Scientific report

Search and Stochastic Phenomena in Complex Physical and Biological Systems

Organizers

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- Raul Toral Institute for Cross-Disciplinary Physics and Complex Systems Campus UIB, 07122 Palma de Mallorca, Spain.
- Horacio Wio Institute of Physics of Cantabria, University of Cantabria Av. Los Castros s/n 39005 Santander Spain.

Timeslot

from 28^{th} of May 2012 to 1^{st} of June 2012

Summary

The international workshop "Search and Stochastic Phenomena in Complex Physical and Biological Systems" was organized at the University of the Balearic Islands on the central subject of First Passage Time techniques and its application to understand stochastic phenomena, particularly the ones observed in biological and in small physical systems. The main objective was to create a lively and fruitful atmosphere of intensive research and mutual interactions between the participants. To this aim, each day of the workshop was structured in 9 talks of 40 minutes each, and contemplated a long break at lunch time and free time in the afternoon to ensure some time for free informal discussions. This workshop attracted 44 participants, among them world-leading experts in the field, as well as a reasonable number of PhD students and young researchers.

Scientific content

Search processes are ubiquitous among physical, chemical, and biological systems. Representative examples include diffusion-limited encounter of molecules involved in a chemical reaction; the dynamical or stochastic search for a global minimum in a complex energy landscape, relevant to systems such as glasses, protein (folding), and others; oil recovery from mature reservoirs; proteins searching for their specific target sites on DNA in gene regulation; transition rates of mechanochemical cycles of molecular motors; animal foraging; survival at the edge of extinction due to low availability of energetic resources; automated search of registers in high-capacity databases, search engines (e.g., "crawlers") that explore the internet, and even pizza delivery in a jammed traffic system of a medium-size town. In this way, the subject is interesting, challenging and inherently multidisciplinary, and has very recently become an important scientific area of investigation.

The search for a desired target may depend on a variety of conditions. Targets may be sparse, hidden, difficult to detect even when found. The targets may be mobile or immobile, they may try to avoid searchers, there may be one target or many. They may have a finite life-time and vanish before they are detected. Searchers may search "blindly", detecting the target only upon encounter, or may perceive distant targets and adjust their motion accordingly. They may have no memory of previously visited areas, or they may avoid such areas. The searchers may act individually or in swarms, optimizing their search efficiency by exchanging information. Finally, the "efficiency" of a search may be judged by a variety of measures, including the time to reach a target or targets, the number of encounters of searchers and targets per unit time, or the exploration range of space per unit time. In general, for each specific situation different search strategies may be appropriate. The quest for optimal strategies has motivated a great deal of work in the past and currently represents one of the most rapidly growing fields of research.

Although the applications are diverse, the underlying physical mechanisms are often the same. Moreover, the inherent complexity of the problem, the abundance of ideas and methods found in this interdisciplinary, innovative field of research is studied in many areas of physics. In particular, the concepts and methods of statistical mechanics are particularly useful to the study of random search. On the one hand, it centers on how to find the global or local maxima of search efficiency functions with incomplete information. This is, naturally, related to the long tradition in physics of using different conceptual and mathematical tools to optimize relevant quantities, e.g., energy, entropy, and action. Such ideas and approaches are very important to solve computationally complex problems involving optimizations in very high dimensional energy landscapes, e.g., in protein folding. On the other hand, random search can also be studied from the perspectives of diffusion and transport properties, stochastic processes, Lévy walks and flights, complex systems and fractal geometry. Some important questions in random search, especially in the case of discrete landscapes, are also associated with graph theory, random lattices, and complex networks.

The highly innovative character of the subject stems from a cross-fertilization of approaches, ideas and fruitful synergies between condensed matter and statistical physics,

quantitative biology and mathematics. In particular, analyzing the data gathered by biologists on the trajectories of lizards, fish, or birds searching for food, one introduces random search strategies, based either on Lévy-type or on intermittent random motion, (in which slow search phases alternate with fast relocations), which explore most of the available space within a minimal time, with minimal oversampling and having the best chances of success. As one important outcome, one may introduce more efficient computer algorithms for the search for global minima in non convex (multiple extrema) energy landscapes by simulated annealing it appears that a random search with Lévy-type jump-length distributions allows for a faster cooling scheme, and hence, for a considerable reduction of computer time, than standard algorithms (Boltzmann machine) based on a nearest-neighbor exploration. An observation that in reality a protein finds a specific binding site on a DNA 103 times faster than it is predicted by conventional chemical kinetics, prompted a very deep understanding of the role of non-specific parts of the DNA. Being inert with respect to the reaction, they act as very efficient antennae reducing the overall search time, essentially in the same way as cell bound glycoproteins, extending in the extracellular medium, enhance the efficiency of chemoreception by capturing the ligands and facilitating their transport to the cell bound receptors. Indeed, finding the target in a finite amount of time is of fundamental importance for many biological processes in the cell, in particular for protein diffusion along DNA. In vivo biological cells are characterized by a high degree of molecular crowding and under some conditions, by an inhomogeneous environment, affecting not only the way proteins and biological molecular motors carrying them move, but perhaps even the internal functioning of the molecular motor and its efficiency. For this the stochastic aspects of thermodynamics of such systems are of particular interest for the experimentalists, due to the recent advance in the technologies of manipulating systems at nano and micro scales.

The scientific program was centered around these modern developments in statistical physics and covered a broad spectrum of topics ranging from fundamental questions to application of statistical methods to the modelling of small biological and physical systems. Among the main topics covered during the five days of the conference included cell kinetics, DNA dynamics active and passive search strategies and foraging, molecular motors and nano-engines, single-molecule experiments, fractional diffusion.

The workshop was organized in 35 talks of 40 minutes plus 4 short talks of 20 minutes, presented by some of the junior participants. The total number of participants was 44 and, as the number show, almost everyone was able to present their research. Special emphasis was given to informal discussions and working group meetings and for this, the schedule of the workshop was structured in order to have some free time periods. This lively exchange between the participants as well as the possibility to immediately work out new ideas in some detail was supported by the pleasant environment of the University of the Balearic Islands. During the workshop, the UBI offered free wi-fi internet access to all of the participants and reserved a large conference room with all the necessary equipment for the realization of the workshop. It is worthwhile mentioning that also younger colleagues were involved and actively participating in the informal discussions, allowing them to discuss their research to the experts in the field and obtain important feedback.

