

Andreas Deutsch
Sabine Dormann

Cellular Automaton
Modeling of Biological
Pattern Formation

Characterization, Applications, and Analysis

Foreword by Philip K. Maini

Birkhäuser
Boston • Basel • Berlin

Andreas Deutsch
Dresden University of Technology
Center for High Performance Computing
D-01062 Dresden
Germany

Sabine Dormann
University of Osnabrück
Department of Mathematics
D-49069 Osnabrück
Germany

AMS Subject Classifications: 00A72, 0001, 0002, 9208, 92B05, 92B20

Library of Congress Cataloging-in-Publication Data

Deutsch, Andreas, 1960-

Cellular automaton modeling of biological pattern formation : characterization, applications, and analysis / Andreas Deutsch, Sabine Dormann.

p. cm — (Modeling and simulation in science, engineering & technology)

Includes bibliographical references and index.

ISBN 0-8176-4281-1 (alk. paper)

1. Pattern formation (Biology) 2. Cellular automata—Mathematical models. I. Dormann, Sabine. II. Title. III. Series.

QH491.D42 2004
571.3—dc22

20030638990
CIP

ISBN 0-8176-4281-1 Printed on acid-free paper.

©2005 Birkhäuser Boston

All rights reserved. This work may not be translated or copied in whole or in part without the written permission of the publisher (Birkhäuser Boston, c/o Springer Science+Business Media Inc., Rights and Permissions, 233 Spring Street, New York, NY 10013, USA), except for brief excerpts in connection with reviews or scholarly analysis. Use in connection with any form of information storage and retrieval, electronic adaptation, computer software, or by similar or dissimilar methodology now known or hereafter developed is forbidden.

The use in this publication of trade names, trademarks, service marks and similar terms, even if they are not identified as such, is not to be taken as an expression of opinion as to whether or not they are subject to proprietary rights.

Printed in the United States of America. (TXQ/MV)

9 8 7 6 5 4 3 2 1 SPIN 10855758

Birkhäuser is a part of *Springer Science+Business Media*
www.birkhauser.com

Contents

Foreword	vii
<i>Philip K. Maini</i>	
List of Figures	xv
List of Notation	xxi

Part I General Principles, Theories, and Models of Pattern Formation

1 Introduction and Outline	3
2 On the Origin of Patterns	13
2.1 Space, Time, and the Mathematics of Pattern Formation: A Brief Historical Excursion	13
2.1.1 Greek Antiquity: Static and Dynamic World Conceptions . . .	13
2.1.2 The Prescientific Age	19
2.1.3 The Deterministic World of Classical Mechanics	19
2.1.4 Discovering the History of Time	24
2.1.5 From Equilibrium to Self-Organizing Systems	27
2.2 Principles of Biological Pattern Formation	31
2.2.1 Preformation and Epigenesis	31
2.2.2 Ontogeny and Phylogeny	34
2.2.3 On Organizers and Embryonic Regulation	35
2.2.4 Molecular and Genetic Analysis	37
2.2.5 Self-Assembly	38
2.2.6 Physical Analogues	39
2.2.7 On Gradients and Chemical Morphogens	41
2.2.8 Self-Organization and Morphogenesis	42
2.2.9 Cell–Cell Interactions	42

3	Mathematical Modeling of Biological Pattern Formation	45
3.1	The Art of Modeling	45
3.2	How to Choose the Appropriate Model	46
3.2.1	Model Perspectives	51
3.2.2	From Individual Behavior to Population Dynamics	53

Part II Cellular Automaton Modeling

4	Cellular Automata	59
4.1	Biological Roots	60
4.2	Cellular Automaton Models of Pattern Formation in Interacting Cell Systems	63
4.3	Definition of Deterministic, Probabilistic and Lattice-Gas Cellular Automata	67
4.3.1	Lattice Geometry and Boundary Conditions	67
4.3.2	Neighborhood of Interaction	70
4.3.3	States	71
4.3.4	System Dynamics	73
4.4	Analysis and Characterization	79
4.4.1	Chapman-Kolmogorov Equation	81
4.4.2	Cellular Automaton Mean-Field Equations	83
4.4.3	Linear Stability Analysis	90
4.5	From Cellular Automata to Partial Differential Equations	97
4.6	Further Research Projects	100

