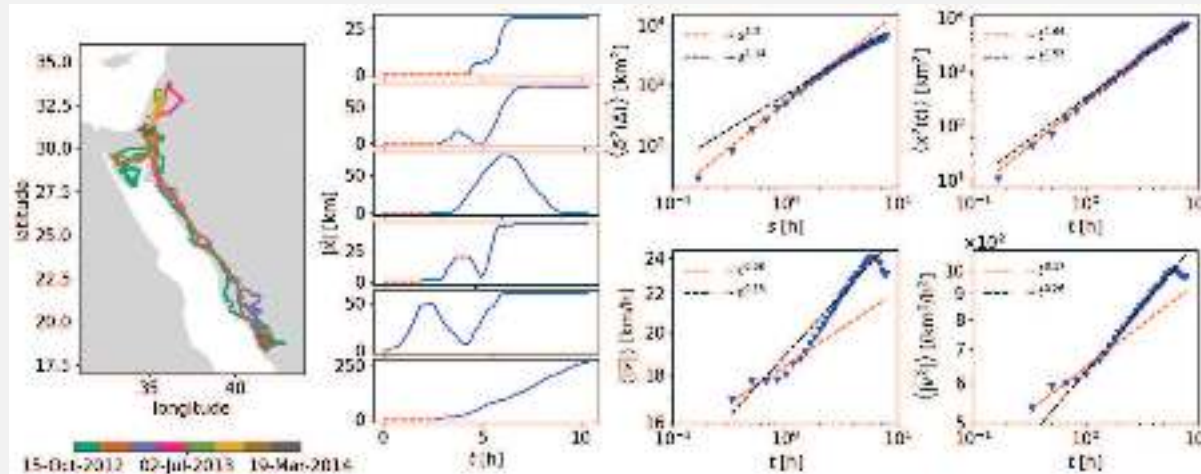
Large-deviation result:

$$P((\xi - 1) \geq \varepsilon) \leq \exp(-a\mathcal{H}(b)), \quad \mathcal{H}(b) = 1 + b - \sqrt{1 + 2b}; \quad a, b = f(\Delta, \dots)$$



Scaling analysis of anomalous diffusion

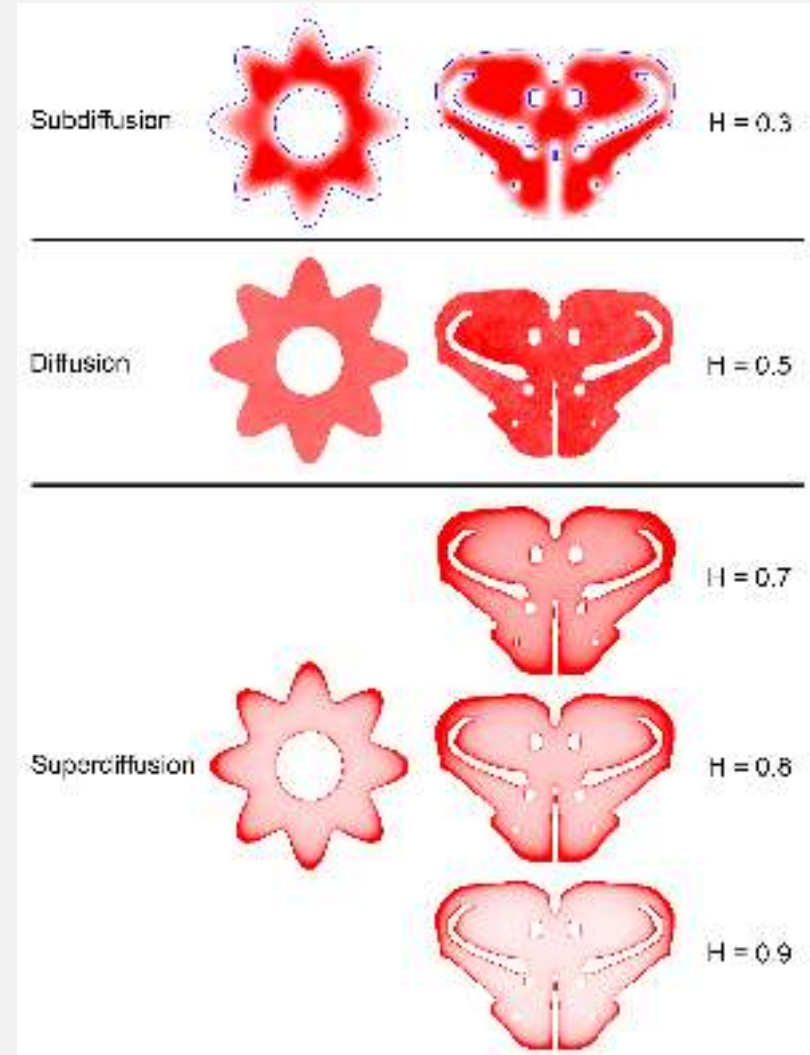
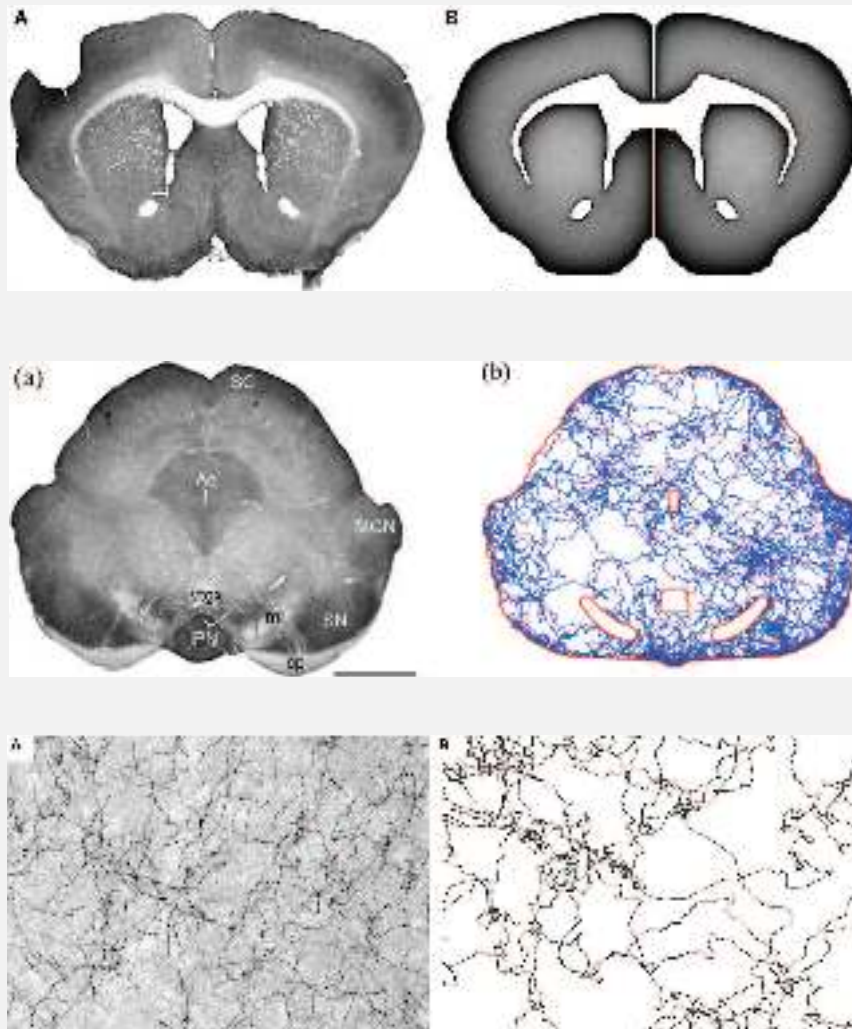
Joseph: long-range correlations; Noah: fat tails of increment PDF; Moses: non-stationarity



