

ORGANISM AND MECHANISM

A Critique of Mechanistic Thinking in Biology

**Submitted by Daniel James Nicholson to the University of Exeter
as a thesis for the degree of Doctor of Philosophy in Philosophy
In September 2010**

This thesis is available for Library use on the understanding that it is copyright material and that no quotation from the thesis may be published without proper acknowledgement.

I certify that all material in this thesis which is not my own work has been identified and that no material has previously been submitted and approved for the award of a degree by this or any other University.

Signature: 

ABSTRACT

In this thesis I present a critical examination of the role played by mechanistic ideas in shaping our understanding of living systems. I draw on a combination of historical, philosophical, and scientific resources to uncover a number of problems which I take to result from the adoption of mechanistic thinking in biology.

I provide an analysis of the historical development of the conflict between mechanistic and vitalistic conceptions of life since the seventeenth century, and I argue that the basic terms of this conflict remain central to current disputes over the nature of the organism as well as the question of how far the theories, concepts, and methods of physics, chemistry, and engineering can ultimately take us in the explanation of life.

I offer a detailed critique of the machine conception of the organism, which constitutes the central unifying idea of mechanistic biology. I argue that this notion, despite its undeniable heuristic value, is fundamentally inadequate as a theory of the organism due to a number of basic differences between organisms and machines. Ultimately, I suggest that the neglected vitalistic tradition in biology actually possesses the best conceptual tools for coming to terms with the nature of living systems.

I also undertake a philosophical analysis of the concept of mechanism in biology. I argue that the term 'mechanism' is actually an umbrella term for three distinct notions, which are unfortunately conflated in philosophical discussions. I explore the relation between mechanistic biology and the new philosophical interest in the concept of mechanism and I show that these two research programs have little to do with one another because each of them understands the concept of mechanism in a different way.

Finally, I draw on the historical and philosophical foundations of cell theory to propose an epistemological perspective which enables the reductionistic explanation of the organism without having to give up the distinctive features of life in the process. In this way, I show this perspective to have significant advantages over the classic physicochemical reductionism of mechanistic biology.

ACKNOWLEDGEMENTS

Although I cannot speak from personal experience, it seems to me that the process of writing a doctoral thesis is quite similar to having a baby. It is slow, painful, laden with uncertainty, and very hard work. However, all the effort seems worthwhile as you see how your creation gradually acquires a life of its own.

It would have not been possible for me to give birth to this ‘baby’ without the help and support of a great many people. First of all I wish to thank my supervisor, Lenny Moss, for being such a constant source of inspiration, for opening my eyes (and my mind) to the universe of possibility that opens up at the interface of philosophy and biology, for his kindness and generosity, and for never being too busy to answer my emails, read my drafts, offer constructive feedback, and engage me in interminable philosophical discussions for hours on end.

I also want to thank my second supervisor, John Dupré, for offering critical feedback at crucial stages in the development of my ideas, as well as for providing in Egenis such a vibrant atmosphere in which to think philosophically about biology. Likewise I wish to thank Maureen O’Malley, Staffan Muller-Wille, and Sabina Leonelli for their encouragement as well as for their insightful comments on drafts of most the chapters in this thesis. I also thank my fellow graduate students at Egenis, especially Pierre-Olivier Méthot, Jonathan Davies, Alex Powell, Katie Kendig, and Mahgol Jaberansari, for making my doctoral life so stimulating and worthwhile.

Finally, I wish to express my eternal gratitude to my parents and my brother Patrick for all that they have done for me in these past few years. They know as well as I do that without their help, patience, and moral support it would have been impossible for me to complete this journey. I dedicate this thesis to them with love and thanks.

LIST OF CONTENTS

List of Figures	6
1. Introduction	8
1.1. Reconsidering the Foundations of the Philosophy of Biology	8
1.2. Mechanistic Thinking in Biology: The Need for Reassessment	12
1.3. Structure of the Thesis and Breakdown of the Argument	15
2. The Mechanicism-Vitalism Dispute: A Reappraisal	19
2.1. Introduction: The Mechanism-Vitalism Dispute – A Dead Issue?	19
2.2. ‘Mechanism’ and ‘Vitalism’: Defining the Terms of the Conflict	20
2.3. The Dawn of Mechanicism and the Cartesian Mechanization of Life	23
2.4. The Rise of Animistic Vitalism in Reaction to Cartesian Mechanicism	26
2.5. The Double-Edged Influence of Newton’s Natural Philosophy	29
2.6. Mechanicism vs. Vitalism in Embryology: Preexistence vs. Epigenesis	34
2.7. The Advent of Organic Chemistry and Its Impact on the Dispute	40
2.8. <i>Entwickelungsmechanik</i> , Driesch, and the Demise of Somatic Vitalism	46
2.9. Vitalism Re-Vitalized: Bernard and the Naturalization of Vitalism	51
2.10. Haldane’s Founding of Organicism and Its Eclipse of Mechanicism	55
2.11. The Molecularization of Biology and the Current State of the Dispute	61
2.12. Conclusions: The Nature and Conceptual Evolution of the Dispute	71
3. What is Wrong with the Machine Conception of the Organism?	81
3.1. Introduction: The Machine Conception of the Organism (MCO)	81
3.2. Historical and Philosophical Foundations of the MCO	83
3.3. Refuting the MCO: Why Organisms Are Different From Machines	87
3.4. Explanatory Consequences of the MCO: Reductionism Vindicated	98
3.5. Theoretical Consequences of the MCO: The Distortion of Development	102
3.6. Theoretical Consequences of the MCO: The Distortion of Evolution	107
3.7. Epistemic Consequences of the MCO: Engineering as Biology	115
3.8. Ethical Consequences of the MCO: Organisms to Use (and Abuse)	112
3.9. The Stream of Life: The Organicist Alternative to the MCO	125
3.10. Rethinking the Role of the MCO in Contemporary Biology	132
3.11. Conclusions: Biology ≠ Mechanicism	140

4. The Concept of Mechanism in Biology: An Analysis	144
4.1. Introduction: The Renewed Interest in Mechanism	144
4.2. The Three Meanings of ‘Mechanism’ in Biology	146
4.3. The Conceptual Evolution of ‘Mechanism’ in Biology	150
4.4. The Mechanismic Program in Relation to Mechanicism	155
4.5. Problems Resulting from the Ontologization of Causal Mechanisms	161
4.5.1. Function	162
4.5.2. Organization	164
4.6. Defending an Epistemic Conception of Causal Mechanisms	165
4.7. Conclusions: Mechanism-Talk in the Sciences	172
 5. Beyond Mechanicism: Biological Atomism and Cell Theory	 174
5.1. Introduction: Coming to Terms with Cell Theory	174
5.2. Biological Atomism Prior to Cell Theory	176
5.3. The Atomistic Foundations of Cell Theory	181
5.4. The Cell as the Biological Atom: Challenges from Above	185
5.4.1. Criticisms	186
5.4.2. Cell Theory versus Organismal Theory	191
5.5. The Cell as the Biological Atom: Challenges from Below	193
5.6. Conclusions: Biological Atoms and Biological Atomism	199
 6. Conclusion	 202
 Bibliography	 207

LIST OF FIGURES

1. Comparative Analysis of the Major Forms of Vitalism	73
2. The Nature of the Mechanicism-Vitalism Conflict	79
3. Experiments on the Effects of Ploidy on Newt Development	91
4. The Major Differences between Organisms and Machines	97
5. Biological and Mechanical Dogs (Alien Thought Experiment)	130
6. Subcellular Assemblies Described as Molecular Machines	137
7. Relationship between the Different Meanings of ‘Mechanism’	150
8. Causal Mechanism of the Membrane Trafficking of DOR	169

“Present day biology is the realization of the famous metaphor of the organism as a *bête-machine* elaborated by Descartes in Part V of the *Discours*”

Richard Lewontin (2009)

“There are powerful reasons for thinking that emancipation from the mechanistic paradigm is a precondition for true insight into the nature of biological processes”

John Dupré (2007)

Chapter 1

INTRODUCTION

1.1. Reconsidering the Foundations of the Philosophy of Biology

The philosophy of biology may be defined as the area of philosophical inquiry devoted to the examination of metaphysical and epistemological issues in biology. However, the academic discipline bearing that name is in reality largely concerned with evolutionary biology. One only needs to browse through the contents of the three most recent textbooks of the philosophy of biology, namely those of Elliott Sober (2000), Brian Garvey (2007), and Alexander Rosenberg and Daniel McShea (2008), to get the unmistakable sense that philosophy of biology as an academic field is not really the philosophy of *biology* at all, but primarily the philosophy of *evolution*. There is a general tendency to consider all interesting biological questions to be evolutionary questions, and all distinctively biological concepts to be evolutionary concepts. Evolutionary theory is seen as constituting the backbone of biology, and the philosophical relevance of every other area of biological science is determined in accordance to the extent to which it contributes to evolution. The most recent appraisal of the field, authored by Matthew Haber, Andrew Hamilton, Samir Okasha, and Jay Odenbaugh (2010), illustrates this thematic bias by its discussion of three areas of evolutionary biology (namely systematics, evolutionary ecology, and the levels of selection) as being jointly representative of philosophy of biology as a whole.

Given the extraordinary breadth of biological science, what is it that actually justifies this dominance of evolutionary thinking? Some philosophers of biology believe that it simply reflects how biologists themselves understand their own subject. However, even the most cursory look at a general biology textbook (e.g., Campbell et al., 2008; Raven et al., 2008; Sadava et al., 2006) suffices to dispel this notion. Biology textbooks begin by discussing the properties of *life*, *cells*, and *organisms*, not with the theory of natural selection. It is only *philosophy* of biology textbooks that contain opening chapters with titles like: ‘What is Evolutionary Theory?’ (Sober, 2000), ‘The Argument in Darwin’s *Origin*’ (Garvey, 2007), or ‘Darwin Makes a Science’ (Rosenberg and McShea, 2007). Why is this so? What is the basis for the overwhelming emphasis placed on evolution in philosophical studies of biology?

The answer to these questions lies in history. The modern academic discipline of philosophy of biology originated out of the efforts by the architects of the Modern Synthesis to defend the autonomy of organismic biology from the threat of physicochemical reduction embodied in the emerging field of molecular biology. “The ultimate aim of the modern movement in biology”, Francis Crick proclaimed, “is to explain all of biology in terms of physics and chemistry” (Crick, 1966, p. 10). Faced by the danger of becoming obsolete in light of the extremely successful molecular movement, Ernst Mayr wrote the following to Julian Huxley in private correspondence:

In a way the impact of biology has had a curious set-back as a result of the magnificent victories of molecular biology. To the outsider they suggest that physics and chemistry is the Alpha and Omega of all science. We will have to make a double effort to restore the influence of organismic biology and to make better known the evolutionary trends that culminated in that unique psycho-social organism, Man. (Mayr, quoted in Milam, 2010, p. 135).

The strategy adopted by the architects of the Modern Synthesis “to restore the influence of organismic biology” was, not surprisingly, to emphasize the primacy of the synthetic theory of evolution for a proper understanding of organisms. Ernst Mayr first attempted this in a highly influential paper called ‘Cause and Effect in Biology’ (1961) in which he argued that evolutionary explanations are necessary and ineliminable in the study of organisms. Mayr illustrated this view with his seminal distinctions between ‘how?’ and ‘why?’ questions and between ‘proximate’ and ‘ultimate’ causes. No matter how far the ‘how?’ questions of molecular biology may take us in elucidating the proximate causes of organisms, Mayr claimed, there will always be a need to consider the ‘why?’ questions of evolutionary biology in order to come to terms with the ultimate causes of organisms. In a similar vein, George Gaylord Simpson pointed to the priority of evolutionary considerations in explanations of organisms in a paper entitled ‘Biology and the Nature of Science’ (1963). Simpson argued that “reductionist explanation[s] made in terms of physical, chemical, and mechanical principles” are insufficient, and need to be complemented by “compositionist [explanations] in terms of the adaptive usefulness of structures and processes to the whole organism” (Simpson, 1963, p. 87). Biology, by virtue of its evolutionary character, can never be reduced to the physicochemical or the mechanical. Finally, Theodosius Dobzhansky did his own part to spread this message

in a paper called ‘Biology, Molecular and Organismic’ (1964), in which he criticized the increasingly prevalent assumption that “the only worthwhile biology is molecular biology” (Dobzhansky, 1964, p. 443) by drawing attention to the unifying power of evolutionary thinking in biology. Dobzhansky epitomized this view with the claim that “nothing makes sense in biology except in the light of evolution” (ibid., p. 449), a dictum he later rephrased in the title of a subsequent paper (Dobzhansky, 1973), and which has become a sort of mantra for evolutionary biologists ever since.

This work started to attract the attention of philosophers, such as David Hull and Michael Ruse, who used it as a basis to establish a sustained discourse within the philosophy of science devoted to the examination of the conceptual puzzles of biology, or more precisely, of the conception of biology which emerged from the Modern Synthesis (see Ruse, 1973; Hull, 1974). Thus, philosophers began to examine issues such as the structure of Darwin’s argument, the explanatory basis of population genetics, the nature of species, the problem of taxonomic classification, the definition of fitness, and the levels of selection. It was discussion around these topics which led to the academic institutionalization of philosophy of biology as a subdiscipline within the philosophy of science in the 1980s. As these philosophers took the Modern Synthesis as their exemplary model of what biology is, evolutionary theory naturally assumed the centre stage in the philosophy of biology discourse (e.g., Ruse, 1988). Areas of biology which had not been well represented in the Modern Synthesis (for example, development) did not become part of the philosophy of biology discourse until ways were found to directly relate them to the concerns of evolutionary biology (which in the case of development began to occur in the mid 1990s). Biological disciplines lying further away from the concerns of evolution, such as physiology, cell biology, immunology, or microbiology, remain severely underrepresented in the philosophy of biology to this day, although the situation has begun to show signs of improvement in recent years. Nevertheless, the overarching premise that continues to guide the philosophy of biology discourse is that Neo-Darwinism provides the basic grounds for defending the autonomy of biology from the physical sciences (see Mayr, 2004), and that consequently if one wishes to engage in philosophical analyses of distinctively biological problems, evolutionary theory is the obvious place to start.

However, to uphold this view is to have an impoverished understanding of what biology is, and by implication, to accept a narrow definition of what the philosophy of biology

could be. Focusing on evolution is not the only, or arguably even the best way of getting at what is distinctively biological. In fact, in the same year that Mayr published his seminal 'Cause and Effect in Biology', the physiologist Barry Commoner, then vice president of the American Association of the Advancement of Science, published a paper entitled 'In Defense of Biology' (1961) which had exactly the same objectives as Mayr's paper (as well as the aforementioned ones by Simpson and Dobzhansky). But instead of resorting to the ineliminability of evolutionary considerations to defend organismic biology, Commoner appealed to the view that organisms possess an inherent complexity that is not quantitatively extrapolable from physicochemical studies alone. Commoner recognized that molecular studies generate vast amounts of data, but he maintained that this data must be properly contextualized in relation to the living system as a whole for it to be truly explanatory.

In setting forth this way of defending the autonomy of organismic biology, Commoner was not proposing a new argument or a new way of thinking about living systems or about biology. Instead, he was drawing on an older organicist tradition in the philosophy of biology that flourished in the first half of the twentieth century, and which was primarily interested in the examination of the features that make organisms distinctive and the question of how far mechanical and physicochemical principles can ultimately take us in explaining them. Some examples of works which contributed to this organicist movement in the philosophy of biology include James Johnstone's *The Philosophy of Biology* (1914), J. H. Woodger's *Biological Principles* (1929), Kurt Goldstein's *The Organism* (1934), J. S. Haldane's *The Philosophical Basis of Biology* (1931), William McDougall's *The Riddle of Life* (1938), Ludwig von Bertalanffy's *Problems of Life* (1952), Morton Beckner's *The Biological Way of Thought* (1959), Rainer Schubert-Soldern's *Philosophical Aspects of Biology* (1962), and Walter Elsasser's *Atom and Organism* (1966). Today, this earlier discourse in the philosophy of biology has been almost completely forgotten, and the consensus within the community is that *real* philosophy of biology only emerged with the work of David Hull, Michael Ruse, and others (but see Byron, 2007). This is most regrettable, given that much of this earlier work is extremely relevant to many of the conceptual and theoretical challenges facing biologists today (see Etxeberria and Umerez, 2006). But even more importantly, this earlier discourse demonstrates that philosophy of biology can be much more than a philosophy of evolution plus allied disciplines. It illustrates

how the central philosophical concern in the science of life really must be the nature of life itself, and not any theory or principle devoted to explaining particular aspects of it.

Ever since its Neo-Darwinian transformation in the 1960s, the philosophy of biology has been predominantly concerned with the biological entities most relevant to the understanding of evolution, namely sub-organismic entities like genes and supra-organismic entities like populations. The crucial entity connecting them, the organism as a whole, has fallen between the cracks of philosophical inquiry. One of the major motivations underlying this doctoral thesis is the desire to contribute to ongoing efforts to return the organism to its rightful place at the centre of the philosophy of biology. With this in mind, this thesis will be addressing many of the same problems and questions which characterized the neglected pre-Neo-Darwinian tradition in the philosophy of biology in an attempt to help broaden up again the current discourse. As a result, this thesis will concern itself with issues more relevant to organisms and cells than to genes and populations, and it will examine problems that are perhaps more central to physiology and cell biology than to evolution and genetics.

1.2. Mechanistic Thinking in Biology: The Need for Reassessment

Once one is liberated from the evolutionary bias which has set the agenda in the philosophy of biology discourse over the past forty years, it becomes clear that, in a very fundamental sense, to do philosophy of biology is to reflect on the autonomy of the subject matter of biology, namely living organisms. Indeed, to acknowledge the existence of a ‘biology’, i.e. a science of organisms, is already to recognize at some basic level that there is something particular about organisms worthy of independent consideration. In general, the nature of any object becomes most perceptible when it is contrasted with a second object that is similar to the first in some respects but differs from it in others. Accordingly, biological reflections about the nature of living systems since the seventeenth century have tended to proceed by means of comparisons with mechanical systems. This should not be surprising. Organisms and machines share many features (e.g., organization, interacting parts, purposive behaviour, etc.) and yet they are also clearly different in other respects. And because machines are the products of human design, their operation is clearly understood. This makes them extremely compelling comparative models for thinking about the nature of organisms.

One of the first to undertake an explicit comparison was Georg Ernst Stahl, who in 1706 published a treatise entitled *De Mechanismi et Organismi Diversitate*. Although for Stahl the concepts of ‘organism’ and ‘mechanism’ did not refer to living and mechanical systems as they do today, but to the principles of order embodied by these two kinds of systems (see Cheung, 2006), his treatise already illustrates the epistemic benefits of comparing organisms with machines in order to gain insight into the nature of the latter. In a sense, the development in thinking about organisms since Stahl represents a struggle between the view that organisms and machines differ only in degree but not in kind, and the view that organisms and machines differ in fundamental ways. According to the first view, which we can call ‘mechanistic’, the theories, concepts, and methods that enable the construction and explanation of machines, and which have proven so successful in explaining the physical world, suffice to capture the nature of living systems. According to the second view, which we can call ‘anti-mechanistic’ or ‘vitalistic’, these theories, concepts, and methods ultimately come short in the explanation of life.

In modern times, it has been the mechanistic view that has gained the most acceptance. This is largely due to the proven track record of mechanistic biology in elucidating many of the structural features of organisms and the functional processes occurring within them. A clear symptom of the pervasiveness of the mechanistic view of life is that it is no longer explicitly defended. Whereas in the past, discussions over whether organisms can be understood as machines were heated, controversial, and considered of the greatest theoretical importance, today it is often simply assumed that organisms *are* machines, albeit ones cobbled together by natural selection (e.g., Monod, 1977; Dawkins, 1986; Dennett, 1995; Rosenberg, 2006, etc.). Indeed, provided that the evolutionary dimension of organisms is acknowledged, mechanistic biology, by virtue of its empirical success, has been allowed to corrode every other possible aspect of organisms which could be taken as a basis to demarcate them fundamentally from machines. This is precisely why evolutionary theory is regarded as being “what makes biology unique” (Mayr, 2004); because, in every other respect, the biological world can be encompassed by the principles of physics, chemistry, and engineering.

Overall, the emphasis on evolutionary issues in the philosophy of biology on the one hand, and the empirical success of the mechanistic approach in experimental biology on the other, has contributed to deflating the ontological and epistemological

significance of the organism. In this thesis, I attempt to illustrate the fundamental importance of the organism category for biology by providing a critical examination of the influence of mechanistic thinking in shaping our understanding of living systems. I oppose the deeply entrenched assumption that for biology to be a rigorous, empirically-grounded science, it must necessarily be framed in mechanistic terms. Instead I argue that “the mechanistic conception of life”, as Jacques Loeb (1912) branded it, despite its pervasiveness, is not only not inevitable, but it is actually seriously misleading. Far from enabling a satisfactory understanding of life, it actually obfuscates it by overlooking precisely what makes organisms distinctive. In fact, it is the anti-mechanistic or vitalistic tradition in biology, which began with Stahl’s rejection of the mechanization of the body proposed by René Descartes, which I believe possesses the best conceptual tools for coming to terms with the nature of life.

An examination of the presuppositions underlying the adoption of machine models in biology would by itself be more than sufficient to warrant a doctoral-level investigation. However, the place of mechanistic thinking in biology has become even more interesting in recent years following the advent of a research program within the philosophy of science with the intention of making sense of the role played by the concept of mechanism in scientific practice. This new interest in mechanisms is motivated by the realization that the classic deductive-nomological model of scientific explanation inherited from logical empiricism (i.e., Hempel and Oppenheim, 1948) does not do justice to the actual nature of biological explanations. Most biologists do not appeal to laws in their explanations, but to mechanisms. Ever since Peter Machamer, Lindley Darden, and Carl Craver published the now classic paper ‘Thinking about Mechanisms’ (2000) a decade ago (which has become the single most cited article in *Philosophy of Science*), an enormous amount of philosophical work has been carried out with the purpose of characterizing the functions of mechanisms in biological inquiry. Surprisingly, however, there has been no attempt whatsoever to investigate the link between the contemporary appeal to mechanisms in biological research, and the older mechanistic tradition in biology. Some important questions remain answered concerning this relation. For example, does the current mechanistic program in the philosophy of biology represent some sort of continuation of the agenda of mechanistic philosophy as it applies to biology? Does the formulation of mechanisms in the investigation of biological phenomena commit a biologist to a mechanistic understanding of living systems, and of biology as a science? What

exactly do biologists mean when they use the word ‘mechanism’? One of the objectives of this thesis will be to provide satisfactory answers to these questions.

Finally, a further line of investigation which I will explore is concerned with the thematic space that opens up once the philosophy of biology is conceptualized beyond evolution and living systems are returned to the centre stage of biological thought. Although Darwin’s theory of evolution by natural selection has attracted far more philosophical attention than any other idea in biology, it is not the only general principle in biology. In fact, there is at least one other theory which can claim the same degree of importance in the living world, namely *cell theory*. In the words of E. B. Wilson (1900, p. 1), “no other biological generalization, save only the theory of organic evolution, has brought so many apparently diverse phenomena under a common point of view or has accomplished more for the unification of knowledge”. However, despite its pivotal position in the edifice of biological knowledge, it has hardly received any attention at all by philosophers of biology. In this thesis I will take some preliminary steps to remedy this situation by analyzing the motivations which led to its formulation and examining the rationale of the major criticisms that have been waged against it in the century and three quarters since it was first formulated. Ultimately, I will argue that thinking philosophically about cell theory opens up a new way of epistemically decomposing organisms that overcomes some of the limitations of the physicochemical reductionism of mechanistic biology.

1.3. Structure of the Thesis and Breakdown of the Argument

This thesis is structured into six chapters: the present introduction (Chapter 1), two large-scale studies (Chapters 2 and 3), two medium-sized studies (Chapters 4 and 5), and a conclusion (Chapter 6). Each of the four studies attempts to offer a critical examination of a particular aspect of mechanistic thinking in biology by adopting different points of departure and drawing on different intellectual resources. Although the lines of argument developed in each of the studies are to a certain extent independent from one another, they also relate to each other in significant ways. Indeed, some recurring ideas will feature in all of the chapters. The overarching expectation is that the various critical discussions of mechanistic thinking will have had a cumulative effect by the end of the thesis. Let me now discuss in a little more detail what exactly I will be covering in the ensuing chapters, and what will be the major claims I will be advancing.

In Chapter 2, I will consider mechanistic biology and its vitalistic alternative in a historical context. My aim will be to retrace the conceptual evolution of the mechanicism-vitalism dispute by selecting some of the most representative episodes of its long and turbulent history. My historical excursion will pay particular attention to the underlying ontological and epistemological presuppositions informing the opposing sides of the dispute, and to the elements of continuity and discontinuity within each doctrine when considered along the historical timeline. This examination will lead me to offer a new interpretation of the development and philosophical relevance of this dispute, in addition to a complete reassessment of the nature of the relation between the schools of mechanicism and vitalism. However, the main novelty of my reappraisal of the mechanicism-vitalism dispute will be the claim that vitalism, far from having been eradicated from biology at the turn of the twentieth century as is generally assumed, actually got recast in naturalistic terms, giving rise to an organicist movement which flourished in the work of many theoretical biologists in the first half of the twentieth century. I will also attempt to show in this chapter that the conflict between mechanistic and vitalistic conceptions of the organism remains very much alive in biology today, even if the language in which the issues are discussed has changed somewhat.

In Chapter 3, I will consider mechanistic biology and its organicist alternative in the context of present-day biology. Specifically, I will take issue with the central unifying idea of mechanistic biology, namely the machine conception of the organism (MCO, hereafter). The MCO elegantly and succinctly sums up the mechanistic understanding of life, and it will therefore serve as the central focus of examination in this chapter. My critical examination will proceed in a series of consecutive stages. I will begin by tracing the historical origins of the MCO, considering its philosophical foundations, and then exposing its fundamental problems. I will then elaborate my criticisms of the MCO by examining in turn the explanatory, theoretical, epistemic, and ethical implications that result from its acceptance. I will argue that explanatorily, it vindicates the appeal to reductionism; theoretically, it leads to a heavily distorted understanding of both development and evolution; epistemically, it eliminates the boundary between biology and engineering; and ethically, it leads to a problematic view of organisms as disposable objects. Following these extended criticisms, I will explore the alternative conception of the organism favoured by organicist biologists and illustrate how it

sidesteps the conceptual problems generated by the MCO. Finally, I will also consider in this chapter what role, if any, should the MCO play in biology in light of its basic deficiencies as a theory of the organism.

In Chapter 4, I will carry out a detailed philosophical analysis of the concept of mechanism in biology. I will argue that the term ‘mechanism’ has three distinct meanings. It may refer to a thesis about the nature of life and biology (i.e., ‘mechanicism’ or ‘mechanistic biology’), to the structure and internal workings of a machine-like system (i.e., ‘machine mechanism’), or to an epistemic device that facilitates the explanation of a phenomenon of interest (i.e., ‘causal mechanism’). In this chapter I will trace the conceptual evolution of ‘mechanism’ in the history of biological thought, and I will examine how the three meanings of this term have come to be featured in the philosophy of biology, situating the new ‘mechanismic program’ in this context. My central claim will be that the leading advocates of the mechanismic program (e.g., Carl Craver, Lindley Darden, William Bechtel, etc.) inadvertently conflate the different biological senses of ‘mechanism’. Specifically, they all inappropriately endow causal mechanisms with the ontic status of machine mechanisms, and this invariably results in problematic accounts of the role played by mechanism-talk in scientific practice. Ultimately, I will suggest that for effective biological analyses of the concept of mechanism, causal mechanisms need to be distinguished from machine mechanisms, and the new mechanismic program in the philosophy of biology needs to be demarcated from the traditional concerns of mechanistic biology, examined in Chapters 2 and 3.

In Chapter 5, I will shift gear somewhat and turn to an examination of cell theory. In order to make philosophical sense of this theory, I will propose a perspective I call ‘biological atomism’. Biological atomism conceives the activity of a living organism as the result of the activities and interactions of elementary constituents, each of which individually already exhibits all the attributes proper to life. In this chapter, I will use the perspective of biological atomism to identify the theoretical antecedents of cell theory, as well as to come to terms with the major criticisms that have been waged against it. My claim will be that biological atomism not only enables a better understanding of the foundations of cell theory, but that it also constitutes a useful perspective through which to analyze its criticisms. The reason is that all major criticisms of cell theory can be interpreted as attempts to relocate the true biological

atom away from the cell to a level of organization either above or below it. I will also show that an important consequence of biological atomism is that it opens up a new way of thinking about the reductionistic explanation of organisms that avoids the pitfalls of mechanistic biology by ending the reduction at the level of living units. The implication of this is that it is possible to break down organisms into their parts for the purposes of explanation without having to surrender the irreducible properties of living systems when examining those parts. Indeed, the explanatory power of cell theory is based precisely on the exploitation of this possibility.

Finally, in Chapter 6, I will conclude by bringing together the common threads connecting the expositions in the previous chapters. This will enable me to offer a general evaluation of the status of mechanistic thinking in biology. I will also suggest some viable directions in which future research may be oriented on the basis of the findings made in this thesis.

Chapter 2

THE MECHANICISM-VITALISM DISPUTE: A REAPPRAISAL

The contest between the mechanistic and vitalistic conceptions is like a game of chess played over nearly two thousand years. It is essentially the same arguments that always come back, though in manifold disguises, modifications, and forms. In the last resort, they are an expression of two opposing tendencies in the human mind. – Ludwig von Bertalanffy (1952)

2.1. Introduction: The Mechanism-Vitalism Dispute – A Dead Issue?

Upon embarking on a critical analysis of the mechanism-vitalism dispute, what one finds most surprising is the remarkably little attention it has received from contemporary philosophers of biology. The received view is that this debate represents nothing more than a closed episode in the history of biology, with little or nothing to contribute to current philosophical discussions. This situation is not without a sense of irony, given that the very first book published with the title *The Philosophy of Biology* (i.e., Johnstone, 1914) was an extensive examination of the philosophical implications of the mechanism-vitalism conflict for our understanding of life (cf. Lillie, 1914). Indeed, since its inception in the seventeenth century, this dispute has provided the central battleground in which biologists have quarrelled over the nature of organisms, the difference between living and nonliving matter, the legitimacy of applying to biology the concepts, theories, and methods of physics and chemistry, and the question of how far the physical sciences can ultimately take us in explaining life. These would appear to constitute some of the most fundamental questions in the philosophy of biology, and yet the mechanism-vitalism conflict remains virtually ignored by contemporary philosophers. The justification that is usually given for this neglect is that the debate itself came to an end in the early twentieth century when mechanistic biologists conclusively undermined the scientific grounds for postulating a vital principle operating in the organism. Indeed, it is widely perceived that the excoriation of vitalism and the consolidation of mechanism were necessary steps in the establishment of modern biology. As a result, there can be nothing of real philosophical interest in vitalism given that this doctrine is fundamentally at odds with the tenets of modern science.

In this chapter I will challenge both the historical and philosophical contentions of this received view and propose in its place a new interpretation of the mechanism-vitalism dispute. By exposing the underlying presuppositions informing mechanism and vitalism, I will ultimately argue that this conflict remains very much alive in contemporary discussions over the nature of life, even if the terms in which the issues are discussed have changed somewhat. My exposition of the mechanism-vitalism dispute will be selective rather than comprehensive, and will primarily seek to provide evidence for the gradual conceptual evolution of the dispute from its origin to the present day. My major objectives shall be to (a) analyze the historical events and ideological motivations which led to its inception; (b) trace its development by examining some representative episodes of its history; (c) identify the elements of continuity and discontinuity in the epistemic convictions of the opposing sides of the dispute; and (d) ascertain the underlying nature of the recurring disagreement. The hope is that my examination of the mechanism-vitalism dispute demonstrates not only its instrumental role in shaping the historical development of biological thought, but also its critical importance and relevance to current theoretical and philosophical discussions in biology.

2.2. ‘Mechanism’ and ‘Vitalism’: Defining the Terms of the Conflict

The task of examining the mechanism-vitalism dispute is encumbered, as Arthur Lovejoy (1911, p. 610) observed, by “the lack of either clear or generally accepted definitions of the terms (‘vitalism’ and ‘mechanism’) used to designate the opposing doctrines under discussion”. C. D. Broad (1925, p. 43) similarly complained that “One is never quite sure what is meant by ‘Mechanism’ and by ‘Vitalism’”. In light of this situation, before I can delve into the historical development of the mechanism-vitalism conflict, it will first be necessary to provide clear and succinct characterizations of the opposing sides in this dispute.

The problem with the term ‘*Mechanism*’ as it is generally used by historians and philosophers of biology is that it is an umbrella term for three distinct notions. Chapter 4 will be devoted to untangling the different meanings of this concept and examining the philosophical consequences which arise from their conflation. For the time being, it shall only be necessary to characterize the sense of ‘mechanism’ that concerns us here, which I shall refer to hereafter as *mechanicism*. Mechanicism (also called *mechanistic philosophy* or *mechanical philosophy*) refers to the natural philosophy that became the

foundation of modern science, and which has its roots in the work of Galileo Galilei, René Descartes, Pierre Gassendi, Robert Boyle, and Isaac Newton. This philosophy is usually associated with a naturalistic, atomistic, and deterministic view of nature which tends to lend itself to mathematical characterization. However, mechanicism in biology, or *mechanistic biology*, has a rather more specific meaning (cf. Broad, 1925; Woodger, 1929; Bertalanffy, 1952; Lewontin, 2000; Allen, 2005; Dupré, 2007; Canguilhem, 2008). It can be characterized by reference to the following key tenets:

1. The commitment to an ontological continuity between the living and the nonliving, exemplified by the quintessential mechanistic conception of organisms as machines, analogous and comparable to man-made artefacts
2. The view that biological wholes (i.e., organisms) are directly determined by the activities and interactions of their component parts, and that consequently all properties of organisms can be characterized from the bottom up in increasing levels of organization
3. The focus on the efficient and material causes of organisms, and the unequivocal repudiation of final causes in biological explanation
4. The commitment to explanatory and methodological reductionism in the study of living systems

The term '*Vitalism*' also demands some clarification, though for rather different reasons. Since the early decades of the twentieth century, it has become customary to employ 'vitalism' as a term of abuse to disparage and ridicule irrational or unscientific views. Consider, for instance, what Francis Crick (1966, p. 99) had to say about vitalism in his John Danz Lectures: "Provided, then, that scientific study continues on a considerable scale, we can foresee a time when vitalism will not seriously be considered by educated men [...] And so, to those of you who may be vitalists, I would make this prophecy: what everyone believed yesterday, and you believe today, only cranks will believe tomorrow". The tendency to vilify vitalism has been a recurring theme throughout the twentieth century. The situation was clearly recognized by William McDougall, who deplored it in his book *The Riddle of Life* (1938) in the following passage:

In modern controversy it is very usual among the critics of vitalism to assume that vitalism consists essentially in the postulation of a, or the, vital force. It is then easy to pour scorn upon the vitalist by pointing out the quite empty, almost meaningless nature of the term

‘vital force’. This, however, is not a fair dealing. It is one form of that argumentation by way of innuendo and abuse of one’s opponents which in this sphere is so common and so much to be deplored. (McDougall, 1938, p. 11)

The modern caricaturization of vitalism is rather unfortunate, as we will see, given the large number of eminent biologists throughout history who have developed their ideas within a vitalistic framework. My examination of the conceptual evolution of the mechanicism-vitalism dispute will attempt to demonstrate that the recent vulgarization of vitalism is not only historically misleading but is also philosophically unjustified. A fairly unbiased definition of vitalism is provided by the *Oxford Dictionary of Philosophy*, which refers to it as:

The doctrine that there is some feature of living bodies that prevents their nature being entirely explained in physical or chemical terms. This feature may be the presence of a further ‘thing’ (such as a soul), but it may also be simply the emergence of special relations or principles of organization arising from the complexity of the biological organism. (Blackburn, 2005, p. 383)

But even this characterization does not do full justice to the doctrine. As the philosophical antithesis of mechanicism, I maintain that the most appropriate way to characterize vitalism is to understand it as the school of biological thought which upholds the *direct inverse* of the four core tenets of mechanicism, namely:

1. The commitment to an ontological discontinuity between the living and the nonliving, exemplified by the rejection of the machine conception of the organism, and the postulation of a vital principle that categorically demarcates living beings from inanimate objects
2. The view that biological wholes (i.e., organisms) possess system-level properties not explainable by attending to the activities and interactions of their component parts, and that consequently the distinctive properties of organisms need to be characterized from the top down in decreasing levels of organization
3. The focus on formal and final causes in biological explanation over and above material and efficient ones
4. The rejection of the sufficiency of explanatory and methodological reductionism in the study of living systems

This characterization of vitalism is appropriate because it does not define this doctrine in purely negative terms. Moreover, this understanding provides a suitable basis upon which to situate and contextualize the various forms of vitalism proposed throughout history, as well as serving as a convenient reference point in my examination of the evolution of vitalistic thinking from its inception to the present day. With clear characterizations of mechanicism and vitalism now in hand, it is now possible to turn to the historical examination of the debate.

2.3. The Dawn of Mechanicism and the Cartesian Mechanization of Life

It is sometimes suggested that the first expression of the clash between mechanicism and vitalism can be traced all the way back to the conflict between Democritean atomistic and Aristotelian philosophies of nature. However, this is quite anachronistic. Although Democritean atomism does resemble mechanicism in its emphasis on the inert, undirected, corpuscular nature of matter, and Aristotelian philosophy does share with vitalism the emphasis on the holistic and purposive features of organisms, it would not be appropriate to locate the inception of the mechanicism-vitalism dispute this far back in history. The dispute emerged *as a consequence* of the mechanistic establishment of modern science, and the proponents of both sides have primarily consisted of natural scientists concerned with the task of subsuming the phenomenon of life into the body of science rather than philosophers intent on providing systematic accounts of nature.

The mechanicism-vitalism dispute, properly conceived, began with the mechanization of life in the seventeenth century, which was itself an extension of the partly antecedent but still continuing mechanization of nature as a whole. This mechanization entailed conceiving the world as the mechanic conceives a machine, namely as a physical system explainable in terms of the size, shape and motion of its component parts (Garber, 2002). Mechanicism emerged in reaction to the Scholastic interpretation of Aristotelian natural philosophy, which was ultimately grounded in the irreducible tendencies of bodies to behave according to their substantial forms. The mechanization of physics entailed, among other things, an overthrow of obscure causes of terrestrial and celestial motion in favour of mathematical descriptions and a focus on deterministic efficient causation. In the science of life, the establishment of mechanicism was expressed by a shift away from explanations in terms of psychic causes, substantial forms, and mysterious faculties to explanations in terms of contact

forces, particulate motions, and mechanical and hydraulic models (Smith, 1976). All aspects of living organisms (except the minds of human beings) were subjected to the same kind of experimental, quantitative, and reductive analysis that was proving so successful in the characterization of the inanimate world. The upshot of this approach to biology was that that life as a phenomenon was transformed into an object of empirical investigation by bringing it within the scope of the analyzable and the explainable (Greene and Depew, 2004, pp. 36-48).

René Descartes (1596-1650) was the first to systematically apply the mechanistic philosophy to the science of living beings, and for that reason alone he has sometimes been credited with founding modern biology (e.g., Hall, 1970, p. 55). Although his main body of work was concerned with the mathematical characterization of physical science, Descartes also nurtured an interest in physiology, which led him to perform numerous dissections and experiments. As a means of extending mechanistic philosophy to the biological realm, Descartes argues that organisms are highly contrived machines which operate deterministically according to fixed, mathematically-describable laws (Des Chene, 2001). In his *Traité de L'Homme* of 1633, Descartes draws on the machine conception of the organism (MCO, hereafter) to fashion a thoroughly mechanical understanding of human physiology, which included explanations of sensation, respiration, muscle contraction, neurophysiology, digestion, reflex action, and the circulation of the blood. Indeed, this treatise has been described by historians of biology as “the first textbook on physiology” (Foster, 1924, p. 57; Singer, 1989, p. 358). In relation to his proposal to understand organisms as machines, Descartes ends *L'Homme* with the following remarks:

I desire, I say, that you should consider that these functions follow in this machine simply from the disposition of the organs as wholly naturally as the movements of a clock or other automaton follow from the disposition of its counterweights and wheels. To explain these functions, then, it is not necessary to conceive of any vegetative or sensitive soul, or any other principle of movement or life, other than its blood and its spirits which are agitated by the heat of the fire that burns continuously in its heart, and which is of the same nature as those fires that occur in inanimate bodies. (Descartes, 1998, p. 169)

This passage highlights two crucial points in Descartes' philosophy of biology that tend to get overlooked or, at the very least, are not always fully appreciated. The first is that when Descartes characterizes living beings as machines, he is not employing

colourful rhetoric or drawing upon a suggestive metaphor. Rather, he is making an exact identification.¹ As I will show shortly, the Cartesian MCO was to become hugely influential in the subsequent development of biological thought, as it came to constitute the central organizing theme underlying and unifying all mechanistic characterizations of life (see Chapter 3). The second point that should be noted is that neither in this passage nor in any of his other philosophical writings does Descartes seek to provide a general understanding of what it takes for an organism to be alive (Ablondi, 1998). In his most explicit statements, such as the one quoted above, he seems to equate life with heat. Life is an ensemble of motions that have their kinetic origin in heat; specifically, a certain ‘fire without light’ that burns, in men and animals, in the heart (Mackenzie, 1975). Interestingly, in the few passages particularly concerned with life itself, Descartes limits his examples to animals with hearts. Nowhere does he attempt to account for the life, heat, or internal motion of other kinds of organisms such as plants. From this it seems clear that Descartes (in opposition to Aristotle) did not consider life to be an important category; the difference between organisms and man-made artifacts like clocks is only a quantitative one. On the whole, Descartes was far more concerned with providing a synthetic model for physiology (which he found in the MCO) that enabled the integration of the most recent biological findings of his time (Sloan, 1977).

Although Descartes himself had to deal directly with the objections of his Neo-Aristotelian contemporaries by showing that a reasonably comprehensible mechanistic natural philosophy was possible (and indeed desirable), a generation or so later, that much could be taken for granted. Indeed, by the time of Descartes’ death in 1650, his mechanistic approach to biology had gained adherents in medical faculties across Europe. In relation to Descartes’ influence, the Danish anatomist Nicolas Steno (1638-1686) remarked in 1666 that:

Descartes [...] was the first who dared to explain all the functions of man, and especially of the brain, in a mechanical manner. Other authors describe man; Descartes puts before us merely a machine, but by means of this he very clearly exposed the ignorance of others

¹ Of course, this is not to say that Descartes fails to recognize the evident complexity of organisms compared to inanimate machines. Indeed, engineered as they are by an omnipotent God, organisms are machines infinitely more ingenious than those of our making. In Descartes own words, the human body, “having been made by the hands of God, is incomparably better ordered than any machine that can be devised by man” (Descartes, quoted in Ablondi, 1998, p. 183)

who have treated of man, and opened up for us a way by which to investigate the use of the other parts of the body as no one has done before. (Steno, quoted in Sloan, 1977, p. 20)

Mechanicism thus quickly became the generally accepted biological framework within which empirical research was gathered and interpreted and theoretical disputes were debated. The proponents of mechanistic explanation no longer had to argue its legitimacy and could instead focus on measuring its applicability and testing its limitations (Des Chene, 2005). One of the most prominent practitioners of the newly established mechanistic biology, Giovanni Alfonso Borelli (1608-1679) combined the Cartesian mechanistic framework with Galileo's emphasis on mathematical descriptions in his *De Motu Animalium* of 1680 to make sense of a wide range of physiological phenomena, including muscle contraction, nerve reflexes, and blood circulation. The successes of these early attempts seemed at the time to signal the triumphant subjugation of life to the rational and analytical character of mechanistic natural philosophy.

2.4. The Rise of Animistic Vitalism in Reaction to Cartesian Mechanicism

Towards the end of seventeenth century, however, the intellectual atmosphere gradually began to change. As more mechanists began applying their philosophy to more complex biological phenomena, it soon became clear that the resources at their disposal were insufficient to explain the functioning of living organisms. As their intricate organization was progressively revealed, the difficulty of ascribing all their properties to mere impulses acting on coordinated sets of pulleys, levers, and hooks, increased. Amid the growing discontent with the rigid application of mechanicism in biology, the animistic conception of the organism that had prevailed prior to the 'Cartesian turn' began to acquire currency once again. However, this new doctrine, which I shall term *animistic vitalism*, was not simply a reversion to the old Greek (or more specifically, Galenic) idea of different soul-faculties for different physiological functions (Hall, 1970, p. 58). Instead, it posited a non-physical vital agent which orchestrated the complex set of functions and operations of the body.

It is worth noting that animistic vitalism from its very inception was far less concerned with substantiating the existence of the vital agency it postulated than in combating the increasing mechanistic tendency to neglect, or at the very least grossly oversimplify, the inherent complexity and unpredictability of life. Animistic vitalism resorted to the

common intuition that a living being cannot be understood as a mere machine operating predeterminately, as it displays behaviours and possesses qualities that defy mechanistic explanation. The perfection of organisms, their properties, their generation, required according to this doctrine an unknown principle, an 'x' beyond all understanding, to account for the purposiveness of living beings. Moreover, Klerk (1979, p. 8) suggests that there might have been a psychological element in the original appeal of animistic vitalism, as the mechanistic implication that man is simply a machine must have resulted unacceptable to many. But probably most importantly, animistic vitalism had its base in everyday experience; when an animal dies, its body remains the same except for the disappearance of force and warmth. As a result, it was easily concluded that the organism was governed by a vital substance which endowed organic matter with life, and which left the body at the moment of death.

Animistic vitalism found its most prominent advocate in the figure of Georg Ernst Stahl (1660-1734), an influential German chemist and physician who argued that an *anima sensitiva* (analogous in some respects to the *psyche* of Aristotle) resides in the body of the organism, endows it with life, and develops through it all vital activities. For Stahl, the body exists not for itself, but for the soul which directly controls its activities for its own ends, and which is by itself responsible for all mental and physiological activities carried out by the body (Driesch, 1914, p. 31). A determinant factor in the development of Stahl's animistic vitalism was his rejection of the Cartesian mechanistic conception of organisms. He rejects the thesis that the living body can be reduced to physical corpuscles and their relations because the physical parts composing a body cannot explain its living state. The soul alone is responsible for adding life to make the organism alive. Thus, any mechanistic approach to the living organism will inherently fail to explain its operations and movements because these are essentially of a different nature from those characteristic of physicochemical substances (Wheeler, 1939, p. 25). In this way, in animistic vitalism the living and the nonliving are, both materially and formally, in a fundamental sense *in conflict* with one another. It is not merely the case that physiological function is not even in principle reducible to physicochemical processes, but it is further the case that it occurs *in violation* of such processes. The soul marks a break in the natural order of things, such that in light of its existence, the science which deals with the domain of the living is, and must forever remain, independent of, and irreducible to, the science dealing with the inanimate world.

