Book Reviews

Toward a Philosophy of Systems Biology

Systems Biology: Philosophical Foundations
Fred C. Boogerd, Frank J. Bruggeman, Jan-Hendrik S. Hofmeyr, and Hans V. Westerhoff, eds
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Systems Biology: Philosophical Foundations is an insightful and timely book that fuses scientific and philosophical insights in a highly effective and mostly accessible manner. Numerous books address scientific aspects of the emerging and expansive field of systems biology (SB) but this is the first to deal specifically with its underlying philosophical issues. Contributors include life scientists as well as philosophers of science, who, besides introducing readers to the field, address topics ranging from the nature of explanation to the definition of life. Although the editors have divided the various chapters into three themes (*SB Research Programmes, Theories and Models,* and *Organization*), we found it helpful to group the contributions slightly differently and let certain chapters appear in more than one theme.

Theme One consists of overviews, background, and characterizations of SB. Chapters 1, 2, 9, and 14 are prime expositions of these topics, which are rooted in an appreciation of the limitations of biochemical, molecular biological, and genomic approaches for the attainment of deep biological understanding. Chapter 9 (Krohs and Callebaut) sets out a clear and compelling "topography" of SB and its three roots, which are helpfully connected to top-down and bottom-up approaches. This description, along with the characterizations in Chs. 1 and 2, more accurately illuminates the variety of SB approaches than do earlier typological attempts (e.g., O'Malley and Dupré 2005).

Theme Two—the bulk of the book—is concerned with the nature of system-level explanation and its implications for the philosophy of science. Chapter 1 in particular exposes the shortfalls of existing philosophy of science and biology—a view contested here only by Ch. 3 (Sulman)—and argues that mechanistic explanation trumps narrowly construed reductionist explanation. Mechanisms are discussed in accord with accounts that now dominate the philosophical literature. These favor explanations based on multilevel regularity producing mechanisms over mereologically or theoretically reductionist explanations (e.g., Bechtel and Richardson 1993; Machamer et al. 2000; Glennan 2002). The distinctive feature of such mechanistic explanations and their relevance for systems biology is that constitutive and interacting elements of the mechanism must be dealt with in their systemic context. Chapter 6 (Richardson and Stephan) expands on mechanistic explanations as highly detailed and dynamic redescriptions of system behaviors in terms of the context-dependent behaviors of their parts (see also Boogerd et al. 2005). These authors raise but do not resolve the questions of what exactly levels are and what the relationship is between organizational and explanatory levels.

Chapter 2 (Westerhoff and Kell) extends the mechanism discussion to argue that emergent properties such as life are calculable, although the calculations involved relate necessarily to nonlinear interactions. In Ch. 7 Schaffner proposes a more abstract account of mechanisms that may capture "emergent simplifications" of systems (p. 155). Although it would have been good to see more systems-biologic interrogation of current philosophies of mechanism, the book makes it clear that a common orientation to mechanism is conducive to profitable engagement between biologists and philosophers of science.

An associated general topic about which there is less consensus is the issue of what theories, models, and simulations are. The status of theories in biology is an issue raised in Ch. 2 (Westerhoff and Kell) and is one that recurs elsewhere in the book. Theories have often been troublesome entities in the philosophy of biology, due to the nature

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of biological explanation and its disharmony with the once-popular conception of theories as appeals to exceptionless, quantitatively precise laws. Chapter 9 (Krohs and Callebaut) argues that now genomics has demonstrated the explanatory bankruptcy of theoretically unorganized data, the role of theory must be addressed anew for systems biology to flourish. The diversity of approaches to theory covered in the book ranges from Westerhoff and Kell's identification of candidates for "law"-based theories (p. 45) and Moreno's "principles of organization" (p. 241) to Schaffner's "overlapping interlevel causal-temporal prototypical models." Obviously, these are very different sorts of "theories," and future philosophies of SB will no doubt direct attention toward the types of theory that prove helpful in the development of the science and show how they function.

