

Abstracts – Animal swarms workshop

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MODELING OF CELL MOTION ON PATTERNED ADHESIVE AND DEFORMABLE SUBSTRATES

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Computational modeling of eukaryotic cells navigating on rigid substrates and responding to external stimuli is an extraordinary complex task: regulatory pathways are intertwined and forces are not fully understood. Additional difficulties arise when the substrate becomes deformable and heterogeneous, leading to a highly nontrivial cell response. We develop an effective computational model for motile cells and cell fragments, based on a generalization of phase field approach, to account for cell shape deformation, explicit dynamics of adhesion site formation and substrate compliance. Treating the substrate as an effective elastic spring, we were able to reproduce key experimental observations and make new predictions. Our model displays steady motion versus stick-slip transitions with concomitant shape oscillations as a function of the actin protrusion rate, the substrate stiffness, and the rates of adhesion. Implementing a patterned surface, exemplified by alternating stripes of high and low adhesiveness, we were able to reproduce the correct motility modes and shape phenomenology found experimentally, as well as to predict novel nontrivial behavior: the motion of the cell is directed perpendicular to stripes of low adhesion strength contrasted by motion parallel to stripes on more adhesive substrates.

SWARMING OF VERY LONG BACTERIA

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Bacterial swarming is a type of motility characterized by a rapid and collective migration of bacteria on surfaces. Most swarming species form densely packed dynamic clusters in the form of whirls and jets where hundreds of cells move in circular and straight patterns, respectively. Recent studies have suggested that short-range steric interactions may dominate hydrodynamic interactions, and that geometrical factors, such as cell's aspect ratio, may become important for how bacteria swarm. However, the aspect ratio for most swarming species is only up to 5 and the swarming of bacteria with much larger aspect ratios has never been studied systematically. Therefore, the role of aspect ratio in swarming is yet to be determined.

In this talk I will present a study of the dynamics of *Paenibacillus dendritiformis* C-morphotype, a very long swarming bacterium with an aspect ratio of more than 20. We find that the dramatic increment in aspect ratio indeed leads to a totally different type of collective motion. Instead of swarming in whirls and jets as observed in most species including the shorter T-morphotype of *P. dendritiformis*, the C-morphotype moves in densely packed straight, but thin, long lines. Within these lines, all bacteria show periodic reversals, with a typical reversal time of 20 s, independent of their neighbours and any environmental parameter tested. The evolutionary advantage of this unique to-and-fro swarming remains unclear.

PDE/ODE MODELS OF COLLECTIVE SWIMMING: VISCOSITY, INTERACTIONS AND COLLISIONS

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We present a review of our work on PDE models of swimming bacteria.

- Analytical study of dilute suspensions. We introduced a stochastic PDE model for a dilute suspension of self-propelled prolate spheroids with tumbling and obtained an explicit asymptotic formula for the effective viscosity (E.V.) that explains the mechanisms of the drastic reduction of E.V.
- Analytical and numerical study of dilute and semi-dilute bacterial suspensions. We introduced a semi-dilute model for swimming bacteria that includes pairwise interactions and obtained an explicit asymptotic formula for the E.V. We also conducted numerical modeling of a large number of interacting bacteria with excluded volume constraints. Comparison with the dilute case leads to a phenomenon of stochasticity arising from a deterministic system.
- Analytical and numerical studies based on kinetic models: beyond Mean-Field. We seek to capture a phase transition in the bacterial suspension – an appearance of correlations and large scale structures with an increase of concentration. Collisions of the bacteria, ignored in most of the previous works, play an important role in this study, which is based on the kinetic theory approach. We introduced an analytical model of two swimmers, and show that collisions must be modeled by the Navier boundary conditions (with slip) rather than the commonly used no-slip.

Collaborators: PSU students S. Ryan and B. Haines, and V. Gyrya, PSU postdoc M. Potomkin, and DOE scientists I. Aronson and D. Karpeev (both Argonne Nat. Lab)

SWARMING BY NATURE AND BY DESIGN

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The cohesive movement of a biological population is a commonly observed natural phenomenon. With the advent of platforms of unmanned vehicles, this occurrence is attracting renewed interest from the engineering community. This talk will review recent research results on both modeling and analysis of biological swarms and also design ideas for efficient algorithms to control groups of autonomous agents. For biological models we consider two kinds of systems: driven particle systems based on force laws and continuum models based on kinematic rules. Both models involve long-range social attraction and short-range dispersal and yield patterns involving clumping, mill vortices, and surface-tension-like effects. For artificial platforms we consider the problem of boundary tracking of an environmental material and consider both computer models and demonstrations on real platforms of robotic vehicles. We also consider the motion of vehicles using artificial potentials.

MACROSCOPIC MODELS OF SELF-ORGANIZATION

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Self-organization and emergence phenomena appear in systems consisting of autonomous agents interacting locally without leaders. They can be observed in virtually all contexts (physics, biology, social sciences) and at all scales to such an extent that they must be considered as the rule rather than as an exception in the universe. However, their theoretical study (from a mathematical perspective) is still at its infancy, because they raise fundamentally new questions that classical methods of kinetic theory can hardly solve. Such a fundamental question arises when one attempts to (quasi)-rigorously derive macroscopic (or continuum) models from Individual-Based (particle-like) models. The problem, which has already been recognized as one of the major difficulties in models of collective dynamics (see introduction of [1]) is the loss of conservation laws (such as momentum conservation). Indeed, conservation laws are the corner-stone of most macroscopic models and of their specific structures and properties. We will use models of self-propelled particles interacting through alignment (see review [1]) to discuss the difficulties brought by the non-preservation of momentum in the system and present a new methodology allowing to bypass them. This talk will be based on a series of works [2-6].