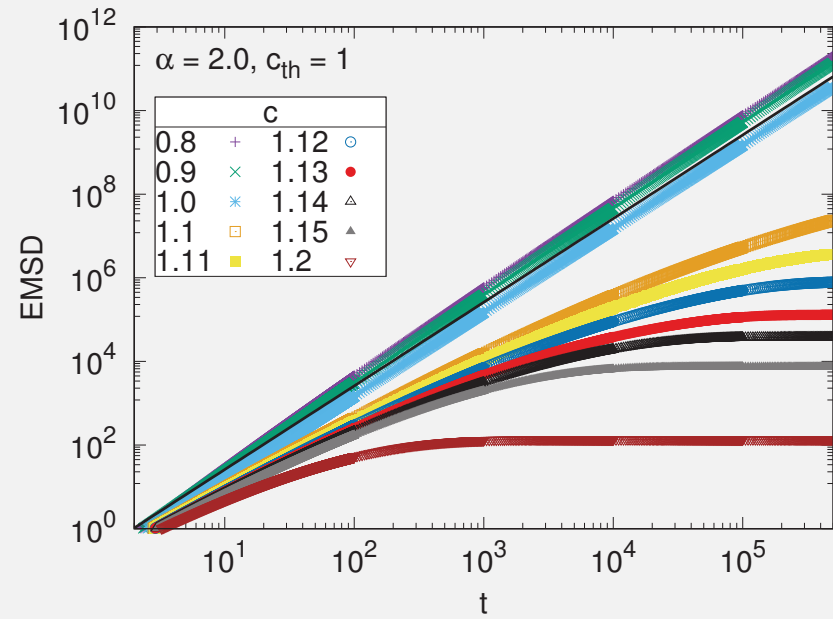
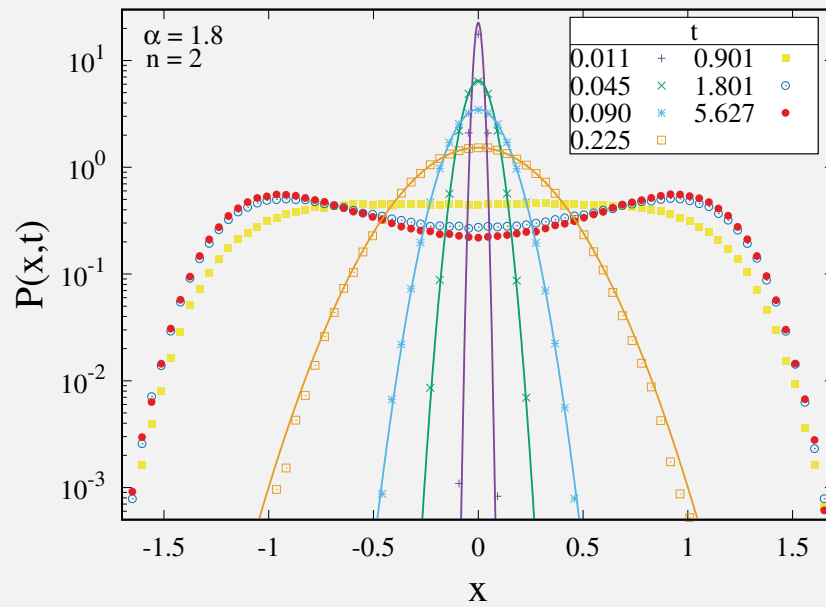
Brain serotonergic axons as FBM paths

**DIVERSION
AHEAD**

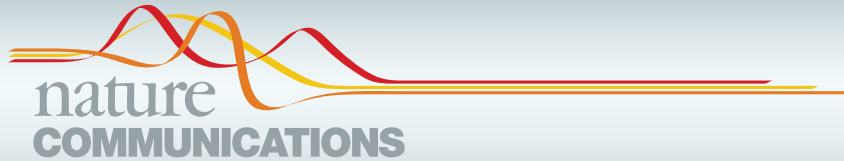
Correlated fluctuations effect non-flat profile



