Soft Matter

EDITORIAL

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Cite this: *Soft Matter*, 2020, **16**, 7185

Introduction to Active Matter

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DOI: 10.1039/d0sm90137g

rsc.li/soft-matter-journal

Introduction

Active matter includes living and non-living systems that have in common that they contain energy-consuming and force-generating microscopic constituents that drive emergent dynamic properties on larger scales. As 'activity' is a fundamental property of living organisms, we begin with an introduction to active biological matter.

Biological systems self-assemble into highly complex structures and display dynamics over broad ranges of time- and length-scales. At the molecular scale, biochemical reactions, diffusion and active transport generate spatial and temporal patterns,[1] prominently in the cytoskeleton that is assembled from protein polymers (filaments).[2] Filament assembly and disassembly is tightly controlled. All filaments have a defined chirality. Actin and microtubules possess polarity, intermediate filaments don't. The polar filaments direct the path of cytoskeletal mechano-enzymes (motors) that convert chemical energy (ATP) into mechanical work.[3,4] Motors and filaments together render the cytoskeleton a unique active material, a motile and adaptable scaffolding spanning the cell, which can dramatically change its large-scale architecture, mechanical response and force generating properties with subtle changes in the activity of the associated molecular control machinery.[5,6] At the mesoscopic scale, cells transmit cytoskeleton-generated stresses to their tissue environment,[7–16] which emerges as a higher-level active material. Collectively, cell-generated forces and regulated mechanical properties drive large scale tissue motion and growth,[17–20] for example in developing embryos.[21] At even larger length scales, organisms can influence each other's motion by physical force,

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including hydrodynamic forces,[22] or by non-reciprocal interactions.[23–25] This can again lead to emergent active dynamics as in swarms of insects[26,27] or fish, flocks of birds,[28] or even collective motions of human crowds.[29] Thus, emergent dynamical phenomena in biological active materials are observed on the molecular scale,[30] the cell scale,[31] the multicellular scale in bacterial suspensions[32] or epithelial tissue monolayers,[33] and on the organismal scale. Active collective phenomena in these systems show interesting analogies to conventional phase transitions and are essential for the maintenance of life. The interdisciplinary study of active matter seeks to obtain a quantitative, mechanistic understanding of these processes by experiment, theory, and the construction of non-living model systems.

At the microscopic scale, the force-generating elements of an active system are supplied with energy from their surroundings; in biological systems typically in the form of metabolically derived chemical energy. Constant dissipation of energy is the basis for the spontaneous emergence of complex hierarchical structures and large-scale collective dynamics in living systems. The flow of energy within active systems can lead to novel symmetries, conservation relationships and material properties. Although thermodynamics and statistical physics put fundamental limits on the loss of entropy or generation of order tied to the input of energy, *it is difficult to quantify experimentally how much energy is dissipated in the assembly or dynamics of active living materials when they perform particular biological processes*.

The emergent properties observed in active matter cannot be understood using equilibrium statistical physics. These properties can often be reproduced by numerically modeling these systems as polymer networks controlled by internal stress generators,[34–36] or as collections of self-propelled Brownian particles with contributions from particle shape and polarity, interfacial forces, and the structure and curvature of confining walls or underlying surfaces.[5,37–43,51] This successful approach has led, in turn, to the development of non-biological experimental model systems that often attempt to mimic biological or other natural processes, or seek to drive emergence *de novo*. Examples include the development of self-propelled particles,[44] driven nematics,[45] and vibrated granular materials.[46] Such systems can exhibit non-equilibrium phase transitions, such as the emergence of giant density fluctuations,[47–49] while they allow one to precisely control the system parameters. Furthermore, they can be amenable to theoretical modelling, which can describe the dynamic evolution of interesting phenomena.[22,50,51]

The goals of active matter research include an understanding of how living systems regulate, partition and optimize the throughput of energy to self-assemble into the amazingly complex and dynamic structures we observe. We will gain new insights into biological systems, in the generation and control of forces in cells and by cells, but also into mechanosensory mechanisms. With that understanding it becomes conceivable to be able to exploit these strategies to engineer new technical active materials and metamaterials with novel and useful properties and functionalities, for example smart biocompatible microscopic robots for drug delivery or through the development of soft robotics that integrate with flexible sensors and actuators.[52–54] In this research, we also constantly seek new frameworks and tools for non-equilibrium statistical mechanics.

