

Stochastic Modeling of Anomalous Dynamics in Complex Physical and Biological Systems



Hugo Steinhaus (1887-1972)

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Wrocław University of Technology, Poland**

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Programme

Thursday, 14th May

- 09:00-09:30 **Ralf Metzler** (University of Potsdam, Germany)
Anomalous diffusion in many particle systems
- 09:30-10:00 **Krzysztof Burnecki** (Wrocław University of Technology)
Estimating the anomalous diffusion exponent for single particle tracking data with measurement errors. An alternative approach
- 10:00-10:30 **Tapio Ala-Nissila** (Aalto University School of Science, Finland)
Driven polymer translocation with iso-flux Brownian dynamics tension propagation theory
- 10:30-11:00 **Coffee break**
- 11:00-11:30 **Matthias Weiss** (University of Bayreuth, Germany)
Causes and consequences of diffusion heterogeneities and anomalies in biological fluids
- 11:30-12:00 **Nir S. Gov** (Weizmann Institute of Science, Israel)
Actin flows mediate a universal coupling between cell speed and cell persistence
- 12:00-12:30 **Gerald R. Kneller** (CNRS, France)
Anomalous diffusion in biomolecular systems by non-equilibrium statistical mechanics and computer simulations
- 12:30-14:00 **Lunch**
- 14:00-14:30 **Davide Calebiro** (University of Würzburg, Germany)
Single-molecule analysis of G protein-coupled receptor signaling
- 14:30-15:00 **Jean-Baptiste Masson** (Institut Pasteur, France)
Biomolecules Random Walks, Heterogeneities and Model Selection: What Information is accessible from experimental Biomolecules Random Walks?
- 15:00-15:30 **Emanuele Cocucci** (Harvard Medical School, USA)
In vivo molecular interactions in membrane traffic
- 15:30-16:00 **Coffee break**
- 16:00-16:30 **Yuval Garini** (Bar-Ilan University, Israel)
The genome in the nucleus: snaky, soft and well organized
- 16:30-17:00 **Carlo Manzo** (The Institute of Photonic Sciences, Spain)
Weak ergodicity breaking in receptor motion on living cell membranes
- 17:00-17:30 **Vasily Zaburdaev** (Max Planck Institute for the Physics of Complex Systems, Germany)
Meiotic chromosomes: Brownian bridges in an external field
- 18:30-21:00 **River cruise**

Friday, 15th May

- 09:00-09:30 **Eli Barkai** (Bar-Ilan University, Israel)
1/f Noise and the Low-Frequency Cutoff Paradox
- 09:30-10:00 **Takuma Akimoto** (Keio University, Japan)
Anomalous Fluctuations in Inhomogeneous Diffusion Processes
- 10:00-10:30 **Ariel Amir** (Harvard University, USA)
Cell size control in microorganisms
- 10:30-11:00 **Coffee break**
- 11:00-11:30 **Diego Krapf** (Colorado State University, USA)
Anomalous diffusion in the cell membrane: from diffusion in fractals to Lévy flights
- 11:30-12:00 **Yael Roichman** (Tel Aviv University, Israel)
Diffusion of a nano-wire in a field of soft scatters
- 12:00-12:30 **John Lapeyre** (Institute of Environmental Sciences and Water Research, Spain)
Weak Ergodicity breaking and Brownian Motion
- 12:30-14:00 **Lunch**
- 14:00-14:30 **Igor M. Sokolov** (Humboldt-Universität zu Berlin, Germany)
Continuous time random walks and their close relatives
- 14:30-15:00 **Stas Burov** (Bar-Ilan University, Israel)
Vortex Like Structures in Molecular-Motors Movement
- 15:00-15:30 **Aurélien Bancaud** (LAAS-CNRS, Toulouse, France)
Motion analysis of chromosomes in budding yeast: Evidence for Rouse dynamics in DNA, chromatin, and chromosomes
- 15:30-16:00 **Coffee break**
- 16:00-16:30 **J. Miguel Rubi** (Universitat de Barcelona, Spain)
Anomalous law of cooling
- 16:30-17:00 **Jakub Ślęzak** (Wrocław University of Technology, Poland)
From physical linear systems to discrete-time series. A guide for analysis of the sampled experimental data
- 17:00-17:30 **Enrico Carlon** (KU Leuven, Belgium)
Anomalous dynamics in single polymers: from DNA hairpin folding to unwinding dynamics

Saturday, 16th May

- 09:00-09:30 **Thomas Franosch** (Leopold-Franzens-Universität Innsbruck, Austria)
Exact Nonlinear Response in Driven Microrheology
- 09:30-10:00 **Agnieszka Wyłomańska** (Wrocław University of Technology, Poland)
Subordinated continuous-time autoregressive (CAR) processes with applications
- 10:00-10:30 **Andreas Dechant** (FAU Erlangen-Nürnberg, Germany)
Scaling Green-Kubo relation and application to aging systems
- 10:30-11:00 **Coffee break**
- 11:00-11:30 **Wojbor A. Woyczynski** (Case Western Reserve University, Cleveland, USA)
Multiscale conservation laws driven by Lévy stable and Linnik diffusions: asymptotics, shock creation, preservation and dissolution
- 11:30-12:00 **Hong Wang** (University of South Carolina, USA)
Fast methods for space-fractional PDEs and their analysis
- 12:00-12:30 **Bartłomiej Dybiec** (Jagiellonian University, Poland)
Escape from bounded domains driven by multi-variate α -stable noises
- 12:30-14:00 **Lunch**
- 14:00-14:30 **Eldad Kepten** (Bar-Ilan University, Israel)
Stochastic Analysis of in-vivo Chromatin Dynamics
- 14:30-15:00 **Grzegorz Sikora** (Wrocław University of Technology, Poland)
Guidelines for the Fitting of Anomalous Diffusion Mean Square Displacement Graphs from Single Particle Tracking Experiments
- 15:00-15:30 **Johannes H.P. Schulz** (Bar-Ilan University, Israel)
Duality in anomalous diffusion processes: infinite densities and heavy-tailed distributions
- 15:30-16:00 **Joanna Janczura** (Wrocław University of Technology, Poland)
Ergodicity testing for anomalous diffusion: Small sample statistics