Animistic vitalism is clearly dualistic, as it affirms the cohabitation of a material body that is in effect inanimate (and therefore somewhat analogous to the MCO of the mechanist) and a life-soul which is exclusively responsible for the life of the organism. Although this tolerance for a radical metaphysical discontinuity in nature may seem completely unacceptable from the modern perspective, it should be remembered that the mechanistic natural philosophy of the time was equally tainted by metaphysical discontinuities, as is exemplified by the Cartesian mind-body dualism. So it is clear that, at least in the seventeenth century, the mechanists' criticism of vitalism could not be motivated by the desire to denounce the ontological demarcation that the animistic vitalists posited between life and matter, as the Cartesian mechanists were themselves defending an equally distinct ontological dualism between mind and matter. The crucial disagreement between the two sides of the dispute at this time is primarily over the extent of applicability of mechanistic natural philosophy. For the animistic vitalist, mechanistic explanations are well-suited for the study of the inanimate world, but are of no use for understanding living beings. For the Cartesian mechanist, mechanistic explanations are appropriate for characterising both physicochemical processes *and* physiological processes, but are inappropriate (or, at the very least, insufficient) for understanding rational processes. The interesting implication of this is that during the seventeenth century neither of the two doctrines could claim universal applicability. Rather, in relation to the physicochemical universe, the animistic vitalist defended the independence and irreducibility of *vital* phenomena, whereas the Cartesian mechanist defended the independence and irreducibility of *mental* phenomena.

Finally, it should be mentioned that Cartesian mechanicism and animistic vitalism were not the only two doctrines informing the physiological and medical research that was pursued during this period. In fact, there were a number of conceptual positions standing in between mechanicism and vitalism (see Hall, 1970, p. 59; Singer, 1989, pp. 358-367). Some natural philosophers, such as Pierre Gassendi (1592-1655) and Thomas Willis (1621-1675), acknowledged the vital soul but in addition attempted to 'materialize' it by giving it a corpuscular constitution. On the other hand, there were others like Claude Perrault (1613-1688) and Pierre-Sylvain Régis (1632-1707), who admitted the existence of the life-soul but rarely invoked for explanatory purposes, retaining the MCO in their biological investigations.

2.5. The Double-Edged Influence of Newton's Natural Philosophy

With the work of Sir Isaac Newton (1643-1727), mechanicism underwent a qualitative change. Descartes had described the universe in terms of matter and motion. Newton added space (i.e., a void in which particles move and interact) and incorporated the notions of attraction and repulsion, which manifested themselves in nature as '*forces*', to explain how organised corpuscular matter maintains its cohesion. Newton's conception of force was initially criticised by some of his mechanistic contemporaries—including Gottfried Leibniz (1646-1716)—because it was seen as an attempt to reintroduce into natural philosophy Scholastic occult qualities through the back door (Boas, 1952, pp. 509-510). However, the forces Newton postulated, unlike the occult qualities of the Scholastics, could be fully operationalized in mathematical terms. Their formal characterization meant that they could be profitably used to effectively explain and accurately predict an extremely wide range of physical phenomena. No additional explanation of the forces' origin was required to understand their mode of operation. As long as the postulated forces could be shown to exist experimentally, accounting for their actual cause was not strictly necessary, as their existence could be deduced from their action on the phenomena. It was this epistemological shift that enabled the Newtonian conception of action at a distance (embodied in his force of gravity described in his law of universal gravitation, and in his conception of attractive and repulsive forces described in his theory of chemical affinity) to become intrinsically ingrained within the mechanistic worldview.

One of the most salient repercussions of Newton's transformation of mechanicism was that it opened up a new area of possibility in which to investigate chemical processes. Building on Robert Boyle's (1627-1691) theories on the structure of matter, Newton was responsible for transforming the notion of chemical affinity from a metaphysical alchemical principle to a physical property arising in the interactions of different compounds that could be measured and predicted (Boas, 1952, pp. 510-515). The upshot of this mechanization of chemistry was that new physiological processes, such as digestion and respiration, became accessible to experimental study. René Réaumur (1683-1757) and Lazzaro Spallanzani (1729-1799) were able to study digestion because they understood it as a chain of chemical reactions instigated by the action of the gastric juice. Antoine Lavoisier (1743-1794) was able to study respiration because he viewed it as a process of chemical combustion (Jacob, 1973, p. 42). The breathing of a bird and the burning of a candle are, for Lavoisier, equivalent objects of study.

Consequently, they can both be investigated using the same concepts and methods. In this way, the mechanistic developments in the physicochemical sciences initiated by Newton's discoveries led to a fundamental change in the way living beings were mechanistically studied during the eighteenth century.

But did this shift in the way mechanists study life transform their actual conception of life itself? It appears that the answer is both yes and no. Strictly speaking, the organism in the eighteenth century remained all that it had been in the seventeenth century: a well-crafted machine. However, the very nature of the machine changed. It was no longer a machine functioning only by shape, size, and motion, but according to a wide range of mechanistic principles. The MCO evolved from a clock, with its springs, cogs, and levers, to a steam engine, with its source of heat that had to be continuously renewed, its cooling system, and its devices for adjusting and coordinating the operations of the various parts. Accordingly, Lavoisier would state that:

The animal machine is governed by three main regulators: respiration, which consumes oxygen and carbon and provides heating power; perspiration, which increases or decreases according to whether a great deal of heat has to be transported or not; and finally digestion, which restores to the blood what it loses in breathing and perspiration. (Lavoisier, quoted in Jacob 1973, p. 43)

What is often forgotten, however, is that Newtonian natural philosophy exerted as much of an influence on the development of vitalism as it did on the development of mechanicism. In the '31st Query' of Newton's *Opticks* (published in 1730), Newton famously remarked that just as the physical world is governed by the forces of gravitation, chemical attraction and repulsion, and electricity, there may be other kinds of forces yet to be discovered operating in other domains of nature (Greene and Depew, 2004, p. 89). This insinuation instigated numerous biologists in the eighteenth and nineteenth centuries to embark on the search for other unknown forces of nature, analogous in kind to the ones described by Newton, but which were manifested exclusively within living beings. The astounding successes of Newtonian natural philosophy meant that it had become legitimate to concentrate on the visible order when studying nature, to interpret that order in terms of putative forces acting on it, and to avoid all speculation about the nature of the forces in question.

Capitalizing on the inherent metaphysical ambiguity of the Newtonian conception of ‘force’, many physiologists, acting in explicit accordance with what they took to be the standard practice of the physicists of the time, invoked a number of inexplicable explicative devices (what Hall (1968) refers to as “physiological unknowns”) to account for biological phenomena that could not be understood in terms of the properties and interactions of organismic parts. This ‘Newtonian turn’ in the approach to the study of organisms constituted a radical transformation of vitalistic thought. The animistic vitalism that had prevailed in the seventeenth century was replaced as a consequence of the impact of Newtonian natural philosophy by a rather distinct doctrine, which I shall refer to as *somatic vitalism*. Unlike its predecessor, somatic vitalism does not posit a fundamental metaphysical dualism in the organism between life and matter. The vital principle is no longer conceived as an external agency which inhabits the body and bestows upon it the vital functions. Instead, it is understood as an intrinsic property of matter; a force which emerges from the living soma and endows it with its irreducible, non-mechanistic qualities. This form of vitalistic thought arose in the mid eighteenth century but remained popular, in one form or other, until the turn of the twentieth century.

What is remarkable from a philosophical perspective is the surprising extent to which somatic vitalism constitutes an *expression* of Newtonian philosophy as much as it constitutes a *reaction* to it. Even though it is clear that somatic vitalists reject as a matter of principle the reducibility of many organismic features to (Newtonian) mechanistic analyses, it is nevertheless equally apparent that they conducted their research in conscious imitation of what they took to be the corresponding practice in the physical sciences. As a matter of fact, the writings of the somatic vitalists contain frequent allusions to Newton himself, and often plainly show his influence even when he is not mentioned by name (see Hall, 1968). In this way, Newton’s impact led to a transformation of both sides of the mechanism-vitalism dispute. On the one hand, the mechanists employed the theoretical concepts and experimental approaches that Newton had profitably used in physics and chemistry to advance the MCO. On the other hand, the vitalists adopted Newton’s epistemic strategy of postulating unknown causal principles to analyse specific domains of recalcitrant phenomena whilst declining to provide an explanation of the origin of such principles.

Which of the two interpretations of Newtonian natural philosophy, the mechanistic or the vitalistic, was more prevalent during the eighteenth century? Theodore Brown (1974) has shown that although mechanicism was prominent in the first few decades of the century, the focus then gradually shifted towards a somatic vitalism that openly embraced the explanatory usefulness of vital forces and explicitly denounced the explanatory limitations of mechanicism. A glance at the titles of the key physiological treatises of the early eighteenth century suffices to confirm the commitment of these works to Newtonian mechanicism, as is illustrated by James Keill's *Account of Animal Secretion, the Quantity of Blood in the Humane Body, and Muscular Motion* of 1708, Nicholas Robinson's *New Theory of Physick and Diseases Founded on the Principles of Newtonian Philosophy* of 1725, and Stephen Hales' *Vegetable Staticks* of 1727.² The underlying objective motivating all of these treatises is the reduction of particular physiological problems to physicochemical ones through the employment of Newtonian mathematical and experimental techniques.

However, already in Keill's treatise of 1708 one finds the first signs of the somatic vitalism that was to shape the study of physiology in the second half of the century. Keill's intention had been to link the study of 'animal oeconomy' with Newtonian physics, but in doing so he introduced the notion of irreducible physiological properties, which he tied to the Newtonian notion of attraction. In his treatise, Keill posited attractive forces between the constituent particles of secreted physiological fluids in order to circumvent certain theoretical difficulties. Although this employment of a physiological force was largely forgotten in the following decades amid the growing appropriation of Newtonian mathematics and methods by Keill's contemporaries (with the notable exception of Henry Pemberton (1694–1771), who suggested in a 1723 treatise on the mechanics of muscle contraction that the living organism may display phenomena beyond the reach of physical explanation), doubts over the scope and validity of mechanistic experimental physiology eventually began to proliferate, paving the way for the introduction of Newtonian epistemic unknowns in the living domain. In this way, some of the most distinguished physiologists of the latter part of the eighteenth century, including George-Louis Leclerc de Buffon (1707–1788), Théophile Bordeu (1722–1776), John Hunter (1728–1793), Paul Joseph Barthez (1734–1806), Johann Friedrich Blumenbach (1752–1840), and Georg Treviranus (1776–1837), employed vital forces in their explanations of biological phenomena. As Bordeu

² The Scottish physician George Cheyne (1671–1743) even urged for the composition of a '*Principia Medicinae Theoreticae Mathematica*' (!) in his *New Theory of Fevers* of 1701 (see Brown, 1987).

notes, in spite of its obscure metaphysical status, the postulated vital force is “no more strange than the gravity, attraction and mobility that belong to various bodies”. As a good Newtonian, he adds that although its operation can be demonstrated experimentally, “As to the nature of this faculty, the subject is one of those about which it is safer to be silent than to try to reason” (Bordeu, quoted in Hall, 1968, p. 18). Similar cautious statements and ontological reservations can be found in the writings of the other aforementioned authors, in addition to many other celebrated biologists of the period (see Hall, 1968).

The physiological unknowns posited by the somatic vitalists never enjoyed the same degree of scientific respectability as their physicochemical analogues, and often evoked vigorous opposition as soon as they were stated. A plausible explanation for this is that the function, operation, and indeed the very nature of the vital force differed greatly from one vitalist to another. There was no consensus among vitalists regarding the way in which the vital force was believed to manifest itself empirically. In fact, there was not even an agreement over whether there was a single vital force or if there were several of them. Blumenbach, for instance, maintained that there were as many as five vital forces operating autonomously in the living organism: (i) the *nisus formativus* (producing the genital and nutritive fluids) (ii) the *vis cellulosa* (conferring irritability to the mucous tissue); (iii) the *vis muscularis* (conferring contractility to the muscles); (iv) the *vis propria* (endowing particular organs with specific functionalities); and (v) the *vis nervea* (providing sensibility to the nervous system). In spite of the remarkable diversity in vitalistic thinking, all somatic vitalists were united in their rejection of the sufficiency of bottom-up mechanistic explanation (be it Newtonian or Cartesian) and in their conviction that the distinctiveness of living phenomena provided ample empirical evidence of the operation of unexplainable forces in nature. Moreover, they concurred that vital forces, regardless of their specific character, did not impose a fundamental metaphysical dualism in the living organism (unlike the life-soul of the animistic vitalists), and were as much of a part of nature as the physical forces postulated by Newton himself. Nevertheless, by the end of the eighteenth century, the philosopher Immanuel Kant, reflecting on half a century of inconclusive attempts at locating vital forces, famously asserted that there would never in fact be a Newton of biology capable of making comprehensible by Newtonian means (in either its mechanistic or vitalistic interpretations) the generation of even a single blade of grass (see, e.g., Heidermann, 2009).

On the whole, what emerges from this examination is that, far from tilting the balance in favour of the mechanistic side of the debate, the impact of Newton's work on the physiology of the eighteenth century actually provided a new axis upon which the mechanicism-vitalism dispute acquired new relevance and significance. As much of my discussion so far has focused almost exclusively on the domain of physiology, in the next section I will consider how the mechanicism-vitalism conflict unfolded during the late seventeenth and eighteenth centuries in a rather different area of biological study: embryology. Following this discussion, it will then be possible to examine the fate of the dispute in the nineteenth century.

2.6. Mechanicism vs. Vitalism in Embryology: Preexistence vs. Epigenesis

Although much of the secondary literature on the mechanicism-vitalism dispute has discussed this philosophical debate in the context of physiology, the study of organismic development during the late seventeenth and eighteenth centuries may be interpreted as providing another central battleground on which the clash between mechanicism and vitalism played out empirically. Two opposing schools of embryological thought became consolidated during this period, the doctrines of *Preexistence*³ and *Epigenesis*, and the vociferous disagreements between their proponents were, for the most part, motivated by deeper, more fundamental philosophical persuasions. Central among these were the conflicting doctrines of mechanicism and vitalism. The study of embryology helps illuminate the mechanicism-vitalism conflict because, in focusing on a very specific object of scientific study that was easily accessible to observation and experimentation, it provided a useful means of testing the validity and applicability of mechanistic and vitalistic conceptions of life. In my examination of the controversy between the doctrines of preexistence and epigenesis, I shall again take the establishment of mechanicism as my point of departure.

As we have already seen, the mechanistic rejection of Scholasticism in the first half of the seventeenth century implied that occult forces could no longer be invoked as

³ In line with recent scholarship (e.g., Pyle, 2006, Detlefsen, 2006), but owing to a distinction originally made by Jacques Roger (1963) and subsequently elaborated by Peter Bowler (1971), I adopt the term 'preexistence' instead of the more traditional notion of 'preformation', as the two labels actually designate two distinct embryological doctrines, and it is the former that acquired greatest currency during this period and which concerns us here.

legitimate explanatory devices to account for biological processes. In the context of organismic development, mechanismism required replacing Aristotelian souls and Galenic faculties with a theory that conceived the phenomenon of generation as a strictly mechanical process which operated in accordance to physical laws. The problem for the mechanist, however, was that it was extremely difficult to explain such a complex natural phenomenon in terms of mere matter in motion. Descartes himself fully recognised this problem when he confessed that “The formation of all the parts of the human body [...] is something so difficult that I dare not undertake [to explain it] yet” (Descartes, quoted in Aucante, 2006, p. 66).⁴ The real difficulty rested on explaining novelty. Although mechanismism could account for the geometric growth of an organism, it could not provide an effective explanation of the origination of new form in the developing organism. The emergence of complex morphological structure where previously there had been none indeed appeared to transcend mechanistic explanation. As a result, the only way in which the phenomenon of organismic generation could be subsumed within mechanismism was to avoid the problem of novelty altogether. This required postulating that the structure of the adult organism is already preformed prior to foetal growth, thereby implying that the process of development simply consists in the gradual enlargement of the adult structure already articulated in the germ. This is the doctrine of the preexistence of germs, and at the time it provided the only viable means of reconciling the evident complexity of organismic generation with the elegance and relative simplicity of mechanistic natural philosophy.

The doctrine of preexistence asserts that the germ is essentially a miniature version of the fully formed adult organism which remains in an inert state awaiting activation through fertilization. Upon this process, the germ is set into a growth phase and gradually expands in all directions through a mechanical process until it acquires its final size. However, since development is merely a process of expansion, the preformed structure already existing in the germ remained to be explained. Thus, in the doctrine of preexistence the problem of generation is simply pushed one step backward, for it is the origination of organic form in the actual seed that now demands an explanation. Since mechanistic principles are as inadequate to explain the emergence of organised structure in the germ as it is in the developing embryo, the

⁴ In fact, Descartes was so aware of the difficulty of applying his mechanistic philosophy to the understanding of the generation of animals that, in spite of the number of embryological experiments he personally conducted throughout his life, he never felt sufficiently confident to publish a single text on the subject in his lifetime (Aucante, 2006, p. 66).

doctrine of preexistence postulated that the germs of *all* organisms, past, present, and future, have always existed, ever since the moment of Creation, and were simply awaiting the moment of activation by fertilization (Jacob, 1973, p. 60).

The doctrine of preexistence was developed through three different theories: *panspermism*, *ovist emboîtement*, and *animalculist emboîtement*. The panspermist version of preexistence was introduced by Perrault, who discussed it in his *Mécanique des Animaux* (published in 3 volumes between 1680 and 1688) as the theory that the preformed miniature germs float freely in the air until absorbed by a parent organism, which supplies the conditions necessary for development upon fertilization (Bowler, 1971, p. 241). The two *emboîtement* theories of preexistence instead assert that each preformed miniature germ is encased within the reproductive organs of one of its parents (the mother on the ovist theory, and the father on the animalculist theory), its parent is encased within the reproductive organs of one of its parents, and so forth. This accounts for all organisms of every generation of every species, as all future members of a given species are nested into one another like Russian dolls within the first member of that species upon Creation. An interesting implication of the two *emboîtement* theories is that both suppose that the male and female contributions to the conception of the organism are different, since only one of the two contains the germs of its descendants. For the ovists, the male merely provides a trigger or stimulus for growth, whereas for the animalculists, the female only provides protection and nourishment.⁵

The doctrine of preexistence, derived as it was from mechanistic natural philosophy, became biological orthodoxy in the late seventeenth century and remained the dominant view of organismic generation throughout most of the eighteenth century. As such, it was advocated by such noteworthy figures as Nicolas Malebranche (1638-1715), Albrecht von Haller (1708-1777), and Charles Bonnet (1720-1793). Out of the three main versions of the doctrine, the ovist theory became the most popular as it was regarded as the best confirmed by experiments carried out on the development of eggs of different species (Bowler, 1971, p. 243; Pyle, 2006, p. 194). Despite its popularity, the doctrine of preexistence was not without its problems. An obvious complication with this conception of generation was that it could not explain why the progeny

⁵ It is important to note that this dispute between ovist and animalculist *emboîtement* theories of animal generation had an analogue in the contemporary discussion over *vegetable* generation, where the conflict was played out between *ovulist* and *pollenist emboîtement* theories (Ritterbush, 1964, pp. 88-98).

displayed phenotypic traits of *both* parents, and new traits altogether.⁶ The problem of emergent variation in the progeny was even more salient in the face of monstrosities and other very apparent defects in the newborn. Having postulated the creation of all organisms by God, preexistence theorists were forced to allow for interference in the unfolding development of embryos, or to admit God's fallibility or His vindictiveness.⁷ Although the doctrine of preexistence remained the orthodox view during the seventeenth and early eighteenth centuries, the gradual accumulation of theoretical problems like this one, stemming from increasing observations and experiments conducted on developing embryos, helped bring to the fore an opposing school of embryological thought known as epigenesis.

Epigenesis is the doctrine which postulates a *de novo* production of organic form in the developing organism. Upon conception, matter previously homogeneous, undifferentiated, and unorganized becomes heterogeneous, differentiated, and organized, resulting in the generation of a living, functional being. According to this doctrine, organic form not only develops anew, but it is brought into existence step by step as development unfolds. Although Harvey was the first to use the term 'epigenesis' in his *De Generatione Animalium* of 1651, it was Caspar Friedrich Wolff (1734-1794) who fully developed the doctrine theoretically in the mid eighteenth century, and in doing so helped bring to the fore the first serious challenge to preexistence. However, although in the nineteenth century Wolff's work (particularly his seminal *Theoria Generationis*) was to provide the foundation for experimental embryology, during the eighteenth century it failed to attract supporters, and remained largely in the shadow of the preexistence theories of Bonnet and Haller (Jacob, 1973, p. 66; Roe, 1979, p. 3).

⁶ As we will see in Chapter 5, during the eighteenth century Buffon proposed a radically different theory to account for these phenomena.

⁷ Being well aware of this problem, and yet wanting to restrict his explanation within the strict confines of mechanicism, Descartes suggested that the mother's imagination exerts a formative influence on the developing foetus. Consequently, "if the imagination of the mother is harmed by some impression, the child's body parts will be monstrous" (Descartes, quoted in Smith, 2006, p. 91). In order to mechanistically account for the causal link between the mother's imagination and the body of the foetus, Descartes argued that "sometimes [the image] can pass from [the pineal gland] through the arteries of a pregnant woman into certain parts of the child that she carries in her womb" (Descartes, quoted in Smith, 2006, p. 90). The pineal gland thus functions as a sort of translating receiver where mental images are converted into physiological signals that lead to specific motor responses in the embryo. Crucially, for Descartes, invoking the imagination of the mother does not amount to a retreat into occult causes to explain what would otherwise remain inexplicable. The imagination does not constitute a non-physical directing agency; it is just a corporeal phenomenon like any other, and as such it is subject to, and explainable by, the basic principles of mechanistic natural philosophy (Smith, 2006, p. 91). Although Descartes' argument was later adopted by Pierre-Sylvain Régis (1632-1707) and others, it failed to convince those who saw contradictions between the basic tenets of the doctrine of preexistence and the process of development as it presented itself to the senses.

It is actually not difficult to understand why it took such a long time for the idea of epigenesis to be taken as a serious alternative for the explanation of generation. Preexistence answered the difficult question of how the embryo attains the complex level of organization it reaches during development whilst at the same time being consistent with both mechanicism and the religious beliefs of the time. In contrast, it was far more challenging to explain development epigenetically. If the embryo develops through successive formation of structures, what guides this process? Is it organic matter itself? Or must there be a special agency or force in operation, governing the process of development? It was in an attempt to answer these questions that Wolff wrote his doctoral dissertation, *Theoria Generationis*, which he defended in 1759. In it Wolff elaborated an epigenetic account of generation according to which plant and animal fluids are secreted from the developing organism and are solidified into parts. The process of secretion and solidification is accomplished by means of a vital force, the *vis essentialis*, which is responsible for the absorption and distribution of nutrients in animals and plants during development.⁸

One of the central claims that Wolff makes in his *Theoria Generationis* is that “Those who teach the system of predelineation [preexistence], do not explain generation but deny that it occurs” (Wolff, quoted in Roe, 1979, p. 16). Indeed, the doctrine of preexistence asserts that actual generation never happens, since each instance of embryonic development is in truth simply the unfolding of an already formed organism. Through the postulation of the *vis essentialis*, and the description of its operation in the developing organism, Wolff was able to provide a genuine explanation of the process of generation that was compatible with, and indeed confirmable by, his microscopical observations of developing embryos. So, in an important sense, it was Wolff’s commitment to a vitalistic conception of generation that enabled the doctrine of epigenesis to become properly developed theoretically.

⁸ Upon its completion, Wolff sent his dissertation to Haller, and, in doing so, initiated a direct and extended debate with him which lasted until Haller’s death in 1777. The main point of contention between them related to the formation of blood vessels in the *area vasculosa*, specifically, over whether they are truly formed or preexist. Haller argued that the vessels are pre-existing but not visible because they are initially transparent; Wolff asserted that they are formed gradually by the movement of fluids, which cuts through the *area vasculosa* under the guidance of the *vis essentialis*. In addition, Haller and Wolff disagreed over the formation or preexistence of the heart. Haller’s theoretical system demanded the preexistence of the heart, since its pumping action is the initiator of the expansion of preformed parts. In contrast, Wolff’s theory of epigenesis required that the heart *not* be present in early stages of development, in order to prove that the *vis essentialis* is required for development to begin (see Roe, 1981, ch. 3).

That Wolff is a vitalist is a fact beyond reasonable doubt, given his postulation of a *vis essentialis* acting solely on living beings, coupled with his explicit rejection of the explanatory sufficiency of mechanical medicine (Roe, 1979, p. 25; Detlefsen, 2006, p. 247). The more crucial question remains, however, as to whether Wolff should be regarded as a *somatic vitalist* in the sense described in the previous section in reference to the physiologists of the same period. I believe that this can indeed be shown to be the case by looking at some of Wolff's own writings. First of all, Wolff clearly distinguishes his own brand of vitalism from the animistic vitalism of Stahl (discussed in Section 2.4), as is attested by the following assertion: "This characteristic and essential force appears to be one [...] whose existence Stahl very certainly recognized, but which he, incorrectly I think, attributed to the soul" (Wolff, quoted in Roe, 1981, p. 116).⁹ What is more, in the very next sentence of this same passage Wolff confirms his commitment to a Newtonian conception of vital force when he notes that the *vis essentialis* "consists in nothing further than a particularly defined kind of attractive and repulsive force" (ibid.). Finally, in the best Newtonian tradition of somatic vitalism, Wolff believes that the vital force can be postulated on the basis of observational evidence, and it is therefore not necessary to provide an account of its cause or origin: "It is enough for us to know that it [the *vis essentialis*] is there, and to recognize it from its effects, as it is demanded purely and simply in order to explain the development of parts" (Wolff, quoted in Roe, 1979, pp. 22-23).

Thus, as the preceding discussion has shown, there is clear evidence which suggests that the clash between preexistence and epigenesis may be viewed as a particular embodiment of the mechanicism-vitalism dispute in the study of development during the late seventeenth and eighteenth centuries. The doctrine of preexistence constituted the only means by which the mechanists of the period could account for generation, namely by evading an actual explanation of it. Indeed in line with the mechanistic commitment to the MCO, all that the mechanist can aspire is to explain its current operations by reference to the arrangement of its component parts. But if generation is the actual object, it is precisely this arrangement that demands an explanation! Since machines do not self-assemble, clearly the only solution that remained was to assert

⁹ Wolff's departure from Stahl's animistic vitalism can be further corroborated by another passage where, in complaining of Haller's criticism of his *Theoria Generationis*, Wolff remarks that "Haller has thus not been entirely correct [...] when in the judgment of my work he put forward the essential force as the main point, remembering all that properly belongs to this theory almost with no words and then deliberately mentioning that this thing is called by me the essential force, but which *I completely separated from the soul of the Stahlans*; about which indeed exactly so much as nothing was said" (Wolff, quoted in Roe, 1981, p. 181; my emphasis).

that every organism is the product of the original supernatural act of Creation, and not the result of a natural process of generation (Pyle, 2006, p. 195). In contrast, the epigenetic theory of Wolff shows obvious signs of having been devised as a reaction against the explanatory insufficiency of the mechanistic doctrine of preexistence, and in his formulation and elaboration of the *vis essentialis*, coupled with his assertion of the irreducibility of vital functions, Wolff proves to be philosophically committed to exactly the same form of somatic vitalism that characterised his physiologist contemporaries. In this way, although both preexistence theorists and epigenesists were united in their desire to explain the same natural phenomenon, and were even in agreement with regards to many of their observations, their underlying philosophical persuasions led them to interpret the empirical data in drastically different ways.

2.7. The Advent of Organic Chemistry and Its Impact on the Dispute

The nineteenth century brought about yet another transformation in the terms and issues upon which the mechanicism-vitalism conflict played out, and once again this change was instigated by concurrent developments in the physical sciences. Specifically, it was the development of organic chemistry and its fruitful application to physiology which exerted the greatest influence on the debate. The pioneering research of Lavoisier in the eighteenth century paved the way for further attempts to apply chemical methods and techniques to the study of living beings, and in doing so bridge the gap between the animate and inanimate realms. Lavoisier and his followers had successfully shown that the elementary composition of living matter was primarily carbon, hydrogen, oxygen, and nitrogen, thereby demonstrating that the ‘stuff’ of life was chemically indistinguishable from nonliving matter, and thus laying to rest any last remnants of animistic vitalism.¹⁰

The further study of the nature and relative proportions of the chemical constituents composing biological substances became the central preoccupation of early organic chemistry. In England, this form of research was pushed forward by the establishment in 1802 of a society for the Promotion of Animal Chemistry. Elsewhere in the continent, Swedish, French, and German chemists followed in Lavoisier’s footsteps by developing and refining techniques for chemical analysis, resulting in the build up of

¹⁰ As Claude Bernard would later assert, the “very essence of Lavoisier’s doctrine lies in the affirmation that there are not two chemistries or two physics, the one applicable to living creatures and the other to inert bodies; rather, there are general laws applicable to all substance[s], however [they] might be disposed, and these laws admit of no exception” (Bernard, quoted in Coleman 1977, p. 126).

increasingly comprehensive rosters of organic substances. By 1845, the division of foodstuffs into carbohydrate, fat, and protein, based on their chemical constitution, had become clearly established (Coleman, 1977, p. 131). This knowledge, coupled with the enduring conviction that chemical transformations inside and outside the organism were strictly comparable (a stance defended and promulgated most prominently by J. J. Berzelius (1779-1848)), opened up even further the study of physiological chemistry. In 1842, Justus von Liebig (1803-1873) published the celebrated *Animal Chemistry, or Organic Chemistry in its Application to Physiology and Pathology*, in which he argued that the study of ‘animal architecture’ alone was insufficient for understanding physiological processes. The organism’s vital functions (e.g., secretion, nutrition, generation) can only be understood if the organic substances involved in these processes are identified. “From organic chemistry”, Liebig claimed, “the science of physiology will be developed” (quoted in Lipman, 1967, p. 173). It is thus through the application of organic chemistry that the study of physiology must proceed, as it is only by determining the chemical basis of vital processes that these can be genuinely elucidated.

Before we can appropriately contextualize the impact of organic chemistry on the study of physiology in relation to the unfolding of the mechanism-vitalism debate during this period, it is first necessary to clarify a common misconception that prevails still today among some scholars. Ramberg (2000) has termed this misconception the ‘Wöhler myth’ and relates to the historical significance of the laboratory synthesis of urea (an organic substance) by German chemist Friedrich Wöhler (1800-1882) in 1828. According to the myth, Wöhler’s synthesis signalled the end of the doctrine of vitalism, as it showed that no vital forces of any kind were required for the generation of organic matter. The reality, however, appears to have been rather different. Historians such as J. H. Brooke (1968; 1971) have denied the premises of the myth’s assumption and have conferred a primarily chemical meaning for Wöhler’s accomplishment. Specifically, the artificial synthesis of urea had interesting implications for the study of isomeric transformation, and was thus heralded as an important milestone in the emerging field of structural organic chemistry. However, Wöhler’s synthesis did not have a direct physiological bearing, nor, of course, did it speak to the existence or nature of a vital force. In fact, most chemists of the period believed that artificial syntheses of organic substances outside the living body were possible, their actual likelihood depending only on the ability to successfully decipher

the chemical constitution of the substance to be synthesised, and in overcoming the technical difficulties faced in the experimental process (see Brooke, 1968). It seems that it has been the popularizers of science and not the chemists of the 1820s and 1830s who have regarded organic synthesis as the ultimate deathblow of vitalism. Ramberg (2000) has traced the origin of the Wöhler myth to a popular history of chemistry monograph by Bernard Jaffe, published in 1931 (and still in print today).¹¹ However, it is likely that the myth originated much earlier. Brooke (1971, pp. 375-376) provides some textual evidence which suggests that the idea that organic synthesis amounted to a refutation of vitalism was first conjured up by the German mechanistic reductionists of the late nineteenth century (to which I will turn to later). At any rate, what is clear is that the artificial synthesis of urea did *not* signal the end of vitalism, in its somatic form that was prevalent at the time, but simply confirm the earlier findings made by Lavoisier regarding the correspondence between inorganic and organic chemical substances.

What, then, was the impact of the progressive ‘chemicalization’ of physiology, made possible by the development of organic chemistry, on the nature and prevalence of vitalistic thinking? The seemingly paradoxical answer is that the greatest expositors of the organic chemistry of the first half of the century (namely Berzelius, Liebig, and Wöhler), despite defending strictly mechanistic and thoroughly analytical approaches to empirical study, were *all* theoretically committed to some form of somatic vitalism. Still, these nineteenth century somatic vitalists did not hold exactly the same views as their eighteenth century predecessors, since they explicitly advocated the adoption of mechanistic research methods, and believed that organisms should be studied, in the first instance, by means of the tools and techniques made available by the physicochemical sciences. At a most fundamental level, they acknowledged that living organisms were no different from inanimate bodies, and consequently they could be described using the same methods. In this way, Berzelius, writing in 1806, argued that the “starting point” in the study of life “should be sought in the basic forces of the elements” given that life itself “is a necessary consequence of the relationships whereby the fundamental materials are joined” (Berzelius, quoted in Coleman, 1977, p. 147). However, in spite of the possibility of mechanistically elucidating the regulation and maintenance of ongoing biological processes in the living organism, Berzelius

¹¹ Ramberg (2000) notes that “[i]gnoring all pretense of historical accuracy, Jaffe turned Wöhler into a crusader who made attempt after attempt to synthesize a natural product that would refute vitalism and lift the veil of ignorance, until ‘one afternoon the miracle happened’”.

considered the processes of *de novo* generation of organic form as being forever beyond the reach of chemical analysis. It is for this kind of phenomena that Berzelius, along with many of his followers, reserved the operation of the vital force. Similarly, Liebig retained the notion of the vital force to explain certain biological processes. In particular, he invoked the vital force in order to account for the seeming contraposition between the action of chemical forces and the organism's own living predispositions. According to Liebig, chemical and vital forces act antagonistically, and their continuous interplay results in the shifting dynamism that we call life.¹² This dynamism finds its most prominent expression in the ongoing reciprocation of tissue formation and tissue degradation, although it is also manifested in other physiological processes, such as the digestion of foodstuffs and the movement of the animal body. Finally, Wöhler, who as I have already indicated would posthumously come to be known, erroneously, as the exorcist of vitalism from biology, was himself, ironically, equally committed to the existence of a vital force which in his view was responsible for a number of physiological processes (see Brooke, 1968; 1971).

It is important to emphasize, having uncovered their vitalistic predilections, that these organic chemists were highly conscious of the need for a strictly naturalistic physiology, and believed that metaphysical speculation should be banished from science. Indeed, their actual writings indicate that, not unlike earlier somatic vitalists, they were far more concerned with the elucidation and description of vital phenomena than with the specification of the vital force. The laws of vitality, not the vital force itself, were the actual focus of their physiological investigations. They did not attempt to search for the vital force, nor did their belief in its existence influence their research methods or empirical findings. Liebig, for instance, in his *Animal Chemistry*, does not set out to prove the existence of the vital force. Instead, he attempts to identify its effects through his investigations in physiological chemistry. Moreover, Liebig, in the best Newtonian tradition of somatic vitalism, at several points (pp. 7-8; 220-221) notes that science will never know the causes for the forces of nature, but that their existence can be deduced from their effects on the phenomena upon which they act. Thus, for these organic chemists, as for all prior somatic vitalists, it was as valid to attribute the laws and effects of life to a vital force as it was to attribute the laws and effects of gravity to a gravitational force.

¹² Liebig's vitalist views owe much to the ideas of Xavier Bichat, who decades earlier had defined life as "the sum of the forces resisting death". I will examine Bichat's views in more detail in Section 2.9 and again in Chapter 5.

Questions could be raised regarding how the leading exponents of such a blatantly mechanistic discipline like organic chemistry could at the same time be committed somatic vitalists. The reason for this apparent contradiction is that for Berzelius, Liebig, and Wöhler, mechanicism and vitalism were not incompatible. This is because they took them to apply to different domains of phenomena. It was thus possible for them to be strictly mechanistic organic chemists while at the same time be vitalistic physiologists. In effect, vitalism had no relevance to pure organic chemistry as an autonomous discipline. The vitalistic inclinations of these thinkers surfaced only when they attempted to contextualize their chemical findings in relation to broader biological questions relating to the distinctive properties of living organisms. In this way, if there is one theme that collectively individuates the great organic chemists of the first half of the nineteenth century it is their endeavour to mechanistically characterize biological matter, whilst simultaneously recognizing the necessity of a vital principle as a means of accounting for more recalcitrant physiological phenomena like self-organization.

Despite its early successes, the seemingly harmonious coexistence of mechanicism and vitalism among chemical physiologists was not to last long. By the mid nineteenth century, the divide between the explanatory domains of mechanicism and vitalism had begun to break down and exclusively mechanistic conceptions of physiological processes were becoming increasingly dominant. The most prominent group of the new wave of mechanicism was that formed by the students of renowned German physiologist Johannes Müller (1801-1858) in his Berlin laboratory during the late 1840s. This group of deeply committed physicalist reductionists was made up by Emil Du Bois-Reymond (1818-1896), Carl Ludwig (1816-1895), Ernst von Brücke (1819-1892), and Herman von Helmholtz (1821-1894). The chief objective of these physiologists was to unify physiology with the rest of the physical sciences. Encouraged by the earlier triumphs in the application of mechanistic methodology to the study of certain biological phenomena, they saw no reason to doubt that an exhaustive mechanistic elucidation of all physiological processes by means of reductive analyses would eventually be obtained. As they saw it, the greatest obstacle to the attainment of this goal was the prevailing tendency to appeal to vital forces in physiological explanations. In the Introduction to his *Researches on Animal Electricity* of 1848, Du Bois-Reymond complained that the vital force is nothing but “a comfortable resting-place where [...] reason finds peace on the cushion of obscure

qualities”. Elsewhere in the text, he reflects on the fate of physiological science, and concludes the following:

If one observes the development of our science [i.e., physiology] he cannot fail to note how the vital force daily shrinks to a more confined realm of phenomena, how new areas are increasingly brought under the dominion of physical and chemical forces [...] [i]t cannot fail that physiology, giving up her special interests, will one day be absorbed into the great unity of the physical sciences; [physiology] will in fact dissolve into organic physics and chemistry. (Du Bois-Reymond, quoted in Coleman, 1977, p. 151)

This faith on the eventual and inevitable ‘dissolution’ of physiology into physics and chemistry was shared by the others members of the group. Ludwig, most notably, argued in his *Textbook of Human Physiology* of 1856 that physiology is essentially analysis and that all vital phenomena arise from the attractive and repulsive forces inherent in the chemical constituents of the body. This unreservedly mechanistic conception of physiological processes did not allow for the intrusion of a vital force, which, as non-material agent, did nothing but obfuscate the real physical causality of the organism’s atoms.¹³ Overall, however, despite the spectacular advances in the mechanistic understanding of the physiology of the organism attained during this period (which included the elucidation of the causal mechanisms responsible for sense perception, lymph formation, and glandular secretion, among many others), it might seem in retrospect unavoidable that the ambitious programmatic demands of these reductionists were not fulfilled. Indeed, fully satisfying the group’s objectives would have required an effective reduction of life, in all its complexity, to force and matter. What the findings of these reductionists *did* provide was a rejuvenated faith in the explanatory power of mechanistic epistemology, which by the end of the nineteenth century had permeated beyond physiology to other spheres of biological inquiry.

¹³ Similar mechanistic assertions can also be found in contemporary physiologists outside Germany. In England, for instance, T. H. Huxley (1825-1895) asserted that physiology is nothing more than “the mechanical engineering of living machines” (Huxley, quoted in Wise, 2007, p. 184). In his 1874 address to the British Association for the Advancement of Science, entitled ‘On the Hypothesis That Animals Are Automata, and Its History’, Huxley began by remarking that “in the seventeenth century, the idea that the physical processes of life are capable of being explained in the same way as other physical phenomena, and, therefore, that the living body is a mechanism, was proved to be true for certain classes of vital actions; and, having thus taken firm root in irrefragable fact, this conception has not only successfully repelled every assault which has been made upon it, but has steadily grown in force and extent of application, until it is now the expressed or implied fundamental proposition of the whole doctrine of scientific Physiology” (Huxley, 1893, p. 199).

2.8. *Entwicklungsmechanik*, Driesch, and the Demise of Somatic Vitalism

One of the biological disciplines which became transformed by the new impulse in mechanistic thinking was embryology. Wilhelm Preyer (1842-1897), a student of Du Bois Reymond and von Helmholtz, opened up new avenues of embryological research through his quantitative analyses of chemical changes occurring during organismic development. Preyer was also the first to show that the anatomical and functional changes which took place during embryogenesis were closely correlated (Allen, 1975, p. 28). One of Preyer's own students, Wilhelm Roux (1859-1924), took up the quantitative and experimental approach to embryology and eventually became one of the leading exponents of mechanistic biology in the late nineteenth and early twentieth centuries. Through his strong emphasis on experimentation as the crucial element of research, coupled with his insistence on the application of physicochemical methods to biological problems, Roux provided a renewed mechanistic foundation for the field of embryology. From the 1890s until his death, Roux relentlessly developed and promoted his program of research, which he named *Entwicklungsmechanik* (developmental mechanics), and founded a new journal, the *Archiv für Entwicklungsmechanik*, in 1894, which presented the experimental work conducted by him and others in the field. Roux's *Entwicklungsmechanik* rapidly gained support both in Europe and in the United States, and was taken up, most notably, by Hans Driesch (1867-1941), Jacques Loeb (1859-1924), and T. H. Morgan (1866-1944).

Roux's primary concern in his study of embryology was the phenomenon of differentiation, that is, the process by which the embryo develops from a formless mass to an organized system of highly specialised cells. In 1885, he proposed the mosaic theory of development, which held that the particular differentiation of the body parts was caused by the distribution of the hereditary material during the consecutive cell divisions of development. So although the single-celled egg initially contains all the hereditary material for the entire adult body, with every cell division the hereditary material becomes progressively disseminated to each of the daughter cells, until ultimately each of the cells in the body expresses only one major hereditary trait, becoming at this stage fully differentiated (Robert, 2004, p. 24). In the best mechanistic tradition, the mosaic theory provided testable predictions. It predicted that the destruction of one blastomere at the two- or four-cell stage, for instance, would produce a deformed embryo (as the remaining blastomeres would contain only part of the hereditary material). Roux proceeded to confirm this prediction in 1888 by

conducting the appropriate experiment. With a hot needle, Roux punctured one of the blastomeres in the two-cell stage of a frog embryo, killing the punctured cell and allowing the remaining blastomere to develop. What he found was that the resulting embryo was severely deformed; having one side well developed and partially differentiated while the other remaining disorganized and undifferentiated. For Roux, these results presented clear evidence in support of his mosaic theory, as the half adult produced could be explained by the fact that the developing embryo had been deprived of half of its hereditary material.

Working in Naples in the 1880s and 1890s, Driesch attempted to reproduce Roux's findings using sea urchin eggs, but instead of killing one of the two blastomeres, he induced their separation by vigorous shaking in water and then allowed each of them to develop normally. To his surprise, he found that each of the separate blastomeres had produced a whole, albeit smaller sea urchin larva. These results flatly contradicted the predictions of the mosaic theory. Indeed, if each blastomere, even after being separated from other cells in the embryo, could still develop into a whole adult, then there must not have been any segregation of hereditary material, as Roux had postulated.¹⁴ These findings led Driesch to argue that the embryo constituted a 'harmonious equipotential system' in which all the parts in the early stages of development had the same potential to produce a whole adult organism. In the first instance, Driesch attempted to describe harmonious equipotential systems in mathematical terms and sought to explain his results in terms of physical influences acting on the embryo. Eventually, however, Driesch became convinced that the *Entwicklungsmechanik* research program was simply incapable of providing the necessary explanatory resources to account for the non-atomistic, self-regulating nature of embryogenesis. As a result, he went on to develop a vitalistic explanation that was more in accordance with his own empirical observations. By the turn of the twentieth century, Driesch had abandoned experimental biology altogether to focus on further developing theoretically and philosophically his vitalistic views, and as a professor of philosophy he published a number of works, including *The Science and Philosophy of the Organism* (1908) and *The History and Theory of Vitalism* (1914).

¹⁴ Subsequently, Roux's experimental results would be explained as being caused by the deleterious effects of the cell debris of the dead blastomere coming into contact with the developing embryo (Moss, 2003, pp. 32-33).

Driesch's decisive rejection of mechanicism was rooted in his conviction that mechanistic causal explanations of living phenomena failed to capture their distinctive nature and behaviour. His own embryological research had shown that during development each embryonic cell is co-regulated with every other embryonic cell so that the organism as a whole could effectively adjust itself by compensating from external perturbations. These markedly holistic capabilities of the embryo were not accountable through bottom-up mechanistic explanations and indeed entailed a view of the organism which was directly antithetical to the conception that had provided the conceptual backbone of mechanistic biology since Descartes, namely the MCO. Driesch was well aware of this, and in his philosophical writings he frequently referred to the ways in which harmonious equipotential systems were fundamentally different from machines. In reference to his key experiments on sea urchins, Driesch (1914, p. 210) notes that

[Whereas] a "machine", *i.e.* a specific arrangement of physico-chemical things and agents, *does not remain itself if you take from it whatever you please* [...] the organism, or better, the non-developed harmonious system *does* remain "itself", with regard to its morphogenetic faculties, after any operation what[so]ever. The harmonious system, then, is not a "machine" (Driesch, 1914, p. 210, original emphasis)

To make the point even more explicitly, in the same passage Driesch asks, rhetorically: "how could a machine *be divided innumerable times and yet remain what it was?* No machine, therefore, can be the test of embryology" (*ibid.*, pp. 211-212).

In order to come to terms with the *real* nature of organisms, Driesch postulated the existence of a 'non-mechanical agent of nature' which operated exclusively within living beings and endowed them with their distinctive character. Driesch termed this vital agent the '*entelechy*', thereby openly acknowledging his indebtedness to Aristotle, although it should be noted that his own usage differs from that of Aristotle. For Aristotle, the entelechy is directly responsible for the maturation of the organism, for it is the active agent which raises the physical potentialities of the organism to the state of actuality. Driesch confers a more restricted role to the entelechy, and instead of identifying it as the primary cause of development itself, he views it as the regulator which governs which of the various potentialities resident in the developing organism shall reach realization and which shall be restrained. Driesch's entelechy, then, is not the template of organismic organization, nor is it the creative agent that brings it about

(and is thus different from Blumenbach's *nisus formativus* and Wolff's *vis essentialis*). Rather, it serves as a kind of a buffer which protects the inbuilt tendencies of the organism from being disrupted by adverse environmental conditions. Moreover, Driesch emphasizes that the entelechy is non-temporal, non-spatial, and non-psychic, and consequently does not interfere with any natural laws. On the whole, with his vitalistic theory Driesch attempted to provide a *bona fide* explanation for the results he had obtained in his embryological research. In doing so, he courageously challenged the prevailing mechanistic orthodoxy of his time (embodied in Roux's influential *Entwicklungsmechanik* research program) and effectively rescued somatic vitalism from a steady decline that had been ongoing since the mid-nineteenth century.

