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# Thermodynamic Network Analysis of Biological Systems

2nd Corrected and Updated Edition

With 14 Figures

Springer-Verlag
Berlin Heidelberg New York 1981

# Preface to the Second Edition

The first edition of this book was greeted with broad interest from readers engaged in various disciplines of biophysics. I received many stimulating and encouraging responses, however, some of the book's reviewers wanted to stress the fact that an extensive literature of network theory was not included or reported in the book. But the main aspect of the book is intended to be substantive rather than methodical: networks simply serve as a remedy for doing some first steps in analysing and modelling complex biological systems. For an advanced stage in the investigation of a particular system it may be appropriate to replace the phenomenological network method by more detailed techniques like statistical equations or computer simulations.

According to this intention, the second edition of the book has been enlarged by further biological examples for network analysis, not by more network theory. There is a completely new section on a network model for photoreception. For this section I am obliged to J. Tiedge who did most of the detailed calculation and to my colleague Professor Stieve with whom we have had a very fruitful cooperation. Also I would like to mention that this work has been sponsored by the "Deutsche Forschungsgemeinschaft" in the "Sonderforschungsbereich 160".

Recent results for excitable systems represented by feedback networks have also been included in the second edition, especially for limit cycle networks.

Once more I have to thank Dr. H. Lotsch and the Springer-Verlag for taking care of this book, and Miss Marie-José Rozenboom for taking care of the manuscripts.

Aachen, January 1981 *J. Schnakenberg*

# Preface

This book is devoted to the question: What fundamental ideas and concepts can physics contribute to the analysis of complex systems like those in biology and ecology? The book originated from two lectures which I gave during the winter term 1974/75 and the summer term 1976 at the Rheinisch-Westfälische Technische Hochschule in Aachen. The wish for a lecture with this kind of subject was brought forward by students of physics as well as by those from other disciplines like biology, physiology, and engineering sciences. The students of physics were looking for ways which might lead them from their monodisciplinary studies into the interdisciplinary field between physics and life sciences. The students from the other disciplines suspected that there might be helpful physical concepts and ideas for the analysis of complex systems they ought to become acquainted with.

It is clear that a lecture or a book which tries to realize the expectations of both these groups will meet with difficulties arising from the different trainings and background knowledge of physicists and nonphysicists. For the physicists, I have tried to give a brief description of the biological aspect and significance of a problem wherever it seems necessary and appropriate and as far as a physicist like me feels authorized to do so. For the nonphysicists, the physical background information is represented in the book as far as possible, for example a brief introduction into the fundamentals of thermodynamics in Chapter 3. I would be glad if this book stimulates the physicists to further reading of physiological texts, and the nonphysicists to study a more rigorous text of irreversible thermodynamics.

The latter remark leads me to point out the significance of thermodynamics for the intention of this book. Very rigorously, one could suspect that its title is only a fashionable paraphrase of simply "the role of thermodynamics in life sciences". For two reasons, however, this would not hit the point. First, it is not just thermodynamics but thermodynamics of situations very far from equilibrium which plays the role of a ground theme for all our considerations in this book. Secondly, the conditions imposed by the fundamental laws of nonequilibrium thermodynamics will automatically be satisfied by utilizing a network language for the analysis of the systems that we have in view.

At this point, I would like to express my deep gratitude to the late Aaron Katchalsky. The lecture, "Network Thermodynamics of Membranes", which he gave on the occasion of the Israelian-German workshop in Göttingen in May 1972 and the

discussions with him a few days before he was murdered on his way home to Israel represented a good deal of stimulation for me to give the lectures mentioned earlier and to write the present text.

I would also like to thank many of my colleagues in Aachen and at other universities for many helpful and elucidating discussions. In particular, I feel indebted to my coworkers Hans Josef Bebber, Christian Hook, Hans-Peter Leiseifer and Günter Wuttke who have contributed valuable results, elucidations and stimuli by their diploma theses. Thanks are expressed also to Dr. H. Lotsch (Springer Verlag) for encouraging and formulating the plan for this text. Last but not least thanks to Miss Marie-José Rozenboom for patiently, untiringly and promptly typing the manuscript.

Aachen, October 1976 J. Schnakenberg

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