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An applied mathematician's perspective on Rosennean complexity

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ABSTRACT

The theoretical biologist Robert Rosen developed a highly original approach for investigating the question "What is life?", the most fundamental problem of biology. Considering that Rosen made extensive use of mathematics it might seem surprising that his ideas have only rarely been implemented in mathematical models. On the one hand, Rosen propagates relational models that neglect underlying structural details of the components and focus on relationships between the elements of a biological system, according to the motto "throw away the physics, keep the organisation". Rosen's strong rejection of mechanistic models that he implicitly associates with a strong form of reductionism might have deterred mathematical modellers from adopting his ideas for their own work. On the other hand Rosen's presentation of his modelling framework, (M, R) systems, is highly abstract which makes it hard to appreciate how this approach could be applied to concrete biological problems. In this article, both the mathematics as well as those aspects of Rosen's work are analysed that relate to his philosophical ideas. It is shown that Rosen's relational models are a particular type of mechanistic model with specific underlying assumptions rather than a fundamentally different approach that excludes mechanistic models. The strengths and weaknesses of relational models are investigated by comparison with current network biology literature. Finally, it is argued that Rosen's definition of life, "organisms are closed to efficient causation", should be considered as a hypothesis to be tested and ideas how this postulate could be implemented in mathematical models are presented.

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1. Introduction

When for the first time I heard about Robert Rosen's life-long quest for the secrets of life, his theory of (M, R) systems and his approach to complexity I didn't quite know what to make of all this. There was an obviously highly original idea for investigating a question which is so hard to answer that it is, in fact, rarely asked: What is life? Also the methods that Rosen used for his work, borrowed from the highly abstract theory of categories, do not quite fit in the classical arsenal of the applied mathematician's toolbox. Could category theory, an area of mathematics so abstract that, in fact, even some of its pioneers referred to it as "abstract nonsense" be successfully applied to a fundamental real-world question "What is life?" which at the same time happens to be one of the hardest scientific questions that one may possibly ask?[1] That sounded interesting, very interesting, indeed!

So I asked two questions that I usually ask myself when I hear about something new and exciting to me in science:

1. Which of Rosen's ideas can I steal for my own work? (more about stealing later, see Section 5.3!)
2. Do I believe Rosen's answers to his research questions "What is life?" and "What is a complex system?"

I will present my answers to these questions as my personal perspective on Robert Rosen's work. The purpose of this is two-fold: First, in my opinion, Rosen's highly original work deserves

[1] Rosen's work on (M, R) systems is by no means the only application of category theory to the sciences. Best-known are perhaps applications in computer science—two examples for textbooks are Pierce (1991) and Barr and Wells (2012)—as well as mathematical physics (Coecke, 2011). A recent introduction to category theory with a view towards applications in the sciences by Spivak (2014) underlines the fact that the trend of category-theoretic ideas in science is increasing. But Rosen's work is one of the earliest, if not the earliest application of category theory outside mathematics.

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more attention from the mainstream of mathematical biologists. Second, I believe that Rosen's frustration that his ideas were not more widely and openly accepted (Mikulecky, 2001) is not completely coincidental—there are important differences between Rosen's theoretical concept of a model and the understanding of modelling within the applied mathematics community. These differences are on the one hand philosophical—Rosen demands that a model accurately represents the causal relationships between the elements of the system to be modelled (see Section 4) whereas models typically built by applied mathematicians can be regarded as formal representations of a *hypothesis* regarding a possible mechanism underlying the system behaviour (see Section 5). On the other hand, Rosen applies mathematical notions, in particular, category theory, in a different spirit than most applied mathematicians would. This issue—which is related to Rosen's presentation of his ideas rather than the ideas themselves—is more important than it may look at a first glance because this difference in using mathematical tools may deter an audience with a mathematical background from Rosen's ideas (Section 6.2.1). My presentation is based on the original publications Rosen (1958a,b, 1959, 1971, 1973, 1991) and Rosen (2000) but I will most often refer to Rosen (1972) because this, in my opinion, is the best summary of Rosen's early publications and to his monograph "Life Itself" (Rosen, 1991) which is the most comprehensive account of the philosophical basis of Rosen's work. Another good introduction into Rosen's thinking are his "Autobiographical Reminiscences" (Rosen, 2006).