Posters

Janusz Gajda, Agnieszka Wyłomańska – *Subordinated continuous-time autoregressive (CAR) processes a link to continuous time series models*

Arkadiusz Jędrzejewski – *Difficulty is critical*

Aleksander Stanislavsky, Karina Weron, Serge Yerin – *Less Typical Case of the Fractional Two-Power Laws of Relaxation: Modeling and Interpretation*

Aleksander Stanislavsky, Karina Weron, Serge Yerin – *Relationship between different relaxation laws*

Marek Teuerle – *Scaling limits and numerical simulations of multidimensional Lévy walks*

Jakub Ślęzak, Sławomir Drobczyński – *Time series methods in analysis of the optical tweezers*

Tomasz Żórawik – *Densities of Levy walks and the corresponding fractional equations*

Abstracts

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Anomalous Fluctuations in Inhomogeneous Diffusion Processes

Anomalous diffusion, where the mean square displacement (MSD) does not increase linearly in time, has been found in various phenomena ranging from transports in disorder materials to biological transports in cells. Calculating the MSD, we can use two different operations for the average, i.e., the ensemble and time averages. In some biological experiments, the time-averaged MSD, defined by

$$\overline{\delta^2(\Delta; t)} \equiv \frac{1}{t - \Delta} \int_0^{t-\Delta} dt' [\mathbf{r}(t' + \Delta) - \mathbf{r}(t')]^2,$$

grows linearly with time whereas the ensemble-averaged MSD grows sublinearly in time. Moreover, time-averaged MSDs exhibit large fluctuations. Such large fluctuations are observed in continuous-time random walk (CTRW), which is a stochastic model of anomalous diffusion (subdiffusion). In CTRW, diffusion coefficients are intrinsically random and the distribution converge to a non-trivial distribution even when the measurement time t goes to infinity.

In this talk, I will present anomalous fluctuations of time-averaged MSD in Langevin equation with fluctuating two-state diffusivity:

$$\frac{d\mathbf{r}(t)}{dt} = \sqrt{2D(t)}\mathbf{w}(t),$$

where $\mathbf{r}(t)$ is a position, $D(t)$ is a stochastic process, and $\mathbf{w}(t)$ is a white Gaussian noise. We consider the stochastic process $D(t)$ as a dichotomous process, i.e., $D(t) = D_+$ or D_- . When sojourn times for the two states have finite means, the system can be equilibrated (equilibrium renewal process). In equilibrium processes, the time-averaged MSD, $\overline{\delta^2(\Delta; t)}$, for a fixed Δ converges to a constant as $t \rightarrow \infty$. When the sojourn time distributions have heavy tails but have finite means, we show that the convergence is extremely slow. Moreover, when the sojourn times do not have finite mean (non-equilibrium process), we provide two novel distributional limit theorems for time-averaged diffusion coefficients.

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Driven polymer translocation with iso-flux Brownian dynamics tension propagation theory*

The dynamics of driven polymer translocation is controlled by the propagation of a tension front on the cis side of the chain, as originally proposed by Sakaue in a series of works, starting from [1]. Based on this idea, Ikonen and collaborators developed a formalism using Brownian dynamics approach coupled with tension propagation (the Brownian Dynamics Tension Propagation or BDTP model), which quantitatively explains finite-chain and pore size effects on translocation dynamics [2]. In this talk I will report some recent progress made in further developing the BDTP approach. In particular, based on an explicit iso-flux assumption at the pore, we have developed an Iso-Flux Tension Propagation (IFTP) model that can quantitatively describe various additional aspects of polymer translocation, such as the waiting times, the translocation time distribution, and the translocation exponents. In addition, results obtained by incorporating thermal fluctuations of the initial configurations in the IFTP theory are in very good agreement with available Molecular Dynamics simulation data [3].

*Work done in collaboration with Timo Ikonen and Jalal Sarabadani.

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Cell size control in microorganisms

Microorganisms in all kingdoms of life face a challenge of regulating the size and shape of their cells, control of which is essential for their viability. For decades, a popular hypothesis has been that cells can measure their absolute size, and that reaching a critical size triggers the division process. This would imply that a cell that was born smaller than average will not be smaller than average when it divides – in contrast to experiments showing that such correlations exist, and that size is partly “inherited”. I will present a stochastic model that sheds new light on this problem, showing that a cell does not need to know its absolute size to regulate size robustly, quantitatively explaining the experimentally measured correlations in various organisms, and predicting that average cell size should depend exponentially on the growth rate.

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Motion analysis of chromosomes in budding yeast: Evidence for Rouse dynamics in DNA, chromatin, and chromosomes

The organization of the genome remains the subject of intense research due to its fundamental role in gene expression, DNA replication and stability. This domain is increasingly involving physicists, who rely on polymer physics to build models of chromosome organization in living systems. Chromosome folding and dynamics in the yeast *S. Cerevisiae* has for instance been recently revisited with polymer models, which appeared to be in reasonable agreement with experimental data. In this talk, we will focus on the spatio-temporal fluctuations of chromosomes, which appear to be in remarkable agreement with the Rouse polymer model [1]. We will then demonstrate that this model allows us to estimate the persistence length and the viscous friction of DNA, chromatin, or chromosome. Finally we will discuss these results in terms of compaction and flexibility of chromosomes in vivo.

