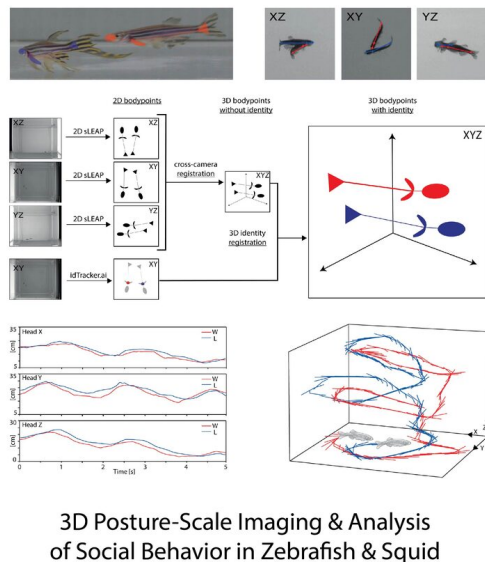


Biological Physics Theory Unit (Greg Stephens)

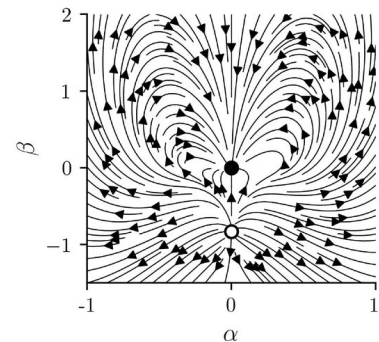
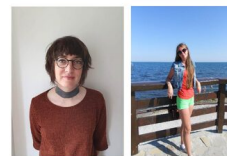
FY2021 Annual Report

Biological Physics Theory Unit

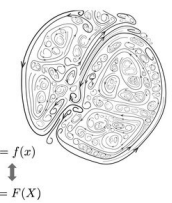
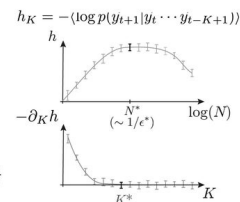
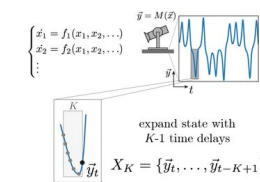
Professor Greg J Stephens



Theory of Slender Animal Behavior



Maximally-Predictive Delay Embedding



Single-organism and Collective Behavior from Data



Abstract

Research in the Biological Physics Theory Unit is organized to seek deep understanding in animal behavior through a combination of quantitative measurements, theory and modeling, and biological insight. We draw and develop experience in each theme from both within the unit and through collaborative partners, at OIST and internationally. In published work we have sharpened our theoretical and modeling focus through a series of approaches aimed at a principled understanding of posture dynamics and developed experimental and tracking techniques that open unparalleled opportunities for high-resolution behavioral analysis, from single organisms to small groups, to collectives. In our future plan we seek to solidify our understanding of single-animal movement and increasingly explore more complex organisms and social situations. In doing so we will ultimately approach questions traditionally associated with our own human experience, but from a novel direction: one rooted in a complete quantitative language which embraces natural behavior, strives to be free of constraining assumptions and attempts to infer rather than postulate the behavioral strategies employed. Our current work is organized around four projects in three primary directions:

- Quantitative analysis of social behavior in zebrafish (Project 1) and in the group dynamics of squid (Project 2), the latter resulting from a new collaboration with the Reiter Unit. Despite remarkable recent effort in high-resolution measurement of animal behavior, tracking and analysis in social settings are comparatively under explored. In zebrafish are extending our work on fighting to well-chosen mutants in collaboration with the Masai Unit and to the longer timescales necessary to

understand (and even predict) fight outcome. We will expand to other social situations in small groups, and with more posture degrees of freedom to resolve subtle social signals. In squid we are performing the first quantitative analysis of group behavior in this evolutionary distant species, including visual communication through skin patterning.

- Effective theories for slender-animal posture-scale movement (Project 3). Theories and principles of movement arise in a wide variety of fields, from robotics and biomechanics to neuroscience and physics of complex matter, but with varying frameworks and complexity that hinder general understanding. We are exploring a simple unifying perspective that is both consistent with recent, data-driven approaches (such as from *C. elegans* and *Drosophila* larva) and predictive of locomotory behavior in diverse settings and animals.
- Dynamical, data-driven approaches for longer-time behaviors and collective systems (Project 4). Physics offers countless examples for which theoretical predictions are astonishingly powerful, such as the first detection of gravitational waves from atomic-scale deformations in kilometer-scale interferometers. But it's hard to imagine a similar precision in complex systems where the number and interdependencies between components simply prohibits a first-principles approach. We are extending to collective systems our successful "inverse" perspective in which we integrate information theory, dynamical systems and statistical physics to extract understanding directly from measurements of both model and real systems.