Assessment of the results

We think that this meeting was very fruitful and successful. The presentations covered a wide spectrum of topics in the physics of small biological and physical systems. Concerning the quality of presentation and of the scientific work, the overwhelming majority of the contributions were well beyond the "average" one is used to from other workshops. Therefore, the participants could gain a comprehensive overview of the state-of-the-art in the field as well as learn about the new developments on first-passage times techniques, and more importantly on recent experimental research.

Everyone participated enthusiastically during the lectures presented and in informal working discussions. We have found that most of the participants were positive concerning the free allocated time for such discussions. As a matter of fact, after the conclusion of the workshop we received very positive and enthusiastic evaluations from most of the participants. Many of them referred to this workshop as "very interesting and pleasant", as "with a very good balanced topics". Moreover, during the workshop it was mentioned that open problems could be solved as a result from the interaction between participants, and that new collaborations were initiated.

This workshop was a good opportunity for the local community of Spanish researchers in the area of stochastic processes and first-passage time, to strength existing collaboration and create new ones with other European and non European research groups.

Projecting the responses of the participants, we expect that a few research articles will be published as a direct outcome of this meeting.

Last, we would like to mention that the success of this workshop has motivated other colleagues to organize future workshops in this subject. In particular we may mention a workshop on "Search and Exploration" to be held in 2013 in the Island of Cargese, France.

Remarks on the budget

The funding sources supporting the realization of this workshop were:

- The European Science Foundation (ESF) through the research networking programme "Exploring the Physics of Small Devices".
- The EU IRSES programme FP7-PEOPLE-2010-IRSES 269139 DCP-PhysBio "Dynamics and Cooperative Phenomena in Complex Physical and Biological Media", in association with the Laboratory J-V Poncelet CNRS and the Independent University of Moscow.
- The University of the Balearic Islands (UBI).
- The Institute for Cross-Disciplinary Physics and Complex Systems (IFISC).

Economic support was obtained from

ESF	10000 EUR
UBI	3000 EUR
EU IRSES	5600 EUR
Registration fee from non invited participants	$1440 \ \mathrm{EUR}$

In addition to this, the IFISC provided each participant with office supplies such as notebooks, pens, folders and organized the identity badges. The UBI also supported the workshop by offering internet access and the seminar room facilities for free. Also, the workshop attracted 8 non invited participants, to whom we asked to pay a small registration fee of 180 EUR.

The funds from ESF and IRSES was used to cover totally or partially the accommodation expenses of most of the participants, and in few cases, we have covered or contributed to the their travel expenses. The travel and living expenses were totally covered with the workshop funding, except for Marcela Reale from Argentina to whom we only covered her living expenses. The lunch was organized in the main cafeteria of the UBI and it was covered with the workshop funds. The funds from UBI and from registration fees were used to cover a social dinner and the coffee breaks.

Appendix A: Program of the meeting

The programme of the workshop is annexed at the end of this report.

Appendix B: List of participants

The full list of participants is annexed at the end of this report.

The Scientific Organizers

Carlos Mejia-Monasterio, Raul Toral and Horacio Wio

IFISC, Palma de Mallorca, May 28 – June 1, 2012

Programme and book of abstracts

Scientific coordination:

Carlos Mejia-Monasterio, Technical University of Madrid, Spain Raúl Toral, IFISC (CSIC-UIB), Palma de Mallorca, Spain Horacio Wio, University of Cantabria, Santander, Spain

Secretary:

Marta Ozonas, IFISC (CSIC-UIB)



Instituto de Física Interdisciplinar y Sistemas Complejos

PROGRAMME:

	Мо	nday	Tuesday	Wed	nesday	Thursday	Friday
9:00 - 9:40	8:30 - 9:30 9:30 - 9:40	Registration Welcome	Benichou	Lind	enberg	Ritort	Viot
9:40 – 10:20	C	Cox	Parmeggiani	Lomholt		Kafri	Imparato
10:20 - 11:00	D	ean	Kolomeiski	Campos		Oddershede	Parrondo
11:00 – 11:30	coffe	e break	coffee break	coffee break		coffee break	coffee break
11:30 – 12:10	Diaz-	Guilera	Cleuren	Horowitz		Mattos	Martinez-Mekler
12:10 – 12:50	Eli	iazar	Sancho	12:10 - 12:30 12:30 - 12:50	Duque Martinez Garcia	San Miguel	Hernández-García
12:50 – 15:00	lu	ınch	lunch	12:50 - 13:10 13:10 - 13:30	Reale Lafuerza	lunch	lunch
15:00 – 15:40	A	bad	Majumdar	Lunch & free afternoon		Jardat	Newby
15:40 – 16:20	Casa	demunt	Larralde			Boyer	Lopez
16:20 – 17:00	Me	etzler	Oshanin			Talbot	Esposito
17:00 – 17:30	coffe	ee end	coffee end			coffee end	closing remarks
20:30				Social Dinner			

FINANTIAL SUPPORT:







EU IRSES programme FP7-PEOPLE-2010-IRSES 269139 DCP-PhysBio / Dynamics and Cooperative Phenomena in Complex Physical and Biological Media /



In association with Laboratory J-V Poncelet CNRS & Independent University of Moscow



Palma de Mallorca, May 28 - June 1, 2012

WIFI network guide for the meeting

 1. Connect to the WiFi (or SSID) "uib" network.

 2. Activate the dynamic IP configuration (DHCP). It's very usual to have dynamic configuration set on the wireless interfaces. Typically it won't be necessary to perform this step.

 3. Open a web browser and try to access a website. Insert the following credentials in the web page that will appear:

 Username
 Password

 search
 uib2012

WIFI network guide for EDUROAM users

Participants coming from an institution that belongs to the Eduroam program can connect to the "eduroam" wireless network using the credentials (username/password) served by the foreign institution.

Note:

• The connection to the "uib" and "eduroam" wireless networks can be established from anywhere in the UIB campus.

Terms and conditions of use of the WiFi user account:

- Anyone using the account must be somehow related to the "Search and Stochastic Phenomena in Complex Physical and Biological Systems" meeting.
- The organization (Search and Stochastic Phenomena in Complex Physical and Biological Systems) is responsible for any action taken from this service with this user account.
- The wrong usage of the network service will cause the definitive deactivation of the account in addition to the corresponding measures taken by the Universitat de les Illes Balears.



