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Mini-Workshop: Mathematics of Differential Growth, Morphogenesis, and Pattern Selection

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Abstract. Living structures are highly heterogeneous systems that consist of distinct regions made up of characteristic cell types with a specific structural organization. During evolution, development, disease, or environmental adaptation each region may grow at its own characteristic rate. Differential growth creates a balanced interplay between tension and compression and plays a critical role in biological function. In plant physiology, typical every-day examples include the petioles of celery, caladium, or rhubarb with a slower growing compressive outer surface and a faster growing tensile inner core. In developmental biology, differential growth is critical to the organogenesis of various structures including the gut, the heart, and the brain. From a structural point of view, these phenomena are close associated with instabilities, of twisting, looping, folding, and wrinkling. From a mathematical point of view, the governing equations of organogenesis are highly nonlinear and often characterized through multiple bifurcation points. Bifurcation is critical in symmetry breaking, pattern formation, and selection of shape. While biologists are studying differential growth, morphogenesis, and pattern selection merely by observation, our goal in this workshop is to explore, discuss, and advance the fundamental theory of differential growth to characterize morphogenesis and pattern selection by mathematical modeling. This workshop will bring together scientists with similar interests and complementary backgrounds in applied mathematics, mathematical biology, developmental biology, plant biology, dynamical systems, biophysics, biomechanics, and clinical sciences. We will identify common features of growth phenomena in living systems with the overall objectives to establish a unified mathematical theory for growing systems and to identify the necessary mathematical tools to address challenging questions in biology and medicine.

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Introduction by the Organisers

The miniworkshop *Mathematics of Differential Growth, Morphogenesis, and Pattern Selection* organized by Krishna Garikipati (Ann Arbor), Alain Goriely (Oxford), Ellen Kuhl (Stanford) and Andreas Menzel (Dortmund) brought together 16 participants with a diverse geographic representation from Europe and the United States. The workshop was organized in five subsections on One-dimensional Problems, Nonlinear Elasticity and Wrinkling, Patterning and Instabilities, Diffusion and Mechanics, and Selected Applications.

Living systems undergo a continuous turnover in response to microenvironmental cues. Alterations in these cues, in particular during development and disease, may cause the system to grow. This workshop brought together scientists with diverse backgrounds to discuss the mathematical modeling of growth with various applications including arteries, tumors, lungs, plants, skin, muscle, the heart, and the brain. From a biological point of view, these types of growth are histologically different and intrinsically unrelated. From a mathematical point of view, however, they have a lot in common: They all fall within the same nonlinear field theories of mechanics, supplemented by the concept of incompatible configurations. Irrespective of the nature of growth, the incompatible configuration is uniquely defined in terms of a single tensorial internal variable, the second order growth tensor. Throughout the course of this workshop, we have jointly identified suitable formats of the growth tensor and systematically categorized existing growth models by means of two criteria, the microstructural appearance of growth and the microenvironmental cues that drive the growth process.

Morphogenesis and growth-induced instability phenomena have been studied extensively in plant physiology, developmental biology, applied mathematics, and theoretical mechanics. Yet, scientists of the individual disciplines hardly ever interact with one another. This workshop will has stimulated cross-disciplinary discussion to show that growth phenomena in these fields indeed share a unified driving mechanism: Constraining deformation during growth induces structural instabilities, which may trigger a change in shape or surface morphology to release the growth-induced residual stress. Typical examples include twisting, looping, folding, and wrinkling. The underlying phenomena are highly nonlinear and require the analysis of evolving instabilities beyond the linear regime. We jointly discussed the mathematical tools necessary to explore growth-induced instabilities in the linear and nonlinear regime. Our goal was to establish unified scaling laws for living systems, for example, to correlate wavelengths or surface amplitudes to surface geometry, stiffness ratios, or growth rates. Understanding the morphogenesis and origin of shape has immediate biomedical applications in the diagnosis and treatment of chronic diseases like asthma, gastritis, obstructive sleep apnea, and tumor invasion. Beyond these biomedical applications, the scientific understanding of growth-induced morphological instabilities has important implications in geology, tectonophysics, material sciences, manufacturing, and microfabrication, with applications in soft lithography, metrology, and flexible electronics.