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1/f Noise and the Low-Frequency Cutoff Paradox

Recent experiments on blinking quantum dots, weak turbulence in liquid crystals, and nanoelectrodes reveal the fundamental connection between $1/f$ noise and power law intermittency. The nonstationarity of the process implies that the sample power spectrum ages and noise level decrease with the increase of the measurement time as reported in a recent experiment [1]. The spectrum is random- a manifestation of weak ergodicity breaking and we discuss its fluctuations characterize by the Mittag-Leffler distribution [2]. We solve in this case an outstanding paradox on the nonintegrability of $1/f$ noise and the violation of Parseval's theorem. We explain why there is no physical low-frequency cutoff and therefore why it cannot be found in experiments.

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Estimating the anomalous diffusion exponent for single particle tracking data with measurement errors - An alternative approach

Accurately characterizing the anomalous diffusion of a tracer particle has become a central issue in biophysics. However, measurement errors raise difficulty in the characterization of single trajectories, which is usually performed through the time-averaged mean square displacement (TAMSD). We study a fractionally integrated moving average (FIMA) process as an appropriate model for anomalous diffusion data with measurement errors. We compare FIMA and traditional TAMSD estimators for the anomalous diffusion exponent. The ability of the FIMA framework to characterize dynamics in a wide range of anomalous exponents and noise levels through the simulation of a toy model (fractional Brownian motion disturbed by Gaussian white noise) is discussed. Comparison to the TAMSD technique, shows that FIMA estimation is superior in many scenarios. This is expected to enable new measurement regimes for single particle tracking (SPT) experiments even in the presence of high measurement errors.

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Vortex Like Structures in Molecular-Motors Movement

Experimentally observed anomalous transport in intracellular environment, specifically appearance of power-law waiting times, needs to be supplemented with appropriate microscopic theory. We seek for crucial ingredients of such theory that will stimulate appearance of broadly distributed dwell times and aging in intracellular environment. A model of molecular motors moving on a two dimensional network is presented. The structure of the network imposes local vortices of motor trajectories. Those vortices act as dynamical traps which dictate anomalous transport of motor-driven vesicles and consequently can be possible candidates for the origins of anomalous transport in living cells.

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Single-molecule analysis of G protein-coupled receptor signaling

G protein-coupled receptors (GPCRs) are the largest family of cellular receptors. They mediate the effects of several hormones and neurotransmitters and represent major pharmacological targets. In our lab we are using single-molecule microscopy and single particle tracking to investigate the organization of GPCR signaling cascades at the surface of living cells [1], [2]. Using this approach we could show that three prototypical GPCRs have very different localization, mobility and tendencies to form supramolecular complexes [1]. The formation of such complexes is due to transient receptor/receptor interactions, which can be directly visualized with our approach. Interactions between receptors and the underlying cytoskeleton seem to play an important role in defining the spatial arrangement of receptors. Our results reveal that GPCR signaling cascades are at the same time very dynamic and yet highly organized in space and time. These data suggest the existence of dynamic receptor nanodomains on the surface of cells, which might be required for achieving high signaling efficiency and specificity.

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Anomalous dynamics in single polymers: from DNA hairpin folding to unwinding dynamics

Single polymers can often display complex and anomalous dynamics. A paradigmatic example is the translocation of a polymer through a narrow pore on a membrane, which has been intensively studied in the past years [1]. Here we review some examples of single polymers anomalous dynamics recently studied by our group: the DNA hairpin folding [2] and the unwinding of a polymer from a rod [3], [4]. Simulations show that in both cases there is an “anomalous” power-law dependence $\sim t^\alpha$ of various quantities as a function of time. We show how the numerical results can be explained by force balance arguments, using a multiphase picture of the polymer conformations.

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In vivo molecular interactions in membrane traffic

Stochastic interactions between molecules are the foundation of any complex physiological process. High-speed fluorescence high sensitivity microscopy approaches coupled with the computational ability to detect and track, in an unbiased way, single diffraction limited objects and gene-editing techniques permits to observe protein interactions in real time at the real concentration avoiding over-expression artifacts. We adopted these techniques to study the molecular interactions happening in the formation of clathrin-coated vesicles (CCVs), structures responsible for the entrapment and sorting of nutrients, receptors, and synaptic vesicle components [1]. CCVs assemble by the subsequent recruitment of adaptor protein complex 2 (AP2) and clathrin triskelions; dynamin is recruited at the end of the assembly and mediates vesicle release by breaking the membrane neck [2]. Despite the detailed information present in the literature on clathrin coat and dynamin structures, an understanding of how CCVs start and how dynamin pinching happens is still missing. The overall result is that CCVs initiate by a stochastic process involving two subsequent steps of recruitment of one clathrin and two adaptor AP2 complexes during the first 5 seconds of life of a clathrin-coated pit [3]. Besides, I defined that dynamin is recruited as dimers and that a large fraction of budding coated pits recruit between 26 and 40 dynamins (between 1 and 1.5 helical turns of a dynamin collar) during the recruitment phase associated with neck fission; since 26 are enough to induce fission, our data suggest a model where a progressive, circumferential twist is induced by dynamin assembly [4].

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Scaling Green-Kubo relation and application to aging systems

The Green-Kubo formula relates the spatial diffusion coefficient to the stationary velocity autocorrelation function. We derive a generalization of the Green-Kubo formula valid for systems with long-range or nonstationary correlations for which the standard approach is no longer valid. For the systems under consideration, the velocity autocorrelation function $\langle v(t + \tau)v(t) \rangle$ asymptotically exhibits a certain scaling behavior and the diffusion is anomalous $\langle x^2(t) \rangle \simeq 2D_\nu t^\nu$. We show how both the anomalous diffusion coefficient D_ν and exponent ν can be extracted from this scaling form. Our scaling Green-Kubo relation thus extends an important relation between transport properties and correlation functions to generic systems with scale invariant dynamics. This includes stationary systems with slowly decaying power law correlations as well as aging systems, whose properties depend on the the age of the system. Even for systems that are stationary in the long time limit, we find that the long time diffusive behavior can strongly depend on the initial preparation of the system. In these cases, the diffusivity D_ν is not unique and we determine its values for a stationary respectively nonstationary initial state.