These directions are broadly supported by current and arriving unit members: postdoctoral scholars Hiroi Makoto (Project 2), Jane Loveless (Project 3), Christian Esperza Lopez (Project 4); technician Tatsuo Izawa (Project 1) and OIST graduate student Akira Kawano (Project 1). We also closely co-advise graduate students with related interests (Lakshmipriya Swaminathan, Stephens & Uusisaari Units; Irina Korshok, Stephens & Miller Units; Mariia Pavelchenko, Stephens & Masai Units).

1. Staff

- Prof. Greg J. Stephens
- Naoko Ogura-Gayler, Research Administrator
- Dr. Makoto Hiroi, Postdoctoral Scholar
- Dr. Jane Loveless, Postdoctoral Scholar
- Dr. Christian Esparza Lopez, Postdoctoral Scholar
- Tatsuo Izawa, Technician
- Akira Kawano, Graduate Student (joint with Masai Unit)
- Lakshmi Swaminathan, Graduate Student (joint with Uusisaari Unit)
- Irina Korshok, Graduate Student (joint with Miller Unit)
- Mariia Pavelchenko, Graduate Student (joint with Masai Unit)
- Liam O'Shaughnessy, Visiting Research Student
- Dr. Antonio Carlos Costa, Visiting Researcher

2. Collaborations

2.1 Social Behavior of Zebrafish in 3D

- Seeded with HFSP program grant (closed July 2021)
- The physics of social behavior in the 3-dimensional shoaling of zebrafish
- Type of collaboration: Joint research
- Researchers:
 - Professor Ichiro Masai, OIST Graduate University
 - Professor Joshua Shaevitz, Princeton University

2.2 Physics of Social Insect Behavior

- Type of collaboration: Joint research
- Researchers:
 - Professor Orit Peleg, University of Colorado
 - Professor Kasia Bozek, University of Cologne

2.3 Dynamical Approaches to Complex Systems

- Type of collaboration: Joint research
- Researchers:
 - Dr. David Jordon, Cambridge University

2.4 Physics of Squid Behavior

- Type of collaboration: Joint research
- Researchers:
 - Prof Sam Reiter, OIST Graduate University

2.5 Biomechanics of *Drosophila* Larval Locomotion

- Type of collaboration: Joint research
- Researchers:
 - Prof Ellie Heckscher, University of Chicago

3. Activities and Findings

3.1 Research Highlights

Behavior of Single Organisms (Antonio Costa, Jane Loveless, Irina Korshok, Lakshmi Swaminathan)

Our work on the behavior of single organisms offers our most mature demonstration for what we mean by "physics of behavior". We address three primary questions: How do we characterize and understand the variability of posture-scale behavior, how can we use this variability to infer behavioral strategies and control, and how can we understand natural behavior from a general theoretical perspective? We integrate statistical physics, dynamical systems and information theory, using both a conventional "forward" style in which we create and explore models and their consequences, but also importantly in the "inverse" where we interrogate precision measurements to infer important quantitative concepts directly from data. We believe that such an inverse approach is an essential component in understanding animal behavior for which we may not know *a priori* the right universality class or even the most relevant theoretical concepts.

We introduced a framework for the principled extraction of coarse-grained, slow dynamics directly from time series data (Costa et al, 2021). We combine delay embedding, fine-scale partitioning, and a Markov approximation of the resulting sequence entropy to reconstruct a maximally predictive state space. We analyze dynamics through ensemble evolution directed by transfer operators approximated from transition probabilities between partitions, and we identify long-lived states through the eigenvalues and eigenfunctions of these operators.

Such data-driven approaches employed in the Stephens Group have revealed important and surprising aspects of whole-animal behavior including indications of a damped and driven Hamiltonian structure, strongly suggesting that the animal's motion may be understood in terms of an effective mechanical

theory governing the postural kinematics. However, a framework that would contextualize these results, and enable us to derive behavioral theories from basic principles is lacking. Complementary to existing efforts in integrative understanding we are building such a framework using the tools of continuum mechanics and employing a renormalization group approach to systematically construct simple theories of animal behavior.

Slenderness is a common morphological trait shared by diverse animal species, including several commonly studied model organisms, in which individuals are much larger in one dimension than in the other two. This property can be exploited to describe a slender animal's mechanical configuration in terms of two scalar fields, measuring strain and curvature along the body axis. To build a statistical field theoretic description of slender animal movement, we choose to work within a "Riewe" theory space, in which driven and/or dissipative Langevin dynamics can be derived from a complex action functional containing higher- and fractional-order derivatives. In the spirit of effective field theory, we write down a generic action functional for the strain and curvature fields then follow through with a renormalisation procedure. This allows us to predict and explain the coarse-grained behavioural dynamics of slender animals that dominate at low frequencies and long wavelengths.