Contributions

Enrique Abad, Santos Bravo Yuste, Katja Lindenberg Departamento de Física Aplicada, Universidad de Extremadura, Badajoz, Spain

Survival probability of a target in a sea of moving traps: incorporating subdiffusion and death processes via fractional equations

In this contribution we deal with a number of target search problems of possible relevance in a wide variety of situations (predator-prey models, animal foraging, etc.). Our starting point is the CTRW model with a long-tailed waiting time distribution and a jump length distribution with finite variance. In the appropriate limit, this model is known to yield a macroscopic integrodifferential equation for the probability density for a particle to be found at a certain position r after a time t. This equation contains a so-called Riemann-Liouville fractional derivative and can be shown to yield subdiffusive behavior on long time scales. If one allows for the possibility that the walker undergoes an spontaneous death process governed by time-dependent rate constant (evanescence), the CTRW equations can be accordingly modified so as to yield a generalized fractional equation (GFE) accounting both for transport and reaction [1]. The GFE differs significantly from its counterpart for classical diffusion, since the reaction rate constant also appears in the transport term. However, it can be reduced to a pure transport equation via a suitable variable transformation.

We apply the GFE to compute the survival probability (SP) of an immobile target immersed in a d-dimensional sea of evanescent, fully absorbing traps which move subdiffusively. The ongoing death processes change the behavior of the SP dramatically, i.e., in any spatial dimension d the target is annihilated with certainty if the traps do not evanesce, but it survives with a finite probability if the decay law for the trap density is sufficiently fast. The situation becomes more complex when the target is also allowed to move diffusively or subdiffusively [2,3]. Time permitting, we shall also discuss this setting, thereby restricting ourselves to the case of non-evanescent subdiffusive traps.

[1] E. Abad, S. B. Yuste, and K. Lindenberg, Reaction-subdiffusion and reaction-superdiffusion equations for evanescent particles performing continuous-time random walks, Phys. Rev. E 81, 031115 (2010).

[2] Reactions in Subdiffusive Media and Associated Fractional Equations, S. B. Yuste, E. Abad, and K. Lindenberg, in Fractional Dynamics: Recent Advances, ed. by S. C. Lim, J. Klafter, and R. Metzler (World Scientific, Singapore, 2011).

[3] R. Borrego, E. Abad, and S. B. Yuste, Survival probability of a subdiffusive particle in a d-dimensional sea of mobile traps, Phys. Rev. E 80, 061121 (2009).

Olivier Benichou CNRS, Paris, France

First-passage times of diffusion processes and Geometry-controlled kinetics

It has long been appreciated that transport properties can control reaction kinetics. This effect can be characterized by the time it takes a diffusing molecule to reach a target - the first-passage time (FPT). We will present a method of determination of the statistics of the FPT in confined geometries, and show that transport processes as various as regular diffusion, anomalous diffusion, diffusion in disordered media and in fractals fall into the same universality classes. Beyond this theoretical aspect, this result could have potential impact on standard reaction kinetics. More precisely, we argue that geometry can become a key parameter so far ignored in this context, and introduce the concept of "geometry-controlled kinetics". These findings could help understand the crucial role of spatial organization of genes in transcription kinetics, and more generally the impact of geometry on diffusion-limited reactions.

Denis Boyer, Meg Crofoot, Peter Walsh, Vian Gomez Universidad Nacional Autonoma de Mexico, Mexico City, Mexico

Individual displacements of animals and humans: between order and randomness

Individual displacements within populations have a strong impact on large scale phenomena such as the spread of epidemics or the diffusion of cultural traits. The availability of quantitative individual movement data has increased in recent years through the widespread use of GPSs on foraging animals and, in the case of humans, the ability to track cell phones. Whereas they look like L\'evy walks at short times, human displacements are not well described by Markovian processes. Instead, trajectories asymptotically exhibit ultra-slow diffusion as well as unusual scaling laws in their recurrent properties, resulting from the tendency of individuals to revisit more frequently a small number of familiar locations. We observe similar features in non-human primates and other animal species in the wild, suggesting that strongly recurrent movements are generic and possibly the outcome of efficient search processes in disordered environments. We further study the emergence of home ranges and heterogeneous visitation patterns in a search model with learning and memory use.

Daniel Campos, Vicenç Méndez, Frederic Bartumeus Universitat Autònoma de Barcelona, Barcelona, Spain

Velocity, intermittence and perception: new insights into search processes

Random search theory has been previously explored for both continuous and intermittent scanning modes with full target detection capacity. Recently we have explored a new class of random search problems in which a single searcher performs flights of random velocities, the detection probability when it passes over a target location being conditioned to the searcher speed. Starting from this case, in the present contribution we plan to discuss the influence and advantages that velocity models offer over other approaches on this field. The emphasis will be put in showing that microscopic differences between velocity and jump or diffusion models can influence the mean search time to detect the target.

The consequences of including non-perfect detection performance (perception) will be also sketched. As a result of this new effect, detection involves an N-passage process for which the mean search time can be analytically obtained through a renewal approximation. This can be directly used to study random animal foraging since a fast movement is known to significantly degrade perception abilities in many animals. We show that perception allows us to introduce naturally the idea of intermittent motion (which is recurrently observed in nature) as a solution to the compromise between fast relocations and target detection capability.

Jaume Casademunt, David Oriola University of Barcelona, Barcelona, Spain

Dwell time and mechanics: the paradoxical Brownian motor KIF1A

Monomeric kinesin (KIF1A) is a motor protein that is driven by a ratchet mechanism and is specific for some of the most demanding tasks in intracellular traffic: transport of very large vesicles along very long distances in neuron axons, a type of traffic that is critical for neuron functioning and whose deficits are associated to neurodegenerative diseases. Paradoxically, this molecular motor is extremely inefficient when compared to conventional (dimeric) kinesin (KIF5), ubiquitous in ordinary intracellular traffic. Recently, it has been shown that, in transport of soft cargoes like vesicles, the Brownian ratchet mechanism is particularly well adapted to cooperative action. The high cooperativity of KIF1A has thus been proposed to solve the above paradox. Here we show that, in particular, the existence of a dwell time in the motor cycle plays a

crucial role in improving the noise-rectification of the ratchet mechanism thus giving rise to a giant increase of the collective stall force. In fact, while the stall force of an individual KIF1A molecule is around 50 times smaller than that of KIF5, a group of 10-15 KIF1A's outperforms a group of any number of KIF5's. Moreover, self-organized groups of KIF1A can eventually overcome any arbitrary force by recruiting more motors, a feature that is not possible with conventional kinesin.

