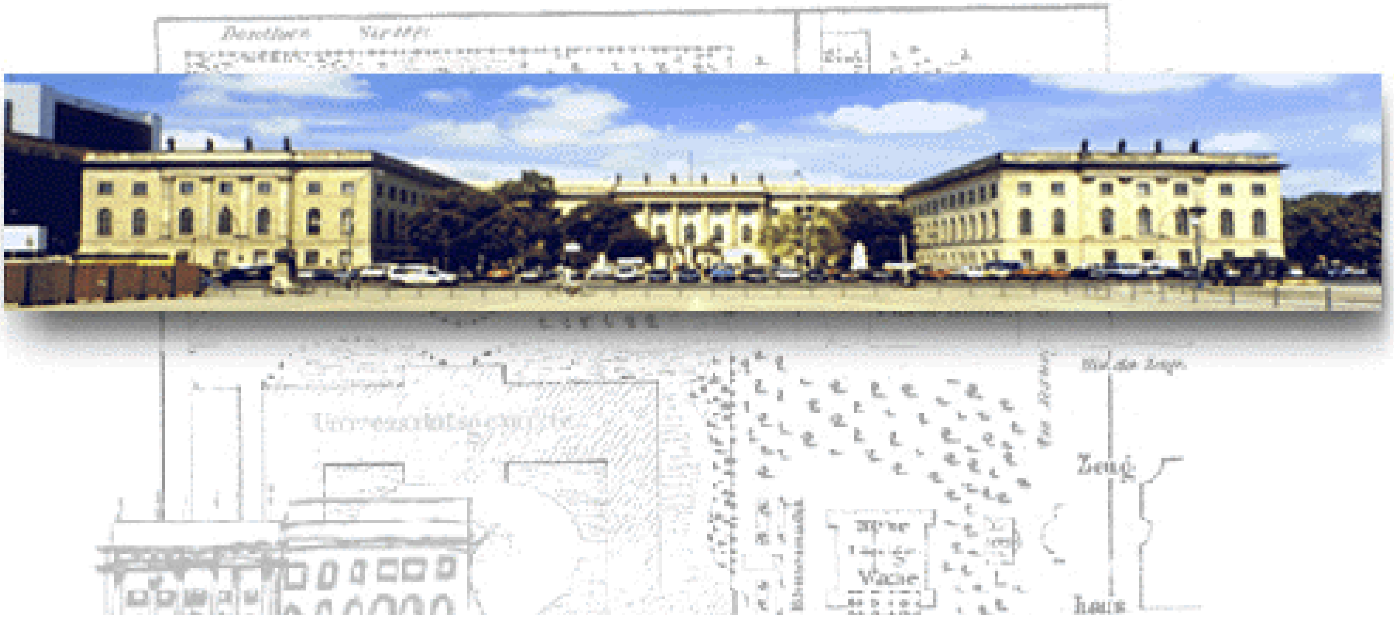
Igor Sokolov, Humboldt-Universität zu Berlin



Diffusion in crowded environments: Models, properties, instruments

25th Smoluchowski symposium, Cracow 2012

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REVIEW

Models of anomalous diffusion in crowded environments

Igor M. Sokolov*

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Different stories to tell:

- Normal diffusion
- Subdiffusion: Experiments, models, and mathematical instruments
  - CTRW
  - Percolation
  - Slow modes of multiparticle models
- Aging
- Case study 1: REM
- Case study 2: “The twins”: exactly solvable examples
- Conclusions

Emergence of normal diffusion

Einstein (1905)

Non-correlated increments

Postulates:

0) $n(x,t) \rightarrow P(x,t)$

i) $\exists$ time interval $\tau < \infty$, so that the particle's motion during the two consequent intervals is *independent*

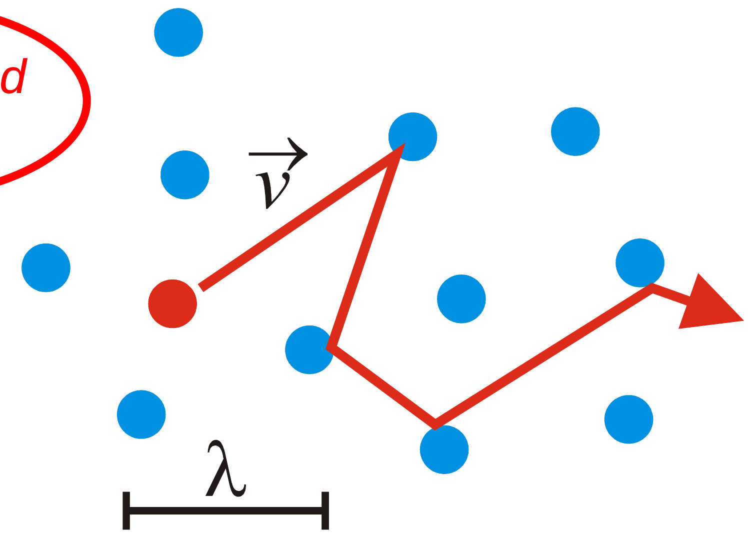
ii) The displacements s during subsequent τ-intervals are *identically distributed*.

Stationary increments

For unbiased diffusion: $\phi(s) = \phi(-s)$

iii) The second moment of s exists

$$\lambda^2 = \int_{-\infty}^{\infty} s^2 \phi(s) ds < \infty$$



Essentially, a Random Walk Model (1880, 1900, 1905×2)

Motion as a sum of small increments: $x(t) = \sum_{i=1}^{N} s_i$

mean free path

$$\lambda = \left\langle s_i^2 \right\rangle^{1/2}$$

$$0 < \lambda < \infty$$

mean relaxation time

$$\tau \propto \lambda / \left\langle v^2 \right\rangle^{1/2}$$

$$0 < \tau < \infty$$

$N \cong t / \tau$ *stationary*

non-correlated

$$\left\langle x^2(t) \right\rangle = \left\langle \left(\sum_{i=1}^{N} s_i \right)^2 \right\rangle = N \left\langle s^2 \right\rangle + \cancel{2N \left\langle s_i s_j \right\rangle} \quad \sim t^1$$

the central limit theorem (for independent steps)

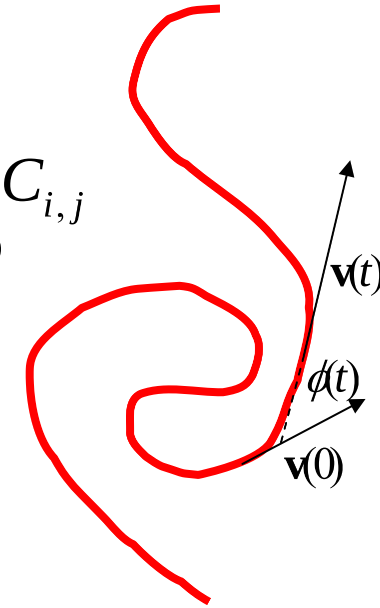
$$P(x,t) = (4\pi K t)^{-1/2} \exp\left(-\frac{x^2}{4Kt} \right)$$

with $K \propto \left\langle v^2 \right\rangle \tau \equiv \lambda^2 / \tau$

RW models vs. continuum models

Discrete $\mathbf{x}_t = \sum_{i=0}^{t} \mathbf{s}_i$

$$\left\langle \mathbf{x}_t^2 \right\rangle = \left\langle \sum_{i,j=0}^{t} \mathbf{s}_i \mathbf{s}_j \right\rangle = \sum_{i,j=0}^{t} C_{i,j}$$



Continuous

$$\mathbf{x}(t) = \int_0^t \mathbf{v}(t')dt'$$

$$\left\langle \mathbf{x}^2(t) \right\rangle = \left\langle \int_0^t \int_0^t \mathbf{v}(t')\mathbf{v}(t'')dt'dt'' \right\rangle$$

$$= \int_0^t \int_0^t C(t',t'')dt'dt''$$

Stationary velocity process → x-process with stationary increments

$$C(t',t'') = C(|t'-t''|), \quad 0 < \int_0^\infty C(t')dt' < \infty$$

$$\left\langle \mathbf{x}^2(t) \right\rangle = dDt$$

$$D = \lim_{t\to\infty} \frac{\left\langle x^2(t) \right\rangle}{t} = \int_0^\infty C(t')dt'$$

Stationarity of increments
=
Stationary (equilibrium) state
of the bath

An increasing number of natural phenomena do not fit into the relatively simple description of diffusion developed by Einstein a century ago

Anomalous diffusion spreads its wings

$$\left\langle x^2(t) \right\rangle \propto t^\alpha$$

$$\alpha \neq 1$$

Joseph Klafter and Igor M Sokolov

AS ALL of us are no doubt aware, this year has been declared "world year of physics" to celebrate the three remarkable breakthroughs made by Albert Einstein in 1905. However, it is not so well known that Einstein's work on Brownian motion – the random motion of tiny particles first observed and investigated by the botanist Robert Brown in 1827 – has been cited more times in the scientific literature than his more famous papers on special relativity and the quantum nature of light. In a series of publications that included his doctoral thesis, Einstein derived an equation for Brownian motion from microscopic principles – a feat

Strange behaviour – albatrosses fly by the rules of anomalous diffusion.

Tony Palliser/BirdLife

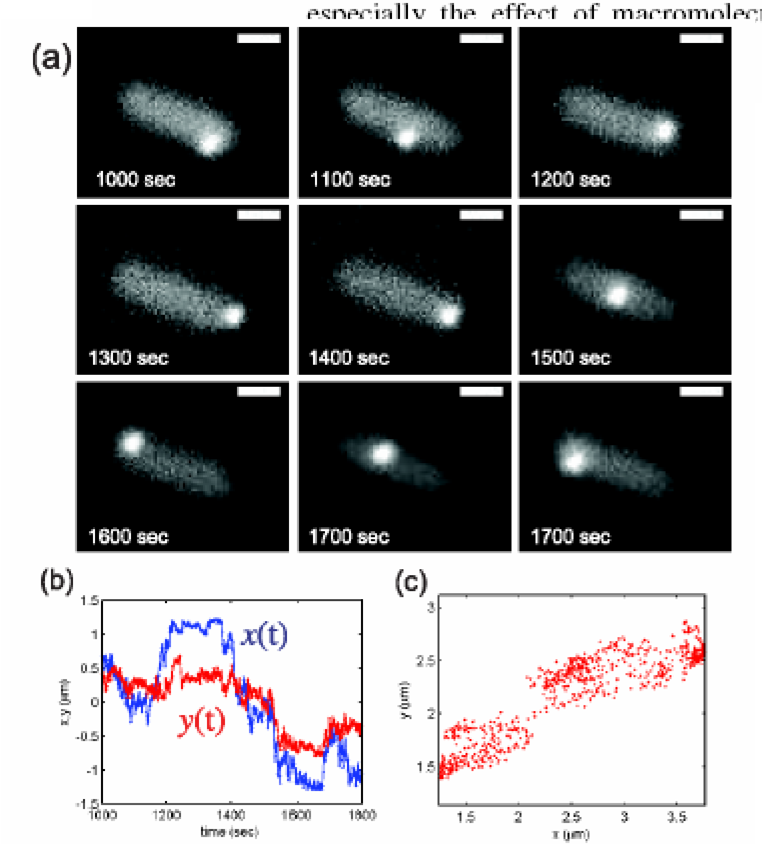
in living organisms. In 1855 Fick published the famous diffusion equation, which, when written in terms of probability, is $\partial p/\partial t = D\partial^2 p/\partial x^2$, where p gives the probability of finding an object at a certain position x, at a time t, and D is the diffusion coefficient. Fick went on to show that the mean-squared displacement of an object undergoing diffusion is $2Dt$.

