FINAL REPORT

on Heisenberg Grant

by German Science Foundation (Deutsche Forschungsgemeinschaft, DFG)

1 General Information

DFG reference number: **421143374**
Project number: FR 3429/4-1&2

Project title: **Physics of active matter: Coupled systems of active and passive matter**

Names of the applicants:

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Reporting period (entire funding period):

01.04.2020 - 31.03.2025

Date of submission of final report to DFG: 30.06.2025

Approval of final report by DFG: 19.03.2026

a. Academic progress

Since 01.04.2025, I am a tenured professor for Biological Dynamics and Self-organization (W2) at the Center for Molecular and Cellular Bioengineering (CMCB) of TU Dresden. Thus, one of the main aims of the Heisenberg program, preparing for a leadership role in Academia, was achieved. My group is a core group of the recently renewed Cluster of Excellence Physics of Life, with secondary affiliation at the Faculty of Physics.

During the funding period 01.04.2020-31.03.2025, we successfully completed most of the proposed research in all three research topics (with 23 peer-reviewed publications since the start of funding, including 1x eLife, 2x PRX Life, 3x PNAS, 1x Nature Physics, 1x Science Advances), with minor adjustments to the original research plan. Additionally, we introduced one fourth research topic 'Pattern formation in cells and tissues', as announced already in the interim report. These changes became necessary by my appointment as Heisenberg professor at the Cluster of Excellence 'Physics of Life' at TU Dresden.

Research highlights from the funding period

C. Ringers, S. Bialonski, M. Ege, A. Solovev, J.N. Hansen, I. Jeong, B.M. Friedrich, N. Jurisch-Yaksi: Novel analytical tools reveal that local synchronization of cilia coincides with tissue-scale metachronal waves in zebrafish multiciliated epithelia. *eLife* **12**, e77701, 2023

Motile cilia are slender cell appendages, whose regular bending waves propel microorganisms and pump fluids in multi-cellular organisms. Dense carpets of cilia exhibit collective dynamics in the form of metachronal synchronization, which is expected to enhance fluid transport. Using our multi-scale simulation framework Lagrangian Mechanics of Active System, we simulate cilia carpet incorporating experimentally measured 3D beat patterns, incorporating (to the best of knowledge for the first time) active noise of cilia beating in realistic simulations. In two closely related theory papers, we first demonstrated a dynamic analogue of the celebrated Mermin-Wagner theorem, showing that the relaxation times of long-wavelength perturbations diverge. This implies that in the presence of active cilia noise, only local but not global synchronization is possible. Finally, in this theory-experiment collaboration with the Jurisch-Yaksi lab (NTNU, Trondheim, Norway), by developing new analysis tools, we could identify and quantify such local synchronization in the ciliated epithelium of the zebrafish nose pit.

I. Babenko, N. Kröger, **B.M. Friedrich**: Mechanism of branching morphogenesis inspired by diatom silica formation. *Proc. Natl. Acad. Sci. U.S.A.* **121**(10), e2309518121, 2024

The formation of minerals by living organisms is ubiquitous across the evolutionary tree-of-life. The ornate silica-based cell walls of diatom microalgae represent an ideal model system to study species-specific biomineral architectures with outstanding materials properties that still defy their reconstitution *in vitro*. In this publication, we developed a minimal mathematical model based on known biosilica chemistry that quantitatively explains the formation of branched patterns of silica ribs. The proposed mechanism exemplifies guided self-organization, where spatial confinement and initial conditions direct a self-organized pattern formation processes to reliable shape functional patterns. Rare, aberrant structures can be explained by the same model assuming perturbed initial conditions. Similar mechanisms may apply in the biological morphogenesis of other branched structures, such as corals or bacterial biofilms.