Bart Cleuren, Bob Rutten, Massimiliano Esposito, Christian Van den Broeck Hasselt University, Diepenbeek, Belgium

Energy conversion in small engines

Improving the efficiency of energy conversion has been a long-time challenge. With the advent of nano-scale machines and recent theoretical developments, new aspects have emerged. In this talk I will present a number of small-scale machines and discuss universal features of their efficiency at maximum power output.

[1] B. Rutten, M. Esposito, B. Cleuren, "Reaching optimal efficiencies using nano-sized photoelectric devices", Phys. Rev. B 80, 235122 (2009)

[2] B. Cleuren, B. Rutten, C. Van den Broeck, "Cooling by Heating: Refrigeration Powered by Photons", Phys. Rev. Lett. 108, 120603 (2012)

Edward Cox, Tom Kuhlman Princeton University, Princeton, USA

How transcription factors find their targets

The diffusion of the canonical transcription factor LacI within living Escherichia coli has been measured directly by in vivo live tracking to be characterized by a diffusion coefficient of $D = 0.4 \mu m2/s$. At this rate, LacI can diffuse from one end of E. coli to the other in 1-10 seconds, and simple models of diffusion lead to the expectation that LacI and other proteins will rapidly homogenize throughout the cell. Here we test this expectation of spatial homogeneity by single molecule visualization of LacI molecules non-specifically bound to DNA in fixed cells. Contrary to expectation, we find that the distribution depends on the spatial location of its encoding gene.

Furthermore, we demonstrate that the spatial distribution of LacI is also determined by the local state of DNA compaction, and that E. coli can dynamically redistribute proteins by modifying the state of its nucleoid. We propose a model for intranucleoid diffusion which can reconcile these results with previous measurements of LacI diffusion, and we discuss the implications of these findings for gene regulation in bacteria and eukaryotes

David Dean Dean, Vincent Demery Universite de Bordeaux, Bordeaux

Diffusion in fluctuating fields

We study the effective diffusion constant of a Brownian particle linearly coupled to a thermally fluctuating scalar field. We use a path integral method to compute the effective diffusion coefficient perturbatively to lowest order in the coupling constant. This method can be applied to cases where the field is affected by the particle (an active tracer), and cases where the tracer is passive. Our results are applicable to a wide range of physical problems, from a protein diffusing in a membrane to the dispersion of a passive tracer in a random potential. In the case of passive diffusion in a scalar field, we show that the coupling to the field can, in some cases, speed up the diffusion corresponding to a form of stochastic resonance. Our results on passive diffusion are also confirmed via a perturbative calculation of the probability density function of the particle in a Fokker-Planck formulation of the problem. Numerical simulations on simplified systems corroborate our results.

Albert Diaz-Guilera, Luce PRignano Universitat de Barcelona, Barcelona, Spain

Exploring complex networks by means of adaptive walkers

Finding efficient algorithms to explore large networks with the aim of recovering information about their structure is an open problem. Here, we investigate this challenge by proposing a model in which random walkers with previously assigned home nodes navigate through the network during a fixed amount of time. We consider that the exploration is successful if the walker gets the information gathered back home, otherwise, no data is retrieved. Consequently, at each time step, the walkers, with some probability, have the choice to either go backward approaching their home or go farther away. We show that there is an optimal solution to this

problem in terms of the average information retrieved and the degree of the home nodes and design an adaptive strategy based on the behavior of the random walker. Finally, we compare different strategies that emerge from the model in the context of network reconstruction. Our results could be useful for the discovery of unknown connections in large scale networks.

Juan Ramón Duque Rodríguez, Carlos Mejía-Monasterio, David Gómez-Ullate Universidad Poltécnica de Madrid, Madrid

First passages in olfactory search with spatial and temporal constraints

We study numerically the robustness and effectiveness of different olfactory search strategies in terms of the probability distribution of search times.

In particular, we look into the problem of spatially and temporally correlated infotaxis in two dimensions, in which an agent is forced to perform its walk on a proper subset of the search space or in conditions of partial gain of information (the agent is not able to gather information for a certain time interval following each detection). The spatial constraints are simulated by a lattice with frustration, while the errors committed in sensing occur randomly with probability p.

Iddo Eliazar, Joseph Klafter Holon Institute of Technology, Holon, Israel

Randomized Central Limit Theorems

The Central Limit Theorems (CLTs) characterize the macroscopic statistical behavior of large ensembles of independent and identically distributed random variables. The CLTs assert that the universal probability laws governing ensembles' aggregate-statistics are either Gaussian or Lévy, and that the universal probability laws governing ensembles' extreme-statistics are either Fréchet, Weibull or Gumbel. The scaling schemes underlying the CLTs are deterministic -- scaling all ensemble-components by a common deterministic scale. However, there are "random environment" settings in which the underlying scaling schemes are stochastic -- scaling the ensemble-components by different random scales. Examples of such settings include Holtsmark's law for gravitational fields, and the Stretched Exponential law for relaxation times. In this talk we establish a unified theory of Randomized Central Limit Theorems (RCLTs) -- in which the deterministic CLT scaling schemes are replaced by stochastic scaling schemes -- and present "randomized counterparts" to the classic CLTs. The RCLT scaling schemes are shown to be governed by Poisson processes with power-law statistics, and the RCLTs are shown to

universally yield the Lévy, Fréchet and Weibull probability laws.

Massimiliano Esposito

University of Luxembourg, Luxembourg

Stochastic thermodynamics: A powerful tool to control small systems

Small systems are often subjected to strong fluctuations and can easily be driven far from equilibrium. My aim is to show that stochastic thermodynamics is a powerful theory that can help us better understand how to manipulate and control small systems in an efficient way. I will discuss in particular how a stochastic driving or a feedback control can be used to make small systems, such as single level quantum dots, operate as efficient thermodynamic machines.

