Soft Active Materials Workshop
Syracuse University
May 2009

Invited Talks

Aparna Baskaran
Syracuse University, USA
Self propelled Particles: From Microdynamics to Hydrodynamics

In this talk I will illustrate the derivation of a unified continuum description of the large scale collective behavior of active matter from two specific physical microscopic dynamical models: stroke-averaged swimmers moving through a viscous fluid and self-propelled hard rods moving on a substrate. New results at large scales include a lowering of the density of the isotropic-nematic transition, an enhancement of longitudinal diffusion of the self-propelled orientable units, and a strong enhancement of boundary effects in confined self-propelled systems.

This work was done in collaboration with M. Cristina Marchetti, with support of NSF grants DMR-0705105 and DMR-0806511.

Iain Couzin
Princeton University, USA
Collective Motion and Decision-Making in Animal Groups

Animal groups such as bird flocks, insect swarms and fish schools are spectacular, ecologically important and sometimes devastating features of the biology of various species. Outbreaks of the desert locust, for example, can invade approximately one fifth of the Earth's land surface and are estimated to affect the livelihood of one in ten people on the planet.

Using a combined theoretical and experimental approach involving insect and vertebrate groups I will address how, and why, individuals move in unison and investigate the principals of information transfer in these groups, particularly focusing on leadership and collective consensus decision-making.

For very large animal groups, despite huge differences in the size and cognitive abilities of group members, recent models from theoretical physics ('self-propelled particle', SPP, models) have suggested that general principles underlie collective motion. Such models demonstrate that some group-level properties may be largely independent of the types of animals involved. I shall present recent experimental work on locusts that validates some of the predictions of simple mechanistic models including a density-dependent "phase transition" from disordered to ordered motion.

Details of the mechanism by which individuals interact, however, also provide important biological insights into swarm behaviour. Using laboratory studies involving nerve manipulation and field experiments we demonstrate that some swarming insects are in effect on a "forced march" driven by cannibalism.

These results will be discussed in the context of the evolution of functional complexity and pattern formation in biological systems.

Rumi De
Brown University, USA

Dynamics of Active Cellular Response Under Mechanical Stress

Forces exerted by and on adherent cells are important for many physiological processes such as wound healing and tissue formation. In addition, recent experiments have shown that stem cell differentiation is controlled, at least in part, by the elasticity of the surrounding matrix. Using a simple theoretical model that includes the forces due to both the mechanosensitive nature of ells and the elastic response of the matrix, we predict the dynamics of orientation of cells. The model predicts many features observed in measurements of cellular forces and orientation including the increase of the forces generated by cells in the absence of applied stress and the consequent decrease of the force in the presence of quasi-static stresses. We also explain the puzzling observation of parallel alignment of cells for static and quasi-static stresses and of nearly perpendicular alignment for dynamically varying stresses. In addition, we predict the response of the cellular orientation to a sinusoidally varying applied stress as a function of frequency. The dependence of the cell orientation angle on the Poisson ratio of the surrounding material can be used to distinguish systems in which cell activity is controlled by stress from those where cell activity is controlled by strain.

References

[1] R. De, A. Zemel, and S. A. Safran. Dynamics of cell orientation. Nature Physics, 3, 655 (2007).
[2] R. De, A. Zemel, and S. A. Safran. Do cells sense stress or strain? Measurement of cellular orientation can provide a clue. Biophys J., 94, L29 (2008).
[3] R. De and S. A. Safran. Dynamical theory of active cellular response to external stress. Physical Review E, 78, 31923 (2008).