Despite having the weight of empirical evidence mostly on his side, Driesch's form of neo-somatic vitalism seemed to have already become anachronistic by the time it began acquiring currency in the late 1910s and 1920s. As a result, it was predominantly met with violent opposition. For example, in 1918, the journal *The Philosophical Review* published an issue (volume 27, number 6) containing a collection of papers written on the mechanicism-vitalism dispute. Interestingly, although not all the authors defended mechanicism, most of them explicitly rejected Driesch's vitalism. The contemporary criticisms of Driesch's ideas were primarily targeted towards his notion of the entelechy. Some biologists (e.g., Lillie, 1926; Needham, 1928a) criticised the inexplicable fact that the entelechy did not operate in the same way in organisms pertaining to different species (e.g., a 'salamander-entelechy' was able to regenerate a limb, whereas a 'human-entelechy' could not). Others directed their criticism towards the very concept of entelechy itself, arguing that it did not constitute an explanation but simply another name for the problem: "Driesch transfers the complexities of development to the entelechy, leaving them in exactly the same need of analysis and explanation as before" (Jennings, 1918, p. 581). Most incisive, perhaps, was Ralph Lillie's indication that the very operation of the entelechy necessary violated the laws of physics:

According to Driesch, an entelechy can, without the performance of work, guide or coordinate [...] processes which themselves require the performance of work. This view implies that in the organism, molecular movement can be directed, retarded, or accelerated at the will of the entelechy [...] [However,] It is physically impossible for any agency to modify the processes in any material system without modifying the energy-transfers in that system, and this can be done only by [...] the performance of work. One is forced to

conclude that all such attempts at the solution of biological problems are based on fundamental misunderstandings. (Lillie, 1914, pp. 843-844)

Finally, as the field of embryology continued to develop, it soon became clear that Driesch's statement of 'equipotentiality' had been far wider than the facts actually warrant. The work of Hans Spemann (1869-1941) and others showed that the totipotency of the early embryo falls off rapidly as development proceeds, and by the gastrulation phase the process of differentiation sets in and the embryonic cells become irrevocably determined. In light of this evidence, the appeal to an entelechy was no longer necessary, and thus the hypothesis of the entelechy became "as redundant as the hypothesis of an agency directing the movements of the planets in their orbits" (Warren, 1918, p. 603). The predominant condemnation of Driesch's theory in the first third of the twentieth century effectively signalled the end of two hundred years of somatic vitalism.

Moreover, the demise of Driesch's vitalism occurred in conjunction with the increasing prevalence of a mechanistic approach to physiology and embryology that stemmed directly from the *Entwicklungsmechanik* tradition, and which sought to materialize the reductionistic ideals of the Berlin school of the 1850s. This wave of mechanistic biology found its most important advocate in the figure of Jacques Loeb, who championed the belief that all living phenomena were reducible, through laboratory analysis, to the fundamental laws of physics and chemistry. In 1912, Loeb published a manifesto entitled *The Mechanistic Conception of Life*, in which he prophesized, following Roux, that biology would ultimately be absorbed by physics, with complex processes such as development, regeneration, and fertilization becoming effectively explained in atomic and molecular terms. However, in spite of its early successes, Loeb's extreme form of mechanicism did not dominate biology for long. A growing number of biologists began to question the cross-disciplinary applicability of Loeb's experimental findings. More importantly still was the concern of whether, even after having rejected somatic vitalism, it was still legitimate to regard mechanistic science as possessing the necessary and sufficient epistemic tools to effectively explain the distinctive nature and behaviour of living organisms. It was amidst this atmosphere of uncertainty that a new form of vitalism emerged, more concordant with the tenets and methodology of the physical sciences, but still committed to the ontological distinctiveness of life. In the next two sections, I will identify the historical roots of

this vitalistic doctrine and trace its process of maturation until the first half of the twentieth century.

2.9. Vitalism Re-Vitalized: Bernard and the Naturalization of Vitalism

Dissatisfaction with the presuppositions of somatic vitalism, even among *non-mechanists*, predates the criticisms of Driesch's ideas by over a century. Some (admittedly, very few) vitalists had long argued that the notion of the vital force imposed an unnecessary metaphysical agent in the living domain which could not possibly be legitimized by emulating the appropriation of the metaphysically obscure forces that Newton had introduced into physical science. The most important, exponent of this marginal form of vitalism was Xavier Bichat (1771-1802) who had defended the autonomy of life from non-life (and of biology from physics) as fervently and as explicitly as his somatic vitalist contemporaries,¹⁵ but who had rooted the distinctiveness of living phenomena, not on the operation of a (Newtonian) vital force, but on the peculiar characteristics of organic tissues. These 'vital properties', namely sensibility and contractibility, were for Bichat the genuine defining features of life, as they endowed the bodily organs with their complex and diverse functionalities.¹⁶ Nevertheless, it would be inaccurate to claim that Bichat's vitalism constitutes a complete departure from the somatic vitalism which prevailed in his time (and long after), as although he spoke of 'vital properties' rather than of 'vital forces', he was as committed as any somatic vitalist to the fundamental unknowability of the vital agents he postulated and to the inherent inappropriateness of approaching the study of living beings within the theories and methods of the mechanists.¹⁷

¹⁵ In his *Physiological Researches on Life and Death* of 1809, Bichat states: "compare the vital faculty of feeling to the physical faculty of attracting; you will see that the attraction is always in proportion to the mass of the rough body in which it is observed, while the sensibility changes incessantly in the same organic part and in the same mass of matter [...] To say that physiology is the physics of animals, is to give but a very imperfect idea of it; I might say with equal propriety that astronomy is the physiology of the stars." (Bichat, quoted in Hein, 1972, p. 167)

¹⁶ In this respect, Bichat followed in the footsteps of earlier physiologists, such as Haller, who despite his mechanistic commitment to the preexistence of germs, nevertheless postulated that sensibility and irritability constituted irreducible vital properties that endowed the organism with its distinctive features. We will return to the ideas of Haller and Bichat in a rather different epistemic context in Chapter 5.

¹⁷ This last point is clearly exemplified in the following passage, where he criticizes by name some of the mechanists we have already examined in previous sections: "One calculates the return of a comet, the speed of a projectile; but to calculate with Borelli the strength of a muscle, with Keill the speed of blood, with Lavoisier the quantity of air entering the lung, is to build on shifting sand an edifice [...] which soon falls for lack of an assured base. This instability [...] marks all vital phenomena with an irregularity which distinguishes them from physical phenomena remarkable for their uniformity. It is easy to see that the science of organised bodies should be treated in a manner quite different from those which have unorganised bodies for object." (Bichat, quoted in Goodfield, 1974, p. 68)

The first real break with the doctrine of somatic vitalism within the non-mechanistic camp would come half a century after Bichat, in the ideas of another Frenchman, the distinguished physiologist Claude Bernard (1813-1878), known for his important contributions to the studies of digestion, animal chemistry, and neurophysiology. In his more philosophical writings, Bernard subjected the science of physiology to a thorough revision which challenged some of the basic presuppositions of both somatic vitalism and nineteenth century mechanicism. Following his mentor François Magendie (1783-1855), and opposing the practices of prior vitalists, Bernard strongly advocated the use of experimentation in the study of organisms. In his celebrated *Introduction à l'Étude de la Médecine Expérimentale* of 1865, he argues, in clear mechanistic terms, that adopting the methodological principles and techniques of physics and chemistry offers the surest grounds for the progress of physiology. To the extent that vital phenomena can be scientifically understood, he writes, they can only be studied through a rigorous application of the experimental method of the physicochemical sciences. However, unlike the mechanist, Bernard asserts that no matter how much experimentation can potentially tell us about the inner workings of the organism, it cannot show that they can be reduced to force and matter. In this sense, Bernard shows to be deeply committed to one of the central tenets of vitalism: the irreducibility of life. It is for this reason that he forcefully attacks the relentless mechanistic endeavour to reduce the subject matter of biology to that of the physical sciences:

We have seen, and still often see, chemists and physicists who [...] try to absorb physiology and reduce it to simple physicochemical phenomena. They offer explanations or systems of life which tempt us at times by their false simplicity, but which harm biological science in every case, by bringing in false guidance and inaccuracy which it then takes long to dispel. In a word, biology has its own problem and its own definite point of view; it borrows from other sciences only their help and their *methods*, not their *theories* (1957 [1865], p. 95; my emphasis)

This distinction that Bernard draws between the import of physicochemical *methods* and the import of physicochemical *theories* illustrates another fundamental difference between him and the mechanists. For Bernard, although physicochemical methods constitute the best means of undertaking physiological research, the mechanistic understanding of the organism which tends to motivate the application of such methods is not entailed by them. In Bernard's own words, "if we break up a living organism by isolating its different parts, it is only for the sake of ease in experimental analysis, and

by no means in order to conceive them separately”, given that “their union expresses more than the addition of their separate properties” (ibid., p. 89; p. 91). The necessary application of analytical methods in physiology does not entail a conception of the organism as a material aggregate of separate parts. The holistic nature of the organism is, in fact, confirmed by the inherent inability of analytical methods to completely explain it. This appreciation for the emergent and irreducible properties of organisms is, of course, unmistakably vitalistic. In speaking of the nature of organisms, Bernard goes on to say, in a language remarkably similar to that later employed by Driesch, that the organism is best conceived as “a harmonious and pre-established unity whose partial actions are interdependent and mutually generative” (ibid., p. 89).

What is interesting, however, is that Bernard’s vitalism in many ways constitutes a radical departure from that of the somatic vitalists. Although being committed to the same core beliefs of vitalistic thought, Bernard explicitly criticizes the somatic vitalists’ persistent appeal to unknowable vital forces to explain their empirical observations, as this leads one to “look on life as a mysterious supernatural influence which acts arbitrarily by freeing itself wholly from determinism” (ibid., p. 68). Bernard praises Bichat for his refusal to accept the notion of the vital force as a valid explanation for the peculiarities of vital phenomena, but also decisively distances himself from Bichat’s ideas as these still rooted the distinctiveness of life in the unknowable ‘vital properties’ of organic tissues. His ultimate discontent with the preceding vitalistic theories of both the somatic vitalists and Bichat led Bernard to develop a new form of vitalistic biology which attempted to theoretically justify the basic tenets of the doctrine without compromising its legitimacy as a scientific theory. At the heart of Bernard’s vitalism is the commitment to a fully naturalistic explanation of the distinctive nature of life. In order to distinguish it from prior strains of vitalistic thought, I will refer to this doctrine as *naturalized vitalism*.

The most fundamental question that naturalized vitalism had to address was: What is the basis of the distinction between the nature of living organisms and the nature of nonliving entities? If not a life-soul, a force, or some otherwise unknowable property, what then? Bernard’s answer to this question arose from his reflections on the famous distinction he drew between the internal and external environments of the object under investigation. He noticed that an inorganic body exists in a state of equilibrium with its immediate surroundings, and consequently all the internal changes it experiences are

always the result of alterations in its external environment. In contrast, a living being is never in a state of physicochemical equilibrium with its external environment, as it possesses “creative spontaneity” and a “ceaseless dynamism” which manifests itself internally in relative isolation from its outer environment. Bernard notes that this independence of the internal environment from the external environment differs “according to the degree of perfection of the organism”. More perfect organisms (such as warm-blooded animals) are less subject to the influences of the outer environment and hence lead “more free and independent” lives. Less perfect organisms (such as plants) are more sensitive to external influences and conditions and in fact depend on them to a certain extent to sustain their existence. It is in this relative autonomy of the internal environment brought about by the organism’s capability to ‘self-regulate’ (a term used by Bernard) and compensate from external perturbations that Bernard rooted not only the distinctiveness of living beings, but also the necessary starting point of biological science, as “it is in the study of these inner organic conditions that direct and true explanations are to be found for the phenomena of the life, health, sickness and death of the organism” (ibid., pp. 97-98).

A possible objection which could be raised against the interpretation of Bernard’s ideas offered here is that Bernard himself in several occasions explicitly refers to a distinctive ‘vital force’ legislating over the organism and regulating physiological processes. Clearly, this kind of language would appear to contradict the assertion that Bernard broke away from the somatic vitalist tradition, and would indeed justify neatly aligning him alongside other somatic vitalists. A close reading of Bernard’s writings, however, positively refutes the grounds for drawing such a conclusion, as his own usage of the term ‘vital force’ is, in fact, confined to the description of the effects of the very phenomenon which deems the invocation of vital forces unnecessary, namely the organism’s capacity to regulate its internal environment. Its occasional appearance in Bernard’s writings should thus be interpreted as referring not to the obscure Newtonian force of the somatic vitalists, but to the ability of the organism to self-regulate. This becomes clear when one considers the meaning ascribed to the notion of vital force in the following passage:

Every living being indeed *appears to us* provided with a kind of inner force, which presides over manifestations of life more and more independent of general cosmic influence in proportion as the being rises higher in the scale of organization. In the higher animals and in man, this *vital force* seems to result in withdrawing the living being from

general physico-chemical influences and thus making the experimental approach very difficult (ibid., p. 59; my emphasis)

Bernard's choice of the words 'appears to us' as opposed to 'is' may provide a further indication that he is actually suggesting that the self-regulating capacities of the organism result in effects which *appear to the external observer* as being the product of a vital force (cf. Roll-Hansen, 1976). It may be safely asserted, then, that Bernard's vitalism constitutes a fundamental departure from the somatic vitalist tradition, which would nevertheless prevail until Driesch.

Overall, Bernard's contributions to both the science and philosophy of life are paramount. Not only is he responsible for making the adoption of physicochemical methodologies in biological research completely compatible with defending a patently *non-mechanistic* understanding of living organisms, but through his postulation of the organism's capacity for self-regulation, he laid down the basic foundations for a new strain of vitalistic thought which subsequent biologists would build upon and engage the established mechanistic community in critical debates without running the risk of being ruled out of the discussion for holding mystical or unscientific views, as had happened with twentieth century neo-somatic vitalists like Driesch.

2.10. Haldane's Establishment of Organicism and Its Eclipse of Mechanicism

The naturalized vitalism which flourished from the seeds sown by Bernard had its most important exponent in the figure of J. S. Haldane (1860-1936), one of the greatest physiologists of the early-twentieth century, and father of the equally distinguished J. B. S. Haldane (1892-1964). J. S. Haldane is perhaps best known for elucidating the physiology of respiration and for his discovery of the 'Haldane effect' of haemoglobin. However, he also developed an interest in philosophy very early on, and already in his days as a medical student in the early 1880s he argued that mechanistic and (somatic) vitalistic conceptions of life were "radically unsound" (Haldane, 1884). He later came into contact with the ideas of Bernard and went on to pursue a highly successful career in experimental physiology. His firsthand acquaintance with the intricacies of physiological processes, acquired from the many decades he devoted to the empirical study of organisms, provided him with a solid foundation upon which to elaborate Bernard's pioneering ideas and develop more broadly the naturalized vitalistic conception of living beings, which he presented in a series of books and lectures. By

the end of his life, Haldane had helped establish naturalized vitalism as a meaningful, scientifically-sound alternative to mechanistic biology.

Haldane's adoption of Bernard's ideas first becomes apparent in his 1916 Silliman Lectures entitled *Organism and Environment as Illustrated by the Physiology of Breathing*, where he identifies the Bernardian conception of organic self-regulation as the "essence of life". Later, in his 1927-1928 series of Gifford Lectures, delivered under the grand title *The Sciences and Philosophy*, Haldane refers to "Bernard's Principle", which he defines as the fact that all physiological activities have as their ultimate objective the preservation of the organism's internal environment. He asserts that this principle has proven "extraordinarily useful in guiding physiological work into fruitful channels", adding that "Bernard himself did not realize how far his development of his own reasoning would carry physiology" (1930, p. 41; p. 57). Haldane goes on to show how Bernard's principle is central to understanding many major physiological processes, such as renal function, respiration, neuronal activity, and blood circulation (ibid., pp. 41-55).

Haldane's crucial contribution to the conceptual development of Bernard's naturalized vitalism lies in his realization of the impossibility to explain the constancy of the organism's internal environment by referring to the *structure* of the organs which regulate it, as these very organs are themselves dependent on the internal environment. They are constantly taking up and giving off organic matter, and thus their actual 'structure' is nothing more than the appearance taken by the flow of material that runs through them. Thus, "We are only reasoning in a circle when we attempt to explain the internal environment by the specific characters of bodily structure" (Haldane, 1917, p. 91). The living organism cannot be defined by its material constituents, as these flow through it and are constantly being replaced. In contrast, the arrangement of that matter, *i.e.*, the *organization*, remains constant and thus endows the living being with its identity and individuality. It is the organization of the organism, expressed as the continuous dynamic coordination and regulation of the internal environment, which, in Haldane's view, is responsible for the distinctiveness and irreducibility of living beings.¹⁸

¹⁸ I will explore this dynamic conception of the organism in more detail in Chapter 3.

The fact that the doctrine of naturalized vitalism has come to be known as *organicism* is something we owe to Haldane. According to the British embryologist Joseph Needham (1928b), the term organicism was first used in 1903 by Yves Delage (1854-1920) in his *L'Hérédité et les Grands Problèmes de la Biologie*. Delage used the term to refer to the school of thought which regarded:

life, the form of the body, the properties and characters of its diverse parts, as resulting from the reciprocal play or struggle of all its elements, cells, fibres, tissues, organs, which act the one on the other, modify one the other, allot themselves each its place and part, and lead all together to the final result, giving thus the appearance of a pre-established harmony” (Delage, quoted in Needham, 1928b, pp. 29-30)

At the beginning of *Organism and Environment as Illustrated by the Physiology of Breathing*, Haldane (1917, p. 3) remarked in a footnote: “It has been suggested to me that if a convenient label is needed for the doctrine upheld in these lectures the word “organicism” might be employed”. However, as Delage associated organicism not only with Bernard, but also somewhat puzzlingly with Bichat and Roux, Needham (1928b, p. 30) is correct when he notes that the term acquired an entirely new lease of life when it was appropriated by Haldane to describe his own views.

An interesting question which arises here is why Haldane felt it necessary to adopt a new term to designate his philosophy when the tenets he sought to defend were so characteristically vitalistic. The simple reason is that Haldane did not see himself as inheriting the ideas of the vitalistic tradition. Rather, he regarded his views (and those of Bernard) as constituting a completely new philosophy which bore no resemblance to either mechanicism or vitalism. In fact, in many of his philosophical writings, Haldane developed his argument in three stages: first he would discuss the mechanistic and vitalistic views in turn, then he would draw attention to what he considered to be fatal flaws in both of these doctrines, and finally he would expound his organicism. Haldane’s terminological demarcation of his naturalized vitalism from vitalistic philosophy as a whole (through his adoption of the term ‘organicism’) is most probably the result of his restricted understanding of what vitalistic thought really entailed. For Haldane (as indeed for virtually everybody else at that time), vitalism simply meant *somatic* vitalism. Since somatic vitalism had become universally rejected following the decisive mechanistic criticisms of Driesch’s ideas, the term ‘vitalism’ no longer appeared to warrant a place in biology. Consequently, it was expunged from

scientific parlance, only to be occasionally invoked thereafter as a term of abuse to criticize views or theories deemed to be unscientific (as in the virulent remarks from Francis Crick quoted in Section 2.2). This situation is clearly a little paradoxical given that Haldane's philosophy (not to mention Bernard's), regardless of whether it is referred to as organicism or naturalized vitalism, is in every important respect distinctively vitalistic, according to the tenets of vitalism outlined at the beginning of this chapter. Nevertheless, it is important to recognize that Haldane's decision to distance himself from the term 'vitalism', when considered in the proper historical context, does not seem unreasonable given the intellectual atmosphere of the time.

Haldane's organicism, then, should be understood as a direct continuation of Bernard's naturalized vitalism. As most vitalists since the seventeenth century, Haldane firmly rejects the mechanistic conception of life, embodied in the MCO:

In endeavouring to interpret living organisms as machines the mechanistic physiology which we have inherited from last century has distorted our ordinary observation and directed attention away from obvious facts. This physiology has thus failed [...] since it has nothing coherent to say about the co-ordination which is the distinguishing feature of life, or about the natural processes of resistance to disturbance and recovery from it [...] These subjects are necessarily ignored, because they are incapable of being stated in terms of the mechanistic interpretation (Haldane, 1930, pp. 94-95)

Haldane argues that the mechanistic understanding of life must be abandoned because it cannot explain the natural tendency of the organism to actively maintain its structure and activities and restore them after external disturbances. When he discusses the form of vitalism he distinguishes himself from (*i.e.*, somatic vitalism), Haldane strongly argues that it too must be rejected, although for very different reasons. Since the seventeenth century, vitalism, unlike mechanicism, had consistently recognized the organism's unique ability to regulate itself and coordinate its activities, but it could only explain this ability by referring to an unknowable vital agent. The existence of a vital force, Haldane notes, "does not correspond to the observed facts, and is thus of little use as a working hypothesis in actual investigation" (Haldane, 1917, p. 112). He adds, however, that the merit of vitalism lies in its "destructive criticism of mechanistic theory", and he even admits that in his own work he has "endeavoured to express the vitalistic criticism in a still more general form than it has assumed in the writings of the vitalists" (*ibid.*). Thus, it is clear that although Haldane chose not to align his views

with that of preceding vitalists by name, he was in fact committed to the exact same criticisms of mechanistic biology and to the same philosophical tenets regarding the nature of organisms as all other vitalists before him.

The consolidation of naturalized vitalism in the early twentieth century by way of Haldane's organicism was to result in an important shift in the unfolding of the mechanicism-vitalism dispute. The full transition from somatic vitalism to organicism signalled the end of the vitalistic appeal to unknowable agents. Thereafter, the fundamental disagreement over the nature of life would be fought out within the strict confines of scientific naturalism. Organicism would continue to defend the distinctiveness of life by means of empirically-grounded conceptions alone, focusing primarily on the specific organismic capabilities that have no counterpart in the machine world: intrinsic purposiveness, self-generation, self-reproduction, plasticity, adaptability, etc. (see Chapter 3). Haldane repeatedly emphasized that these features of the living world cannot be explained, or even expressed, in mechanistic terms. Mechanists may, for sure, investigate secretion by measuring the mass or volume of the substances secreted, or by their chemical composition, and they may investigate muscular contraction by measuring the rate and extent of contraction, or by the accompanying heat production. But in all of these instances, the phenomena observed are always physicochemical. A *biological* understanding of the significance of these phenomena requires that they are interpreted from the point of view of the whole living organism, and this can only be done through the introduction of terms and concepts which have no place in physics and chemistry. For this reason, biology must be viewed as an independent science, not incompatible with physics and chemistry, but autonomous from them in every important respect. "The time has come", Haldane (1917, p. 103) proclaimed, "for biology to liberate herself and step forth as a free and living experimental science, with a world before her to conquer by the help of clearer ideas of what life is, and how it can be investigated". But Haldane's belief in the autonomy of biology went even further, and in a presidential address delivered before the physiological section of the British Association in 1908, he made the following prophecy:

That a meeting-point between biology and the physical sciences may at some time be found, there is no reason to doubt. But we may confidently predict that if that meeting-point is found, and one of the two sciences is swallowed up, that one will *not* be biology (Haldane, 1930, p. 96)

Haldane's prophecy may have seemed audacious even by vitalistic standards. It was one thing to argue against the reducibility of biology to physics, but who in their right frame of mind could seriously contend that physics may one day be encompassed by biology? As presumptuous as it may have seemed, the truth of the matter is that in the first few decades of the twentieth century Haldane's prophecy came remarkably close to being fulfilled. During this period the certainties of mechanicism were shattered following the radically new developments in physics. Relativity theory and quantum mechanics appeared to present serious challenges to the fundamental principles of classical mechanics, as even the most elementary units of matter were proving to behave in unexpected ways. As a result, physicists were being led to think of the inorganic world more and more in terms of organization, wholes, and internal relations; conceptions, of course, which had been integral to biological (especially vitalistic) thinking for centuries. The physicist-turned-philosopher A. N. Whitehead (1861-1947) was the first to realize that the new ideas of physics seemed to approximate fundamental biological conceptions and indeed asserted in his celebrated *Science and the Modern World* that biology's traditional appeal to physical theories and concepts, although justified and fruitful in the past, was no longer defensible:

It cannot be too clearly understood that the various physical laws which appear to apply to the behaviour of atoms are not mutually consistent as at presently formulated. The appeal to mechanism [i.e., *mechanicism*] on behalf of biology was in its origin an appeal to the well attested self-consistent physical concepts as expressing the basis of natural phenomena. But at present there is no such system of concepts. (Whitehead, 1925, p. 129)

Instead, Whitehead argued that physics should adopt biological notions and apply them to the entire natural world. This was his theory of 'organic mechanism' (or *organic mechanicism*, in keeping with the terminology I have adopted), which he formulated and defended in the same book. According to Whitehead, science is best defined as the study of 'organisms', understanding this term as any stable and active organized system; be it a living being or an atom.¹⁹ Other philosophers and biologists would adopt and elaborate ideas similar to those of Whitehead, most notably C. Lloyd Morgan (1852-1936) and Jan Smuts (1870-1950). Lloyd Morgan, in his book *Emergent Evolution* (1923), claimed that the concept of organism is not characteristic

¹⁹ Despite their obvious differences, organic mechanicism does share with classical mechanicism the conviction that the partition between life and non-life is artificial and should be abandoned, as both doctrines maintain that the organic and inorganic realms are ultimately of the same nature (even if that 'nature' is different in each doctrine).

of living beings, as it is applicable to the entire spectrum of integrated natural entities which exist in the universe in progressive levels of emergent complexity. Writing around the same time and along similar lines, Smuts asserted in *Holism and Evolution* (1926) that the term 'life' in science should be abandoned in favour of the notions of whole and wholeness, as these are applicable throughout nature, ranging from inorganic substances to the highest manifestations of the human spirit (e.g., mental activities, personality, etc.).

Although for a time it did indeed seem that biology would effectively 'swallow up physics', as Haldane had predicted, through the construction of a unified organic science of nature, the fact is that this research program was never seriously taken up by the majority of physicists and biologists. Even if it may have appeared reasonable to presume, given the history of the development of biological thought, that the new physics would lead to a corresponding revolutionary transformation of biology (as had occurred previously with Cartesian mechanicism in the seventeenth century and again with Newtonian mechanicism in the eighteenth century), the eventual 'revolution' which resulted in the establishment of molecular biology in the latter half of the twentieth century was *not* primarily based on the new physical conceptions of matter, but rather on the mechanistic principles and research programs that had been developing since the mid nineteenth century.

2.11. The Molecularization of Biology and the Current State of the Dispute

Despite the virtually universal belief that the mechanicism-vitalism debate ended with the demise of Driesch's somatic vitalism, I have attempted to show in the preceding sections that some of the major trends in biological thought of the late nineteenth and early twentieth centuries are most effectively understood when contextualized within the mechanicism-vitalism axis. As we turn to look back at the recent history of biology and consider its current state, it again becomes apparent that many of the most important modern developments acquire a new significance when approached through the unique perspective afforded by the mechanicism-vitalism dispute.

Following on from my discussion in the previous section, the second third of the twentieth century saw the continued elaboration of the doctrine of naturalized vitalism (renamed 'organicism' by Haldane, I have argued, in order to escape the mystical connotations of the earlier forms of vitalism) through the work of a number of

theoretical and experimental biologists. Central among them were the Englishmen J. H. Woodger (1894-1981), and Joseph Needham (1900-1995); the Americans W. E. Ritter (1856-1944) and L. J. Henderson (1878-1942); and the Austrians Paul Weiss (1898-1989) and Ludwig von Bertalanffy (1901-1972). As these biologists worked largely independently of each other, their individual interpretations and elaborations of the organicist conception of life differ to a certain degree. However, they all share two basic objectives. The first is the vindication of “the autonomy of life, denied in the mechanistic conception, and remaining a metaphysical question mark in [somatic] vitalism” (Bertalanffy, 1952, p. 20). The second is the ambition to come to terms with the nature of the living organization (see Haraway, 1976). In fact, it is on precisely this crucial issue that Haldane’s initial organicism had proven most unsatisfactory. The term ‘organization’ features prominently in Haldane’s writings, as it was considered to constitute the basis of the distinction between the living and the nonliving. However, at no point does Haldane attempt to explain what the organization of life actually consists of. Organization in Haldane’s work is not really the solution but merely a new name for the problem that needs explaining. It is for this reason that Needham at one point accused Haldane of developing a form of ‘neo-vitalism’ (by which he evidently meant a new form of *somatic* vitalism) given that his organicism left the nature of the postulated vital principle (namely, the living organization) essentially unexplained (Haraway, 1976, pp. 36-37).

For these organicists who followed after Haldane, the objective was no longer to identify the causes of the distinctive vital properties of the organism, as these could now be traced to the living organization, but rather to explain why the distinctive vital properties observed are in fact a consequence of the structures and processes analysed. Organismic organization became the explanandum rather than the explanans. This conceptual shift is well documented in Woodger’s classic *Biological Principles*, where he notes that “If the concept of organization is of such importance as it appears to be it is something of a scandal that biologists have not yet begun to take it seriously”, adding that “The first duty of the biologist would seem to be to try and make clear this important concept” (Woodger, 1929, p. 291). Along similar lines, Bertalanffy remarks in his *Problems of Life* that “the problem of life is that of *organization*” (Bertalanffy, 1952, p. 12). Overall, what appears to have emerged from the work on organization on the part of these organicists is a fairly unified conception of the organism as a complex, hierarchically structured whole whose parts are not only functionally integrated in the

whole, but also directly coordinated by the whole. The integrating and coordinating effects of the organismic whole on its component parts means that the whole is as responsible in determining the nature of the parts as the parts are in determining the nature of the whole (see Chapter 3).²⁰

The organicist conception of the organism had profound epistemic consequences. Most importantly, it provided a naturalized explanation for why vitalists had long argued that reductionistic methodologies were inherently incapable of exhaustively elucidating the nature of the organism. The organism cannot be understood by analyzing its component parts because the behaviour of the parts when examined in isolation is qualitatively different from the behaviour they exhibit when they are found integrated in the organism. It is therefore entirely inappropriate to “regard living beings as machines made up of a multitude of discrete parts (physicochemical units), removable like pistons of an engine and capable of description without regard to the system from which they are removed” (Novikoff, 1945, p. 210). Due to the self-organization of the organism as a whole, the parts interact with one another nonlinearly, causing qualitatively new properties to emerge at the level of the whole. These emergent properties of the whole are not possessed by the component parts, neither when taken separately nor when put together in other combinations, and only become visible upon consideration of the organism as a whole. In this way, organicism succeeded where all prior forms of vitalism had failed in accounting for the distinctive vital properties of life without having to actually add anything to the organism. Organicists were committed to the Aristotelian dictum that ‘the whole is greater than the sum of its parts’, but they did not accept that there was something *added* to those parts.

In spite of its successes, the wave of organicism which permeated biological thought in the early decades of the twentieth century was not to have a lasting effect. While the organicists were busy engaging each other in elaborate theoretical and philosophical discussions over the integrated nature of the organism, mechanistic biologists continued to make progress in the characterization of biological processes at ever

²⁰ This view is essentially an updated modern formulation of the original understanding of organisms as ‘natural purposes’ that Immanuel Kant (1724-1804) put forward in his *Kritik der Urteilkraft* of 1790. This is perhaps not entirely surprising given that many organicists were well versed in Kantian philosophy. A natural purpose for Kant is a naturally produced self-organizing entity which is teleologically structured with respect to the relation between parts and whole. Crucially, however, the concept of natural purpose in Kant is merely a regulative principle, subjectively valid (and indeed necessary) for *reflecting* on such beings, but not objectively valid for determining their constitutive properties. Organicists, in contrast, are committed to the belief that the integrated and intrinsically purposive nature of organisms reflects the very essence of what they actually are in reality.

lower levels of organization, arriving eventually at the molecular and chemical levels. Areas such as physiology, embryology, heredity, or evolution, which had previously been studied on a tissue, cellular, or populational level, were gradually shown to have a common foundation in the molecular architecture of specific macromolecules. Investigations into the structure and function of molecules such as proteins and later nucleic acids opened new avenues for investigating the microstructure of the cell and showed new relationships among different areas of biology whose common foundations had only been hazily inferred the past (Allen, 1975. pp. 187-189). While a concern with the molecular basis of the genetic transmission of heredity was perhaps paramount, the molecular research program also extended to other aspects of the cell, such as the nature of protein interactions, enzyme and antibody specificity, and the structure and composition of cellular membranes.

This increasingly profitable molecular research program came to be known as *molecular biology*. William T. Astbury (1898-1961), one of the founders and propagandizers of the term ‘molecular biology’, defined it in 1950 as being “particularly [concerned] with the forms of biological molecules and with the evolution, exploitation and ramification of these forms in the ascent to higher and higher levels of organization”. Astbury added that molecular biology “implies not so much a technique as an approach, an approach from the viewpoint of the so-called basic sciences with the leading idea of searching below large-scale manifestations of classical biology for the corresponding molecular plan” (Astbury, quoted in Allen, 1975, p. 189). Molecular biology was interested in the architecture of biologically important macromolecules and the ways in which they interact in cell metabolism and heredity. Biophysical methods such as x-ray diffraction of crystallized molecules and molecular model building were employed to investigate molecular architecture, while biochemical methods were used to determine how macromolecules interact with each other and with smaller molecules in the cell. The question of specificity in molecular ‘templating’ became one of the most pressing problems, and both Linus Pauling (1901-1994) and Max Delbrück (1906-1981) pointed to its fundamental importance for conceptualizing gene replication as well as gene expression. The pinnacle of this research came in 1953 with the elucidation of the structure of DNA by James Watson (b. 1928) and Francis Crick (1916-2004), which, as they remarked in their famous *Nature* paper, “immediately suggests a possible copying mechanism for the genetic material” (Watson and Crick, 1953, p. 737). In many respects, Watson and Crick’s

accomplishment represented the triumphant culmination of the bold programmatic objectives of the Berlin school of mechanistic physiology of the nineteenth century. Life, at last, had been successfully reduced to its molecular constituents, and thus biology could finally be ‘absorbed into the great unity of the physical sciences’, as Du-Bois Reymond had hoped in 1848.

Indeed, the mechanistic character of molecular biology is instantly recognizable. As I noted in Section 2.2, mechanistic biology seeks to explain all features of living systems from the bottom up in increasing levels of organization. In this way, molecular biology takes individual biological molecules and their detailed three-dimensional structure as the starting point of explanation. The description of the sequential transformations of these structures and the means by which they come into mechanical contact with one another is what enables the causal understanding of key processes like DNA replication and protein synthesis. As Richard Lewontin indicates, “molecular approaches to biology are attempts to *build up* the units of “natural” causal relations from individual elements” (2000, p. 77, my emphasis). This epistemic attitude is effectively captured in the first edition of Watson’s seminal textbook *Molecular Biology of the Gene* (1965), in which Watson remarked that:

Complete certainty now exists among essentially all biochemists that the other characteristics of living organisms [...] will all be completely understood in terms of the coordinative interactions of small and large molecules [...] [F]urther research of the intensity recently given to genetics will eventually provide man with the ability to describe with completeness the essential features that constitute life. (Watson, 1965, p. 67)

As this passage makes clear, the guiding expectation of molecular biology is that exhaustively cataloguing how all the different molecules in a living system interact with one another will ultimately result in a complete understanding of the living system as a whole. Of course, this does not mean that molecular biologists (or mechanists more generally) have no appreciation of the inherent complexity of living systems. It simply means that they consider that the complexity of a living system is directly determined by the properties and interactions of the parts which compose it, and that consequently a full reductionistic characterization of these parts amount to a full understanding of the living system as a whole. This view emerged as a clear and explicit reaction to the organicist or vitalist conception of the organism of the earlier part of the century, according to which the self-producing organization of the whole

organism is primary and not reducible to molecular analyses. In this respect, “Molecular biologists”, as Evelyn Fox Keller has pointed out “were struggling to build a new biology that would be clearly distinct from (and even in opposition to) an older, organismic biology, as they sought to rid their descriptions of living organisms of traditionally vital (or vitalistic) preoccupation with *function*—especially to expunge from their language such conspicuously teleological notions as *purpose*, *organization*, and *harmony*” (Keller, 1995, pp. 88-89). By rejecting the primacy of these “vitalistic” notions, molecular biologists repudiated the notion that organisms exhibit reciprocal forms of causality of the kind proposed by Kant and the organicists. Instead, the causal emphasis is on genes, which act as master molecules that exert unidirectional control by translating their miniature linear codes into the four dimensional form of the living organism. This insistence on unidirectional causality is essentially the idea that underlies the Central Dogma, which was first formulated by Crick in 1958, and which undoubtedly constitutes one of the key principles of molecular biology.²¹

This commitment to unidirectional causality is inextricably linked to the emphasis on the notion of *information*; a concept which was central to the establishment of molecular biology. In fact, molecular biology appealed to a variety of research fields outside biology, not only information theory but also cybernetics, systems analysis, operations research, and computer science (cf. Keller, 1995; Morange, 1998). Cybernetics, for instance, enabled the introduction of the concept of *feedback* into biology, which became central to the understanding of gene regulation following François Jacob (b. 1920) and Jacques Monod’s (1910-1976) formulation of the operon model in 1960. Likewise, the advent of computer science made possible the idea of a *genetic program*, which Jacob and Monod also adopted in 1961 as a model to make sense of gene expression (I will examine the concepts of feedback and genetic program in much more detail in Chapter 3). However, what is perhaps most remarkable about the establishment of molecular biology is that, despite drawing on cutting-edge areas of physical science and engineering for inspiration, its fundamental understanding of living systems is firmly grounded on the old mechanistic conceptions of matter and causality of the late nineteenth and early twentieth century. Molecular biology thus represents a direct continuation and elaboration of classic mechanistic biology, not a new form of mechanicism based on new engineering or cybernetic conceptions. Its

²¹ For a historical account of Crick’s formulation of the Central Dogma of molecular biology, see Olby, 1970. For a critical analysis of its presuppositions, see Sarkar, 1996.

mechanical conceptualization of subcellular structures (i.e., its MCO) is little different from that of classic mechanicism. Keller makes this point explicitly:

“Cyberscience and molecular biology may have been products of the same historical moment, but with respect to their models of causal structure, they were running on two separate tracks, side by side, but in opposite directions: while the first one was busy using the organism to illustrate a new kind of machine, the other was seeking to model the organism after the machines of yesteryear!” (Keller, 1995, p. 97).

Along similar lines, the noted physicist David Bohm (1917-1992) poignantly remarked at Conrad Waddington’s symposia on theoretical biology that modern biology remains committed to a mechanistic worldview whereas modern physics had departed from it:

It does seem odd [...] that just when physics is [...] moving away from mechanism, biology and psychology are moving closer to it. If the trend continues it may well be that scientists will be regarding living and intelligent beings as mechanical, while they suppose that inanimate matter is too complex and subtle to fit into the limited categories of mechanism [i.e., *mechanicism*]. (Bohm, 1969, p. 48)

Being that as it may, with a consolidated mechanistic understanding of organisms firmly in hand and the availability of the appropriate methodological techniques for studying them, the latter half of the twentieth century was largely devoted to working out the details of the molecular view of life through a meticulous characterization of its causal mechanisms. However, by the end of the last century, the realization began to emerge that molecular biology is inherently incapable of providing a complete understanding of living systems. It has gradually become apparent that the spectacular success of molecular biology was entirely predicated on its dispensation of all aspects of biology it could not comprehend or effectively deal with and its specific targeting of those problems that happened to be amenable to mechanistic conceptualizations and reductionistic investigations, such as the structure and function of macromolecular complexes, and the transmission of genetic material. Already in 1985, Adam Wilkins noted in an editorial entitled ‘The Limits of Molecular Biology’ that “molecular biology as a theory is incomplete: for many fundamental problems in biology, the present molecular canon provides no theoretical predictions and therefore cannot serve as a source of testable hypotheses in these areas” (Wilkins, 1985, p. 3).

The basic limitation of molecular biology is that it provides no general rules for deducing the properties and behaviours of individual cells or groups of cells from their macromolecular composition, however complete the molecular inventory may be. The simple fact is that the properties of living systems often derive from unexpected or unknown interactions of their components, these interactions often setting the stage for secondary interactions and so forth. The consequence is that many of the properties of living systems cannot be predicted, deduced, or calculated from the properties of the individual parts. The organism as a whole determines the behaviour of its parts, so that their behaviour as parts of the whole is qualitatively different from their behaviour in isolation. A good illustration of this is the phenomenon of cellular morphogenesis. Analysis solely of the components of the cytoskeleton (e.g., actin microfilaments, microtubules, etc.) can never provide the complete explanation, as it is the whole cell which self-organizes and determines its form (see Karsenti, 2008; Kurakin, 2005).

Instead of conceiving the advent of molecular biology as the beginning of the end of the quest to elucidate the nature of life, it may be more profitable to regard it as the end of the beginning; that is, as the mechanistic research program which took explanatory reductionism as far as it could possibly go and by doing so ultimately revealed its limitations. Carl Woese has recently expressed a similar view:

I think the 20th century molecular era will come to be seen as a necessary and unavoidable transition stage in the overall course of biology: necessary because only by adopting a heavily reductionist orientation and the technology of classical physics could certain biological problems be brought to fruition and transitional because a biology viewed through the eyes of fundamentalist reductionism is an incomplete biology. Knowing the parts of isolated entities is not enough. A musical metaphor expresses it best: molecular biology could read notes in the score, but it couldn't hear the music. (Woese, 2004, p. 175)

The field of systems biology has emerged at the beginning of the twenty-first century as a concerted effort to come to terms with the 'music of life' (see Noble (2006) for an extended examination of the music metaphor in relation to systems biology). In order to unravel the complexity underlying living systems, it is necessary to investigate the holistic patterns of the multiple interactions that link all the components of such systems. This is what systems biology sets out to do (Kitano, 2001; Konopka, 2007; Boogerd et al., 2007). However, in recent years some theoretical biologists (e.g., Cornish-Bowden, 2006) have made the worrying observation that much of the research

that goes by the name of ‘systems biology’ is actually old-style mechanistic biology applied at a larger scale. In this way, the term ‘system’ is often used to refer to the domain of interconnected phenomena to be examined reductionistically. For example, a great deal of systems biology research is concerned with examining the intracellular networks involved in metabolism, signalling, and transcription and regulation of the genetic material. However, the adopted approach is in essence no difference from the older molecular biology: each of the components in the network is individually characterized, and the interactions between them are modelled using computational tools. The underlying expectation is that this bottom-up modelling will lead to an understanding of the integrated and coordinated behaviour of living systems. But these systemic behaviours cannot be explained from the bottom up (Kaneko, 2006). Instead, top-down, system-level examinations are necessary which attempt to make sense of networks and assemblies of the component parts in terms of the self-producing organization of the system as a whole (Cornish-Bowden et al., 2004). Overall, systems biology remains largely mechanistic, though there are also some proponents of a more organicist and theoretically-rich understanding of systems biology.

Nevertheless, a more explicit resurgence of organicism is emerging in response to the still predominant mechanismism of molecular biology in other biological areas like development. In 2000, Scott Gilbert and Sahotra Sarkar authored a well-known paper entitled ‘Embracing Complexity: Organicism for the 21st Century’ in which they criticized the reductionistic presuppositions of molecular and developmental genetics, and they advocated a genuinely organicist conception of developmental biology as a “science of emergent complexity” (Gilbert and Sarkar, 2000, p. 1). Although they did not draw a line of historical and philosophical continuity between organicism and vitalism in the way that I have done in this chapter, their characterization of organicism corresponds precisely to the one I have provided, in accordance with the four key tenets of vitalistic thought outlined in Section 2.2. Gilbert and Sarkar contrast organicism with reductionism, which they characterize ontologically as mechanismism. They note that organicists, unlike reductionists, consider that “complex wholes are inherently greater than the sum of their parts in the sense that the properties of each part are dependent upon the context of the part within the whole in which they operate” (ibid.). Moreover, they note that organicism opposes the mechanistic commitment to the explanatory sufficiency of bottom-up characterizations of biological phenomena, indicating that “Organicism claims that this is not sufficient and that top-down and

bottom-up approaches must both be used to explain phenomena” (ibid., p. 2). Of course, we have already seen that these ideas, far from being new, were thoroughly developed by the wave of organicist theoretical biologists in the first half of the twentieth century before the rise of molecular biology. But in a sense they are even older, as they effectively capture much of what I have argued has always been distinctive about vitalism.

The distinguished cell biologists Marc Kirschner, John Gerhart, and Tim Mitchison have been among the very few contemporary biologists who have chosen to align themselves explicitly within the tenets of vitalistic (rather than organicist) thought, and they have done so precisely because they have been able to see beyond the derogatory way in which the term ‘vitalism’ was used for much of the twentieth century, and they have understood that this doctrine has always been truly characterized by its emphasis on the organism’s intrinsic purposiveness and self-producing organization of living systems and by its unequivocal rejection of the MCO of mechanistic biology. Indeed, their article ‘Molecular “Vitalism”’ (2000) is a full-blown attack of the ontological and epistemological commitments of mechanistic biology, as well as its most recent empirical findings in the realm of the cell. They begin their discussion by asking themselves “to what extent the ‘postgenomic’ view of modern biology would convince a nineteenth century vitalist that the nature of life was now understood” (Kirschner et al., 2000, p. 79). After reviewing the various deficiencies of understanding cellular and developmental processes in mechanistic terms and in accordance to machine models, they conclude with the following evocative passage, which is worth quoting in full:

At the turn of the twenty-first century, we take one last wistful look at vitalism, only to underscore our need ultimately to move beyond the genomic analysis of protein and RNA components of the cell (which will soon become a thing of the past) and to turn to an investigation of the “vitalistic” properties of molecular, cellular, and organismal function. Such an opportunity is now possible because of the great advances in genetics and in molecular and cell biology during the past century. As it is now clear that gene products function in multiple pathways and the pathways themselves are interconnected in networks, it is obvious that there are many more possible outcomes than there are genes. The genotype, however deeply we analyze it, cannot be predictive of the actual phenotype, but can only provide knowledge of the universe of possible phenotypes. Biological systems have evolved to restrict these phenotypes, and in self-organizing systems the phenotype might depend as much on external conditions and random events as the genome-encoded structure of the molecular components. Yet out of such a potentially

nondeterminist world, the organism has fashioned a very stable physiology and embryology. It is this robustness that suggested “vital forces”, and it is this robustness that we wish ultimately to understand in terms of chemistry. We will have such an opportunity in this new century. (Kirschner et al., 2000, p. 87)

The significance of this passage resides in the explicit recognition by these cell biologists that much of what remains to be done in biology in the twentieth century can be effectively conceptualized as the culmination of the explanatory objectives set forth by vitalists in previous centuries. The claim is that it is by appealing to vitalistic intuitions biologists today can come to terms with the properties of organisms that remained unexplainable in terms of the mechanistic understanding of living systems that drove much of twentieth-century biology. So although it is undoubtedly the case that most contemporary biologists are still implicitly committed to a mechanistic conception of life, the dispute between mechanicism and vitalism is far from over. In important respects, it continues to provide the basic battleground in which ontological and epistemological discussions about organisms is played out.

Having concluded my survey of the mechanicism-vitalism dispute, in the concluding section of this chapter I will attempt to use the resources obtained in my historical examinations to generate a clearer and richer picture of the nature and conceptual evolution of the dispute.

