Complexity, Chaos, and Biological Evolution

Edited by
Erik Mosekilde and
Lis Mosekilde

NATO ASI Series

Series B: Physics Vol. 270

Complexity, Chaos, and Biological Evolution

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Plenum Press
New York and London
Published in cooperation with NATO Scientific Affairs Division

Proceedings of a NATO Advanced Research Workshop
on Complex Dynamics and Biological Evolution,
held August 6-10, 1990,
in Hindsgavl, Denmark

Library of Congress Cataloging-in-Publication Data

NATO Advanced Research Workshop on Complex Dynamics and Biological Evolution (1990 : Hindsgavl, Middelfart, Denmark)
Complexity, chaos, and biological evolution : [proceedings of a NATO Advanced Research Workshop on Complex Dynamics and Biological Evolution, held August 6-10, 1990, in Hindsgavl, Denmark] / edited by Erik Mosekilde and Lis Mosekilde.
p. cm. -- (NATO ASI series. Series B, Physics ; v. 270)
"Published in cooperation with NATO Scientific Affairs Division."
Includes bibliographical references and index.
ISBN 0-306-44026-1
1. Biophysics--Congresses. 2. Evolution (Biology)--Congresses. 3. Biological systems--Congresses. 4. Chaotic behavior in systems--Congresses. 5. Morphogenesis--Congresses. 6. Molecular biology--Congresses. 7. Dynamics--Congresses. I. Mosekilde, Erik. II. Mosekilde, Lis. III. Title. IV. Series.
QH505.N333 1991
574'.01'1--dc20 91-26491
CIP

ISBN 0-306-44026-1

A Division of Plenum Publishing Corporation
233 Spring Street, New York, N.Y. 10013

Printed in the United States of America

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PREFACE

From time to time, perhaps a few times each century, a revolution occurs that questions some of our basic beliefs and sweeps across otherwise well guarded disciplinary boundaries. These are the periods when science is fun, when new paradigms have to be formulated, and when young scientists can do serious work without first having to acquire all the knowledge of their teachers.

The emergence of nonlinear science appears to be one such revolution. In a surprising manner, this new science has disclosed a number of misconceptions in our traditional understanding of determinism. In particular, it has been shown that the notion of predictability, according to which the trajectory of a system can be precisely determined if one knows the equations of motion and the initial conditions, is related to textbook examples of simple, integrable systems. This predictability does not extend to nonlinear, conservative systems in general. Dissipative systems can also show unpredictability, provided that the motion is sustained by externally supplied energy and/or resources. These discoveries, and the associated discovery that even relatively simple nonlinear systems can show extremely complex behavior, have brought about an unprecedented feeling of common interest among scientists from many different disciplines.

During the last decade or two we have come to understand that there are universal routes to chaos, we have learned about stretching and folding, and we have discovered the beautiful fractal geometry underlying chaotic attractors. Hand in hand with this development we have seen a rapidly growing interest in the application of concepts from far-from-equilibrium thermodynamics. In analogy with the behavioral complexity that can arise in nonlinear dynamic systems, we observe the spontaneous unfolding of structure in spatially extended systems as the throughflow of energy and resources lift them further and further above the state of thermal equilibrium.

In the years to come, much of this research will be directed towards understanding the types of complexity that follow after chaos: hyperchaos, higher-order hyperchaos, spatio-temporal chaos and, perhaps, fully developed turbulence. This will lead to the integration of nonlinear dynamics and irreversible thermodynamics into a theory of complex physical systems. However, it is equally important to try to apply the ideas of nonlinear dynamics and irreversible thermodynamics to living systems. Such systems clearly depend on a continuous supply of energy and resources to maintain their functions and, frankly speaking, the concepts of conventional physics have never been of much help to the biological sciences. In many contexts, these concepts are inappropriate, if not directly meaningless, and it is hard to imagine that a greater contrast can exist than that which is found between the simple ideas of classical mechanics and equilibrium thermodynamics and the spontaneous morphogenesis, differentiation, and evolution that we observe in the living world.