Many living systems are characterized by a multi-layered organization with a highly functionalized microstructural architecture to perform a wide range of tasks. In mammals, histological differences in tissue anatomy originate from early embryonic development after a series of processes, which are shared across a many species. For example, membrane or tubular structures often differentiate into two or more layers, a thin protective surface layer and one ore more thick internal layers. The required functionality determines the surface morphology of the thin layer as it evolves into longitudinal folds, radial folds, isolated mountains and ridges, or finger-type protrusions. Different rates of cell proliferation gives rise to residual stresses to promote a mechanical instability, which triggers the occurrence of regional specificities. The resulting tensile and compressive forces at the interface activate signaling pathways at the cellular level and interact with individual morphogens and transcription factors to determine the expression of a specific form of cell differentiation to create surface structure and shape. Pathological states are often characterized by a disturbance of this homeostatic state, which may trigger cell proliferation and abnormal growth. Mathematically, these phenomena fall into the broad category of pattern formation and are associated with one or more bifurcation points that distinguish characteristic morphologies. During this workshop, we have actively discussed critical conditions for bifurcation and identified examples where appropriate pattern selection is critical to biological function.

After discussing the common mathematical theory for growing systems and identifying analytical solutions for simplified model systems, we have focused on the computational modeling of differential growth. Computational modeling, for example within a nonlinear finite element framework, has the potential to provide mechanistic insight into the causes and effects of growth. It can uniquely integrate information from multiple length and time scales towards providing a holistic view of morphogenesis and pattern selection. Yet, despite intense efforts, computational modeling of growth is far from completely understood. To convert current computational models into truly predictive tools, controlled experiments are needed to acquire quantitative biochemical and biomechanical information across multiple spatial scales at multiple points in time. We have identified the urgent need for more sophisticated experiments to build confidence in the mathematical modeling and computational simulation of differential growth. Once calibrated and validated, growth models have immediate applications in biologically and clinically relevant fields such as atherosclerosis, in-stent restenosis, tumor invasion, tissue expansion, chronic bronchitis, mitral regurgitation, limb lengthening, tendon tear, plant physiology, dilated and hypertrophic cardiomyopathy, and heart failure. All participants concluded that modeling differential growth, morphogenesis, and pattern formation of living systems is a challenging but rewarding task: It may inspire improved medical devices design and optimize personalized treatment options.

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Abstracts

Active stress as a local regulator of global size in morphogenesis

Davide Ambrosi

There is a big debate about the physical mechanisms that control organs' size during the morphogenetic process. In embryo development, cells stop proliferating at homeostasis, a target state in terms of physical conditions that can represent, for instance, the shape and size of an organ. However, while control of mitosis is local, the spatial dimension of a tissue is a global information. How is global information transmitted? While morphogen factors are demonstrated to play a key role in morphogenesis, they seem unable to produce a global control on size by themselves because they satisfy reaction–diffusion equations characterized by a fixed characteristic length, independent on the size of the domain. In this talk I have investigated the conjecture that active mechanics plays a role, looking for solutions of balance equations where the signal, e.g., the stress or its derivative, has a form of the type $f(x;L) = f1(L)\,f2(x/L)$ where L is the size. Solution of boundary value problems of this type are admissible conveyor of information on size but, unfortunately, the most simple mechanical systems do not yield solutions of this type.

Self-focussing elastic energy

Martine BenAmar

Embryogenesis offers a real laboratory for pattern formation, buckling, and postbuckling induced by growth of soft tissues. Each part of our body is structured in multiple adjacent layers: the skin, the brain, and the interior of organs. Each layer has a complex biological composition presenting different elasticity. Generated during fetal life, these layers will experience growth and remodeling in the early postfertilization stages. Common to many mammalians, these instabilities are a precursor of the villi, finger-like projections into the lumen. Many debates and biological studies are devoted to these specific morphologies, which regulate cell renewal. After reviewing experimental results about morphogenesis, we showed that a model based on simplified hypothesis of differential growth can explain buckling and postbuckling instabilities.

Dripping of an elastic rod and snake locomotion

Davide Bigoni

Eshelby-like forces are shown to develop in elastic structures which can change their configuration through a release of energy. A simple example is the axial force developing in an elastic rod constrained with a sliding sleeve at one end and loaded transversally at the other. This force is proportional to the square of the curvature at the sliding sleeve edge. Configurational forces are shown to be responsible for the motion of an elastic rod, which can slip without friction inside a frictionless rigid channel. This mechanical setting corresponds to the problem of serpentine locomotion of a snake in a frictionless but confined environment. Finally, it is shown, both theoretically and experimentally, that Eshelby-like forces make self-encapsulation, or dripping, possible for an elastic rod loaded transversally at midspan between two fixed sliding sleeves.

