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Movements of molecular motors: Ratchets, random walks and traffic phenomena

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Abstract

Processive molecular motors which drive the traffic of organelles in cells move in a directed way along cytoskeletal filaments. On large time scales, they perform motor walks, i.e., peculiar random walks which arise from the repeated unbinding from and rebinding to filaments. Unbound motors perform Brownian motion in the surrounding fluid. In addition, the traffic of molecular motors exhibits many cooperative phenomena. In particular, it faces similar problems as the traffic on streets such as the occurrence of traffic jams and the coordination of (two-way) traffic. These issues are studied here theoretically using lattice models.

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1. Introduction

The idea of constructing nanometer-sized devices and machines has created a lot of excitement during the past years. Despite the progress made, the functionality of artificial nano-devices is, however, still rather limited. At the same time, more and more biomolecular nano-machines have been identified in the cells of living beings where they accomplish a huge variety of tasks. Many of these molecular motors are now rather well studied and were found to work with an amazing degree of precision and efficiency as a result of billions of years of evolution [1,2]. In the following, we will focus on one class of molecular motors which has been studied quite extensively during the last decade, namely processive cytoskeletal motors which drive the traffic of vesicles and organelles within cells. These motors hydrolyze adenosinetriphosphate (ATP) and convert the free energy from this chemical reaction into directed

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movements along filaments of the cytoskeleton. This class of motors contains kinesins and dyneins, which move along microtubules, and certain myosins, which move along actin filaments. These motors walk along the filaments by performing discrete steps with a step size which corresponds to the repeat distance of the filament, 8 nm for kinesins and 36 nm for myosin V. They are called processive if they make many steps while staying in contact with the filament.

From a physical point of view, much of the interest in molecular motors is due to the fact that the difference in size compared to macroscopic engines implies also conceptual differences. The typical energy of macroscopic motors is much larger than the thermal energy, $k_B T$, while the typical energies of molecular motors are of the order of $k_B T$. For example, the hydrolysis of ATP releases about $20\,k_B T$. On the one hand, molecular motors have to cope with perturbations arising from thermal fluctuations; on the other hand, the unavoidable presence of noise suggests that evolution has created motors which make use of this noise in order to generate work or directed movement.

From a technological viewpoint, the amazing properties of single biological motor molecules and the complexity of the systems into which they are integrated in the cell provide inspiration for the design of artificial nanoscale transport systems [3,4].

In this article, we discuss several theoretical aspects of the motor movements. In Section 2, we start by summarizing some recent experimental results and discuss the question whether noise-driven mechanisms are used by these motors. In Section 3, we discuss another effect of noise, namely the detachment of motors from their tracks due to thermal fluctuations, which leads to peculiar random walks. We derive the asymptotic behavior of these random walks using the statistical properties of the returns of motors to the filament. Finally, in Section 4, we summarize our recent studies of traffic problems which arise in systems with many molecular motors due to their mutual exclusion from binding sites of the filaments. These topics are also addressed in the review article [5].

2. Active movements of molecular motors

Molecular motors can be studied outside cells using biomimetic model systems. In these experiments, the biological complexity is reduced to a minimal number of components, namely motors, filaments, and ATP. An example is shown in Fig. 1. By these experiments, one can observe movements of single motor molecules and measure transport properties such as velocities, step sizes, and forces [1,2].

On the one hand, these experiments provide insight into the motor mechanisms. A major breakthrough was to resolve the discrete steps of the motors and to measure their step size which corresponds to the repeat distance of the filament. This has first been achieved for kinesin using an optical tweezers setup [6]. More recently, it has been shown that kinesin [7,8] and also myosin V [9] move in a hand-over-hand way, i.e., that the two heads of the dimer step forward in an alternating fashion such that the rear head always moves in front of the leading head, similar to human walking. Further progress is expected from combining mechanical methods and particle tracking with fluorescence techniques.

On the other hand, using these biomimetic motility assays, one can measure the transport properties systematically varying external control parameters. Here the main focus has been on the velocity as a function of the ATP concentration and of the force applied with, e.g., optical tweezers to oppose the movements, see, e.g., Ref. [10]. Other quantities that have been measured are the one-dimensional diffusion coefficient of motors bound to filaments or the randomness parameter and the walking distance before unbinding from the filament. These measure-

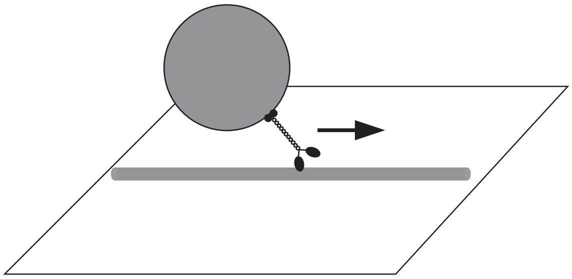

Fig. 1. The ‘bead assay’ constitutes a biomimetic model system: a molecular motor transports a (glass or latex) bead along a filament which is immobilized on a surface.