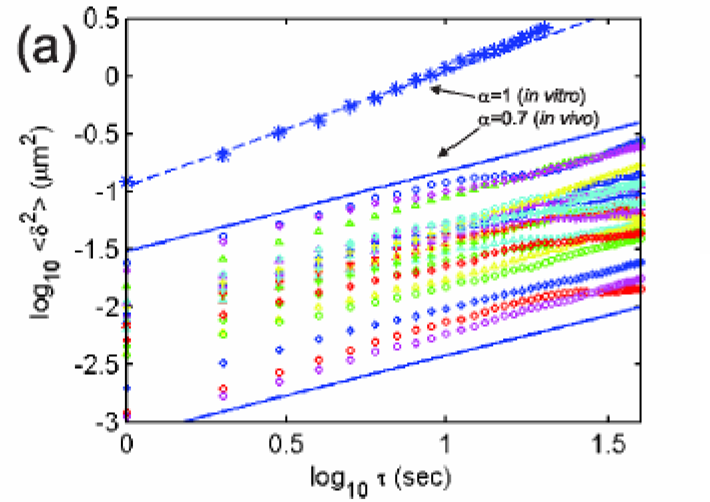
However, Fick's approach was purely phenomenological, based on an analogy with Fourier's heat equation – it took Einstein to derive the diffusion equation from first principles as part of his work on Brownian motion. He did this by assuming

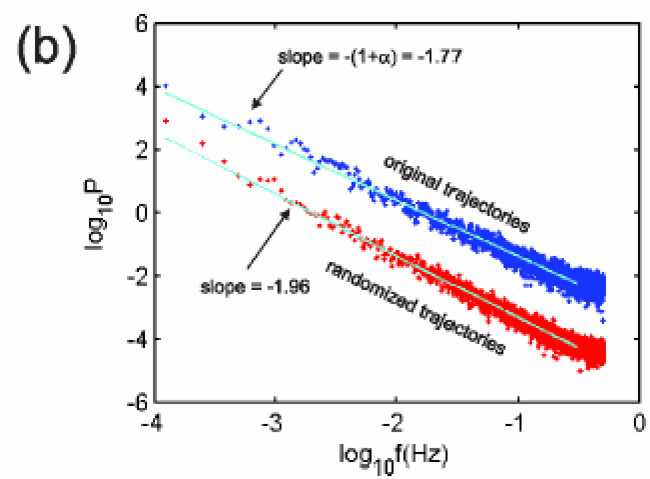
Physical Nature of Bacterial Cytoplasm

Ido Golding and Edward C. Cox
Department of Molecular Biology, Princeton University, Princeton, New Jersey 08544, USA
(Received 10 November 2005; published 10 March 2006)

We track the motion of individual fluorescently labeled mI
find that the motion is subdiffusive, with an exponent that is ro
disruption of cytoskeletal elements. By modifying the parame
cell, we are able to examine the possible mechanisms tha
especially the effect of macromolecular crowding. We als
gene regulation, in par







Ergodic and nonergodic processes coexist in the plasma membrane as observed by single-molecule tracking

Aubrey V. Weigel[a], Blair Simon[b], Michael M. Tamkun[c,d], and Diego Krapf[a,b,1]

[a]School of Biomedical Engineerin
State University, Fort Collins, CO
[d]Department of Biochemistry anc

Edited* by Jennifer Lippincott-Sch

Diffusion in the plasma mem
display anomalous dynamics.
this diffusion pattern remain:

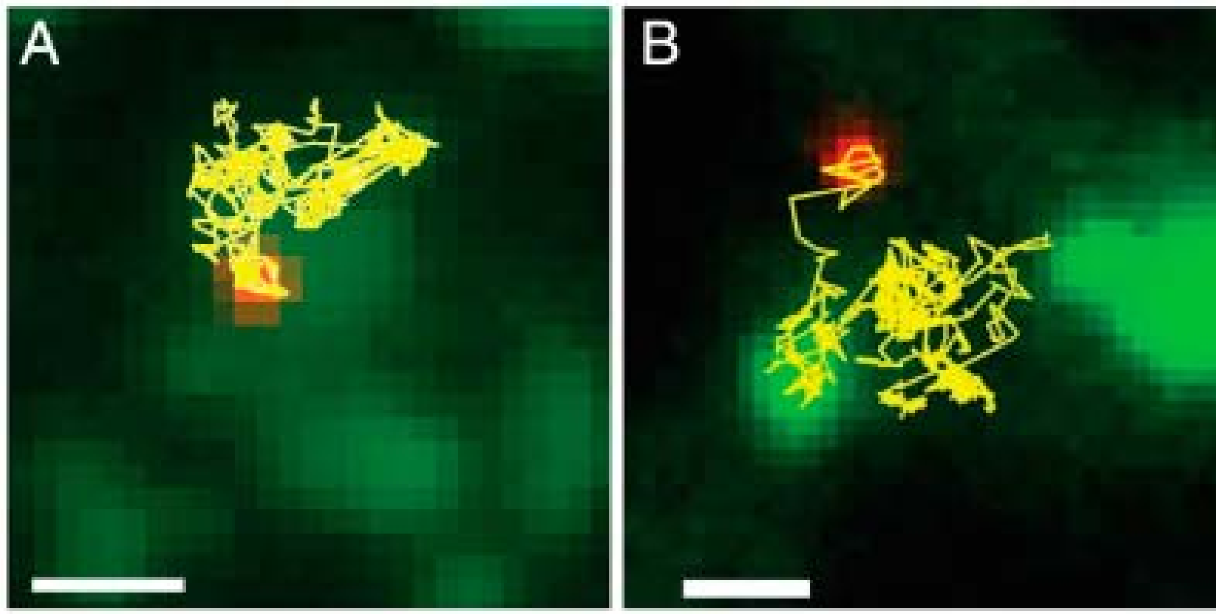


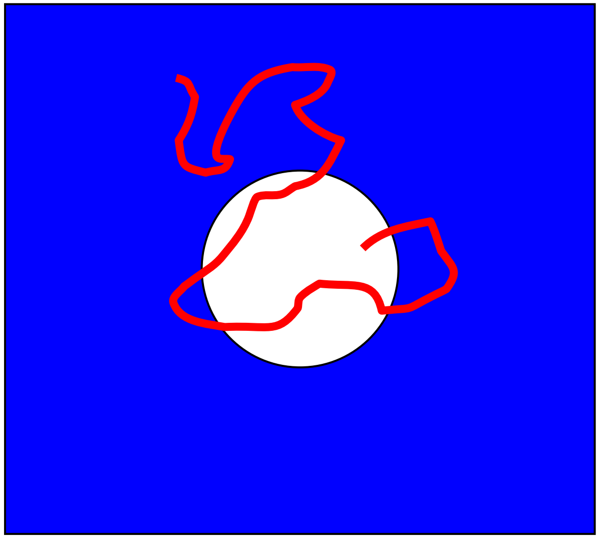
Fig. 1. Overlay image of GFP-tagged Kv2.1 clusters and individual QDs. Kv2.1 clusters are shown in green and QD-tagged channels in red. The trajectories of (*A*) a clustered and (*B*) a nonclustered (free) Kv2.1 channels are shown. Interestingly, the nonclustered channel ignores the compartment perimeters and the channel travels freely into and out of a cluster. Scale bars: 1 μm.

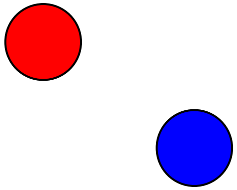
Experimental techniques

- Ensemble properties:
  - measurements of mass transport, current or polarization
  - FRAP

- Single-particle properties:

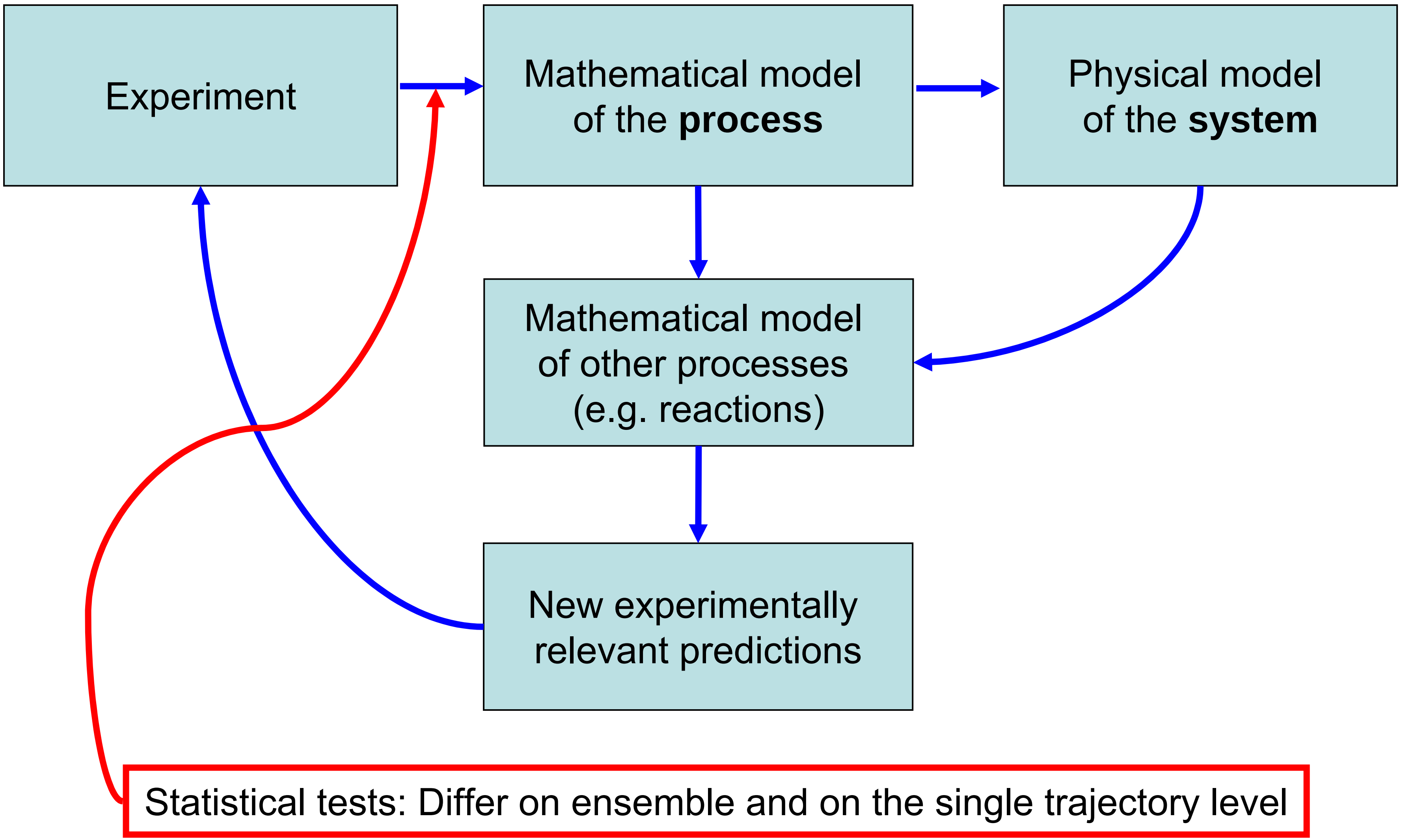
- Trajectories
  - single-particle tracking
- First passage times
  - FRET
- Sojourn times
  - FCS





"Measure and fit!"

Why do we need it?



Physical models

Crowded environments: experiments hint onto subdiffusion:

$\alpha < 1$, or $D = 0$.