With the concepts and ideas of complex systems theory it now appears that the biological sciences have acquired a set of tools which will allow us to describe the behavior, function and evolution of living systems in much more detail. As a step in this direction, small as it may be, this book reproduces a collection of papers which were delivered at the NATO Advanced Research Workshop on Complex Dynamics and Biological Evolution which took place at Hindsgavl Conference Center near Middelfart, Denmark, August 6-10, 1990.

Attended by some 60 participants, this workshop succeeded as one of the relatively unusual events where clinically oriented medical doctors, experimental biologists, chemists, physicists and mathematicians are able to find a common language and to communicate freely across conventional barriers. Surely, confronted with the real life observations of biologists and doctors, some of the physicists may have been struck by the extreme oversimplification of their approach to the complexity of the living world. Some of the doctors, on the other hand, may have felt a little intimidated by their lack of mathematical background.

However, mediated in part by the pleasant surroundings of the conference site, all such feelings rapidly disappeared to make way for a common experience of a worthwhile and interesting endeavor. We would like to extend our thanks to all the participants and invited speakers for contributing to the success of the meeting.

The workshop offered lectures by leading experts in the fields of theoretical biology, morphogenesis, evolution, artificial life, hormonal regulation, bone remodeling, population dynamics, and chaos theory. In addition to the presentations given by the invited speakers, many of those attending the workshop also reported on their recent results within these and related areas. A list of participants is given at the end of the proceedings.

As editors of the proceedings we would like to thank The NATO Science Committee, The Danish Natural Science Foundation, and The Technical University of Denmark for sponsoring the meeting. We would also like to thank Janet Sturis and Ellen Buchhave for their assistance in preparing the proceedings.

Erik and Lis Mosekilde

Copenhagen, February 1991

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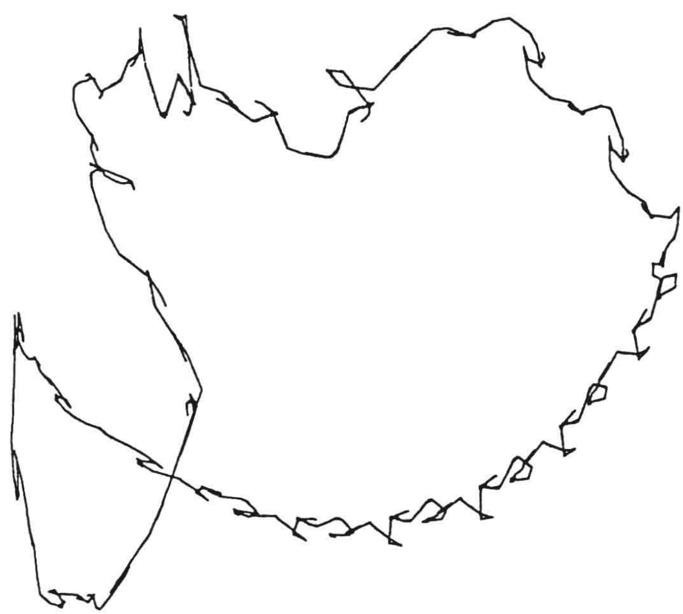
Section I
An Introductory Overview

With the development of nonlinear dynamics we have acquired a completely new set of tools for the description of the complex dynamic phenomena we observe in the living world.



STRUCTURE, COMPLEXITY AND CHAOS IN LIVING SYSTEMS

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ABSTRACT

Although homeostasis of the internal environment is almost axiomatic in the physiological sciences, it is apparent that rhythms occur in the levels of a variety of bodily functions, ranging in time from a few cycles per millisecond for the firing of the central nervous system to the monthly period of the menstrual cycle. As an example of such a rhythm, this introductory overview describes how self-sustained oscillations arise in the pressure and flow regulation of individual nephrons as a result of a delayed action of the juxtaglomerular apparatus. The same problem is dealt with in considerably more detail in the contribution by Marsh et al., and one of the purposes of the present discussion is to speculate on the biological significance of such cycles.