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Escape from bounded domains driven by multi-variate α -stable noises

We explore properties of escape processes from bounded domains driven by multi-variate α -stable noises in order to elaborate differences between various types of α -stable noises. The special attention is given to the so-called spherical and Cartesian Levy flights.

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Exact Nonlinear Response in Driven Microrheology

One of the principal strategies to probe material properties is to apply an external stimulus and monitor the system's response. The fundamental link between the deterministic response of a system and the correlation functions of intrinsic fluctuations is provided by the celebrated fluctuation-dissipation theorem (FDT). The framework applies whenever the unperturbed system is in thermal equilibrium and the forces are sufficiently small such that the response is linear.

It came as a big surprise that the equilibrium correlation functions yielding the transport coefficients display power-law tails rather than an exponential decay. First found in computer simulations [1] of the velocity autocorrelation function (VACF) these persistent correlations have been derived rigorously for dilute gases by systematically going beyond the Boltzmann equation. Then repeated collisions with the same particle yield a non-analytic dependence of the diffusion coefficients on density, frequency, and wavenumber.

We determine the nonlinear time-dependent response of a tracer on a lattice with randomly distributed hard obstacles as a force is switched on [2]. The calculation is exact to first order in the obstacle density and holds for arbitrarily large forces. In particular, we show that the nonlinear drift velocity in the stationary state becomes non-analytic in the driving force. Furthermore we demonstrate that the stationary velocity is approached exponentially fast for any finite value of the force, in striking contrast to the power-law relaxation predicted within linear response. We generalize our results to a dilute colloidal suspension where a force acts on a single tracer particle only.

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Subordinated continuous-time autoregressive (CAR) processes a link to continuous time series models

We study properties of the continuous-time autoregressive (CAR) processes driven by α -stable Lévy motion delayed by inverse stable subordinator. Such processes can be applied to high-frequency data with visible jumps and co-called "trapping-events". Those properties are often observable in financial time series but also in technical data describing the rotational speed of a machine working under various load regimes or data related to

indoor air quality. We concentrate on the main characteristics of the examined subordinated process expressed in the language of the measures of dependence which are main tools used in statistical investigation of real data. We calculate the codifference, which is the most general measure of dependence defined for wide class of processes. Moreover we present the simulation procedure of the considered system and indicate how to estimate its parameters. Theoretical results we illustrate by analysis of the simulated data.

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The genome in the nucleus: snaky, soft and well organized

The DNA in a human cell is ~ 3 meters long. Although there are no definite structures that maintain the order in the nucleus, the genome is well organized, though dynamic. What are the mechanisms that organizes the DNA in the nucleus?

Dynamic methods in live cells are ideal for studying the genome organization. By labeling specific genetic sites and using optical microscopy, time paths can be measured and analyzed, so as other dynamic properties.

We used single particle tracking (SPT) and continuous photobleaching (CP) that are adequate for live-cell imaging. Data is analyzed according to diffusion analysis methods that we developed. In normal cells, the sites we measured, mainly telomeres and centromeres, exhibit anomalous diffusion (viscoelastic) with a power law of $\sim 0.3-0.7$ and the diffusion was found to belong to the family of fractional Brownian motion anomalous diffusion.

We rationalized that the viscoelasticity results from a cross-linking mechanism that is most likely mediated by a protein or a protein complex. We identified the source protein and showed that a phase transition from viscoelastic to viscous diffusion occurs when its expression is inhibited. We suggest a rather simple mechanism that explains the organization maintenance of the chromosomal territories and is strongly supported by the whole set of our dynamic measurements.

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Actin flows mediate a universal coupling between cell speed and cell persistence

Cell movement has essential functions in development, immunity and cancer. Various cell

migration patterns have been reported, but no general rule has emerged so far. Here [1], we show on the basis of experimental data in vitro and in vivo that cell persistence, which quantifies the straightness of trajectories, is robustly coupled to cell migration speed. We suggest that this universal coupling constitutes a generic law of cell migration, which originates in the advection of polarity cues by an actin cytoskeleton undergoing flows at the cellular scale. Our analysis relies on a theoretical model that we validate by measuring the persistence of cells upon modulation of actin flow speeds, and upon optogenetic manipulation of the binding of an actin regulator to actin filaments. Beyond the quantitative prediction of the coupling, the model yields a generic phase diagram of cellular trajectories, which recapitulates the full range of observed migration patterns. The same model can be extended to describe the transitions from stable to oscillatory motility, which is observed in certain types of immune cells.

References

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Ergodicity testing for anomalous diffusion: Small sample statistics

An analysis of trajectories recorded in experiments often requires calculating time averages instead of ensemble averages. According to the Boltzmann hypothesis they are equivalent only under the assumption of ergodicity. In this paper we implement tools that allow to study ergodic properties. This analysis is illustrated for two classes of anomalous diffusion processes: fractional Brownian motion and subordinated Ornstein-Uhlenbeck process. We show that only first of them is ergodic. We demonstrate this by applying rigorous statistical methods: mean square displacement, confidence intervals and dynamical functional test. Our methodology is universal and can be implemented for analysis of many experimental data not only if a large sample is available, but also when there are only few trajectories recorded.