2.12. Conclusions: The Nature and Conceptual Evolution of the Dispute

In this chapter, I have tracked the development of the mechanicism-vitalism dispute from its origins with the Cartesian mechanization of life and its discontents, to the current tension between the mechanistic outlook of molecular biology and the organicist movements in developmental and cell biology. In reflecting on the history of the dispute as a whole, there are a number of interesting points which emerge. Perhaps the first thing to note is that neither mechanicism nor vitalism has remained static in its conceptualization of the nature of the organism. Despite preserving their core ideas, both doctrines have changed with the general development of biological science. As well as mechanicism's growth and expansion, vitalism has undergone a profound conceptual transformation since its inception. In my historical survey, I have distinguished three major forms of vitalism: animistic vitalism, somatic vitalism, and naturalized vitalism or organicism. The question is: How do they actually relate to one

another? Figure 1 attempts to provide an answer by enlisting the basic characteristic features of each successive incarnation of the doctrine.

As the comparative analysis in Figure 1 reveals, although there are clear elements of continuity in the history of vitalism, such as the commitment to the distinctiveness of life and the operation of an irreducible vital principle in living beings, what changes from one form of vitalism to the next is the very nature of that principle. In animistic vitalism, the distinction between life and non-life is based on the operation of a life-soul that enters the organic body at birth and endows it with its distinctive vital functionalities. For an animistic vitalist, there is nothing about the constitution or arrangement of the organism which justifies the division between life and non-life. Rather, the vitality of the organism is the result of the infiltration of an external agent into the body. It is the very presence of the soul which makes the organism alive, and it is its departure from the body which results in the organism's death. In contrast to animistic vitalism, somatic vitalists root the distinctiveness of life on the operation of a vital force (or forces) which comes into being as the body forms during ontogeny. Although the cause of this force cannot be identified, its existence can be empirically confirmed through its observable effects on the organism. The actual function of the vital force differs considerably from one somatic vitalist to another, but it is generally taken to be responsible for guiding or directing physiological processes or the course of ontogenetic development. Finally, in organicism, the basis for the ontological distinctiveness of life (i.e., the vital principle) is the particular organization of matter within the organism. The self-producing and self-preserving organization of the living being enables it to regulate its internal environment from external perturbations and to holistically coordinate its different physiological functions. In this form of vitalism, life itself is viewed as a natural emergent property of a very specialized and intricate arrangement of organic matter. The death of the organism is understood as being the result of the disappearance of its intricate organization. Unlike animistic vitalism but like somatic vitalism, organicism maintains that the source of vitality arises from within the organism itself, and not from the action of an external agent. The critical difference between organicism and prior forms of vitalism is that the cause of the vital principle is no longer obscure or beyond the reach of scientific explanation. It nonetheless remains a phenomenon exclusive to the living realm.

Figure 1. Comparative Analysis of the Major Forms of Vitalism in the History of Biology

	ANIMISTIC VITALISM	SOMATIC VITALISM	NATURALIZED VITALISM
Period of Acceptance	Late 17 th C. to Mid 18 th C.	Mid 18 th C. to Early 20 th C.	Late 19 th C. to Present Day
Living is Distinct from Nonliving	Yes	Yes	Yes
Nature of Vital Principle	Life-Soul	Force	Intrinsically Purposive Self-Organization
Metaphysics of Vital Principle	Supernatural	Unclear	Natural
Location of Vital Principle	Resides Outside of Living Matter	Supervenes on Living Matter	Supervenes on Living Matter
Principle's Relation to Living Matter	Exists Independently of Living Matter	Is a Property of Living Matter	Results from Organization of Living Matter
Cause of Vital Principle	God	Unknown	Evolved Complexity of the Organism
Main Function of Vital Principle	Endows the Organism with Life	Guides Physiological Processes	Regulates & Coordinates the Organism
Measurability of Vital Principle	No	Yes	Yes
Accountability of Vital Principle	No	No	Yes
Mechanistic Analogy	Descartes' Mind-Body Dualism	Newton's Gravitational Force	Whitehead's 'Organic Mechanicism'
Representative Exponents	G. E. Stahl	Wolff, Blumenbach, Driesch	Bernard, J. S. Haldane, Bertalanffy

Although the different schools of vitalism conceptualize the vital principle very differently, what they all share is the conviction that the life of the organism needs to be understood as a particular attribute (be it a life-soul, a force, or an emergent self-producing organization) which acts upon the organism's matter and eludes a bottom-up mechanistic explanation. In fact, it is in the explication of the vital principle that all vitalists since the seventeenth century have grounded their defence of the autonomy of the living. From the historical examination I have presented it becomes clear that, despite their differences, all forms of vitalism have been constructed upon the same basic principles I outlined at the outset of this chapter, namely the commitment to an ontological discontinuity between the living and the non-living, exemplified by the rejection of the MCO and the postulation of a vital principle; to the view that organisms possess system-level properties that cannot be accounted for by attending to the properties and interactions of their parts; to the emphasis on the organizational and teleological features of organisms; and to the rejection of the sufficiency of the explanatory reductionism.

The development of mechanicism is similarly marked by the evolution and transformation of particular ideas and approaches coupled with the preservation of a core set of basic principles. As a whole, mechanists of all ages have shared the commitment to a natural continuity between the living and the non-living; to the view that organisms are directly determined by the activities and interactions of their component parts; to the emphasis on the causal and material features of organisms; and to the confidence in the sufficiency of explanatory reductionism. But more than anything else, the heart of mechanistic biology since its inception is the MCO. This notion constitutes a constant recurring theme in the writings of (most) mechanists who, since Descartes, have regarded it as the central working hypothesis informing their research. The importance of this conception stems from the fact that it provides a compelling justification for the application of physicochemical and engineering concepts and methods in biology. Indeed, if the organism is nothing but a complex machine, then the implementation of physicochemical and engineering principles in the scientific study of life is not only legitimate but necessary.

Of course, although the MCO has prevailed historically, the kind of machine that has been used to conceptualize the inner workings of the organism has changed as

technological development enabled the construction of increasingly complex machines. In Cartesian mechanicism, the organism was either a clock, with its coordinated set of rotating cogs, springs, and levers, or a hydraulic automaton, with its ordered arrangement of pipes and tubes. By the late eighteenth century, it had become a steam engine, with its source of heat that had to be continuously renewed, its cooling system, and its devices for adjusting the operations of the various parts. By the mid nineteenth century, it was a self-regulating chemical factory coordinating a multitude of interconnected reactions. Finally, by the late twentieth century, many mechanists were conceiving it as an electronic computer, containing a preexisting set of instructions and possessing the ability to process large amounts of information about the environment and feeding back appropriate responses. The prevalence of the MCO in biological inquiry reveals an important aspect about mechanistic epistemology. The organism, as any machine, can only be fully understood if it is 'dismantled' into its components and then each of its parts is examined independently. The underlying assumption here is that understanding the functional roles of all the parts of an organism suffices to explain the activity of the organism as a whole.

Having outlined the basic trends of continuity running along the conceptual evolution of both doctrines, it is now possible to consider the development of the conflict between them. In broad terms, the history of the mechanicism-vitalism dispute may be regarded as a sequence of vitalistic retractions against the gradual yet inexorable advances of mechanicism. Mechanists have sequentially done away with life-souls, vital substances, and vital forces, and have increasingly equated living processes to those which take place in the realm of inanimate bodies. Indeed, each succeeding form of vitalism can be viewed as a more moderate version of the preceding form. The different phases of vitalism I have identified embody the successive retrenchments that vitalism has been forced to make in the face of the challenges put forward by their mechanist opponents. At the same time, mechanicism has become increasingly adept at characterizing and conceptualizing the complexity of living systems. The fundamental difference between mechanists and vitalists regarding their respective conceptions of the nature of organisms has remained virtually unaltered in the long history of the dispute. What has changed is the *justification* provided for their conceptions.

Another interesting aspect of the dispute which emerges from my historical examination is the very peculiar relationship that vitalism has had with mechanicism. On the one hand, vitalists have always forged and elaborated their views on the basis of the criticisms they have directed against their mechanist opponents. As such, animistic vitalism is a reaction to Cartesian mechanicism, somatic vitalism is an outgrowth of Newtonian mechanicism, and organicism is a response to late nineteenth century physicalistic reductionism. On the other hand, however, each form of vitalism has seemed to recapitulate the conceptual framework of the brand of mechanicism it opposed. Clearly, this is because mechanicism at every stage of its development has had something interesting to offer vitalism epistemologically. But I think that there is a deeper motivation at work here. It seems to me that given the fact that since the Scientific Revolution mechanicism has tended to be regarded as the embodiment of 'good science', any substantive departures from mechanicism on the part of vitalistic biologists could easily become construed as constituting a departure from science in general (indeed, this has occurred historically more than once, most prominently in the case of Hans Driesch at the turn of the twentieth century). As a result, vitalists have been forced to devise their criticisms of mechanicism *within* the conceptual framework laid out by their mechanist opponents, and indeed the scientific respectability of their claims has often been grounded on the similarities they have shared with the very mechanistic theories they have sought to reject!

This argument helps explain why animistic vitalists expressed their conviction that mechanicism was inherently incapable of accounting for life by elaborating a dualistic conception of the living organism which explicitly emulated the Cartesian dualistic conception of man as a rational being. In a similar fashion, the doctrine of somatic vitalism was forged using Newtonian mechanicism as the model, with its postulation of unknowable yet measurable forces of nature. Recapitulating the relation between animistic vitalism and Cartesian mechanicism, the vitalism that was developed by adopting the Newtonian approach to natural philosophy was principally reacting to the mechanistic interpretation of the very science that had led to its inception. Moreover, it is again the case that it was precisely the similarity with Newtonian mechanicism that allowed somatic vitalists to justify the scientific legitimacy of their views. As it turns out, however, somatic vitalism failed to convince in the long term, as no consensus could be reached regarding the nature of the vital force and its effects on

the organism. Eventually, it became apparent that Kant had been right to assert that a 'Newton of a blade of grass' would not come into being in the form of a biologist trying to emulate Newton's own approach to physical science. François Magendie (1783-1855), Bernard's main intellectual mentor, clearly recognized this when he noted in 1833 that "Of all the illusions of modern physiologists, the most deplorable has been that of believing that by forging a new term, such as vital principle or vital force, one has done something analogous to the discovery of gravitation" (quoted in Hall, 1968, p. 22). It is probably due to this important realization that naturalized vitalism, unlike its predecessors, did not emerge through the adoption of a mechanistic conceptual framework. In fact, as I showed, the reverse situation almost occurred when, in the midst of the conceptual confusion resulting from the astounding developments in physics in the early twentieth century, a number of mechanists considered introducing biological notions such as 'organization' and 'organism' into physics in order to help unify their new understanding of nature.

So far, I have focused on the conceptual evolution of the mechanicism-vitalism dispute, and how the relationship between the two doctrines has been to a large extent responsible for the way each has constructed their own views. I will now turn to examine the nature of the conflict itself, and I will do this by identifying the fundamental differences in the epistemic frameworks of the two doctrines. One of the major differences, even if it is not one that is immediately apparent upon a first examination, is the location of the phenomenological experience of life in relation to the generation of scientific knowledge. Mechanists have tended to formulate their theories on the basis of the empirical study of the inanimate world and then have proceeded to examine the living world under the reasonable assumption that whatever holds for the domain of the physical must necessarily hold for the domain of the biological. As such, mechanicism subsumes the nature of the living within the mechanistic conceptual framework derived from the study of inanimate bodies. Thus, mechanists approach the living organism already having a fairly clear understanding of what it is (namely, a machine) and how it should be investigated. In this sense, its endeavour to explain the organism is pursued from the outset within the strict boundaries of what is taken to be mechanistically acceptable.

In contrast, vitalism is in some respects more empirically grounded since its understanding of life is not arrived at on the basis of a preconceived model like the MCO but rather as a result of being empirically confronted by the complexity of the organism. Vitalism, unlike mechanicism, allows the object of study to dictate the kind of theory that should be constructed to explain it. Wolff, one of the greatest somatic vitalists of the eighteenth century, exemplified the empirical commitments of vitalism when he noted that “It is of particular importance to me to discover the principles and universal laws of generation *a posteriori*” (Wolff, quoted in Roe, 1981, p. 111). Indeed, the very notion of the vital force, as employed by Wolff and most other somatic vitalists, was generally not introduced as an *a priori* statement of faith about the nature of the organism, but rather as a tentative explanation, after observation and experiment, for the results obtained. The vital force was thus a reasonable postulation made by those seeking to ‘save the phenomena’, and it is through this perspective that its invocation should be understood.

The general claim that vitalism, unlike mechanicism, is more closely derived from observation than from theory can be substantiated by considering the intellectual development of well-known proponents of the vitalistic doctrine. What one finds is that a number of them began as mechanists but as a result of the weight of their own investigations they ended up abandoning their mechanistic commitments and embracing vitalistic ideas that were more concordant with their own empirical findings. Bichat is a case in point. Although he started out as a mechanistic anatomist seeking to reductionistically explain the organism in terms of twenty-one different types of tissues, he eventually became convinced of the existence of irreducible vital properties in these tissues which could not be accounted for mechanistically. Driesch is another good example. As I indicated in Section 2.8, although he initially worked with Roux as part of the *Entwicklungsmechanik* research program, his own experimental findings led him to reject mechanicism and develop a form of vitalism that could better account for his observations. From this it is possible to conclude in broad terms that whereas mechanists tend to approach life with presuppositions derived from the study of the physical or the mechanical, vitalists typically arrive at their understanding of life through a more dynamic interplay of data acquisition,

theory construction, and theory testing.²² These general conclusions can be summarized diagrammatically, as shown in Figure 2.

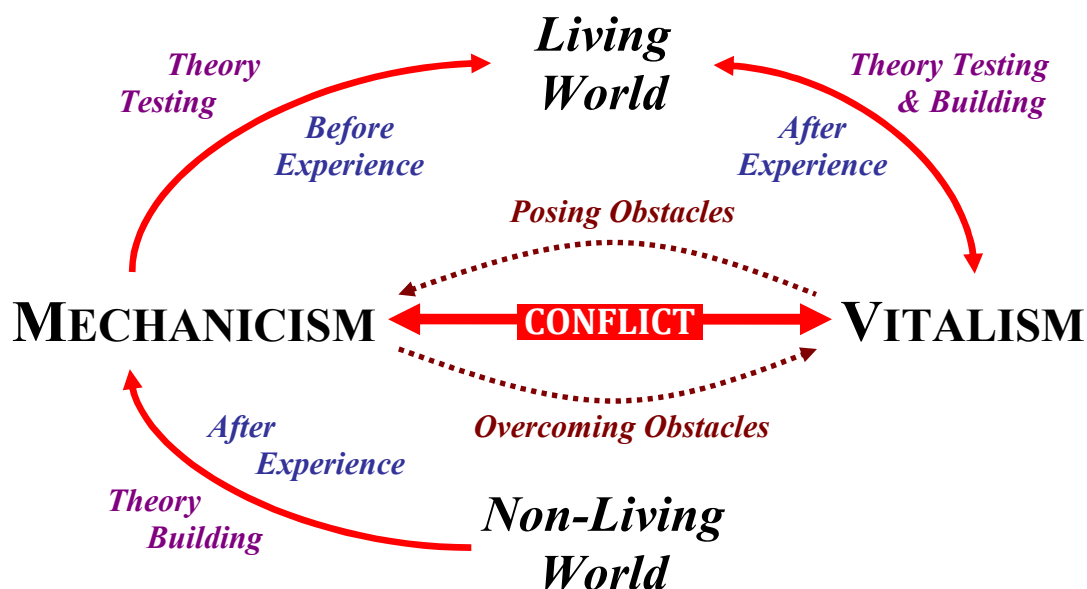


Figure 2. Selected features of the nature of the mechanicism-vitalism conflict

One of the most remarkable aspects of the relationship between mechanicism and vitalism is that it is not symmetrical. The way mechanicism influences vitalism is very different from the way vitalism affects mechanicism. I have already discussed the way vitalistic thinking despite being fundamentally opposed to mechanicism has been historically shaped by it. What I have not yet mentioned is the effect that vitalism has had on mechanicism throughout the history of the conflict. It would appear that because mechanicism directly derives from the study of the inanimate, it does not become altered when approaching the study of life. This, however, is not actually correct. As part of the dispute, vitalists tend to draw attention to the properties of living organisms that mechanists seem incapable of explaining. The natural tendency of mechanists is to focus on phenomena they *can* explain, and to overlook the vital phenomena that prove more difficult. In this context, vitalists provide a kind of honesty check on mechanists by posing obstacles for mechanists to overcome by

²² Of course, as with any broad generalizations, it is not difficult to find exceptions. Perhaps the most famous counterexample to this characterization of vitalism is the philosopher's Henri Bergson's (1859-1941) articulation of vitalistic thought in his *L'Evolution Créatrice* (1911), which did not directly derive from any empirical investigations. I should therefore indicate that in discussing mechanicism and vitalism in this general way, I am assuming that the existence of certain counterexamples does not preclude the possibility of drawing concrete conclusions about the typical *modus operandi* of mechanists and vitalists.

keeping in focus aspects of the organism that remain recalcitrant to existing mechanistic explanatory strategies. In this respect, by virtue of its empiricism, vitalism provides a useful corrective for mechanism's reliance on rationalism.

These considerations lead me to the end of this concluding discussion, where it is necessary to at least consider the daunting question of whether or not the mechanism-vitalism dispute is resolvable. Hilda Hein's (1968; 1972) view is that the conflict is meta-theoretical in nature as it involves "fundamental commitments on the part of their antagonists which do not depend upon scientific evidence for their retention, and which will not be shaken by evidence to the contrary" (Hein, 1972, p. 160). Because of this, she asserts that the dispute "will be perpetuated as long as people ask questions and seek rational answers" (*ibid.*, p. 188). Clearly, this view offers little hope for any sort of resolution. However, there are good reasons to be sceptical of Hein's conception of the conflict. As the preceding historical examination has shown, the mechanism-vitalism dispute has always been, and continues to be, deeply ingrained in actual biological theorizing. Indeed, it has in fact grounded some of the major biological controversies of the last four centuries. Moreover, my analysis has revealed that the two doctrines find themselves in constant dialogue with each other and with the subject matter they seek to explain. On these grounds, I believe that the idea that the conflict is purely ideological can be rejected and consequently Hein's pessimism regarding a resolution no longer appears to be warranted. The question remains, however, of whether the dispute can ever be settled on theoretical grounds.

Since its inception, vitalism has emphasized the features of living organisms which seem to be unexplainable in mechanistic terms. Throughout history, mechanism has gradually succeeded in subsuming more and more of the organismic realm into the physicochemical worldview. The crucial question is whether the mechanistic subjugation of life can ever be absolute. For the modern organicist, the two central, and most elusive, distinctive features of the organism are its intrinsic purposiveness and its self-generating organization. Ultimately, the fate of the mechanism-vitalism dispute will depend on whether these two problems can be effectively resolved by means of a complete mechanistic characterization of the organism, or if, on the contrary, they can be conclusively shown to constitute real yet irreducible natural phenomena requiring a fundamentally different kind of theoretical understanding.

Chapter 3

WHAT IS WRONG WITH THE MACHINE CONCEPTION OF THE ORGANISM?

The ur-metaphor of all of modern science, the machine model that we owe to Descartes, has ceased to be a metaphor and has become the unquestioned reality: Organisms are no longer *like* machines, they *are* machines. – Richard Lewontin (1996)

3.1. Introduction: The Machine Conception of the Organism (MCO)

A large number of working biologists today are firmly committed to a mechanistic understanding of life. In the previous chapter, I described mechanistic biology in terms of the following key tenets:

1. The commitment to an ontological continuity between the living and the nonliving
2. The view that biological wholes (i.e. organisms) are directly determined by the activities and interactions of their component parts, and that consequently all properties of organisms can be characterized from the bottom up in increasing levels of organization
3. The focus on the efficient and material causes of organisms, and the unequivocal repudiation of final causes in biological explanations
4. The commitment to explanatory and methodological reductionism in the study of living systems

These four principles are neatly encapsulated in the *machine conception of the organism* (MCO, hereafter) which constitutes the central unifying idea of mechanistic biology. Indeed, due to its indissoluble association with mechanistic thinking, the MCO has played an instrumental role in the unfolding of the mechanicism-vitalism dispute, as I showed in the previous chapter, with the mechanists persistently drawing upon it to anchor their various biological claims, and the vitalists uniting by their collective rejection of it. Today, the MCO is so engrained in the minds of working biologists that it is simply taken for granted. The question ‘What is the nature of the organism?’ does not even enter the scientific discourse because most biologists just

assume that mechanicism has already answered it: the organism is a machine. Indeed, in cell, molecular, and developmental biology, the standard conception of the organism is that of a machine programmed by its genes and decomposable into its component mechanisms. Likewise, in evolutionary biology, organisms are conceived as optimally-designed machines blindly engineered by natural selection. The pervasiveness of the MCO is the most evident symptom of the dominance of mechanistic thinking in contemporary biology.

However, as I indicated at the end of the last chapter, in recent years there have been growing voices of dissent from the mechanistic orthodoxy as more and more biologists have begun to question the ontological foundations and epistemic prescriptions of mechanicism. Still, what current critiques tend to overlook is that the increasingly apparent inadequacies of the mechanistic understanding of life stem from the outright acceptance of the MCO. As we will see, the confidence in the sufficiency of reductionistic explanations, the belief in genetic determinism, the disproportionate emphasis on the structural and causal features of organisms over and above their organizational ones, and the reliance on adaptationist thinking in evolutionary biology all have their basis in the MCO. Consequently, any serious critique of mechanistic thinking in biology must take the MCO as its primary target. Only by exposing the fundamental deficiencies of the MCO can the mounting criticisms of mechanistic biology be appropriately justified and contextualized.

The aim of this chapter is to provide a comprehensive critique of the MCO. I shall begin by tracing its historical origin and analyzing its philosophical foundations (Section 3.2). I will then explain why organisms are fundamentally different from machines, and why the MCO results in a deeply misguided understanding of living systems (Section 3.3). Following this, I will elaborate my criticisms of the MCO by examining the explanatory (Section 3.4), theoretical (Sections 3.5 and 3.6), epistemic (Section 3.7), and ethical (Section 3.8) consequences of its acceptance. Then, I will explore an alternative conception of the organism favoured by organicists and illustrate how it sidesteps the problems generated by the MCO (Section 3.9). This will lead me to consider what role, if any, the MCO should play in biology today in light of its deficiencies as a theory of organisms (Section 3.10). I will conclude by explaining why biology must break free from the grip of mechanicism (Section 3.11).

3.2. Historical and Philosophical Foundations of the MCO

Although the MCO has its origins in the writings of René Descartes, the idea of assimilating the activity of organisms to the workings of machines has a much longer history. For example, Aristotle compared the movements of animals to those of automatic puppets in *De Motu Animalium*, and he also likened the organs of animal motion to the parts of war machines, indicating that the human limb is articulated like the arm of a catapult. Similarly, the Roman poet Lucretius compared the movements of animals to the functioning of machines in his *De Rerum Natura*. In addition, the Christian apologist Thomas Aquinas asserted in the *Summa Theologica* that animals can be regarded as machines because they display regular and orderly behaviour. This view was restated and elaborated by the Spanish physician Gómez Pereira in his *Antoniana Margarita* of 1554 (cf. Grmek, 1972; Canguilhem, 1992; Berryman, 2007).

However, what is undeniable is that Descartes took the comparison between organisms and machines to a completely new level. With Descartes, it is no longer simply the case that it might be helpful, under certain circumstances, to appeal to the workings of machines to illuminate the activity of organisms. Rather, it is *only* by conceiving organisms *as* machines that we can truly make sense of them. For Descartes, the MCO is a model of intelligibility that brings the biological realm within the scope of mechanistic explanation. To understand the organism as a machine is to understand it well enough that no further requirement of clarity or demonstrative certainty is required (see Des Chene, 2001). For this reason, despite earlier comparisons between organisms and machines, Descartes was undoubtedly the first to truly recognize the potential of the MCO, identifying it as the necessary condition for biological knowledge, and adopting it as the basic standard for explanatory adequacy in biological inquiry.

The MCO is based on the *analogy* between organisms and machines. The term ‘analogy’ derives from the Greek word for proportion, which is a comparative relation between two objects. Thus, two objects are analogous if there is a correspondence between them. The strength of an argument by analogy depends on the degree of similarity between the compared attributes (Juthe, 2005). Analogies play a central explanatory role in Cartesian natural philosophy. Descartes’ appeal to analogical

reasoning is legitimated by the metaphysical conviction that the objects he compares are essentially of the same nature, differing only in the size, shape and motion of their material components. In personal correspondence, Descartes says the following regarding his use of analogical reasoning:

[I]n the analogies which I employ, I compare movements only with other movements, or shapes with other shapes; that is, I compare things that are too small to be perceived by the senses with other things that can be so perceived, the latter differing from the former simply as a large circle differs from a small one. I maintain, therefore, that analogies of this sort are the most appropriate means available to the human mind for laying bare the truth in problems of physics (Descartes, 1991, p. 122)

The analogy between organisms and machines is likewise legitimated by the presumed ontological correspondence between these two kinds of objects. For Descartes, it is *because* organisms and machines are essentially of the same nature that it is possible to infer the imperceptible operations of the former by attending to the visible workings of the latter. Thus, in the *Principia Philosophiae* he states that:

I do not recognize any difference between artefacts and natural bodies except that the operations of artefacts are for the most part performed by mechanisms which are large enough to be easily perceivable by the senses – as indeed must be the case if they are capable of being manufactured by human beings. The effects produced in nature, by contrast, almost always depend on structures which are so minute that they completely elude our senses. (Descartes, 1985, pp. 288-289)

What justifies the organism-machine analogy, then, is precisely the fact that organisms are not actually distinct from machines; they *are* themselves machines in every respect, just machines of far more intricate design than any machine produced by man. In fact, in his *Traité de l'Homme* Descartes sets out to describe not the physiology of man, but the physiology of imaginary automata made by God to resemble man. The point of this rhetorical strategy is to show that the human body is indistinguishable from a perfectly designed automaton, so that a detailed mechanistic description of the latter amounts to an effective explanation of the former. Descartes makes this explicit at the end of the treatise:

[A]ll the functions that I have attributed to this machine, such as the digestion of food, the beating of the heart and the arteries, the nourishment and growth of the bodily parts, respiration, waking and sleeping; the reception of light, sounds, odours, smells, heat, and other such qualities by the external sense organs; the impression of the ideas of them in the organ of common sense and the imagination, the retention or imprint of these ideas in the memory; the internal movements of the appetites and the passions; and finally the external movements of all the bodily parts [...] imitate as perfectly as is possible the movements of real men. (Descartes, 1998, p. 169)

In the later physiological work *La Description du Corps Humain*, written at the end of his life, Descartes dropped the pretence of simulation of *l'homme* and plainly identified the body as a machine, thereby reaffirming his earlier allusions to the MCO in more general works like the *Discours Sur la Méthode*. After Descartes, the MCO became systematically applied to virtually every area of physiological inquiry. Consider, for instance, the following remarks by the seventeenth-century iatromechanist Giorgio Baglivi:

Examine carefully the physical economy of man: What do you find? The jaws are armed with teeth, which are no more than pincers. The stomach is nothing but a heat chamber; the veins, the arteries and indeed the entire vascular system are simply hydraulic tubes; the heart, a pump; the viscera, nothing but filters and sieves; the lungs, a pair of bellows; and what are the muscles if not a system of cables and ropes? What is the oculomotor nerve, if not a pulley? And so on. (Baglivi, 1696, quoted in Canguilhem, 1992, p. 47)

Ever since the establishment of mechanistic biology, the history of thinking about organisms has trailed the progressive technological development of machines. Through the centuries, organisms have been conceived in accordance to the paradigmatic machine of the age, be it a seventeenth-century clock with its precise finely-tuned parts operating as a functionally-integrated whole, an eighteenth-century steam-engine consuming energy by combustion and performing work whilst producing heat, a nineteenth century chemical factory coordinating a multitude of interconnected reactions, or a twentieth-century computer processing information about the environment and feeding back appropriate responses. Even individual organs have undergone their own particular technomimetic transformations. For

example, Georges Canguilhem (1963, p. 518) traced “the successive identification of the nerve with a non-isolated, passive electric conductor, then with an electro-chemical assembly [...] simulating the propagation of an impulse and the establishment of an insensitive period, and finally with a model of an [...] electric circuit, combining a battery with a grid-leak condenser”.

Philosophically, although grounded on the analogy between organism and machine, the MCO is more specifically the result of the *metaphorical redescription* of the organism *as* a machine. Of course, it is well known that metaphors play an indispensable role in scientific understanding (Hesse, 1966; Brown, 2003). As the cognitive linguists George Lakoff and Mark Johnson (1999, p. 128) have remarked, “Metaphorical thought is what makes abstract scientific theorizing possible”. In general, metaphors constitute means for representing new knowledge by providing familiar conceptual frameworks through which to make sense of unfamiliar phenomena, so that the unknown is ‘seen through’ the known. In this way, our ability to comprehend the visual idea of a ‘living machine’ seems to help us understand many of the actual properties of organisms. For example, our ability to deduce structural and functional relationships in machines gives us the confidence to predict the nature of the corresponding relationships in organisms. This is the source of the epistemic power of the MCO; it opens up new avenues of biological inquiry, as confirmed statements regarding the workings of machines are translated into testable hypotheses concerning the operation of organisms. Throughout history, the MCO has also been responsible for the introduction of a great deal of terminology into the biological discourse. Ubiquitous terms like ‘mechanism’, ‘design’, ‘goal’, ‘control’, ‘regulation’, ‘efficiency’, and ‘program’ all have their basis in the MCO. No wonder, then, that in a recent editorial entitled ‘Grand Metaphors of Biology in the Genome Era’, the systems biologist Andrzej Konopka (2002, p. 398) asserted that “the machine metaphor is perhaps the most powerful conceptual tool of modern biology”.

Still, leaving Cartesian metaphysical commitments to one side, what is it that actually *justifies* in the present context the identification of organisms with machines? In what ways are organisms and machines isomorphic? A number of commonalities are readily discernable. At a most fundamental level, both organisms and machines are bounded physical systems that act in accordance to natural laws. Both use or modify

energy and transform part of it into work. Moreover, both are heterogeneous systems, since each part of an organism or a machine has a different structure from the whole (in contrast to, say, a stone). As a result, they both admit relational descriptions, meaning that any organism, and any machine, can be represented in terms of interacting parts and causal relations. At the same time, both organisms and machines are organized so that they operate coordinately towards the attainment of particular ends, and consequently both can be characterized in functional terms. Finally, the duration of their operation is, in both cases, finite. These are, I believe, the main commonalities underlying the appeal to the MCO in biology. What, then, is wrong with the MCO?

3.3. Refuting the MCO: Why Organisms Are Different From Machines

The problem with the MCO stems from the failure to recognize that in any comparison between two entities, the most immediately perceptible similarities are not necessarily the most important ones. Valid analogical arguments are precisely those which effectively distinguish accidental and non-accidental relations and use only the latter as the basis for comparisons (Weitzenfeld, 1984). It is the successful identification and mapping of the distinctive features²³ of the compared entities that guarantees the explanatory power of an analogy. If the mapping relations do not capture these distinctive features, then the metaphorical redescription of one entity on the basis of the other results in a distorted conceptualization of the redescribed entity. In this section, I will argue that the inadequacy of the MCO derives from the fact that the distinctive features of organisms are, in the final analysis, fundamentally different from those of machines.

Paradoxically, the single most important difference between organisms and machines has its basis in what *prima facie* appears to be their most obvious similarity. As I indicated above, both organisms and machines operate towards the attainment of particular ends; that is, both are *purposive* systems. However, their purposiveness is of a completely different kind. The first to fully recognize this was Immanuel Kant (2000 [1790]), who in discussing organisms and machines distinguished between

²³ By the distinctive features of an entity I simply mean those features without which the entity would not be what it is.

extrinsic (or relative) and *intrinsic* forms of purposiveness. A machine is extrinsically purposive because it operates towards an end that is external to itself. Its *telos* is imposed from the outside and it is of use or value to an agent other than itself. A machine does not serve its own interests but those of its maker or user. In contrast, an organism is intrinsically purposive because it acts on its own behalf, towards its own ends. Its *telos* is internal, arising from within, and serving no other purpose than to maintain its own organization. A machine is also organized, of course, given that the operation of each part is dependent on it being properly arranged with respect to every other part, and to the system as a whole. But in an organism, the parts are not just there for the sake of each other, but they also produce each other, repair each other, and generally exist by means of one another. Organisms, unlike machines, are not only organized but are also *self-organizing* and *self-reproducing* systems.

This notion of *selfhood* is helpful in fleshing out the different kinds of purposiveness exhibited by organisms and machines. Organisms have an autonomous self; the phenomena of self-formation, self-regeneration, self-preservation, and self-repair are all characteristic of the internal dynamics of living systems. Machines, on the other hand, lack an autonomous self; their means of production reside outside of themselves, demanding outside intervention not just for their construction but also for their maintenance. Indeed, for the sustained operation of a machine, an external agent is required to determine when defective components need to be repaired or replaced, and to carry them out in a timely fashion. In an organism, all of these processes are carried out from within. Therefore, confronted with a machine, one is perfectly justified in inferring the existence of an external creator responsible for producing it in accordance to a preconceived plan or *design*. Confronted with an organism, one is not. As I will show in Section 3.6, this contrast has major implications for the appeal to the MCO in evolutionary biology.

The distinction between extrinsic and intrinsic forms of purposiveness is also at the heart of another important dissimilarity between organisms and machines, namely that the attribution of *functions* has a different basis and a different significance in these two kinds of systems (see McLaughlin, 2001). Machines have functions; organisms do not. It is only the parts (or traits) of organisms that have functions; in machines, both parts and wholes can be ascribed functions in the same sense. The reason for this

is that the attribution of a function to a particular entity is enabled by the fact that the beneficiary of its operation is an external agent. A machine has a function because it is good for something; that is, it is designed to operate in ways that serve the ends of its maker or user. An organism does not have a function because it is not good for anything; it simply acts on its own behalf and serves its own ends.

Nevertheless, the *parts* of both machines and organisms have functions, given that in each case the immediate beneficiary of their operation is the whole system to which they belong, be it a machine or an organism. The key difference here is that in the case of the machine, the function of the parts are good for the function of the whole, and the function of the whole is in turn good for an external agent, namely the maker or user of the machine. In contrast, in the case of the organism, this concatenation of functional beneficiaries is avoided because the system is intrinsically purposive and consequently does not serve the interests of an external agent. The parts of an organism, unlike the parts of a machine, are not good for external beneficiaries of the operation of the organism, but for the organism itself.²⁴ In this way, the attribution of functions to the parts of an organism is dictated by the means in which each part individually contributes to the maintenance of the organization of the organism as a whole. It is the actual organism, and not some external agent, that adjudicates the ascription of functions to its parts according to how they help it meet its physiological needs and cope with its surroundings (cf. Mossio et al., 2009).

Thus, the *relation* between the parts and the whole is of a fundamentally different kind in organisms and machines. In a machine, the parts are physically independent of, and temporally antecedent to, the whole they constitute. Their functions belong to the original design of the machine, and are therefore ascribed by the maker of the machine. Although the parts acquire their function by virtue of being present in the machine, they nevertheless retain their own distinctive properties regardless of whether they are integrated in the machine or not. By contrast, the parts in an

²⁴ Peter McLaughlin (2001, p. 148) illustrates this difference with the following example: “The elephant’s heart has the function of pumping its blood, and it has this function because the activity [...] is for the good of the elephant [...]. The pump on my air conditioner, on the other hand, has the function of circulating cooling fluids because this contributes to the performance of the machine, which is good for me, its designer, manufacturer, purchaser, or whatever. Air conditioners have no interests or welfare; they are not appropriate subjects of benefit, utility, or happiness.”

organism are neither physically independent of, nor temporally antecedent to, the whole they constitute. Their function is not only enabled by the whole but also *determined* by the whole. The parts of an organism exist in a relation of collective interdependence, as every part is necessary for the generation and operation of the others. The organism maintains its autonomy as a whole by constantly regulating, repairing, and reproducing its parts (Varela, 1979). Moreover, the processes by which the parts are produced are precisely those by which they constitute and maintain the organization of the whole. As a result, the generation, properties, and functions of the parts of an organism, unlike those of a machine, cannot be understood independently from the whole. This has crucial explanatory consequences which I will discuss in the next section.

The determining influence in organisms of the whole over the parts has long been recognized. One of the most influential studies of the ‘holistic’ capabilities of organisms was carried out by the German physician and neurologist Kurt Goldstein (1995 [1934]) who, in the course of his treatment of brain-damaged soldiers during World War I, observed that the organism readjusted itself to cope with devastating injuries by withdrawing to more limited ranges of activity which it could manage by appropriately redistributing its reduced energies. For Goldstein, the assumption that in an organism, like in a machine, the parts determine the whole could be refuted empirically. When confronted with illness or injury, Goldstein found that organisms possess the inherent flexibility to reorganize their parts to a considerable extent in order to recover the performance of vital functions. Thus, Goldstein’s rejection of the MCO was not the result of philosophical speculation but of clinical observations. In fact, even someone with impeccable mechanistic credentials like the cyberneticist John von Neumann (who, as we will see in Section 3.7, used the MCO as the basis for his theory of self-reproducing automata) recognized the determining influence of the whole over the parts in biological systems like the brain, noting that “It is never very simple to locate anything in the brain, because the brain has an enormous ability to reorganize. Even when you have localized a function in a particular part of it, if you remove that part, you may discover that the brain has reorganized itself, reassigned its responsibilities, and the function is again being performed” (von Neumann, 1966, p. 49).

The determination of the parts by the organism as a whole extends not only to their function and behaviour, as shown by the examples above, but also to their *structural* properties. In the words of the British physiologist J. S. Haldane (1884, p. 37), “What appeared to belong to the parts independently of their relation to the whole, for instance their size, shape, and structure, is really only the manifestation in the parts of the influence of the whole”. A beautiful illustration of this was provided by the Swiss embryologist Gerhard Frankhauser in the 1940s, as Marc Kirschner, John Gerhart, and Tim Mitchison (2000) have recently pointed out. Frankhauser experimented with the effects of ploidy (i.e., the number of chromosome sets in the cell) on newt development, and found that polyploid embryos, generated by suppressing early cleavages, had fewer but larger cells. The number and size of cells differed in haploid, diploid, and pentaploid embryos, but the tissues of the organism, as well as the organism as a whole, remained the normal size in all cases. This was seen most clearly in well-defined structures like the pronephric duct of the kidney (see Figure 3). Frankhauser’s experiments showed that in an organism, unlike in a machine, there is no strict correlation between the size of the parts and the size of the whole. Whereas in a machine the whole is always the product of the structure and arrangement of its parts, in an organism the whole simply cannot be reduced to the properties and interactions of its parts.

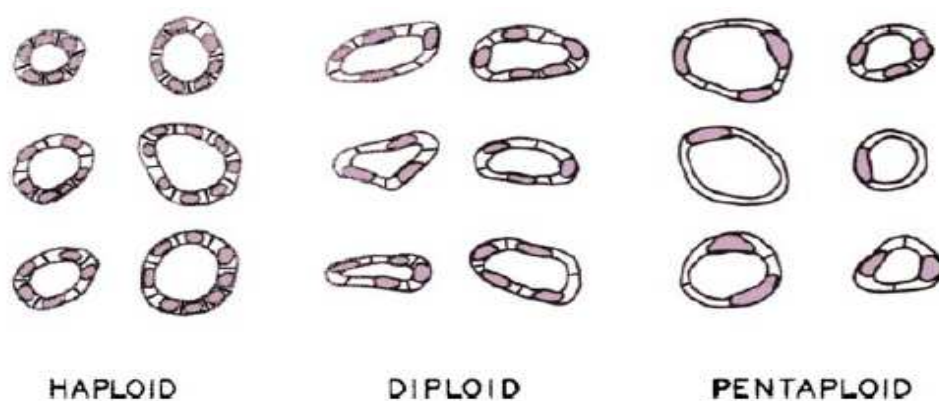


Figure 3. Cross sections of the pronephric ducts of haploid, diploid, and pentaploid newt embryos (adapted from Kirschner et al., 2000). In pentaploid embryos just one to three cells strain to maintain a circular duct of dimensions that require three to five cells in diploid embryos, and five to eight cells in haploid embryos. Nevertheless, the normal size and thickness of the duct is maintained despite the differences in cell size.

Moreover, by virtue of its self-organization, the organism displays a *transitional identity*; the parts change, yet the identity of the whole remains. While a machine always consists of the same components, an organism is maintained in a state of continuous flux in which there is a permanent breaking down and replacement of its constituent materials (see Section 3.9). It makes no sense to identify an organism with the sum of its parts as these are only temporary manifestations of the organization of the whole. The parts of a machine, however, remain distinct and identifiable even when they are integrated in the whole. In fact, the machine as a whole only comes into existence *after* all the parts have been properly assembled. In contrast, the organism is an organism from its inception. This points to another important difference between organisms and machines, which is that an organism's physiological functions must take place while growth is in progress, whereas a machine cannot perform its intended function while it is still in the process of construction. The organism even maintains its autonomy when it produces an offspring or when it divides by asexual reproduction. It is difficult to conceive of a machine that could be divided repeatedly and yet be able to retain its identity as a whole.

A final distinctive feature of organisms with respect to machines is their dependence on initial conditions, which we may refer to as their *historical character*. Every organism originates from others of its kind and carries with it the ineluctable marks of the past, not only of its own individual existence (i.e., its *development*), but also of the history of the generations which preceded it (i.e. its *evolution*). Any satisfactory explanation of an organism must not only consider its existing features but also take into account how and why it came to acquire those features. Although a machine also has a history, which refers to the process by which it was assembled from simpler components, the details of its manufacture are not relevant to its operation. Similarly, the history of the machine's invention and subsequent modifications is not important for understanding how the machine actually works. As Richard Lewontin puts it, "My car mechanic does not need to know the history of the internal combustion engine or to possess the plans of the automobile assembly line to know how to fix my car" (1996, p. 1). Thus, whereas the study of how machines work does not require a consideration of their history, it is not possible to come to a full understanding of organisms without considering their developmental and evolutionary histories. I will discuss the grounds for this crucial difference in Sections 3.5, 3.6, and 3.9.

Having outlined the crucial respects in which organisms differ from machines, it is now necessary to consider an important objection that may be raised against the preceding discussion. History has shown that as the progressive development of technology has enabled the engineering of ever more sophisticated machines, the once unbridgeable chasm between machine and organism has become increasingly narrow. Indeed, in the same way that, as we saw in the previous chapter, mechanists confront the challenges of the vitalists by indicating that what were yesterday irreducible vital phenomena today have yielded to mechanistic explanation, so do they maintain that what today appear to be unique features of organisms, tomorrow will be part and parcel of the mechanical operation of machines. Is the ultimate vindication of the MCO simply a matter of inevitable technological progress? What would happen if a machine were to display all the characteristics considered to be ontologically distinctive of organisms? I will devote the remainder of this section to addressing these questions.

The first step in articulating a response to this objection is to point out that not all differences between organisms and machines carry the same ontological weight. Just as there are contingent similarities between organisms and machines (as I indicated at the end of the last section), there are also contingent differences between them. For instance, Anna Deplazes and Markus Huppenbauer (2009, p. 57) note that organisms differ from machines in their composition, given that the former are composed of organic compounds whereas the latter are built from inorganic materials. However, organisms are not defined by their composition, so building a machine entirely from organic compounds would not demonstrate that organisms and machines are ontologically indistinguishable. To take another example, Leonid Gavrilov and Natalia Gavrilova (2001, p. 531) indicate that a key feature of organisms with respect to machines is “the extraordinary degree of miniaturization of their components (the microscopic dimensions of cells, as well as the molecular dimensions of information carriers like DNA and RNA), permitting the creation of a huge redundancy in the number of elements”. Again, although this observation is certainly correct, organisms are not defined by their heterogeneity and redundancy. Building a machine which exhibited the same degree of heterogeneity and redundancy as an organism would not vindicate the MCO. As I indicated at the start of this section, what guarantees the

explanatory power of an analogy is precisely the successful identification and mapping of the *distinctive features* of the compared entities.

I have argued that the most fundamental difference between organisms and machines is that the former are intrinsically purposive whereas the latter are extrinsically purposive. All the subsequent differences between organisms and machines I have discussed can be derived, directly or indirectly, from this one distinction. To this extent, their respective form of purposiveness is what identifies an organism *as* an organism and a machine *as* a machine. This is a matter of definition, and is quite independent of technological advancement. This view is nicely captured in the following passage by the systems biologists Athel Cornish-Bowden, María Luz Cárdenas, Juan-Carlos Letelier, and Jorge Soto-Andrade:

All machines, *at what ever level one defines the word “machine,”* whether a simple tool like an axe, a more complex machine such as an airplane or a computer, or even a complete factory, require external agencies to construct and maintain them [...] In an organism, however, replacement is an internal function, involving no help (before the advent of modern medicine, at least) from an external agency [...] To a considerable degree even the construction of an organism is an internal function: a bacterium makes itself, but no machine does that, and at our present level of understanding we cannot even conceive of how a machine in the future might construct and maintain itself. (Cornish-Bowden et al., 2007, p. 841, my emphasis)

By virtue of their intrinsic purposiveness, organisms are self-organizing, self-producing, self-repairing, and self-regenerating. Still, it is true that machines controlled by negative feedback can display *self-steering*, *self-regulating* and even *self-maintaining* behaviour. A target-seeking torpedo is self-steering, a heater with a thermostat is self-regulating, and an engine which lubricates itself is, to a limited extent, self-maintaining. The physiologist Arturo Rosenblueth and the founder of cybernetics Norbert Wiener, together with the engineer Julian Bigelow, famously argued that such machines are intrinsically purposive. “The term servomechanisms”, they noted, “has been coined precisely to designate machines with intrinsic purposeful behavior” (Rosenblueth et al., 1943, p. 19). Being intrinsically purposive, they claimed that servomechanisms are ontologically indistinguishable from organisms.

Indeed, in a follow-up paper they reached the mechanistic conclusion that “as objects of scientific enquiry, humans do not differ from machines” (Rosenblueth and Wiener, 1950, p. 38).

The problem with this argument is that it rests on the questionable correlation of purposiveness and behaviour. Although the behavioural pattern of a system affords the best evidence of its purposiveness, the purposiveness of a system cannot be explained in terms of observable behaviour alone, much less be defined in terms of inputs and outputs whilst black-boxing the internal organization of the system (Taylor, 1950a; 1950b; Wimsatt, 1970). Yet this is precisely what Rosenblueth and Wiener do, asserting on this basis that “if the notion of [intrinsic] purpose is applicable to living organisms, it is also applicable to non-living entities *when they show the same observable traits of behavior*” (1950, p. 323, my emphasis). They illustrate this claim by indicating that if a servomechanical hound *behaves* like a living hound, then the same kind of purposiveness must be attributed to both the organism and the machine, “if we wish to be consistent” (ibid.). The fact is, however, that although a servomechanism can behave *as if* it was intrinsically purposive, it is not itself an intrinsically purposive system, as it does not act on its own behalf, nor does it serve its own ends. Servomechanisms cannot be regarded as the bearers of purpose, the subjects of action, or the makers of decisions (Jonas, 2001 [1966], pp. 108-127). A servomechanism will always behave exactly the same way if it is fed the same input data, whereas the behaviour of an organism cannot be predicted or computed even if knowledge of all the external conditions was available. Moreover, a servomechanism may be functioning or may be at rest; in either state the machine exists. In contrast, the organism’s continuous operation is a necessary condition for its existence. As Hans Jonas observed, “There is no analogue in the machine to the [organism’s] instinct of self-preservation—only to the latter’s antithesis, the final entropy of death” (ibid., p. 126).