On the origins of activity and statistical physics approaches to non-equilibrium dynamics

Active matter is commonly defined as soft systems with built-in dispersed and local conversion of energy into forces and motions. In biological systems, energy is typically supplied as chemical energy in the form of adenosine triphosphate (ATP), which in turn is synthesized in the metabolism of nutrients or through photosynthesis. In model systems, energy can also be supplied by mechanical force, electric fields, or light. Energy dissipation maintains the system out of thermodynamic equilibrium, and thus the standard Boltzmann description of classical equilibrium statistical mechanics is not applicable. This fundamentally implies that time-reversal symmetry is broken in the phase space dynamics of the system. A manifestation of this broken symmetry is that the system does not obey detailed balance everywhere in its phase space.[55–58] An interesting question is in *which degrees of freedom the broken detailed balance is manifest in a given system, and if and how the breaking of detailed balance at the molecular scale translates to the breaking of detailed balance on larger scales.* Obviously, the activity of motor proteins in cells can lead to large-scale non-equilibrium motion, such as a person walking down the street, but this requires a particular architecture of the active matter at work. Alternatively stated, *how does the local dissipation of energy relate to what one can define as non-equilibrium phase transitions*, namely the emergence of large-scale collective structural and dynamic order? The extent to which detailed balance is broken is also a measure of how far a system is from equilibrium, *i.e.* how much energy is being dissipated. In a stationary stochastically fluctuating system, the dissipation of energy is directly related to the production of entropy. An important question in biology is how living systems, while they continually produce and dissipate energy, achieve robustness to external perturbations and maintain steady states (homeostasis) using repair processes (regeneration, wound healing, *etc.*).

To approach these questions, one first requires accurate methods to quantify the dissipation of energy in particular degrees of freedom in an active system. One way to do this is to make use of the fluctuation–dissipation theorem, which states that, in equilibrium, the thermal fluctuations in a system are related to the linear response parameters.[59] If one independently measures response parameters directly, one can thus estimate thermal fluctuations and isolate non-equilibrium fluctuations from the total observed fluctuations by subtraction of these estimated thermal fluctuations This method has been used, for example, to characterize the activity of molecular motors within biopolymer networks.[60,61] Often, particularly in glasses, the concept of an "effective temperature" has been used to describe the active fluctuations, but this assumes a particular frequency spectrum for the active forces, which may not be a valid assumption.

The field of stochastic thermodynamics is rapidly developing to provide the theoretical framework necessary to extract thermodynamic parameters such as heat, work or entropy from experimental observations of fluctuating active soft matter systems.[62] Practical methods to observe broken detailed balance have been recently introduced to identify the presence of subtle non-equilibrium dynamics in cells.[55] For example, in some cases vorticity in phase space can be quantified from the dynamic modes of actively fluctuating filaments.[56,57] In addition, one can also take spatial information into account when measuring the breaking of time reversal symmetry, thereby inferring the role of dissipation in the emergence of patterns far from equilibrium.[63–65] These methods can be used to understand the dissipation of energy, which is intrinsically related to biological information processing and the performance of feedback circuits in sensory adaptation.[66] Current challenges involve identifying and capturing the most relevant degrees of freedom in an active fluctuating system to obtain reasonable estimates of the true entropy production. A new approach to achieve this goal is "Dissipative Component Analysis".[68] Ultimately, one would like to be able to deduce the stochastic equations of motion, including the active force terms that drive particular degrees of freedom in an active material, from the observation of fluctuations. Promising methods of stochastic force inference are currently being developed.[67–69]

