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Criticality and supradiffusion in biological membranes: The effect of transverse multiplicative fluctuations

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ABSTRACT

We suggest that the cytoskeleton in contact with the inner surface of biological membranes in cells exhibiting tensegrity, may be considered as a system near critical conditions. This feature will influence the dynamical processes, such as diffusion, associated with the membrane's fluctuations induced by the surrounding medium. In this work we analyze a model for the diffusion of particles attached to the membrane due to the transverse membrane fluctuations when the surrounding fluid is near a critical state. We describe these fluctuations by a multiplicative Langevin equation with colored noise which accounts for the rheological nature of the medium. From the associated Fokker–Planck equation we calculate analytically the mean square displacement (*MSD*) and the dynamic structure factor (*DSF*) of the particles. In the limit of additive white noise, it is well known that the *MSD* and the *DSF* exhibit sub-diffusive behavior with a scaling $MSD \sim t^{2/3}$ and $DSF \sim \exp\left(\Gamma_k^{AW} t\right)^{2/3}$. In contrast, we show that for the case of external fluctuations arising from criticality and modeled by an Ornstein–Uhlenbeck multiplicative noise, the behavior of these quantities becomes supradiffusive, with scalings $MSD \sim t^{5/3}$ and $DSF \sim \exp\left(\Gamma_k^{MC} t\right)^{5/3}$. We suggest that this supradiffusive behavior might be of importance for the biological functions of the cell and compare our work with other approaches which also predict the same transition from a sub-diffusive to a supra-diffusive regime.

1. Introduction

Biological processes take place near criticality where their regulation is easier. Such is the case of the structure of proteins and nucleic acids, where the free energy is much smaller than the enthalpy [1]. The same is valid for other biological systems such as various genetic networks [2], when they are analyzed with the Derrida approach [3]; or for the brain when viewed, at a certain coarse grain, as a relatively small dynamic system. It is known that such systems can reliably generate robust and flexible behavior if they are located near a second order phase transition, because of the abundance of metastable states at the critical point [4]. In the case of the brain it has been shown experimentally that functional brain networks exhibit highly inhomogeneous scale free functional connectivity with the existence of long range correlations [5]. For instance, recent experiments on cortical neural networks have revealed the existence of well-defined avalanches of electrical activity. Such

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avalanches have been claimed to be generically scale invariant, i.e. power law distributed, with many exciting implications in neuroscience [6]. All these experimental results are consistent with the picture of the brain operating near a critical point [7,8].

Another aspect of criticality is the one associated to the so-called tensegrity [9], which may allow us to consider that cell membranes with tensegrity are systems near criticality as will be discussed below. Tensegrity structures are composed by a network of tensed elements linked to a subset of elements that resist being compressed, and thereby bring the entire system to a state of isometric tension. These structures are present in the system of muscles and skeleton where bones resist compression and muscles resist tension. Ingber has shown that cell microtubules can bear compression in living cells, and that they resist inward-directed forces generated by the surrounding contractile actin cytoskeleton. Cell stability would depend on a mechanical force balance in which microtubules struts balance inward-directed compressive forces generated by tensile actomyosin filaments [10,11].

One of the most interesting properties of tensegrity structures is that hierarchical tensegrities can be built, which exhibit force transmission and fine structural coordination across multiple size scales. Coordination between cell surface and nucleus deformation is found and forces applied to surface integrins result in orientation of nucleotides, suggesting that the nucleus itself must contain some type of load-bearing structural network. Integrins are indeed mechano-receptors that transmit mechanical forces across the cell's surface over a specific molecular pathway and facilitate mechanochemical signal conversion inside the cell. Conversely, the application of cell traction forces on integrins and the surrounding extracellular matrix can feedback to alter biochemistry outside the cell, for example, by unfolding fibrobronectin proteins and promoting extracellular matrix fibril formation.

However, we cannot offer a clear justification of why cells with tensegrity may be considered as critical systems; we only make the suggestion that this might be so. This suggestion may be supported by noting that at the critical point of a phase transition of a dynamical system, large dynamic structures emerge; this is the case of a ferromagnetic material even though there are only short range interactions between the system's elements. Thus, at the critical temperature the system exhibits a greatly correlated state which at the same time is able to widely fluctuate in time at all scales. Since as mentioned above, hierarchical tensegrity structures can be built and optimal performance occurs, the behavior of these cells could be better understood by considering that are systems near criticality. However, to our knowledge, there are no experiments in eukaryotic cells where this issue could be clarified [12,13].

A membrane, especially if it is biological, should not be conceived as an abstract boundary surface that merely defines the volume of the cell, preventing the diffusion of its components. Even in the most simple proto-metabolism, the cellular membrane must be a functionally very active part of the system, since it channels the flow of matter–energy necessary for its continuous self-construction [13]. For this reason one wonders if the vicinity of a cell membrane to criticality, could modify as well the dynamic (transport) processes occurring in them; in particular the diffusion processes which play such important roles in many vital processes. The aim of this work is to explore the dynamics of membranes, analyzing a model for diffusion due to transverse membrane fluctuations when the fluid surrounding the membrane is near a critical state, where the role of fluctuations and stochasticity will become more relevant.

Recently there has been an upsurge in the study of diffusion processes in membranes, specifically in the context of biological systems where diffusion plays an outstanding role at cellular level [14–16]. It is common to describe diffusion by assuming an inherent randomness of the dynamics of these systems which gives rise to thermal (internal) fluctuations of their state variables [17–19]. However, since membranes are in general open systems, they may be also subject to fluctuations arising from the variability of their environment. The role of stochasticity and fluctuations in the dynamics of biological cells is drawing the interest of an increasing number of researchers [14,15,20,21]. Yet, the model described below will not try to mimic nature in every single molecular detail, providing an accurate biophysical description of membrane properties and dynamics. It is just meant as a first step with this new stochastic approach to the study of dynamic processes in cell membranes.

Actually, the fluctuations (noise) existing in open systems may be conveniently classified into internal and external (parametric) fluctuations. The former are those self-originated in the system, while the latter are determined by the environment. Internal fluctuations are a consequence of the large number of degrees of freedom averaged out in a macroscopic description. They scale with the size of the system and are small in the thermodynamic limit, except at a critical point where long range order is established, or in non-equilibrium steady states induced by external gradients [19]. Their study is an important and well known part of statistical mechanics [22].

In contrast, external fluctuations exist when the system is under the influence of a natural or induced randomness of the environment of the system. These fluctuations play the role of an external field driving the system and do not scale with the system's size. The behavior of physicochemical systems under the influence of external noise has been the subject of active research. Systems where their effect has been considered include lasers [23] and optical systems [24,25], chemical reactions [26], nuclear reactors [27] and liquid crystals [28,29]. A recent and broad overview of the mechanisms through which noise affects the behavior of a variety of systems is given in [30]. In all these applications the parameters of the deterministic equations describing the macroscopic behavior of the system become random and are described as a stochastic processes [31,32].

The effect of thermal additive fluctuations on the transverse mean square displacement of a tagged particle attached to a membrane has been studied in the limit of large wave numbers which is sensitive to single membrane dynamics. Also, by using a statistical mechanics approach to describe an ensemble of membrane plaquetes at random orientations, the effect