J. Rode, M. Novak, **B.M. Friedrich**: Information theory of chemotactic agents using both spatial and temporal gradient sensing. *PRX Life* **2**, 023012, 2024

Biological systems process information despite noise-corrupted input, often operating at limits imposed by physics. A prime example is chemotaxis, i.e., active navigation in spatial fields of chemical cues, which enables immune cells to find inflammation sites, sperm cells to find the egg, and bacteria and social amoeba to build communities. Intriguingly, cells of different size use different chemotaxis strategies, comparing concentrations in either space or time. Only heuristic arguments exist to explain this evolutionary choice. We developed an information theory of an ideal agent that combines both strategies that allows to quantify 'chemotaxis in bits', and to predict when temporal or spatial gradient-sensing provides more information. Our predictor is consistent with data from 250 chemotactic cells, including unusual bacteria that use spatial gradient-sensing. Our work bridges a gap between extensive previous work that focused exclusively on one strategy, and may suggest bio-inspired search robot designs.

F. Kolley, C. Sidor, B. Dehapiot, F. Schnorrer*, **B.M. Friedrich***: Theory of sarcomere assembly inferred from sequential ordering of myofibril components. *PRX Life* **2**, 013002, 2024

Voluntary motions and heartbeat in animals is driven by contractions of myofibrils, millimeter-long acto-myosin bundles with characteristic periodic patterns of micrometer-sized sarcomere repeat units. Despite enormous progress in understanding sarcomere structure and physiology, there are conflicting hypotheses on the biophysical mechanisms underlying the assembly of these "cytoskeletal crystals". By developing new analysis tools, we could show that myosin molecular motors and actin crosslinking proteins establish periodic patterns first, while actin seems to serve as passive scaffold, prompting a modification of previous theories. This data inspired a new mathematical model of sarcomere self-assembly, which robustly establishes spontaneous periodic sarcomeric patterns in agent-based simulations. We provide testable predictions for genetic perturbation experiments.

C. Rodier, I.D. Estabrook, …, **B.M. Friedrich***, F. Schnorrer*: Muscle growth by sarcomere divisions. *Science Advances*, *in press*

Sarcomeres are the contractile units of muscles. These micrometer-sized units are chained into millimeter-long myofibrils that connect skeletal elements. During development, new sarcomeres are added to myofibrils under high mechanical tension, without comprising their mechanical integrity, yet the mechanism remained elusive. Using unprecedented high-throughput image analysis of developing sarcomeres in the insect flight muscle, we identified and confirmed a mechanism of tension-driven sarcomere addition by which a mother sarcomere divides into two daughter sarcomeres. New sarcomeric proteins are recruited during this division. A similar mechanism prevails in cross-striated muscle, where laterally progressing sarcomere divisions result in characteristic topological defects, and may apply in mammals.

Achievements in the three research topics

Results on Topic 1. Pattern formation in motor-filament systems

Sarcomeres are the contractile units of muscle. Controlled sarcomere contractions drive voluntary movements and heart beat in all animals. Yet, despite their physiological importance, the biophysical mechanisms of their self-assembly remained surprisingly under-researched. In a theory-experiment collaboration with the experimental group of Frank Schnorrer (IBDM, Marseilles, France), we could make quite substantial progress[17,22] on this open and important question, laying the foundation for a long-term continuation of this successful research program.

Together with the group of Frank Schnorrer, we proposed a new model of sarcomere self-assembly[17]. We first investigated the temporal sequence at which different sarcomeric components become ordered, using a newly developed algorithm to characterize autocorrelation functions of emergent periodic patterns. Contrary to previous models, we could show that myosin molecular motors and actin-crosslinking Z-disc proteins form sarcomeric patterns first, while polar actin filaments become polarity-sorted only hours later. Based on this insight, we developed a new mathematical model of sarcomere self-assembly that robustly replicates periodic sarcomeric patterns in agent-based stochastic simulations. Predictions of the model are consistent with experimental data for knock-down conditions as well as genetically engineered versions of the giant sarcomeric protein titin, which directly affects sarcomere length. Results were published in PRX Life[17]. We are currently working on a refined version of this model that is able to reproduce both normal sarcomere self-assembly as well as aberrant liquid-liquid phase separation of sarcomere components recently observed by our experimental collaboration partners in partial myosin knockdown conditions.