The article is structured as follows: In Section 2 we introduce the notions of metabolism-repair systems ((M, R) systems). In Section 3 we present Rosen's proposed characterisation of life as systems that are "closed to efficient causation". We show that this concept is not—as Rosen suggests—a specific property that can be deduced from the architecture of (M, R) systems but should be regarded as a postulate, a hypothesis to be tested by implementing "closure to efficient causation" in mathematical models. Rosen's specific view of modelling which is closely related to his interpretation of category theory is presented in Section 4. I describe the conceptual basis of mechanistic models in Section 5. In particular, I will argue that Rosen's relational models can be regarded as a specific type of mechanistic models. In Discussion (Section 6) I compare mechanistic models with Rosen's perspective on modelling and present some ideas how his concept of an organism could be investigated via mathematical models in physiology and ecology.

2. Rosen's answer to the question "What is life?"

Although most people—with or without a scientific background—seem to have a good intuition when it comes to decide if something is "alive" it is nevertheless very hard to come up with a rigorous scientific definition of life. Thus, definitions of life are usually descriptive—a list of properties that are characteristic of living systems is given such as the following appearing in Campbell (2008):

1. *Order.* Organisms are highly ordered, and other characteristics of life emerge from this complex organization.
2. *Reproduction.* Organisms reproduce; life comes only from life *(biogenesis)*.
3. *Growth and Development.* Heritable programs stored in DNA direct the species-specific pattern of growth and development.
4. *Energy Utilization.* Organisms take in and transform energy to do work, including the maintenance of their ordered state.
5. *Response to Environment.* Organisms respond to stimuli from their environment.
6. *Homeostasis.* Organisms regulate their internal environment to maintain a steady-state, even in the face of a fluctuating external environment.
7. *Evolutionary Adaptation.* Life evolves in response to interactions between organisms and their environment.

But these properties are not necessarily defining: systems that are not usually considered to be living systems may have one or even several of these properties. Indeed, Campbell (2008) refers to this list as emergent properties and processes of life rather than a definition.

Instead of a descriptive definition, Rosen proposes a relational approach for distinguishing systems that are "dead" from systems that are "alive". He starts from a set of components that he explicitly refers to as black boxes i.e. he avoids making any assumptions on the internal structure of these components. Instead his focus is on the relationships between these components—he develops a highly abstract theory with the purpose of demonstrating that the way that components interact determines if a system is "complex" or "simple" and also, if a system is "alive" or "not alive". By developing an approach that intentionally ignores the properties of individual components of a system and emphasising the relationships between these components he followed a motto of his mentor Nicolai Rashevsky (cited according to Rosen (2006))—"Throw away the physics, keep the organisation". More generally, the question of the relationship between structure (i.e., for example, the underlying physics) and function in biology has a long history. For example, the famous Cuvier–Geoffroy debate in front of the French Academy of Sciences in 1830 was ultimately about the two principles "form follows function" which was Georges Cuvier's view whereas Geoffroy Saint-Hilaire argued for the opposite position "structure determines function". In Rosen (1991), his monograph "Life itself", he strongly rejects "structure determines function" which is currently, for example, influential in molecular biology in the theory of protein folding—because the sequence of amino acids (primary structure) to a great extent controls the three-dimensional arrangement (tertiary structure) and this 3D structure determines the function of a protein it is argued that structure determines function (Petsko and Ringe, 2008).

In contrast, Rosen states that biological functions arise from the interactions between the parts of a biological system, independent of the material realisation of the components. In order to explain this idea, let us consider calcium signalling. In many cases when hormonal or electrical signals reach a cell, calcium oscillations are used for propagating these signals within the cell and control a wide range of cellular functions such as the contraction of heart cells or the transcription of particular genes. The shape of these oscillations can be very different between cell types although the Ca^{2+} signalling components involved are the same—voltage-gated Ca^{2+} channels, that allow calcium influx in response to electrical signals, intracellular channels like the inositol-trisphosphate or the ryanodyne receptor, that release large amounts of calcium from intracellular stores when stimulated, and Ca^{2+} pumps, that return Ca^{2+} released to the cytosol back to intracellular stores. How can Ca^{2+} oscillations be so different in different cell types if they are generated by similar sets of Ca^{2+} signalling components? An obvious explanation is that Ca^{2+} oscillations in particular cell types are shaped by relationships between the components that are characteristic of this cell type. This is the concept of the Ca^{2+} "toolbox" which is the basis of our current understanding of Ca^{2+} oscillations (Berridge et al., 2000). But does the fact that differences in the relationships between components are important for explaining the different shape of Ca^{2+} oscillations imply that we should restrict ourselves to investigating relationships and completely ignore structural properties of the components? We

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