Seth Fraden

Brandeis University, USA

Active Emulsions

The Belousov--Zhabotinsky (BZ) reaction is the best known chemical oscillator. We study monodisperse water-in-oil emulsions where the interior of the drops contains the BZ reaction surrounded by a continuous oil phase. Bromine, an intermediate in the BZ reaction, inhibits the oscillation, and being nonpolar readily diffuses through the oil into neighboring drops. For emulsions confined to a one-dimensional capillary this inhibitory coupling leads to anti-phase oscillations whereby neighboring drops are 180 degrees out of phase, or, depending on chemical composition, Turing patterns are observed in which drops alternate in space between the reduced and oxidized states, but are stationary in time [1]. Here we present data and modeling of drops in two-dimensions. Stationary anti-phase coupling is frustrated for two-dimensional hexagonal lattices. We observe that hexagonally arrayed BZ emulsions in 2D either exhibit a mixed state (some drops stationary, some oscillating anti-phase), or all drops oscillate with nearest neighbors 120 degrees out of phase with each other. The behavior is modeled as coupled chemical oscillators.

[1] Diffusively Coupled Chemical Oscillators in a Microfluidic Assembly, M. Toiya, V. K. Vanag, and I. R. Epstein, Angew. Chem. Int. Ed. *47*, 7753 --7755 (2008).

Margaret Gardel

University of Chicago, USA

Assembling Contractile Actomyosin Bundles

The ability of adherent cells to regulate traction forces on their extracellular matrix (ECM) is fundamental to tissue morphogenesis and directed cell migration. While mechanisms of force generation at the molecular level are established, our understanding of how these forces are variably transmitted to cellular length scales by the cellular cytoskeleton is largely unknown. To a large degree, cellular traction forces are regulated by myosin-II generated cell contractility, which promotes the development of contractile F-actin bundles and the engagement and growth of mechanosensitive focal adhesions. To address how myosin-II ATPase activity drives the organization of the F-actin cytoskeleton into structures capable of efficient force transmission, we utilized a combination of high resolution confocal microscopy and traction force microscopy. We found that myosin-II drives a rapid, tight engagement of transmembrane integrins to the adjacent ECM such that the stress dissipated through the integrin-ECM bond decreases nearly two orders of magnitude in 20 seconds. Stabilization of this adhesive bond requires a critical tensile stress between the cellular adhesion and the surrounding ECM such that, when presented with ECM substrates of varying compliance, the cellular-induced strain on the substrate varies. After stabilization of this adhesive bond, the F-actin cytoskeleton rapidly reorganizes into compact bundles at timescales consistent with further increases in force at adhesion sites. We propose that enzymatic activity of myosin

II promotes rapid reorganization of the F-actin cytoskeleton until myosin-II mediated tensile stresses within the cytoskeleton are balanced with traction stresses exerted on the ECM.

Deborah Gordon

Stanford University, USA

How Harvester Ant Colonies use Interaction Networks to Regulate Foraging

Ant colonies operate without central control. Harvester ants adjust the numbers foraging to the availability of food. A forager leaves the nest to search for food, usually a seed. It searches until it finds food and then brings it back to the nest. Each forager makes many trips in a day. When it returns from a trip, it puts down its food fand then waits inside the nest. Whether the forager leaves the nest on its next trip depends on its rate of interaction with returning, successful foragers. The length of a foraging trip depends on how long the forager has to search for food; the more food available, the shorter the trip. Thus the rate of forager return is a measure of food availability. The rate at which foragers leave the nest is tightly coupled to the rate of forager return; experimental manipulation of the return rate leads within minutes to a change in the rate at which foragers go out. Each forager returns to the same site on successive trips, so a forager returning from one location stimulates another forager to search in a different location. Thus, the regulation of foraging in harvester ants does not require any individuals to show others a particular location with abundant food. Instead, a decentralized network of interactions tunes the numbers foraging to current food availability.