Possible sources of anomalous subdiffusion:

1. Trapping models as arising from variants of random potential models (*energetic disorder*, *trapping environment*) often translated to CTRW (in $d = 3$)
2. Trapping models of geometric nature (combs, "spikes") (even closer to CTRW)
3. Diffusion on fractal structures, e.g. on percolation clusters (*geometrical disorder*, or *labyrinthine environment*).
4. Temporal correlations due to *slow modes* (typical for *viscoelastic environments*)

Physical models

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4. Temporal correlations due to *slow modes* (typical for *viscoelastic environments*)

(can be considered as a complex combination of fractal diffusion and projections from state to configuration space)

Mathematical instruments

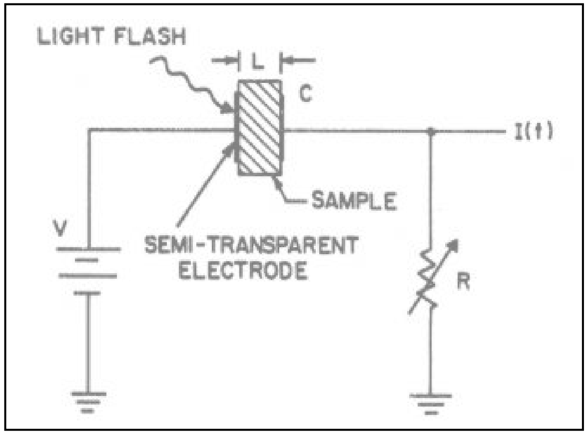
CTRW: Fractional diffusion (or Fokker-Planck) equation, or a couple of Langevin equations describing the evolution of the coordinate and of the clock time as functions of the operational time (Fogedby's approach).

Fractals: Percolation and other labyrinthine models. No equation known. Often approximately described by diffusion equations with distance-dependent diffusion coefficient.

fBm (viscoelastic models): Generalized (integrodifferential) Langevin equation. No Fokker-Planck analogue known.

sBm: "Time-dependent diffusion coefficient taken seriously": Diffusion equation with time-dependent diffusion coefficient. Often used by experimentalists for fitting of anomalous diffusion of unclear origin.

Subdiffusion: In disordered solids…



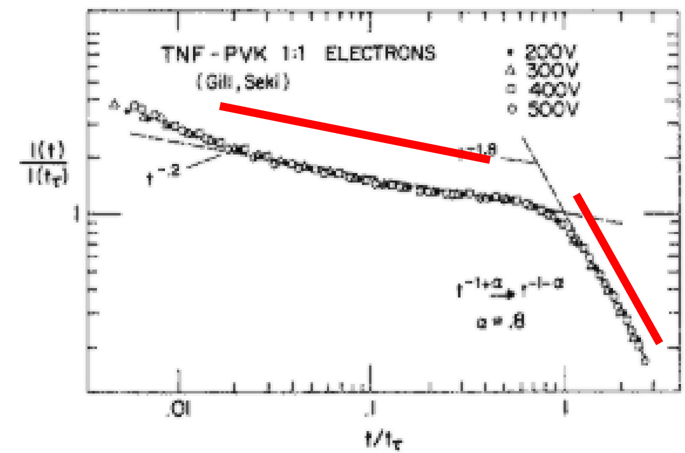
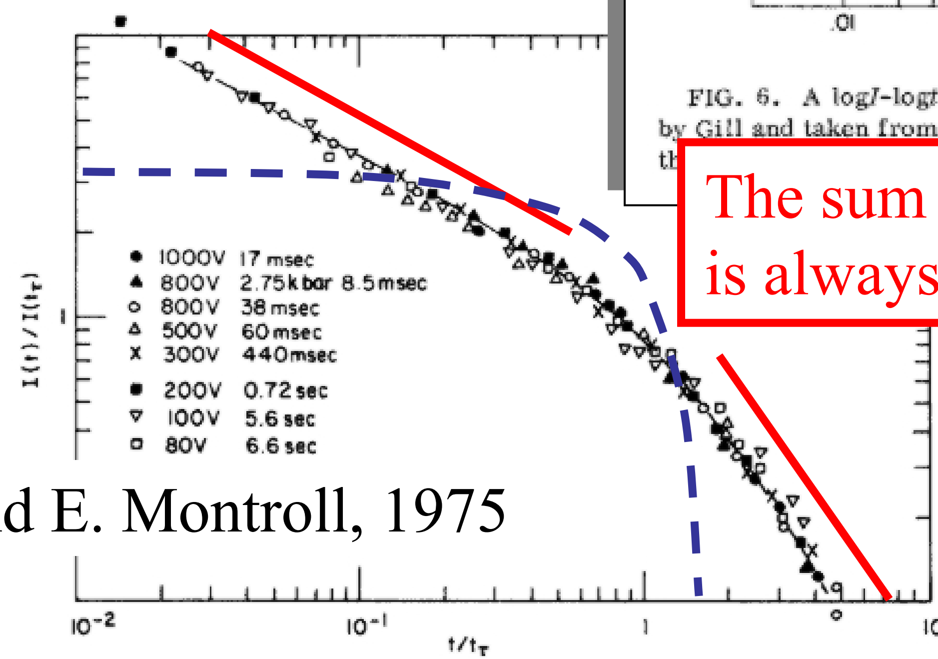


FIG. 6. A log$I$-log$t$ plot for 1:1 TNF-PVK measured by Gill and taken from a paper by Seki. The slopes of th… …pectively.

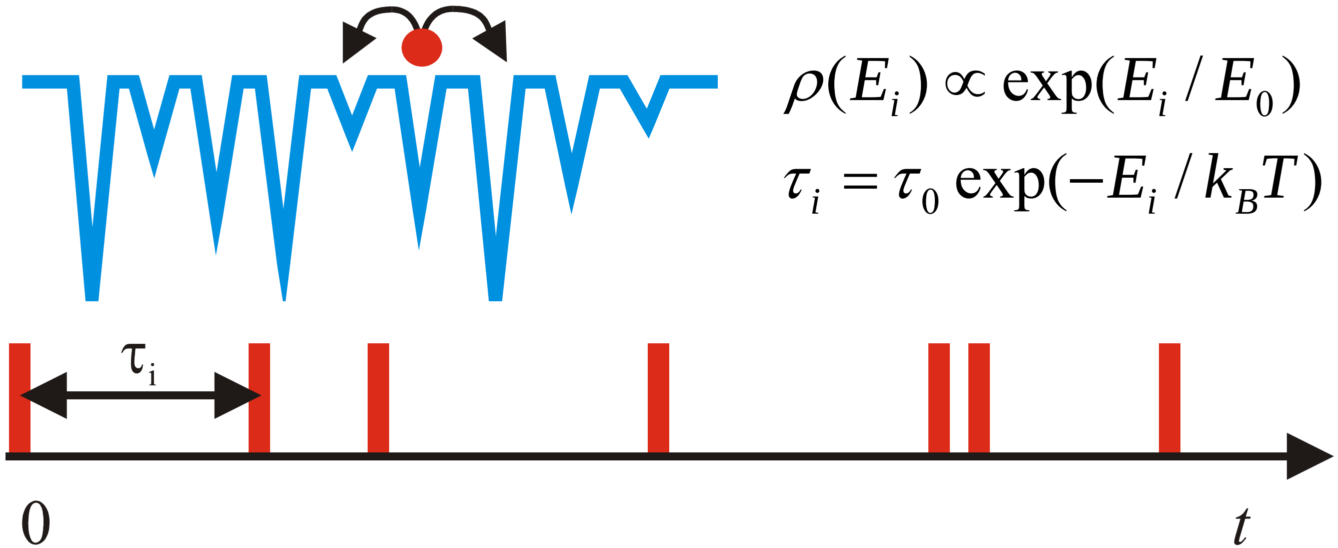


… plot … ange … n … ure- ments by Pfister also include a data set at high pressure (2.75 kbar). The solid line is the theoretical curve.

The sum of slopes is always 2

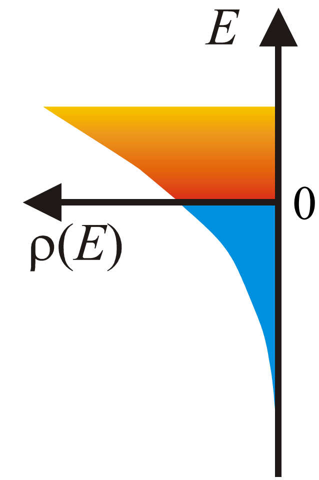
H. Scher and E. Montroll, 1975

Explanation: Multple trapping and CTRW



$\rho(E_i) \propto \exp(E_i / E_0)$

$\tau_i = \tau_0 \exp(-E_i / k_B T)$



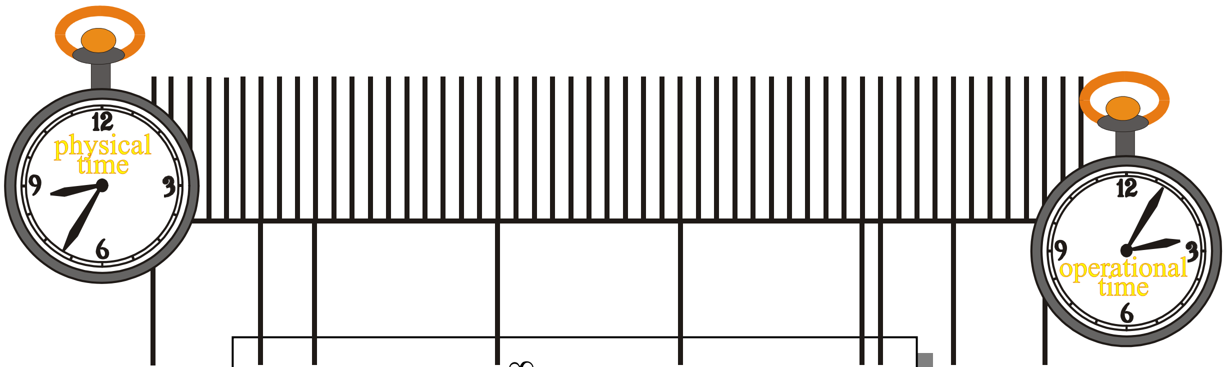
The waiting-time distribution between the two jumps $\psi(t) \propto t^{-1-\alpha}$ with $\alpha = k_B T / E_0$

Diffusion anomalies for $0 < \alpha < 1$: the mean waiting time diverges!