Sarcomere self-assembly and maturation is a multi-step process. Even after the establishment of sarcomeric patterns, new sarcomeres are added to existing myofibrils to enable muscle growth. This is a non-trivial problem, as myofibril are under tension and firmly attached to tendons at their terminal ends, and any opening of myofibrils for sarcomere insertion could result in catastrophic rupture. Our collaboration discovered a new mechanism of “sarcomere division” in which a mother sarcomere divides into two daughter sarcomeres by splitting its myosin stack, and establishing a new Z-disc in between[22]. Discovering this division of sarcomeres become possible through a physics-inspired image analysis pipeline, which allows to accurately track ten-thousands of sarcomeres from multi-channel 3D fluorescence microscopy images. This enabled us to identify rare division events (‘needle-in-haystack’), and even to reconstruct a pseudo-time series of sarcomere division. We could quantitatively show how new sarcomeric proteins are recruited during the division process. Analysis of video microscopy data confirmed the proposed time series and allowed us to calibrate it. This new mechanism of sarcomere addition by sarcomere division applies also in cross-striated larval muscle, which are more similar to mammalian skeletal muscle. There the division site propagates along the short, transversal axis of myofibril bundles in a zipper-like mechanism. A similar mechanism may apply in mammalian muscles. This theory-experiment project crucially relied on the development of several new image and data analysis pipelines by my group[S6] and involved a frequent back-and-forth between the group of Frank Schnorrer and my group to jointly develop and test hypotheses.

Additionally, an invited review on this topic has been submitted to Biophysical Review[S3].

We are continuing this highly successful line of research with a postdoc with expertise on self-organized pattern formation, as well as a guest scientist working on AI-based image analysis. We are additionally recruiting a new PhD student, who will establish agent-based simulations in 3D, through a recently acquired DFG-grant.

Results on Topic 2. Collective dynamics of motile cilia

We successfully implemented a detailed, multi-scale model of cilia carpets using our modeling framework LAMAS[4]. This model allows to incorporate previously measured, three-dimensional cilia beat patterns[9,10], and contains only a minimal number of free parameters. Using a published, three-dimensional beat pattern from multi-ciliated *Paramecium*, we demonstrated for the first time the multi-stability of collective wave modes (="metachronal waves") and could correctly predict the direction of the metachronal wave[9]. A related finding was published by the Golestanian lab, albeit for a minimal model using orbiting spheres (instead of cilia beat patterns taken from experiments, which implies degenerate symmetries and thus cannot predict a unique metachronal wave direction).

Building on this, we next investigated the impact of active cilia noise on collective hydrodynamic synchronization[10]. We showed that active noise can induce reversible transitions between multiple metastable wave modes. To the best of our knowledge, our simulations of collective dynamics in cilia carpets were the first to systematically explore the impact of active noise. We established a new paradigm of local, but not global synchronization, which provides a dynamic analogue of the famous Mermin-Wagner theorem from equilibrium statistical physics. Remarkably, we observed this phenomenon of local but not global synchronization also in an experimental model system of ciliated nose pit of zebrafish studied by our experimental collaboration partner, the lab of Nathalie Jurisch-Yaksi (NTNU, Norway)[16]. For this result, new analysis methods (based on correlations in Fourier space) had to be developed.

Although, project 2.1 is thus completed (and the PhD student successfully graduated with 'magna cum laude'), we will continue this successful theory-experiment collaboration with the Jurisch-Yaksi group. Nathalie Jurisch-Yaksi and myself are both part of a DFG-funded Research Unit on primary cilia dynamics (and jointly contributed to a review on this topic[14]).

Project 2.2 aimed to explore the possibility to build artificial cilia carpets by arranging reactivated axonemes (=the cytoskeletal core of cilia and flagella) on regular synthetic grids. This sub-project is conducted together Marina Medina-Sanchez (CIC NanoGUNE and B CUBE, TU Dresden) and our long-standing experimental collaborator Veikko Geyer (B CUBE, TU Dresden). Due to experimental challenges (notably ensuring regular alignment of cilia), we adjusted the scope of this project, and decided to build a bio-hybrid system consisting of externally actuated artificial cilia and biological cilia from *Chlamydomonas*. This unique setup demonstrates synchronization by direct hydrodynamic interactions. A first publication is in preparation.