- [1] T. Vicsek, A. Zafeiris, Collective motion, Physics Reports, Vol. 517, pp. 71-140, 2012
- [2] P. Degond, S. Motsch, Continuum limit of self-driven particles with orientation interaction, Math. Models Methods Appl. Sci., 18, Suppl. (2008), pp. 1193-1215.
- [3] P. Degond, J-G. Liu, Self-alignment interactions with precession and the Landau-Lifschitz-Gilbert equation, Math. Models Methods Appl. Sci., 22, Suppl. 1 (2012), 1140001.
- [4] A. Barbaro, P. Degond, Phase transition and diffusion among socially interacting self-propelled agents, to appear in Discrete and Continuum Dynamical Systems B.
- [5] P. Degond, A. Frouvelle, J-G. Liu, Macroscopic limits and phase transition in a system of self-propelled particles, to appear in Journal of Nonlinear Science.
- [6] P. Degond, J-G. Liu, S. Motsch, V. Panferov, Hydrodynamic models of self-organized dynamics: derivation and existence theory, arXiv:1108.3160

HETEROSPECIFIC PUBLIC INFORMATION USE GENERATES COLLECTIVE BEHAVIOUR IN MULTI-SPECIES SONGBIRD FLOCKS

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The choice of when and with whom to associate is a fundamental question in the study of animals that live in groups. But understanding the rules that govern the social decisions they make is challenging due to multiple levels of selection and causation that operate. By studying multi-species groups we can study social decisions without confounding effects of kin selection or mate choice. Mixed-species flocks, a ubiquitous case of multi-species group-living, are often described as ‘bird waves’ consisting of individuals from several species that maintain cohesion through time and space. Here we test the relative use of social information from heterospecifics and conspecifics in collectively behaving mixed-species flocks. We also test whether individuals trade-off the mutualistic benefits of collective flocking with increased interference competition. We deployed artificial habitat patches and recorded 91 576 records of feeding events by 1 904 individuals from five species, and found highly synchronised feeding behaviour with active movement by individuals towards high-density parts of the patch. However this pattern was negatively influenced by competition. The high weighting of social information from heterospecifics reflects its importance in the decision-making of foraging groups.

PERSISTENCE AGAINST DISSIPATION: HOW DESERT ANTS MAKE THEMSELVES UNDERSTOOD

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Biological individuals often interact to form cooperative societies that have functional advantages. How the specifics of these interactions constrain collective performance is not well understood. In this context, we study how desert ants inform each other about the presence of food. We use automated tracking to generate a large data-base of ant trajectories and interactions that provides us with sufficient statistics to empirically estimate the efficiency of their communication. This is done, quantitatively, by calculating the information theoretical channel capacity of the ants' pairwise interactions. We find that this channel is noisy to a degree that makes it difficult for ants to tell between a recruiter reporting about food and a random collision within the dark nest environment. To distinguish these ambiguous signals the colony must therefore perform error-correcting on the level of the group. We demonstrate that the ants accomplish this by exhibiting strict control of when to transmit a message and when to respond to received information. This control leads a collective process that couples negative and positive feedbacks and ensures reliable colony performance. Thus, the ants need no language, but just one aptly used "word" pronounced with conviction inside a noisy environment.

HIGH ORDER SOCIAL INTERACTIONS IN SMALL POPULATIONS OF MICE

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Social behavior in mammals is often studied in pairs and under artificial conditions. However, the behavior of groups as a whole, and of individuals within a group, may arise from complex network of dependencies among them. We studied small groups of mice in a semi-natural environment, whose behavior was automatically tracked for several days. To uncover the underlying social interaction network of groups of animals, we built mathematical models of the joint activity patterns of the members of the group. We found that the locations of the mice in the arena were significantly correlated, and synergetic when viewed as a group. We used a maximum entropy framework to model the distribution of mouse configurations, where the state of each animal was given as one of 10 locations in the arena. The maximum entropy model in this case is a generalized Potts model. We found that a pairwise maximum entropy model could account for less than 60% of all correlations among the mice; the third order model, explain 90% of the correlations or more. We then used the interaction terms in the generalized Potts model to construct a social interaction map between the mice. Finally, in spite of the variability in the interactions when we compared groups of mice with environmental or genetic variations we found that groups with similar backgrounds clustered together in terms of their distribution of states.

NOVEL METHODS FOR HIGH-THROUGHPUT AUTOMATED ETHOLOGY

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Recent trends in ethology indicate a new and exciting focus on the research of animal groups, swarms and societies instead of animals as individuals. However, the parallel observation of many individuals requires non-trivial, usually technology-assisted solutions to aid the precious work of the ethologist. To narrow the gap between state-of-the-art technology and the traditional approaches in animal group research, here we show some of our novel, automated methods that can easily be used in a wide range of species as multi-target tracking tools, providing information that can form the basis of subsequent innovative analysis. We present two case studies of “high-throughput ethology”. First, we show a custom made miniature GPS/INS logger weighting only 13g to measure the details of the collective flight of 30 pigeons. Second, we present a computer vision based multi target tracking method that was used for the individual, simultaneous tracking of members of a pigeon society in a loft and several rodents in a group. Both case studies focus mainly on the technological aspects and difficulties of such systems and provide solutions that could be used in a wider context in animal research.

LIVING ARCHITECTURES

BRIDGE CONSTRUCTION IN ARMY ANTS

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Robustness and adaptability are central to the functioning of biological systems, from gene networks to animal societies. Yet the mechanisms by which living organisms achieve both stability to perturbations and sensitivity to input are poorly understood. Here we present an integrated study of a living architecture in which army ants interconnect their bodies to span gaps. We demonstrate that these self-assembled bridges are a highly effective means of maintaining traffic flow over unpredictable terrain. The individual-level rules responsible depend only on locally-estimated traffic intensity and the number of neighbours to which ants are attached within the structure. We employ a parameterized computational model to reveal that bridges are tuned to be maximally stable in the face of regular, periodic fluctuations in traffic. However analysis of the model also suggests that interactions among ants give rise to feedback processes that result in bridges being highly responsive to sudden interruptions in traffic. Subsequent field experiments confirm this prediction and thus the dual nature of stability and flexibility in living bridges. Our study demonstrates the importance of robust and adaptive modular architecture to efficient traffic organisation and reveals general principles regarding the regulation of form in biological self-assemblies.