Paul Janmey

University of Pennsylvania, USA

Response of Cells to Nonlinear Elastic Substrates

Most tissue cells grown in sparse cultures on linearly elastic substrates typically display a small, round phenotype on soft substrates and become increasingly spread as the modulus of the substrate increases until their spread area reaches a maximum value. As cell density in creases, individual cells retain the same stiffness-dependent differences unless there are very close or in molecular contact. On nonlinear strain-stiffening fibrin gels, the same cell types become maximally spread even when the low strain elastic modulus would predict a round morphology, and cells are influenced by the presence of neighbors hundreds of microns away. Fibroblasts and human mesenchymal stem cells on fibrin deform the substrate by several microns up to five cell lengths away from their plasma membrane through a force limited mechanism. Atomic force microscopy and rheology show that these strains locally and globally stiffen the gel, thereby allowing long distance cell-cell communication and alignment. These cells are acutely responsive to the nonlinear elasticity of their substrates and are capable of manipulating these properties to induce patterning.

Jean-Francois Joanny
Institut Curie, France
Cell Dynamics and Active Gels

In many circumstances cells show instabilities of their shapes such as oscillations, the formation of membrane protrusions (blebbing) or the contractile ring observed during cell division in cytokinesis before the final separation of the two cells. All these instablities are driven by the cortical actin layer located just below the cell membrane. In this talk we first show how one can describe the properties of the cortical actin layer using a hydrodynamic theory of active gels. We then use this theory to study the oscillations of fibroblast cells when they are not allowed to adhere, the formation of blebs induced by laser ablation and the formation of contractile rings both around wounds in xenopus eggs and during during cytokinesis.

Arshad Kudrolli
Clark University, USA
Swarming and Swirling: from Granular Rods to Bacterial Colonies

Motivated by bacteria colonies and hoofed animal herds which show collective behavior, we discuss a series of experiments performed with granular rods, dimers, and flexible chains on a vibrated plate to illustrate the effect of particle shape on self-organization. A non-spherical shape is shown to lead to not only states which resemble nematic and smectic phases but also causes novel dynamics. We will then introduce and discuss the dynamics of deformable shapes consisting of a head and a tail composed of a bead chain which is shown to undergo directed motion because of differential friction associated with the head and the body. Recognizing that such a system is a simple physical model of self-propelled particles, we discuss the observed collective behavior such as aggregation at the boundaries and swirling motion in the context of various minimal leaderless models of active living systems. We will discuss the self-propelled particle number fluctuations, flow fields, and orientation order inside a container as a function of number density and excitation, and compare their statistics with recent models of active nematic particles and living cells.

Eric Lauga
University of California, San Diego, USA
The Nonlocal Hydrodynamics of Swimming Cells

Microorganisms swimming in viscous fluids inhabit a world quite different from the one we are used to experiencing. In this talk, we will discuss some properties and recent results of fluid-based locomotion on very small scales where hydrodynamic interactions play a dominant role: (1) The attraction of bacteria by solid surfaces; (2) The influence of interfaces on the propulsive forces generated by swimming eukaryotes; (3) The role of hydrodynamic interactions in collective locomotion at low Reynolds number.

Jacques Prost
ESPCI Paris, France
Mechanics of Tissue Growth

Cynthia Reinhart-King
Cornell University, USA
Endothelial Cell Network Assembly on Soft Substrates

Endothelial cells comprise the nearly impermeable single cell barrier that lines the lumen of all blood vessels. Physiologically, blood vessel formation is important for wound healing; however, aberrant endothelial cell behavior can lead to tumor formation and numerous vascular diseases including atherosclerosis. Work in the Reinhart-King Lab focuses on describing governing parameters that mediate endothelial cell-biomaterial interactions at the molecular, cellular and tissue scales. Using materials of well-characterized chemical and mechanical properties which mimic the in vivo environment, we have characterized fundamental mechanisms of endothelial cell adhesion, spreading, and migration as a function of matrix compliance and chemistry. We have implemented Traction Force Microscopy, a tool that quantifies the magnitude, direction and location of cellular traction stresses, to investigate individual endothelial cell mechanics in response to various extracellular matrix cues. I will discuss our approach to decipher the complex balance between the chemistry and mechanics of the cellular microenvironment, and I will describe our insights into the mechano-chemical regulation of endothelial cell physiology.