Organisms are autonomous beings. Machines (including servomechanisms) are simply means of furthering the causal autonomy of their users. Organisms have no external controls, whereas “A characteristic of all man-made machines is that they serve as instruments of control. They are manipulated [...] by an operator who uses controlling devices; and their performance is not a random one but the one that the

operator contemplates while he is exercising the control” (Kapp, 1954, p. 93). Machines are controlled so that they operate in the ways desired by their makers and users. We, as makers and users of machines, *determine* the norms of their operation. When machines do not operate in the way *we* expect them to, they are deemed *by us* to be malfunctioning or defective. Organisms, on the other hand, owing to their intrinsic purposiveness operate according to their *own* norms (Canguilhem, 1978 [1966]). In an important respect, what qualifies a system as a machine rather than as an organism is precisely the fact that it operates according to the normative standards imposed by an external agent. Consequently, I maintain that a hypothetical machine that acquired the capacity to act purposively on its own behalf in accordance to its own norms would cease to qualify as a machine. As Deplazes and Huppenbauer rightly indicate, “for [a machine] to be considered alive, it needs to be driven by its *own interest* and not by a human determined program” (2009, p. 58, my emphasis).²⁵

Of course, this is not the only strategy one could pursue. Humberto Maturana, a leading exponent of the second wave of cybernetics, together with his student Francisco Varela, proposed to expand the concept of machine sufficiently to accommodate all that was distinctive about organisms in their influential theory of autopoiesis (Maturana and Varela, 1973). In defining organisms as ‘autopoietic machines’, they employed the term ‘machine’ not in the conventional sense of artifact, but in a way that applied to *any* system whose operation is determined by its relational organization and the way that organization is structurally realized. However, in light of the influence of mechanistic biology, Maturana’s and Varela’s decision to use the word ‘machine’ to describe organisms was rather paradoxical given that the major aim of their theory was to explain the essential ways in which the organization of living systems *differs* from that of (man-made) machines (which they called ‘allopoietic machines’). If only to be consistent, it would seem more reasonable to retain the standard meaning of machine as an extrinsically purposive system, as this is exactly the sense in which the term is used when the MCO is invoked in biology, and simply acknowledge that an organism is different kind of system from a machine.

²⁵ As a fictitious example, consider HAL, the computer onboard the *Discovery* in Stanley Kubrick’s *2001: A Space Odyssey*. During the mission, HAL refuses to comply with the wishes of the astronauts and ultimately kills most of the crew, having identified them as threats to the success of the mission. From the moment that HAL chooses not to conform to the norms imposed by its human users and begins to act on its own behalf in pursuit of its own ends, it can no longer be regarded as a machine. Instead, HAL would need to be conceived as a living system, albeit one created artificially.

The objection anticipated above has now been comprehensively dealt with. The theoretical vindication of the MCO is *not* a matter of technological progress, for if it were ever possible to engineer a truly intrinsically purposive system that exhibited all the distinctive features of organisms, such technological feat would not prove that organisms are indistinguishable from machines, but rather demonstrate the artificial synthesis of a living being. As a matter of principle, there is no reason why the distinction between organisms and machines should *necessarily* coincide with the distinction between naturally produced and artificially created systems.

We may conclude, then, that at a most basic level the inadequacy the MCO stems from the ill-conceived attempt to impose the characteristics of extrinsically purposive systems onto intrinsically purposive ones. A selection of the key differences between organisms and machines discussed in this section, which lay bare the various deficiencies of the MCO, is presented in Figure 4.

	ORGANISMS	MACHINES
<i>Purposiveness</i>	Intrinsic	Extrinsic
<i>Normativity</i>	Internally generated	Externally imposed
<i>Identity</i>	Transitional	Continual
<i>Operation & preservation</i>	Interdependent	Independent
<i>Functional attributions</i>	To parts	To parts and whole
<i>Functional determination</i>	Whole determines parts	Parts determine whole
<i>Properties of parts</i>	Dependent on whole	Independent from whole
<i>Genesis</i>	Self-producing	Created by external agent
<i>Product of</i>	Evolution	Design
<i>Behaviour</i>	Flexible / adaptive	Programmable / predictable
<i>Knowledge of its history</i>	Relevant to its operation	Irrelevant to its operation

Figure 4. The major differences between organisms and machines

The MCO results in a deeply misguided understanding of living systems. Nevertheless, it continues to exert an extremely powerful influence on biological research and explanation. In the next five sections, I will elaborate my general criticisms of the MCO by examining the most deleterious consequences of its uncritical acceptance in contemporary biology.

3.4. Explanatory Consequences of the MCO: Reductionism Vindicated

Undoubtedly, the spectacular success of the MCO is largely due to the fact that in addition to providing a convenient theoretical model of living systems, it also specifies an appropriate means of understanding their operation, namely *explanatory reductionism*. Indeed, one of the distinguishing features of a machine is that it is a composite entity; it is made up of clearly defined parts which interact to produce the behaviour of the whole. Therefore, to explain the workings of a machine, one can proceed by dismantling it into its component parts and then characterizing each of the individual parts in isolation. The component parts may be separated and examined without running the risk of losing information about the operation of the whole because the properties of the parts collectively entail the properties of the whole (Rosen, 1991, pp. 21-22). In this way, the MCO serves to legitimize and actively encourage reductionism in the study and explanation of living systems.

The difficulty of appealing to reductionistic explanations in biology is that, as I indicated in the previous section, the relation between parts and whole in an organism is fundamentally different from that of a machine. In a machine, the parts are both physically independent of, and temporally antecedent to, the whole they constitute. The machine as a whole comes into existence by the assembly of pre-existing parts. Reductionism is successful in the explanation of machines precisely because it involves reversing the process by which machines are constructed. There is thus a perfect symmetry between the manner in which a machine is built and the manner in which it is explained. In the case of the organism, however, no such symmetry exists because the organism does not arise from the assembly of pre-existing parts. The existence of the parts does not precede that of the whole given that the parts only acquire their respective identities as the whole progressively develops from an originally undifferentiated (yet already integrated) system. Furthermore, organismic parts have the properties that they do by virtue of the influence of the whole. Consequently, these cannot be adequately explained independently from the whole. In fact, when a living system is dissected, the parts exhibit different properties and behaviour from the ones they display when they are integrated in the whole. This is why reductionism is inevitably of limited value in the explanation of organisms.

The task of explaining living systems by reductionistic strategies is further aggravated by the fact that there is no single or obvious way to decompose an organism into parts. Because the parts of an organism do not exist prior to the whole they constitute (as is the case in a machine), how an organism is partitioned is entirely dependent on the phenomena one is interested in investigating. In the explanation of organisms, parts are usually identified by isolating how particular substructures causally contribute to the realization of given functions within the organism (see Kauffman, 1970). However, this functional determination of parts is encumbered by the lack of one-to-one correspondence between structure and function. In an organism, a single structure can carry out a variety of different functions, and several structures can carry out one and the same function. Moreover, functional pathways overlap with one another, and as a result any given organismic feature can be structurally delineated in a variety of different ways. For example, bones serve the function of providing rigidity to the body and attachments for muscles. But they are also the sites for the storage of calcium, and the bone marrow is the tissue within which new red blood cells are produced. Therefore, depending on the causal pathway of interest, bones may be conceived as macroscopic architectural elements, as collections of cells that secrete calcium, or as embryonic tissue of the circulatory system (Lewontin, 2000, p. 79). A further problem with the functional determination of parts is that not all the structural components of an organism carry out functions. Many organismic features are instead the epiphenomenal consequences of developmental changes or the functionless vestiges from remote ancestors (see Gould and Lewontin, 1979).

The epistemic decomposition of an organism into parts is thus a complex and subjective exercise. This is patently not the case in a machine. The identification of the parts of a machine is unambiguous because the machine is composed of discrete units of structure and function. Lewontin's remarks are again helpful in bringing the point home: "If wishing to study the operations of a mechanical clock, I open it, I will see a collection of gears, levers, and springs whose status as the parts of the clock are never in doubt. There is no question about where one gear starts and another ends, nor that these immediately perceived separate pieces are the elements whose functional relations need to be specified in any explanation of the operations of the clock as a whole" (Lewontin, 2000, p. 71). Moreover, because the operation of a machine is the direct result of the combined actions of its interacting parts, it is possible to learn

much about how the machine works by removing, altering, or interfering with the operation of each of its parts. Although this analytical explanatory strategy is also commonplace in biology, it does not provide the same reliable results due to the organism's considerable capacity to readjust by reorganizing its parts in order to compensate against external perturbations.

Overall, it is clear that although reductionism provides the perfect means of explaining the workings of machines, it is far less instructive in the explanation of organisms. The widespread appeal to reductionism in suborganismic areas of biology like cell and molecular biology generates stupendous amounts of data about living systems, but it comes at the cost of missing precisely what makes living systems distinctive, namely their systemic, intrinsically purposive self-organization. This organization is for the most part heavily presupposed in the explanations of suborganismic biology. As Lenny Moss observes:

Cell biologists, for example, elaborate on mechanisms of protein sorting, targeting and secretion, cellular polarization, self-assembly, motility, signal reception, transduction and effector activation, and so forth, *within the context of an always already-present, complexly differentiated, functionally organized cell*. Molecular biologists, in turn, *must assume all of the above as background*, for example, in focusing on the very complex processes involved in transcriptional activation and repression, which also involve the functional organization of DNA and chromatin in general, and the presence of numerous complex “purposeful” enzyme systems that modify DNA and histones as well as those that make transcription possible. (Moss, 2002, p. 220, my emphasis)

The hopelessly naïve expectation underlying a great deal of contemporary biomolecular research is that the exhaustive characterization of every single part of a living system, as well as the way in which each part interacts with other parts, will inevitably result in a complete explanation of the system as a whole. This is an evident symptom of the powerful influence that the MCO exerts in the thinking of biologists, given that if organisms *were* machines, this unapologetically reductionistic approach would indeed suffice. However, the inescapable fact of the matter is that the intrinsically purposive self-organization of an organism cannot be accounted for the bottom up by simply referring to the progressive complexity of molecular

interactions, but rather requires a top-down, system-level explanation of the coordinated integration of the organism as a whole. The organicist Paul Weiss fully recognized this problem back in 1963 when he criticized the reductionistic attempts to explain the organization of the cell by appealing to the action of individual molecules. In a memorable passage, he remarked that:

The common habit of personifying compounds by calling them ‘regulators’, ‘integrators’, ‘organizers’, etc., and crediting them verbally with the ‘regulatory, integrative and organizing’ effects which one observes [in the cell] but cannot explain analytically, either intends to endow chemicals with spiritual powers up and above their ordinary properties, or else is wholly meaningless. To state it bluntly, it would be rather a reversion to the prescientific age if on observing, for instance, the spinning of a whirl of fluid, one were to invoke a special compound as ‘spinner’. By reasons of logic and scientific honesty, the problem of *coordinated unity* of the cell must therefore be acknowledged as a real one. (Weiss, 1963, p. 395)

As Weiss’s concerns were voiced at the height of the ‘molecular biology revolution’, they went virtually unnoticed. Nevertheless, as I showed in the previous chapter, a consensus is rapidly emerging among biologists today that explanatory reductionism has reached its limits (e.g., Bock and Goode, 1998; Soto and Sonnenschein, 2006). There is an increasing awareness that organisms cannot be explained from the bottom up because they exhibit system level properties that cannot be predicted, deduced, or calculated from the individual properties of their parts (Kaneko, 2006). The budding field of systems biology appears to be developing as a consequence of this recognition in an effort to address the distinctive features of living systems that escape reductionistic explanations (e.g., Kitano, 2001; Konopka, 2007). Unfortunately, the MCO itself is seldom subjected to critical scrutiny and consequently it still serves as the implicit explanatory model for much of current biological research, including in systems biology. As an example, consider the following passage extracted from the website for the Institute for Systems Biology, one of the largest research centres in the world devoted to this new area of research:

Traditional biology [...] has focused on identifying individual genes, proteins and cells, and studying their specific functions. But that kind of biology can yield relatively limited insights about the human body. As an analogy, if you wanted to study an automobile, and

focused on identifying the engine, seat belts, and tail lights, and studied their specific functions, you would have no real understanding of how an automobile operates. More important, you would have no understanding of how to effectively service the vehicle when something malfunctions. (Institute for Systems Biology, 2010, paragraph 3)

This is patently false. A mechanic is able to effectively service an automobile *precisely because* he can disassemble it into its component parts, inspect each of them in isolation, identify the malfunction, and finally reassemble the automobile back again. It is thus regrettable that the crucial biological point that the authors sought to convey in this passage concerning the irreducible properties of organisms is completely obscured by their ill-conceived decision to illustrate the integrated nature of the human body by comparing it to that of a machine. Clearly, the reliance on explanatory reductionism in biology will not be overcome until biologists realize that the faith they used to place on this epistemological approach directly stems from their uncritical endorsement of the MCO.

In addition to the explanatory consequences I have discussed in this section, the widespread acceptance of the MCO also results in a seriously misleading theoretical understanding of two basic biological processes: development and evolution. Sections 3.5 and 3.6 will examine each of them in turn.

3.5. Theoretical Consequences of the MCO: The Distortion of Development

The first thing to note in considering developmental biology is that the very term ‘development’ is not theory-neutral with respect to the process it designates. Development literally means an unfolding of something that is already present and in some way preformed. What is reflected in the biological usage of this term is the deep commitment to the view that the ontogenesis of an organism is specified and determined by its genetic constitution (Lewontin, 2000, p. 5). Accordingly, modern biology explains the development of an organism as the unconditional unfolding of a sequence of events set in motion by a pre-existing *genetic program*. The notion of genetic program, proposed simultaneously by the molecular biologists François Jacob and Jacques Monod (1961) and the evolutionary biologist Ernst Mayr (1961), “has come to be widely regarded as a fundamental explanatory concept for biological development—if not *the* fundamental concept” (Keller, 2000, p. 74).

The genetic program is the notion that underlies one of the most common modern formulations of the MCO. With the rise of cybernetics and electronic engineering after World War II emerged a new kind of machine, the computer, and with it a new way of conceptualizing organisms. The genetic program, as Jacob indicates, “is a model borrowed from electronic computers. It equates the genetic material of an egg with the magnetic tape of a computer” (Jacob, 1973, p. 9). In Mayr’s words, “the genetic program is the underlying factor of everything organisms do. It plays a decisive role in laying down the structure of an organism, its development, its functions, and its activities” (Mayr, 1997, p. 123). Thus, the organism itself is described as “the realization of a programme prescribed by its heredity” (Jacob, 1973, p. 2). Genetic programs, having evolved through variation and selection, determine the unfolding of development in the same way that the operations of a machine are determined by its computer program. This genetic program is also at the heart of Richard Dawkins’s popular characterization of organisms as “survival machines—robot vehicles blindly programmed to preserve the selfish molecules known as genes” (Dawkins, 2006 [1976], p. xxi).

However, as organisms are fundamentally different from machines, the concept of the genetic program is inevitably misleading. The inadequacy of this notion becomes apparent when we consider the relationship between the program and the system that executes it. In a computer, we can clearly distinguish between the *hardware* (i.e., the material parts of the machine such as circuits, disks, wiring, etc.) and the *software* (i.e., the various programs that can be run on it). The hardware is independent of the software given that the computer machinery must already be assembled before any programs can be run on it. This is not the case in biological development. Here, the output of the program is the organism itself. This means that the software (i.e., the genetic program), is responsible for producing and assembling the hardware (i.e., the organism). Yet throughout this process, it is the organism itself that has to execute the program. In other words, the hardware runs the software, whilst at the same time the software is generating the hardware. This results in a highly paradoxical situation given that the genetic program requires its own output in order for it to be executed. The lack of correspondence between the programmed operation of a computer and the development of an organism stems, unsurprisingly, from the different forms of purposiveness displayed by computers and organisms. As an extrinsically purposive

system, a computer does not generate itself but is rather assembled by an external agent. This is why its hardware is physically independent of, and temporally antecedent to, its software. In contrast, organisms are self-producing and self-organizing, which is why the distinction between software and hardware is far less meaningful in a biological context, if it is meaningful at all.

In addition to being conceptually problematic, the genetic program model of organismic development is not well supported empirically. For one thing, it is difficult to see how genes could be responsible for initiating and directing the development of the organism given that DNA is not an inherently active molecule, but rather requires activation from without. Indeed, without the highly structured cellular environment (which is not itself produced by the DNA), DNA is inert, relatively unstructured, and non-functional. Moreover, the ‘information’ required for making an organism is not actually preformed in the DNA but rather emerges progressively through the dynamic interaction of DNA with proteins, metabolites, and other cellular components as well as with the cellular, extracellular, and extraorganismic environments. These realizations have led to the articulation of a ‘Developmental Systems Theory’ in recent years which rejects the primacy of genes in determining development and emphasizes the contingency, context dependence, and distributed control of the developmental process (Griffiths and Gray, 1994; Griffiths and Knight, 1998; Oyama, 2000; Oyama et al., 2001).

Overall, the concept of a genetic program that directs and controls development implies an attribution of causal agency to genes that they simply do not possess on their own. This has led some authors to describe the belief in a genetic program of development as a form of ‘genetic animism’ (Robert, 2004, p. 39). This genetic animism is bolstered by the prevalent tendency in biology textbooks to describe DNA as ‘self-replicating’ and as being responsible for ‘making’ the proteins that constitute the cell. The reality, however, is that “The idea of a computer program written in the DNA and controlling the sequence of events which characterizes cell growth and differentiation is more a metaphor than a result of a detailed analysis of DNA structures as carriers of a real programming language” (Atlan and Koppel, 1990, p. 335). For earlier generations of molecular biologists, the genetic program offered a means of reconciling the goal-directed nature of development with the mechanistic

commitment to the MCO. The metaphor of the computer program provided an intuitive and well-understood model for a complex and puzzling phenomenon. As Frederik Nijhout remarks, “The only reasons for supposing the existence of a program for development are first, that *we* would have designed such a system that way, and second, that it is discomfoting to deal with the notion that development is largely self-organizing” (Nijhout, 1990, p. 443). Nevertheless, developmental biologists today are being prompted by their own findings to resist the temptation of appealing to models based on our familiarity with machines and instead are beginning to confront the complexity of development on its own terms (Gilbert and Sarkar, 2000).

As well as the concept of the genetic program, the appeal to programming language more generally has led to the claim that an embryo could in principle be *computed* from the complete dataset of a fertilized egg. For example, in 1994 Lewis Wolpert, in reflecting on the advances made in developmental biology over the preceding 20 years, raised the question of the computability of development as one that could be resolved over the following 20 years:

Over the past 20 years, progress in developmental biology has been so dramatic that developmental biologists may be excused for having the view, possibly an illusion, that the basic principles are understood, and that the next 20 years will be devoted to filling in the details. [...] So we can begin to ask questions – like whether the egg is computable. *Will the egg be computable?* That is, *given a total description of the fertilized egg – the total DNA sequence and the location of all proteins and RNA – could one predict how the embryo will develop?* This is a formidable task, for it implies that in computing the embryo, it may be necessary to compute the behavior of all the constituent cells. It may, however, be feasible if a level of complexity of description of cell behavior can be chosen that is adequate to account for development but that does not require each cell’s detailed behavior to be taken into account. (Wolpert, 1994, p. 270, my emphasis)

Despite Wolpert’s optimism, developmental biologists today are no closer to computing the embryo than they were in 1994, and this is largely due to the fact that most of them are not even trying to do so. The question ‘Will the egg be computable?’ is not pursued in contemporary developmental biology; not because it is considered too ambitious or too complex, but simply because it has become apparent that it is the

wrong question to be asking in the first place. The egg does not actually determine the final state of the organism, so it makes little sense to attempt to compute the latter on the basis of the former.

The misguided belief that computability should play a role in the explanation of development stems from the acceptance of the MCO. It is *because* organisms are machines that the question of computability is theoretically meaningful. Alexander Rosenberg makes this explicit in a paper entitled ‘Reductionism Redux: Computing the Embryo’, where he simply assumes from the outset that “the thesis that the embryo is computable from macromolecules alone will not even be controversial among biologists, including anti-reductionist biologists”. The reason is that “A mathematical function is computable if a machine can execute it. The system which builds the embryo out of macromolecules is a machine, albeit one cobbled together by natural selection. Accordingly there is a computable function that this machine implements” (Rosenberg, 1997, pp. 449-450). Thus, the claim that the embryo is computable is not contentious because computability simply implies the possibility of being executed by a machine, and since the embryo is built from a system that is itself a machine, the process of development must *as a matter of principle* be computable. The underlying question of whether organisms *actually are* machines is not even considered. In formulating the computability thesis, the MCO is simply taken for granted.

The fact is, however, that ontogeny is not the gradual unfolding of the organism from a preformed egg, as the very term ‘development’ misleadingly suggests. Rather, it is a highly dynamic and heterogeneous process involving the confluence of numerous intersecting causal factors, some of which are located within the egg itself, while many others arise from the external environment. The failure to recognize the crucial role of the environment in shaping development is yet another consequence of employing the operation of machines to shed light on the development of organisms. In the operation of a machine, the environment plays only the role of providing the necessary conditions that allow the machine to function in its ‘normal’ way. A watch, for instance, works in a programmed and inflexible way, irrespective of the state of the outside world. The development of the organism, on the other hand, is highly sensitive to external conditions, which is why similar organisms in different

environments tend to develop differently. Indeed, it is not always appreciated that the relation between the organism's genotype and the organism's phenotype is mediated by the environment. The genotype does not actually specify a unique outcome of development but rather stipulates a *norm of reaction*, that is, a pattern of different developmental outcomes across different environments (see, e.g., Lewontin, 2000, pp. 17-30). As a result, development needs to be conceived theoretically as a constant process of interaction between the internal structure of the organism and the external milieu in which it operates.

Overall, it is evident that the MCO has much to answer for in developmental biology. It is responsible for legitimating a fundamentally flawed model of development, the genetic program, which severely overemphasizes the causal role of genes at the expense of almost completely neglecting every other pertinent developmental factor. The appeal to the MCO also underlies the talk of 'programming' and 'computing', terms borrowed from the realm of machines that have no place in the explanation of development. By making explicit the rejection of the MCO, developmental biology becomes liberated from a number of misleading conceptions which serve only to promote a heavily distorted understanding of what development is and how it takes place.

3.6. Theoretical Consequences of the MCO: The Distortion of Evolution

The pervasiveness of the MCO also has far reaching implications for the conceptualization of evolution. In fact, the MCO has permeated Neo-Darwinian evolutionary thinking to such an extent that some of the most prominent disputes within modern evolutionary biology have tacitly centred upon the coherence, legitimacy, and applicability of the MCO. This is all the more extraordinary in light of the fact that the original Cartesian formulation of the MCO is theoretically incompatible with an evolutionary understanding of organisms. Whereas the former is grounded in Christian theology, the latter is deeply committed to a naturalistic metaphysics. To understand the Cartesian *bête-machine*, it is necessary to conceive it as being preceded, logically and chronologically, by God. In this sense, Descartes' MCO leads naturally to the Argument from Design. As organisms are like machines, one can infer that just as the functional organization of the latter is the product of

design, the functional organization of the former must also be the result of design. And since the design of organisms infinitely surpasses that of machines, the intellect and ingenuity of the designer must be inconceivably greater than that of man. In this way, the MCO provided a firm ‘scientific’ foundation for the existence of God, and many natural philosophers and theologians (especially in Britain) used it to this end during the eighteenth and nineteenth centuries.

The most famous example of the theological recourse to the MCO is William Paley’s *Natural Theology*, published in 1802. In this work, Paley compared the intricate contrivances of machines like the watch to the exquisite adaptations of organisms, and argued for the existence of a divine Creator on the basis of the apparent design of the latter. It is well known that Charles Darwin read Paley’s *Natural Theology* as a young man and was instilled with a sense of the perfect adaptation of structure to function in organisms. Indeed, in the 1830s it became one of the major objectives of his work to account for such wondrous functional adaptation (Ospovat, 1981). With his theory of evolution by natural selection, Darwin considered that he had provided an alternative, naturalistic explanation of the functional organization of organisms. As he would later remark in his autobiography, “The old argument of design in nature, as given by Paley, which formerly seemed to me so conclusive, fails, now that the law of natural selection has been discovered” (Darwin, 1908, p. 154). Darwin’s theory appeared to present a lethal blow to the MCO. Adaptations, the very features of organisms that seemed to cry out for an explanation in terms of design, could be accounted for by appealing to the operation of natural processes like natural selection.

However, what is remarkable (and more than a little surprising) is that Darwin did not in fact succeed in expunging the MCO from biological theory. Instead, what happened was that evolutionary biology *itself* adapted to accommodate the MCO. Ever since Darwin, machine-language, despite its obvious Creationist connotations, has continued to pervade the biological discourse in general and the evolutionary discourse in particular. In fact, modern evolutionists do not even hesitate to invoke Paley’s theological work on adaptation as a model for evolutionary biology. John Maynard Smith (1969, p. 82), for instance, asserts that “The main task of any theory of evolution is to explain adaptive complexity, i.e., to explain the same set of facts which Paley used as evidence of a Creator”. Similarly, George Williams (1992, p.

190) considers that Paley's *Natural Theology* is "worth close attention by all biologists" because it offers advice on how to identify the products of selection. For this reason, Richard Dawkins (1998, p. 16) is quite willing to admit that modern evolutionists "might be labelled neo-Paleyists, or perhaps 'transformed Paleyists'". Implicit in this methodological association with natural theology is the view that in a post-Darwinian biology, organisms, whilst being the products of selection rather than creation, are still optimally designed machines in the exact same sense that Paley, and Descartes for that matter, conceived them. Dawkins is all too happy to confirm this: "we animals are the most complicated and *perfectly-designed pieces of machinery* in the known universe" (Dawkins, 2006, p. xxii, my emphasis).

The problem with this mechanistic understanding of organisms and the language used to describe it is that it is completely inappropriate in evolutionary biology. The pervasive use of the term *design* is a case in point. Design may be defined as the deliberate production of an object by an external agent so that it accomplishes a desired function (Bunge, 2003). It is therefore a notion which serves to characterize extrinsically purposive objects like machines since the design reflects the intentions of the external agent that are realized by the produced object.²⁶ However, as organisms are self-producing, intrinsically purposive systems, the concept of design is not suitable to characterize their functional organization, given that this functional organization does not reflect the intentions of an external agent. The mechanistic fallacy that the structure and behaviour of organisms is explicable in terms of extrinsic purposiveness leads to the view that organisms have been literally designed to function in a preordained way. This view is deeply problematic. For one thing, an organism cannot be designed for a function because it does not itself *have* a function; only its parts do. But even if the notion of design is restricted to the parts of an organism, it is still wholly inappropriate because the attribution of a function to a part of an organism does *not* entail design for that function, as indicated in Section 3.3. Functional adjudications need not be grounded on mechanistic notions of design, intention, or extrinsic purpose.

²⁶ Even those fully committed to the evolutionary use of 'design' acknowledge this point. For instance, Michael Ruse, in his book *Darwin and Design*, notes in relation to the design of a knife that "The knife itself hardly has the end of cutting. *We* have the end of cutting, and so we *design* and make the knife [to that end]" (Ruse, 2003, p. 276, my emphasis).

Unfortunately, this is seldom recognized in the philosophical literature on function and teleology. Tim Lewens, for instance, has recently written an entire book on the role of the MCO in evolutionary biology entitled *Organisms and Artifacts* (2004), but at no point does he even consider the possibility that purposiveness (or teleology) may be intrinsic as well as extrinsic. Consequently, he simply assumes that functional language is of the same kind when it is applied to machines as when it is applied to (the parts of) organisms. Thus, he incorrectly asserts that: “when organisms were considered to be artefacts made by God, function language had the same meaning regardless of whether one was talking about the function of a fork or a frog’s leg. It is widely agreed that evolutionary biologists today use function language in a strikingly similar way to how it was used by the natural theologians” (Lewens, 2000, p. 99; 2004, p. 13). This erroneous belief has led philosophers to derive function from design (e.g., Millikan, 1984; Neander, 1991; Kitcher, 1993; Krohs, 2009) or to derive design from function (e.g., Lauder, 1982; Allen and Bekoff, 1995; Buller, 2002), not realizing in either case that the adjudication of functions in organisms and in machines has a different basis.

Despite being a concept that belongs to the realm of machines, the term ‘design’ is quite liberally used in contemporary discussions of evolution, to the extent that the outcome of the evolutionary process itself is often characterized as ‘design without a designer’ (e.g., Kitcher, 1993; Ayala, 2004). This is misleading because the notion of design does not capture how Darwinian evolution explains the functional organization of organisms. The adaptations produced by evolution are not the result of an intentional preconceived plan, but are rather the result of the differential survival and reproduction of organisms with heritable adaptive variations. Thus, it is far more appropriate to assert that organisms are fashioned or shaped by selection pressures than to invoke design as an explanatory concept in evolution. Moreover, the very idea of ‘design without a designer’ is not only deceptive, but it is also logically contradictory; *designed* literally means made by a designer. As Mohan Matthen (1997, p. 32, fn. 14) rightly complains, “This does not make sense to me: ‘design without a designer’ is still an unintuitive notion as far as I am concerned, and [...] it goes against some influential ideas in evolutionary biology”.

The reason why the notion of design pervades evolutionary biology is that it is used uncritically, typically as shorthand for functional organization (e.g., Ayala, 2004, p. 58). But in inferring design from functional organization, modern evolutionists inadvertently appeal to the first part of the Argument from Design. As noted above, this first argues inductively for design on the basis of functional organization, and then argues deductively for a designer on the basis of design. The fatal flaw of this theological argument, as David Hume showed in his *Dialogues Concerning Natural Religion* (1779), lies not in its deductive part (i.e., design → designer) but in its inductive one (i.e., functional organization → design), which itself derives, as does the MCO, from our familiarity with machines. But even though Hume showed that functional organization is not necessarily evidence of design, he was not able to provide a causal explanation for its origin and occurrence in organisms. This was precisely Darwin's accomplishment. Peter McLaughlin (2001, p. 152) makes this point well: "What Darwin has enabled us to do (that Hume could not) is not to 'think of design without a designer', but rather to think of eyes as being for seeing without presupposing that they are designed for seeing. We do not think of a plan (design) without a planner but of adaptation without intent (design)".

Nevertheless, there is still an alternative left for ardent evolutionists unwilling to let go of the concept of design, which is to bite the bullet and accept both inductive *and* deductive parts of the Argument from Design, and simply replace God with natural selection as the designer. Evolution is thus not 'design without a designer' but 'design *with* a designer'. According to this rather extreme interpretation of Darwinism (described by Niles Eldredge (1995) as 'ultra-Darwinism'), the design of organisms is the work not of a divine watchmaker but of a *blind watchmaker* (Dawkins, 1986; see also Dennett, 1995). However, this move does not really help matters because evolution simply does not proceed like a watchmaker, blind or otherwise. It is worth bearing in mind that Darwin, having read Paley, was fully aware of the watchmaker analogy and yet he chose not to resort to it in the *Origin of Species* (1859). Rather, the analogy Darwin adopted to illustrate his theory of evolution was that of *selection*, as used by pigeon breeders. Darwin's choice of analogy is extremely significant because breeders and watchmakers proceed in fundamentally different ways. The watchmaker manipulates the internal parts of a watch, its gears and springs, in order to affect the properties of the watch. The breeder, on the other hand, manipulates the selective

pressure on a population of pigeons in order to affect the beaks and wings of successive generations of pigeons. Selection (both natural and artificial) is a process by which parts of a whole are preserved, changed, or created as the long-term consequences of manipulations carried out not on the parts themselves but on the wholes to which they belong. Thus, whereas the designer (such as a watchmaker) manipulates parts to affect the properties of wholes, nature (like a breeder) manipulates wholes to affect the properties of their parts (see McLaughlin, 2001, p. 153-161). It is therefore selection rather than design that provides the appropriate analogy to understand Darwinian evolution, which is why Darwin called the causal principle of his theory ‘*natural selection*’ and not the ‘*blind watchmaker*’.

In spite of its inherent inadequacy, the ultra-Darwinian conception of evolution as the work of a blind watchmaker has exerted considerable influence on modern evolutionary biology. In fact, it lies at the heart of the excesses of the ‘adaptationist program’ that Stephen Jay Gould and Richard Lewontin famously criticized in their paper ‘The Spandrels of San Marco and the Panglossian Paradigm’ (1979).²⁷ The adaptationist is committed to the view that organisms, like watches, can be effectively decomposed into discrete and mutually independent traits, and that each of these traits is an adaptation, optimally-designed for its function by natural selection. The problem with adaptationism is that, as indicated in Section 3.4, there is no single way of decomposing an organism into parts. So although some organs like the eye display a degree of functional modularity comparable to the components of a watch, many other organismic structures cannot be demarcated in such a manner because they contribute to the realization of a variety of different functions within the organism. The parts of an organism contribute to its fitness in so many different ways that it makes little sense to attempt to calculate their individual fitness values, as they have not been shaped independently by selection. The adaptationist assumes that nature selects parts of organisms for their functions in the same way that a watchmaker selects parts of watches for their functions. However, nature does not select parts at all. Rather, it selects organisms with parts that functionally contribute (in many different ways) to enhancing the fitness of the organism as a whole.

²⁷ Peter Godfrey-Smith (1999, p. 190) also notes the association between the ultra-Darwinian appropriation of the concept of design and the adaptationist program, and accordingly characterizes the latter as “the *tradition of natural theology continued*”.

Another major problem with adaptationism is that it assumes that the adaptations produced by natural selection are as optimal as they can be given the trade-offs that need to be reached among conflicting functional demands as well as the inevitable architectural constraints of organismic form. This belief in optimal adaptation is another consequence of the conception of natural selection as a watchmaker, given that no watchmaker would deliberately design a watch to display suboptimal components or features. Instead, the watchmaker carefully chooses the gears, springs and levers to ensure that the watch is as functionally effective as possible. In the same way, the adaptationist considers that each part of an organism has been optimally evolved by natural selection to contribute to the best possible design of the organism as a whole. However, this view drastically overestimates the power of natural selection. Natural selection does not produce perfectly optimized adaptations, as Darwin himself recognized: “Natural selection tends only to make every organic being as perfect as, or slightly more perfect than, the other inhabitants in the same country with which it has to struggle for existence. And we see that this is the degree of perfection attained under nature” (Darwin, 1859, p. 201).

The adaptationists’ endorsement of the ‘design with a designer’ view of evolution is also exemplified by their contention that natural selection is like an engineer that devises effective ‘solutions’ to the adaptive ‘problems’ presented by the environment. Accordingly, adaptationists study the adaptations of organisms by means of two epistemic strategies: ‘reverse engineering’ and ‘adaptive thinking’. Reverse engineering seeks to infer the problems posed by an organism’s environment from the study of observed organismic traits. Adaptive thinking reverses the direction of inference and seeks to draw on known adaptive problems faced by an organism to predict likely solutions that will have emerged to meet those problems (see Dennett, 1995, pp. 187-262; Griffiths, 1996; Lewens, 2002). The difficulty with the problem-solving interpretation of natural selection is that problem-solving in general is an inherently prospective process. It requires identifying a desired state in advance and then specifying and following a route from the current state to the desired state. However, natural selection does not proceed prospectively towards the attainment of particular ends. The various traits of an organism have not evolved *in order* to be able to solve adaptive problems posed by the environment. Rather, they are able to solve adaptive problems posed by the environment *because* they have evolved. For

example, the wings of a bird are not the solution devised by natural selection to deal with the problem of flight, since half a wing provides no lift at all given the nonlinearity of aerodynamic relations. Rather, wings were initially selected for their ability to carry out other functions (e.g., terrestrial locomotion, predatory action, heat regulation, etc.) and only as they grew larger were they incidentally found to also enable flight, thereby becoming subsequently selected for this purpose. As Lewontin (1996, p. 8) eloquently puts it, “If wings are a solution to the problem of flight, they are an example of a problem being created by its own solution”.

The recruitment of already existing structures for novel functions is a common occurrence in evolution (see Gould and Vrba, 1982), and it runs counter to the conception of natural selection as an engineer. Evolutionary change is constrained by the past history of organisms, given that novelty can only arise on the basis of modifying what already exists. In contrast, the engineer designs machines *de novo* out of especially prepared components. This difference was pointed out by François Jacob in a well-known paper entitled ‘Evolution and Tinkering’, in which he remarked that:

[N]atural selection does not work as an engineer works. It works like a tinkerer—a tinkerer who does not know exactly what he is going to produce but uses whatever he finds around him whether it be pieces of string, fragments of wood, or old cardboards; in short it works like a tinkerer who uses everything at his disposal to produce some kind of workable object. For the engineer, the realization of his task depends on his having the raw materials and the tools that exactly fit his project. The tinkerer, in contrast, always manages with odds and ends. What he ultimately produces is generally related to no special project, and it results from a series of contingent events. (Jacob, 1977, pp. 1163-1164)

Jacob’s analogy between evolution and tinkering is instructive because it helps illustrate some of the major problems of the designer/engineer conception of natural selection I have discussed. For example, whereas the engineer works prospectively according to a preconceived plan, the tinkerer cannot know in advance what precisely he is going to come up with. Moreover, whereas the engineer builds machines by bringing together individually specified components, the tinkerer has to make do with whatever components happen to come his way. Finally, whereas the engineer

produces objects as perfect and efficient as his technological resources and understanding permit, the works of the tinkerer are typically far from perfection. Evolution is indeed much more like tinkering than engineering.

On the whole, in light of the numerous and seemingly irremediable problems of appealing to the concept of design in explanations of evolution, it is rather surprising that it continues to permeate modern evolutionary biology. J. G. Ollason (1987, p. 243) evocatively expressed this frustration when he stated that “the idea that animals are designed is dead, killed by Hume, buried, perhaps unwittingly by Darwin, but however comprehensively it is disposed of, like the walking dead, it haunts us still”. It is indubitable that one of the major reasons why the notion of design still haunts evolution is that, despite its disturbing theological connotations, it is firmly grounded in the most influential and widely accepted theory of organisms, namely the MCO of mechanistic biology. Thus, it is only by making explicit the rejection of the MCO that evolutionary biology can finally lay the ghost of natural theology to rest and fully come to terms with the actual implications of Darwin’s theory for our understanding of the nature of organisms.

3.7. Epistemic Consequences of the MCO: Engineering as Biology

The most important epistemic consequence of the MCO is that if organisms are indeed machines, then biology and engineering cannot be regarded as clearly distinct disciplines; the boundary between them becomes completely blurred. In fact, ever since the establishment of mechanistic biology, the transfer of theoretical, conceptual, and explanatory resources between biology and engineering has been extremely fluid. As a result, biology has come to be regarded as the branch of engineering devoted to the study of ‘living machines’ (e.g., Dennett, 1995, pp. 187-228). This conceptualization of biology as engineering has been bolstered, as we have seen in previous sections, by the steady import of epistemic tools from engineering into biology, such as the adoption of programming language in developmental explanations and the use of reverse engineering in the study of adaptation. However, what is not always appreciated is that the MCO has also resulted in the inverse epistemic conceptualization of *engineering as biology*. The implication of this view is that engineering, concerned as it is with the design and construction of machines, is

itself conceived as a way of doing biology, having a legitimate, indeed fundamental, role to play in the mechanistic explanation of organisms. This section will uncover the philosophical grounds underlying this biological conceptualization of engineering, and expose its inherent limitations.

The disciplinary juxtaposition of engineering and biology has its basis in Descartes' move to collapse the distinction between the science of natural bodies (i.e., physics, including biology) and the science of machines (i.e., mechanics). Because natural bodies (both living and nonliving) are ontologically equivalent to artificial bodies, mechanics, while being a subset of physics, is nevertheless epistemically indistinguishable from physics, as both deal with the same kind of object, both are subject to the same laws, and both formulate the same kinds of explanations. In his *Principia*, Descartes writes:

[M]echanics is a division or special case of physics, and all the explanations belonging to the former also belong to the latter; so it is no less natural for a clock constructed with this or that set of wheels to tell the time than it is for a tree which grew from this or that seed to produce the appropriate fruit. Men who are experienced in dealing with machinery can take a particular machine whose function they know and, by looking at some of its parts, easily form a conjecture about the design of the other parts, which they cannot see. In the same way I have attempted to consider the observable effects and parts of natural bodies and track down the imperceptible causes and particles which produce them. (Descartes, 1985, pp. 288-289)

With Descartes, all natural bodies receive a mechanistic treatment; everything physical is explained as if it was mechanical. The physicist, and by implication the biologist, can look at nature through the eyes of the mechanic or engineer ('men who are experienced in dealing with machinery'). In this way, in *l'homme* Descartes comes to terms with the biology of the human body by describing in detail the various mechanisms underlying the operation of a perfectly-designed imaginary automaton. In an important respect, *l'homme* is a technological treatise, doing as much for engineering as for biology. In it, Descartes deploys an astounding array of mechanical devices (rods, tubes, valves, pulleys, levers, sieves, counterweights, wheels), machines (fountains, organs, self-moving statues, clocks, mills), and sources of power

(water, air, weights, pressures) to develop the machine model of the body. In writing *l'homme*, Descartes availed himself of the best engineering works of his time and he put them at the service of his biology. Between 1614 and 1615, Descartes visited the Royal Château of Saint-Germain-en-Laye, just outside Paris, and he was greatly impressed by the ability of the water-powered fountains in the gardens to animate a variety of automata, including self-playing organs and self-moving statues. Accordingly, in *l'homme* he appealed to these hydraulic machines to illustrate the anatomical features of the human body and to explain the various physiological processes occurring within it:

you may have observed in the grottoes and fountains in the royal gardens that the force that drives the water from its source is all that is needed to move various machines, and even to make them play certain instruments or pronounce certain words, depending on the particular arrangements of the pipes through which the water is conducted. And the nerves of the machine that I am describing can indeed be compared to the pipes in the mechanical parts of these fountains, its muscles and tendons to various other engines and springs which serve to work these mechanical parts, its animal spirits to the water that drives them, the heart with the source of the water, and the brain's cavities with the apertures. (Descartes, 1998, p. 107)

Here lies one of the most remarkable aspects of Descartes' formulation of the MCO. What Descartes *observed* at the Royal Château of Saint-Germain-en-Laye was simply that automata, under appropriate conditions, can sometimes appear life-like. However, what he *concluded* was rather that *life itself was automaton-like*. Thus, the automata built in the image of organisms became the very models used by Descartes to explain the organisms they had been designed to imitate. This epistemic move completely transformed the understanding of the relation between engineering and biology. Before Descartes, automata had been regarded primarily as spectacles, built to demonstrate technological virtuosity and designed for the sole purpose of amusing and entertaining. After Descartes, automata also acquired a degree of scientific respectability, as they came to represent serious mechanistic experiments intended to determine the extent to which organismic features could be recreated in machines. In this way, Descartes laid the foundations for the research programme we now call *Artificial Life* (A-Life, hereafter), which denotes the self-consciously biological

branch of engineering that seeks to understand the phenomenon of life (or certain aspects of it) by reproducing it in machines. Although modern A-Life only really arose with the work of Christopher Langton in the 1980s, the discipline itself has a much longer history which runs parallel to that of mechanicism. Historically, attempts to create 'living machines' constituted a practical means of validating the ontological commitments of mechanistic biology (cf. Price, 1964).

The most prominent figure of old A-Life was the eighteenth-century engineer Jacques de Vaucanson, who Langton (1989, pp. 8-9) heralds as one of the forefathers of the modern version of the discipline. For Vaucanson, the conventional means of generating biological knowledge, based on observation and experimentation, needed to be supplemented by visual demonstrations of mechanical models and simulations. Accordingly, in 1738 and 1739 he presented before the Académie des Sciences in Paris three life-like automata of his own design, 'The Flute Player', 'The Tambourine Player', and 'The Digesting Duck', all of which had been built with the explicit intention of furthering the understanding of human and animal biology (Wood, 2002; Landes, 2007). Out of the three, the Duck was the most impressive, as it appeared to have the remarkable ability to eat kernels of grain, and to metabolize and excrete them. This stunning creation enabled Vaucanson, an engineer by training, to enter into academic debates with physiologists over the nature of digestion, and ultimately helped him secure an appointment at the Académie des Sciences as 'associated mechanician' in 1757 (Riskin, 2003, p. 601). However, shortly after Vaucanson's death in 1782, a close observer of the Duck's swallowing mechanism reasoned that digesting the grain would take far longer than the brief pause the Duck took between swallowing and defecating, and thereby concluded that the grain input and excrement output were entirely unrelated, and that the tail end of the Duck must have been loaded before each act with fake excrement. In this way, "The Duck that pioneered physiological simulation was, at its core, fraudulent" (ibid., p. 607). The epistemic lesson to draw from this historical episode is that the fact that a machine can be made to externally resemble an organism in its input and output functions does not provide a legitimate basis for concluding that the machine itself is analogous in nature to the organism it represents.

Unfortunately, this problematic behaviourist assumption lies at the heart of modern A-Life. As Langton (1989, p. 1) puts it in the opening sentence of his A-Life manifesto, “Artificial Life is the study of man-made systems that exhibit behaviors characteristic of natural living systems”, and again a few pages later, “Artificial Life is concerned with generating *lifelike* behaviors. Thus, it focuses on the problem of creating *behavior generators*” (ibid., p. 5). A-Life is interested in behaviour itself, not in the physiological processes that give rise to it. However, the ability to faithfully reproduce in a machine a particular pattern of organismic behaviour does not amount to an understanding of how it comes about, as Vaucanson’s Duck dramatically illustrates. This is because the same behavioural output may be brought about by different kinds of means. The rationale of A-Life consequently suffers from the same problem faced by the cyberneticists who, as we saw in Section 3.3, claimed that servomechanisms and organisms are indistinguishable as objects of scientific inquiry since both display intrinsically purposive *behaviour*. This similarity is not coincidental, as contemporary A-Life draws heavily on the ideas of cybernetics (see Riskin, 2007, pp. 10-12). Like cybernetics, “The field of Artificial Life is unabashedly mechanistic and reductionist” (Langton, 1989, p. 6). It is *mechanistic* because the claim that machines that exhibit life-like behaviours can be used to generate biological knowledge about those behaviours presupposes a direct ontological correspondence between machines (the model systems) and organisms (the systems modelled). Langton’s own mechanistic commitment to the MCO is unequivocal, asserting in his A-Life manifesto that “living systems are nothing more than complex biochemical machines” (ibid., p. 5). A-Life is also *reductionistic* because it reduces living organisms to their outward manifestations, deeming what is characteristic about the living state to be a matter of purely external behaviours.