INDIVIDUAL-BASED ASSESSMENT OF INFORMATION CENTERS IN GRIFFON VULTURES (*GYPS FULVUS*)

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Information transfer among conspecifics regarding food patches may decrease foraging costs and facilitate recruitment to discovered patches, providing an evolutionary advantage for communal roosting. The Information Center (IC) hypothesis was suggested as a possible mechanism for information transfer, but empirical support is lacking. This hypothesis ascribes that naïve individuals (missing prior information on a specific patch) may benefit from following informed individuals returning from roosts to previously visited food items. Therefore, IC is expected to generate coordinated movements of animals, based on differential access to information about food resources.

We tested this hypothesis and its prerequisites by tracking foraging movements of 47 free-ranging griffon vultures (*Gyps fulvus*) tracked over 316 ± 30 days (mean+SD) using GPS/ACC transmitters in high spatiotemporal resolution and demonstrated that birds returned to the same eating sites in sequential days and that naïve individuals follow informed ones. Unlike previous studies we were able to reject the occurrence of other social foraging mechanisms such as local enhancement by observing long joint flight events. Our results provide strong quantitative support for most of the IC prerequisites suggesting that vultures' colonies serve as information centers. This highlights the potential detrimental effects of declining populations on the individual ability to forage efficiently. It also marks a mechanism generating coordinated movements among conspecifics, which might be extended to multiple animal species of the same guild.

RECEPTIVE FIELD MODEL ACCURATELY PREDICTS INDIVIDUAL ZEBRAFISH BEHAVIOR IN A GROUP

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One of the most intriguing features of collective behavior is the ability of groups of animals to perform synchronized motion and collective decisions without apparent leadership or centralized control. Here, we studied the group behavior of adult Zebrafish in a controlled laboratory environment. We used fast video recording and automatic tracking to reconstruct the trajectories of individual fish and obtain a detailed quantitative description of their swimming behavior. To characterize collective motion in these groups, we modelled the directional response of a single individual based on a “receptive field” model of its surrounding. We used our high temporal resolution data to learn the weights that a fish gives to the movement of the other fish in space, taking into account the specific direction and angle of a neighbor relative to the center fish. Our model predictions show very strong agreement with actual fish swimming behavior at a single point in time. We further found that including the effect of arena walls on the fish in our model improved our predictions significantly. Thus, although zebrafish do not show highly synchronized and polarized motion as a group, individual behavior can be predicted accurately from the group. This approach enabled us not only to get an accurate description of fish behavior but also to compare different theoretical assumptions (such as metric distances vs. topological ones).

THE IMPORTANCE OF UNINFORMED INDIVIDUALS IN CONSENSUS DECISION-MAKING

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Collective systems are pervasive across all scales of the natural and engineered world, in part due to their ability to make rapid, accurate decisions even in complex environments or amidst conflicting needs. A substantial body of work has emerged to explain how these groups are able to leverage numbers to amplify environmental signals, dampen noise, and exhibit other forms of collective intelligence. The sheer diversity of these systems, however, has made it difficult to address central questions about collective decision-making in any unified manner. Key questions include (A) How and when are groups able to achieve consensus? (B) How does the mechanism by which organisms act on social information influence group outcomes? (C) How should one express individual opinions and pool social information simultaneously? Recent work by Couzin et al. has shown that uninformed individuals in animal groups play a crucial role in consensus decision-making, shaping both the process and outcomes in two-choice foraging tasks [1]. Uninformed individuals, or those who have no bias/preference regarding outcome, are ubiquitous across collective systems from populations of neurons to animal groups, and yet have been largely overlooked or misunderstood. Here we employ models and experiments to demonstrate that, for a wide range of conditions, a strongly opinionated minority can dictate group choice, but the presence of uninformed individuals spontaneously inhibits this process, returning control to the numerical majority. Our results emphasize the role of uninformed individuals in achieving democratic consensus amid internal group conflict and informational constraints.

[1] Couzin, Iain D., et al. "Uninformed individuals promote democratic consensus in animal groups." *Science* 334.6062 (2011): 1578-1580.

CELLULAR NAVIGATION: FROM AMOEBA TO CANCER

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Cellular migration is a central part in diverse biological processes, from development and immune response to cancer metastasis. In many cases, cellular motility is guided by directional cues, such as a gradient of a nutrient or a growth factor. The motion of a cell is also restricted by the structure of its surrounding environment, which typically includes other cells as well as the extracellular matrix (ECM). The migrating cell therefore needs to perform a complicated task of navigation under physical constraints.

We start with the basic amoeboid motion in a complex environment, from motion in an obstacle-free environment to navigation between obstacles and finally to moving in a maze. We show that cells employing simple chemotactic strategies will often be unable to navigate through maze-like geometries, but a simple chemical marker mechanism serves as a “memory” and significantly improves success rates.