Mean number of steps $n(t) \propto t^{\alpha}$ Mean rate of steps $M(t) = \dfrac{dn}{dt} \propto t^{\alpha-1}$

Mean squared displacement $\langle x^2(t) \rangle \propto t^{\alpha}$ with $\alpha < 1$

The subordination



$$P(x,t)=\sum_{n=0}^{\infty} W(x,n)\chi_n(t)$$

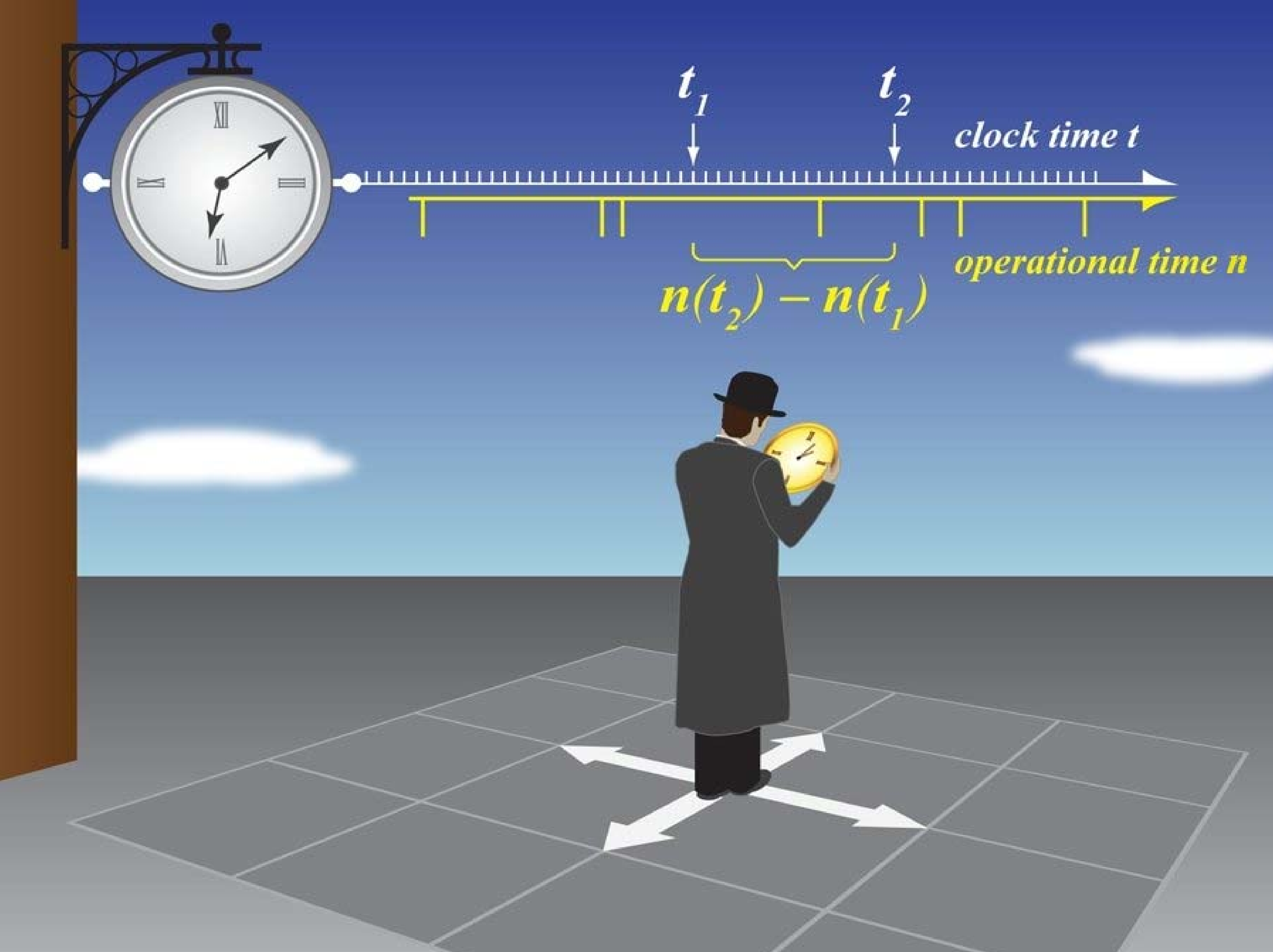
PDF of the particle's position after *n* steps (say, a Gaussian)

Probability to make exactly *n* steps up to the time *t*

Transition to continuum:

$$P(x,t)=\int_0^{\infty} W(x,\tau)T(\tau,t)d\tau$$

operational time



t_1
t_2
clock time t
operational time n
$n(t_2) - n(t_1)$

Short way to the result:

- Independent steps => $\langle x^2(t)\rangle = a^2\langle n(t)\rangle$

•Steps follow inhomogeneously in the physical time *t*.

•The number of steps up to the time *t* may be calculated using the renewal approach:

no steps up to time *t*: $\chi_0(t) = 1 - \int_0^t \psi(t')dt'$

1 step up to time *t*: $\chi_1(t) = \int_0^t \psi(t')\chi_0(t-t')dt'$

....

n steps up to time *t*: $\chi_n(t) = \int_0^t \psi(t')\chi_{n-1}(t-t')dt'$

$$\langle n(t)\rangle = \sum_{n=0}^{\infty} n\chi_n(t) = ?$$

After Laplace-transform: $\tilde{\chi}_n(u) = \dfrac{1-\tilde{\psi}(u)}{u}\tilde{\psi}^n(u)$

$$\left\langle \tilde{n}(u) \right\rangle = \frac{1-\tilde{\psi}(u)}{u}\sum_{n=0}^{\infty} n\tilde{\psi}^n(u) = \frac{1-\tilde{\psi}(u)}{u}\sum_{n=0}^{\infty}\tilde{\psi}(u)\frac{d}{d\tilde{\psi}}\tilde{\psi}^n(u)$$

$$= \frac{1-\tilde{\psi}(u)}{u}\tilde{\psi}(u)\frac{d}{d\tilde{\psi}}\sum_{n=0}^{\infty}\tilde{\psi}^n(u) = \frac{\tilde{\psi}(u)}{u\left[1-\tilde{\psi}(u)\right]}.$$

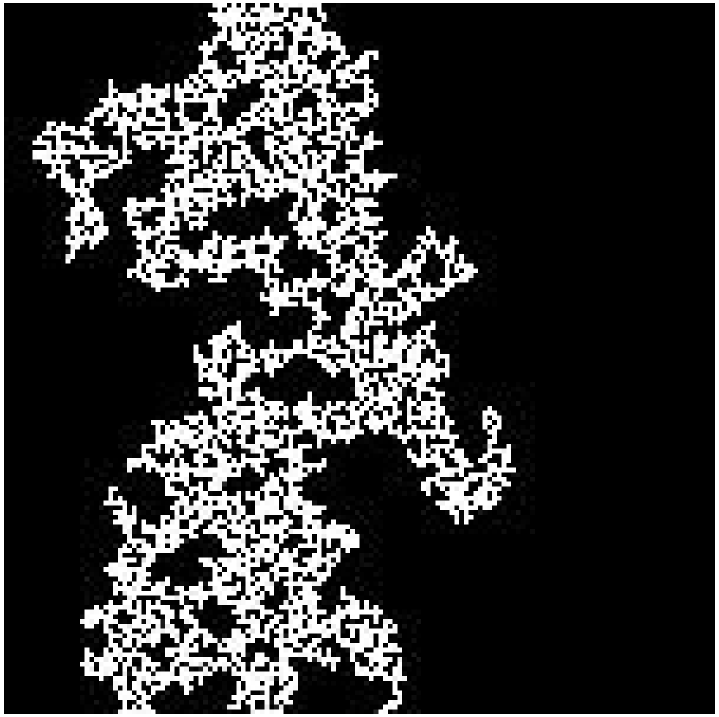
$$\boxed{\psi(t) \propto t^{-1-\alpha}} \longrightarrow \boxed{\tilde{\psi}(u) \cong 1 - cu^{\alpha} + \ldots}$$

$$\downarrow$$

$$\boxed{\left\langle n(t) \right\rangle \propto t^{\alpha}} \longleftarrow \boxed{\left\langle \tilde{n}(u) \right\rangle \cong c^{-1}u^{-1-\alpha}}$$

The the FDE can be derived from the properties of the parent process and those of subordinator (operational time)

Other relevant models: Percolation



Geometric disorder: Percolation cluster at criticality: Markovian model with non-iid steps. Mapped on a non-Markovian model after averaging over realizations

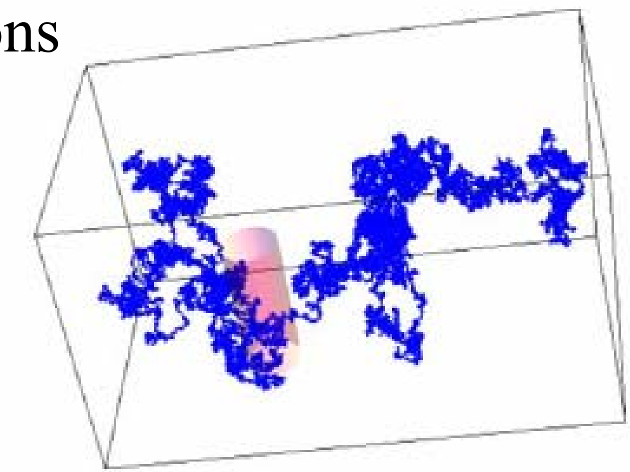


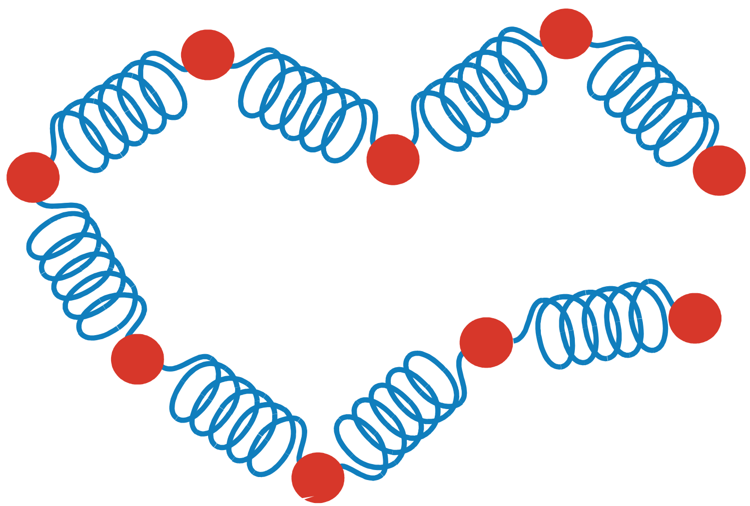
Fig. (4). The measurement system: 3D translational anomalous diffusive motion within the observation volume $\Delta V = 0.14$ fL (in pink color). Simulation steps n=10000.

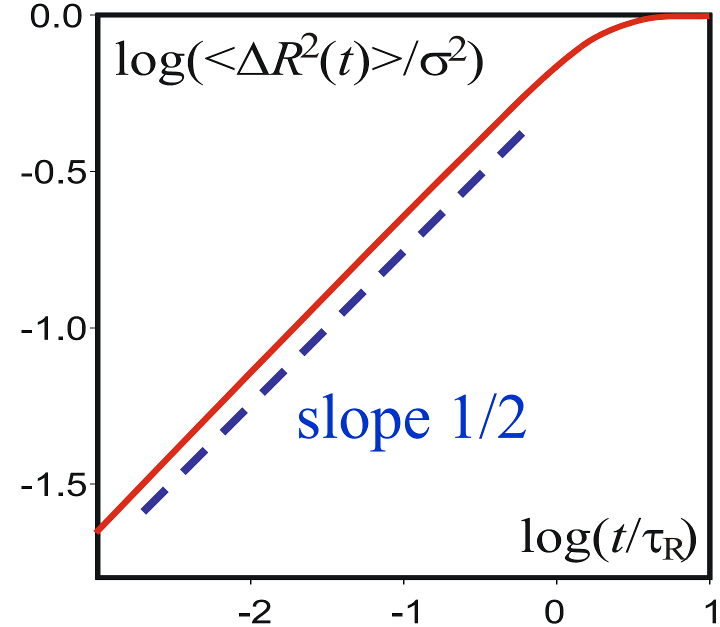
Current Pharmaceutical Biotechnology, 2010, *11*, 527-543 527

Meaningful Interpretation of Subdiffusive Measurements in Living Cells (Crowded Environment) by Fluorescence Fluctuation Microscopy

Gerd Baumann[1,*], Robert F. Place[2,3] and Zeno Földes-Papp[1,4,*]

Other relevant models: Polymers





Slow modes: Subdiffusion in a Rouse polymer chain.
Each mode normally diffusing (OU-process).
More complex models: polymer networks, intramolecular interactions etc.
Close relative: Single file diffusion in a 1d tube

The whole process is a non-Markovian process with stationary increments

Back to basics

Normal diffusion was a process with stationary, non-correlated increments.