FBM in anharmonic potentials



The ANomalous Diffusion challenge



ARTICLE



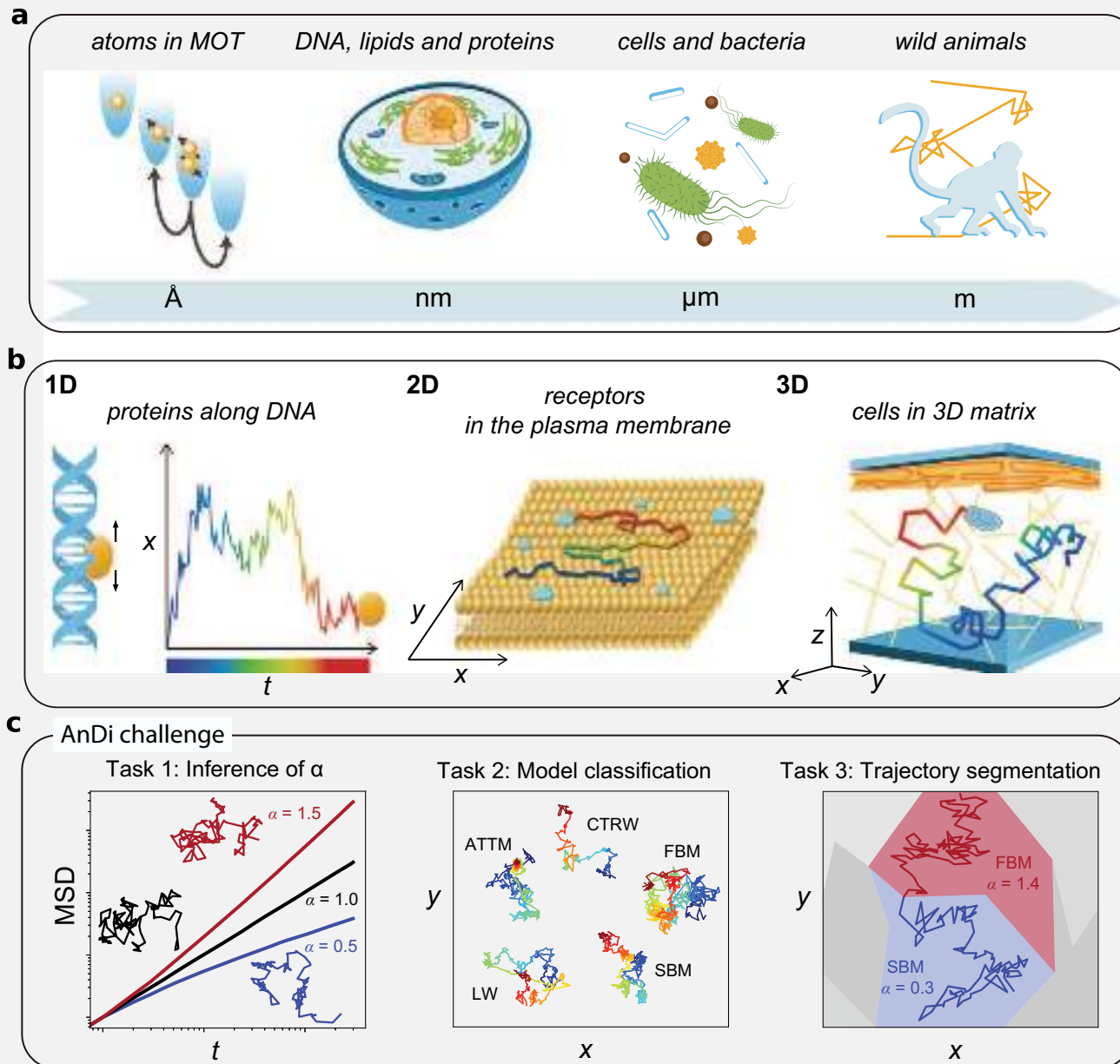
<https://doi.org/10.1038/s41467-021-26320-w>

OPEN

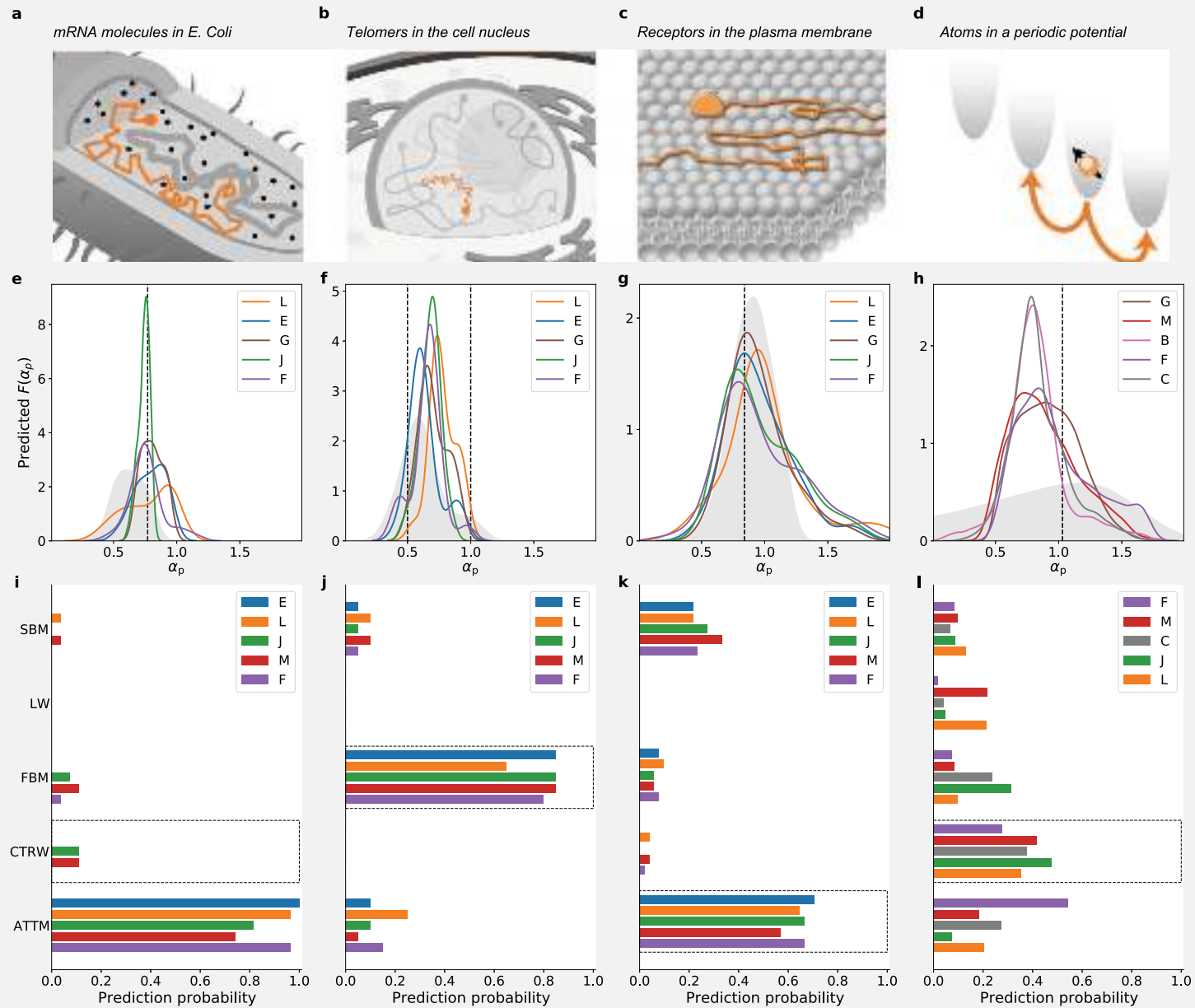
Objective comparison of methods to decode anomalous diffusion