[1] M. Esposito, "Stochastic thermodynamics under coarse-graining", Phys. Rev. E 85, 041125 (2012)

[2] M. Esposito, N. Kumar, K. Lindenberg and C. Van den Broeck, "Stochastically driven single level quantum dot: a nano-scalefinite-time thermodynamic machine and its various operational modes", Phys. Rev. E 85, 031117 (2012)

[3] M. Esposito and G. Schaller, "Stochastic thermodynamics for 'Maxwell demon' feedbacks", arxiv:1204.5671

Emilio Hernandez-Garcia, E. Tew Kai, V. Rossi, J. Sudre, H. Weimerskirch, C. Lopez, F. Marsac, V. Garçon IFISC (CSIC-UIB), Palma de Mallorca, Spain

Following the line: Marine birds fly on top of ocean coherent structures

Statistical properties of animal displacements have been usually interpreted as consequences of purely random process or of efficient search strategies. Here we point out the importance of environmental heterogeneity by showing, from combined oceanographic and ecological datasets on the Mozambique channel, that frigatebirds fly on top of ocean structures known as Lagrangian Coherent Structures. These are the edges of ocean eddies or, more generally, stable or unstable manifolds of hyperbolic locations in the sea surface flow. These structures are located from a finite-size Lyapunov exponent analysis of sea surface velocities, as measured by satellite altimetry. Our findings imply that the strong intermittency of the physical medium in which the

birds and their prey live strongly constrains animal behavior, with implications on optimality of search processes.

Todd Horowitz

Brigham & Women's Hospital, Harvard Medical School, Cambridge, MA

Exit strategies: Quitting time problems in visual search

Visual search is a ubiquitous cognitive task performed by humans hundreds of times each day. You search for your keys on your desk, or a ripe tomato in the market. Socially-critical visual search tasks include search for threats in luggage or tumors in mammograms. A major theoretical problem in visual search is understanding quitting times. In tasks where the target is always present, the answer is simple: find the target and then quit. However, in many laboratory search tasks, a single target is present on 50% of trials (i.e., 50% prevalence). Classical theories of visual search assumed sampling without replacement, which meant that observers should quit when they found the target, and search the display exhaustively otherwise. Work from my lab and others has demonstrated that this assumption is likely to be false; search without replacement is slow and difficult, and the visual system tends to favor a faster but more random sampling strategy. Under these circumstances, deciding when to quit becomes more difficult. An additional complicating factor is target prevalence. I will discuss research demonstrating that when target prevalence is low (e.g., 2%), observers are more likely to miss targets. This is an important phenomenon in both practical and theoretical terms, because low prevalence is characteristic of socially-critical search tasks. Finally, I will report ongoing research into visual foraging in contexts with many targets but limited time and resources.

Alberto Imparato, N. Golubeva, L. Peliti Aarhus University, Denmark

Efficiency of molecular machines with continuous phase space

We consider a molecular machine described as a Brownian particle diffusing in a tilted periodic potential. We evaluate the absorbed and released power of the machine as a function of the applied molecular and chemical forces, by using the fact that the times for completing a cycle in the forward and the backward direction have the same distribution, and that the ratio of the corresponding splitting probabilities can be simply expressed as a function of the applied force. We explicitly evaluate the efficiency at maximum power for a simple sawtooth potential. We also obtain the efficiency at maximum power for a broad class of 2-D models of a Brownian machine and find that loosely coupled machines operate with a smaller efficiency at maximum power than their strongly coupled counterparts.

Marie Jardat University Pierre et Marie Curie, Paris, France

Diffusion with electrostatic interactions from numerical simulations

Long-range electrostatic interactions have a strong influence on the diffusion properties in bulk and in disordered charged porous media. Firstly, I will focus on the dynamics of DNA-binding proteins and address the following question: Why are proteins able to perform a one dimensional diffusion along DNA ? We have computed from Monte Carlo simulations the effective nonspecific interaction potential between model DNA and model proteins, and have shown that a counterintuitive repulsion between the two oppositely charged macromolecules exists at a nanometer range. For the concave shape of DNA binding proteins, and for realistic protein charge densities, the DNA-protein interaction free energy has a minimum at a finite surface-to-surface separation, in which proteins can easily slide. Secondly, I will focus on the diffusion in modeled charged nanoporous media. We have used Brownian dynamics simulations to compute the self-diffusion coefficients of ions in the presence of charged obstacles. For a dilute concentration of charged obstacles, counterions are on average slower than co-ions because part of them is strongly attracted to the obstacles. In the opposite case of high concentration of obstacles, counterions can hop from one obstacle to another and increase their diffusion coef?cient in comparison with the co-ions. The latter are, namely, trapped in the crowded region between the obstacles.

Yariv Kafri

Technion, Haifa, Israel

Classes of fast and specific search mechanisms for proteins on DNA

Problems of search and recognition appear over different scales in biological systems. The talk will focus on the challenges posed by interactions between proteins, in particular transcription factors, and DNA and possible mechanisms which allow for a fast and selective target location. Initially it will be argued that DNA-binding proteins can be classified, broadly, into three distinct

classes which we illustrate using experimental data. The classification is directly related to the binding energy landscape of the proteins to the DNA. Each class calls for a different search process and we discuss the possible application of different search mechanisms proposed over the years to each class. Time permitting I will also discuss a new barrier controlled search mechanism as well as the non-trivial influence of the binding energy landscape on the Hill coefficient of transcription factors.

Anatoly Kolomeisky, Alex Veksler Rice University, Department of Chemistry, Houston, Texas, USA

Mechanism of Fast Protein Search for Targets on DNA: Strong Coupling between 1D and 3D Motions

One of the most critical aspects of protein functioning in cells is the ability of protein molecules to quickly find and recognize specific targets on DNA. Kinetic measurements indicate that in many cases the corresponding association rates are surprisingly large. For some proteins they might be even larger than maximal allowed 3D diffusion rates, and these observations stimulated strong debates about possible mechanisms. Current experimental and theoretical studies suggest that the search process is a complex combination of 3D and 1D motions. Although significant progress in understanding protein search and recognition of targets on DNA has been achieved, detailed mechanisms of these processes are still not well understood. The most surprising observation is that proteins spend most of the search time being non-specifically bound on DNA where they supposedly move very slowly, but still the overall search is very fast. Here we propose a possible mechanism that might explain fast protein search for targets on DNA. Using exact calculations by analyzing first passage distributions, it is shown that strong coupling between 3D and 1D motions accelerate the search. The coupling behaves as an effective potential that drives the search of the protein molecules that are non-specifically bound to DNA. Our theoretical analysis is supported by Monte Carlo computer simulations. Physical-chemical aspects of the mechanism are also discussed.