Position-position correlation function $\phi(t,s) = \langle x(t)x(s) \rangle$

Displacement during the time interval between s and t ($t > s$)

$$\left\langle [x(t) - x(s)]^2 \right\rangle = \left\langle x^2(t) \right\rangle + \left\langle x^2(s) \right\rangle - 2\langle x(t)x(s) \rangle$$

Anomalous diffusion with stationary increments: $\left\langle x^2(t) \right\rangle = Kt^\alpha$

$$\left\langle [x(t) - x(s)]^2 \right\rangle = \left\langle x^2(t-s) \right\rangle$$

e.g. $\phi(t,s) = \frac{K}{2}\left[t^\alpha + s^\alpha - |t-s|^\alpha \right] \rightarrow$ fractional Brownian Motion

No age, no aging!

Process starting at t_0

$$\left\langle [x(t-t_0) - x(s-t_0)]^2 \right\rangle = \left\langle x^2(t - t_0 - s + t_0) \right\rangle = \left\langle x^2(t-s) \right\rangle$$

Anomalous diffusion with symmetric non-correlated increments

$$\phi(t,s) = \langle x(t)x(s) \rangle = \langle x(s)x(s) \rangle + \langle \Delta x(t-s)x(s) \rangle = \langle x^2(s) \rangle$$

Displacement during the time interval between s and t ($t > s$)

$$\langle [x(t)-x(s)]^2 \rangle = \langle x^2(t) \rangle + \langle x^2(s) \rangle - 2\langle x(t)x(s) \rangle = \langle x^2(t) \rangle - \langle x^2(s) \rangle$$

Anomalous diffusion: $\langle x^2(t) \rangle = Kt^{\alpha}$

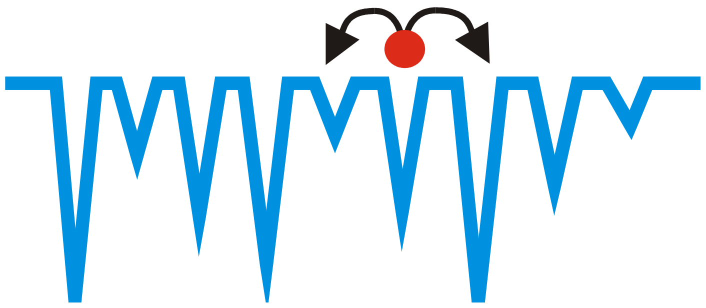
$$\langle [x(t)-x(s)]^2 \rangle = Kt^{\alpha} - Ks^{\alpha}$$

Process starting at t_0

$$\langle [x(t-t_0)-x(s-t_0)]^2 \rangle = K(t-t_0)^{\alpha} - K(s-t_0)^{\alpha}$$

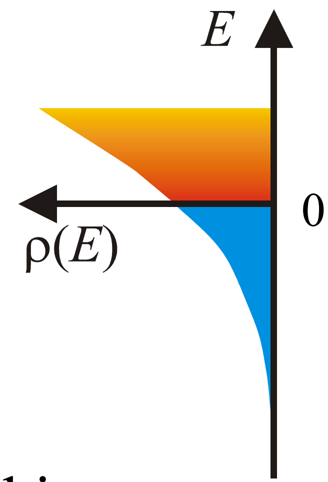
Age $s - t_0$ at beginning of observation can be determined for $\alpha \neq 1$

Resampling of CTRW

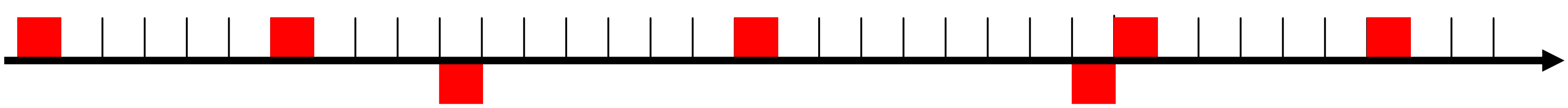


$$\rho(E_i) \propto \exp(E_i / E_0)$$

$$\tau_i = \tau_0 \exp(-E_i / k_B T)$$



CTRW as a process with dependent, yet uncorrelated increments

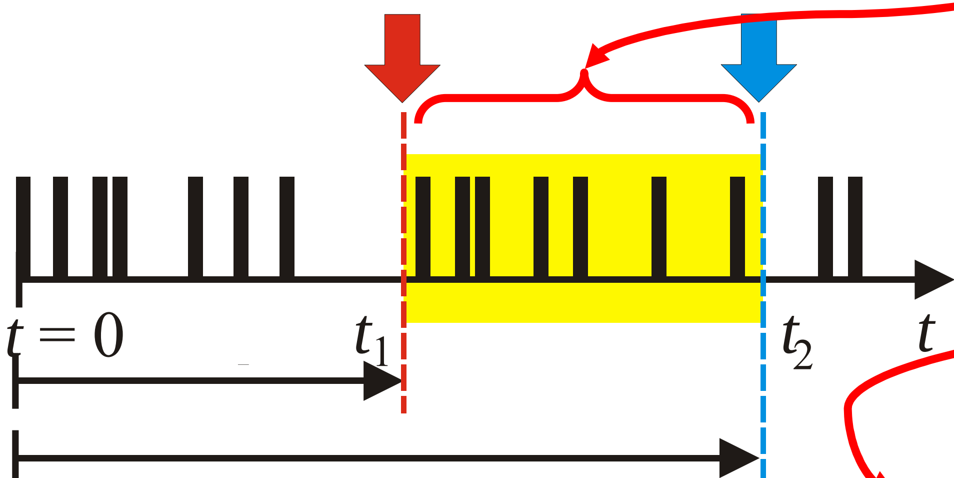


Aging properties in CTRW

In normal diffusion: $\left\langle \left[x(t_2)-x(t_1)\right]^2 \right\rangle = \left\langle x^2(t_1-t_2) \right\rangle = 2D(t_1-t_2)$

Explanation: Since $\left\langle n(t) \right\rangle = t/\tau,\ \left\langle n(t_2) \right\rangle - \left\langle n(t_1) \right\rangle = \left\langle n(t_2-t_1) \right\rangle$

In CTRW $\left\langle \left[x(t_2)-x(t_1)\right]^2 \right\rangle \propto \left\langle n \right\rangle = \left\langle n(t_2) \right\rangle - \left\langle n(t_1) \right\rangle$



$\propto t_2^{\alpha} - t_1^{\alpha}$

$$= \begin{cases} t_2^{\alpha} & t_2 - t_1 >> t_1 \\ t_1^{\alpha-1}(t_2 - t_1) & t_2 - t_1 << t_1 \end{cases}$$

The process ***ages***.

Moving time average

$$\langle n(t) \rangle_{\text{ens}} \cong At^{\alpha}$$

$$\langle x^2(t) \rangle = a^2 \langle n(t) \rangle_{ens}$$

$$\left\langle [x(t_2) - x(t_1)]^2 \right\rangle_{\text{ens}} = a^2 \left[\langle n(t_2) \rangle_{\text{ens}} - \langle n(t_1) \rangle_{\text{ens}} \right]$$

•Ensemble average of moving time averages
= moving time average of ensemble av.

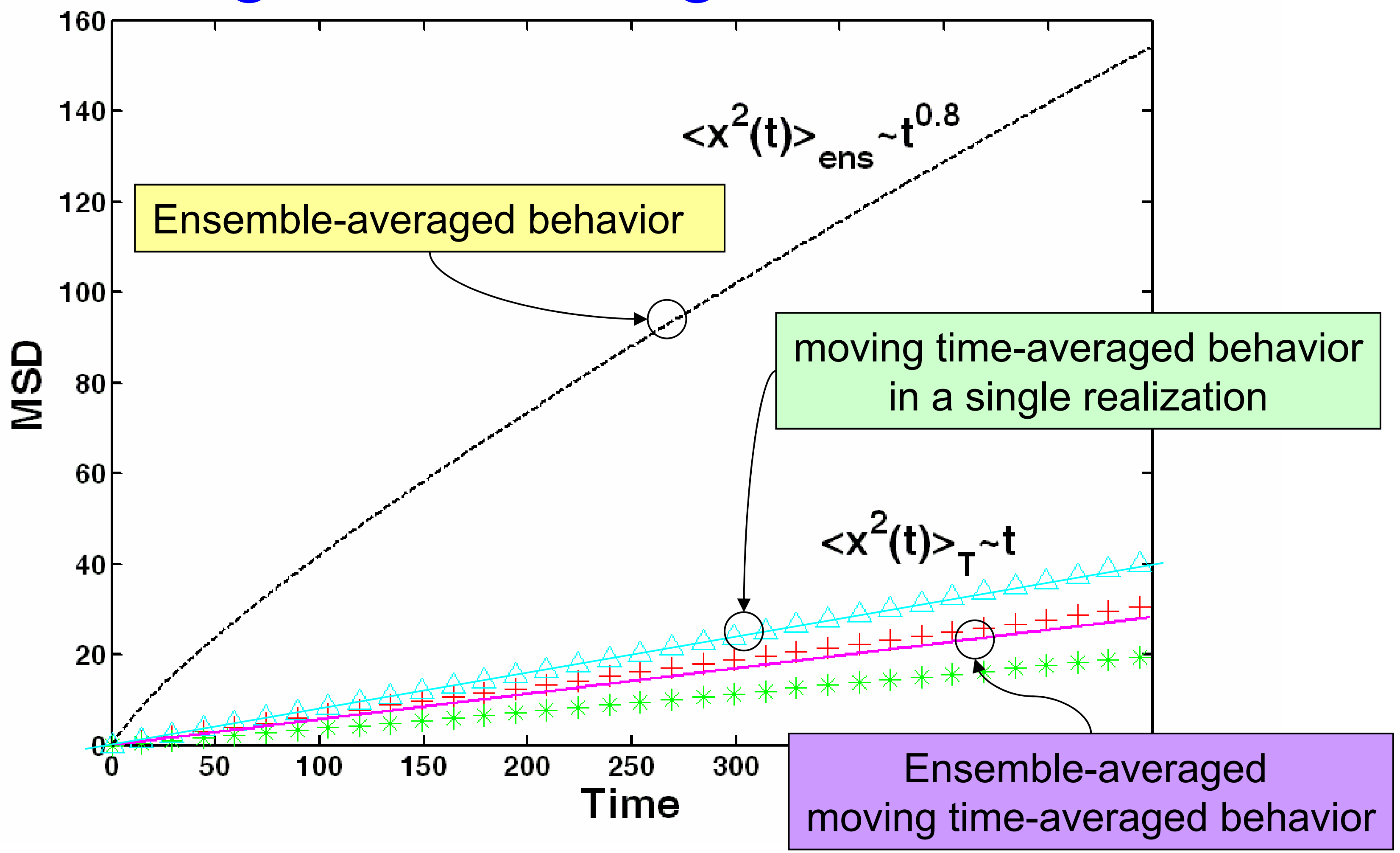
$$\left\langle \left\langle x^2(t) \right\rangle_T \right\rangle_{\text{ens}} = a^2 \frac{1}{T} \int_0^T \left[\langle n(t'+t) \rangle_{\text{ens}} - \langle n(t') \rangle_{\text{ens}} \right] dt' = \frac{a^2 A}{T} \int_0^T \left[(t'+t)^{\alpha} - t'^{\alpha} \right] dt'$$

•For $t << T$ one gets: $\left\langle \left\langle x^2(t) \right\rangle_T \right\rangle_{\text{ens}} = a^2 A T^{\alpha-1} t$

•**Prediction:** time dependent mean diffusion coefficient

$$K_{\text{eff}}(T) = a^2 A T^{\alpha-1} / 2$$

Moving time averages in CTRW



Some numerical results for the case $\psi(t) \sim t^{-1.8}$

A. Lubelski, IMS, J. Klafter, PRL **100**, 250602 (2008)

Y. He, S. Burov, R. Metzler and E. Barkai, PRL **101**, 058101 (2008)

Test on ensemble level

PRL **103**, 038102 (2009) PHYSICAL REVIEW LETTERS week ending 17 JULY 2009

Elucidating the Origin of Anomalous Diffusion in Crowded Fluids

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(Received 12 December 2008; published 15 July 2009)