The theory of mechanobiological stability

Christian Cyron

Aneurysms are focal dilations of blood vessels that often keep growing until the vessel ruptures. They are among the leading causes of death in industrialized countries. Yet, their driving mechanism remains unclear to date. Recently, the theory of mechanobiological stability was introduced, which emphasizes an important difference between living tissue and engineering materials. Living tissue is subject to a continuous turnover of mass, which induces an inelastic relaxation towards a preferred homeostatic stress. This turnover induces a potential so-called mechanobiological instability which is kept under control by the capacity for mechano-regulated growth (i.e., deposition of additional fibers in the tissue). The factors which can be demonstrated to decrease mechanobiological stability, i.e., faster mass turover, lower capacity for mechano-regulated growth and lower stiffness, are exactly the ones which have been known for decades among experimentalists and clinicians to promote aneurysmal enlargement. Mechanobiological instability may thus be the governing principle of aneurysmal enlargement, which opens up promising perspectives to develop new therapies against aneurysms on the basis of this mathematical concept. To this end, it is important to further explore its mathematical foundations, where several open questions remain to date. The Mathematisches Forschungsinstitut Oberwolfach provides the ideal environment to address these questions on the basis of a presentation and subsequent personal discussions.

Growth laws in morphoelasticity

Alexander Erlich

We are studying the growth of soft, elastic, actively growing tissue. The question we are addressing is: How does stress influence the growth and remodelling of such tissues, thus effectively regulating and driving their shape evolution? Our description of the interaction between stress and growth is based on the framework of morphoelasticity. In this viewpoint, the post-grown reference configuration of the body is evolving in time. Its time evolution depends on the difference between the current local stress of the system and the genetically encoded local homeostatic stress. We model several systems of actively growing tissues with stress feedback with one and two independent growth directions. For instance, we study networks of one-dimensional growing elastic rods in parallel and series connections, as well as tubular structures in which radial and tangential stress contributions are competing for their influence on shape evolution. The dynamics of such systems can be described both from the point of view of shape evolution and stress evolution. We focus on stationary states of such systems in which either the geometric shape and/or the stress field of the tissue is stationary and characterise the stability of such states in terms of linear stability analysis. This permits us to uncover parameter margins under which the systems have stable / unstable dynamics, which in biological applications can identify margins for physiological / pathological behaviour.

Patterning and morphology in developmental biology

Krishna Garikipati

A central question in developmental biology is how size and position are determined. The genetic code carries instructions on how to control these properties to regulate the form, shape and size of structures in the developing organism. Transcription and protein translation mechanisms implement these instructions. However, this cannot happen without sampling epigenetic information on the current form, shape and size of structures in the organism. The only robust description of this nature in physics is represented by spatio-temporal partial differential equations. Reaction-transport equations starting from simple Fickian diffusion, through the incorporation of reaction, advection and phase segregation terms can represent much of the patterns seen in the animal and plant kingdoms. Morphology, requiring the development of three-dimensional structure also can be represented by these equations. The recognition that physical forces play controlling roles in shaping tissues is behind the common use of nonlinear elasticity driven by volumetric growth to model morphology. Notably, the combination of reaction-transport equations with those of elasto-growth opens up the ability to model a potentially unlimited spectrum of patterning and morphology in developmental biology.

Folding and faulting of an elastic continuum as the response to a material instability

Panos Gourgiotis

Materials with extreme mechanical anisotropy are designed to work near a material instability threshold where they display stress channelling and strain localization, effects that can be exploited in several technologies. Extreme Cosserat solids are introduced and systematically analyzed in terms of several material instability criteria: positive-definiteness of the strain energy, strong ellipticity, plane wave propagation, ellipticity, and the emergence of discontinuity surfaces. In contrast with the classical elasticity case, ellipticity and wave propagation are not interdependent conditions, so that it is possible for waves not to propagate when the material is still in the elliptic range and, in very special cases, for waves to propagate when ellipticity does not hold. Failure of ellipticity is related to the emergence of discontinuity surfaces. The Greens functions for an applied concentrated force and moment are obtained analytically for Cosserat elastic solids with extreme anisotropy, which can be tailored to bring the material in a state close to an instability threshold such as failure of ellipticity. Accordingly, the Greens functions are used as perturbing agents to demonstrate in an extreme material the emergence of folding and faulting of a Cosserat continuum in single or cross modes, phenomena which remain excluded for a Cauchy elastic material.