Gorka Muñoz-Gil ¹, Giovanni Volpe ²✉, Miguel Angel Garcia-March³, Erez Aghion⁴, Aykut Argun², Chang Beom Hong⁵, Tom Bland⁶, Stefano Bo ⁴, J. Alberto Conejero³, Nicolás Firbas ³, Òscar Garibo i Orts ³, Alessia Gentili ⁷, Zihan Huang ⁸, Jae-Hyung Jeon ⁵, Hélène Kabbech ⁹, Yeongjin Kim⁵, Patrycja Kowalek ¹⁰, Diego Krapf ¹¹, Hanna Loch-Olszewska ¹⁰, Michael A. Lomholt¹², Jean-Baptiste Masson ¹³, Philipp G. Meyer ⁴, Seongyu Park ⁵, Borja Requena ¹, Ihor Smal⁹, Taegeun Song ^{5,14,15}, Janusz Szwabiński¹⁰, Samudrajit Thapa ^{16,17,18}, Hippolyte Verdier ¹³, Giorgio Volpe ⁷, Artur Widera ¹⁹, Maciej Lewenstein ^{1,20}, Ralf Metzler ¹⁶ & Carlo Manzo ^{1,21}✉

The ANomalous Diffusion challenge

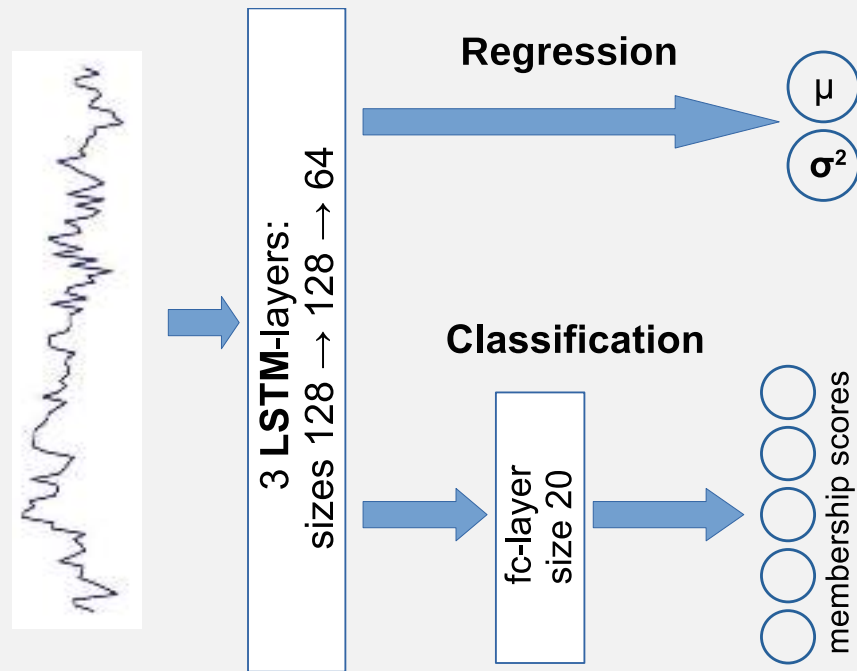


The ANomalous Diffusion challenge



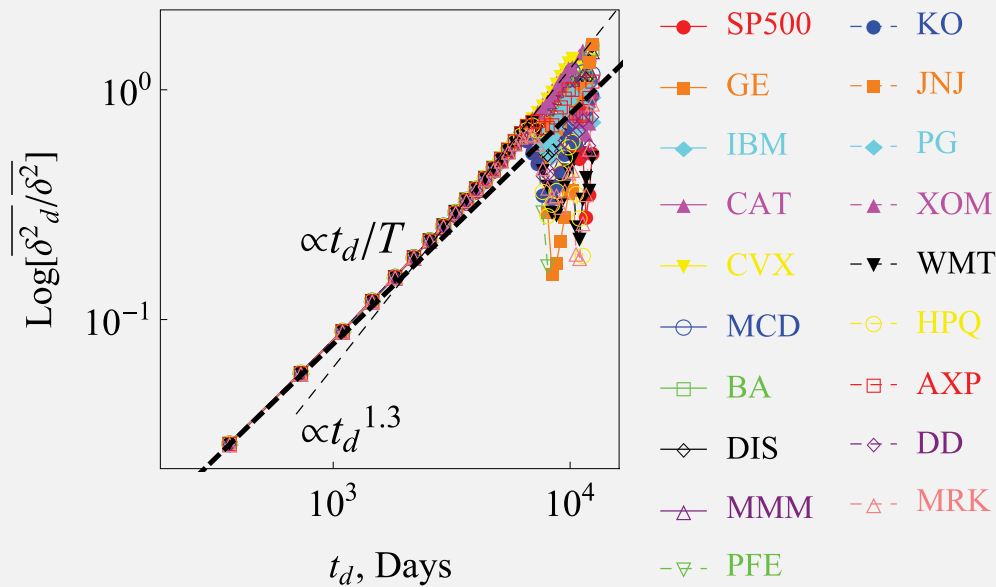
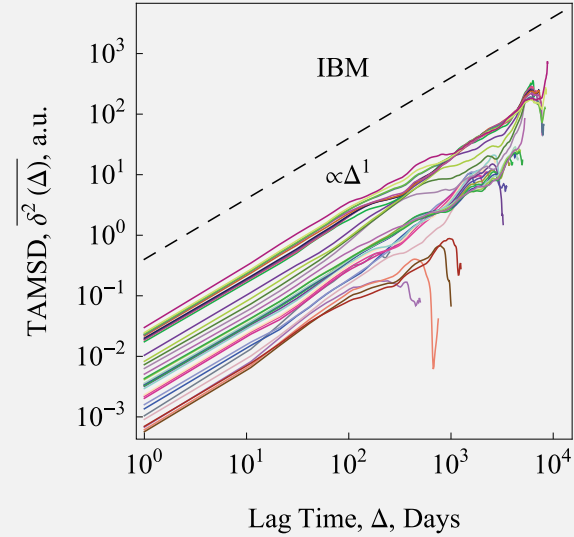
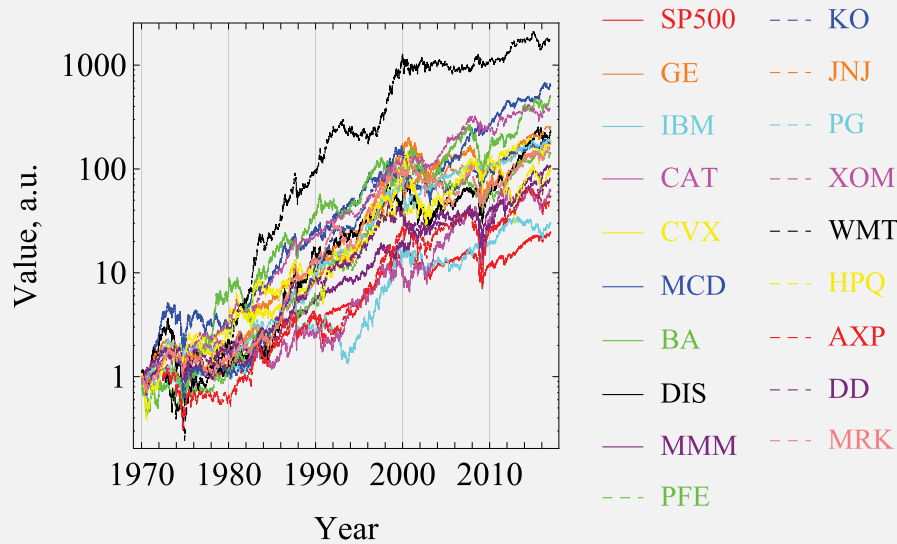
Bayesian-weighted deep learning model selection