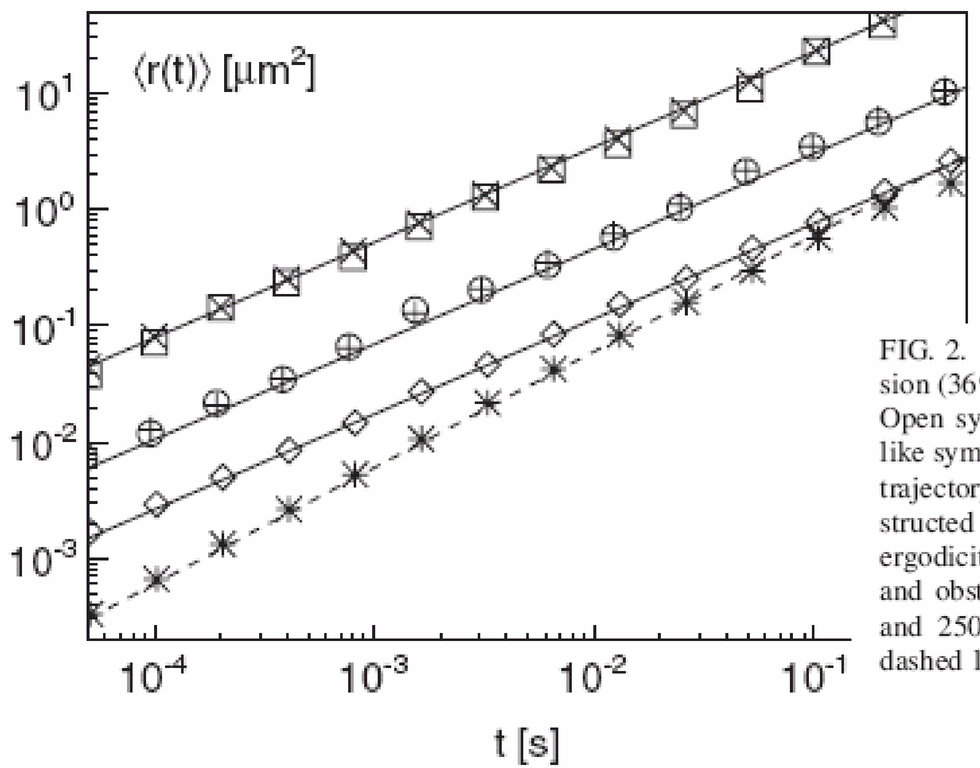

FIG. 2. Mean square displacement $\langle r(t)^2 \rangle$ for obstructed diffusion (36% obstacle concentration), FBM, and CTRW (from top). Open symbols denote the ensemble-averaged MSD, and cross-like symbols denote the time-averaged MSD for a representative trajectory. While both approaches coincide for FBM and obstructed diffusion, the curves differ for the CTRW due to weak ergodicity breaking. For better visibility, MSD curves for FBM and obstructed diffusion have been shifted upwards (factor 50 and 250, respectively). Full lines scale as $\langle r(t)^2 \rangle \sim t^{0.82}$; the dashed line is linear in time.

Test on single trajectory level

p-variance test for temporal homogeneity

PRL **103**, 180602 (2009) PHYSICAL REVIEW LETTERS week ending 30 OCTOBER 2009

Fractional Brownian Motion Versus the Continuous-Time Random Walk: A Simple Test for Subdiffusive Dynamics

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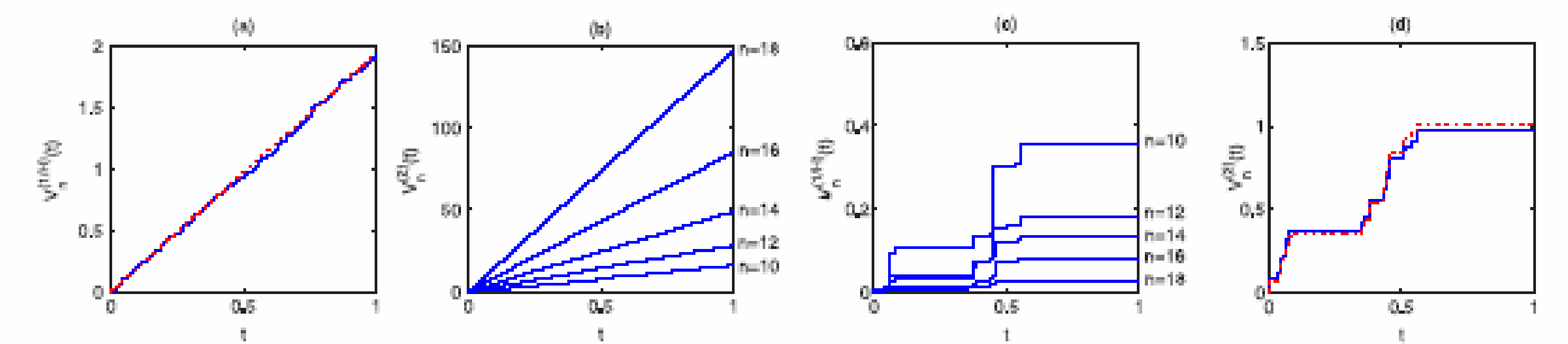
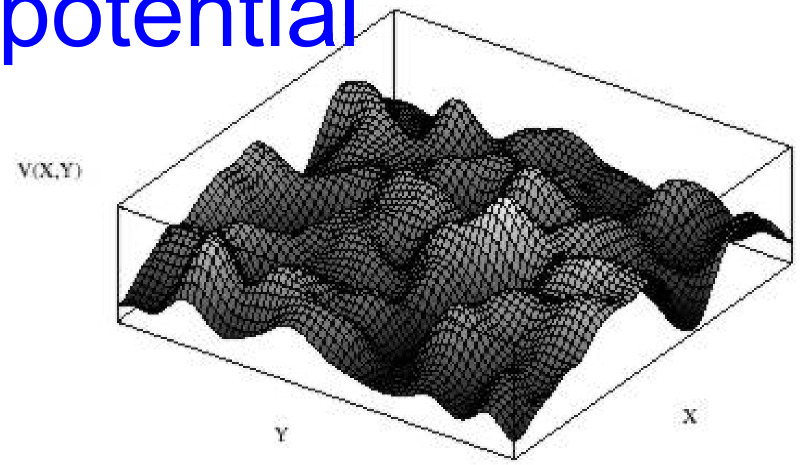


Properties of the most popular models of subdiffusion

Environment	Model	Correlations	Aging prop.	Moving time av.	PDF
trapping	CTRW	none	aging	normal	non-Gauss.
labyrinthine	fractal	antipersistent	equilibr.	anomal.	non-Gauss.
“changing”	sBm	none	aging	normal	Gaussian
viscoelastic	fBm	antipersistent	equilibr.	anomal.	Gaussian

- Anomalous is normal
- Happy families are all alike; every unhappy family is unhappy in its own way

Case study: Non-interacting particles in a random potential

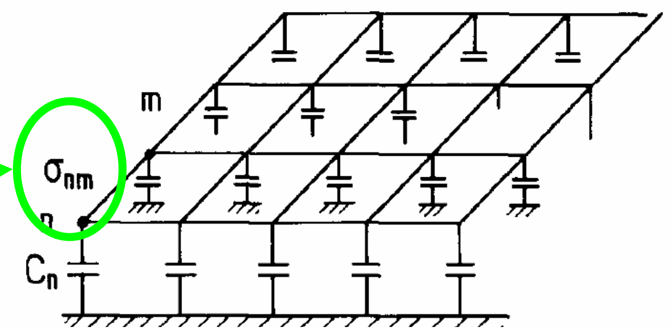


$$\dot{n}_i = \sum_j \left(w_{ij} n_j - w_{ji} n_i \right)$$

detailed balance

$$w_{ij} n_j^0 = w_{ji} n_i^0 \qquad \text{with}$$

$$n_i^0 = \frac{M}{N} \exp\left(-\frac{E_i}{kT} \right)$$



$$D^* = a^2 \frac{\left\langle w_{ij} \exp\left(-\frac{E_i}{kT} \right) \right\rangle_{EM}}{\left\langle \exp\left(-\frac{E_i}{kT} \right) \right\rangle}$$

$$\sigma = \overline{n}\, e\, \overline{\mu}$$

$$\overline{\mu} = \frac{\overline{D}}{kT}$$

$$D^* = a^2 \frac{\left\langle w_{ij} \exp\left(-\frac{E_i}{kT}\right)\right\rangle_{EM}}{\left\langle \exp\left(-\frac{E_i}{kT}\right)\right\rangle}$$

• Superdiffusion is impossible: The enumerator never diverges in finite dimensions and the denominator never vanishes

Two (and only two) sources of subdiffusion in our system:

• Either $\left\langle \exp\left(-\frac{E_i}{kT}\right)\right\rangle$ diverges ("strong energetic disorder")

• or the percolation concentration in the system is unity, e.g. on the percolation threshold, in 1*d*, or on a finitely ramified fractal ("structural disorder"). No anomalous diffusion in random barrier models in $d > 1$.

• both can apply simultaneously ("subdiffusion of mixed origins") e.g. in 1d barrier model

F. Camboni & IMS, Phys. Rev. E **85**, 050104(R) (2012)

Two (and only two) sources of subdiffusion in our system:

- Either $\left\langle \exp\left(-\frac{E_i}{kT}\right)\right\rangle$ diverges ("strong energetic disorder")

  The disorder-averaged partition function diverges (at lower limit). Different realizations of a finite system might be strongly different.

- or the percolation concentration in the system is unity, e.g. on the percolation threshold, in 1*d*, or on a finitely ramified fractal ("structural disorder").

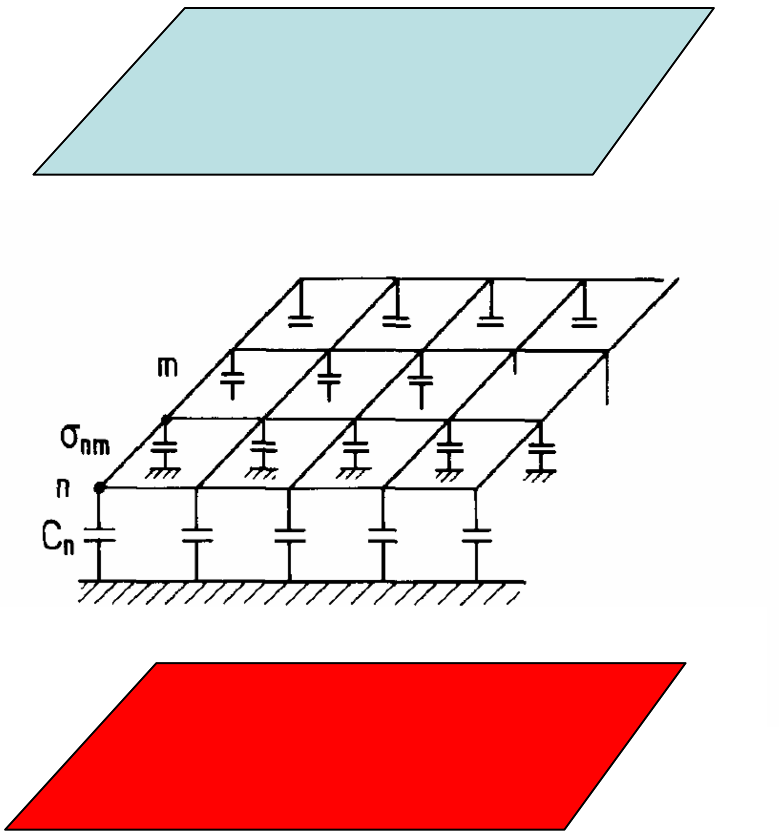
  The system may not homogenize even at largest scales. Different realizations of a finite system might be strongly different.