A viral or bacterial infection is an example of an instability where a small initial population of foreign agents is allowed to multiply over several decades before the immune system or other reactions of the body finally establishes the defence required to cope with the infection. In a recent paper by Anderson and May, it was suggested that the response of the immune system to the simultaneous infection by HIV and another virus that activates the same T-cells can produce chaotic bursts of free HIV with intervals of the order of 20 weeks. We have performed a more detailed mathematical analysis of this model, including a construction of phase space trajectories as well as Poincaré

Complexity, Chaos, and Biological Evolution, Edited by E. Mosekilde and L. Mosekilde, Plenum Press, New York, 1991

sections and return maps. At least one route to chaos in the model has been identified and found to proceed through a cascade of period-doubling bifurcations. Even though more recent observations seem to indicate that the Anderson and May model is incorrect in certain respects, it can still be expected that the immune system is capable of producing very complicated responses.

In contrast to the conventional picture of a relatively quiescent dynamics, it has always been acknowledged that the spatial structure of physiological systems is exceedingly complicated. Advances in experimental techniques over recent decades have made it possible to illuminate this complexity in even more detail, and the time has come when we must try to relate the complexity of the physiological structures with the dynamical processes involved in their formation and maintenance. As a final problem we thus discuss some of the difficulties involved in relating bone structure with bone remodeling processes. This problem will also be dealt with at greater length in a subsequent contribution by Lis Mosekilde.

INTRODUCTION

A variety of new experimental techniques in molecular biology, physiology and other fields of biological research constantly expand our knowledge and enable us to make increasingly more detailed functional and structural descriptions of living systems. Over the past decades, the amount and complexity of available information have grown manyfold, while at the same time our basic understanding of the nature of regulation, behavior, morphogenesis, and evolution in biological systems has made only modest progress. A key obstacle in this process is clearly the proper handling of the wealth of data. This requires a stronger emphasis on mathematical modeling through which the consistency of the adopted explanations can be checked and general principles may be extracted. As a much more serious problem, however, it appears that the proper concepts for the development of a theoretically oriented biology have not hitherto been available. Classical mechanics and equilibrium thermodynamics, for instance, are inappropriate and useless in some of the most essential biological contexts. Fortunately, there is now convincing evidence that the concepts and methods of the newly developed fields of nonlinear dynamics and complex systems theory will enable us to establish much more detailed descriptions of biological processes (Nicolis and Prigogine 1989).

Contrary to the conventional assumptions of homeostasis, many biological and biochemical control systems are unstable and operate in a pulsatory or oscillatory mode (Glass and Mackey 1988, Degn et al. 1987, Holden 1986). This is true, for instance, for the release of hormones such as growth hormone, luteinizing hormone, and insulin. The latter case is described in considerable detail in the contribution to this proceedings by Sturis et al. As discussed by Prank et al., the hormonal release process may also become more erratic, and the question arises whether the information associated with the temporal variation in hormone concentration has significance for the regulatory function. While this problem still remains at the speculative level, it is evident that disruption of certain rhythms can be associated with states of disease while, on the other hand, new types of oscillations may appear in connection with other diseases.

Many cells exhibit pulsatory variations in their membrane potential with extremely complicated patterns of slow and fast spikes. Heart cells, for instance, have been found to produce chaos and complicated forms of mode-locking when stimulated externally (Glass and Mackey 1988). Similarly, as discussed in the contribution by Colding-Jørgensen, the interaction between nerve cells can give rise to nonlinear dynamic phenomena with frequency locking and chaotic firing influencing the flow of information. Liebovitch and Czegledy, and Østergaard et al. present more detailed models of neural function while Babloyantz shows how one can characterize signals from the central nervous systems by means of fractal dimensions and other measures from nonlinear dynamics. In line with this research, Herzel et al. analyze examples of newborn infant cries and voiced sound to illustrate the occurrence of bifurcations and chaos.

Rhythmic signals also seem essential in intercellular communication (Goldbeter 1989). Besides neurons and muscle cells which communicate by trains of electrical impulses, examples range from the generation of cyclic AMP pulses in the slime mold *Dictyostelium discoideum* to the pulsatile release of hormones. While in these instances the oscillatory dynamics characterize the extracellular signal, recent observations indicate that signal transduction itself may be based on oscillations of intracellular messengers. In his contribution to this volume, Goldbeter assesses the efficiency of pulsatile signaling. It appears that periodic signals are more effective than constant, stochastic or chaotic stimuli in eliciting a sustained physiological response.