Additionally, we explored active, non-equilibrium fluctuations of beating axonemes[20]. These active fluctuations put tight constraints on the possibility of cilia to synchronize. Moreover, axonemal fluctuations are interesting in their own respect as they represent a mesoscopic signature of the collective dynamics nanoscopic stochastic molecular motors. In a theory-experiment collaboration with Veikko Geyer, we could for the first time measure active axonemal fluctuations as function of motor number (using an experimental protocol for partial extraction of dynein molecular motor proteins). The observed reduction of oscillation quality with decreasing motor number can be rationalized by a minimal model of a traveling excitation wave on a domain with increasing number

of defects. Results were published in PNAS[20]. Building on this result, we are currently extending the existing minimal model and have already formulated a detailed model of cilia beating that accounts for the stochastic binding and unbinding dynamics of molecular motors, the first of its kind.

Progress on Topic 3. Stochastic dynamics of biological microswimmers

Subproject 3.1: This sub-project had been successfully completed. In brief, using multi-scale modeling in the spirit of LAMAS[4], we could identify a novel navigation paradigm of cells performing chemotaxis in the presence of small-scale turbulence[5]. External flows are omnipresent in physiological chemotactic environments, yet are often ignored - a particularly pronounced examples being sperm chemotaxis in external fertilizers, which spawn sperm and egg cells directly into the sea. There, flows distort the concentration fields of chemoattractant released by a source, here by an egg cell, into slender concentration fields. Sperm cells can "surf" along these filaments towards the egg. Our theory can explain for the first time (to the best of our knowledge) a previously reported optimum of fertilization success at a non-zero flow rate. Additionally, our analytical theory as well as agent-based simulations are in very good agreement with previous experiments. We believe that a similar mechanism applies in bacterial chemotaxis.

Original plans to study bacterial chemotaxis in small-scale-turbulent flow had to be postponed as the talented post-doctoral fellow working on this project had been awarded a research group leader position at a different institution, and a new hire was more suited for an at least equally exciting, yet slightly different direction to continue this research: Generalizing from the specific example of sperm chemotaxis, we considered the problem of chemotactic navigation more broadly and started to develop an information theory of chemotaxis[6,11,15,19]. Chemotactic navigation of biological cells represents a prime example of cellular information processing corrupted by noise, with known input and output, and a single objective. First cases considered include spatial sensing of an external concentration gradient[6] and optimal run-and-tumble chemotaxis as employed by bacterial cells[15]. By combining analytical theory and extensive simulations, we identified novel scaling laws for the optimal sensing time and other key parameters as function of sensing and motility noise.

Ultimately, we addressed the long-standing question as of why different biological cells use fundamentally different chemotaxis strategies[11,19]: Small and fast bacteria sense concentration gradients in time while moving actively, whereas large and slow eukaryotic cells with crawling motility sense concentration gradients across their diameter in space. Only heuristic arguments exist to explain this evolutionary choice of either gradient-sensing in time or gradient-sensing in space. To address this open question, we developed an information theory of an ideal agent that combines both gradient-sensing strategies[19]. By deriving analytical formulas for the information gain, we can decompose the information gain of temporal and spatial gradient-sensing and thus quantify 'chemotaxis in bits'. This theory of Bayesian chemotaxis generalizes information-greedy infotaxis as formulated by Vergassola et al. (Nature, 2007) to spatially extended agents with motility noise (and an egocentric map). Using information decomposition (made possible by our analytical theory[11,19]), we could predict when each gradient-sensing strategy provides more information as function of a powerlaw that combines the three fundamental parameters of this problem: agent size, motility noise and sensing noise into a single predictor. This predictor is consistent with data from 250 chemotactic cells, including unusual bacteria that use spatial gradient-sensing. Our idealized model of Bayesian chemotaxis assuming unlimited information processing capabilities thus serves as a benchmark for the chemotaxis of biological cells. The

corresponding publication in PRX Life represents one of the research highlights of the funding period[19].