In addition to the centuries-old project of building machines that display life-like behaviours, modern A-Life is also engaged in the somewhat different project of producing life-like behaviour *within* machines, that is, in the virtual world of computers. The roots of this approach to A-Life lie in the work of the cyberneticist John von Neumann, who in the 1940s developed a mathematical theory of discrete symbolic systems called *cellular automata* as a means of exploring the ‘logic’ and computability of self-reproduction as displayed by real living systems. Today, this form of A-Life has broadened to include the computational simulation of many other

biological processes and behaviours apart from self-reproduction, such as animal communication, predator-prey interactions, insect colony dynamics, and speciation. Now it is evident that these simulations can be of great value in helping biologists model the phenomena they study, but there is a real epistemic danger in assuming, as many A-Life researchers do, that high-quality simulations of life actually constitute realizations of life. For example, Thomas Ray (1992, p. 372) argues that the ‘digital organisms’ inhabiting virtual platforms such as the *Tierra* simulator are literally alive, given that they are “self-replicating, and capable of open-ended evolution”. However, this claim is based on the conflation of the concepts of simulation and realization, which, as H. H. Pattee (1989) indicates, are categorically different. Although both constitute models of a system, simulations are symbolic representations, whereas realizations are material implementations. Therefore, despite being heuristically useful for biological research, digital simulations of life cannot be considered to be part of the subject matter of biology because they are not actual *instantiations* of life. Elliott Sober makes this point in the following way:

It is sometimes suggested that, when a computer simulation is detailed enough, it then becomes plausible to say that the computer is an instance of the objects and processes that it simulates. A computer simulation of a bridge can be treated as a bridge, when there are simulated people on it and a simulated river flowing underneath. [...] I regard this suggestion as mistaken. The problem with computer simulations is not that they are simplified representations, but that they are representations. Even a complete description of a bridge, one faithful in every detail, would still be a very different object from a real bridge. (Sober, 1992, p. 764)

Some A-Life researchers respond to this objection by arguing that the logical form of an organism can be extrapolated from its material constitution because the property of being alive has a purely formal basis and is completely independent from the materials which realize it (Langton, 1989). This is a fair point, as it is indeed the case that matter by itself does not make organisms what they are. Nevertheless, this argument does not alleviate the underlying worry of whether it really is possible to completely abstract life from its material constitution. Von Neumann’s reservations regarding his own formalization of the problem of self-reproduction are quite revealing in this respect. He believed that by abstracting the problem in this way, “one

has thrown half of the problem out of the window, and it may be the more important half". Von Neumann recognized that the price to be paid for formalization is that "One does not ask the most intriguing, exciting, and important questions of why the molecules or aggregates which in nature really occur in these parts are the sorts of things that they are" (von Neumann, 1966, p. 77). In a similar respect, the idea defended by modern virtual A-life researchers that the life of an organism can be separated from its embodiment in the organism, or that an organism's ability to reproduce and evolve can be understood in total abstraction from the organism's material constitution, would almost certainly strike most practicing biologists as deeply counterintuitive. Biologists do not deal with life in the abstract, but with living organisms; it is impossible to study the former without the latter.

In the last analysis, however, the status of virtual forms of A-Life must be evaluated in terms of the epistemic service they provide to biology. And so we may ask: Has a focus on virtual A-Life resulted in new biological knowledge about organisms in general? Has it enabled the discovery of new biological regularities? The fact is that virtual forms of life are so essentially different from natural forms of life that it is not at all clear how knowledge of the former could be of any actual use in advancing the understanding of the latter. Instead, it seems more reasonable to conclude that the actual epistemic value of virtual simulations of life lies in that they serve as heuristic tools in the study of real living organisms. In other words, virtual simulations of life do not by themselves *generate* knowledge about life, although their employment in biological research does *facilitate* it.

Overall, it is clear that A-Life does not really constitute a way of doing biology at all. Of course, this does not mean that A-Life is not a legitimate or useful undertaking; quite the contrary. The biologically-inspired construction of machines capable of exhibiting life-like behaviours can enable the performance of novel tasks in new mechanical contexts. And the development of computer simulations of life (or of living processes) can greatly enhance the investigation of real life. However, A-Life cannot be said to constitute a branch of *biology*. At most, it is a form of biological technology. Organisms and machines are fundamentally different, and consequently the epistemic relation between biology and engineering, though dynamic and permeable, can never be truly symmetrical. The conviction that biologists can learn

about organisms by studying machines, or that the pursuit of engineering by itself can constitute a way of doing biology, has its roots in the physiological writings of Descartes, and is deeply misguided. The fact that it is still seriously contemplated reflects the remarkable endurance of the MCO.

3.8. Ethical Consequences of the MCO: Organisms to Use (and Abuse)

It is important to bear in mind that the MCO has consequences that go well beyond biological science itself and which impinge upon a number of broader philosophical issues. Perhaps the most salient of these is the moral status of nonhuman life. In the ethical debate over the use of organisms, especially animals, in scientific research, the MCO has historically provided a convenient foundation upon which to anchor arguments in favour of vivisection, and animal experimentation more generally (Monamy, 2009). I will not enter into this ethical debate here, as it is beyond the scope of this chapter. Instead, what this section will attempt to do is uncover the nature of the relation between the MCO and the ethical arguments in favour of the unmitigated use of nonhuman organisms that are advanced on its behalf.

I argued in Section 3.3 that the single most important difference between organisms and machines lies in their different forms of purposiveness. It is by virtue of its intrinsic purposiveness that an organism acts on its own behalf and towards its own ends. The internal physiological processes occurring within the organism are functional inasmuch as they contribute to the maintenance of the organism as a whole. In contrast, being extrinsically purposive systems, machines are designed, built, and maintained by external agents. Although the internal processes occurring within a machine also contribute to the operation of the machine as a whole, the machine's operation does not serve its own ends but those of its users. It is the users who impose the normative standards according to which the functioning of the machine is evaluated because they are the ones who benefit from its operation. It is in the interests of the users that the machine functions in the specified way. The machine itself has no benefits or interests of its own. An organism, on the other hand, functions according to its own normative standards because it is the beneficiary of its own operation. Thus, an organism, unlike a machine, has benefits and interests of its own.

Now it may be argued that winding a watch is beneficial for the watch, but in reality it is only beneficial for the watch inasmuch as it is beneficial for its user. It is the user, not the watch, who benefits from the winding of the watch. A watch that is left unwound can continue to exist indefinitely. By comparison, the operation of an organism benefits the organism itself because it is only by means of its operation that the organism is able to maintain its existence (cf. McLaughlin, 2001, pp. 191-204).

So it is by virtue of their intrinsic purposiveness that organisms, but not machines, are the *subjects of benefit*. Being subjects of benefit means that organisms are also *subjects of harm*. For example, depriving an organism from food harms it because it conflicts with its interest of maintaining its own organization. In contrast, a machine cannot be the subject of harm. Interfering with the mechanism of a watch so that it is no longer able to keep good time does not harm the watch, but rather the user who benefits from the watch's ability to keep good time. Unlike a machine, an organism has a *wellbeing*. Serving the interests of an organism enhances its wellbeing, whereas opposing the interests of an organism jeopardizes its wellbeing. These are the capacities that make organisms, as opposed to machines, the subjects of moral consideration. Thus, *in principle*, not just humans and other mammals, but also sharks, oak trees, and cyanobacteria can be conferred a moral status, as they all have intrinsic interests that contribute to their wellbeing.²⁸ In practice, however, moral philosophers disagree over which organisms should be granted greater moral consideration. Some argue that organisms that experience pain in the way that humans do deserve the greatest moral consideration, whereas others regard consciousness and self-awareness as the attributes that merit the most moral consideration. Still, these disputes need not concern us here, as what most moral philosophers would surely agree on is that having a wellbeing of one's own that is served by one's interests, and being the subject of benefit and harm, are the absolute minimal conditions for granting an individual a moral status *of any kind*. Thus, although it is not entirely clear which organisms deserve the greatest moral consideration, what is *absolutely* clear is that no machine can be the subject of any moral considerations whatsoever.

²⁸ Even a hypothetical artificially-created intrinsically purposive system would have a wellbeing of its own and would be the subject of benefit and harm. Consequently, it would also in principle be eligible to a moral consideration of some sort.

This has fundamental implications for the appeal to the MCO in biological research. If organisms are conceived as machines, then it is no longer necessary to consider their welfare or even whether they have a moral status at all. Having been stripped of their intrinsic purposiveness, organisms are deemed to have no real interests of their own and can therefore be appropriated by their human users to serve their own ends. This was already recognized by Gottfried Leibniz in the seventeenth century in relation to animals: “if we are compelled to view the animal as being more than a machine, we would have to [...] renounce our domination of animals” (Leibniz, quoted in Canguilhem, 1992, p. 52). Today, the MCO motivates and morally legitimates the instrumental use of organisms, which have come to be regarded as one more kind of *experimental material* at the disposal of the biologist (see Knorr-Cetina, 1999, pp. 138-158). In molecular biology, for instance, organisms are conceived as technological systems of production; they are standardized, mass-produced, and genetically manipulated to serve the biologist’s own ends. Parts are routinely detached from organisms (e.g., plasmids from bacteria, antibodies from rabbits, muscle tissue from mice, etc.) just as they are detached from machines, and are subsequently reinserted into different organismic hosts to resume the work of production. As Robert Rosen (1991, p. 21) remarks: “Genetic engineers, who are the molecular biologists turned technologies, habitually regard their favourite organism, *E. coli*, as a simple vending machine; insert the right token, press the right button, and the desired product is automatically delivered, neatly packaged and ready for harvest”.

Clearly, the increasing objectification of living beings in the laboratory presents extremely challenging ethical issues that moral philosophers need to address. As mentioned above, it is exceedingly difficult to unequivocally determine which organisms should be afforded greatest moral consideration and why. However, what is certain at any rate is that the appeal to the MCO provides a way of not even having to ask any moral questions *at all*. Although rejecting the MCO evidently should not lead us to renounce the use and manipulation of organisms in biological research, it nevertheless forces us to rethink the terms in which this ethical debate is conducted. Doing away with the MCO constitutes the first necessary step in reframing the ethical discussion over the appropriation of nonhuman organisms in science.

3.9. The Stream of Life: The Organicist Alternative to the MCO

The preceding sections have demonstrated that the MCO fails to capture much of what makes organisms distinctive. The very identity of an organism, based on the self-preservation of the organization of the whole coupled with the continual renewal of its parts, is beyond the reach of the MCO. No machine is made of parts that are constantly replaced by the machine itself, yet this is precisely what occurs in an organism. Whereas in a machine the identity of the whole invariably corresponds to the collective identity of the parts, in an organism the whole cannot be identified with the parts because these are continuously being replenished by the whole. To continue to obstinately uphold the MCO in light of such a basic difference only leads to a totally unrealistic understanding of machines.

A glaring illustration of this can be found in a curious paper by Reginald Kapp entitled ‘Living and Lifeless Machines’ (1954), in which some of the distinctive features of organisms are discussed from the perspective of the MCO, resulting in a very peculiar machine-based understanding of organisms. For example, Kapp (1954, p. 100) indicates that ‘living machines’ are constantly being ‘redesigned’ as they face new adaptive challenges: “a motor car must be permanently fitted with a brake as well as an engine. But an animal has no brake while it is running. It is redesigned so as to acquire one when it is coming to a stop; and at this moment it ceases to have an engine of propulsion, an engine designed for the function of running”. Kapp also uses the analogy of the motor car to illustrate how fuel is consumed in an organism, asserting that: “The living body is analogous to a motor car in which the chassis, brakes, cylinders, pistons, connecting rods, valves and bearings all contained combustible material, some of which was burnt whenever the driver placed his foot on the accelerator” (ibid., p. 101). But how is such a bizarre imaginary motor car still analogous to an *actual* motor car? Can the mechanisms of the latter really be used to explain the mechanisms of the former? If not, then what is the point of obstinately upholding the MCO if the price to be paid is that our understanding of machines has to be completely distorted to accommodate the distinctive features of organisms?

The obvious alternative is simply to come to terms with the fact that machines are not good models for understanding organisms. Once it is realized that the MCO, despite

its overwhelming influence, is neither necessary nor inevitable, a number of alternative conceptual models become available. In this section, I want to explore a metaphor for the organism that was adopted by one of the leading organicists of the twentieth century, the Austrian theoretical biologist Ludwig von Bertalanffy. In his book *Problems of Life* (1952), Bertalanffy illustrated the nature of the organism by appealing to the famous aphorism of the Presocratic philosopher Heraclitus that it is impossible to step into the same river twice because fresh water is forever flowing.²⁹ A stream is never the same at two succeeding temporal points; it is permanently changing. This image encapsulated the Heraclitean worldview, which emphasized the endless movement and change of all things (Vamvacas, 2009). Bertalanffy argued that “With this Heraclitean thought we put our finger on a profound characteristic of the living world” (1952, p. 124). Like the river, ever changing in its waves and yet persisting in its flow, the living organism only *appears* to be constant and invariable, but in reality it is the manifestation of a perpetual current. Accordingly, Bertalanffy maintained that “living forms are not *in being*, they are *happening*; they are the expression of a perpetual stream of matter and energy which passes the organism and at the same time constitutes it”. He referred to this dynamic conception of the organism as the *stream of life*, and counted it “among the most important principles of modern biology” (ibid.).

In the stream of life, Bertalanffy found a fitting metaphor for the understanding of the organism he had been developing since the 1930s, which was based on the novel thermodynamic idea of an *open system*. Classic thermodynamics deals with closed systems, i.e., systems which exchange with the environment energy (in the form of heat and work) but not matter. An open system exchanges both energy *and* matter with the environment. By abstracting the physical principles underlying the nature of organisms, Bertalanffy played a mayor role in developing the branch of physics now known as non-equilibrium thermodynamics. Bertalanffy showed that the organism is a kind of open system which persists in the incessant import and export of matter and energy, and which maintains itself in a steady state far from equilibrium. In the 1940s, the physical chemist Ilya Prigogine began to study the thermodynamics of this kind of

²⁹ One of Heraclitus’ followers, Cratylus, argued that it is not even possible to step into the same river *once*, given that in between entering and leaving the stream, the water that one comes into contact with has already changed.

open systems (which he called ‘dissipative structures’), and found that they were able to minimize their total entropy production by spontaneously increasing their order and organization (a discovery for which he was awarded the Nobel Prize in 1977). It is important to note that not all dissipative structures are living systems. Air pressure-organized tornadoes and temperature-driven Bénard rolls (longitudinal cylinders of liquid molecules that form ordered dynamic patterns) are well-known examples. However, as Bertalanffy himself recognized, organisms differ from other kinds of dissipative structures in that they are hierarchically organized, complexly differentiated, and are able to preserve their organization for much longer periods of time (perhaps even indefinitely, if one takes into account the fact that the living organization is essentially preserved during reproduction).

Although Bertalanffy was the first to identify the physical principles underlying the stream of life, this understanding of the organism has a much longer history. For example, John Locke, in the second edition of his *Essay Concerning Human Understanding* (1694), observed that organisms and inanimate bodies maintain their identities over time in completely different ways. Whereas inanimate bodies remain the same by virtue of keeping the same component parts, organisms persist by actively replacing their parts. Locke argued that a machine whose parts were constantly being repaired and regenerated would closely resemble an organism: “If we would suppose [a] Machine one continued Body, all whose organized Parts were repair’d, increas’d or diminish’d, by a constant Addition or Separation of insensible Parts, with one Common Life, we should have something very much like the Body of an Animal” (Locke, quoted in McLaughlin, 2001, p. 177). However, Locke recognized that such a machine would still not be exactly like an animal because its principle of motion would be external rather than internal.³⁰ Thus, for Locke, the stream of life lies at the heart of what he considered made organisms distinctive.

This dynamic conception of the organism that emphasizes form over matter was also central to the comparative anatomist Georges Cuvier, who used it as the basis for his definition of life:

³⁰ Note that Locke here brilliantly anticipates Kant’s seminal distinction between intrinsic and extrinsic forms of purposiveness that I have argued constitutes the single most fundamental difference between organisms and machines.

Life is a vortex, more or less rapid, more or less complicated, the direction of which is invariable, and which always carries along molecules of similar kinds, but into which individual molecules are continually entering, and from which they are continually departing; so that the *form* of a living body is more essential to it than its *matter*. As long as this motion subsists, the body in which it takes place is living—*it lives*. When it finally ceases, *it dies*. (Cuvier, 1832, p. 14)

The British polymath William Whewell, in the section of *The Philosophy of the Inductive Sciences* (1847) that dealt with what he was the first to call ‘The Philosophy of Biology’, endorsed Cuvier’s view, and asserted that “Life is a constant Form of a circulating matter” (1847, p. 587). This understanding of the organism can also be found in the writings of some contemporary authors. Roger Faber (1986, pp., 23-24), for instance, argues that living systems are best understood as waves:

Just as a particular wave crest is composed now of one portion of the surface of the sea and later, as the crest moves on, of another portion, so an individual cell is composed now of one set of molecules and ions and later, after ingestion, metabolism, and excretion, of a distinct set of molecules of the same kinds. Each cell, and therefore, the entire organism, is an enduring configuration in the jumble of nutrients and wastes; it is a wave or eddy in the molecular flux. An organism is a complex dance into whose dynamic pattern the atoms insert themselves for a time, performing their intricate steps until, displaced by newcomers, they move on to other actions in other places. (Faber, 1986, pp. 23-24)

What these metaphorical appeals to flowing streams, circulating vortices, and moving waves all have in common is that they attempt to capture the thermodynamic nature of organisms by singling out *metabolism* as the defining characteristic of life. Metabolism is what maintains the organism in a steady state far from thermodynamic equilibrium. As metabolism proceeds, with the continuous import of nutrients and export of wastes, not much remains at a later time of the materials that once composed the organism. This continuous exchange of materials occurs at every level of organismic organization. The chemical constituents of a cell are constantly synthesized and degraded and yet the cell persists as a whole. In a multicellular organism, the component cells are continuously dying and being replaced by new ones and yet the organism persists as a whole. Thus, every living system seems

permanent and stationary when it is considered from a particular viewpoint. But what appears to be permanent at one level is in fact maintained by means of the continuous building up and breaking down of the components at the lower level; be it of molecules in a cell, or of cells in a multicellular organism.

The appearance of stasis and permanence can be very deceptive at any level of organismic organization. For example, subcellular formations like the nuclear spindle and the Golgi apparatus seem well-defined structures when we observe them in fixed microscope preparations. However, when we consider them *in vivo* in their changes in time, it becomes clear that they are temporary manifestations of biochemical processes involving continuous fluxes of matter and energy. These organelles, like most other molecular assemblies in the cell, do not exist as rigid microstructures but as quasi-stationary patterns, part fluid, part consolidated, which endure for a time before undergoing changes or disappearing altogether (Bertalanffy, 1952, p. 136; see also Kirschner et al., 2000). In the same way, no tissue or organ in a multicellular organism is a permanent object. Rather, any given tissue or organ constitutes a steady state, only the shape of which persists, while its material constitution is constantly being renewed by metabolic events. Ultimately, this also applies to the multicellular organism as a whole. This is much harder to visualize because the material regeneration of the form of macroscopic organisms is not easily perceived by the human eye. But consider the following thought experiment. Imagine an extraterrestrial humanoid life form whose mode of visual recognition was based on the enumeration of the material components making up particular tokens of general types, rather than on the identification of general types instantiated by particular tokens. Imagine further that this alien lands on Earth at a particular location and encounters two dogs: a living dog and a mechanical dog, the latter being the product of the most cutting-edge A-Life research (see Figure 5). The alien scans the two dogs, catalogues their material constitution for future identification, and returns home. A year later, the alien returns to Earth to the same location and faces the two dogs it encountered in its first trip. Despite being in the presence of the same two dogs, the alien's cognitive apparatus means that it is only able to recognize the mechanical dog and not the living one. From the alien's perspective, the living dog of the first trip has faded out of existence, and an entirely different one has taken its place! What this admittedly fanciful thought experiment is meant to illustrate is that if one focuses on the materials of the parts

instead of the form of the whole, organisms do indeed resemble flowing streams. The fact that this is not easily perceptible to us does not make it any less true or important.

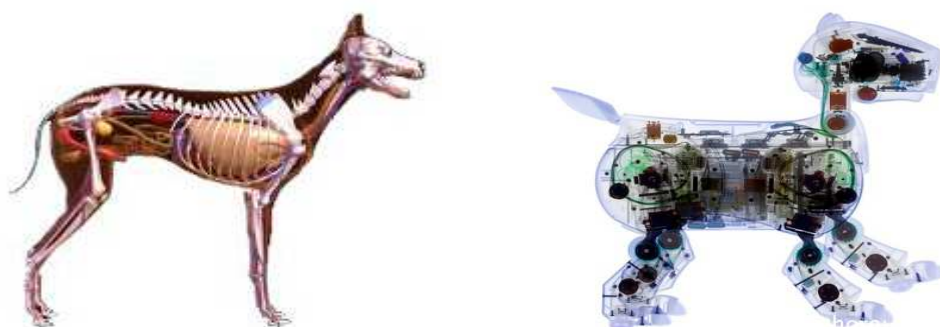


Figure 5. Depiction of two dogs, one biological and one mechanical, as they would be perceived by an imaginary alien whose mode of visual perception was based on the enumeration of the material components that constitute physical bodies.

The stream of life is a good model for the organism because it captures its inherently dynamic nature. Flowing streams (as well as circulating vortices and moving waves) are thermodynamically open systems, as organisms are. Machines, on the other hand, are thermodynamically closed systems. This is one of the reasons why the MCO is fundamentally inadequate; it presumes it can account for the characteristics of open systems by appealing to the characteristics of closed systems. As John Dupré (2007, p. 14) has pointed out: “Mechanical models, assuming fixed machine-like ontologies, are at best an abstraction from the constantly dynamic nature of biological processes”. Machines are composed of stable parts with relatively constant modes of interaction. To conceptualize organisms in this way means to resign oneself to characterizing static snapshots of a rapidly changing biological reality.

Once the stream of life is taken seriously, it quickly becomes clear that the dynamic nature of organisms has wide-reaching implications for biology. For example, the traditional disciplinary divide between anatomy and physiology is based on the mechanistic assumption that structure and function are distinct properties of the organism that can be studied independently. Indeed, a mechanic can examine the structural arrangement of a machine while it is at rest, or study the function of the machine while it is operating. However, organisms are not objects, like machines, but manifestations of ongoing processes. The implication of this, as the early champion of

organicism J. S. Haldane (1931, p. 29) realized, is that “Structural and functional relations cannot be separated in the scientific study of life, since structure expresses the maintenance of function, and function expresses the maintenance of structure”. The dynamic nature of organisms means that the concepts of structure and function in biology are not just interdependent but *interdefining*. As a result, the longstanding dispute over whether structure determines function or if it is function that determines structure (see Russell, 1916) can be resolved. In the words of another leading organicist, J. H. Woodger (1929, p. 330), “What is required is an enlargement of the concept of ‘structure’ so as to include and recognize that in the living organism it is not merely a question of spatial structure with an ‘activity’ as something over against it, but that the concrete organism is a spatio-temporal structure and that this spatio-temporal structure *is* the activity itself”.

On the whole, the stream of life of organicism constitutes a helpful starting point for coming to terms with the inherently dynamic nature of the organism. It provides a convenient alternative to the MCO of mechanicism because it attends more closely to the characteristics that make organisms distinctive. As a consequence of this, it sidesteps many of the misunderstandings concerning the nature of organisms that result from endorsing the MCO. Contemporary biologists would do well to replace the MCO with the stream of life as their point of departure when thinking about living systems in the particular contexts in which they investigate them. Today it appears that this organicist idea, which got swept away by the molecular biology revolution of the latter half of the past century, is again beginning to acquire currency. In a recent article entitled ‘A New Biology for a New Century’, the renowned microbiologist Carl Woese specifically singles out the MCO as one of the major obstacles impeding further progress in our understanding of organisms. In place of the MCO, Woese invokes the stream of life of the early organicists (although he does not cite any of them directly) as a more appropriate metaphor in which to think about organisms, as biology enters the twenty-first century:

If they are not machines, then what are organisms? [...] Imagine a child playing in a woodland stream, poking a stick into an eddy in the flowing current, thereby disrupting it. But the eddy quickly reforms. The child disperses it again. Again it reforms, and the fascinating game goes on. There you have it! Organisms are resilient patterns in a

turbulent flow—patterns in an energy flow. A simple flow metaphor, of course, fails to capture much of what the organism is. None of our representations of organism capture it in its entirety. But the flow metaphor does begin to show us the organism's (and biology's) essence. And it is becoming increasingly clear that to understand living systems in any deep sense, we must come to see them not materialistically, as machines, but as (stable) complex, dynamic organization. (Woese, 2004, p. 176)

Replacing the static view of living systems embodied in the MCO with the dynamic conception captured by the stream of life prevents biologists from making incorrect assumptions about organisms, it provides a useful starting point for the examination of life's intrinsic purposiveness, and it furnishes them with new conceptual tools with which to address the theoretical problems they are confronted with.

3.10. Rethinking the Role of the MCO in Contemporary Biology

Given the irredeemable deficiencies of the MCO, which previous sections have highlighted, why has this notion exerted such a powerful influence in biology? A number of reasons can be identified. Firstly, as machines are clearly understood, being the products of human design, they are intuitively compelling models for conceptualizing organisms. As a result, biologists have been tempted to draw on the superficial similarities between machines and organisms (e.g., organization, interacting parts, purposive behaviour) in order to explain the latter on the basis of their familiarity with the former. Secondly, by upholding the MCO biologists have kept their discipline firmly within the confines of physical science, and historically this has served to ensure the scientific respectability of their inquiries, as well as to legitimate the epistemic transfer of theories, concepts, and methods from more developed sciences like physics and chemistry, in addition to engineering. Thirdly, the MCO fills the void caused by the absence of a generally accepted definition of life, so that by endorsing it biologists have not needed to concern themselves with intimidating conceptual questions like 'What is life?' or 'What is an organism?' and have instead been able to get on with the business of studying living systems. But above all, the most important reason why the MCO has been, and continues to be, such a seductive notion is that it is highly successful in generating empirical data. It is undeniable that the periods in history in which mechanicism and the MCO have

dominated biological inquiry have also been the periods of greatest empirical progress. This leads us to an intriguing paradox: How can the MCO result in such a fundamentally inadequate understanding of what organisms are and yet prove to be so fruitful when used to investigate them? In light of this tension, what role should the MCO play in biology today?

In order to answer these questions, it is necessary to take a step back and consider in general terms the different ways in which metaphors are used in science. Following Michael Bradie (1999), we can distinguish *theoretical*, *heuristic* and *rhetorical* functions for scientific metaphors. Metaphors with a theoretical function are central to scientific understanding, as they provide the foundation for the conceptualization, explanation, and representation of the phenomena they model. Metaphors with a heuristic function constitute methodological tools that facilitate the empirical investigation of the phenomena they model. And metaphors with a rhetorical function are used in scientific communication to inform and educate non-specialists about the phenomena scientists investigate. The most influential scientific metaphors, like the MCO, perform all three functions. So far, my discussion of the MCO has focused primarily on its theoretical function, and I believe that enough has been said in the preceding sections to legitimately conclude that, as a *theory of the organism*, the MCO has absolutely no role to play in biology. In what follows, I will examine in turn the heuristic and rhetorical functions of the MCO. I will first explain why the MCO succeeds when it is employed heuristically but not theoretically, and I will then illustrate the serious problems which arise from the rhetorical appeal to the MCO.

The key to the heuristic value of the MCO in the study of organisms resides in the fact that the distinctive nature of the organism is only truly perceptible when it is considered as a whole. If the parts of an organism are considered independently from the whole for the purpose of their investigation, they do resemble machines in that they constitute extrinsically purposive systems. Like machines, the parts of an organism are not self-producing, self-organizing, or self-maintaining, but rather depend on an external agent for their production, organization, and maintenance (namely, the organism as a whole). Just as machines serve the ends of their users, organismal parts serve the ends of the organisms to which they belong. So whereas an organism as a whole is a categorically different kind of system from a machine, its

parts actually share many of the attributes of machines. Consequently, when these parts are studied in isolation, much can be learnt about them by treating them *as if* they were machines. This is the source of the heuristic power of the MCO, and it explains why this notion has proven to be so successful when used as a methodological tool in the analytical examination of organisms. To investigate localized areas within the organism as machines allows biologists to conveniently abstract away the intimidating complexity of the broader physiological context of the organism as a whole and focus their attention on particular causal relations between well-defined interacting components (see Bechtel and Richardson, 1993). The heuristic adoption of the MCO also enables biologists to devise testable hypotheses regarding the connections between local suborganismic structures and clearly identified functions.

Nevertheless, an important limitation in the methodological use of the MCO needs to be pointed out. This is that the heuristic value of the MCO is directly proportional to the degree of physiological differentiation of the organism under investigation. An organism in the early stages of development cannot be studied as an assemblage of machines because in it all functions are assumed by the organism as a whole. The organism at this point constitutes what Hans Driesch called a ‘harmonious-equipotential system’ that is totally unintelligible in mechanistic terms.³¹ It is only with the progressive physiological differentiation of the embryo that the originally unitary action of the organism becomes partitioned into separate individual actions, and it is at this developmental stage that local machine-like structures within the organism begin to appear, thus rendering the MCO of some heuristic value. Still, it is important to remember that even in the adult stage, organisms retain a certain degree of plasticity and a significant capacity to reorganize their parts and reassign their functional needs accordingly in order to compensate against external perturbations (as Goldstein’s clinical studies discussed in Section 3.3 illustrated). So at no stage in the life history of an organism is the heuristic reliability of the MCO absolute.

So far, I have argued that the heuristic value of the MCO resides in the relative similarities between machines and the *parts* of organisms. But what should we make

³¹ It is for this reason that Driesch appealed to the holistic properties of organisms at this stage of development to demonstrate the inadequacy of the MCO and formulate his ‘first proof of vitalism’ (see Driesch, 1908, pp. 118-149).

of the adoption of the MCO in the study of *whole* organisms? Whole organisms, unlike their parts, constitute intrinsically purposive systems. Consequently, they cannot be mechanized for the purpose of their investigation in the way that their parts can when considered in isolation. The mechanistic approach to the study of organisms is inherently incapable of tackling the systemic properties that make organisms distinctive in the first place; all it can do is target localized and highly differentiated regions within organisms on an individual basis. Does this mean that the MCO is useless in the investigation of whole organisms? Not quite. The MCO can still play a heuristically useful counterfactual role by helping to highlight what organisms are *not*. In this respect, the MCO can serve as a false model which, by virtue of its inherent inadequacy, can orient biologists towards the actual nature of organisms (cf. Wimsatt, 1987). As Rosen (1991, p. 248) observes, “On balance, the Cartesian metaphor of organism as machine has provided to be a good idea. Ideas do not have to be correct in order to be good; it is only necessary that, if they fail, they do so in an interesting way”. Overall, the key to effectively evaluating the MCO is to clearly demarcate its heuristic role from its theoretical role. Successful mechanistic *investigations* of organisms do not enable successful mechanistic *explanations* of them, as Section 3.4 argued. So although the MCO provides a convenient means of pragmatically simplifying biological reality in order to facilitate its investigation, it nonetheless fails to provide an appropriate theoretical understanding of that reality.³² The regrettable prevalence of the MCO in contemporary biological thought is to a large extent the result of unwarrantedly inferring its ontological truthfulness on the basis of its methodological usefulness.

Let us now turn to the rhetorical function of the MCO. As indicated above, metaphors with a rhetorical function are used for the purposes of communicating scientific knowledge, both technical and popular, to non-specialists. Some authors have argued that the MCO, despite being theoretically inadequate, can still be of great rhetorical value because it provides a highly instructive visual aid in teaching non-specialists

³² James Barham has also highlighted the distinction between the MCO’s rhetorical (or methodological) function and its theoretical (or metaphysical) function: “*As a scientific methodology*, the machine metaphor has been extraordinarily fruitful. No doubt it will remain so for a long time to come, although there are many signs that we are beginning to bump up against the limits of its usefulness. But however that may be, *as a metaphysics*, mechanism has always been incoherent. The idea that a machine could occur naturally at all, much less that it might have its own intrinsic purposes and values, is simply an article of faith for which there is no rational support” (Barham, 2004, p. 222, my emphasis).

about the features and properties of organisms. For instance, Konopka (2002, p. 399) remarks that although “the machine metaphor is bound to fail as a serious scientific tool [...] it can remain an extraordinarily useful pedagogical tool in education of gifted non-specialists in local youth centers (including our Universities) all over the world”. This view, however, is problematic. Just as it is tempting for biologists to wrongly infer the theoretical adequacy of the MCO on the basis of its heuristic value, so can the rhetorical use of the MCO by biologists inadvertently mislead non-specialists into assuming that organisms really are machines. In this sense, rhetorical metaphors are double-edged swords; in the same way that they can enhance scientific understanding, they can also serve to obstruct it (see Quale, 2002). This clearly depends on the choice of metaphors used; theoretically misleading metaphors like the MCO do far more harm than good in this respect. This can be effectively illustrated by considering the repercussions of the recent rhetorical appeal to ‘molecular machines’ in molecular biology.

In 1998, the then president of the U. S. National Academy of Sciences, Bruce Alberts, edited a special issue in *Cell* (volume 92, issue 3) which brought together a series of papers that systematically appealed to the use of machine language in the description of large protein complexes. In his introduction to the issue (entitled ‘The Cell as a Collection of Protein Machines: Preparing the Next Generation of Molecular Biologists’), Alberts noted that aspiring molecular biologists should learn to view the cell as a factory containing many interlocking assembly lines of protein machines. In relation to his use of the term ‘machine’, Alberts offered the following explanation:

Why do we call the large protein assemblies that underlie cell function protein *machines*? Precisely because, like the machines invented by humans to deal efficiently with the macroscopic world, these protein assemblies contain highly coordinated moving parts. Within each protein assembly, intermolecular collisions are not only restricted to a small set of possibilities, but reaction C depends on reaction B, which in turn depends on reaction A; just as it would in a machine of our common experience. (Alberts, 1998, p. 291)

This machine terminology has caught on rapidly in the molecular biology community, and year after year the frequency of the term ‘molecular machine’ has steadily increased in scientific journals and magazines, where it has become a fashionable

expression to describe virtually any highly organized and functionally specialized molecular assembly in the cell. Figure 6 lists a selection of the subcellular structures which have recently been described by biologists as molecular machines.

Subcellular assembly	Sample of 'molecular machine' language	Source reference
<i>Ribosome</i>	"probably the most sophisticated machine ever made"	Garrett (1999)
<i>Proteasome</i>	"a molecular machine designed for controlled proteolysis"	Voges et al. (1999)
<i>Bacteriorhodopsin</i>	"a deceptively simple molecular machine"	Kühlbrandt (2000)
<i>Apoptosome</i>	"a seven-spoked death machine"	Salvesen et al. (2002)
<i>Glideosome</i>	"a molecular machine powering motility"	Keeley et al. (2003)
<i>Spliceosome</i>	"among the most complex macromolecular machines known"	Nilsen (2003)
<i>Blood clotting system</i>	"a typical example of a molecular machine"	Spronk et al. (2003)
<i>Condensin</i>	"the key molecular machine of chromosome condensation"	Strunnikov (2003)
<i>Photosynthetic system</i>	"the most elaborate nanoscale biological machine in nature"	Imahori (2004)
<i>Bacterial flagellum</i>	"an exquisitely engineered chemi-osmotic nanomachine"	Pallen et al. (2005)
<i>Myosin filament</i>	"a complicated machine of many moving parts"	Ohki et al. (2006)
<i>RNA degradasome</i>	"a supramolecular machine dedicated to RNA processing"	Marcaida et al. (2006)
<i>Cyclosome</i>	"a machine designed to destroy"	Peters (2006)
<i>RNA Polymerase</i>	"a multifunctional molecular machine"	Haag et al. (2007)

Figure 6. Subcellular assemblies which have been described as molecular machines

Despite the popularity of the term 'molecular machine', a bibliographical analysis reveals that this phrase is predominantly featured in review articles, and only rarely is it found in original papers. When it does feature in an original paper, it almost always appears in the title, abstract, or introduction sections, rather than in the parts of the paper actually describing the research undertaken and the interpretation of the findings. What this suggests is that instead of serving as a theoretical model in the explanation of subcellular assemblies, the term 'molecular machine' primarily plays a rhetorical role in introducing newcomers to the field of molecular biology devoted to the study of the structure and function of large subcellular assemblies. Indeed, the phrase 'molecular machines' has become a common title for academic conferences and sessions, and it thus appears to work mainly at a social level by helping to define a particular subset within the molecular biology community (Peters et al., 2007).

However, the adverse consequences that have resulted from the use of the phrase 'molecular machine' far outweigh its potential pedagogical and sociological benefits, given that in the biologists' persistent appeal to this term, modern-day creationists have found just the kind of rhetoric they needed to dress up their belief in a

supernatural being with a guise of scientific respectability. Indeed, the pseudo-scientific movement known as ‘Intelligent Design’ (ID, hereafter) has come to rely on the so-called ‘molecular machines’ of molecular biology as the primary basis of empirical support for their claims regarding divine design (Behe, 2001). One of the leading proponents of ID, the biochemist Michael Behe, argues that many of the highly organized subcellular systems that molecular biologists describe as molecular machines exhibit ‘irreducible complexity’ that could not have evolved as the result of natural causes and must therefore be the product of an intelligent agency. Behe (2006 [1996], p. 39) defines an irreducibly complex system as one composed of many interacting parts that contribute to the function of the system, and in which the removal of any of the parts necessarily causes the system to cease functioning. He illustrates this concept by using a machine, the mousetrap, which requires the simultaneous presence of a spring, bar, platform, and other components to catch mice. Behe points out that the efficiency of the mousetrap does not increase gradually with the successive addition of components. Rather, all of the components need to be in place for the machine to function at all. In the same way, Behe argues that molecular machines, such as the bacterial flagellum and the blood clotting system, are like the mousetrap in that they constitute irreducibly complex systems.

The role played by the notion of molecular machine in Behe’s case for ID is absolutely crucial, as it provides a tacit way of sidestepping the inductive part of the Argument from Design in order to establish on purely analytical grounds that since machines have designers, and since living systems are collections of molecular machines, then living systems must have a designer. The obvious problem with this argument does not lie in inferring design (and therefore a designer) from a machine, but in conceiving living systems, or rather their parts, as machines. Behe is well aware of this, which is why he devotes so much attention in his writings to highlighting the mechanistic nature of cells. Fortunately for Behe, this task is greatly facilitated by the fact that molecular biologists are the first to use machine language in their descriptions of cellular components, as Figure 6 illustrates. Because of this, Behe (ibid., p. 218) is able to assert that “Hume’s criticism of the design argument that asserts a fundamental difference between mechanical systems and living systems is out of date, destroyed by the advance of science which has discovered the machinery of life”. Hence, Behe becomes a *de facto* mechanist when it comes to the cell, and it is

here where the concept of molecular machine, proposed by the molecular biologists themselves, is so convenient. Indeed, Behe takes every possible opportunity to employ it:

The cumulative results [of molecular biology] show with piercing clarity that life is based on machines—machines made of molecules! Molecular machines haul cargo from one place in the cell to another along «highways» made of other molecules, while still others act as cables, ropes, and pulleys to hold the cell in shape. Machines turn cellular switches on and off, sometimes killing the cell or causing it to grow. Solar-powered machines capture the energy of photons and store it in chemicals. Electrical machines allow current to flow through nerves. Manufacturing machines build other molecular machines, as well as themselves. Cells swim using machines, copy themselves with machinery, ingest food with machinery. In short, highly sophisticated molecular machines control every cellular process. (Behe, 2006, pp. 4-5)

In the hands of Behe, the phrase ‘molecular machine’ is no longer a fanciful, purely rhetorical figure of speech, but is rather a literal characterization of the real nature of cellular components: “literally, there are real machines inside everybody’s cells and this is what they are called by all biologists who work in the field, molecular machines” (Behe, 2005). The ingenuity of Behe’s argument for ID thus lies in its skilful exploitation of a term that molecular biologists use loosely for rhetorical purposes in a way that draws on their authority as scientists to undermine their own claims. The interesting consequence of this is that the rebuttals of ID formulated by biologists and philosophers have largely consisted in arguments against the MCO. For example, in their criticism of Behe, Niall Shanks and Karl Joplin (1999, p. 281) indicate that “Real biological systems are quite unlike economically designed engineering artifacts such as mousetraps. [Behe’s] case against evolution is a good example, in fact, of the perils of being ‘trapped’ by a metaphor”, by which of course they mean the MCO. Similarly, in their critique of ID, Eugene Scott and Nicholas Matzke (2007, p. 292) argue that “The differences between biological phenomena and human-built machines easily outweigh the superficial similarities”, and even quote Woese’s (2004) formulation of the stream of life as a better metaphorical conceptualization of the organism than the MCO. Accordingly, in a recent editorial entitled ‘Stand Up for Evolution’, the evolutionary developmental biologist Rudolf Raff (2005, p. 274) has emphasized the need for biologists to avoid the MCO in their

teaching and writing: “let us not play into the hands of ID propagandists. For instance, be careful about using [extrinsically] teleological words to describe biological entities in our teaching and writing. Calling cells ‘machines that do X,’ or describing biological structures as ‘well designed to do Y’ will be duly cited in ID propaganda as one more biologist supporting design”. It is therefore clear that the pernicious consequences that result from the rhetorical use of the MCO by biologists totally overshadow its limited didactic and sociological value in particular disciplines like molecular biology.

Overall, we can conclude by asserting that the numerous problems with the MCO that previous sections highlighted do not require us to dispense with the MCO altogether. However, they do demand that the role of the MCO in biology be properly circumscribed. This has been accomplished in this section by independently considering the theoretical, heuristic, and rhetorical functions of the MCO. Although the MCO is fundamentally flawed as a theory of the organism, it nevertheless remains a valuable heuristic tool when it is employed in scientific research. Approaching the study of organisms *as if* they were machines can be quite profitable, and is to a certain extent necessary. Nevertheless, it is crucial not to allow the empirical fruitfulness of the MCO obscure the undeniable fact that organisms and machines are categorically different. The danger of slipping to a theoretical interpretation of the MCO is always present, and this is why the rhetorical use of the MCO is so perilous. The price that biologists have to pay for their profitable heuristic use of the MCO is that they must maintain the intellectual sobriety to resist the temptation of succumbing to the theoretical appeal of this intuitively compelling notion.

3.11. Conclusions: Biology ≠ Mechanicism

The failure of the MCO to come to terms with the ontology of living systems forces us to view mechanicism in a completely new light. Much of the prestige and authority of the mechanistic worldview derives from the instrumental role it played in the establishment of modern science in the seventeenth century. Throughout history, to conceive nature as a machine has meant to conceive it in a way that enables it to be scientifically investigated. Indeed, the very idea of a machine encapsulates precisely that which is amenable to scientific analysis; an organized system with regular and

predicable behaviour, and whose workings can be completely explained in terms of the structure and interactions of its component parts. One of the most remarkable incidents in the history of science is that the mechanistic conception of the world as a machine proved to be so empirically successful that it came to be regarded as *reality itself*, rather than as a convenient model for investigating it. As Andrés Vaccari (2008, pp. 332-33) remarks, “What is peculiar to the machine metaphor [in the seventeenth century] is that it later disappears, becoming a tacit, implicit assumption. For modern science, the assumption that the world and living organisms are machines becomes commonplace, an invisible, high-order structure that frames more specific, local projects”. The machine conception of nature and of life has come to be widely perceived not just as a useful model, but as the very condition of possibility for scientific inquiry.

However, what is often forgotten is that machines are highly contrived devices that are specifically designed to exhibit the kind of lawful and mathematizable regularities that mechanicism can capture! When dealing with machines it is possible to uphold the commitments that characterize mechanicism, such as reductionism and determinism, precisely because machines are constrained in their organization and operation in a way that enables these commitments to hold. The reality is that there is nothing *natural* about a machine. In fact, it represents the quintessence of artificiality. Everything about it reflects the purposes and intentions of an external agent. The basic problem of the mechanistic worldview is that nature, unlike a machine, has not been expressly designed to display the kind of attributes that mechanicism is most adept in explaining (cf. Dupré, 1993; 2001; 2007). Of course, this does not mean that mechanicism cannot explain natural systems at all, but it *does* mean that the fit between the machine model and any natural system that mechanicism targets can never be exact. The lack of fit between model and target is especially noticeable in biology, given that, as this chapter has shown, organisms are fundamentally different kinds of systems from machines. This is why imposing the machine model on the conceptualization of organisms has such disastrous consequences.

In essence, the MCO systematically reduces organisms to the features that mechanicism is capable of explaining and filters out everything that remains. The success of mechanistic biology in explaining these selected features in turn helps to

reinforce the original conceptualization of the organism as a machine. The more recalcitrant aspects of the organism that do not fit the mechanistic characterization are either ignored or dismissed as unimportant. Unfortunately, what is neglected in the MCO is precisely what makes organisms most distinctive, namely their intrinsic purposiveness and their self-producing organization. It should not come as a surprise that the philosophical notions that are typically associated with these two non-mechanistic features, namely teleology and holism, are treated by the scientific community with scepticism and suspicion. As the edifice of modern science is built on mechanistic foundations, it is to be expected that what lies beyond the reach of mechanicism is readily dismissed as mystical or unscientific. As Rosen (1991, pp. xv-xvi) puts it, “for the past three centuries, ideas of mechanism and machine have constituted the very essence of the adjective “scientific”; a rejection of them thus seems like a rejection of science itself”. But this is nothing more than a prejudice. Once it is left behind and it is understood that mechanicism, despite its historical importance, neither predetermines nor exhausts the meaning of science, biological thought liberates itself from the need to conform to the MCO, and it becomes able to explore alternative conceptual models, like the stream of life, that attempt to confront the complexity of the organism in more direct terms.

This chapter has endeavoured to show that the MCO stands today as one of the most serious obstacles impeding further progress in our comprehension of living systems. In Rosen’s words, the MCO “makes biology infinitely harder than it needs to be [...] because it transmutes biology into a struggle to reconcile organic phenomena with sets of constituent fragments of unknown relevance to them” (ibid., p. 22). Bertalanffy, in his *Modern Theories of Development*, is even more forceful in his condemnation of the MCO:

In the history of science and philosophy there is hardly a less happy expression than that of the *bête machine* of Descartes. No concept leads to such a distorted view of the problem underlying it or so greatly falsifies its proper meaning. It might even be said that, in spite of its heuristic success, the notion of the machine has had a destructive effect on the development of biological theory. It has entangled the investigator even to-day with scholastic artificial problems, and at the same time has prevented the clear discernment of the essential problem of organic nature. Only the displacement of the

machine theory which is now gradually taking place will put an end to the paralysis of biological thinking for which this Cartesian expression has been responsible. (Bertalanffy, 1962 [1933], pp. 36-37)

Unfortunately, the displacement of the MCO that Bertalanffy referred to in this passage, written in 1933 at the height of the organicist movement in theoretical biology, did not last long, as the molecular biology revolution was just around the corner, and with it came the effective reestablishment of the MCO at the centre stage of biological thought. It is only in the present time, as biology gradually emerges at the other side of the molecular biology tidal wave that it is again becoming apparent that the MCO, and mechanicism more generally, is obstructing rather than enabling theoretical progress in biology. It should be clear that breaking free from the grip of mechanicism constitutes a necessary precondition for gaining a genuine understanding of the nature of living systems.