By virtue of the positive feedback associated with replication, and because of maturation and other delays, many problems in ecology, microbiology and population dynamics lead to complex dynamic phenomena involving different types of competition between erratic bursts and deterministic oscillations. Olsen et al. give a detailed analysis of this type of behavior in their contribution on epidemics of children's diseases. As shown in an example below, similar phenomena can arise in the response of the immune system of an AIDS patient to an opportunistic infection.

With recognition of the fractal geometry underlying chaotic attractors, and with the establishment of universal scaling laws for the transition to chaos, we can now describe behaviors which previously appeared to be hopelessly complex and which, for that reason, were usually neglected or ascribed to random exogenous processes (Devaney 1986, Holden 1986, Christiansen and Holden 1989). Similarly, the understanding of spontaneous structure formation in open thermodynamic systems under far-from-equilibrium conditions has provided us with a new paradigm for the description of fundamental biological processes such as morphogenesis, evolution and differentiation (Nicolis and Prigogine 1977, Haken 1978).

As demonstrated in the contribution by Meinhardt, biological pattern formation can be described in terms of instabilities and nonlinear dynamic phenomena in biochemical reaction-diffusion equations. A similar approach is adopted by Hunding in his study of early *Drosophila* embryogenesis. This model rests on the idea of Turing systems of the second kind in which a prepattern generates position dependent rate constants for a subsequent reaction-diffusion system. Maternal genes are assumed to be responsible for setting up gradients from the anterior and posterior ends as needed to stabilize the double period prepattern suggested as underlying the read out of the gap genes. The resulting double period pattern again stabilizes the following prepattern in a hierarchy of increasing structural complexity. Without such hierarchical stabilization, reaction-diffusion mechanisms yield highly patchy short wavelength patterns.

By combining reaction-diffusion equations with equations for the mechanical behavior of the cell membrane, Goodwin illustrates how similar ideas can be used to address the problem of biological morphogenesis for the single-celled alga *Acetabularia*. Because of its basic simplicity, this organism lends itself to experimental and theoretical studies of form formation. A model of the morphogenetic field and a finite element simulation of its behavior are presented which show that spatial patterns generically similar to those observed in the alga arise naturally, suggesting that normal morphogenesis can be described as an attractor of a moving boundary process. This approach can form the basis for a whole new discipline of theoretical study of developing organisms with the goal of identifying the generic properties which result in robust but highly modifiable structures.

At present this is mostly a vision, and there are enormous difficulties to overcome. One major difficulty is associated with experimental problems of identifying the morphogenes which appear in the various reaction-diffusion equations, not to mention the problems of measuring the nonlinear rate constants involved in their interactions. Another difficulty is associated with the strong preoccupation of many biologists with genetic control mechanisms. It is clear, however, that the genetic approach can never stand alone, as this approach does not help us understand how a gene codes for a specific form.

Parallel with the above developments we see attempts to describe evolutionary processes from a more formal point of view, including attempts to investigate life forms in alternative chemistries (Ebeling and Feistel 1982, Langton 1988, Stein 1989). This line of research is represented by the contributions on evolutionary theory and artificial life by Ebeling, by Blomberg and by Knudsen et al. In the latter field, one is primarily concerned with finding ways of formulating evolutionary dynamics as an open-ended problem, i.e., as a problem where the various roads that evolution can take have not already been laid down by the modeler. This has brought about a study of life forms in other media with the aim of elucidating the very definition of life. Emmeche, on the other hand, in his contribution on formalization of biological systems, challenges this approach with the claim that formal evolutionary models show general aspects and higher order behavior of living systems for which there is no existing experimental background.

Within the scope of this short introduction it has not been possible to give credit to all contributors to the present volume. There are, for instance, important contributions by Müller on vortex formation in excitable media, by Bohl on structural amplification in chemical networks, by Das et al. on boundary operator and distance measure for cell lineage of *Caenorhabditis elegans* and for the pattern in *Fusarium solani*, by Lloyd on timekeeping for intracellular dynamics, and by Rössler et al. on an optimality approach to ageing. In addition, Andresen and Rauch-Wojciechowski have contributed a couple of more mathematically oriented papers. Finally, we have included two contributions on higher-order chaos, even though these are not directly related to concrete biological problems. The idea has been to convey to the reader an impression of the richness of new ideas which arise from the interaction between the biological sciences and complex systems theory. We would also like to convey a little of the