We continue to study the more complex case of cellular invasion, which also includes the ability to degrade the surrounding ECM, as represented by the maze walls. This is typically the case for early metastasizing cancer cells, which secrete matrix metalloproteases (MMPs) which degrade the ECM. Using the maze platform together with energy considerations, we investigate how the different tasks of the cell, i.e. proliferation, invasion and migration, need to be balanced in order to optimize the overall dissemination. Interestingly, we find that a different priority set is needed for different resource levels. This implies that different cellular phenotypes, such as highly invasive or highly proliferative, are optimal for different conditions. We conclude that tumor plasticity, namely the coexistence of different phenotypes (also termed “proliferation-invasion dichotomy”), can be explained as optimization for dynamic conditions, as tumors typically go through cycles of hypoxia (low resources) and angiogenesis (high resources). Our simulation platform can be used to study additional diverse phenomena, such as collective vs. independent motility, cellular motility mode selection and cell decision making.

STABILITY AND CLUSTERING OF SELF-SIMILAR SOLUTIONS OF AGGREGATION EQUATIONS

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We consider the linear stability of a family of exact collapsing similarity solutions to the aggregation equation in a general dimension, where the density has a power law interaction with the exponent γ . It was previously observed that radially symmetric solutions are attracted to a self-similar collapsing shell profile in infinite time for $\gamma > 2$. We compute the stability of the similarity solution and show that the collapsing shell solution is stable for $2 < \gamma < 4$. For $\gamma > 4$, we show that the shell solution is always unstable and destabilizes into clusters that form a simplex which we observe to be the long time attractor. We then classify the stability of these simplex solutions and prove that two-dimensional (in-)stability implies n -dimensional (in-)stability.

COLLECTIVE DECISION MAKING IN STARLING FLOCKS

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Turning flock of starlings can be viewed as a paradigm for a synchronized rapid change of direction in moving animal groups. How birds in a flock decide when to turn and in what direction, and if changes in the direction of motion are instantaneous for all the birds in the flock are some of the questions which one would like to answer. In order to elucidate the origin and the mechanism of this collective decision making, we use newly obtained 3D trajectories of individual birds in flocks of starlings for the entire duration of a turning event.

We present the results for the turning flocks of up to 500 individuals, obtained using a variety of correlation functions for velocities and accelerations of individual birds. We show that the turning decision starts typically as a self-generated fluctuation in the direction of motion of one or few individual birds. In particular, we were able to extract a well-defined ranking of each individual bird in the flock, according to its reaction delay time: time it starts to turn after the initiating bird has started to turn. From such ranking, several important properties of the turning mechanism clearly emerge.

DOES DARWIN OR EINSTEIN EXPLAIN MOVEMENT IN SELF-ORGANIZED MUSSELS BEDS?

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Brownian motion has been the default template to model movement and dispersal of animals. However, the use of Brownian motion as a description of large-scale animal movement has been challenged by empirical studies, which show that many searching animals are found to do a Lévy walk, in which short movement steps are alternated with long moves. Currently, there exist significant controversy about which search model, Brownian or Lévy walks, best describes animal movement on both individual and population levels.

Here, we report on a change in observed movement patterns in self-organized “swarms” of mussels – establishing mussel beds. In mussel beds, short-range interactions between moving mussels leads to the development of regularly clumped patterns (1), a process which is akin to swarming of birds and school formation in fish. Based on a combination of experimental work and individual-based models of mussel movement during spatial self-organization, we show that mussel movement changes with density: it is best described by a Lévy walk (2) when mussel density is low, but changes to Brownian motion as the density of mussels increases.

To alternative explanations exists to explain observed shift in movement patterns. The first explains the shift from Brownian to Lévy movement by adaptation, as Brownian movement may provide a fitness advantage at high density (Darwinian hypothesis). The second hypothesis explains the shift by increasing rates of encounter (“collisions”) between the mussels at high density, blocking long-range movement. This hypothesis follows Einstein’s explanation for Brownian movement, caused by physical collisions between molecular particles in solution.

Separation in our experiments of free moving mussels from those whose movement is hindered by other mussels, revealed that the shift from Lévy-movement to Brownian movement resulted from physical encounters between mussels, following Einstein’s explanation for Brownian movement. Our results show that at low density, movement is determined by the intrinsic movement strategy of the mussels, shaped by Darwinian evolution. At high density, however, encounters between mussels lead to Brownian motion, and Einstein’s “collision” process dominates mussel movement patterns. Our results highlight the universality of Einstein’s explanation for Brownian movement, showing that collisions and (more general) encounters are important drivers of diffusion throughout nature.

[1] Van de Koppel et al, 2008, *Science* 322:739; [2] De Jager, et al 2011, *Science* 332:1551.

CLUSTERING OF MIGRATING BRAIN TUMOR CELLS: TYPICAL BEHAVIOR AND RARE EVENTS

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Glioblastoma tumors are highly invasive; therefore, the overall prognosis of patients remains poor, despite major improvements in treatment techniques. Cancer cells detach from the inner tumor core and actively migrate away [1]. Invasive cells have a very low proliferation (division) rate compared to those on the tumor surface. Unfortunately, these invasive cells may eventually switch back to the “proliferative” phenotype, after a cell has migrated a large distance from the original solid tumor; this gives rise to recurrent tumors.

The mechanisms of the phenotypic switch are poorly understood. We proposed [2] that it can be related to the observed clustering of invasive cells. Once such clusters are formed in the invasive region, cells on the surfaces of the clusters can become proliferative again, like the cells on a surface of a primary tumor. To investigate the mechanisms of cell clustering on a substrate, we formulated [2] a discrete stochastic model for cell migration. The model accounts for cells diffusion, proliferation and adhesion. We predicted that cells *typically* form clusters if the effective strength of cell-cell adhesion exceeds a certain threshold. Our prediction was confirmed in a series of experiments [2].

However, for many glioma cell lines, the effective strength of cell-cell adhesion is below the threshold value necessary for cluster formation. For sub-critical adhesion, the invasive cells do not *typically* form clusters; despite this, tumor recurrence does exist for these cell lines. We hypothesize that recurrent brain tumors can be triggered by a rare event - spontaneous clustering of invasive tumor cells [3]. Once a sufficiently large cluster is formed due to a large fluctuation, cells on the surface of the cluster may become proliferative, triggering rapid tumor growth.