Long Short-Term Memory approach (recurrent neural network architecture)



Predicted model	attn	0.54	0.048	0.065	0.0013	0.099
	ctrw	0.1	0.93	0.033	0	0.0025
	fbm	0.13	0.014	0.73	0.01	0.14
	lw	0.0061	0	0.015	0.98	0.01
	sbm	0.22	0.0071	0.16	0.0082	0.75
		True model				
		attn	ctrw	fbm	lw	sbm

Time averages & ageing in financial market time series



$$dX(t) = \mu X(t)dt + \sigma X(t)dW(t)$$

$$\overline{\delta_d^2(\Delta)} = \frac{\int_{t_d}^{T-\Delta} [X(t+\Delta) - X(t)]^2 dt}{T - t_d - \Delta}$$

$$\sim \frac{\Delta}{T - t_d} X_0^2 \left(e^{\sigma^2 T} - e^{\sigma^2 t_d} \right)$$

$$\log \left[\frac{\langle \overline{\delta_d^2(\Delta, t_d)} \rangle}{\langle \overline{\delta^2(\Delta)} \rangle} \right] \sim t_d/T$$

Universality of delay-time averages for financial time series

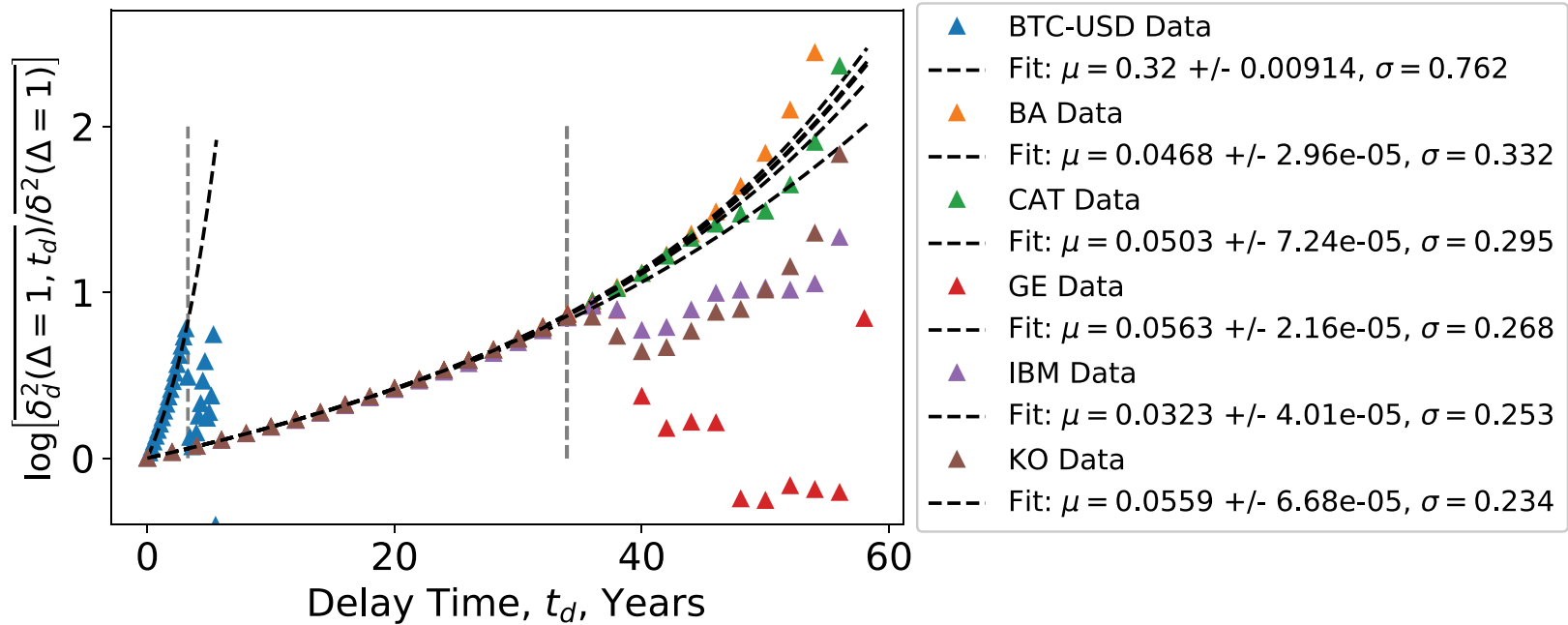
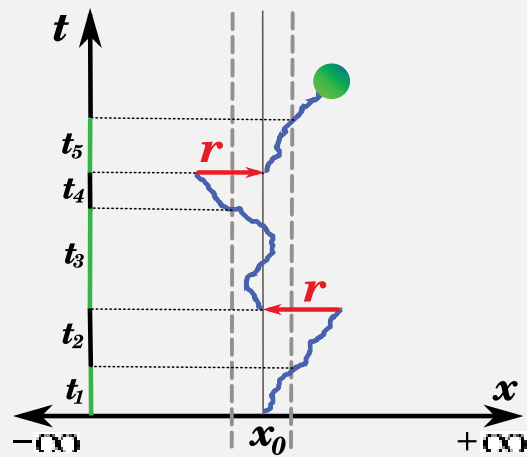


Figure 9. Delayed TAMSs calculated for the stocks- and cryptocurrency-data plotted versus the delay time t_d . The time periods of the FTS used for the determination of optimal drift and volatilities are 1962–2020 and 2014–2019, for the classical stocks and cryptocurrencies (BitCoin), respectively. The optimal annualized volatility found from equation (C5) and the value of drift found from the single-parameter fit of $\delta_{d,i}^2(\Delta)$ are listed in the legend. The two vertical dashed lines shown on the t_d -axis at the end of 1995 and 2017 help to assess the positions, respectively, of the 1997–1999 financial crisis for the stocks and of the crash late December 2017 for Bitcoin. These lines define the range of the delayed-TAMSD data used to obtain the parameter μ from the respective fits to the data, see appendix C for details.