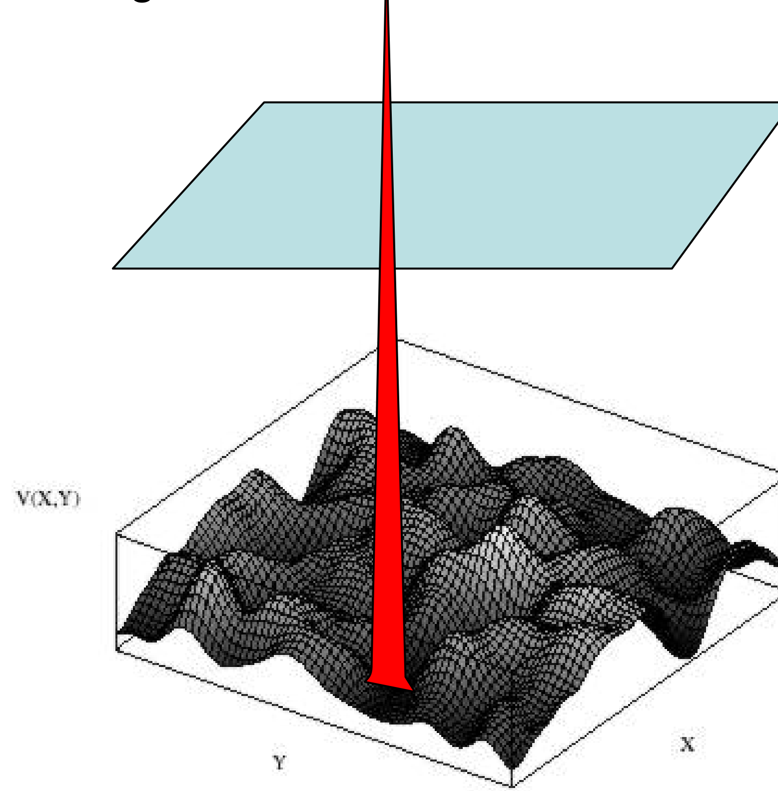
- both can apply simultaneously ("subdiffusion of mixed origins") e.g. in 1d barrier model

Formal theory: Y. Meroz, IMS and J. Klafter, PRE **81** 010101 (2010)

Aging and closeness to equilibrium

Initial distribution: Homogeneous



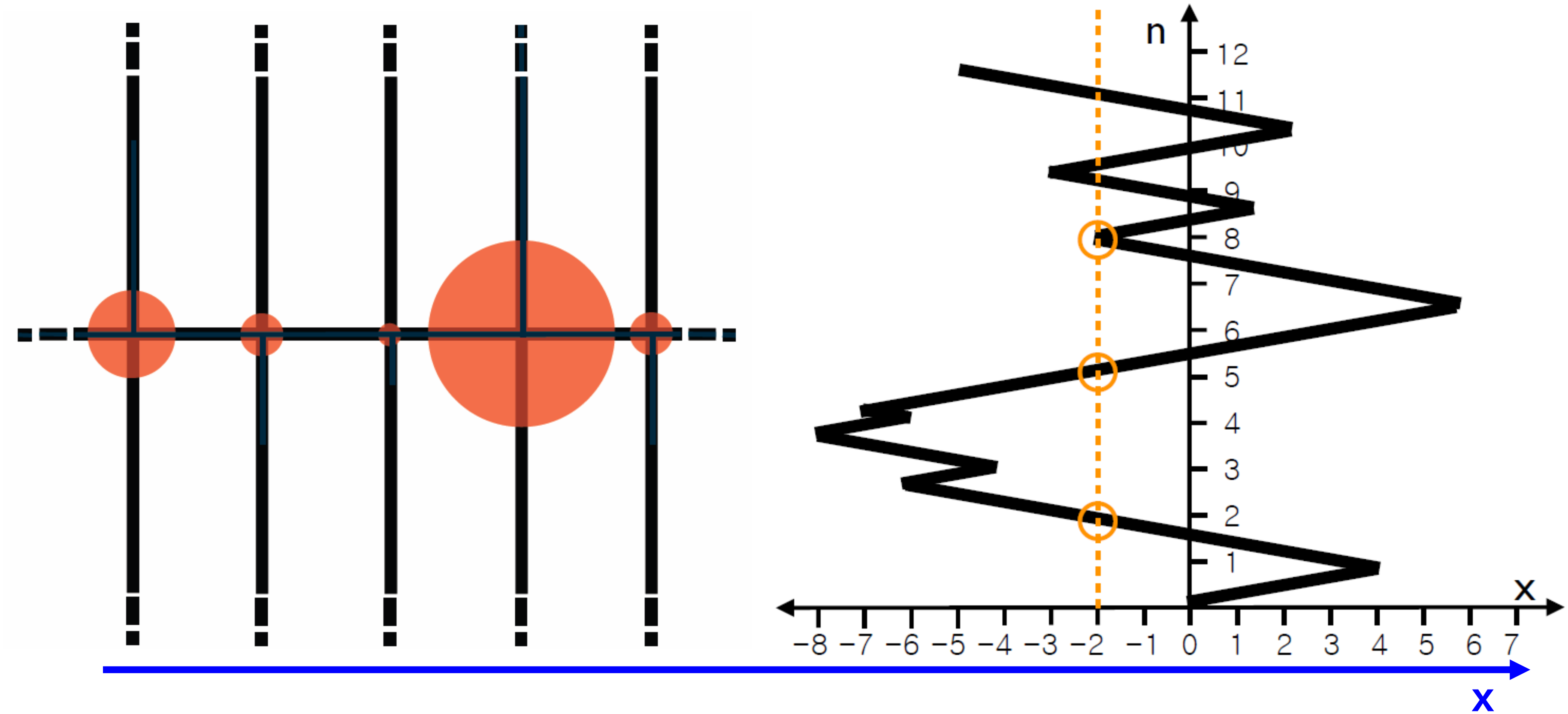


Final (equilibrium) distribution:
homogeneous

Final (equilibrium) distribution:
all particles in the deepest trap.
(Sub)diffusion without dispersion
(Anderson localization, not in CTRW*)