Additionally, we investigated the motility of microswimmers. While a DFG-proposal on collective dynamics in dense sperm suspensions was not funded, we made considerable progress in our understanding of individual cilia[8,9,21]. A key bottleneck is our insufficient understanding of three-dimensional cilia beat patterns, which determine the chiral swimming paths of ciliated microswimmers. In a first theory-experiment collaboration using digital-inline holography, we provided evidence for the presence of traveling torsion waves that propagate from the proximal to the distal end along the length of cilia, yet the method was limited in spatial resolution[9]. In a second theory-experiment collaboration[21], a different method was employed: beating axonemes swimming close to a glass-water interface imaged by defocused dark-field microscopy will locally get in and out of focus as the z-position changes, which can be precisely calibrated. In fact, these measurements achieved a positional precision in tracking beating axonemes of 2 nm in *z*-direction and 2 Angstrom in *xy* (after Fourier averaging), which required advanced data analysis and error calculation. This precision was necessary to accurately determine torsion (which mathematically amounts to a third spatial derivative, which amplifies any uncertainty in the raw measurement data). Twist was inferred by tracking the motion of gold-nanoparticles attached to axonemes. This study published in Nature Physics (to which I contributed as co-corresponding author) represents the first measurements of dynamic twist of beating axonemes[21]. As key result, this study demonstrated that torsion and twist are coupled during cilia beating. This insight informs models of cilia beating and motor coordination in the axoneme, the conserved cytoskeletal core of cilia and flagella.

Additional research topic: Pattern formation in cells and tissues

At the time of writing of my Heisenberg proposal, it was still open, which proposals for clusters of excellence (EXC) at my host institution would receive funding. The former EXC cfaed (where I had been an independent research group leader) was not funded for a 2nd phase; as a consequence, I decided to put subproject 1.2 (=information-processing motor-filament systems) of the original proposal on hold. On the other hand, the EXC-proposal 'Physics of Life (PoL)' (where I am one of 25 core-PIs) was funded and offered me a tenure-track professorship. To strengthen ties with 'Physics of Life', I opted to include a new project area on pattern formation on the cell and tissue scale (in addition to a project on sub-cellular pattern formation in the original proposal, p. 22).

Additional sub-project 4.1: Axolotl limb regeneration: Together with experimental collaboration partners, Elly Tanaka (IMP and IMBA, Vienna) and Tatiana Sandoval-Guzman (CRTD, TU Dresden), we investigated limb regeneration in axolotl[S1] (1 PhD student, funding: D-A-CH FR3429/5-1). Regeneration of lost body parts must not just recapitulate developmental programs, but also adjust to the size of the adult organism. The control mechanisms enabling such size-adaptive morphogenesis are not well understood. Inspired by axolotl limb regeneration, we proposed a simple, yet effective mechanism for robust growth arrest by a pair of oppositely-oriented morphogen gradients, which together promote growth. Tissue growth decreases the overlap between both gradients and eventually halts morphogen signaling and arrests tissue growth. For this mechanism to work robustly that a subset of morphogen parameters scale proportionally with animal size (yet stay constant during regeneration). Remarkably, AI-assisted quantification of SHH and FGF8 morphogen dynamics in 3D (data provided by Sandoval-Guzmán lab, CRTD Dresden), we could confirm this theory prediction. A first manuscript is in revision in

PNAS[S1]. The PhD student has submitted her thesis and is expected to graduate soon. [Addition: the PhD student successfully defended her thesis 18.12.2025.]

A second PhD student is currently working on a related project on fin regeneration in zebrafish (core funding) together with experimental collaboration partner Rita Mateus (PoL, TU Dresden and MPI CBG).