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Difficulty is critical

Empirical results from the domains such as agriculture, medicine or technology show that external constraints may effectively hinder the adoption of innovation. In the promising agent-based modeling approach, however, person-independent costs of adoption that amount to difficulty of engagement in innovation have not been considered before. In this paper, we present a model in which aside from the social influence (conformity or non-conformity), difficulty is included as a factor affecting the process of adoption. We propose a model that is inspired by the so-called diamond model of social response and empirical results of classical social experiments. Formally, the model that we study here is a generalization of the q -voter model with independence that additionally takes into account the context dependent difficulty. Using Monte Carlo simulations (for small-world networks) and analytic calculations (for the complete graph) we provide evidence that introducing the idea of difficulty leads to a completely new macroscopic behavior and may be critical in understanding diffusion of innovation, especially in the context of so-called green products and practices.

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Stochastic Analysis of *in-vivo* Chromatin Dynamics

Recent studies have shown that accurate spatial organization and dynamics of nuclear DNA strands is crucial for cellular genetic activity. However, nuclear dynamics and organization are intimately dependent, both creating and disrupting each other, in ways that are yet to be fully understood. We study the stochastic motion of chromatin loci (DNA with its accompanying proteins) with the use of fluorescent microscopy, in order to identify and characterize the underlying physical and biological mechanisms. By measuring the relative dynamics between thousands of chromatin loci pairs, we are able to extract significant traits, despite the high inherent randomness of the system. Through the application

of novel stochastic characterization techniques, an anisotropic distance dependent anomalous diffusion is found, with a varying memory kernel. Such relative dynamics have not been seen before, and lead us to define and validate a new diffusion mechanism – contractile diffusion. Possible biophysical implications of chromatin diffusion will be discussed.

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Anomalous diffusion in biomolecular systems by non-equilibrium statistical mechanics and computer simulations

Anomalous diffusion and slow non-exponential relaxation in biomolecular systems are studied within the theoretical framework of non-equilibrium statistical physics. The focus is on the relation between transport coefficients and the asymptotic form of statistical observables, such as the mean square displacements of the diffusing particles, their velocity autocorrelation function, and the associated memory function which is the key element in the Generalized Langevin Equation[1]. It is shown that fractional diffusion equations describe anomalous diffusion asymptotically correctly [2]. In this context, molecular dynamics simulations are an essential tool to illustrate theoretical results, in particular the relation between anomalous diffusion and the caging effect of diffusing particles in their respective environments. Examples are presented for the lateral diffusion of molecules in lipid bilayers [3], [4] and for the relaxation backbone dynamics in proteins [5].

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Anomalous diffusion in the cell membrane: from diffusion in fractals to Lévy flights

Lipids and proteins are known to exhibit complex anomalous diffusion on the surface of mammalian cells. In this talk I will present evidence from single-particle tracking measurements for three different mechanisms affecting the motion of membrane proteins: (i) a subdiffusive continuous time random walk (CTRW); (ii) diffusion in a fractal structure; and (iii) a superdiffusive Lévy flight.

A heavy-tail CTRW takes place in the motion of potassium channels, because they reversibly bind to non-stationary structures yielding a power-law immobilization-time distribution $\psi(\tau) \sim \tau^{-(1+\alpha)}$ with $\alpha < 1$ [1]. As a consequence, the dynamics of potassium channels exhibit aging and weak ergodicity breaking [2]. Furthermore, the motion of potassium channels has a signature of diffusion in a fractal environment. Statistical analysis shows that the data cannot be modeled by fractional Brownian motion but it fits well within a model of diffusion in a fractal. To test this hypothesis, we image the actin cytoskeleton in close proximity to the plasma membrane with superresolution in live cells. It is found that the cortical forms a self-similar structure that compartmentalizes the motion of membrane proteins.

I will also describe experimental observations of superdiffusive Lévy flights performed by membrane targeting proteins [3]. These measurements are obtained in reconstituted lipid bilayers. We observe that the proteins often dissociate from the lipid bilayer, perform a three-dimensional Brownian motion, and eventually re-associate to the membrane. The bulk excursions induce long jumps with step sizes distributed according to power laws.

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Weak Ergodicity breaking and Brownian Motion

I will discuss anomalous diffusion arising from Brownian motion on heterogeneous media. A well-known example is the random walk on a critical percolation process. I will show, however, that a different source of disorder produces an anomaly that is associated with weak ergodicity breaking. I will place the models in the context of recent work on the continuous-time random walk and trapping models. I will give illustrative examples of applications to biological and physical systems. These include motion of receptors in cell membranes and flow in porous media.

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Weak ergodicity breaking in receptor motion on living cell membranes

Molecular diffusion in the plasma membrane of living cells regulates numerous processes underlying biological functions. In the last decade, advances in single-molecule techniques have provided novel insights on the dynamics of multiple receptors at unprecedented spatiotemporal resolution. These experiments have revealed that the complexity of the membrane environment often produces deviation from purely Brownian behavior, leading

to anomalous and confined diffusion. Recently, it has also been shown that some cellular components display nonergodic dynamics, but its implications for the cellular function are not fully understood.

We have applied single-particle tracking to study the dynamics of DC-SIGN, a receptor that facilitates capture and internalization of viral pathogens [1],[2]. The analysis of time- and ensemble-averaged mean-square displacement of single receptor trajectories revealed that, besides anomalous diffusion, DC-SIGN dynamics exhibits weak ergodicity breaking and aging [4]. In contrast to other systems showing analogous behavior, DC-SIGN nonergodicity is not induced by transient immobilization and therefore cannot be modeled as a continuous-time random walk. We model and quantitatively interpret this dynamics within the framework of a new family of stochastic models [5], assuming inhomogeneous Brownian diffusion with random diffusivity on scale-free media. To further explore the molecular causes of DC-SIGN nonergodic subdiffusion, we comparatively investigated three mutated forms of the receptor [4] as well as performed complementary measurements by means of super-resolution imaging (STED) and functional assays [1],[2].