[1] A. M. Stein et al, Biophys. J., 92, 356 (2007);

[2]. E. Khain et al, EPL 88, 28006 (2009);

[3]. E. Khain, M. Khasin, L.M. Sander, in review (2012).

FLOCKING MODELS OF TISSUE DYNAMICS

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The collective motion of cells constituting a tissue is a balance between factors affecting individual cell polarization and factors related to cell-cell physical and chemical interaction. Recent experiments by Trepap et al (for normal epithelial cells) and Zaritsky et al (for cancer cell lines) have shown that this balance can lead to surprising results, including the fact that tissues can be under large-scale tensile stresses, that free edges can lead to wave-like phenomena and that the cells can support swirling patterns of activity. We present a simple “flocking” type model of these dynamics, where the main notion is that cell polarization (i.e. the direction in which the cell tries to move) is strongly affected by forces arising from neighboring cells. This simple hypothesis explains much of the data and can form the basis of more quantitatively realistic models that include the role of activating chemicals and the effect of phenotypic variability.

THE COMPLEXITY OF DECISION MAKING IN GROUPS OF FISH

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One advantage for animals of living in groups is the ability to process information collectively to make better decisions than individuals on their own. Experiments have shown that shoals of fish can improve their decision making with increasing group size [1, 2]. In theory this effect can be derived from a variety of principles such as the ‘Many Wrongs’ [3] and ‘Many Eyes’ [2] hypotheses, and Condorcet’s Jury Theorem [4]. Recent work by [5,6] has shown how an optimal Bayesian approach to utilising social information leads to accurate group decisions. Based on this work we show how our experiments suggest that group decision making may be even simpler than such theory assumes, with a variety of fish species showing evidence of acquiring social information from only a small number of conspecifics, in line with recent results concerning the motion of individual fish in groups [7]

[1] Ward *et al.* P.N.A.S. 2011

[2] Couzin *et al.* Science 2011

[3] Simons T.R.E.E. 2004

[4] Condorcet 1785

[5] Pérez-Escudero & de Polavieja PLoS Comp. Biol. 2012

[6] Arganda *et al.* ArXiv 2012

[7] Herbert-Read *et al.* P.N.A.S. 2011

PATTERN FORMATION IN A SECOND-ORDER KINETIC SWARMING MODEL

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We consider a second-order self-propelled interacting particle system, which has been frequently used to model complex behavior of swarms such as fish schools or birds flocks. The interaction between animals is modelled as some combination of attractive, repulsive and alignment forces. For a large number of particles or individuals, continuous descriptions in terms of kinetic PDEs become increasingly desirable.

After an introduction of the model and the derivation of characteristic equations for certain particular solution, such as flocks and mills, we present some of the recent advances: First, we show that radial densities of flock or mill states can be computed explicitly for particular interaction potentials. Among others, this includes Quasi-Morse potentials in higher spatial dimension. Second, we show how the given model can be extended with behavioural rules inspired by biological observations, and how such new effects influence coherent patterns of motion on the level of the particle model, the kinetic equation as well as the hydrodynamic limit. Exemplarily, we will focus on the behaviour of starlings to overpass a preferred roosting area.

RISK AND INFORMATION DETERMINE COLLECTIVE DECISIONS IN ANIMAL GROUPS

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During consensus decision-making, individuals in groups balance personal information (based on their own past experiences) with social information (based on the behavior of conspecifics), allowing the group to reach a single collective choice. Previous studies of consensus decision-making processes have focused on the informational aspects of behavioral choice, assuming that individuals make choices based solely on their likelihood of being beneficial. However, decisions by both humans and non-human animals systematically violate such expectations. Furthermore, the typical experimental paradigm of assessing binary decisions, those between two mutually exclusive options, risks confounding two aspects common to most group decisions: minimizing uncertainty and minimizing risk.

Here we experimentally disassociate risk-based decisions from information-based decisions using a three-choice paradigm and demonstrate that both factors are crucial to understanding the collective decision-making of schooling fish. In addition, we demonstrate how multiple informational dimensions (here color and stripe orientation) are integrated within groups to achieve consensus, even though no individual is explicitly aware of, or has a preference for, the consensus option. Balancing of social and personal information by individuals in key frontal positions in the group is shown to be essential for such group-level capabilities. Our results demonstrate the importance of both information-based and risk-based considerations when explaining the collective capabilities of group living animals.

TRAFFIC MODELS FOR PEDESTRIAN AND THEIR COMPARISON WITH EXPERIMENTAL DATA

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Understanding the various factors which determine pedestrian flow efficiency is an important societal issue (e.g. traffic safety, optimization of traffic flow). With this aim, a simple traffic flow model is constructed and calibrated on the basis of experimental recordings. The novelty of the model relies on the introduction of a two direction flow depending on co and counter-moving pedestrians. A comparison between data and model is performed and we observe a good agreement for the apparition of clusters and traveling bands. However, some discrepancies are observed, which are due to the inhomogeneities of the pedestrians comfort walking speeds. To account for these inhomogeneities, we propose an extension of the model (model of second order) which improves the agreement with the experimental data.

COLLECTIVE MOVEMENT AND SOCIALITY IN EURASIAN JACKDAWS (*CORVUS MONEDULA*)

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The recent emergence of the movement ecology paradigm parallels an immense growth in interest on animal collective movements. Both themes have been strongly facilitated by new modeling tools developed to discern the underlying forces and rules, along with technological advances providing high resolution data of multiple animals on the move. Quantifying and modeling coordinated movements of free-ranging animals in large-scale real-life settings is a general major challenge hindering progress in these lines of research, especially for highly social animals. However, sociality is common among many animal species and has been regarded a key mechanism underlying coordinated movements. This motivates direct tests of how social interactions shape collective moves of free-ranging animals.