The (unequal) twins

Y. Meroz, IMS and J. Klafter, PRL **107,** 260601 (2011)

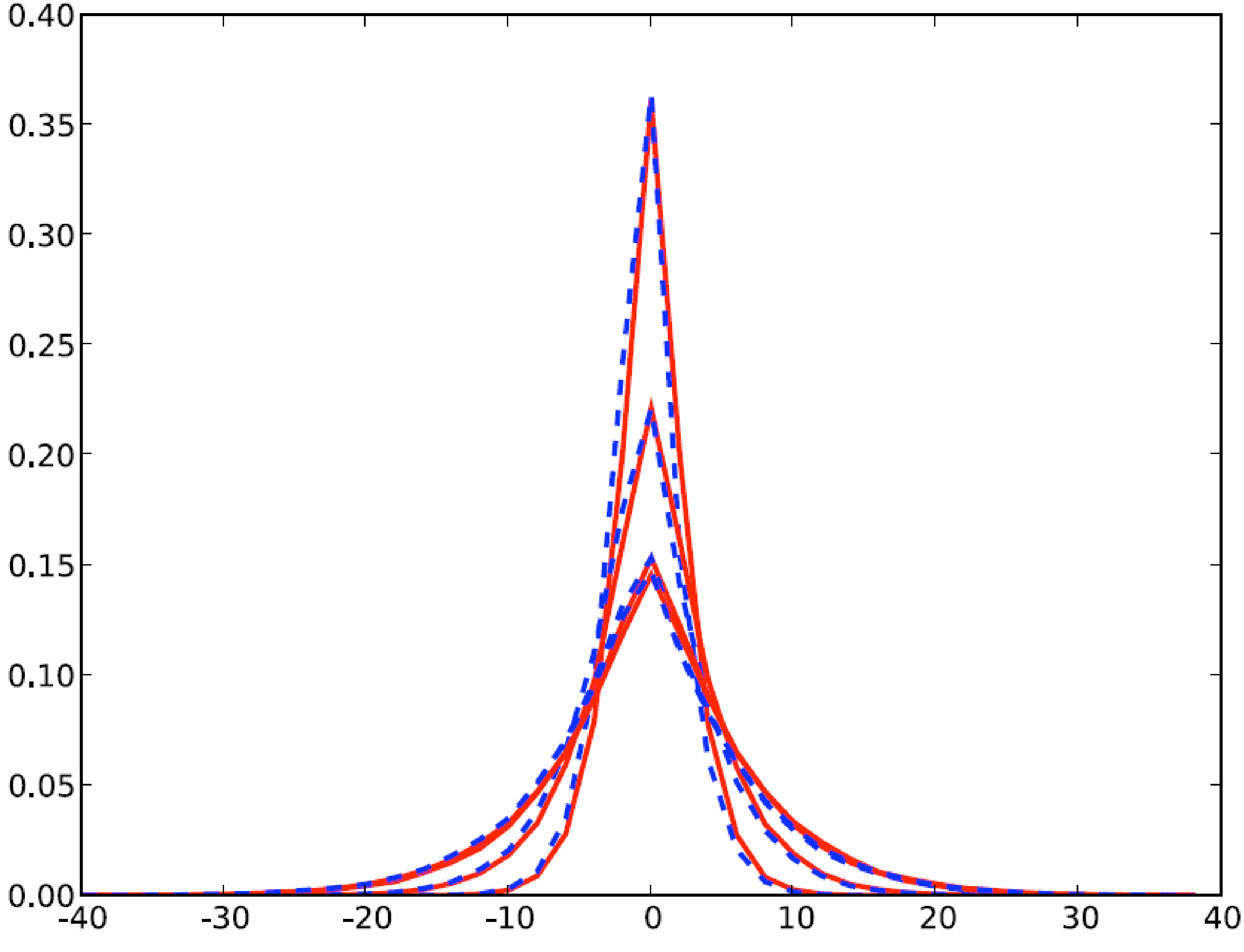


G. H. Weiss and S. Havlin, Physica A 134, 474 (1986)

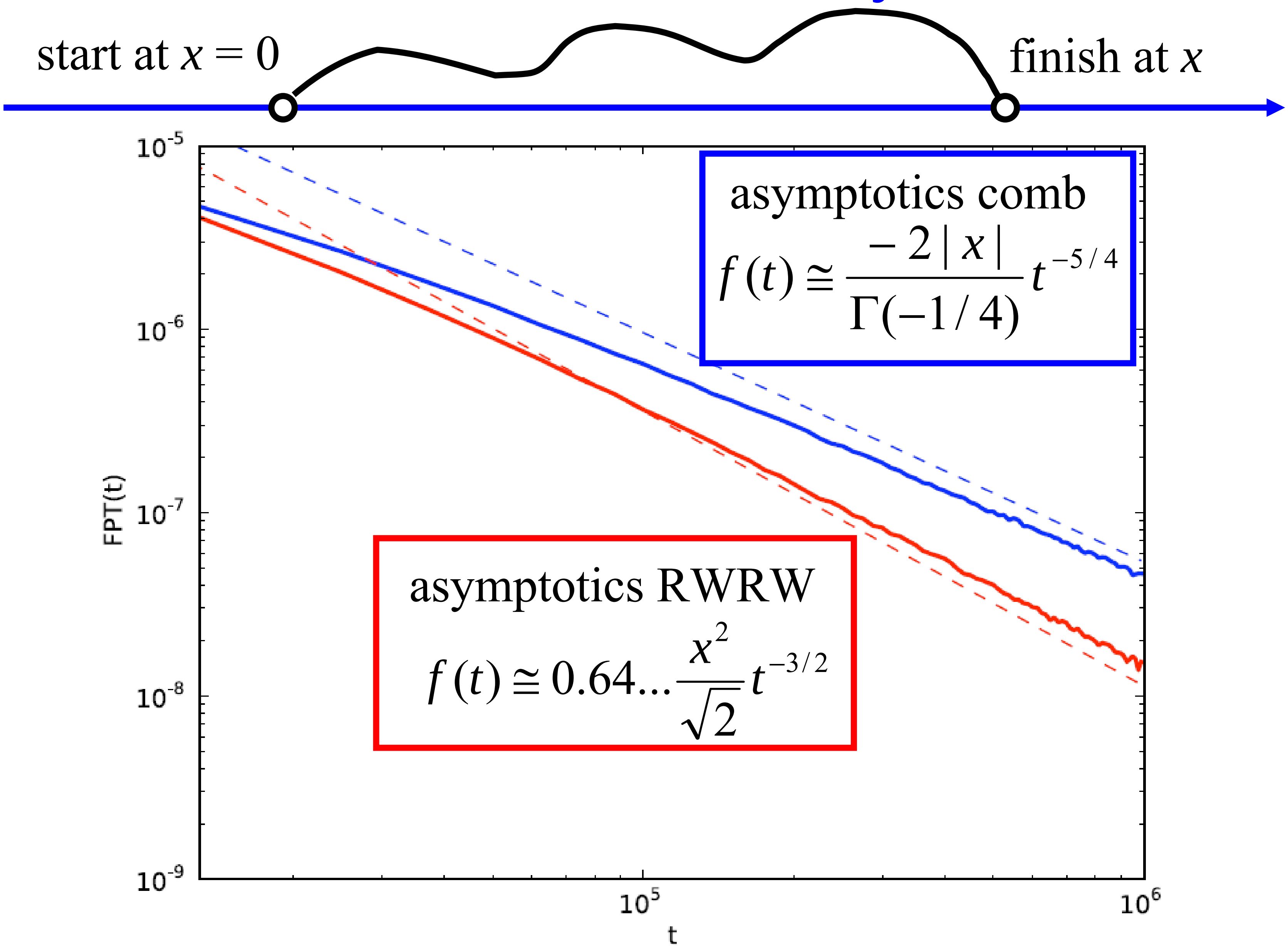
K. W. Kehr and R. Kutner, Physica A 110, 535 (1982)

Markovian RW models, mapped on non-Markovian models under projection (and averaging over realizations in RWRW)

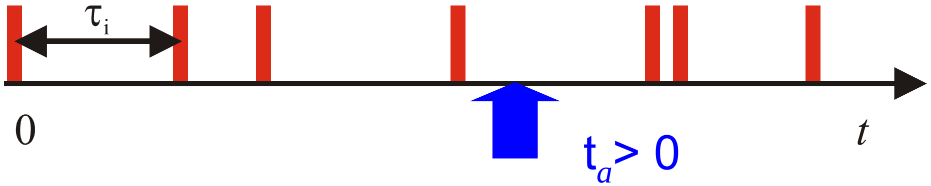
The PDFs



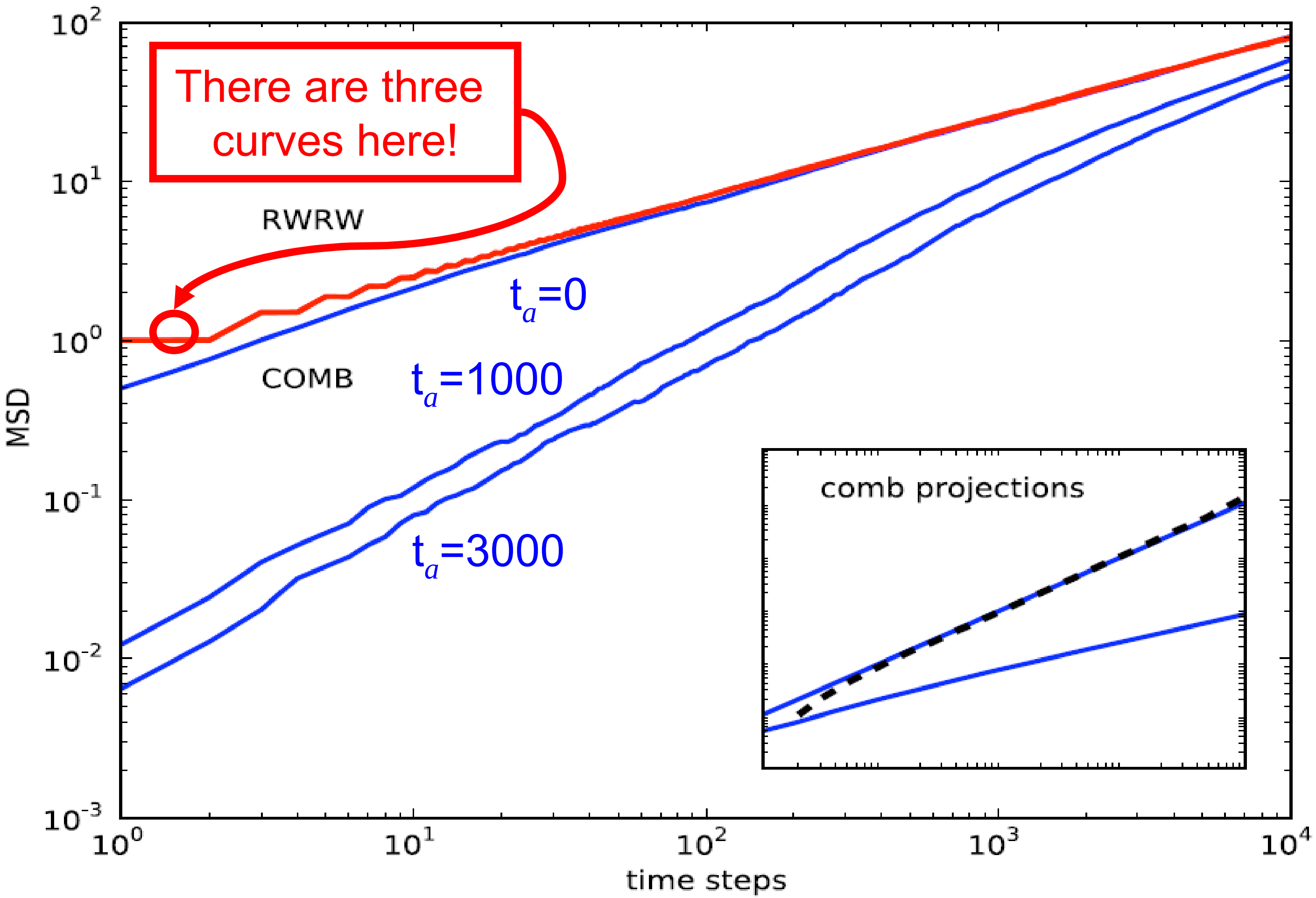
The FPT density

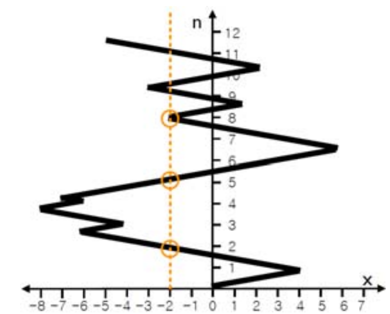


Aging properties

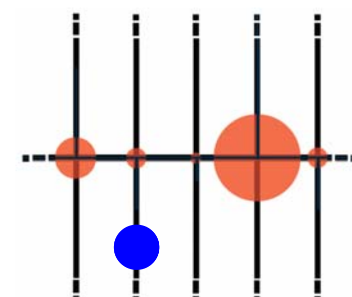


$$\left\langle x^2(t)\,\big|_{t_a} \right\rangle = \left\langle \left[x(t_a + t) - x(t_a)\right]^2 \right\rangle$$





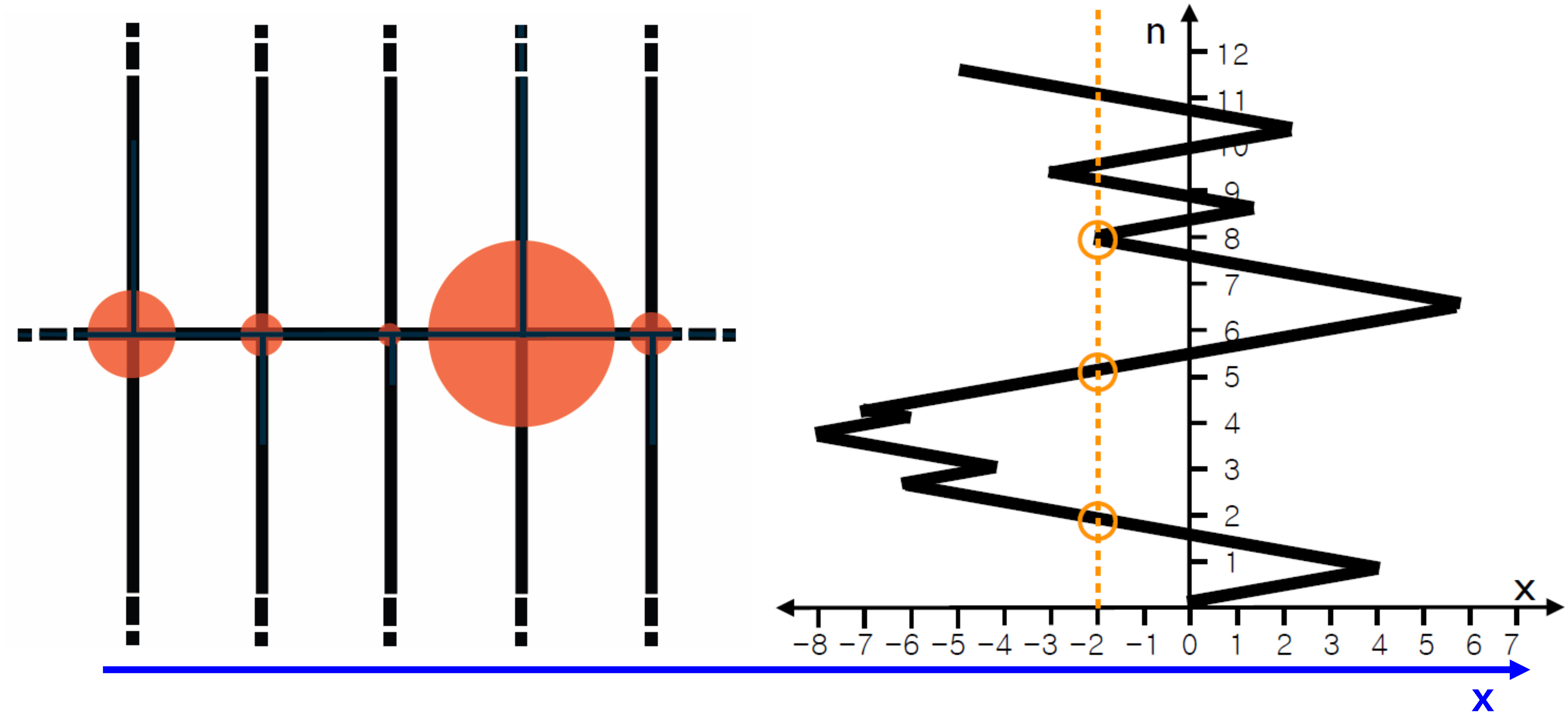
stationary



non-stationary

The (unequal) twins

Y. Meroz, IMS and J. Klafter, PRL **107,** 260601 (2011)



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Take home messages

- Anomalous is normal
- Happy families are all alike; every unhappy family is unhappy in its own way
- Knowledge of the PDF as a function of time (and even of an equation for this function) is not too much
- The most important distinction has to be made between models with stationary increments and models with uncorrelated increments.
- Models of mixed origin make the situation even more complex