Additional sub-project 4.2: Biomineral pattern formation of the silica cell wall in diatoms: A theory-experiment project on pattern formation on the sub-cellular scale from the original proposal addressed the morphogenesis of diatom silica cell walls[12,18,23] (1 PhD, funding by a 'Physics of Life' nucleation grant to Nils Kröger, B CUBE Dresden and myself). This project resulted in a last-author publication in PNAS as listed in the research highlights[23].

The formation of minerals by living organisms is a widespread biological phenomenon occurring throughout the evolutionary tree of life. The silica-based cell walls of diatom microalgae are impressive examples featuring intricate architectures and outstanding materials properties that still defy their reconstitution *in vitro*. We developed a minimal mathematical model that explains the formation of branched patterns of silica ribs, the first step of silica morphogenesis in diatoms. The generic mechanism of branching morphogenesis identified here represents a "non-classical Turing mechanism" and might apply in the biological morphogenesis of other branched structures, such as corals or bacterial biofilms[23].

Within this collaboration, we additionally contributed new analysis tools to characterize regular pore patterns in diatom silica cell walls, which were likewise published in PNAS[12], and wrote a book chapter[18]. This successful line of research will be continued with a new DFG-funded project jointly awarded to our experimental collaborator Nils Kröger and myself.

Modifications of the original research plan:

- *In subproject 1.3 on self-assembly of motor-filament oscillators,* we strategically decided against bottom-up synthesis of a cytoskeletal oscillator, but instead "deconstructed" an ubiquitous cytoskeletal oscillator, the axoneme, which constitutes the well-studied core of cilia and flagella and which is amenable to controlled perturbations. Using calibrated extraction of molecular motors, our team could quantitatively show how the precision of axonemal oscillators gradually decreases upon reduction of motor number, consistent with a minimal mathematical model, see above (published in PNAS[20]). A follow-up project now develops a more detailed stochastic mathematical model and thus addresses *Subproject 3.3 on intra-flagellar synchronization.*

- *Subproject project 2.2 on artificial cilia carpets* turned out to be technically challenging and our theory-experiment collaboration jointly decided to instead investigate hydrodynamic synchronization between artificial and biological cilia (manuscript in preparation together with experimental collaboration partners Mariana Medina-Sanchez (nanoGUNE San Sebastian, Spain) and Veikko Geyer (B CUBE, TU Dresden).

- *Subprojects 3.2 on collective dynamics in sperm suspensions and 3.4 on mammalian chemotaxis:* here, we will took a broader information-theoretic perspective, which includes sperm chemotaxis but goes beyond[6,7,11,15,19], see above.

b. Progress during the funding period and academic career advancement

At the start of the 2nd year of my DFG-funding (01.04.2021), I was appointed as Heisenberg professor at TU Dresden (pay scale W2, tenure track). I successfully completed the tenure evaluation and have been appointed as of 01.04.2025 as tenured professor at TU Dresden with the new denomination 'Biological Dynamics and Selforganization'. This professorship is a core group of the recently renewed Cluster of Excellence of 'Physics of Life' and formally affiliated to the Center for Molecular and Cellular Bioengineering (CMCB) of TU Dresden. I hold a secondary affiliation at the Faculty of Physics, where I am also teaching. I continued to expand my strong network in Dresden, with an additional affiliation at the Center for Systems Biology Dresden (CSBD), active membership in the graduate school DIGS-ILS for Interdisciplinary Life Sciences, as well as multiple research collaborations with the Max-Planck Institute for Molecular Cell Biology and Genetics (MPI CBG).

Since the start of funding, my group published 23 publications in peer-reviewed journals as well as 4 preprints (3555 citations according to google scholar, h-index = 32 as of 30.06.2025), see detailed publication list below. With several recent graduates, my research group currently comprises 3 PhD students, 1 PostDoc (as well as Master and Bachelor students); one more PhD student and one more PostDoc will join soon. This group size allows for close interactions with weekly one-to-one meetings, which is crucial for theoretical research.