These data allowed us to correlate receptor motion with molecular structure, thus establishing a link between nonergodicity and DC-SIGN capability in pathogen capture and internalization [4]. Our findings highlight the fundamental role of disorder in cell membranes and postulate a connection with function regulation.

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Biomolecules Random Walks, Heterogeneities and Model Selection: What Information is accessible from experimental Biomolecules Random Walks?

The development during the last 20 years of single biomolecule tagging allows unprecedented access to single biomolecule dynamics. Thus, large amount of random walks are now accessible. These random walks bear information on both the biomolecule dynamics and on the environment properties. One of the key questions is how to exploit these random walks to gain quantitative information on the biological processes taking place and the nature of these random walks.

Biological environments differ significantly from the usual medium where random walks were historically studied. Trajectories can bear unusual and sometimes contradictory set of properties. Furthermore, Biological media are often characterised by high temporal/spatial heterogeneities and complex geometries. Thus, analysing biological random walks remain a challenge.

Growing number of data being accessible multiple statistical hypothesis can be tested. Bayesian Inference [1] is a natural tool to handle multiple environment models, large amounts of data and multiple statistical hypothesis. We will discuss the use of Bayesian Inference to analyse single biomolecule trajectories[2], [3], [4], show various local models to describe biomolecule dynamics, methods to analyse multi-scale dynamics and describe transitions to anomalous dynamics [5]. We will also comment on out-of-equilibrium dynamics and stochastic integrals dilemma.

We will show two applications of the Inference Schemes on the Glycine Receptors dynamics at the full cell scale in both neurons and transfected Hela Cells and on the GAG dynamics at HIV-1 platform assembly. Finally, we will quickly introduce InferenceMAP a user-friendly software to analyse random walks trajectories.

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Anomalous diffusion in many particle systems

I will present three cases in which many particle interactions effect distinct anomalous diffusion. The first system follows a tracer particle in a flexible gel made up of excluded volume particles connected by Morse springs. From the time averaged van Hove correlation functions and the tracer mean squared displacement the highly co-operative dynamics is analysed for the relevant case when the size of the tracer is comparable to the typical mesh size of the gel [1].

The second case is that of single file diffusion in a disordered environment. This is a one-dimensional gas of excluded volume particles, which can be trapped in space. The associated waiting times are power-law distributed. It is shown that while a single particle would perform continuous time random walk subdiffusion, the many particle interactions lead to a ultraslow, logarithmic growth of the mean squared displacement of a labelled tracer particle [2].

Finally, the third case is that of a granular gas with either constant restitution coefficient of pair-colliding particles or with a relative speed dependence of the restitution coefficient. The temperature of this gas, defined in terms of the kinetic energy, decays in power-law fashion. We will discuss the weakly non-ergodic properties of this process and show to what extent simple, single particle scaled Brownian motion can describe the observed granular gas dynamics.

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Diffusion of a nano-wire in a field of soft scatters

We investigate experimentally the movement of hard rods in a 2D environment of randomly distributed obstacles. This is done by following the diffusion of silver nano-wires in a field of optical traps which are created using holographic optical tweezers (HOTs). We find that at a certain normalized density threshold a transition from normal diffusion to super diffusion occurs. This is unlike previous numeric results which have indicated changes in the diffusion coefficient but not in movement type. These results are explained in terms of the worm like chain model of polymers.

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Anomalous law of cooling

We have investigated the relaxation of the temperature of a system that undergoes anomalous diffusion and is in contact with a thermal bath. We have performed an analysis based on a generalized Langevin equation to derive an expression for the relaxation equation for the temperature of the system which resembles Newton's law of cooling but with a nonconstant coefficient that depends on the nature of the diffusion process. Temperature relaxation exhibits significant differences with respect to the case of normal diffusion in which Newton's law of cooling holds. In particular, the temperature of the system may oscillate because of memory effects. These memory effects can be relevant in small-scale systems, since the reduction of the observational scales modifies the interactions of the particles with the thermal bath and leads to a time-dependent friction coefficient. The results obtained can be used to analyze heat transfer at small scales.

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Duality in anomalous diffusion processes: infinite densities and heavy-tailed distributions

We discuss several processes where a physical observable exhibits biscaling. That means, the bulk statistics of the observable have a different time scaling behavior (in our case: faster) than the extreme value statistics. Examples include the strong anomalous diffusion of Lévy walks [1], the fluctuations of occupation times in ergodic continuous-time random walks [2] and the Brownian diffusion in a logarithmic potential [3].

We present strong evidence that this type of biscaling is generically caused by an interplay of two types of limiting laws: the infinite density of large deviations complements a heavy-tailed bulk distribution. Neither of these two should be interpreted as a stand-alone limiting law, as each has its own deficiency: the infinite density has an infinite norm (despite particle conservation), while the heavy-tailed distribution has an infinite variance (although all the dynamics are bounded). These unphysical divergences are remedied by consistent use and interpretation of both formulas.

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Guidelines for the Fitting of Anomalous Diffusion Mean Square Displacement Graphs from Single Particle Tracking Experiments

Single particle tracking is an essential tool in the study of complex systems and biophysics and it is commonly analyzed by the time-averaged mean square displacement (MSD) of the diffusive trajectories. However, past work has shown that MSDs are susceptible to significant errors and biases, preventing the comparison and assessment of experimental studies. Here, we attempt to extract practical guidelines for the estimation of anomalous time averaged MSDs through the simulation of multiple scenarios with fractional Brownian motion as a representative of a large class of fractional ergodic processes. We extract the precision and accuracy of the fitted MSD for various anomalous exponents and measurement errors with respect to measurement length and maximum time lags. Based on the calculated precision maps, we present guidelines to improve accuracy in single particle studies. Importantly, we find that in some experimental conditions, the time averaged MSD should not be used as an estimator.