Interestingly, we have found that endothelial cell assembly varies based on substrate mechanics. Moreover, we showed for the first time that endothelial cells are able to communicate mechanically through their substrate using contractile forces. Such insights into the mechanics of endothelial cell behavior will enable rational design of tissue-engineered therapeutics and a greater understanding of how perturbations in the cellular microenvironment lead to disease progression.

Lev Tsimring
University of California, San Diego, USA
Growth-Induced Ordering and Streaming in Dense Bacterial Populations

The structure of bacterial populations is governed by the interplay of many physical and biological factors, ranging from properties of surrounding aqueous media and substrates to cell-cell communication and gene expression in individual cells. The biomechanical interactions arising from the growth and division of individual cells in confined environments are ubiquitous, yet little work has focused on this fundamental aspect of colony formation. We analyze the spatial organization of Escherichia coli growing in a microfluidic chemostat. We find that growth and expansion of a dense colony of cells leads to a dynamical transition from an isotropic disordered phase to a nematic phase characterized by orientational alignment of rod-like cells. Furthermore, an interplay between cell growth and mobility in a confined environment leads to a novel cell streaming instability. We develop a continuum model of collective cell dynamics based on equations for local cell density, velocity, and the tensor order parameter. We use this model and discrete-element simulations to elucidate the mechanisms of cell ordering and streaming, and to quantify the relationship between the individual cell dynamics and the structure of the whole population.

Tamas Vicsek

ELTE, Budapest, Hungary

Collective Motion: Some Models and Experiments

We address the question of finding unifying principles describing the essential aspects of collective motion, being one of the most relevant, widespread and spectacular manifestation of collective behaviour. After an introduction to the topic, several models as well as a few new experiments will be discussed. The models have been designed to capture both the general features of group motion as well as the behaviour of specific systems including tissue cell cultures and panicking people. The experimental observations involve groups of migrating keratocites, a system of self-propelled “toys” and a study of bird flight trajectories.

Roy Welch

Syracuse University, USA

Genomics of Emerging Order Within a Biofilm

Self-organizing phenomena are characterized by the emergence of patterns at the global level of a system that arise solely from numerous interactions among lower-level components. With this in mind, the emergence of globally-ordered patterns in a developing Myxococcus xanthus swarm was investigated to determine the parameters that control swarm self-organization. Through the identification and tuning of critical system parameters, M. xanthus swarms were observed to produce patterns on multiple scales. The genomic underpinnings of these patterns involves a complex signal transduction network. A targeted disruption of this network frequently produces phenotypic abnormalities that can only be observed as subtle alterations in the formation of swarm patterns. These alterations represent the first clue to reverse engineering self-organization at genome scale.

Mingming Wu

Cornell University, USA

Collective Dynamics in Swimming E. Coli Bacteria

Collective dynamics plays critical roles in living systems both at the molecular and the cellular levels. At molecular level, proteins coordinate through protein reactions and conformational changes to orchestrate cellular function; at cellular level, cells of various types interact via mechanical and chemical cues to mediate various physiological processes. In this talk, I will present two research projects that illustrate the importance of collective dynamics at molecular and cellular levels using swimming *Escherichia coli* (*E.coli*) as a model system. Project 1: Receptor–receptor coorperativity in bacterial chemotaxis. In this part, I will talk about our studies of bacterial chemotaxis using a combination of quantitative experiments and theoretical modeling. We demonstrate that receptor-receptor coorperativity plays a key role in bacteria's ability to sense a very small amount of chemicals, as well as to maintain high chemo-sensitivity in a wide chemical concentration range. Project 2: Role of cell-cell interactions in mass transport within a bacterial suspension. In this part, I will present our experimental and theoretical investigations on how cell-cell interact via hydrodynamic forces, and how this interaction leads to the unusual mass transport properties in a swimming *E.coli* bacterial suspension.