Soft resets of Lévy walk

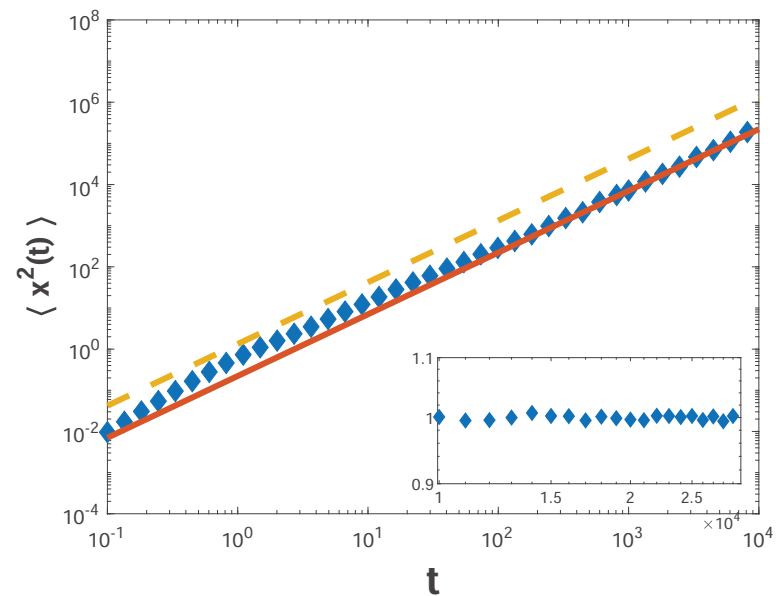
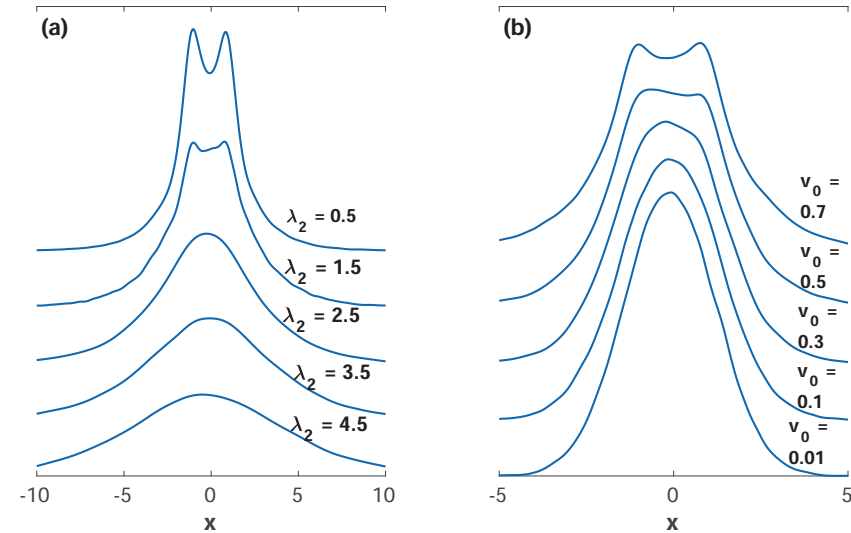


Soft reset phase: motion in harmonic potential with Hooke constant γ :