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Continuous time random walks and their close relatives

Continuous time random walks (CTRW) are a popular model of anomalous diffusion. The model has a clear physical interpretation as an approximate description of trapping in high dimensions, and a clear mathematical structure as a process subordinated to simple random walks, and, in the corresponding limit, to Brownian motion. We discuss several models closely related to CTRW. Thus, we show that the scaled Brownian motion (sBm) as described by the Bachelor's equation (in the subdiffusive case) is a mean field (Gaussian) approximation of CTRW, and discuss the similarities and the differences between these models. Both models are non-stationary and share the same aging properties, but differ in the finer characteristics of their behavior. Thus the sBm is weakly ergodic [1] while CTRW shows weak ergodicity breaking. We moreover consider other situations corresponding to more general models of motion in random potentials [2] and to models subordinated to fractional Brownian motion [3]. In cases when the behavior can be described by subordination, we discuss which properties are dominated by the parent process and which ones (like the ergodicity breaking parameter) by the directing one.

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Less Typical Case of the Fractional Two-Power Laws of Relaxation: Modeling and Interpretation

We pay our attention to the dielectric susceptibility fitting the less typical relaxation responses derived from the limit theorems of probability theory and the subordination approach to anomalous diffusion. The link between the microscopic world of interacting components forming the relaxation system and macroscopic reaction responding to an external force field is provided through the internal structure evolution of random relaxation changes. They can be considered in two ways, either in time or in space. The space representation is convenient to formulate from relaxation rates of complex systems [1]. Another representation of relaxation is based on the analysis of subordinators, and therefore the scheme is called temporal [2]. As applied to the fractional two-power laws of relaxation, the key point plays a description of cluster and supercluster structures in the organization of component interactions during the process of relaxation. The origin in the appearance of clusters and superclusters is due to the self-similar dynamics of system components on micro, meso and macroscopic levels in the evolution of complex systems. For fixing the spatial structure of clusters in time, one can pass from the subordinated random processes to the Continuous Time Random Walk (CTRW) limit of random variables in one instance. Consequently, the subordination analysis of relaxation transforms into the description in relaxation rates [3]. The obtained results reinforce the physical significance of the empirical discovered forms of relaxation as well as integrate the method of random relaxation rates into the anomalous diffusion approach based on subordinators.

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From physical linear systems to discrete-time series. A guide for analysis of the sampled experimental data

Modelling physical data with linear discrete time series, namely Autoregressive Moving Average (ARMA), is a technique which achieved attention in recent years. In order to provide physical background of this model, we show that time series of this type can be regarded as sampled trajectories of the coordinates governed by system of linear stochastic differential equations with constant coefficients. We show concrete application of these results, analysing the recorded trajectories of the stochastic harmonic oscillator as ARMA time series. We provide exact form of the aliased power spectral density of these measurements, which previously had to be calculated numerically, and calculate ARMA parameters of the time series distorted by the video camera blur and additive noise.

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Time series methods in analysis of the optical tweezers

We show how treat recorded trajectories of the beads trapped in optical tweezers as discrete-time linear filters and analyse them using time series methods. Using this techniques we obtain simple analytical formula for the aliased power spectrum density. Moreover, we separate influences of the noise and blur induced by the video camera from the physical content of the measurements, providing simple tools to detect and account for these distortions.

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Scaling limits and numerical simulations of multidimensional Lévy walks

The model of Lévy walk (LW) was proposed for the first time by M.F. Shlesinger, J. Klafter and Y.M. Wong (1982). That model assumes that a walker trajectory consists of sum of jumps (or flights), which are characterized by a constant velocity within some heavy-tailed period of time. Moreover after every jumps the walker randomly changes the direction of next jump. Our analysis is based on a model which is very close to the one described above, but not exactly the same. Namely, it arises as a special class of continuous-time random walk (CTRW) which is generated by the sequence of iid heavy-tailed pairs of jumps and respective waiting times. A strong coupling introduced within every pair between the jump and the waiting time implies a finite second moment over whole trajectory [1]. In our work [1], [2] we analyze a multidimensional LW, which is a CTRW process generated by sequence of iid heavy-tailed pairs of jumps and respective waiting times, such that the length of every multidimensional jump is equal to the length of waiting time raised to some fixed positive real power γ . We investigate the detailed description of the scaling limit by means of their Levy triplet. Another part of our research is devoted to the fractional diffusion equations which governs the pdf of obtained scaling limits. Moreover, we discuss the possible anomalous diffusion regimes (superdiffusion, quasi-normal diffusion and subdiffusion) of the scaling limit, which may be obtained by proper choice of parameter γ . It worth be noticing that our asymptotical analysis of LW also includes its modification, in which every waiting time is proceeded by a jump leading to so-called ‘jump first’ or ‘jump-wait’ scenario (in contrary to ‘wait first’ or ‘wait-jump’ which arise naturally in CTRW model). The last part of our work describes the algorithm of simulating trajectories of the studied processes and present some Monte Carlo results.

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Fast methods for space-fractional PDEs and their analysis

Traditional second-order diffusion PDEs model Fickian diffusion processes, in which the particles follow Brownian motion. However, many diffusion processes were found to exhibit anomalous diffusion behavior, in which the probability density functions of the underlying particle motions are characterized by an algebraically decaying tail and so cannot be modeled properly by second-order diffusion PDEs. Fractional PDEs provide a powerful tool for modeling these problems, as the probability density functions of anomalous diffusion processes satisfy these equations.

Fractional PDEs present new difficulties that were not encountered in the context of integer-order PDEs. Computationally, the numerical methods for space-fractional PDEs generate dense matrices. Direct solvers were traditionally used, which require $O(N^3)$ computations per time step and $O(N^2)$ memory, where N is the number of unknowns.