Shapes and buckling instabilities of elastic shells

Jan Kierfeld

When spherical shells, such as plastic balls or microcapsules, are deflated or compressed, they always go through the same sequence of shapes: For small volume reduction, they remain spherical. Then they undergo the classical buckling instability where an axisymmetric dimple appears. Finally, upon further volume reduction, they lose their axisymmetry and the dimple becomes polygonal. Using membrane-shell theory we discuss the classical buckling instability and the associated shape bifurcations for axisymmetric shells in terms energy diagrams and including collapsed states. Apart from the classical buckling threshold marking the stability limit of the spherical shape we define a critical buckling volume where buckling becomes energetically favorable. We also explain the secondary buckling transition as a wrinkling transition under a compressive hoop stress, which develops during the primary classical buckling instability. In the secondary buckling instability, the dimple become polygonal by developing wrinkles in the vicinity of the dimple edge. All three buckling volumes, the classical buckling volume, the critical buckling volume where buckling becomes energetically favorable and the secondary buckling threshold, scale with a characteristic power of the Foeppl-von-Karman number.

Brain development as a mechanical instability problem

Ellen Kuhl

Arguably, the brain is the most complex organ in the human body, and, at the same time, the least well understood. Today, more than ever before, the human brain has become a subject of narcissistic study and fascination. The fields of neuroscience, neurology, neurosurgery, and neuroradiology have all seen tremendous progress over the past two decades; yet, the field of neuromechanics remains underappreciated and poorly understood. Here we show that mechanical stretch, strain, stress, and force all play a critical role in modulating the structure and function of the brain. We discuss the role of neuromechanics across the scales, from individual neurons via neuronal tissue to the whole brain. We review current research highlights, and discuss challenges and potential future directions. Using the nonlinear field theories of mechanics, we illustrate three phenomena which are tightly regulated by mechanical factors: neuroelasticity, the extremely soft behavior of the brain independent of time; neurodevelopment, the evolution of the brain at extremely long time scales; and neurodamage, the degradation of the brain at extremely short time scales. We hope that this review will become a starting point for a multidisciplinary approach to the mechanics of the brain with potential impact in preventing, diagnosing, and treating neurological disorders.

Geometric condition for the stability of one-dimensional systems

Thomas Lessinnes

Given a functional for a one-dimensional physical system, a classical problem is to minimize it by finding stationary solutions and then checking the positive definiteness of the second variation. Establishing the positive definiteness is, in general, analytically untractable. We discussed how a global geometric analysis of the phase-plane trajectories reveals the positive definiteness in a straightforward way. In particular, when applied to mechanical systems, the stability or instability of entire classes of solutions can be obtained effortlessly from their geometry in phase-plane, as illustrated on problems of a mass hanging from an elastic rod with intrinsic curvature and on the formation of stable perversions of the ladder invented.

A view on homogenisation and material instability

Andreas Menzel

Energy relaxation methods are well-established in the mathematics and mechanics community – especially in the field of the modelling of solid-solid phase transformations. This concept, however, is often considered as a purely mathematical tool with restricted physical significance. In this contribution we aim at emphasising the significance of energy relaxation methods for the modelling of dissipative solids and especially microstructure formation as well as microstructure evolution. In particular, we shall point out aspects and advantages of this concept which are not straight forward to achieve within alternative modelling approaches. A key ingredient of relaxation methods is exemplified in the introduction of a displacement perturbation field. We focus on two different concepts for the derivation: The first method is based on a laminate approach whereas the second framework to approximate the quasiconvex energy hull is achieved by the discretisation of the displacement perturbation field by means of the finite element method. The latter approach can be related to computational homogenisation schemes such as the so-called FE2 framework. While the motivation of identifying approximations of the quasi-convex hull is driven by concepts of energy minimisation, biological systems and adapting materials may also tend to maximise energy contributions, respectively tend to miximise their loading capacity.