Active matter, especially when involving complex interacting "particles" on larger length scales, such as whole organisms, can also involve complex interactions that are not simple physical forces between constituents and their environments. The symmetry of Newton's third law does not apply, for example, when sensory perception and information processing are involved, such as in a school of fish. In equilibrium, interactions are reciprocal – in that particle A interacts with particle B in the same way that B interacts with A. Interactions between constituents can also be non-reciprocal, for example, when a composite system consisting of different species interacts with an environment that is out of equilibrium. As a result, collective behaviors can arise.[70] For example, non-equilibrium dynamics and active self assembly can occur in a mixture of colloids with asymmetric mutual diffusiophoretic interactions.[23] In this case, the magnitude of the non-reciprocity is determined by the relative disparity in activity. Non-reciprocal interactions can be seen in synthetic model systems[71,72] and in biological systems.[73,74]

Engineering metamaterials

The engineering of materials with non-equilibrium properties remains a major challenge in materials science. The activity of constituent particles can give rise to emergent material properties. Current efforts include the activation of a wide range of materials, from active colloids and driven grains to molecular motors. In these cases, topological defects,[75] mechanical properties and shape memory can be controlled.[2] However, *it remains a challenge to control the amount of activity internally as well as to be able to exert spatial and temporal control*. To address this challenge, experimental methods have been designed to control the extent to which detailed balance is broken on a molecular level using external fields. For example, light has been used to activate molecular rotors[76] or to activate colloidal particles that self-assemble into dynamic "living crystals".[77] In biological materials, using optogenetics, molecular motors are engineered to change their walking velocity or direction in response to different wavelengths of light.[78]

Active systems break symmetries and violate conservation laws and reciprocity relations. As a result, *it remains a challenge to describe active material (mechanical) behaviors with conventional continuum theories*. For example, in chiral active fluids, in which internal activity drives colloidal particles with a torque, the constitutive equations that describe the mechanical response of viscoelastic materials do not obey standard symmetry arguments. This causes the response to exhibit an anomaly and an odd viscosity.[79] Cases where internal chiral activity can result in rotations abound in both biological and non-biological materials. In biological materials, molecular motors walk along chiral protein filaments, which self-assemble into nematics,[31,75,80–85] leading to large-scale continuous coherent flows,[86–88] but also unexpected behaviors such as oscillations.[47] Activity can also result in elasticity absent in the corresponding passive system, entering the odd part of the static elastic modulus tensor.[48] Thus, for example, axial stresses can couple to rotations, creating novel material properties unavailable in passive systems. Controlling internal activity and modeling its impact on material properties will make strides towards enabling the design of intelligent active materials that can be programmed to self-heal, organize, sense and move to create work on user-defined time scales.

How does dissipation of energy boost the performance of living systems?

The efficiency of biological processes is a current topic of extensive research and debate. There is an obvious need for energy consumption in building ordered structures and in producing forces and motions, *i.e.* performing external work, but there is also energy dissipated to heat. There are many subtle benefits for an active material in dissipating energy to maintain a steady state, such as the capability to maintain temperature or chemical gradients, adaptability or regenerability, and possibilities for repair after damage. Living systems are generally robust and resilient, and can actively evolve, reproduce, and survive in a continuously fluctuating and changing environment. Presumably, this robustness and the resistance to perturbations costs energy. To obtain a precise understanding of the interplay between energy dissipation and robustness, speed and accuracy of sensing and response, adaptation and repair,[66] we need to identify mechanisms and estimate the associated dissipation of energy. This knowledge will both advance basic biology and open up new ways of engineering active technical materials.

Acknowledgements

MD and MM acknowledge discussions with participants at the KITP 2020 Workshop on Symmetry, Thermodynamics, and Topology in Active Matter which was supported in part by NSF Grant No. PHY-1748958, NIH Grant No. R25GM067110, and the Gordon and Betty Moore Foundation Grant No. 2919.02. MD further acknowledges support from NSF Grant No. CBET-1604712, NSF Grant No. DMR 1808026, NSF Grant No. EF-1935277. MM acknowledges support from ARO MURI W911NF-14-1-0403, the National Institutes of Health (NIH) U54 CA209992, NIH RO1 GM126256, and Human Frontiers Science Program (HFSP) grant number RGY0073/2018. CFS acknowledges discussions at the Aspen Center for Physics, which was supported by NSF grant PHY-1066293 and support by the European Research Council under the European Union's Seventh Framework Programme (FP7/2007–2013)/ERC grant agreement no. 340528.

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