In addition, I expanded my international network, which now includes experimental collaboration partners in France, Austria, Italy, Spain, Norway, Finland, and the US. In addition to the collaborations with Frank Schnorrer (IBDM, Marseilles, France; sarcomere self-assembly), Nathalie Jurisch-Yaksi (NTNU, Trondheim, Norway; cilia synchronization), Elly Tanaka, (IMP and IMBA, Vienna, Austria; axolotl limb regeneration) detailed above, I keep ties with Israel (scientific exchange with Assaf Gal and joint DFG-ISF proposal with Eyal Karzbrun at the Weizmann institute). A letter of intent for an HFSP collaborative grant with Arnold Matthijssen (US) and Caroline Wagner (Canada) was recently selected to submit a full proposal (as one of 82 letters out of 1180 submitted). Furthermore, I gave 39 invited talks and seminars and 80 contributed talks at international conferences in Europe, Israel, US, China, Japan, Singapore.

Joint initiatives:

I was PI in the DFG-proposal for a collaborative research center CRC 1492 on biomineralization led by Nils Kröger, which passed to the 2nd stage, yet eventually was not funded. Nonetheless, as member of the internal advisory board (who read and commented on all other projects), I gained valuable experience regarding the preparation of consortia proposals. This proposal formed the nucleus of a proposal for a research training group RTG 3142 'The biological making of materials' led by Prof. Yael Politi, where I am involved with two projects, with on-site visit scheduled in August this year. Further, I am PI in the DFG-funded research unit FOR 5547 led by Dagmar Wachten and Jay Gopalakrishnan on the 'Dynamics of primary cilia in health and disease' studying morphogenesis of pancreas duct network with a putative role of primary cilia as flow sensors together with Prof. Anne Grapin-Botton (MPI CBG, Dresden).

Service for the scientific community:

As core PI of the Cluster of Excellence 'Physics of Life', I contributed to the writing of the renewal proposal, which has just been evaluated successfully, with new funding period 2026-2032. I am head of the teaching committee of our cluster, as well as active member of its outreach committee

and its faculty council. I regularly supervise BSc and MSc theses, am member of thesis-advisory committees (5x), PhD committees (10x), and one appointment committee (W2). I regularly serve as reviewer for scientific journals (e.g., Science, Nature Physics, PRL, PNAS), grant agencies (e.g., Alexander-von-Humboldt, ANR-DFG), and PhD theses.

Teaching:
Together with colleagues, I had the privilege to jointly design and implement a new Master course Physics of Life at TU Dresden, which could welcome its first students in 2022. In addition to defining study modules and study documents, I devised and now teach three new lecture courses in this new Master course, covering topics from Statistical Physics, Nonlinear Dynamics, Stochastic Processes and Continuum Mechanics. I am currently head of the teaching committee of this research-oriented Master course, and oversee the further development of its curriculum.

Additionally, I am teaching at the Faculty of Physics, where I am involved in the education of physics teachers. Here, I teach 'Theoretische Mechanik für das Lehramt' (3+2 h/week; taught 2020, 2021, 2024, and again 2027). About 100 students enroll each year in this foundational, obligatory lecture, with 5 tutorial classes running in parallel.
I also give guest lectures in other study programs of TU Dresden. Within the national research unit FOR 5547, I am giving an online lecture course on statistics, data and image analysis, and an introduction to programming in Python to mostly biological and biomedical PhD students.

Mentoring:
I consider mentoring early-career scientists a key responsibility. I am proud and feel honored that four former postdocs in my group could secure independent positions in academia (Prof. Dr. Maja Novak (2018-2020, now assistant professor University of Zagreb; Prof. Dr. Stephan Bialonski, postdoc 2017-2018, now professor University of Applied Sciences Aachen; Prof. Dr. Steffen Werner, PhD and postdoc 2011-2016, now assistant professor University of Wageningen; Dr. Steffen Lange, postdoc 2017-2019, research group leader HTW Dresden). Several PhD students are continuing their academic training in other research groups; other alumni moved on to challenging jobs in R&D, IT, and finance.