> **Luis F. Lafuerza**, Raul Toral IFISC (CSIC-UIB), Palma de Mallorca, Spain

Collective fluctuations in systems of non-identical random walkers

We consider a population of non-identical random walkers. We are interested in the

distribution of the number of walkers occupying a given site and how it depends on the degree of heterogeneity in the population. We show that the fluctuations of this occupation number may increase or decrease with the heterogeneity, depending on the specific form of the system. For independent walkers, heterogeneity in the preference for the site decreases the variability of the occupation number of this site. We show how fluctuations in a collective variable give information about the degree of heterogeneity in the system. We develope a systematic approximation method to analytically study systems of stochastic heterogeneous particles.

Hernán Larralde Instituto de Ciencias Físicas, UNAM, Cuernavaca, México

On the number of distinct sites visited over the last 25 years.

In this talk I intend to present a short survey of some of the results on the statistics of the number of distinct sites visited by random walkers, that have been discussed in the literature over the last 25 years or so. These results will be presented in their relation to searching and trapping problems, in connection to various notions of "searching efficiency". Finally, some unstudied extensions and variations of these problems will be also be discussed.

Katja Lindenberg, S. I. Denisov, S. B. Yuste, Yu. S. Bystrik, H. Kantz University of California, San Diego, La Jolla, CA, USA

Continuous-time random walks with superheavy-tailed waiting time and heavy-tailed jump length distributions

We study the long-time behavior of decoupled continuous-time random walks characterized by superheavy-tailed distributions of waiting times and symmetric heavy-tailed distributions of jump lengths. Our quantity of principal interest is the limiting probability density of the position of the walker multiplied by a scaling function of time. We show that the probability density of the scaled walker position converges in the long-time limit to a non-degenerate density only if the scaling function behaves in a certain way. This function as well as the limiting probability density are determined in explicit form. Also, we express the limiting probability density which has heavy tails in terms of the Fox H-function and find its behavior for small and large distances. **Michael Lomholt**, Leila E. Sereshki Ralf Metzler University of Southern Denmark, Odense, Denmark

The subfacilitated diffusion of the restriction enzyme EcoRV

The restriction enzyme EcoRV searches for its specific target on DNA via facilitated diffusion exploiting a combination of 1D sliding along DNA and 3D bulk diffusion. This has been demonstrated in several experiments. However, in vitro measurements of the overall search time of EcoRV give results that are much smaller than the predictions of standard models for facilitated diffusion. The discrepancy can be explained by EcoRV having an inactive state. But this seems to introduce a paradox, since the survival of E. coli bacteria depends on the efficiency of the EcoRV target search. In this talk I will explain how this paradox can be resolved under in vivo conditions, and how the inactive state turns out to be an advantage under conditions leading to subdiffusion.

Cristóbal López, E. Heinsalu, E. Hernández-García. IFISC, Palma de Mallorca, Spain

Competitive Brownian and Levy walkers

Population dynamics of individuals undergoing birth and death and diffusing by short or long ranged two-dimensional spatial excursions (Gaussian jumps or Levy flights) is studied. Competitive interactions are considered in a global case, in which birth and death rates are influenced by all individuals in the system, and in a nonlocal but finite-range case in which interaction affects individuals in a neighborhood. The conditions for the clustering of organisms are analyzed.

Satya Majumdar, Martin R. Evans CNRS (France), Universite Paris-Sud (Orsay), Orsay, Paris South, France

Diffusive search by stochastic resetting

We study simple diffusion where a particle stochastically resets to its initial position at a constant rate r. A finite resetting rate leads to a nonequilibrium stationary state with non-Gaussian fluctuations for the particle position. We also show that the mean time to find a stationary target by a diffusive searcher is finite and has a minimum value at an optimal resetting rate r^* . Resetting also alters fundamentally the late time decay of the survival probability of a stationary target when there are multiple searchers: while the *typical* survival probability decays exponentially with time, the *average* decays as a power law with an exponent depending continuously on the density of searchers.

Ricardo Martinez Garcia, Cristobal Lopez IFISC (CSIC-UIB), Palma de Mallorca, Spain.

A nonlocal spatial model for savannas.

Savannas are very important ecosystems mainly characterized by a long time coexistence between a continuous grass layer and dispersal clusters of trees.

We propose a stochastic nonlocal macroscopic equation to model savannas which takes into account two of the factors that are thought to be crucial to structure semiarid savannas: tree-tree competition and fire [1].

We study the spatial structures in the model, and the impact of fluctuations (demographic and environmental) on them. The phase transition from an active phase where grass and trees coexist, to an absorbing one, characterized by the absence of trees, is also analyzed in detail [2].

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[2] R. Martinez-Garcia, C. Lopez, in preparation.

Gustavo Martinez-Mekler, J. Espinal, A. Guerrero, M. Aldana, R. Verduzco, J. Carneiro, C. Wood, A. Darszon. Instituto de Ciencias Fisicas, UNAM, Cuernavaca, Mexico

Chemotaxis in Sea Urchin Fertilization

Fertilization is a fundamental process of life in which the spermatozoon must find its female

gamete partner. This requires that the spermatozoon be motile and endowed with swimming strategies to locate the oocyte. Chemotaxis is an exploration mechanism governed by a gradient of chemical signals released by the egg. We look into the behavior of the sperms of two sea urchin species for which the binding to the flagellum of an oocyte secretion (speract), triggers Ca^2 + concentration fluctuations that reorient their swimming. In one of these cases chemotaxis is encountered, in the other it is absent. In previous work we implemented a logical network model for these fluctuations, which recovered experimental observations and predicted new phenomenology, subsequently corroborated in our laboratory. In recent experimental work, our group showed that the interplay between the signaling network and the external speract gradients produces a marked difference in the Ca^2 + oscillations, depending on whether the sperm is swimming up or down the gradient. Here we summarize these experimental results and study with our model the operation of drugs that disorient sperm navigation. We also further develop our model by coupling spatially the former networks. With this module oriented, spatio-termporal dynamics, we analyze the hypothesis that density of receptors may be a feature that determines the transition from the absence of chemotaxis to its presence in spatial exploration.