Mathematical difficulties include the loss of coercivity of the Galerkin formulation for variable-coefficient problems, non-existence of the weak solution to inhomogeneous Dirichlet boundary-boundary value problems, and low regularity (the solution to homogeneous Dirichlet boundary-value problem of a one-dimensional fractional PDE with constant coefficient and source term is not in the Sobolev space H^1).

We present the recent developments of accurate and efficient numerical methods for space-fractional PDEs, which has optimal storage and almost linear computational complexity. We will also address mathematical issues such as well-posedness and regularity of the problems and their impact on the convergence behavior of numerical methods.

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Causes and consequences of diffusion heterogeneities and anomalies in biological fluids

Diffusion of macromolecules in crowded biological fluids is a key determinant of biochemical reactions. We had shown previously that the frequently observed subdiffusion of macromolecules in biological fluids shows signatures of a fractional Brownian motion, i.e. the crowded fluid appears to be viscoelastic [1], [2], [3]. In dividing cells the diffusion

anomaly even varies anisotropically, i.e. the degree of subdiffusion is significantly different along and perpendicular to the mitotic spindle [4].

Excluded-volume interactions with 'crowders' and an enhanced rebinding of reaction partners due to a crowding-induced viscoelasticity have been hypothesized to shift chemical equilibria towards the associated state. We have dissected these facets of crowding in an experimentally accessible system: Exploiting fluids with the same crowder and similar occupied volume fractions but different viscoelasticities, we predict and verify an increased fraction of closed DNA hairpins in crowded fluids that feature an anomalous diffusion [5], [6].

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Multiscale conservation laws driven by Lévy stable and Linnik diffusions: asymptotics, shock creation, preservation and dissolution

Some fractal conservation laws driven by Lévy α -stable diffusions exhibit shocks for bounded, odd, and convex on the positive half-line, initial data when the parameter $\alpha < 1$. For the Lévy α -Linnik diffusions the local behavior is strikingly different, although we are able to establish analytically that the large time behavior of the two types of conservation laws are similar. But the main new insights obtained via large-scale numerical experiments is that, for any $0 < \alpha \leq 2$, the conservation laws driven by α -Linnik diffusions display shocks that do not dissipate over time while those for α -stable diffusion ($0 < \alpha \leq 1$) do. (Joint work with B. Gunaratnam)

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Subordinated continuous-time autoregressive (CAR) processes with applications

We study properties of the continuous-time autoregressive (CAR) processes driven by α -stable Lévy motion delayed by inverse stable subordinator. Such processes can be applied to high-frequency data with visible jumps and co-called "trapping-events". Those properties are often observable in financial time series but also in technical data describing the rotational speed of a machine working under various load regimes or data related to indoor air quality. We concentrate on the main characteristics of the examined subordinated process expressed in the language of the measures of dependence which are main tools used in statistical investigation of real data. We calculate the codifference, which is the most general measure of dependence defined for wide class of processes. Moreover we present the simulation procedure of the considered system and indicate how to estimate its parameters. Theoretical results we illustrate by analysis of the simulated data.

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Meiotic chromosomes: Brownian bridges in an external field

Chromatin movement and structure are central to many processes in cells such as gene expression, DNA replication, mitosis, and meiosis. In fission yeast, a model organism of cell biology, the process of meiosis is marked by a phase of pronounced nuclear oscillations. It was suggested that these oscillations promote the alignment and facilitate recombination of homologous chromosomes. However, the physical mechanisms responsible for the alignment of chromosomes are still poorly understood. In this work, we use a physical model of polymer loops pulled through a viscous fluid to describe the statistics of chromosome alignment. We introduce an external force field to the Brownian bridge concept of random walks and derive the resulting statistics of loop configurations in space. For each point of the loop, average and variance of its position are determined by the location on the loop and the ratio of the pulling force to the intrinsic noise level. We can further

generalize the model by introducing additional constraints between the chromosomal loops corresponding to newly appearing recombination spots, or recombination independent interactions of the centromeric regions on DNA. By comparing the results of the model to the available experimental data we show that molecular motors driving the oscillations in yeast are capable to generate a pulling force sufficient to counterbalance fluctuations and align the chromosomes.

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Densities of Levy walks and the corresponding fractional equations

In this presentation we provide explicit formulas for the densities of Levy walks. Our results cover various types of these processes: jump-first, wait-first and continuous Levy walks. The obtained densities solve certain fractional differential equations involving fractional material derivative operators. To calculate the densities we use two different methods based on [1] and [2]. The results show perfect agreement with the Monte Carlo simulations.

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	Thursday, 14.05	Friday, 15.05	Saturday, 16.05
09:00-09:30	R. METZLER	E. BARKAI	T. FRANOSCH
09:30-10:00	K. BURNECKI	T. AKIMOTO	A. WYŁOMAŃSKA
10:00-10:30	T. ALA-NISSILA	A. AMIR	A. DECHANT
10:30-11:00	COFFEE	COFFEE	COFFEE
11:00-11:30	M. WEISS	G. KRAPF	W. WOYCZYNSKI
11:30-12:00	N. GOV	Y. ROICHMAN	H. WANG
12:00-12:30	G. KNELLER	H. LAPEYRE	B. DYBIEC
12:30-14:00	LUNCH	LUNCH	LUNCH
14:00-14:30	D. CALEBIRO	I. SOKOLOV	E. KEPTEN
14:30-15:00	J-B. MASSON	S. BUROV	G. SIKORA
15:00-15:30	E. COCUCCI	A. BANCAUD	J. SCHULZ
15:30-16:00	COFFEE	COFFEE	J. JANCZURA
16:00-16:30	Y. GARINI	M. RUBI	CLOSING
16:30-17:00	C. MANZO	J. ŚLĘZAK	
17:00-17:30	V. ZABURDAEV	E. CARLON	
18:30-21:00	RIVER CRUISE		