We propose an attractive system to cope with this challenge, investigating coordinated movements of Eurasian Jackdaws (*Corvus Monedula*). Jackdaws establish long-term pair bonds, exhibit strict monogamy with no extra-pair fertilization, and form a strong linear hierarchy in which high-ranking birds consistently win contests over low-ranking birds under variable circumstances. Jackdaws frequently fly in pairs, and also exhibit highly coordinated flock flights.

Our project, still in an initial stage, utilizes a video system to document flights of jackdaw flocks by two high resolution cameras, using image analysis tools to deduce the three-dimensional flight trajectories of each individual bird. We hypothesize that the social structure of jackdaws impacts flight patterns, including highly coordinated flights of pair mates and consistent leader-follower relationships in the group. Testing these hypotheses first requires quantifying flight patterns, followed by analysis of the dynamics of nearest neighbors, and the directional correlation delay time for each pair and between each bird and the rest of the group. In a more long-term perspective, we aim at linking the findings of this work with quantitative data on social hierarchy and associations among tracked individuals.

MECHANISMS UNDERLYING COLLECTIVE BEHAVIOUR IN DESERT LOCUST NYMPHS

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From biblical times and still today, the devastating effects of mass migrating insects, specifically those of the desert locust (*Schistocerca gregaria*), have attracted much attention. However, our understanding of swarm formation and of the complex interactions within a locust swarm is still very far from complete. Synchronized movement is seen not only in flying adult locusts but also in bands of juveniles, in which the wingless hoppers form a marching swarm that can extend over kilometres. What are the mechanisms that allow a swarm to move in coordination?

We used video recording and cutting-edge methods of movement tracking to monitor the marching behaviour of five-instar desert locust nymphs. 30-50 crowd-reared locusts in our experimental system will spontaneously generate robust and consistent coordinated marching behaviour. Using high temporal and spatial resolution analysis in a MatLab environment, we investigated the early stages and maintenance of this behaviour. We show that the order parameter, which quantifies the level of synchronisation within the experimental arena, correlates with the fraction of walking nymphs. We therefore focused on investigating the stimuli that cause walking initiation. Individual animals within the crowd intermittently switch between standing and walking, a switch that can be triggered by tactile or visual stimuli. We report that initiation (or resumption) of walking that is not preceded by touch depends on a decrease in the number of moving animals in close proximity. This finding suggests a role of visual stimuli in establishing and maintaining synchronized movement in marching locust bands. While continuing to study further collective behavioural rules in the system, we also take advantage of the locust as an established neurophysiological preparation in order to investigate the underlying neural mechanisms that allow this collective behaviour among locusts.

COLLECTIVE DECISION MAKING IN PIGEON FLOCKS

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Groups of animals accumulate information and reach decisions in ways that often result in informational benefits from being gregarious. There is growing empirical evidence that animals use social information to increase their navigational accuracy. At the same time, it is now possible to choose and calibrate models of collective behavior using empirical data. This leads to the question of whether a model calibrated on local responses in small groups predicts the global features of decision-making across a range of group sizes. In this study, we analyze how pigeons respond to each other while reaching a consensus homing route, using high-resolution GPS tracking. In addition, we estimate each bird's relative influence on the flock's choice of route, by comparing the flock's route to the preferred homing route each pigeon had established when flying alone. Larger flocks are less likely to follow one bird with a minority preference. We test how well various models predict this effect, focusing on how pigeons respond to multiple neighbors and whether this improves the flock's ability to collectively process navigational information.

A COGNITIVE APPROACH TO COLLECTIVE BEHAVIOR

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I will describe a program to understand the cognitive underpinnings of collective behaviour. First, I will describe a theoretical approach that uses very general features of how brains process information [1]. This approach is shown to give simple theoretical expression for decisions in animal collectives that compare very well with data in different species. Second, I will describe a new tracking method that allows the study of animal groups by identification, with the advantage of following individuals across different experiments. Third, I will describe neurobiological techniques in zebrafish that will allow the study of the impact of attention, motivation, emotions and sensorimotor processing in group behaviour.

[1] S. Arganda, A. Pérez-Escudero, G. G. de Polavieja 'A common rule in collective decision-making across species' PNAS (early edition, 2012)

THE VICSEK MODEL IN THE LARGE VELOCITY REGIME - ANISOTROPIC BEHAVIOR AND CORRECTION

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Numerical investigations of the classic Vicsek model of self-propelled particles show that in the large velocity limit the boundary of the domain of simulation has a substantial effect on the isotropy of the dynamics [1]. In particular, the order parameter has preferred directions. This anisotropy may even change the type of the phase transition.

We have investigated this phenomenon numerically to find the characteristics of this anisotropy. We find it is strongly dependent on the speed of particle and increases with system size. In this case, it may affect the qualitative behaviors of the system and the phase transition. The precise speed threshold for which this behavior becomes significant is unclear.

We suggest a perturbed model in which the macroscopic anisotropy is compensated by introducing a microscopic anisotropy. This is achieved by making the noise depend on the particle direction.

[1] M. Nagy, I. Daruka, and T. Vicsek, *Physica A* **373**, p. 445 (2007).

MODELING LOCUST SWARM MOTION AND THE BUILDUP OF SYNCHRONIZATION

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A simplified model is developed in order to show how interactions between individual locusts lead to coherent motion in a swarm. All model parameters are calibrated according to experimental results in which several dozens of marching locust nymphs move freely in a circular arena. Experiments reveal that the order parameter, which is a measure of the degree of order in the system, is correlated with the number of walking locust. In addition, order is meta-stable, meaning that coherent motion is a long lived state, but unstable. Experiments also suggest that walking initiation is the critical mechanism in the buildup of synchronization. Movement is initiated due to two reasons: touch (tactile stimulus) and other locusts moving away.