Simulations are addressed in Ch. 4 (Fell), which concisely outlines metabolic control analysis and its history (also neglected in the history and philosophy of biology, but often proposed in this book as a good example of a system-level theory) within a broader discussion of the relationship between simulation and comprehension. Complex systems such as cells, argues Fell, may be fully simulable but still not readily comprehensible (p. 99). Models (primarily mathematical ones) and modeling are discussed generally and specifically throughout the book, but not in relation to the more general accounts of models, theories, and simulations found in contemporary philosophy of science (e.g., Cartwright 1999; Giere 1999; Morgan and Morrison 1999; Winsberg 2001). Some reflection on this literature would have been interesting, as would a more systematic discussion of the different types of simulation.

Several chapters mention or dwell on Robert Rosen's relational biology, and Ch. 8 (Wolkenhauer and Ullah) teases out a central element of Rosen's thinking about the nature of complex systems and their models. Although this is still a very technical interpretation, it may make Rosen less opaque to at least some readers. Chapter 10 (Hofmeyr) fleshes out some of Rosen's abstract ideas with examples drawn from contemporary biochemical science. How useful Rosen will be for SB has yet to be established, but some serious attention to his ideas from historians and philosophers of science is long overdue. Although von Bertalanffy is occasionally mentioned (e.g., p. 161), his general systems theory is not pursued at all, and perhaps this represents a shared verdict on its usefulness.

The concluding Ch. 14 offers a sketch of explanatory types in SB, especially as outlined in this book. Types of explanation include causal-mechanical, unificationist (general principles that bring system properties together with molecular ones via quantitative analysis), nomological, design (accounting for how things are functional), and evolutionary. The chapter and the book end by advocating explanatory pluralism, which is consistent with the generally integrative, multidisciplinary aim of SB but may be too generous in its openness to nomological explanation.

Theme Three confronts the nature of systems themselves, with discussions of system definition and theories of organization. Chapter 9 shows how the issue of system individuation relates to modularization or the functional analysis of ontological wholes. The authors suggest that developing a conceptualization of wholeness is crucial to top-down systems biology. The concept of system autonomy is briefly discussed in Ch. 10 (Hofmeyr) and leads to reflections on autopoiesis—not yet a theoretical approach greatly favored by systems biologists, but one mentioned several times in this collection. Chapter 11 (Moreno) examines the concept of system self-maintenance in relation to the origins of life and offers a thermodynamic view of autonomy that Moreno argues is both less abstract than autopoietic accounts and also the precondition for Darwinian evolved systems (p. 257). From this basic form of autonomy, a set of organizational steps leads to the emergence of more complex living systems. Chapter 12 (Bechtel) also focuses on the autonomy of living systems, placing competing accounts within a perspective in which system autonomy is subserved by mechanisms. Bechtel arrives at this position by way of an overview of Gánti's "chemoton" model of the simplest biological system, which he compares with Rosen's (M,R) systems, autopoiesis, and Moreno's account of autonomy.

Chapter 13 (Keller) starts off with some basic questions about the definition of "organism" in an historical overview of how organisms and self-organization were decoupled when mechanical and physical analogies were employed with the development of cybernetics after WWII. She goes on to give an abstract account of how evolved complex (biological) self-organization is different from the organization of machines because the former arises and evolves spontaneously. Despite the book's general position that explanations of system organization have priority over those concerned with system evolution (e.g., p. 325), the latter approach has its advocates. Make sure EvoDevo is brought into the SB picture, says Wimsatt in Ch. 5 (see also Ch. 9, note 16). Robustness is usually considered to be an important system-level property, he argues, and understanding it fully will involve evolutionary and developmental analysis.