Thiago Mattos, Carlos Mejía-Monasterio, Ralf Metzler, Gleb Oshanin Max-Planck Institute for Intelligent Systems, Stuttgart, Germany

First passages in bounded domains: When mean are meaningful?

We study the statistics of the first passages to adsorbing boundaries for a Brownian motion in bounded two-dimensional domains of different shapes and with different configurations of the adsorbing and reflecting boundaries. To highlight the role of the sample-to-sample fluctuations and to quantify the effective broadness of the first passage time distribution we focus on the distribution $P(\omega)$ of the random variable $\omega = \tau_1/(\tau_1 + \tau_2)$, where τ_1 and τ_2 are the times of the first passage to an adsorbing boundary of two different realizations of the Brownian motion trajectories commencing at the same starting point. Evidently, ω probes the likelihood of the event that both trajectories arrive to the adsorbing boundary simultaneously. We realize that, strikingly, the very shape of this distribution - either a unimodal bell-shaped function with a maximum at $\omega = 1/2$ or a bimodal, *M*-shaped function with two maxima close to 0 and 1 and a local minimum at $\omega = 1/2$, - depends crucially on the location of the starting point. Evidently, for the former case the sample-to-sample fluctuations are not very significant and the mean first passage time (MFPT) is a plausible characteristic of the actual behavior, while in the latter case it is meaningless. For each bounded domain, we present a "phase-diagram" for $P(\omega)$ showing the regions in which the distribution has an *M*-shaped and a unimodal bell-shaped forms. Ralf Metzler, Johannes Schulz, Jae-Hyung Jeon, Eli Barkai U Potsdam, Potsdam, Germany

Ageing and ergodicity breaking in anomalous diffusion

In 1905 Einstein formulated the laws of diffusion, and in 1908 Perrin published his Nobel-prize winning studies determining Avogadro's number from diffusion measurements. With similar, more refined techniques the diffusion behaviour in complex systems such as the motion of tracer particles in living biological cells or the tracking of animals and humans is nowadays measured with high precision. Often the diffusion turns out to deviate from Einstein's laws. This talk will discuss the basic mechanisms leading to such anomalous diffusion as well as point out its consequences. In particular the unconventional behaviour of non-ergodic, ageing systems will be discussed within the framework of continuous time random walks. Indeed, non-ergodic diffusion in the cytoplasm of living cells as well as in membranes has recently been demonstrated experimentally.

Jay Newby, Paul Bressloff University of Oxford, Oxford, UK

Population model of unidirectional random intermittent search

I will discuss recent work on directed intermittent search by multiple searchers for a single hidden target. The simplest model is the unidirectional search, where each searcher switches between a single constant velocity moving state and an immobile searching state. I will show results (exact in most cases) for two different scenarios motivated by molecular motor transport in the axon of a neuron. In particular, I will consider two different initial conditions: a large population of searchers starting at the same position at the same instant some distance away from the target and an equilibrium population arising from a constant flux of searchers into the domain. The latter will be compared to a single searcher starting from a uniformly distributed initial position. I will emphasize those cases where results from the population model differ significantly from the single searcher model.

Lene Oddershede, Natascha Leijnse, Tabita Winther, Jae-Hyung Jeon, Ralf Metzler Niels Bohr Institute, Copenhagen, Denmark

Diffusion within living cells

Diffusion of single molecules and organelles in living cells has attracted considerable interest as the most important mechanism behind intra- and intercellular transport and search for a specific target. Using optical tweezers combined with single particle tracking inside living cells we study intracellular diffusion of single proteins and nano-sized organelles. We studied the motion of the lambda-receptor, a porin in the outer membrane of E. coli, and revealed its nano-scale motility. Overall, the receptor exhibits a confined diffusion, which, surprisingly, is not only thermal, but also has an active component connected to the metabolism of the organism. The purpose of this active motility could be to search for the porin's target. We also studied the diffusion of naturally occurring lipid granules inside S. pombe yeast cells and inside human endothelial cells. Most predominantly, lipid granules exhibit sub-diffusion, however, at longer timescales other types of diffusion occur, e.g., superdiffusion, as footprints of biological functions. Interestingly, all granules within the S. pombe cytoplasm exhibit weak ergodicity breaking at short timescales. In the endothelial cells, only granules located within, or close to its nucleus exhibit ergodicity breaking. While ergodicity breaking is expected in large living organisms it is surprising to find it for such a small particle essentially coupled to a thermal heat bath and on biochemically relevant timescales.

Gleb Oshanin

LPTMC, University Pierre & Marie Curie/CNRS, Paris, France

Distribution of the least-squares estimators of a single Brownian trajectory diffusion coefficient

We overview our recent results on the distribution functions of various time-averaged, weighted estimators, which optimize the least-squares fitting of the diffusion coefficient of a single d-dimensional Brownian trajectory. We show that such estimators possess an ergodic property, i.e., the distribution converges to a delta-function centered at the ensemble average value of the diffusion coefficient as the observation time tends to infinity, only for certain weighting functions. Otherwise, the distribution of the estimators tends to a limiting form with a finite variance. In the ergodic case, which we specify, the fluctuations are effectively filtered out so that the ensemble averaged diffusion coefficient can be obtained with any necessary precision

from a single trajectory data, but at expense of a progressively higher experimental resolution. These results are generalized for fractional Brownian motion, for which we also specify the optimal weighting functions producing an ergodic behavior. Finally, we discuss the influence of disorder on the distributions of the time-averaged, weighted least-squares estimators on example of the Slutsky-Kardar-Mirny model of diffusion of a protein along a DNA sequence, affected by random base-pair reading interaction.

Andrea Parmeggiani, I. Neri, A. Raguin, N. Kern

Biological Physics and Systems Biology, DIMNP, University of Montpellier 2, Montpellier, France

Some progress toward a multiscale theory of intracellular cytoskeletal transport

Living cells rely heavily on cytoskeletal transport as an efficient way to deliver vesicles and biochemically active cargos within the cytoplasm for cell viability and function regulation. Non-equilibrium stochastic motion of molecular machines such as motor proteins on cytoskeletal filaments plays a fundamental role in intracellular traffic and cytoplasm dynamical organization, whereas perturbations of these functions are known to lead to diseases.