In our model, particles modeling individual locusts move in a one dimension circular domain representing an annulus in which the locusts effectively move. Particles move either clockwise or counter clockwise at a constant speed. The model specifies the probability of a particle to start or stop moving, and to change its direction (make a U-turn).

Simulations reproduce several experimental results: order is meta-stable because as movement becomes more coherent, locusts are more likely to change direction and join other locust motion. Also, the order parameter and number of walking locust are positively correlated. This is because on average, as movement becomes more ordered, individuals see larger groups moving away. This increases their chance to initiate walk due to visual stimulation.

HUMAN SWARMS, HOW MUCH DOES HUMAN INFORMATION FLOW FIT IMITATION HEURISTICS

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This work considers the percolation of information through social networks, and, particularly, how this flow is affected by herd behavior phenomena.

Let us define the state of a node in the network to be positive as it accepts a new idea. We defined "Full Herd Behavior" (HB) as the extreme "upper bound" where the acceptance of new ideas is only the result of imitation. For example, consider a case where the probability of accepting a new idea is proportional to the average over all states of all members in a population / group. Although full HB is by no doubt only theoretical, we assume that HB is, to some degree, a factor which affects the acceptance of new ideas / products in social groups.

For analysis purpose we simulate the change of states over time in by a synthetically constructed Barabasi-Albert network. We further assume that the probability of infection follows the HB rule.

In comparison to the traditional models of infection spreading with fix probability, the change of states seems to follow a different pattern that better fits an exponential growth compared to a high degree power function of the non HB models.

Using the Google Correlation tools, we look for terms that have been searched in the last years through the Google Search Engine, and follow the exponential growth function (found resulting from the HB synthetic model). We compare terms having an exponential growth to terms having a power growth. Initial result might suggest that information flow of novel concepts follow exponential growth, while power growth characterizes less novel concepts.

Although the research is only in its early stages, preliminary results might suggest that HB is indeed a factor in the adoption of novel ideas. The results trigger several research directions.

COMPLEX COLLECTIVE NAVIGATION IN BACTERIA-INSPIRED MODELS

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We investigate how complex navigation capabilities may arise in simple multiagent systems. Bacteria-inspired agents are simple simulated processing units that have limited computational ability and very short memory. We study the computational and functional abilities of groups of bacteria-inspired agents in the context of natural problems, in particular, collective navigation.

Our study is inspired by bacteria. Bacteria exhibit remarkably sophisticated collective behaviours such as complex expansion patterns, intricate multi-cellular structures, and complicated movement dynamics, in which cells organize into vortices or move collectively in a common direction.

We used mathematical analysis and simulations and found new underlying mechanisms beneficial to collective navigation which may exist in bacteria: adaptable interactions and molecular communication. Adaptable interactions significantly improved the collective swarming performance of bacteria inspired agents, leading to highly efficient navigation even in very complex terrains [1]. Cargo transport, such as fungal spores, was investigated in such models [2]. We went further, to understand navigation in terrains with obstacles, such as a maze. We found that molecular communication, by a diffusing repellent, allowed simulated swarms to navigate efficiently in a maze and we took a first step into a new form of analysis of navigation around obstacles.

[1] Shklarsh A, Ariel G, Schneidman E, Ben-Jacob E (2011) Smart Swarms of Bacteria-Inspired Agents with Performance Adaptable Interactions. PLoS Computational Biology.

[2] Shklarsh A, Finkelshtein A, Ariel G, Kalisman O, Ingham C, Ben-Jacob E (2012) Collective navigation of cargo-carrying swarms. Interface Focus.

CONTROLLING COLLECTIVE BEHAVIOR IN SUSPENSIONS OF SWIMMING BACTERIA

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A suspension of swimming bacteria *Bacillus subtilis* demonstrates novel physical properties. At concentrations above critical, the system exhibits transition from individual swimming to a collective swarming characterized by large scale coherent structures: jets, vortices, plumes. Correlation length of the bacterial flow in the regime of collective swimming is larger than the size of individual bacteria by an order of magnitude. We experimentally investigated spatial and temporal correlation functions for various swimming speeds and concentrations. Our measurements produced a puzzling result: while the energy injection rate is proportional to the swimming speed and concentration, the correlation length remains almost constant until the noise induced by tumbling of bacteria is negligible [1]. It highlights two dominant interaction mechanisms: hydrodynamic entrainment and steric collisions. Their strength is proportional to the swimming speed and concentration.

Interaction of bacteria with externally induced flow results in a reduction of effective viscosity. Measurements of the shear viscosity in suspensions of swimming bacteria in a free-standing liquid film have revealed that the viscosity can decrease by a factor of 7 compared to the viscosity of the same liquid without bacteria or with nonmotile bacteria [2].

We also present a class of systems in which randomly moving bacteria can rotate submillimeter gears decorated with asymmetric teeth, primitive systems of gears, or actuate V-shape objects. The directional rotation is observed only in the regime of collective swimming and the gears' angular velocities depend on and can be controlled by the amount of oxygen available to the bacteria [3].

[1] A. Sokolov and I.S. Aranson, Phys. Rev. Lett. (2012)

[2] A. Sokolov, I.S. Aranson, Phys. Rev. Lett. **103**, 148101 (2009)

[3] A. Sokolov et al, PNAS **107** 969 (2010)

THE EVOLUTIONARY ECOLOGY OF INSECT MASS MIGRATIONS

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Swarming locusts and Mormon crickets provide some of the most spectacular examples of insect mass migration. Swarms can contain billions of individuals, and in the case of flying adult locusts, are capable of extended flights across continents and oceans. These insect mass movements have been noted by humans throughout history, in no small part due to their ecological and cultural impact as agricultural pests. However, our understanding of the proximate and ultimate mechanisms underlying swarm formation and movement has changed dramatically in a relatively short amount of time. I will provide an overview of these advances, highlighting recent empirical work across disciplines ranging from radiotelemetry and molecular population genetics to collective dynamics and nutritional ecology. Particular emphasis will be placed on ongoing efforts to use field-collected individual-based movement data to test collective movement models.