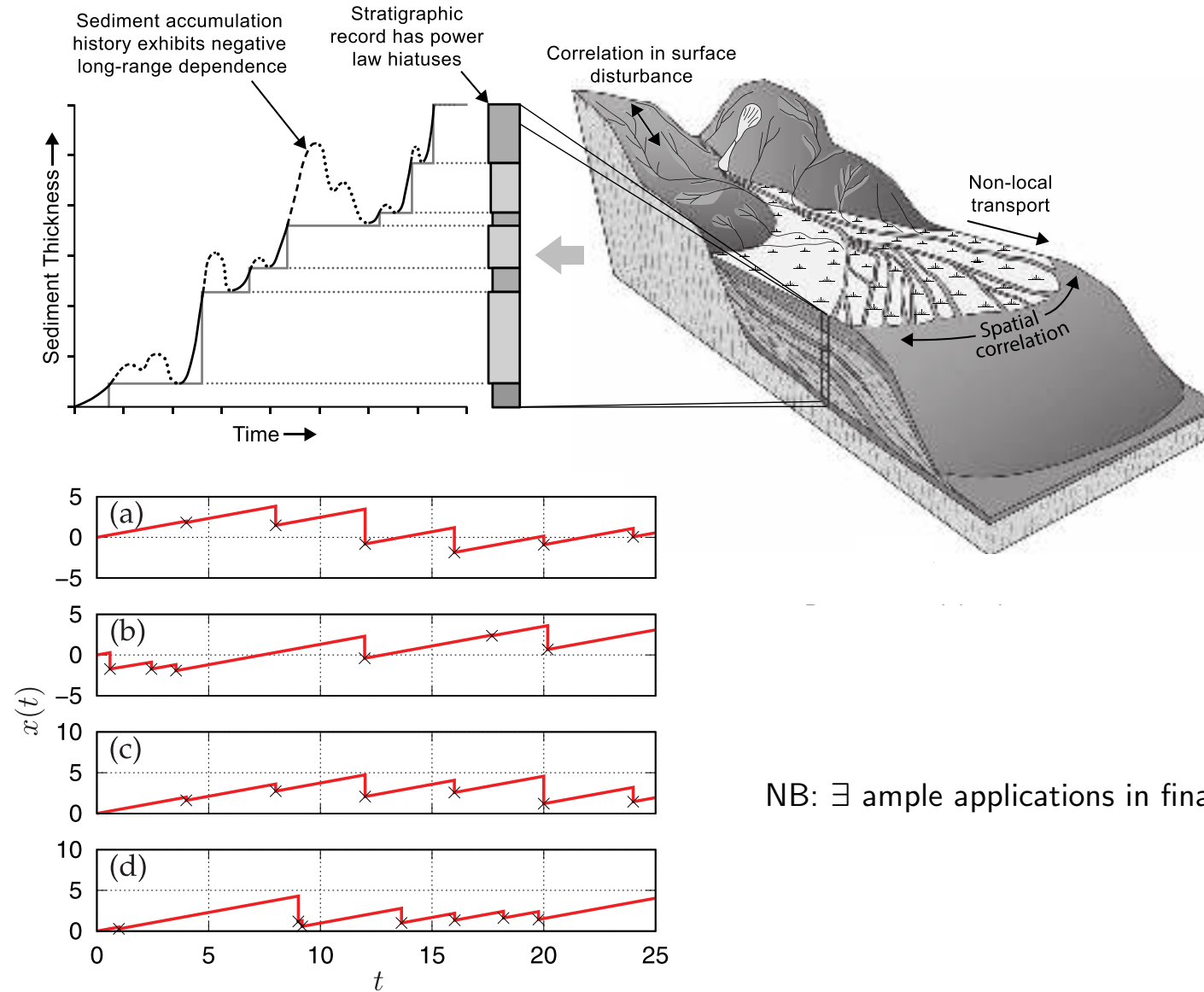
$$m \frac{d^2 x}{dt^2} = -\gamma x$$

Free Lévy walk phase:

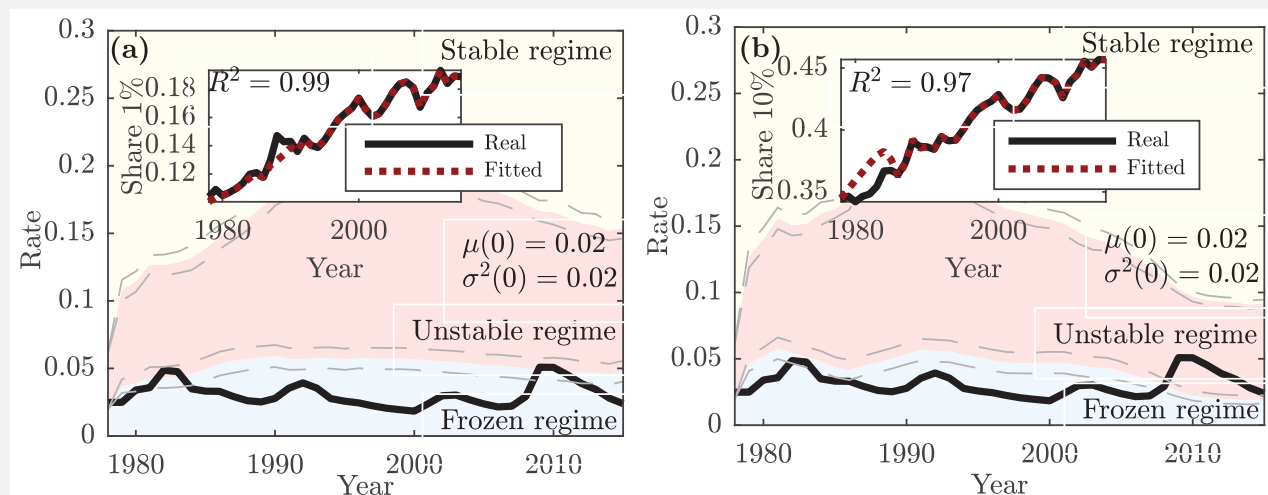
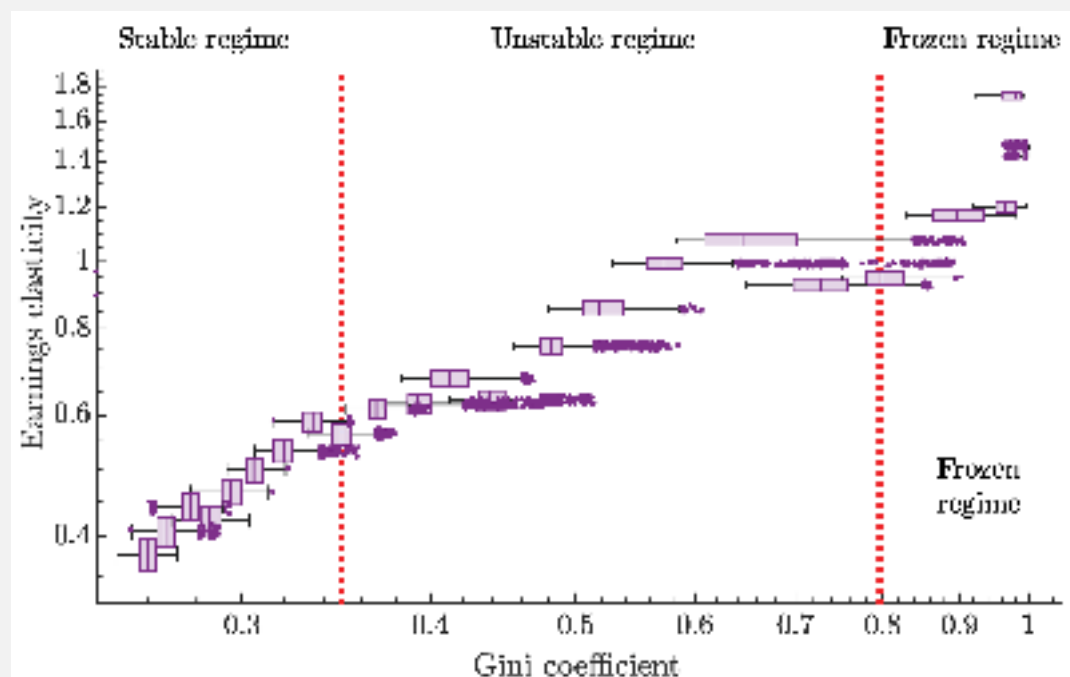
$$\frac{dx}{dt} = \pm v_0$$