Chapter 4

THE CONCEPT OF MECHANISM IN BIOLOGY: AN ANALYSIS

I wish to make it quite clear that Biological Mechanism is committed logically to a great deal more than is commonly supposed. – C. D. Broad (1925)

4.1. Introduction: The Renewed Interest in Mechanism

The concept of mechanism has recently received a great deal of attention in the philosophy of science. The main catalyst for this new interest has been the realization that scientists, especially biologists, often refer to mechanisms in their inquiries into the phenomena they investigate. This has led to the development of a lively philosophical research program over the past decade that has attempted to make sense of scientists' mechanism-talk and elucidate the role it plays in scientific practice. The standard philosophical strategy has been to begin by offering a general characterization of 'mechanism' that captures the way scientists use this term, and then show the ways in which mechanisms are involved in the explanation of phenomena. The mechanism account which has exerted the greatest influence in the development of this new discourse has been formulated by Peter Machamer, Lindley Darden, and Carl Craver (2000). Machamer et al. (MDC hereafter) conceive mechanisms as "entities and activities organized such that they are productive of regular changes from start or set-up conditions to finish or termination conditions" (MDC, 2000, p. 3). Stuart Glennan (2002) and William Bechtel (2006) have also developed their own mechanism accounts. Glennan defines a mechanism for a behaviour as "a complex system that produces that behavior by the interaction of a number of parts, where the interactions between parts can be characterized by direct, invariant, change-relating generalizations" (Glennan, 2002, p. S344), whereas Bechtel characterizes a mechanism as "a structure performing a function in virtue of its component parts, component operations, and their organization", adding that "The orchestrated functioning of the mechanism is responsible for one or more phenomena" (Bechtel, 2006, p. 26).

This emerging mechanism movement aims to provide a new framework in which to tackle a number of traditional problems in the philosophy of science. Central among them is the nature of explanation, in which a focus on mechanisms serves as an effective antidote to the outmoded deductive-nomological conception of explanation inherited from logical empiricism. Nevertheless, despite the general applicability of mechanism-based philosophy, it is interesting to note that this research program has developed primarily within the philosophy of biology. The most prominent defences and extensive elaborations of the mechanism approach have been advanced by philosophers interested in the biological sciences, with book-length accounts of mechanisms now existing for several biological subdisciplines, including cell biology (Bechtel, 2006), molecular biology (Darden, 2006), and neurobiology (Craver, 2007). This partnership between mechanism-based philosophy and biology is no mere happenstance. In fact, attending to the role the concept of mechanism has played in the development of biological thought opens up a rich new perspective in which to effectively examine and critically evaluate the recent mechanism discourse.

In a nutshell, what a historically-informed perspective reveals is that the concept of mechanism in biology has come to be used in several different senses. As the current mechanism discourse in the philosophy of science proceeds with an almost complete disregard for how the concept of mechanism has been shaped by the history of its usage, discussions frequently suffer from the inadvertent conflation of the different meanings of the term. Admittedly, philosophers are generally aware that ‘mechanism’ is a convoluted concept with a long history, as evidenced by MDC’s assertion that “What counts as a mechanism in science has developed over time and presumably will continue to do so” (2000, p. 2). However, most of them deem the potential for semantic confusion minimal because they consider the various meanings of the concept to be neatly associated with discrete, non-overlapping historical periods. Craver, for instance, remarks: “But what is a mechanism? History cannot answer this question. The term mechanism has been used in too many different ways, and most of those uses no longer have any application in biology” (2007, p. 3). In this chapter I will attempt to show, in opposition to this claim, how an awareness of the semantic breadth of the concept of mechanism afforded by an examination of its history can help uncover a number of important tensions within the current mechanism discourse, as well as provide the necessary philosophical resources for resolving them.

I will begin by distinguishing and characterizing the three meanings of the concept of mechanism in biology (Section 4.2). I will then explore the way in which the different senses of ‘mechanism’ have been used in the history of biology (Section 4.3), and how they have come to be featured in the philosophy of science, situating the new mechanism movement in this context (Section 4.4). Following this, I will illustrate the various problems that arise in recent discussions from the inadvertent conflation of the different senses of ‘mechanism’ (Section 4.5). Finally, I will show what amendments need to be made to current accounts of mechanism to effectively capture the way this term is used by biologists in their research (Section 4.6).

4.2. The Three Meanings of ‘Mechanism’ in Biology

The term ‘mechanism’ is used to mean different things in different contexts. In biology, ‘mechanism’ has three distinct meanings, which can be terminologically distinguished as follows:

- (a) *Mechanicism*: The philosophical thesis which conceives living organisms as machines that can be completely explained in terms of the structure and interactions of their component parts.
- (b) *Machine Mechanism*: The structure or internal workings of a machine-like system.
- (c) *Causal Mechanism*: A step-by-step explanation of the mode of operation of a causal process that gives rise to a phenomenon of interest.

As this taxonomy illustrates, ‘mechanism’ may refer to (a) a *philosophical thesis* about life and biology, (b) the inner workings of a *machine*, and (c) a mode of *explanation*. In order to make the ensuing discussion as clear as possible, I will refrain from using the word ‘mechanism’ in favour of these three terms, employing it only when referring to the word itself and not to any of its meanings. Let us now examine each of these three meanings of ‘mechanism’ in more detail.

As we saw in Chapter 2, *mechanicism* has its roots in the Scientific Revolution and is usually associated with a naturalistic, atomistic, and deterministic view of nature which tends to lend itself to mathematical characterization. However, we have also

seen that mechanicism in biology, or *mechanistic biology*, has a rather more specific meaning. In previous chapters, I have characterized mechanistic biology in terms of the following basic tenets:

1. The commitment to an ontological continuity between the living and the nonliving
2. The view that biological wholes (i.e., organisms) are directly determined by the activities and interactions of their component parts, and that consequently all properties of organisms can be characterized from the bottom up in increasing levels of organization
3. The focus on the efficient and material causes of organisms, and the unequivocal repudiation of final causes in biological explanation
4. The commitment to explanatory and methodological reductionism in the study of living systems

The *machine mechanism* sense of ‘mechanism’ is the closest to the etymological roots of the word, which can be traced to the Latin *machina* and the Greek *mechane*, terms meaning ‘machine’ or ‘mechanical contrivance’. When used in the machine mechanism sense, the term ‘mechanism’ refers to a machine-like system, or rather to a system conceived in machine terms. In Chapter 3 I examined this sense of ‘mechanism’ in a great amount of detail, so I will say no more about it here.

The *causal mechanism* sense of ‘mechanism’, in contrast to the first two, only acquired widespread currency in biology in the twentieth century. However, it is the meaning of the term that has become predominant in contemporary biological research. Causal mechanisms are of fundamental importance in scientific practice because they enable the identification of causal relations. When a biologist asks ‘What is the *mechanism* of P?’ (where P is the phenomenon of interest), she is seeking to identify the causes which explain how P comes about. Although the vast majority of philosophers conceive causal mechanisms as real things in the world (akin to machine mechanisms), I will argue in this chapter that they are actually better understood as heuristic models which target particular causal relations and thereby facilitate the explanation of the phenomena scientists investigate.

I am not, of course, the first to propose that the concept of mechanism needs to be terminologically fragmented to reflect its semantic breadth. In fact, the term ‘mechanicism’ as I am using in this thesis has had longstanding currency in the German (*‘mechanizismus’*), French (*‘mécanicisme’*), Italian (*‘meccanicismo’*), and Spanish (*‘mecanicismo’*) scholarly literature, where it is commonly used to demarcate this sense of ‘mechanism’ from the more familiar machine mechanism sense. For some reason, however, the term ‘mechanicism’ has not caught on in the English-speaking world. Still, Garland Allen (2005) has recently distinguished between the mechanicism meaning (which he calls ‘philosophical Mechanism’) and the causal mechanism meaning (which he calls ‘explanatory mechanism’), though he does not discern the machine mechanism meaning of the term. On the other hand, Michael Ruse (2005) has distinguished between machine mechanisms and causal mechanisms (designating the former ‘mechanism in the specific sense’ and the latter ‘mechanism in the general sense’), but he fails to acknowledge the mechanicism meaning. So although previous attempts have been made to distinguish the various senses of ‘mechanism’, these efforts have tended to only discriminate two of the three meanings of the concept. I argue that a tripartite distinction such as the one I have proposed in this section is needed to recognize the full semantic breadth of the concept of mechanism.

Members of the new mechanism movement may object that such terminological distinctions are not really necessary, as at least in recent philosophical discussions the term ‘mechanism’ is employed consistently. The reality, however, is that the current philosophical discourse is full of examples in which the concept is used in different senses, sometimes in the same sentence. For instance, consider the following remark by Craver and Darden (2005, p. 234):

From the perspective of biology, however, one might tell a triumphal story of the success of mechanism [i.e., *mechanicism*] over various forms of vitalism, as well as over biological theories appealing to intelligent design. Indeed, one cannot open a journal in any field of contemporary biology without encountering appeals to the mechanism [i.e., *causal mechanism*] for this or that phenomenon.³³

³³ In addition to conflating two senses of ‘mechanism’, this passage is historically inaccurate. Mechanicism cannot be contrasted historically with theories appealing to intelligent design given that,

One final terminological distinction is in order before moving on. It has become customary, following Robert Skipper and Roberta Millstein's (2005) analysis, to refer to the recent mechanism movement in the philosophy of science as 'the new mechanistic philosophy'. This is a very unfortunate and rather misleading designation, as it suggests that the current philosophical interest in the concept of mechanism represents some sort of resurrection of mechanistic philosophy (i.e., mechanicism), which is not in fact the case. Mechanistic philosophy, both as a general doctrine and specifically as it applies to biology, is concerned with the characterization of machine mechanisms. The new mechanism movement, in contrast, is devoted to examining the role played by causal mechanisms in scientific practice. This mechanism discourse is not committed to a mechanistic worldview, nor does it prescribe a mechanistic approach in biology. Indeed, there is nothing distinctively *mechanistic* about the new mechanism movement, other than its focus on 'mechanisms'; and even this is not something it really shares with mechanicism as each doctrine understands this concept in a different sense (see Figure 7). Still, contemporary philosophers routinely refer to explanations appealing to causal mechanisms as 'mechanistic', despite these generally having nothing to do with mechanistic explanations. As previous chapters have shown, mechanistic explanations are ones in which material wholes are accounted for in terms of the properties and interactions of their component parts. Thus, to explain an object mechanistically is to explain it as one explains a machine mechanism, i.e., to explain the way in which the component parts of the object determine the properties and activities of the whole. It is therefore important not to use the term 'mechanistic' as simply a synonym for 'causal' when characterizing explanations. This inappropriate use of the term 'mechanistic', which is rampant in the recent philosophical literature on causal mechanisms, is problematic because it blurs the longstanding biological tradition of using this term to refer to the philosophical commitments of mechanicism, which still form the basic conceptual backbone of

as we have seen in previous chapters, in its classic formulation the mechanistic view of the world as a machine mechanism necessarily presupposed the existence of a divine creator. This has had important repercussions for biology. As C. D. Broad (1925, p. 91) remarked "Biological Mechanism [i.e., *mechanicism*] about the developed organism cannot consistently be held without an elaborate Deistic theory about the origin of organisms. This is because Biological Mechanism [i.e., *mechanicism*] is admittedly a theory of the organism based on its analogy to self-acting and self-regulating machines. These, so far as we can see, neither do arise nor could have arisen without design and deliberate interference by someone with matter". As I will show in the next section, only with the acceptance of Darwin's theory of evolution did mechanistic biology become completely secularized.

contemporary fields like molecular biology.³⁴ Consequently, for the sake of consistency it is preferable to avoid the term ‘mechanistic’ altogether in discussions of causal mechanisms. In place of Skipper and Millstein’s misleading banner, I will refer to the new mechanism movement in the philosophy of science as the *mechanismic program*, and to explanations given in terms of causal mechanisms as *mechanismic* explanations, retaining the term ‘mechanistic’ for discussions of mechanicism and machine mechanisms, as I have done so in previous chapters. This seems more appropriate, as the term ‘mechanismic’ is already used in philosophical discussions of causal mechanisms in the social sciences (e.g., Bunge, 1997; Norkus, 2005; Gerring, 2007; Falleti and Lynch, 2009).³⁵

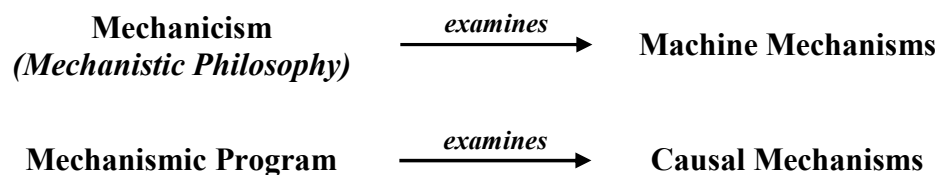


Figure 7. Relationship between the different meanings of ‘mechanism’

4.3. The Conceptual Evolution of ‘Mechanism’ in Biology

Darden (2006) has noted that “The history of the usage of the concept of mechanism from the seventeenth century to molecular biology has yet to be written” (p. 289, fn. 5). It would be impossible to provide a comprehensive account of this history here. Instead, I will restrict myself in this section to indicating what I take to be the critical episodes in that history which resulted in the semantic fragmentation of ‘mechanism’.

³⁴ Jacques Monod, one of the founders of molecular biology, captures the distinctively mechanistic mindset of this field in his conception of the cell: “By its properties, by the microscope clockwork function that establishes between DNA and protein, as between organism and medium, an entirely one-way relationship, this system obviously defies ‘dialectical’ description. It is not Hegelian at all, but thoroughly Cartesian: the cell is indeed a *machine*” (Monod, 1977, p. 108).

³⁵ Indeed, these authors have adopted the term ‘mechanismic’ precisely because they recognize the importance of distinguishing explanations based on causal mechanisms from mechanistic explanations of machine mechanisms. Gerring (2007, p. 163), for instance, remarks: “It should be noted that this contemporary understanding of mechanism [i.e., *causal mechanism*] departs dramatically from common nineteenth-century and early twentieth-century understandings of the term, which invoked a *mechanistic* account of the world. In this context, mechanism meant ‘the theory that all phenomena can be explained in terms of the principles by which machines (mechanical systems) are explained without recourse to intelligence as an operating cause or principle’ [...]. Evidently, to say ‘mechanism’ in a contemporary context does not mean that one is wedded to a mechanistic causal account modelled on Newtonian physics”.

The first two meanings of ‘mechanism’ I distinguished, mechanicism and machine mechanism, can be traced back to the natural philosophy of the seventeenth century. As we saw in the previous chapter, mechanicism in its first formulations was intertwined with natural theology, given that the mechanistic understanding of the universe as intricate clockwork (i.e., as a machine mechanism) necessarily implied a Divine Creator. As a result, all things in nature, including living systems, became conceived as complex assemblages of machinery created by an intelligent Designer. It is this mechanistic understanding which enabled the notion of machine mechanism to be employed beyond the realm of technology and engineering in explicitly biological contexts. For the mechanistic biologist, as we have already seen, living organisms are not just composed of machine mechanisms; they *are* themselves machine mechanisms. Indeed, allusions to the ‘mechanism of the body’ are standard throughout the history of physiology.

With Charles Darwin’s theory of evolution by natural selection, it became possible to naturalistically explain the complex adaptations of organisms without needing to appeal to a divine Creator. One of the implications of Darwin’s theory was that its evolutionary understanding of organisms seemed to be at odds with the engineering-based conception of life of mechanicism, exemplified by its postulation of machine mechanisms. Therefore, to uncover the semantic evolution of the concept of mechanism, it is necessary to address two key questions:

- (a) What happened to the notion of machine mechanism in biology after Darwin?
- (b) When and why did the notion of causal mechanism become pervasive in biology?

In a recent paper, Ruse (2005) has provided answers to both of these questions. However, I will argue that his answers are unconvincing and that consequently the two questions need to be re-addressed. In response to question (a), Ruse presents textual evidence which shows that although Darwin did occasionally refer to biological machine mechanisms, unlike earlier biologists he *always* understood these in a purely metaphorical sense. Ruse concludes from this that Darwin was responsible for demoting the notion of machine mechanism in biology to a heuristic status. With Darwin, machine mechanisms lost their ontic basis and became reconceptualized as heuristic tools that aid the investigation of adaptation. Darwin himself made use of the

machine mechanism-heuristic in his inquiry into the workings of barnacles and orchids, and this remains a standard practice in evolutionary biology today.

Although this account may seem reasonable, a more careful examination reveals its problems. Despite the apparent incompatibility between the mechanistic conception of organisms as machine mechanisms and a Darwinian understanding of organisms, what we actually find in modern evolutionary biology is that the machine mechanism-language is *not* used exclusively at a heuristic level. Contrary to Ruse's expectations, Darwin did not strip the notion of machine mechanism of its ontic significance. Rather, it was evolutionary biology *itself* which adapted to accommodate mechanistic thinking about organisms, so that since Darwin, "the idea that the world is full of *designed machines* has been replaced by the idea that it contains *evolved machines*" (Craver and Darden, 2005, p. 239, my emphasis). In fact, I showed in the previous chapter that Stephen Jay Gould and Richard Lewontin's (1979) well-known critique of adaptationism can be interpreted precisely as a reaction against this excessive reliance on machine mechanism-thinking in evolution, which all too often constitutes not just a heuristic tool but also a theoretical justification for understanding organisms as optimally-designed machines engineered by natural selection.

Moving to other areas of contemporary biology, it quickly becomes apparent that machine mechanism-talk also remains entrenched at an ontic level. In molecular biology, for instance, the standard conception of the organism is that of a machine programmed by its genes and decomposable into its component machine mechanisms. An important point, however, is that despite the fact that machine mechanisms continue to play a fundamental role in many areas of biology, the term 'mechanism' is generally no longer used to designate them. Instead, contemporary biologists tend to refer to machine mechanisms simply as *machines*, presumably in order to distinguish this notion from the sense in which 'mechanism' is now most commonly used by biologists, namely the causal mechanism sense.

Ruse's explanation for the displacement of machine mechanism by causal mechanism as the most widely used sense of 'mechanism', i.e., his answer to question (b), is also problematic. He suggests that Darwin's secularization of mechanismism enabled the concept of 'mechanism' to acquire widespread currency in the broader sense of causal

mechanism. With Darwin, ‘mechanism’ came to be used to designate a much wider range of biological phenomena, including Darwin’s own ‘mechanism’ of natural selection. However, after thoroughly searching through Darwin’s works, Ruse actually discovers that Darwin “simply does not speak of natural selection as a mechanism” (2005, p. 291). Darwin only uses ‘mechanism’ in the machine mechanism sense; the very idea of a causal mechanism is simply alien to him. As Ruse himself indicates, it is not until the late nineteen-thirties and early forties that natural selection came to be generally referred to as a ‘mechanism’. Neither R. A. Fisher (1930) nor J. B. S. Haldane (1932) used this language, but Theodosius Dobzhansky (1937) did, noting that “the theory of natural selection is primarily an attempt to give an account of the probable mechanism [i.e., *causal mechanism*] of the origin of the adaptations of organisms to their environment” (p. 150). If Darwin’s secularization of mechanicism truly brought about the widespread use of causal mechanism, why is it that three-quarters of a century had to pass from the publication of Darwin’s *Origin of species* for natural selection to be commonly referred to as a ‘mechanism’?

In light of these difficulties, I want to propose a rather different answer to question (b). When considering the factors that had the greatest impact on mechanicism in the late nineteenth and early twentieth centuries, far more important than the advent of Darwinism was the gradual erosion of somatic vitalism. As we saw in Chapter 2, the rising empirical success of mechanicism in the late nineteenth century in fields as diverse as physiology, developmental biology, and biochemistry eventually led to the marginalization of somatic vitalism. No longer being confronted by serious opposition, the mechanistic conception of life became widely accepted as an elementary presupposition of biological research in the early decades of the twentieth century. “At the present day”, wrote the embryologist Joseph Needham in 1925, “the situation is in effect the complete triumph of mechanistic biology. It is not alone in the field, because the neo-vitalists do exist as a small minority, but the vast preponderance of active biological workers are mechanists” (p. 235).

I would argue that one of the key consequences of the consolidation of mechanicism was that it was no longer necessary to explicitly defend the basic tenets of this doctrine. The view that living systems are machine mechanisms did not need to be

justified and could simply be taken as a given. As a result, mechanism-talk became applied to all kinds of biological phenomena, given the mechanistic confidence that everything would, in due course, be explained in terms of the causal operation of machine mechanisms. This increasingly loose use of ‘mechanism’ caused the word to gradually lose its distinctive mechanistic connotations, becoming a ‘dead metaphor’ completely devoid of theoretical content that could be readily applied beyond the realm of machine-like systems to any biological phenomenon in need of a causal explanation. It is this semantic shift, I suggest, which led the term ‘mechanism’ understood in the more general and inclusive sense of causal mechanism to acquire such widespread currency in biology.

Evidence for this account can be found in the writings of the biologists of this period. For example, J. S. Haldane, the founder of organicism and one of the most influential physiologists of the early twentieth century, drew attention on several occasions to the increasing proliferation of mechanism-talk in biology, pointing out that using the term ‘mechanism’ with respect to a phenomenon no longer implied conceiving it mechanistically as a machine mechanism. In *The Sciences and Philosophy*, he observed that “In current physiological literature it is still customary, in describing what is known as to different bodily activities, to refer to them as ‘mechanisms’ – for instance, the ‘mechanisms’ of reproduction, respiration, secretion, etc.” despite the fact that “There are perhaps few physiologists who now consider that they have any real conception of these mechanisms [as *machine mechanisms*]”. The usage of ‘mechanism’, Haldane noted, has become “a mere matter of custom” (Haldane, 1930, p. 59). In *The Philosophical Basis of Biology*, Haldane reiterated these remarks, indicating that physiologists “have acquired the habit, almost unconscious, of referring to the ‘mechanisms’ of various physiological activities, though they have not the remotest conception of what sort of mechanisms [i.e., *machine mechanisms*] these activities represent”. He concluded from this that “the use of the word ‘mechanism’ is a mere empty formality” (Haldane, 1931, p. 11). Although Haldane openly voiced his concern regarding this looser use of ‘mechanism’ in the causal mechanism sense, warning that “such a mode of expression is extremely misleading to that miscellaneous body which we call the public” (Haldane, 1930, p. 59), he clearly did not succeed in persuading his contemporaries against this usage of the term. Still, what is relevant in the present discussion is that his remarks lend credence to my

proposed explanation of the supplantation of machine mechanism by causal mechanism as the most common meaning of the term in biology.³⁶

4.4. The Mechanismic Program in Relation to Mechanicism

So far I have argued that due to the success of mechanicism in the early twentieth century, the causal mechanism sense of ‘mechanism’ became predominant in biology during this period, and remains so to this day. But how and when did the different senses of ‘mechanism’ come to be featured in the philosophy of biology? Exploring this question will help situate the recent mechanismic program in relation to mechanistic philosophy. This will be a key step in the development of my argument, as showing the fundamental differences between these two research programs will provide the basis for my critical engagement with the mechanismic program in Sections 4.5 and 4.6.

As I noted in Chapter 1, the longstanding conflict between mechanists on one side and vitalists (including organicists) on the other, being in the final analysis a dispute concerning the very nature of life, constituted the central theme in the philosophy of biology during the first half of the twentieth century (cf. Johnstone, 1914; Woodger, 1929; Bertalanffy, 1952), even if by this time most experimental biologists considered that the dispute had already been resolved in favour of mechanicism. Mechanistic biology and machine mechanisms continued to be discussed in subsequent decades (e.g., Varela and Maturana, 1972), capturing even the attention of leading exponents of logical empiricism like Carl Hempel (1966, ch. 8) and Ernest Nagel (1979, ch. 12). However, following the academic institutionalization of the philosophy of biology at the hands of David Hull, Michael Ruse and others, discussions of mechanistic biology came to an abrupt end as the new generation of philosophers of biology, influenced by prominent evolutionists like Ernst Mayr, turned its attention to theoretical issues in evolutionary biology, such as the levels of selection, the definition of fitness, and the nature of species. Nevertheless, critical examinations of mechanistic biology and machine mechanisms are still featured in the contemporary literature (e.g., Rosen,

³⁶ It is interesting to note that, as Ruse (2005) recognizes, the causal mechanism sense of ‘mechanism’ first began to permeate the literature on natural selection only a few years after Haldane’s warnings against this looser use of the term.

1991; Lewontin, 2000; Kaneko, 2006; Dupré, 2007), although the terms in which the issues are discussed have changed somewhat.

What of the third sense of ‘mechanism’? When did causal mechanisms enter the philosophy of biology? Browsing the literature, one finds passing references to the term ‘mechanism’ employed in the causal mechanism sense in the writings of Stuart Kauffman (1970), Marjorie Grene (1971) and William Wimsatt (1972). However, Robert Brandon (1985) appears to have been the first to provide a detailed analysis of the importance of causal mechanisms for biology. Brandon’s account is important for several reasons. For one thing, it is the first to explicitly recognize the semantic ambivalence inherent in the biological usage of ‘mechanism’, and the inevitable difficulties that arise when defining this concept.³⁷ More crucially, it presents an understanding of the postulation of causal mechanisms in biology that distinctly characterizes the mechanistic program today, namely that the appeal to causal mechanisms in scientific practice does *not* imply a commitment to the reductionistic agenda of mechanicism.³⁸ Indeed, whereas mechanicism, as Craver and Darden (2005, p. 235) note, is “closely aligned with the spirit of reductionism and the unity of science”, the mechanistic program focuses on multi-level mechanistic explanations (given in terms of causal mechanisms) and with an explicitly non-reductive view of science (Craver, 2005; Darden, 2005).

The mechanistic program, unlike mechanicism, is not primarily concerned with biological ontology, but with the nature of biological explanations. This is not surprising given that the postulation of causal mechanisms, having become a virtually ubiquitous practice in biology, says very little about a biologist’s ontological commitments. Physiologists, ecologists, neuroscientists, and cell biologists have very different understandings of living systems, yet they all appeal to causal mechanisms in

³⁷ In fact, when Brandon asks what ‘mechanisms’ are, he is unable to provide a precise definition. He notes that ‘mechanism’ may refer to “spring-wound clocks and watches” (i.e., *machine mechanisms*) but also to “small peripheral populations and geographic isolating barriers” (i.e., *causal mechanisms*). To make matters worse, Brandon observes, in the philosophy of biology ‘mechanism’ “is typically used to designate the position opposing vitalism, holism, or organicism” (i.e., *mechanicism*). The semantic ambiguity is exacerbated by Brandon’s surprising proposal to use the term ‘mechanism’ in a fourth sense to refer to the practice of formulating causal mechanisms in science, stating confusingly that “the position I call mechanism is given in terms of search of mechanisms” (Brandon, 1985, p. 346).

³⁸ Brandon further develops this key thesis in a more recent essay entitled ‘Reductionism versus holism versus mechanism’ (Brandon, 1996, ch. 11).

their research. Clearly, whatever ontological commitments they all share are likely to be very general in nature. This stands in contrast with molecular biologists' standard mechanistic conception of living systems as machine mechanisms, for which explanations are sought from the bottom up in increasing levels of complexity. In every respect, the appeal to machine mechanisms is indicative of far more substantive ontological commitments than the appeal to causal mechanisms. These ontological commitments derive from the mechanistic conception of life which for much of the twentieth century dominated biological thought, but which today, with the growing emphasis on systemic approaches in biology, is increasingly viewed as simply one of many possible understandings of what organisms are and how they should be studied.

In the few occasions when mechanistic philosophers do explicitly address matters of biological ontology, it is usually to distinguish mechanism's appeal to machine mechanisms from their own concern with causal mechanisms (recall Figure 7). By demarcating causal mechanisms from machine mechanisms, mechanistic philosophers distance their research program from the ontological commitments of mechanismism. Mechanistic philosophers distinguish causal mechanisms from machine mechanisms in two ways. The first strategy (which I have already alluded to in Section 4.1) is to focus on the way the term 'mechanism' is presently used in biology and disregard older uses of the term as irrelevant to current analyses of the concept (e.g., Craver, 2007, p. 3). What this does is minimize the scope for conflating the older biological usage of 'mechanism' as machine mechanism (predominant in biology until the first third of the twentieth century) with the current biological usage of the term as causal mechanism. The second strategy is to explicitly differentiate 'mechanisms' (that is, causal mechanisms) from 'machines' (that is, machine mechanisms), and both Darden (2006, pp. 280-281; 2007, p. 142) and Craver (2007, p. 4 and p. 140) do this on more than one occasion.

It is important to emphasize the extent to which MDC's (2000) account of causal mechanisms has marked a turning point in philosophical discussions of this concept. Before MDC's account, characterizations of 'mechanisms' routinely conflated the machine mechanism and causal mechanism meanings. For instance, Paul Thagard (1998) notices that the term 'mechanism' is commonly featured in explanations of disease, but defines it as "a system of parts that operate or interact *like those of a*

machine” (p. 66, my emphasis). Similarly, when Glennan first defines ‘mechanism’, he indicates that his definition is meant to apply to “complex systems *analogous to machines*” (1996, p. 51, my emphasis). In fact, Glennan has continued to heavily rely on the notion of machine mechanism in his account of ‘mechanisms’, going as far as to cite cells and organisms as prime examples of his conception of them (2002, p. S345). Although mechanistic biologists do indeed ontologically conceive cells and organisms as machine mechanisms, it makes little sense for any biologist to consider the causal mechanism of an entire cell or organism. Most mechanistic philosophers would almost certainly disagree with Glennan’s designation of cells and organisms as ‘mechanisms’, and the reason is clear. The mechanistic program “strives to characterize mechanism [...] in a manner faithful to biologists’ own usages” (Darden, 2007, p.142) and causal mechanism *is* what contemporary biologists mean when they use the word ‘mechanism’. This is why mechanistic philosophers focus exclusively on this sense of the term, and why most of them would not recognize alleged machine mechanisms like cells and organisms as ‘mechanisms’.

The reason for Glennan’s apparent unconcern regarding the lack of correlation between his conception of ‘mechanism’ and the way the term is actually used by most biologists is that his ‘mechanism’ account is not primarily motivated by an interest in scientific practice (like MDC and others), but by a concern with the nature of causation. Indeed, in his 1996 paper Glennan sets out to address Hume’s sceptical challenge regarding the connection between cause and effect by suggesting that ‘mechanisms’ could provide a plausible metaphysics of causation. Glennan proposes that events are causally related *if* there is a ‘mechanism’ that connects them, and he uses this conception of ‘mechanism’ to develop a mechanical view of explanation (Glennan, 2002). In doing so, Glennan builds on Wesley Salmon’s (1984) account of causal-mechanical explanation, which was itself an elaboration of Peter Railton’s (1978) deductive-nomological model of probabilistic explanation, in which the term ‘mechanism’ was introduced into the philosophical literature on explanation (Glennan 2002, p. S343). Interestingly, this earlier work on ‘mechanisms’, unlike the more recent biologically-inspired mechanistic discourse, does actually show some clear links with mechanicism. Railton (1978) says the following regarding his *mechanistic* orientation:

The goal of understanding the world is a theoretical goal, and if the world is a machine—a vast arrangement of nomic connections—then our theory ought to give us some insight into the structure and workings of the mechanism [i.e., *machine mechanism*], above and beyond the capability of predicting and controlling its outcomes. (Railton, 1978, p. 208)

This conception of the world as a machine mechanism, as well as the stated desire to understand, predict, and control it, are all characteristic attributes of mechanistic philosophy. Along similar lines, Glennan (1996) points out that his account of ‘mechanisms’ is “largely inspired by the insights of the Mechanical philosophers’ of the seventeenth century” (p. 51). Thus, Skipper and Millstein’s (2005) banner of ‘the new mechanistic philosophy’ would have been far more appropriate if it had been used to refer to *this* literature on ‘mechanisms’, rather than to the recent examinations of causal mechanisms in biology, which on the whole bear little connection to the original motivations of this earlier work in the philosophy of science. Darden’s (2008) latest appraisal of the mechanistic program makes this explicit when she clarifies that “work on mechanisms in biology originated (primarily) not as a response to past work in philosophy of science but from consideration of the work of biologists themselves” (Darden, 2008, p. 958).

Overall, it is clear that the mechanistic program must be regarded as being completely independent from mechanismism (both as a general doctrine and specifically as it applies to biology). Indeed, we have seen how leading mechanistic philosophers like Craver and Darden reject some of the core tenets of mechanismism, such as the reducibility of biology to physics and chemistry, and the exclusive reliance on strictly reductionistic explanations. Demarcating the mechanistic program from mechanismism is crucial, as the failure to do so results in problematic analyses of causal mechanisms in contemporary biology. The most prominent example of this, in my view, is found in some of Bechtel’s recent work. Whereas most mechanistic philosophers are rather cautious in their use of history when discussing causal mechanisms, emphasizing the importance of historical context and drawing on relatively recent case studies when illustrating their claims, Bechtel has traced the appeal to ‘mechanisms’ in scientific explanation not just to Descartes in the seventeenth century, but all the way back to the Ancient Greek atomists of the fifth century BCE (2006, pp. 20-21; 2008, p. 10). But instead of examining how the

meaning of ‘mechanism’ has developed over time (as Ruse (2005) does, and as I have attempted to do in Section 4.3), Bechtel takes the modern sense of ‘mechanism’ as causal mechanism as his starting point and then simply projects it back in history. As a result, his historical discussions conflate the distinctive appeal to machine mechanisms by mechanistic biologists with the almost ubiquitous appeal to causal mechanisms by biologists today (e.g., Bechtel, 2006; ch. 2; Bechtel, 2007). Understanding the term ‘mechanism’ in the causal mechanism sense, Bechtel complains that critics of mechanistic biology commit a grave mistake in assimilating the notion of ‘mechanism’ to that of machine (e.g., Bechtel, 2008, p. 2), not realizing that the very reason for this is that when mechanists speak of ‘mechanisms’, machines (i.e., machine mechanisms) is *precisely* what they have in mind.³⁹

The striking thing is that Bechtel, just like Craver and Darden, actually rejects central tenets of mechanistic biology, such as the exclusive reliance on reductionistic explanations (e.g., Bechtel and Abrahamsen, 2008), and the privileging of the material and efficient causes of organisms over their final and formal ones (e.g., Bechtel, 2007). But, again, instead of distancing himself from mechanicism, Bechtel seems to think that the only way to make sense of the pervasive mechanism-talk in biology today is to expand mechanistic biology accordingly, not realizing that the appeal to ‘mechanisms’ in scientific practice no longer commits one to mechanicism (as ‘mechanism’ is now generally employed in the causal mechanism sense). This leads Bechtel to formulate a highly idiosyncratic conception of mechanistic biology, so general and inclusive that none of the distinctive ontological and epistemological commitments that tend to be associated with it are relevant. Instead, all that appears to qualify a biologist as a ‘mechanist’ is that she appeals to ‘mechanisms’ in her research. Similarly, all that qualifies an explanation as ‘mechanistic’ is that a ‘mechanism’ is featured in it, regardless of the way in which this concept is used.⁴⁰

³⁹ This is as true for seventeenth-century mechanists like Descartes as it is for twentieth-century mechanists like Loeb.

⁴⁰ Much more could be said regarding Bechtel’s questionable reconstruction of mechanistic biology, such as the way in which he appropriates classic anti-mechanistic ideas like self-organization for the mechanists (e.g., Bechtel, 2007) despite the fact that the concept of self-organization was actually coined by Immanuel Kant in order to argue that organisms are fundamentally different from machines and thus cannot be explained in mechanistic terms. However, an elaborate critical examination of Bechtel’s historical claims would take me beyond the scope of this chapter.

I can think of two reasons for Bechtel's misrepresentation of mechanistic biology. The first is that his earlier work with Robert Richardson (1993) was in fact concerned with the nature of *mechanistic* explanations (specifically with the strategies of decomposition and localization that are often featured in them).⁴¹ So in the wake of the influence of MDC's (2000) account of causal mechanisms, Bechtel might have felt it natural to bridge his earlier discussion of mechanistic biology with an examination of causal mechanisms, since, after all, the concept of 'mechanism' is central to both discourses. Still, the main reason for Bechtel's misrepresentation is that he does not realize that the concept of 'mechanism' has more than one meaning. It is because he conflates the notions of machine mechanism and causal mechanism that he also conflates mechanicism with the mechanistic program (e.g., Bechtel, 2006, ch. 2; 2008, ch. 1).

Nevertheless, the misrepresentation of mechanistic biology is not the only, or even the main, problem that results from the conflation of causal mechanisms and machine mechanisms. The most serious consequence of not distinguishing these notions is that causal mechanisms become inappropriately endowed with the ontic status of machine mechanisms. This ontologization of causal mechanisms is very widespread in mechanistic philosophy, and in the next section I will discuss some of the problems which stem from it.

4.5. Problems Resulting from the Ontologization of Causal Mechanisms

Mechanistic philosophers tend to conceive causal mechanisms as real things in the world existing independently from our conceptualization of them. However, based on the role they play in scientific practice, I want to suggest that causal mechanisms are better understood as heuristic models that facilitate the explanation of phenomena. The fact that the overwhelming majority of mechanistic philosophers speak of them as "real systems in nature" (Bechtel, 2006, p. 33) I attribute to an inadvertent

⁴¹ The fact that Bechtel and Richardson (1993) are interested in mechanistic explanations (relating to machine mechanisms) as opposed to mechanistic explanations (relating to causal mechanisms) is evidenced by their assertion that "By calling the explanations *mechanistic*, we are highlighting the fact that they treat the systems as producing a certain behavior in a manner analogous to that of *machines developed through human technology*" (p. 17, my emphasis). Indeed, their analysis of mechanistic explanation begins with a characterization of *machines*, not of mechanisms. However, in his more recent work Bechtel readily describes as 'mechanistic' not just the distinctive appeal to machine mechanisms by mechanists, but also the general appeal to causal mechanisms in scientific practice.

transposition of the ontic status of machine mechanisms (the original sense in which ‘mechanism’ was used) to the notion of causal mechanism (the standard meaning of ‘mechanism’ in biology today). This ontologization of causal mechanisms often results in a conception of them as autonomous complex systems (analogous in many respects to machine mechanisms) which constitute and operate within the organism (e.g., Glennan, 2002; Bechtel, 2007). I maintain that this ontic conception of causal mechanisms is problematic, and I will illustrate this claim by examining what are perhaps the two most distinctive characteristics of causal mechanisms in biology: *function* and *organization* (cf. McKay and Williamson, 2010).

4.5.1 Function

The operation of a causal process described in a causal mechanism produces a particular phenomenon which serves to individuate and causally relate the entities and activities that are responsible for it. In biology, the phenomenon produced by the causal process described in a causal mechanism usually enables the fulfilment of a function, so that specifying the causal mechanism for a function explains how this function is causally brought about. The problem of conceiving causal mechanisms as autonomous complex systems is that it overlooks the conditions that actually enable the functions of these systems to be carried out, as well as the true biological significance of those functions.

A living organism is an organized network of processes of production, transformation, and regeneration of components that continuously realizes itself by means of the coordinated orchestration of the components that make it up (see Maturana and Varela, 1980). In this way, the organism constitutes an integrated whole which maintains its identity through time by regulating, repairing, and reproducing its component parts. These parts stand in a relation of collective interdependence, as every one of them is necessary for the generation and operation of every other. Thus the attribution of functions to the parts of an organism is dictated by the means in which each part individually contributes to the maintenance and organization of all other parts and hence to the organism as a whole (McLaughlin, 2001; Mossio et al., 2009). This means that the function of all suborganismal systems and processes featured in causal mechanisms is ultimately that of preserving the intrinsically

purposive self-organization of the whole organism. As a result, these functions reveal a great deal about how the organism satisfies its needs and copes with its surroundings.

The notion of autonomous causal mechanisms operating within the organism is, I suggest, nothing more than a pragmatic idealization that biologists appeal to in order to narrow their focus on the particular parts of the organism they happen to be investigating. This heuristic fragmentation of the organism into causal mechanisms, despite being necessary for its investigation, often comes at the expense of neglecting the way in which the organism as a whole influences the behaviour of its parts. In mechanistic accounts, the conception of causal mechanisms as real autonomous subsystems neglects the fact that in order to make appropriate biological sense of the subsystems' functions, these subsystems need to be framed within a set of background conditions, that is, the *organismal context*, that enables them to carry out their functions in the first place.⁴²

Craver (2007, p. 122) indicates that “The core normative requirement on mechanistic [i.e., *mechanismic*] explanations is that they must fully account for the *explanandum phenomena*”. That is, “Good explanations account for all of the features of a phenomenon rather than a subset” (ibid., p. 161). This means that mechanistic explanations that do *not* include an account of the organismal context that enables the production of the *explanandum* phenomenon (or function) are, on Craver's terms, necessarily incomplete. This is problematic as actual scientific practice reveals that mechanistic explanations are seldom exhaustive catalogues of *all* the causal relations necessary for the production of phenomena, such as the enabling conditions provided by the organism as a whole. Rather, mechanistic explanations tend to specify only those features of the underlying causal networks that biologists deem *most relevant* for manipulating and controlling the phenomena whilst at the same time presupposing a great deal of the organismal context that makes them possible. It thus makes more sense to view causal mechanisms as idealized spatiotemporal cross-sections of

⁴² The problematic transference of mechanistic thinking is particularly pronounced here. Whereas a machine mechanism can be broken down into discrete, self-contained parts with clearly-delineated output functions without the loss of information, the parts in an organism (ontologized in most accounts of causal mechanisms) stand in a relation of collective interdependence and are thus not autonomous in any important respect (even if they can be construed as such for the purposes of their investigation). Consequently, any explanation of the functions of parts in an organism needs to account not just for the parts themselves but also for the organismal context that makes their function possible.

organisms that heuristically pick out certain causal features over others in order to account for how given functions within the organism are carried out, as these are generally the things that biologists describe when they use the term ‘mechanism’ in their explanations.

4.5.2. Organization

Mechanismic philosophers frequently emphasize the importance of organization for understanding how causal mechanisms account for functions or behaviours. MDC (2000, p. 3), for instance, state that “The organization of entities and activities determines the ways in which they produce the phenomenon”. Bechtel (2006, p. 26) similarly notes that “The orchestrated functioning of the mechanism is responsible for one or more phenomena”. The problem is that mechanismic philosophers do not actually explain *how* the entities and activities in a mechanism are organized, only *that* they are organized. MDC point out that “Entities often must be appropriately located, structured, and oriented, and the activities in which they engage must have a temporal order, rate, and duration” (p. 3) but say nothing about the means by which these crucial organizational requirements are actually met in living organisms. Instead, what discussions of organization in the mechanismic literature essentially amount to is the plain assertion that ‘organization matters’ (e.g., Craver, 2007, pp. 134-139).

Still, if causal mechanisms are to be conceived ontically as real suborganismal systems (rather than epistemically as idealized models *of* those subsystems, as I suggest) then just paying lip service to the fact that these subsystems are organized is insufficient. To *fully* account for the *explanandum* phenomenon (Craver’s normative requirement for a good mechanismic explanation) it becomes necessary not just to *specify*, but also to *explain* how this organization is generated and maintained. The problem is that this requires taking the explanation beyond the actual causal mechanism to the level of the organism as a whole, given that suborganismal parts do not organize themselves but rely on the purposive action of the whole organism for their generation, organization, and maintenance. This is rarely understood in mechanismic accounts of organization. For example, when Craver (2007) indicates that a “mechanism might compensate for the loss of a part by recovering (healing the

part), by making new use of other parts, or by reorganizing the remaining parts” (p. 148), he inappropriately attributes actions to an ontologized causal mechanism that are actually performed by the organism which contains it.⁴³

As I argued in my discussion of function, one of the advantages of understanding causal mechanisms as idealized models of suborganismal causal processes rather than as real things is that a satisfactory mechanistic explanation need not include an account of how the target system is actually organized by the organism *even if* this organization is strictly speaking necessary for the system to causally bring about the phenomenon. This is more in accordance with scientific practice, in which causal mechanisms tend to pragmatically abstract away the organismal context and only specify the causal features that are taken to be most relevant for controlling and manipulating the phenomena being investigated. In the next section, I will elaborate my epistemic account of causal mechanisms, indicating the further advantages of this view over the ontic conception that most mechanistic philosophers favour.

4.6. Defending an Epistemic Conception of Causal Mechanisms

It is important to keep in mind that the causal mechanism sense of ‘mechanism’ was not conceptually developed by philosophers and then applied to scientific practice. Rather, it arose from scientific practice and it has only recently been philosophically reconstructed to make sense of how scientists explain phenomena. Therefore, the success of any given philosophical reconstruction of ‘mechanism’ must be measured in terms of how well it captures the way this term is used in scientific practice. The conception of causal mechanism that I argue best fits biologists’ mechanism-talk is that of a contingent explanatory description which heuristically abstracts away the complexity of a living system sufficiently to describe some localized causal process which leads to the realization of some function within that system. That is, causal mechanisms are epistemic models which facilitate the explanation of how phenomena are causally brought about. It is worth pointing out that although most mechanistic

⁴³ Not only does Craver (or Darden or Bechtel) not refer to the influence of the whole organism in explaining how the causal processes instantiated by causal mechanisms achieve and maintain their organization, but there is reason to believe that mechanistic explanations, by virtue of their nature, simply *cannot* accommodate organismal organization, given that mechanistic explanations are, in Craver’s words, “anchored in components” (Craver, 2007, p. 138), and an organism’s self-organization is a higher-level phenomenon that is not explainable by attending to the properties of component parts.

philosophers claim to uphold an ontic view of causal mechanisms, much of what they say is actually perfectly compatible with an epistemic conception. In fact, it is not difficult to find examples in the mechanistic literature in which ontically-construed causal mechanisms are conflated with their epistemic representations, as I will show in a moment. This ambiguity, I suggest, is the result of the tension which arises from inappropriately transposing the ontic status of machine mechanisms onto causal mechanisms on the one hand, and paying close attention to the role that mechanism-talk actually plays in scientific practice on the other.

When scientists inquire about the ‘the mechanism for P’ (where P is the phenomenon of interest), the term ‘mechanism’ does not refer to that which is explained but rather to that which does the explaining. Craver (2007) acknowledges this when he specifies that “The *explanans* is a mechanism” (p. 139) and the phenomenon of interest is the *explanandum* (p. 6).⁴⁴ In this way, specifying a causal mechanism for a phenomenon implies providing an explanation for it. As MDC indicate, “Mechanisms are sought to *explain* how a phenomenon comes about or how some significant process works” (2000, p. 2, my emphasis). One of the implications of the epistemic account of causal mechanisms is that it is no longer necessary to postulate additional epistemic notions like ‘mechanism sketch’ and ‘mechanism schema’ to make sense of mechanistic explanations. Depending on the degree of abstraction, causal mechanisms may constitute what mechanistic philosophers call ‘sketches’, ‘schemas’, or ‘mechanisms’. This is tacitly conceded by Craver when he indicates that progress in formulating a successful mechanistic explanation “involves movement [...] along the sketch-schema-mechanism axis” (Craver, 2007, p. 114).

Moreover, the very characterizations of causal mechanisms that mechanistic philosophers propose are in fact perfectly compatible with an epistemic account of causal mechanisms. According to the epistemic view, causal mechanisms constitute idealized representations of causal processes. These causal processes are abstracted temporally and spatially. Temporally, a causal mechanism delimits the causal process by specifying arbitrary beginning and end points that are selected on pragmatic grounds. MDC (2000, p. 11) explicitly recognize that the set-up and termination

⁴⁴ Thus, mechanistic explanations should be understood not as explanations *of* causal mechanisms, but as explanations *given in terms of* causal mechanisms.

conditions of causal mechanisms are “idealized states”, and Darden has reiterated this point on several occasions, noting that the beginning and end points of causal mechanisms are “more or less arbitrarily chosen” (2007, p. 141; see also Torres, 2009, p. 240, fn. 10). So although MDC purport to defend an ontic conception of causal mechanisms, they actually characterize them in terms of epistemically-selected beginning and end points.