Social Behavior of Zebrafish & Squid in 3D (Tatsuo Izawa, Liam O'Shaughnessy, Akira Kawano, Mariia Pavelchenko, Makoto Hiroi)

Our 3D imaging apparatus and computational image processing pipeline capable of tracking multiple body- points of multiple fish across three dimensions enable an unparalleled high-resolution view of interacting animals. While our effort on dyadic fighting behavior continues (for which a manuscript is in preparation) we are leveraging this novel system to explore the variety of social behaviors in zebrafish, thus enabling a new understanding of social behavior at the posture scale.

We are extending our analysis of fighting behavior to understand how sequences of short-time maneuvers ultimately resolve in a dominance decision. Unraveling the factors underlying this decision requires principled approaches to analyzing long-time behavioral dynamics and also the capability to produce a much larger dataset of fighting behavior, to capture the variance in fight outcomes. In anticipation of the need for more efficient data collection, we have constructed a second identical imaging system, and we are using both systems to produce a dataset of ~200 fights.

From inception, our zebrafish project suggested a powerful potential synergy: 3D imaging and tracking of multiple organisms in an aquatic environment could ignite new collaborations that leverage the unique natural environment surrounding OIST. With the Reiter Unit we have begun to realize that potential through a project aimed to elucidate the social behavior of *Sepioteuthis lessoniana*, a squid found locally in the waters around Okinawa. We have developed an imaging and tracking system and are exploiting this system to understand group behavior.

Collective Dynamics from Data (Christian Esparza Lopez)

The principled integration of fine-scale degrees of freedom yielding coarse-grained theories that successfully capture large-scale structure is a remarkable achievement in physics and an important example for the quantitative understanding of complex systems, from the ensembles of statistical mechanics to the kinetic theory of fluids. Powerful as they are, such examples require detailed knowledge about the underlying dynamics, symmetries and conservation laws, or a parameterization of the models for tools such as the renormalization group. We seek to emulate this success in situations for which we lack such knowledge, thus opening new systems like collective animal behavior, or the brain, for quantitative understanding.

We recently introduced a framework for the principled extraction of coarse-grained, slow dynamics directly from time series data (**Costa et al, 2021**). We are now extending this approach using diffusion maps to uncover the principles of collective behavior directly from data without making a priori assumptions about the functional form of the dynamics. We have validated our approach in simulated system including Ising and Vicsek models.

3.2 Professional Activities

- GJ Stephens, Co-organizer (with O Peleg), Physics of Social Behavior Focus Session, APS March Meeting, Chicago Mar 14-18 (2022)

3.3 PhD Dissertations

None

4. Publications

4.1 Journals and Preprints

1. A Carlos Costa, T Ahamed, D Jordan & GJ Stephens, Maximally predictive ensemble dynamics from data (2021); bioRxiv <https://doi.org/10.1101/2021.05.26.445816>; arXiv:2105.12811
2. RX Lee, GJ Stephens & B Kuhn, Social relationship as a factor for the development of stress incubation in adult mice, *Frontiers in Behavioral Neuroscience* **6**:854486 (2022); <https://doi.org/doi:10.3389/fnbeh.2022.854486>; bioRxiv <https://doi.org/10.1101/249870>

4.2 Books and other one-time publications

Nothing to report

4.3 Oral and Poster Presentations

1. GJ Stephens, Joint Condensed Matter and Biophysics Seminar, Washington University, St Louis US (March 2022)
2. L O'Shaughnessy, T Izawa, JW Shaevitz & GJ Stephens, APS March Meeting, Chicago US (March 2022)
3. A Kawano & GJ Stephens, APS March Meeting, Chicago US (March 2022)
4. J Loveless & GJ Stephens, APS March Meeting, Chicago US (March 2022)
5. GJ Stephens, APS March Meeting Focus Session on Animal Behavior, Chicago US (March 2022)
6. GJ Stephens, Models of Biosystems Meeting, Online (March 2022)
7. GJ Stephens, AMOLF Autonomous Matter Seminar, Online (Feb 2022)
8. L O'Shaughnessy, T Izawa, I Masai, JW Shaevitz & GJ Stephens, 20th Human Frontier Science Program Awardees Meeting, Online (July 2021)

9. GJ Stephens, Aspen Center for Physics Public Lecture, Aspen US (June 2021)
10. GJ Stephens, BetaBreak, Amsterdam NL (June 2021)
11. GJ Stephens, Amsterdam IAS Workshop on High-order interactions: mixing and matching topological and information theory approaches, Online, (April 2021)

6. Meetings and Events

Travels, Meeting

- GJ Stephens, Washington University, St Louis US (March 2022)
- GJ Stephens, APS March Meeting, Chicago US (March 2022)
- J Loveless & I Korshok, University of Tokyo, JP (March 2022)
- GJ Stephens, University of Cologne, Cologne DE (November 2021)
- GJ Stephens, Aspen Center for Physics, Aspen US (June 2021)

7. Other

Nothing to report.

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