Chemical versus mechanical patterns in 1D

Derek Moulton

Pattern formation is often considered either in terms of biochemical patterns or morphological patterns. Mathematically, these are often treated as separate, non-interacting phenomena. Biochemical pattern formation, such as the famous Turing instability, emerges as solutions of reaction-diffusion equations and can lead to stable patterns emerging from homogeneous initial conditions. Morphological patterns emerge via an elastic instability, characterised for instance by a simple buckling of a beam on a Winkler foundation. While these are governed by different physics, they need not be disjoint phenomena. In fact, there are several striking examples in which a morphological pattern and biochemical pattern perfectly coincide. For instance, in certain species of Mollusc seashells, the shell secreted has an intricate pigmentation pattern and matching morphological pattern. Here, we explore in a simple 1D beam setting possible explanations for mechanical and biochemical patterns coinciding. We consider four scenarios, two scenarios in which a biochemical pre-pattern dictates the morphological pattern, and two in which a morphological pre-pattern dictates the biochemical pattern. We first examine a biochemical pre-pattern that weakens the mechanical stiffness of a beam on a foundation, and uncover an intriguing bifurcation from the desired mechanical pattern as the heterogeneity due to biochemistry increases. We then examine a heterogeneous growth on the mechanical buckling, and show that significant heterogeneity is required to see an effect. In terms of a mechanical pre-pattern, we show that a change in structural shape, with no other influences, has no effect on the biochemical pattern in a 1D system. Finally, if the mechanical pattern creates a non-uniform diffusion, this can affect the biochemical pattern, causing a phase separation of the spatial domain, but not necessarily an imprint of the mechanical pattern.

Wrinkly isometries

Dominic Vella

Poking is a natural way to measure the world around us - how an object resists poking tells us how stiff it is. Similarly, indentation with an atomic force microscope is used to characterise the properties of cells, viruses and other biological capsules. Such objects are very difficult to stretch rather than bend and so their isometries (distance-preserving deformations) are natural ways of understanding their deformation. For example a doubly-curved shell is often assumed to adopt a mirror-buckled profile when loaded. However, numerous experiments show that rather than adopt such shapes, the system buckles. We study why the expected isometric deformations are not in fact obtained - how can other deformations be favourable? We focus in particular on the indentation of a pressurised spherical shell and of a floating elastic membrane. In the first case we show that wrinkling leads the system to a new isometry (not available in the absence of wrinkling) and that this wrinkly isometry is energetically favourable compared to mirror-buckling since it compresses less gas. In the second case, we show that there is again a wrinkly isometry, even though there is no axisymmetric isometry in this case.

Brain indentation measurements and histological stains

Johannes Weickenmeier

Mechanics play a fundamental role in understanding the formation of folds in the developing brain and impacts the progression of tissue damage and morphological changes in common brain diseases such as multiple sclerosis and Alzheimers disease. The presented work addresses the mechanics of the brain on two extreme length scales. On the micro-structural level, we quantified the mechanical properties of neonatal and mature white matter bovine tissue through nano-indentation measurements and visualized the cellular micro-structure of brain tissue by means of histological staining and microscopic imaging. On the other end of length scales, we developed a whole-organ three-dimensional finite element model of the brain for the numerical simulation of specific cases of injury and pathological development. Preliminary numerical simulations of craniosynostosis (premature fusion of bone plates in the growing brain of children) and craniectomy (neurosurgical procedure to release intracranial pressure of a swelling brain by removing parts of the skull) have indicated the relevance of numerical simulations in such medical applications. The experimental campaign revealed a positive correlation between the location specific degree of myelination in white matter and elastic tissue stiffness. The continuous process of myelination in white matter tissue is consequently associated with variable tissue stiffness and might help to explain the onset of folding in the developing brain due to chronic changes of the gray and white matter stiffness ratio.

Electrically induced patterns

Giuseppe Zurlo

The possibility to induce patterns in thin bodies under soft/hard boundary conditions is crucially based on the assumption that the material response exhibits a softening behavior. This assumption, which received considerable attention in the literature on phase transitions since the pioneering works of van Der Waals, leads to the possibility to describe several inhomogeneous bounded equilibrium configurations that may be of interest for the appearance of patterns in biological systems. Here we discuss yet another possibility to induce patterns which does not require softening, but rather the application of living (position dependent) loads on the lateral boundary of a thin body. We show the existence of a critical voltage for which the homogenous configuration becomes unstable and periodic configurations are possible, and we discuss the role of nonlocal (bending) contributions in regularizing such configurations.

Reporter: Ellen Kuhl

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