Conference organization:
I was co-organizer of the international EMBO workshop 'Physics of Living Systems: From physical principles to biological function', which was held at TU Dresden from 03.-07.07.2023. We organizers were positively overwhelmed by the number of applications for this workshop and could welcome 240+ participants from all over the world, in addition to 30 invited speakers (thus, upscaling our original plan of only 120 participants to respond to the high demand). This high interest reflected the importance and timeliness of the topic, as well as the attractiveness of the speaker line-up. Together with Dr. Rita Mateus (PoL, MPI CBG), I was directly involved in funding acquisition, speaker invitation, program planning, organization, and reporting (supported by the senior organizers and the administrative team of PoL).

Additionally, Timo Strünker (University of Münster) and Veikko Geyer (B CUBE, TU Dresden) organized an international Heraus seminar on 'The Biophysics of Motile Cilia' with 70+ participants, held from 30.03.-02.04.2025 in the Physikzentrum Bad Honnef of the German Physical Society, which attracted a large number of high-profile speakers.

Outreach:
My group is continuously active in various outreach activities for the general public (e.g., Girl's Day, Physics on Saturdays, Long Night of Science Dresden, and most recently, contribution to a

science comic series science), which I consider an integral part of my professional role. As possibly largest outreach event so far, I was serving as main scientific curator of a museum exhibition at the Dresden science museum Technische Sammlungen Dresden (TSD), supported by PoL colleague Dr. Marcus Jahnel. This museum exhibition showcased the interdisciplinary research of our Cluster of Excellence PoL, and was opened on 05.05.2023 by the rector of TU Dresden, Prof. Dr. Ursula Staudinger, and a Vice-Mayor of the City of Dresden. Due to high demand, this interactive hands-on exhibition was shown for 1.5 years, followed by a 2 months in an exhibition space in the city's concert hall *Kulturpalast*.

Publications from the funding period

List of publications in peer-reviewed journals (during funding period)

1. F. Striggow, M. Medina-Sánchez, V. Magdanz, G.K. Auernhammer, **B.M. Friedrich**, O.G. Schmidt: Sperm-driven micromotors moving in oviduct fluid and viscoelastic media, *Small* **16**, 2000213, 2020
https://onlinelibrary.wiley.com/doi/abs/10.1002/smll.202000213

2. J. Karschau, A. Scholich, J. Wise, H. Morales-Navarette, Y. Kalaidzidis, M. Zerial, **B.M. Friedrich***: Resilience of three-dimensional sinusoidal networks in liver tissue, *PLoS Comp. Biol.* **16**(6), e1007965, 2020
https://journals.plos.org/ploscompbiol/article?id=10.1371/journal.pcbi.1007965

3. A. Scholich, S. Syga, H. Morales-Navarrete, F. Segovia-Miranda, H. Nonaka, K. Meyer, W. de Back, L. Brusch, Y. Kalaidzidis, M. Zerial, F. Jülicher, **B.M. Friedrich***: Quantification of nematic cell polarity in three-dimensional tissues, PLoS Comp. Biol. **16**(12): e1008412, 2020
https://journals.plos.org/ploscompbiol/article?id=10.1371/journal.pcbi.1008412

4. A. Solovev, **B.M. Friedrich***: Lagrangian Mechanics of Active Systems, *Eur. Phys. J. E,* **44**:49, 2021
https://doi.org/10.1140/epje/s10189-021-00016-x

5. S. Lange*, **B.M. Friedrich**: Sperm chemotaxis in marine species is optimal at physiological flow rates according theory of filament surfing, *PLoS Comp. Biol.*, **17**(4): e1008826, 2021
https://doi.org/10.1371/journal.pcbi.1008826

6. M. Novak, **B.M. Friedrich***: Bayesian gradient sensing in the presence of rotational diffusion, *New J. Phys.,* **23**:043026, 2021
https://doi.org/10.1088/1367-2630/abdb70

7. S. Lange, **B.M. Friedrich***: Network permeability changes according to a quadratic power law upon removal of a single edge, *EPL (Europhysics Letters),* **134** *64002,* 2021
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