Recent progresses in experimental techniques are giving access to a wealth of data down to the single-molecule level in-cellulo, and models are becoming increasingly important in order to interpret these data and understand general mechanisms. One approach to obtain fundamental insights into collective mechanisms and provide predictions for experiments is to use non-equilibrium statistical mechanics transport models. Building on our recent work on one of the most paradigmatic lattice gas models, the "Totally Asymmetric Simple Exclusion Process"-TASEP, we generalize TASEP on networks of increasing complexity: from complex junctions up to large random networks that better mimic the cytoskeleton complexity in cells. We provide a general theoretical framework supported by simulations, numerical and analytical results, to acquire a throughout understanding of collective stochastic transport of motor proteins on simple and complex topologies, with emergent properties, dependent on the network connectivity, and observable in experiments.

Juan MR Parrondo, Martin Depken Stephan Grill Universidad Complutense de Madrid, Madrid, Spain

Diffusive proofreading in transcription

Single-molecule experiments show that DNA transcription and replication are highly stochastic and irregular processes, where the corresponding polymerases frequently pause and even reverse direction. While such behavior is recognized as stemming from a sophisticated proofreading mechanism during replication, the origin and functional significance of irregular transcription dynamics remain controversial. Here, we theoretically examine the implications of RNA polymerase backtracking as a stochastic or diffusive mechanism of proofreading. To explore the competing demands of transcription fidelity, nucleotide triphosphate (NTP) consumption and transcription speed in a physiologically relevant setting, we establish an analytically framework for evaluating transcriptional performance at the level of extended sequences. Using this framework, we reveal a mechanism by which moderately irregular transcription results in astronomical gains in the rate at which extended high-fidelity transcripts can be produced under physiological conditions.

http://arxiv.org/abs/1201.5344

Marcela Reale, A. J. Fendrik and L. Romanelli Universidad Nacional de General Sarmiento, Buenos Aires, Argentina

Currents in defective coupled ratchets

Transport phenomena in a one dimensional system of interacting particles is studied. This system is embedded in a periodic and left-right asymmetric potential driven by a force periodic in time and space. When the density (number of particles per site) is integer, directional current of the particles is collective, that is it involves the whole system since all the sites are equivalents. On the other hand, when the system has a defect a new localized/non-collective current appears due to the migration of defects from one site to another. We show here how this "defective" (defects generated) current can be controlled by white noise.

Felix Ritort, Anna Alemany, Cristiano Valim Bizarro Universitat de Barcelona, Barcelona, Spain

Dynamic force spectroscopy of nucleic acids

Single molecule manipulation makes possible to exert force at the ends of single molecules and, for example, disrupt the molecular bonds that hold native structures in nucleic acids and proteins. In this talk I will present results on the spectrum of unfolding and folding times of single

DNA and RNA hairpins that are mechanically unzipped using optical tweezers. Application of Kramers theory of thermally activated processes makes possible to characterize the position of the transition state and the mechanical fragility of the molecular structures. Finally, I will introduce a new experimentally accessible quantity termed transition-state susceptibility that can be used to discriminate non-specific from specific cation binding in RNA structures.

Maxi San Miguel IFISC (CSIC-UIB), Palma, Spain

Searching for the absorbing state in the voter model

The voter model is a paradigmatic nonequilibrium model of interacting units with two equivalent absorbing states. I will discuss when the absorbing state is reached or when the systems persists in a dynamical regime depending on the topology of the network of interactions and on the hetereogeneity in the timing of the interactions.

José M. Sancho, R. Perez-Carrasco University of Barcelona, Barcelona, Spain

The transduction energy between molecular motors and pumps

An important source of energy inside a cell in the electro chemical potential across the membrane. This energy can be released when is necessary through ion channels and can also be transduced into different kinds of energy. The transmembrane motors F0F1-ATPsynthase and the Bacterial Flagellar Motor (BFM) uses the electrochemical energy to rotate, producing ATP en the first example or to move a bacteria in the second one. Moreover the F0F1 motor can work in the reverse regime hydrolyzing ATP to pump ions across the membrane. For these reasons, the mechano-chemical transduction between electrochemical energy across a membrane and the mechanical energy is an important matter in biophysics [1].

Most work has been devoted to the physics of molecular motors driven by chemical energy such as ATP hydrolysis [2] using flashing ratchet models. The results have been compared satisfactorily with experiments [3]. However, molecular motors working with flux have not received a comparable attention, and accordingly the experimental data on physical observables are scarce. In this work we will focus in the most basic scheme of the energy transduction flux--motion and not in the particular mechanism of an specific motor or its structure, expecting

that our general physical analysis will applied to any motor of this type. Our main observables are: velocity, flux, power and efficiency, which will be calculated for a simple model system. We will show that thermal fluctuations are quite relevant in these devices.

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Julian Talbot, Andrea Gabrielli, Pascal Viot LPTMC-CNRS, Paris, France

Stochastic Models of Blocking in Concurrent and Countercurrent Flows

We investigate models in which blocking can interrupt a particulate flow process at any time. Traffic flow, filtration, and flow in microchannels are examples of such processes. We first consider a concurrent flow model where a Poissonian stream of particles enters a channel. The model is characterized by the rate λ and the transit time τ . If at any time two particles are present, failure occurs. We determine the survival probability for a single component system where all particles move with the same speed and for a binary system where a transit time is associated with each species. We then consider a counterflow model with two opposing Poisson queues. There is no restriction on the number of particles passing in the same direction, but failure occurs if, at any time, two opposing particles are simultaneously present in the passage. We obtain an exact expression for the survival probability as a function of time and $\lambda_1, \lambda_2, \tau_1, \tau_2$.

Pascal Viot, Julian Talbot LPTMC, UPMC, Paris, France

Frictional granular motors

We first review theoretical studies of idealized models of granular motors, in particular, when the device is constructed from two different materials, the motor effect can be obtained for any temperature of the granular gas. However in recent experiments, the phenomenon is only observed if the bath temperature is sufficiently large. The presence of friction could explain the weakening of the motor effect.

Within the framework of a Boltzmann-Lorentz equation, we analyze the dynamics of a granular rotor immersed in a bath of thermalized particles in the presence of a dynamic frictional force acting on the granular motor. Numerical simulation exhibit two scaling regimes at low and high bath temperatures. In the large friction limit, we obtain the exact solution of a model corresponding to asymptotic behavior of the Boltzmann-Lorentz equation. In the limit of large rotor mass and small friction, we derive a Fokker-Planck equation for which the exact solution is also obtained. Finally, we consider the influence of a static dry friction.

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