HETEROPHILIOUS INTERACTIONS ENHANCE FLOCKING IN SELF-ORGANIZED DYNAMICS

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We discuss self-organized dynamics of agent-based models with focus on a prototype model driven by non-symmetric self-alignment introduced in [1].

Unconditional consensus and flocking emerge when the self-alignment is driven by global interactions with a sufficiently slow decay rate. In more realistic models, however, the interaction of self-alignment is compactly supported, and open questions arise regarding the emergence of clusters/flocks/consensus, which are related to the propagation of connectivity of the underlying graph.

In particular, we discuss heterophilious self-alignment: here, the pairwise interaction between agents increases with the diversity of their positions and we assert that this diversity *enhances* flocking/consensus. The methodology carries over from agent-based to kinetic and hydrodynamic descriptions.

[1] A new model for self-organized dynamics and its flocking behavior, *J. Stat. Physics* 144(5) (2011) 923-947.

VISUAL SENSORY NETWORKS AND COLLECTIVE INFORMATION TRANSFER IN SCHOOLING FISH

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Little is known empirically about how information propagates through animal groups. We investigate two functionally important contexts for collective information transfer in schooling fish: the propagation of sudden escape responses through a school, and leadership events. Using computer vision, we tracked the position and reconstructed the visual field of each individual in schools of 70 and 100 conspecifics. We measured a range of visual and non-visual features available to each individual to determine, using Bayesian model selection, the subset of features most predictive of a behavioral response (a startle or following event, respectively). In both experiments, the angular area subtended by a neighbor on the retina was more important than a neighbor's metric or topological distance. Moreover, a network analysis of our experimental data indicates that metric and topological interaction models typically fall within the same class (under a wide range of parameterizations), and are both dissimilar to visual networks based on angular area. Visual networks obtain a consistently lower transitivity and average path length for the same average number of neighbors, suggesting that metric and topological models may underrepresent the rate at which information propagates through a group, while over-representing the degree of correlated information between neighbors.

CONTEXT-DEPENDENT HIERARCHIES IN ANIMAL SOCIETIES

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Social structure has the potential to impact the way that information flows through groups and the group decisions that emerge during collective action. In the case of collective motion¹, the relationship between leadership and social dominance varies among species, but the majority of case studies report that dominant individuals lead group movements. Here we use novel, computer-vision based methods and miniature GPS tracking to study, respectively, social dominance and in-flight leader-follower relations in pigeons and find that dominance and leadership hierarchies are entirely independent of each other. In addition to confirming the existence of multiple independent and context-specific hierarchies in pigeons, we succeed in setting out a novel, robust, and scalable method for the automated analysis of dominance relationships, applicable to many species.

In order to get a deeper insight into the mechanisms favouring the emergence of context-dependent hierarchies we have also used a modeling approach. Groups of animals or people often face problems they need to solve together. During the associated collective decision-making process members of the group typically contribute to finding the best solution with varying degrees of input. Here we introduce a family of models based on the most general features of group decision making to show that – from an approach based on first principles only - the optimal distribution of competences and pliancies is highly skewed with a structured fat tail. We show that such a distribution (order hierarchy) leads to performances exceeding several times those obtained for other common distributions.

We have also addressed the most general question of how and why a hierarchical network of the pairwise interactions is likely to emerge in a group of selfish individuals. Spontaneously arranging interactions into a given structure is a clear sign of cooperative problem solving even if the actors are selfish. In the case of living matter or social systems there must be an advantage of such an organization, because of the permanent evolution of these systems preferring the more efficient (having a larger fitness) variants. But where is this advantage? Better adaptability? A more robust, stable structure? Our calculations provide both some heuristic and quantitative answers to these fundamental questions.

*In collaboration with : Zs. Ákos, D. Biro, M. Nagy, T. Nepusz and A Zafeiris

[1] T Vicsek and Anna Zafeiris, Collective motion, *Physics Reports*, Volume 517, Issues 3-4, 2012, Pages 71-140 and <http://hal.elte.hu/~vicsek>

OVERCOMING SENSORY INTERFERENCE IN A SWARM OF BATS

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Bats are among the most social mammals. Some bat species roost in large colonies of thousands or individuals exhibiting vast social behavior. Many bat species exhibit different forms of swarming behavior including emerging from their cave in a swarm and flying together for many kilometres or foraging in a dense group of many bats at one location. Most of these bats use echolocation as a primary active sensing modality to orient themselves: they emit ultrasonic SONAR signals and analyze returning echoes to perceive their surroundings. Since the echolocation-signal of a specific bat species has evolved to fulfil sensory demands it is very similar across individuals. This results in sensory interference which is unique to bats: when many bats using the same echolocation signal fly together they must distinguish echoes returning from their own emissions from echoes returning from other individuals' calls. This problem increases dramatically with an increase of the number of bats around. Several people have suggested that bats spectrally alter their signals to avoid interference (spectral jamming avoidance), but this was only demonstrated for simple situations in which pairs of bats fly together.

We will present results of several approaches to study the problem of sensory interference when flying in a swarm including carefully controlled behavioral experiments, semi-natural laboratory experiments simulating sensory interference and on-board audio recordings from free-flying bats in the wild.

Our results suggest that spectral jamming avoidance is not the only solution for the entire repertoire of swarming behaviors presented by bats and imply other alternatives.