Stochastic resets with random amplitude & stratigraphy



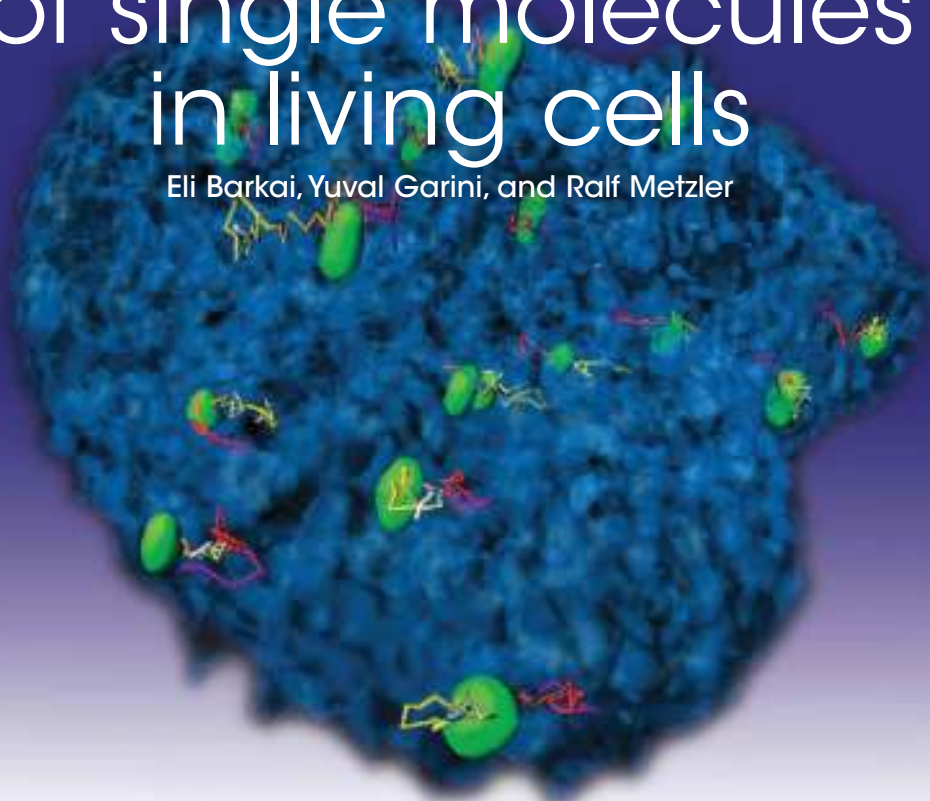
Income inequality & mobility in GBM /w stochastic resetting



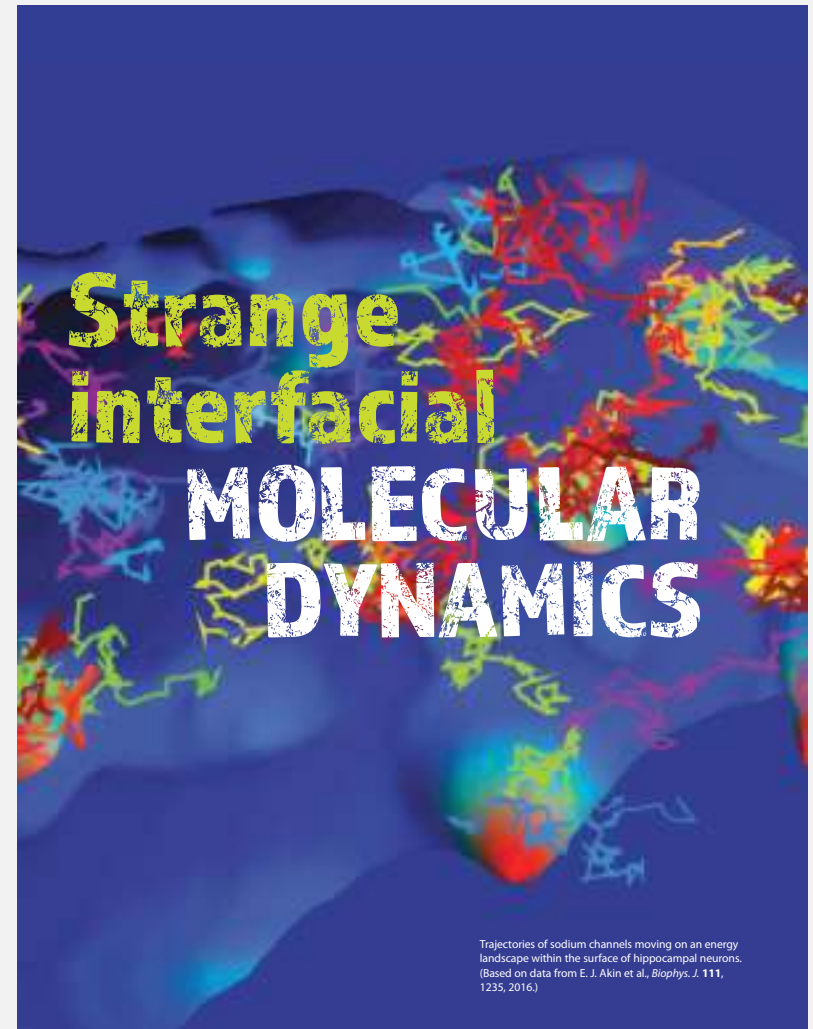
STRANGE KINETICS

of single molecules in living cells

Eli Barkai, Yuval Garini, and Ralf Metzler



The irreproducibility of time-averaged observables in living cells poses fundamental questions for statistical mechanics and reshapes our views on cell biology.



Trajectories of sodium channels moving on an energy landscape within the surface of hippocampal neurons. (Based on data from E. J. Akin et al., *Biophys. J.* 111, 1235, 2016.)

Σ ummary

- I Signalling molecules in cells often occur @ small copy numbers & are inhomogeneously distributed. Associated molecular chemical reaction times show broad distributions $\leadsto$ chemical rate concepts no longer work
- II Non-Gaussian diffusion is observed in a wide range of soft & biological matter systems, based on spatiotemporally fluctuating diffusivities: $\leadsto$ model approaches such as diffusing diffusivity
- III Many different stochastic models are needed to grasp the detail observed in complex systems. They can be identified by complementary statistical observables: e.g., amplitude variation or large-deviation; velocity auto-correlation; single-trajectory power spectra, etc.
- IIII Time-averaged observables $\leftrightarrow$ cognisance of the (non-)ergodic & ageing behaviour of the system
- IIII Bayes/max likelihood or deep learning model determination

For slides or questions: write to rmetzler@uni-potsdam.de

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Christine Selhuber-Unkel (U Heidelberg)

Flavio Seno (Università di Padova)

Igor Sokolov (Humboldt U Berlin)

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Yong Xu (NWPU Xi'an)