A key aim of this book is to bring the philosophy of biology into a new mode of biological thinking and expand the limited range of biological research it has tended to address. This is an aim very likely to be realized as systems biology becomes increasingly a topic of reflection for philosophers of biology. At the recent meeting of the International Society for History, Philosophy, and Social Studies of Biology (Exeter, July 2007), for example, six sessions and a total of 14 papers were dedicated in various ways to systems biology

or discussions of systems (not including developmental systems theory). Does this book say everything that needs to be said? Of course not, and nor does it pretend to. As a doorway into the fascinating developments of systems biology and its philosophical underpinnings, however, no reader could ask for a better entry point. We hope that the book will stimulate further interdisciplinary gatherings along the lines of the one that was the source for this collection of essays, and that as these occur, the literature in both fields will be positively influenced by closer dialogue between systems biologists and philosophers of science.

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Building Blocks in Search of a Theory

Primates and Philosophers: How Morality Evolved
Frans de Waal
Princeton, NJ: Princeton University Press, 2006
(209 pp; $22.95 hbk; ISBN 0691124477)

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Conceived on the occasion of Frans de Waal's Tanner Lectures on Human Values at Princeton University in 2003, *Primates and Philosophers* contains as its first and major part de Waal's essay "Morally evolved: Primate social instincts, human morality, and the rise and fall of 'Veneer Theory,'" followed by his three short appendices: on anthropomorphism in primate research, on theory of mind in apes, and on animal rights, respectively. The second part of the book consists of commentaries on de Waal's essay written by Robert Wright, Christine Korsgaard, Philip Kitcher, and Peter Singer. In the third part, de Waal responds to commentators.

De Waal starts by identifying the opponent he wants to challenge. Naming it the "Veneer Theory" of morality (VT), he defines it as the view according to which morality is "a cultural overlay, a thin veneer hiding an otherwise selfish and brutish nature" (p. 6). De Waal sees VT as a historical constant of both philosophical and evolutionary thinking and singles out as its most disturbing specimen T. H. Huxley's lecture *Evolution and Ethics* (1893). Since "Darwin's bulldog" seems to have suggested that human morality somehow falls beyond the explanatory reach of evolutionary theory, de Waal finds him guilty of the high treason of Darwinism.

Although he opens his case against VT by invoking two historical allies—Charles Darwin and Edward Westermarck—de Waal's chief ally is actually de Waal himself, as he relies mainly on his longstanding primatological research and some of his earlier writings, his main objective being to show that morality is part and parcel of our evolved nature, and not a "veneer." De Waal's basic argument can be stated as follows: in the psychological and social lives of human and nonhuman primates, there are a number of common elements, from empathy to the tendency to harmonize relationships. Since these elements are also the "building blocks" of morality, their presence in both human and nonhuman primates is evidence for his theses about the natural pedigree of human morality. What follows is an abridged two-step reconstruction of this general argument.

Empathy, according to de Waal, is undoubtedly present in nonhuman primates, especially in chimpanzees, which also seem to display "cognitive empathy"—the ability to adopt another individual's viewpoint. Reciprocity, de Waal stresses, is well established among capuchin monkeys and chimpanzees. Drawing on his experiments with capuchin monkeys and their responses to inequitable rewards for the same efforts, de Waal argues that some nonhuman primates also have a certain "sense of social regularity." And finally, says de Waal, in apes there is the tendency to harmonize relationships visible in their "reconciliation behavior," when females or high-ranking males even-handedly smooth relations between conflicting parties with, as it seems, their only aim being to restore peace in the group.

De Waal next presents his views about the constitutive role of the above traits for human morality. First he adopts a view according to which "human morality is firmly anchored in the social emotions, with empathy at its core" (p. 56). Then he postulates that morality is best summarized by the so-called Golden Rule (with reciprocity at its heart) and draws the following corollary: "To know that some of the psychology behind this rule may exist in other species, along with the required empathy, bolsters the idea that morality, rather than a recent invention, is part of human nature" (p. 49). As for the "sense