Part III Applications

5	Random Movement	105
5.1	Brownian Motion	106
5.2	Discrete Random Walk and Diffusion	107
5.3	Random Movement in Probabilistic Cellular Automaton Models	111
5.3.1	Random Walk Rule According to Toffoli and Margolus	111
5.3.2	Random Walk in Probabilistic Cellular Automata with Asynchronous Updating	114
5.4	Random Movement in Lattice-Gas Cellular Automaton Models	115
5.4.1	Stability Analysis for the One-Dimensional Random Walk Model with One Rest Channel	119
5.4.2	Checkerboard Artefact	122
5.5	Growth by Diffusion-Limited Aggregation	126
5.6	Further Research Projects	128

6	Growth Processes	129
6.1	Classical Growth Models	129
6.2	Growth Processes in Cellular Automata	131
6.3	Growth Processes in Lattice-Gas Cellular Automata	136
6.4	Further Research Projects	142
7	Adhesive Cell Interaction	143
7.1	Cellular Patterns Originating from Adhesive Interaction	144
7.2	Adhesive Lattice-Gas Cellular Automaton	146
7.3	Analysis of Aggregation Dynamics in the Single-Cell-Type Adhesion Model	148
7.3.1	Linear Stability Analysis	149
7.3.2	Spatial Pattern Formation	153
7.4	Phase Separation and Engulfment in a Two-Cell-Type Adhesion Model	155
7.5	Further Research Projects	159
8	Alignment and Cellular Swarming	161
8.1	Orientation-Induced Pattern Formation	161
8.2	A Swarm Lattice-Gas Cellular Automaton	164
8.2.1	Linear Stability Analysis	166
8.2.2	The Swarming Instability	168
8.3	Further Research Projects	172
9	Pigment Cell Pattern Formation	173
9.1	Principles of Pigment Cell Pattern Formation	173
9.2	Automaton Model with Adhesive/Orientational Interaction	175
9.3	Simulation of Stripe Pattern Formation	178
9.4	Development and Evolutionary Change	180
9.5	Further Research Projects	182
10	Tissue and Tumor Development	185
10.1	Modeling Contact Inhibition of Movement in Lattice-Gas Cellular Automata	186
10.2	Tissue Growth	187
10.3	A Cellular Automaton Model for Chemotaxis	191
10.4	Avascular Tumor Growth	195
10.4.1	A Hybrid Lattice-Gas Cellular Automaton Model for Tumor Growth	197
10.4.2	Simulations	202
10.5	Further Research Projects	206

- 11 Turing Patterns and Excitable Media** 207
 - 11.1 Turing Patterns 207
 - 11.1.1 Turing Pattern Formation in Macroscopic Reaction–Diffusion Systems 208
 - 11.1.2 A Lattice-Gas Cellular Automaton Model for Activator–Inhibitor Interaction 211
 - 11.1.3 Pattern Formation in One Dimension: Analysis and Simulations 219
 - 11.1.4 Pattern Formation in Two Dimensions 229
 - 11.1.5 Derivation and Analysis of a Macroscopic Description of the Lattice-Gas Cellular Automaton 238
 - 11.2 Excitable Media 243
 - 11.2.1 Introduction 243
 - 11.2.2 Definition of the Automaton Rules 246
 - 11.2.3 Lattice-Boltzmann Equation and Its Uniform Steady States 248
 - 11.2.4 Stability Analysis of the Lattice-Boltzmann Equation 251
 - 11.3 Further Research Projects 255

- 12 Discussion and Outlook** 257
 - 12.1 Cellular Automaton Characterization 258
 - 12.1.1 Cell-Based Instabilities and Cellular Self-Organization 258
 - 12.1.2 Discreteness and Finite Size Effects 259
 - 12.2 Cellular Automata as a Modeling Tool 261
 - 12.3 Diffusive Behavior and Growth Patterns 262
 - 12.4 Adhesive Interactions and Cell Sorting 263
 - 12.5 Collective Motion and Aggregation 268
 - 12.6 Pigment Pattern Formation 272
 - 12.7 Tumor Growth 272
 - 12.8 Turing Patterns and Excitable Media 273
 - 12.9 Outlook 274
 - 12.9.1 Further Applications 275
 - 12.9.2 Further Analysis 276

- Appendices** 279
 - A. Growth Processes: A Mean-Field Equation** 279

 - B. Turing Patterns** 281
 - B.1 Complete Interaction Rule 281
 - B.2 Linear Stability Analysis 282

 - C. Excitable Media: Complete Interaction Rule** 285

D. Isotropy, Lattices, and Tensors 287

 D.1 Isotropic Media and Lattices 287

 D.2 Introduction to Tensors 289

 D.3 LGCA Dynamics and the Influence of the Lattice 290

References 293

Index 319