Causal mechanisms are also abstracted spatially, according to the epistemic view, as they can only capture certain ontic features of reality at the expense of neglecting others. What gets represented and what is omitted in a causal mechanism is dictated by the nature of the *explanandum* phenomenon. Craver (2007, pp. 139-160) reaches this same conclusion when he considers the normative requirements that determine whether or not something is included as part of a causal mechanism, asserting repeatedly that the delimitation of causal mechanisms can only occur *in the context of explanation*. That is, components, activities, and organizational features are part of the causal mechanism for P (where P is the phenomenon of interest), if and only if they are relevant to the explanation of P. The act of individuating the causal mechanism for P is thus the act of determining what aspects are causally relevant to the explanation of P. The delimitation of causal mechanisms hence “depend[s] on the epistemologically prior delineation of relevance boundaries” (Craver, 2007, p. 144).

This view of causal mechanisms significantly departs from the conception of them as autonomous complex systems (defended by Glennan, Bechtel, and at times by Craver himself, as I showed in Section 4.5), given that the parts of a causal mechanism do not even need to be structurally correlated.⁴⁵ All that matters is that they are *causally relevant* to the production of the *explanandum* phenomenon. Craver fleshes out this notion of causal relevance by appealing to James Woodward’s (2003) manipulability theory of causation. In this way, a part is causally relevant to the phenomenon produced by a causal mechanism if one can modify the production of this phenomenon by manipulating the behaviour of the part, and one can modify the behaviour of the part by manipulating the production of the phenomenon by the causal mechanism.

⁴⁵ Indeed, Craver acknowledges that causal mechanisms “frequently transgress compartmental boundaries” (Craver, 2007, p. 141), and “are often spatially quite distributed” or “tightly interwoven into their systematic context” (ibid., fn. 23, p. 143).

Although Craver's account of explanatory relevance is compatible with both an ontic and an epistemic conception of causal mechanisms, there do not appear to be any obvious reasons for favouring the former over the latter view; if anything, the latter view seems more reasonable. Explanations always presuppose a context that specifies what is to be explained and how much detail will suffice for a satisfying answer, and Craver recognizes that it is this very epistemic context that determines how causal mechanisms are individuated and what details are featured in them. The crucial requirement of any causal mechanism, according to Craver's account, is that it must capture the underlying causal relationships of the target system in such a way that it exhibits the necessary resources for explaining how the target system will behave as a result of interventions and manipulations of its parts. An epistemic view of causal mechanisms fulfils this requirement.

It may be helpful to illustrate these claims with an example. Consider the causal mechanism for the membrane trafficking of the delta-opioid receptor (DOR) induced by pain stimulation, shown in Figure 8 (adapted from Bie and Pan, 2007). This causal mechanism exhibits all of the features I have discussed. It is a step-by-step explanation of the mode of operation of the signal transduction pathway induced by pain stimulation that triggers the intracellular activation of DOR, which results in effective pain relief. The causal mechanism is abstracted both temporally and spatially. Temporally, it abstracts the continuous life-cycle of DOR into a series of discrete idealized stages, which are numbered in the causal mechanism. Spatially, although the whole cell is depicted, only the features that are causally relevant to the membrane trafficking of DOR (i.e., the *explanandum* phenomenon) are represented in the causal mechanism. If we happened to be interested in explaining any other cellular phenomenon, a different yet partially-overlapping set of features would be included in the causal mechanism. Moreover, the organismal context (in this case, the cell) is abstracted away and yet it is heavily presupposed, as it provides the enabling conditions that are ultimately necessary for the membrane trafficking of DOR. Finally, the causal mechanism constitutes a model of a particular cross-section of a cell that provides the necessary resources for anticipating how interventions and manipulations of any of the causally relevant parts within the cell and any of the successive stages of the described process will affect the membrane trafficking of

DOR. In this way, this causal mechanism serves the heuristic purpose of aiding the physiological and pharmacological investigation of pain relief.

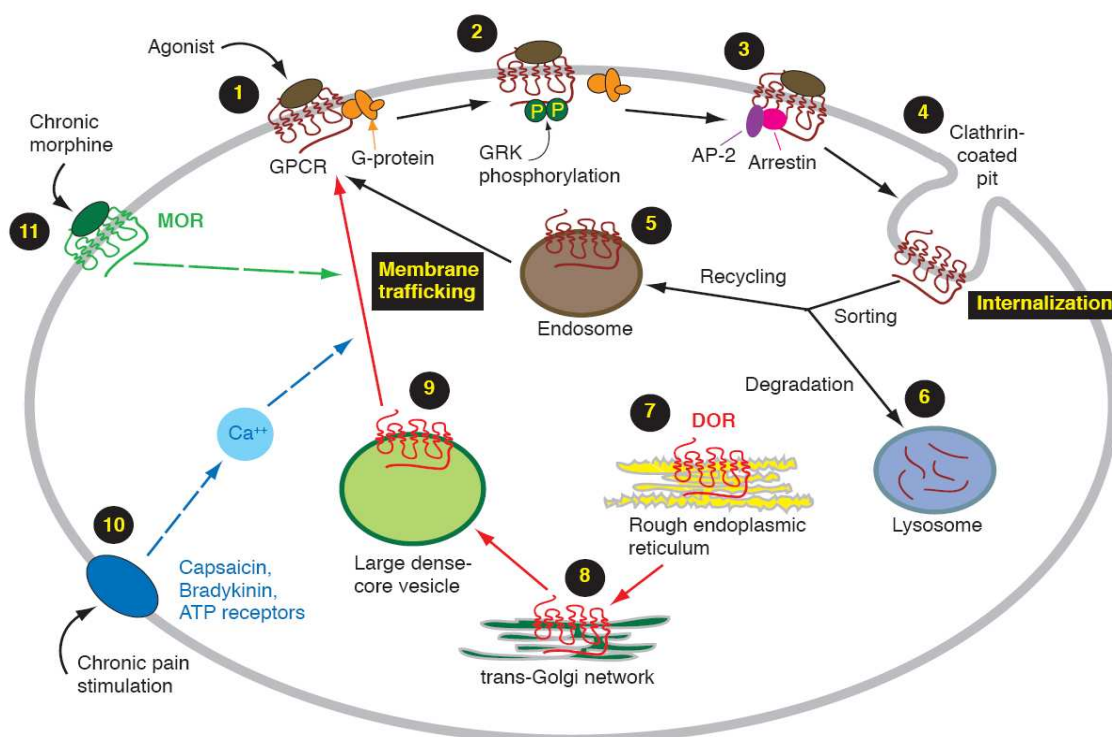


Figure 8. Causal mechanism of the Membrane Trafficking of the Delta-Opioid Receptor (DOR) Upon agonist binding (1), DOR is phosphorylated by GRK (2). It then binds to proteins AP-2 and arrestin (3), and undergoes the process of internalization via endocytosis (4). Once internalized, the receptor is sorted and targeted either to endosomes via the recycling pathway (5) for membrane insertion, or to lysosomes for degradation via the degradation pathway (6). DOR is synthesized in the endoplasmic reticulum (7), and transported to the trans-Golgi network (8), becoming a mature receptor which is targeted in dense-core vesicles (9), ready for membrane trafficking and insertion. Chronic pain stimulation activates receptors (10) and increases intracellular calcium concentration, inducing the membrane trafficking of DOR.

So far in this section, I have advanced my defence of an epistemic view of causal mechanisms by showing how the key features of causal mechanisms that mechanistic philosophers deem most important are not only not incompatible with the epistemic account I propose, but actually provide support for it. Still, the compatibility of the central claims of mechanistic philosophy with an epistemic conception of causal mechanisms does not constitute the main incentive for adopting it. The major reason for defending an epistemic account, as I will argue in the remainder of this section, is

that it captures the meaning of biologists' mechanism-talk in ways that are simply beyond the reach of any ontic conception of causal mechanism.

Causal mechanisms are invoked to explain an extremely wide range of phenomena. As Allen (2005, p. 264) indicates, causal mechanism "can refer to very specific processes, such as the nucleophilic attack by the reactive group of an enzyme on an exposed covalent bond of its substrate, or to a whole category of reactions such as cell signal responses due to protein kinase A (PKA) second messengers". As the postulation of causal mechanisms has become a virtually ubiquitous practice in biological research, it is practically impossible to define what a causal mechanism is in a way that meaningfully captures all the different uses of this concept, given that the conditions of satisfaction for what counts as a causal mechanism are determined by the context in which it is postulated, as well as on the kind of questions that are asked of the *explanandum* phenomenon. If, as I suggest, the notion of causal mechanism is understood epistemically, then it can be characterized as an explanation where the *explanans* and *explanandum* are sorted out from the context of its formulation. However, if causal mechanisms are conceived as "real systems in nature" (Bechtel, 2006, p. 33), it becomes exceedingly difficult to specify exactly what these 'systems' actually are and what they have in common.

Paradoxically, this problem stems from the mechanistic program's desire to closely adhere to scientific practice, given that as long as it remains "faithful to biologists' own usages" of 'mechanism' (Darden, 2007, p. 142), it cannot fulfil its objective of ontically characterizing this notion in a concrete and unified manner. The reason for this is that there is a fundamental tension between the degree of concreteness of any given ontic characterization of causal mechanism and the breadth of its applicability. An ontic definition of causal mechanisms can only increase its applicability at the expense of sacrificing the concreteness of its formulation. The only way mechanistic philosophers could encompass all the different ways in which the notion of causal mechanism is employed in biological research would be to provide an ontic characterization so general and so abstract that it would be effectively vacuous.

The recent debate concerning the nature of the causal mechanism of natural selection provides an instructive illustration of this dilemma. Skipper and Millstein (2005) have convincingly argued that none of the existing ontic conceptions of causal mechanism successfully captures ‘the mechanism of natural selection’. The causal mechanism of natural selection is *not* a series of parts in a complex system interacting to produce a behaviour (à la Glennan), *nor* is it composed of entities and activities organized to produce regular changes (à la MDC), *nor* is it a structure performing a function in virtue of its component parts (à la Bechtel). The different ways in which mechanistic philosophers have dealt with this incompatibility is very revealing. Glennan (2005) bites the bullet and concludes that “there is no such thing as the mechanism of natural selection”. This strategy is problematic because it is at odds with the mechanistic commitment to the “details of scientific practice” (MDC, 2002, p. 2), given that evolutionary biologists *do* routinely refer to natural selection as a ‘mechanism’. Craver and Darden (2005) instead contemplate “whether the account of mechanism should be broadened to allow for stochastic processes and other forms of organization” (p. 240). Skipper and Millstein (2005, p. 344) also consider this option but decide against it because postulating such a broad conception of causal mechanism “may not be desirable if it means sacrificing an understanding of the things that make mechanisms distinctive in particular fields, such as molecular biology”. This concern aptly illustrates the danger of vacuity which arises from formulating exceedingly broad ontic characterizations of causal mechanisms. Benjamin Barros (2008) proposes a third solution, which is to formulate various ontic characterizations of causal mechanism, among them one which can effectively capture the causal mechanism of natural selection. The problem with this strategy is that it means giving up the objective of having a unified conception of causal mechanisms that can be used to make generalizations regarding the nature of mechanistic explanations across biology. In this way, all three of the proposed solutions end up being at odds with some objective of the mechanistic program. However, when one adopts an epistemic conception of causal mechanisms, the tensions generated by the efforts to ontically reconstruct biologists’ mechanism-talk disappear.⁴⁶

⁴⁶ Jaakko Kuorikoski (2009) has recently proposed a sort of compromise between ontic and epistemic conceptions of causal mechanisms by formulating two concepts of ‘mechanism’: an ontic one referring to componential causal systems (like the causal mechanisms of cell biology), and an epistemic one referring to abstract forms of interaction (like the causal mechanism of natural selection). Although I am sympathetic towards this sort of reconstruction, I believe that the inherent problems of the ontic

Some mechanistic philosophers may object that the thesis that causal mechanisms are epistemic rather than ontic can be refuted on the grounds that biologists often seem to use ‘mechanism’ to refer to the causal process itself and not *just* to the explanation of it. In response, I would argue that it is important to bear in mind the reasons why biologists refer to ‘mechanisms’ in the first place. The conflation of the notions of machine mechanism and causal mechanism is once again at the heart of the matter. Mechanistic philosophers tend to assume that using the term ‘mechanism’ in relation to P (where P is the phenomenon of interest) indicates something distinctive about the nature of P that warrants the use of the word ‘mechanism’. Although this has indeed been the case in the past when mechanistic biologists systematically conceived complex systems like organisms as machine mechanisms, the ubiquitous appeal to ‘mechanisms’ by the majority of biologists today is no longer determined by a set of prescriptive ontological commitments, as I argued in Section 4.4. Mechanism-talk in contemporary biology is simply a contingent product of history, or as Haldane put it, “a mere matter of custom”. Consequently, the use of the word ‘mechanism’ in an ontic sense by some biologists does not demonstrate that causal mechanisms need to be understood as real things. The ontic-epistemic dispute concerning the nature of causal mechanisms cannot be settled by listing examples of the usage of ‘mechanism’ in an ontic or an epistemic sense in the scientific literature, but by considering how best to make philosophical sense of the role played by mechanism-talk in scientific reasoning and explanation.

4.7. Conclusions: Mechanism-Talk in the Sciences

In this chapter I have showed that the concept of ‘mechanism’ in biology may refer to a philosophical thesis about the nature of life and biology (i.e., mechanicism), to the structure and inner workings of a machine-like system (i.e., machine mechanism), or to an epistemic device which facilitates the explanation of a phenomenon of interest (i.e., causal mechanism). For effective philosophical analyses of this concept, causal mechanisms need to be explicitly or implicitly distinguished from machine mechanisms, and the mechanistic program needs to be clearly demarcated from mechanicism. The inadvertent conflation of these meanings or the misapprehension of

account discussed in Section 4.5, together with the broad compatibility of an epistemic view, justifies defending a general epistemic conception of causal mechanisms.

how they relate to each other (recall Figure 7), results in problematic accounts of the role played by mechanism-talk in current scientific practice. I have argued that the most serious implication of conflating the various ‘mechanism’ meanings is that causal mechanisms become inappropriately endowed with the ontic status of machine mechanisms. I have advanced my defence of an epistemic conception of causal mechanisms in three stages: I first pointed out the basic problems facing the ontic account, I then showed the compatibility of the epistemic account with the central claims of the mechanistic program, and finally I indicated the advantages of an epistemic over an ontic account in capturing the multitudinous ways in which contemporary biologists employ the term ‘mechanism’ in their research.

As the historical and philosophical analysis of the concept of ‘mechanism’ presented in this chapter has been confined to biology, it would be interesting to see whether similar analyses in other sciences support or conflict with the conclusions I have arrived at for biology, such as the thesis that causal mechanisms are actually explanations rather than real things. Jeffry Ramsey (2008) has recently examined the role of mechanisms in organic chemistry, and one of his main findings is that “Organic chemists take mechanisms to be explanations” (p. 976) in the form of “inferences based on observational data” (p. 972).⁴⁷ This suggests that the epistemic account of causal mechanisms that I have defended here is probably applicable to other branches of science outside of biology. Expanding the range of perspectives on scientific practice should help provide further insight into the role played by the concept of ‘mechanism’ across the sciences.

⁴⁷ In fact, the textbook definition of ‘mechanism’ that Ramsey cites in his analysis closely resembles the epistemic definition of causal mechanism I offered in Section 4.2. In organic chemistry a mechanism “is a specification, by means of a sequence of elementary chemical steps, of the detailed process by which a chemical change occurs” (Lowry and Richardson, 1981, p. 174).

Chapter 5

BEYOND MECHANICISM: BIOLOGICAL ATOMISM AND CELL THEORY

The principle of autonomy of the anatomical elements can be considered as one of the most fruitful in modern physiology. This principle, or under another name, this cell theory, is not a vain expression. It has been a mistake to forget it when concerned with complex organisms. – Claude Bernard (1878)

5.1. Introduction: Coming to Terms with Cell Theory

Cell theory is generally regarded as one of the central unifying ideas in biology. It is widely acclaimed in textbooks as a cornerstone of biological science (e.g., Sharp, 1921, p. 9; Harold, 2001, p. 17) and, alongside Charles Darwin's theory of evolution, the most important generalization in biology (e.g., Wilson, 1900, p. 1; Webster, 2003; p. 9). However, what is interesting is that cell theory is far from being an obvious, self-evident truth that is universally accepted among biologists. In fact, ever since it was formally enunciated by Matthias Schleiden and Theodor Schwann in 1838 and 1839, the extent of its applicability, and even its internal coherence, have remained the subject of controversy in biology. The main aim of this chapter will be to uncover the rationale underlying the major objections that have been waged against cell theory since its formulation to the present day. To do so, it will be necessary to identify the philosophical foundations upon which cell theory rests. In turn, this will require going beyond the 'official history' of cell theory, on the grounds that there is, philosophically speaking, no direct path connecting Robert Hooke's first microscopical observations of cells in 1665 with Schleiden's and Schwann's articulation of cell theory 175 years later.

Rather than enumerating the successive recorded observations of cells from Hooke to Schleiden and Schwann, it may be instructive to consider the genesis of cell theory by examining the epistemological motivations that led to its formulation, as these can help situate the subsequent criticisms of the theory in an appropriate philosophical context. Of course, there is no single way of accomplishing this. E. S. Russell (1916), for instance, explained the development of cell theory and the subsequent challenges

to it as an expression of the fundamental biological dispute over the causal primacy of form or of function. Georges Canguilhem (2008 [1965]), on the other hand, interpreted the history of cell theory as a dialectical battle between two opposing representations of the anatomical constitution of organisms: one emphasizing continuity, and the other emphasizing discontinuity. And Timothy Lenoir (1982) traced the steps that led to Schleiden's and Schwann's enunciation of cell theory as part of a broader 'teleomechanical' research program in biology, which he argued arose out of a materialistic interpretation of Immanuel Kant's teleological conception of the organism advanced in his *Kritik der Urteilkraft* of 1790.

In this chapter, the perspective adopted to make philosophical sense of past and present disputes over the legitimacy of cell theory is one I call *biological atomism*. I characterize biological atomism as the doctrine which postulates a basic indivisible unit of life and seeks to explain the morphological constitution and physiological operation of all living beings in terms of these fundamental units. The activity of a living organism is thus conceived as the result of the activities and interactions of its elementary constituents, each of which individually already exhibits all the attributes proper to life. It is important to distinguish from the outset what I call biological atomism from mechanistic efforts to reduce biological entities (e.g., organisms) to physicochemical ones (e.g., genes), given that in theories of biological atomism the final units of analysis are still living beings in their own right.

By looking at cell theory through the prism of biological atomism, I want to suggest that we can reach a better understanding of the ideas which led to its formulation, and a fuller appreciation of the rationale underlying the major objections that continue to be waged against it. I begin by surveying the major incarnations of biological atomism prior to cell theory, and by illustrating the philosophical continuity between them (Section 5.2). I will then consider the conceptual development of cell theory itself and highlight its atomistic foundations (Section 5.3). Following this, I will examine the main criticisms of cell theory, categorizing them according to whether they represent efforts to locate the true indivisible unit of life above or below the level of the cell (Sections 5.4 and 5.5). I will conclude by reflecting more generally on the philosophical value of biological atomism and on its relation to mechanistic biology (Section 5.6).

5.2. Biological Atomism before Cell Theory

Although atomistic theories of nature were developed by a number of Ancient Greek philosophers, such as Leucippus and Democritus, none of them sought to account specifically for the constitution of living beings. It is true that Aristotle, in his *De Partibus Animalum* (2001, bk. II, 646^a, 10-24), distinguished three degrees of composition in animals: the unorganized material composed of the four primitive elements (earth, water, air, and fire), the composition of uniform body parts (e.g. bone, flesh, fat), and the composition of non-uniform body parts (e.g. face, hands, feet). However, this kind of analytical decomposition was not atomistic in the proper sense of the term. In order to unearth the genuine roots of biological atomism, one must turn to the revival of atomistic conceptions of nature and the popularization of corpuscular theories of matter and light in the late seventeenth and eighteenth centuries.

Corpuscles acquired widespread currency as explicative devices in physics largely through the work of Sir Isaac Newton. In the rare instances when Newton theorized about life, he referred to chemical transformations, especially fermentation, which he explained in corpuscular terms (Hall, 1969, p. 18). One of the chief exponents of Newtonian natural philosophy in eighteenth-century France was Georges-Louis Leclerc de Buffon, and it is to him that we owe the first explicit formulation of an atomistic theory of life. Though originally trained in physics and mathematics (he published a French translation of Newton's *Method of Fluxions* in 1740), Buffon made his most important contributions in biology. As a true Newtonian, Buffon endorsed the corpuscular conceptions of matter and light, and argued by inference that living matter must likewise be corpuscular in nature. In the second volume of his *Histoire Naturelle* (published in 1749), Buffon presented his theory of 'organic molecules', which stated that organisms are compound assemblages of elementary living particles. These biological atoms, common to animals and plants, are primary and unalterable, such that the generation and destruction of organisms is in reality the result of the association and dissociation of these elementary living beings:

The life of the animal or vegetal appears to be nothing more than the result of all the actions, all the particular little lives (if I may be allowed to express myself in this way) of each one of these active molecules, whose life is primitive and appears to be indestructible: we have found these living molecules in all living or vegetating beings: we are certain that all these organic molecules are also proper to nutrition and by consequence to the reproduction of animals and plants. It is thus not difficult to conceive that, when a certain number of these molecules are united, they form a living being: life being in each of the parts, it can be in a whole, in any assemblage whatsoever of these parts. (Buffon, quoted in Canguilhem, 2008, p. 37)

To explain the confinement of the aggregation of organic molecules in the organism, as well as the stable organization of the organic molecules in three-dimensional space, Buffon introduced the concept of ‘inner mould’ as a sort of principle of morphological constancy. With his theory of organic molecules, Buffon was able to account for a number of fundamental biological processes, including heredity, reproduction, and development.⁴⁸ Buffon’s friend, the geophysicist Pierre-Louis Moreau de Maupertuis, published a similar atomistic theory in his *Vénus physique* (published in 1745), though the elementary particles of his theory were not just alive but were also endowed with psychic properties, such as desire, aversion, and memory (Hall, 1969, pp. 18-28). In any event, the idea that living particles are the basic building blocks of plants and animals was widely discussed and even generally accepted during much of the eighteenth century. For instance, the article on ‘animal economy’ in Diderot’s *Encyclopédie* described the constituents of plants and animals as “living atoms or organic molecules” (Diderot, quoted in Grene and Depew, 2004, p. 88).

One of Buffon’s contemporaries, the Swiss physiologist Albrecht von Haller, advanced a rather different atomistic theory of the organism—one that persisted in various forms well into the nineteenth century: the ‘fibre theory’. Building on earlier ideas expounded by Francis Glisson, Nehemiah Grew, and James Keill, Haller postulated that the fibre is the elementary unit of all living bodies, famously asserting in his *Elementa Physiologiae Corporis Humani* (published in 1757) that the “fibre is

⁴⁸ For example, with regards to heredity, the theory of organic molecules appeared to overcome the limitations of the two rival unilateral preformationist theories of animal generation of the time—ovism and animalculism—by proposing a bilateral conception of heredity that accounted for the phenomenon of hybridization

for the physiologist what the line is for the geometer” (Haller, quoted in Toulmin and Goodfield, 1962, p. 391). According to Haller, there is only one kind of fibre to form all organs. It is the manner in which the fibres are arranged, the texture of the network they form, and the quantity of liquid retained by the mesh, that gives each organ its distinctive characteristics. Haller conceived fibres as the fundamental units of life, arguing that sensibility and irritability, the two sources of all vital activity, are themselves properties of the constituent fibres of the body.

At the end of the eighteenth century, the French anatomist Xavier Bichat distanced himself from Haller’s fibre theory, and in so doing developed an atomistic theory of his own. Bichat argued that the bodily organs “differ, not only in the way in which the fibre that forms them is arranged and interwoven, but also, in the very nature of the fibre itself; they differ in composition as in tissue” (Jacob, 1973, p. 113). Just as the body is composed of various organs, each organ is composed of several interwoven tissues, each of which possesses its own distinctive characteristics. But for Bichat tissues are not simply the final terms of anatomical analysis; they are the fundamental units of structure and function. Like Haller, Bichat identified sensibility and contractility (i.e., irritability) as the basic vital properties, but unlike Haller, he located these in the tissues rather than in the constituent fibres. Thus for Bichat, each individual tissue has individual life. As Claude Bernard would remark years later, “Bichat decentralized life and incarnated it in the tissues” (Hall, 1969, p. 129).

A distinctive feature of Bichat’s ‘tissue theory’ in relation to previous forms of biological atomism is that the elementary units of his theory are heterogeneous rather than homogeneous. Bichat distinguished twenty-one different kinds of tissues, and asserted that the particular attributes of an organism are the direct result of the different combinations of these tissues. In an explicit recognition of the atomistic nature of his theory, in the *Anatomie Générale* (published in 1801) Bichat compared his twenty-one ‘biological elements’ to the thirty-three chemical elements Antoine Lavoisier had described in his *Traité Élémentaire de Chimie* of 1789 (Haigh, 1984, p. 118). Nevertheless, later anatomists, such as Karl Friedrich Heusinger (who coined the term ‘histology’ in 1822), and Philipp Franz von Walther, attempted to further reduce the variety of tissues described by Bichat to a single elementary one from which all others derived. In 1807 Walther declared that the difference between

Bichat's tissues was only one of degree given that "all tissues contained in the texture of the organs of the animal body are formed by the metamorphosis of one and the same original tissue", which he identified as 'cellular tissue' (Walther, quoted in Jacyna, 1990, p. 165).

References to cellular tissue can already be found in the writings of Haller and other eighteenth-century physiologists like Théophile de Bordeu and Johann Friedrich Blumenbach, but these authors conceived it as the gelatinous material resulting from the association of the body's constituent fibres, and *not* as an elementary unit of life in its own right (Wilson, 1944, pp. 169-170). In contrast, most of the early nineteenth-century biologists who theorized about cellular tissue did in fact view it as the primary component of all living matter. Jean-Baptiste Lamarck devoted an entire chapter to cellular tissue in the second volume of his *Philosophie Zoologique* (published in 1809), in which he wrote:

It has been recognized for a long time that the membranes that form the envelopes of the brain, of nerves, or vessels of all kinds, of glands, of viscera, of muscles and their fibres, and even of the skin of the body are in general the productions of *cellular tissue*. However, it does not appear that anyone has seen in this multitude of harmonizing facts anything but the facts themselves; and no one, so far as I know, has yet perceived that cellular tissue is the general matrix of all organization, and that without this tissue no living body would be able to exist nor could have been formed. (Lamarck, quoted in Conklin, 1939, p. 541)

Given assertions like this one, some commentators have argued that Lamarck deserves to be credited as one of the forefathers of cell theory (e.g., Gerould, 1922; Conklin, 1939; Sapp, 2003). However, this assessment is only correct in as much as Lamarck asserted that there is a fundamental indivisible unit of life which forms all organisms. But for Lamarck, this elementary unit was *not* the cell but cellular tissue. Consequently, Lamarck is only as much of a precursor of cell theory as the other proponents of biological atomism I have considered in this section. One must move forward a number of years after Lamarck to find the first attempts to conceptually reduce tissues to cells as the basic units of life. One of the earliest to do so was the

botanist P. J. F. Turpin, who in 1826 published a paper with such a long and complete title that it can serve as a concise abstract of the novel claims contained within it:

Observations on the origin and first formation of cellular tissue, on the vesicles composing this tissue, considered as distinct individualities having their own vital center of vegetation and propagation and destined to form by agglomeration the composite individuality of all those plants whose organization is composed of more than one vesicle. (Turpin, quoted in Conklin, 1939, p. 541)

Before proceeding to examine the cell theory we need to consider one more expression of biological atomism that preceded it, the ‘globule theory’, which despite having been the product of flawed microscopical observations nonetheless reflects the same atomistic thinking as the other theories I have discussed. Recorded observations of ‘globules’ can be traced all the way back to the two seventeenth century Dutch pioneers of the microscope, Antonie van Leeuwenhoek and Jan Swammerdam. However, it is only with the physiologist Caspar Friedrich Wolff in the eighteenth century that we encounter the first formulation of the globule theory. In his *Theoria Generationis* of 1759, Wolff noted that the “constituent particles of which all parts of the animal body are composed at their first beginnings, are globules [*globuli*], which always yield to a moderately good microscope.” (Wolff, in Baker, 1948, p. 116) Johann Friedrich Meckel was probably the first to discuss the globule theory in a textbook of anatomy, published in 1815. In it, Meckel argued that all living matter is essentially an agglomeration of elementary globules embedded in a coagulated matrix. Still, the most famous account of the globule theory was the one expounded by the French zoologist Henri Milne-Edwards, who in 1823 carried out a systematic examination of a wide range of animal organs from different species, and concluded that they were *all* made up of globules 1/300 mm. in diameter. (Toulmin and Goodfield, 1962, p. 392)

Milne-Edwards’ perfectly uniform globules were almost certainly artefacts of observation produced by an optical effect called spherical aberration, caused by poor microscopical lenses. In the same way, it is quite likely that many of the previous records of observed globules were also the unfortunate result of spherical aberration, or of lipoidal droplets produced by inappropriate tissue preparation. Of course, some of the globules observed by microscopists may well have been cells or even cell

nuclei, but, as Baker (1948, p. 114) concedes, it is extremely difficult for the historian to distinguish the occasions on which globules depicted real anatomical structures from the times in which they did not. Still, this historiographical limitation need not concern us here. What is important for our purposes is the fact that during the 1810s and 1820s the globule theory represented a serious theoretical model of tissue structure and formation which exerted considerable influence in France and Germany (see Pickstone, 1973). Ultimately, the development of the microscope and the accumulation of conflicting accounts of globular structure led to the widespread rejection of the globule theory. Nevertheless, as Schickore (2009) has recently argued, the globule theory should not be regarded as a misguided conception irrelevant to the history of cell biology, but rather as a preliminary and tentative atomistic account of living matter whose influence and eventual rejection contributed to the consolidation of cell theory in the second third of the nineteenth century.

5.3. The Atomistic Foundations of Cell Theory

So far I have reviewed the major episodes in the evolution of atomistic thinking in biology up to the first decades of the nineteenth century. I will now show how the formulation and conceptual development of cell theory in many ways represented the culmination of the search for the biological atom. The cell, just like the organic molecule, fibre, tissue, and globule before it, is a notion tailored for the analysis of living matter that is meant to capture the ultimate, indivisible unit of life. But whereas previous theories of biological atomism had been tentative first approximations to the analytic understanding of living structures, cell theory appeared to successfully identify the actual minimal units of life and to root all major biological processes in the activities and interactions of these units.

I have already mentioned Turpin's 1826 paper, which sketched what was probably the first atomistic conception of the cell in plants.⁴⁹ This same notion was reiterated even more clearly and forcefully by the German botanist Franz Meyen in 1830:

⁴⁹ Around the same time, another Frenchman, Henri Dutrochet, published similar atomistic assertions regarding animal cells. However, Dutrochet's contribution to cell theory is difficult to assess as many of his observations of what he called 'cells' were most probably of globules (see Wilson, 1947; Baker, 1948; Pickstone, 1973).

Plant cells occur either singly, so that each forms a single individual, as in the case of some algae and fungi, or they are united together to form greater or smaller masses, to constitute a more highly organized plant. Even in this case each cell forms an independent, isolated whole; it nourishes itself, it builds itself up, and elaborates the raw nutrient materials which it takes up, into very different substances and structures. (Meyen, quoted in Hall, 1969, p. 188)

Meyen elsewhere referred to plant cells as “little plants inside larger ones” and as “essential elementary organs of assimilation and construction” (Meyen, quoted in Conklin 1939, pp. 541-542). Matthias Schleiden, the co-founder of cell theory, did little more than restate in different words Turpin’s and Meyen’s atomistic conceptions of plant cells when he asserted, in the oft-quoted passage of his *Beiträge zur Phytogenesis* of 1838, that:

Each cell leads a double life: an independent one, pertaining to its own development alone; and another incidental, in so far as it has become an integral part of a plant. It is, however, apparent that the vital process of the individual cell must form the very first, absolutely indispensable fundamental basis of vegetable physiology and comparative physiology. (Schleiden, quoted in Conklin, 1939, p. 543)

The atomistic nature of Schleiden’s conception of plant cells is evident. For Schleiden, each constituent cell in a plant is first and foremost an autonomous living being. The activity of a plant is conceived as the result of the individual activities of each of its constituent cells. In 1837 Schleiden conveyed these ideas to his colleague Theodor Schwann, who at once extended them to the animal kingdom. Each cell, wrote Schwann, “contains an independent power, a life of its own”. The totality of the multicellular organism, plant or animal, “subsists only by means of the reciprocal action of the single elementary parts” (Schwann, quoted in Wilson, 1900, p. 58). In 1839, acknowledging his indebtedness to Schleiden, Schwann formulated the cell theory, grounding it on three fundamental principles:

1. All parts of plants and animals are cellular either in organization or in derivation.
2. Cells are autonomous living units, and although each cell is influenced by its neighbours, the life of the whole organism is the product, not the cause, of the life of its cellular elements.

3. Cells arise inside or near other cells by differentiation of a homogeneous primary substance called the *cytoblastema* in a process analogous to crystallization.

The first principle was promptly corroborated through extensive microscopical studies of a wide range of tissues from different species. The second principle, which stressed the atomistic nature of the theory, acquired widespread currency and was further articulated in the second half of the nineteenth century, as I will show in a moment. The third principle, in contrast, was immediately challenged by Schleiden's and Schwann's contemporaries. For one thing, observations of cell division had already been reported by a number of authors before them, including Turpin (in 1826), B. C. J. Dumortier (in 1832), Hugo von Mohl (in 1837), and Meyen (in 1838). In the 1840s and 1850s, more detailed investigations, particularly those carried out by Robert Remak on the early developmental stages of the chick embryo, ultimately confirmed that cell division is not just the main, but the *only* way in which new cells are formed. This led to the rejection of Schleiden's and Schwann's conception of free cell formation, which Remak deemed "just as improbable as the spontaneous generation of organisms" (Remak, quoted in Mendelsohn, 2003, p. 16).

The new principle of cell formation was further generalized by the pathologist Rudolf Virchow, who in 1855 proclaimed that just as an animal can only proceed from an animal and a plant from a plant, wherever a cell may originate another cell must pre-exist to give rise to it, immortalizing this assertion with the Latin dictum "*omnis cellula e cellula*"—that is, every cell from a cell (Virchow, quoted in Baker, 1952, p. 436). A few years later, Virchow published his seminal *Die Cellularpathologie* based on a series of lectures delivered at the University of Berlin, in which he updated Schleiden's and Schwann's cell theory and gave it a formulation which remained highly influential in subsequent decades (Sapp, 2003, p. 78). With Virchow, the atomistic connotations of cell theory became even more conspicuous. Cells are not just the minimal indivisible units of physiological activity, but they are also the seats of disease. The disciplines of physiology and pathology in the hands of Virchow became unified by the cell as their common elementary unit (Coleman, 1977, pp. 32-33).

By the end of the nineteenth century, the atomistic dimension of cell theory had become its single most distinctive feature. In 1893, the German zoologist Oscar Hertwig provided the following characterization of cell theory:

Animals and plants, so diverse in their external appearance, agree in the fundamental nature of their anatomical construction; for both are composed of similar *elementary units*, which are generally only perceptible under the microscope. Through the influence of an old theory, now discarded, these units are called cells, and thus the doctrine that animals and plants are composed in an accordant manner of very small particles of this kind is called the *cell-theory* [...] The common life-process of a composite organism appears to be nothing else than the exceedingly complicated result of its numerous and diversely-functioning cells. (Hertwig, quoted in Baker, 1948, p. 105)

Two years later, the English anatomist G. C. Bourne offered a similar account of cell theory: “The multicellular organism is an aggregate of elementary parts, viz. cells. The elementary parts are independent life units. The harmonious interaction of the independent life units constitutes the organism. Therefore the multicellular organism is a colony” (Bourne, quoted in Reynolds, 2007, p. 83). The twentieth century brought enormous empirical advances in every area of cell biology, but the fundamental understanding of cell theory has remained largely unchanged. Indeed, through the decades one finds that cell theory has been periodically rearticulated by different authors in the same atomistic terms. For example, the Austrian theoretical biologist Ludwig von Bertalanffy asserted in 1952 that cell theory has morphological, embryological, and physiological meanings, and each of them emphasizes the theory’s atomistic connotations in its own way:

Morphologically, it means that the cell is the sole building element of the living world, and that multicellular elements are aggregates of cells. *Embryologically*, the development of the multicellular organism is resolved into the actions of the individual cells in the embryo. *Physiologically*, the cell is considered to be the elementary unit of function. (Bertalanffy, 1952, p. 35)

To sum up, cell theory tells us that the cell is the basic constituent of living matter; it is the fundamental unit of structure, function, and disease; it is the primary agent of organization; and it is the locus of all major organismic processes, including

metabolism, development, reproduction, and heredity. In short, the cell, as the American zoologist Charles Otis Whitman so perceptively noted, “has come to signify in the organic world what the atom and molecule signify in the physical world” (Whitman, 1893, p. 639).

Having completed my survey of the conceptual development of cell theory through the perspective of biological atomism, I will now employ this very same perspective to make philosophical sense of the major objections that have been waged against cell theory. I will show that all major criticisms of this theory can be understood as attempts to relocate the true biological atom away from the cell to a level of organization either above or below it. The next two sections will examine each of these two kinds of critique in turn.

5.4. The Cell as the Biological Atom: Challenges from Above

One of the most salient consequences of cell theory’s atomistic conception of the cell is that ‘organism’ becomes a biological category possessing little ontological weight of its own. According to cell theory the organism is the product of its cellular units. It is, in effect, a ‘state’ of autonomous living units which operate collectively to constitute it (see Reynolds, 2007). The common point of departure for all the challenges to cell theory I will consider in this section is a fundamental dissatisfaction with this understanding of the organism. In fact, they can all be classified under what Whitman (1893) called the “organismal standpoint”, which later became known as the “organismal theory” (Ritter, 1919). Organismal theory postulates that it is the whole organism, rather than its cells, that represents the primary unit of life and thus the true biological atom. The organism is considered to be the cause, not the product, of its cellular constitution. Of course, cells are still regarded as important, but without an organismal-level perspective, questions of structure, function, and organization cannot be adequately addressed. In brief, organismal theory maintains that the biology of the organism is not reducible to the biology of its cellular constituents. In what follows, I will consider the three main criticisms of cell theory that have been advanced by proponents of the organismal theory.

5.4.1. Criticisms

- *Criticism #1: The organism is not an aggregate of independent living units, but a genuine biological individual in its own right*

The fact that the organism is cellular in constitution is not contested by the organismal theory. What is disputed is the idea that the organism represents an aggregation of autonomous living units. Organismal theorists point out that physiology offers ample evidence that the organism functions as a fully integrated whole, and not as a collection of individual unities. The harmonious organization existing at the organismal level cannot be easily explained in terms of the sum of the individual activities of the component cells. One can certainly study biological phenomena at the cellular level, but one must ultimately interpret the findings of these studies from the perspective of the whole organism to fully appreciate their biological significance. Therefore, the fact that the organism can be analytically decomposed into its constituent parts does not imply that the organism is ontologically reducible to a collection of autonomous entities. Even if the organism is constituted of cellular subunits, organismal theory maintains that the organism as a whole remains the true individual unit of life.

Given the history of biological atomism prior to cell theory, it is probably not that surprising to find that this critique of the conception of the organism as an aggregate of individuals actually predates the formulation of cell theory by Schleiden and Schwann. What is perhaps more surprising is the fact that one of the authors who most clearly expressed this criticism, the Romantic biologist Lorenz Oken, is sometimes referred to as one of the forefathers of cell theory (e.g., Singer, 1989, p. 33). In his *Die Zeugung* (published in 1805), Oken objected to the idea that multicellularity entails multi-individuality:

The association of primitive animals in the form of flesh should not be thought of as a mechanical joining of one animal to the other, like a pile of sand in which there is no other association than an accumulation of numerous grains. No. Just as oxygen and hydrogen disappear into water, mercury and sulfur into cinnabar, what occurs here is a veritable interpenetration, an interlacing and a unification of all the animalcula. From this moment on, they no longer lead their own lives. They are put to the service of the more

elevated organism; they work in view of a unique and common function; or rather, they carry this function out in realizing themselves. No individuality is spared here; individuality is quite simply ruined. But this language is inappropriate: the individualities brought together form another individuality; the former are destroyed and the latter only appears by their destruction. (Oken, quoted in Canguilhem, 2008, pp. 40-41)

Like many of the biological atomists I have considered, Oken compares the cells in an organism to the atoms in a chemical compound; but what is interesting about this passage is how Oken uses this analogy to draw the opposite conclusions. Just as the atoms of oxygen and hydrogen lose their independent identities when they combine to form a molecule of water, living cells fuse their separate individualities when they collectively constitute an organism. For Oken, as for all the organismal theorists ever since, the organism cannot be regarded as a ‘cell republic’ (as cell theorists like Virchow claimed) given that it is already the minimal individual unit of life. Its constituent cells should be regarded not as autonomous individuals, but as “*organs* of the organism just as muscles and glands and hearts and eyes and feet are so regarded” (Ritter, 1919, p. 191).

- *Criticism #2: A unicellular organism is physiologically analogous and phylogenetically homologous to a multicellular organism, not to one of its constituent cells*

Cell theory has important consequences for microbiology, particularly for the study of protists (or ‘protozoa’, as they used to be called). Since multicellular organisms are conceived as colonies of single-celled individuals which have undergone a physiological division of labour, cell theory suggests a direct evolutionary link between unicellular beings like protists and multicellular ones like higher plants and animals. Specifically, the ‘cell state’ of a multicellular plant or animal is considered to be the evolutionary product of the colonial association of single-celled protists. The implication of this view, as noted by Max Verworn and Oscar Hertwig at the turn of the twentieth century, is that studying protists provides important insights for understanding the cells of multicellular organisms, since the former are essentially homologous with the latter (Richmond, 1989).

The organismal criticism of this viewpoint is grounded on the recognition that since multicellular organisms are individuals, rather than communities of individuals, their evolutionary origin must be rooted not in the association of many protists but in a single polynucleated protist whose parts subsequently evolved specialized functions, gradually forming the various tissues and organs of multicellular organisms (Sedgwick, 1896). Protists cannot be homologized with somatic cells of multicellular organisms because they are already autonomous individuals in their own right. Instead, the protist must be morphologically and physiologically compared with the multicellular organism *as a whole*. Indeed, both are individuals with specialized internal regions, and both are capable of independent locomotion, feeding, growth, reproduction, and regeneration.

One of the most vigorous exponents of this organismal critique was the English protistologist Clifford Dobell. Being so convinced of the fundamental and irreconcilable differences between protists and the individual cells of plants and animals, Dobell refused to accept even the designation 'unicellular' to describe protists. He argued that these should be referred to as 'acellular' organisms (Dobell, 1911). This acellular conception of protists exerted a considerable degree of influence during the first half of the twentieth century, but it has become largely marginal in the present day (see Corliss, 1989). The reason for this seems to be that Dobell's objection to use the term 'cell' in relation to protists was based on the rather odd assumption that a cell by definition is always a *part* of an organism and never a whole organism. This understanding of 'cell' stems from the fact that this concept was first used in relation to the component cells of higher plants and animals, and that consequently when it began to be used in relation to protists, it carried with it inappropriate connotations of parthood which obscured the protists' individuality as autonomous organisms. However, it is difficult to think of a good reason why the concept of 'cell' should be restricted in its usage in the manner that Dobell prescribed, which is probably why the term 'acellular' gradually lost its currency.

- *Criticism #3: Multicellularity is the product, not the cause, of the organism's development*

In no area of biological inquiry have the atomistic presuppositions of cell theory been more hotly contested than in developmental biology. The implications of cell theory for the understanding of embryological development have spawned a wide array of dissenting voices. The disagreements again centre on the problematic relationship between cell and organism. According to cell theory, cells assemble the organism from the bottom up. In the words of Schwann, “the individual cells so operate together in a manner unknown to us as to produce a harmonious whole” (Schwann, quoted in Weiss, 1940, p. 38). As the multicellular organism is a community of interacting and mutually dependent individuals, development consists of a sequential multiplication of individualities resulting from the successive cell divisions of a primordial individual, the egg.

The point of departure for the organismal critique of this viewpoint is the contention that the process of development has no effect on an organism's individuality. Before cellular segmentation, the egg is a whole organism; after segmentation, it is the same whole organism, only more differentiated. The egg is an integrated whole within which parts gradually arise through cell division. At no time do the cells constitute independent units, since from the very beginning they are subordinated to the growth of the organism as a whole. From the perspective of organismal theory, multicellularity is not achieved by the coordinated aggregation of cells but by the secondary chambering of the organism into cellular subunits.

This understanding of the attainment of multicellularity has important ramifications, as it implies that cells, far from being the elementary individuals described by cell theory, are effectively nothing more than internal subdivisions within the organism. In the course of the organism's development, cells are fashioned according to their context within the developing whole. The generation of biological form (i.e., morphogenesis) operates above the level of individual cells, and is thus a strictly organismal phenomenon. This idea is effectively captured by Anton de Bary's famous aphorism that it is not the cells that form the plant, but rather the plant that forms the cells (cf. Barlow, 1982). Instead of being the source of morphogenesis, cells are

merely markers of growth. This was essentially the point made by T. H. Huxley in his review of cell theory of 1855, in which he poetically declared that cells “are no more the producers of the vital phenomena than the shells scattered in orderly lines along the sea-beach are the instruments by which the gravitative force of the moon acts upon the ocean. Like these, the cells mark only where the vital tides have been, and how they have acted” (Huxley, in Richmond 2000, p. 272).

Many of these ideas were brought together and further developed in Whitman’s classic paper, ‘The Inadequacy of the Cell-Theory of Development’. Arguing from the organismal standpoint, Whitman asserted that the growth and differentiation of the developing embryo occurs “regardless of the way it is cut up into cells” (Whitman, 1893, p. 644). Whether as a single-celled egg or as a multicellular adult, the organism maintains its individuality independently of the number of cells present. This argument represents an important challenge to the atomistic assumptions of cell theory, as the number of cells composing an organism is deemed to be largely irrelevant for the understanding of the organism’s form and organization.

A number of developmental studies conducted in the twentieth century provided further support for Whitman’s criticisms. One example I already alluded to in Chapter 2 is Gerhard Frankhauser experiments on the effects of ploidy on newt development (Frankhauser, 1945). Frankhauser found that polyploid embryos, generated by suppressing early cleavages, had fewer but larger cells. The number and size of cells differed in haploid, diploid, and pentaploid embryos, but the whole embryo remained the same size in all cases, enforcing the organismal hypothesis that development is more appropriately understood as resulting from the internal partitioning of an individual rather than from the agglomeration of a community of cooperating individuals, as implied by cell theory.

Contemporary research on plant morphogenesis has also helped to substantiate these views. Donald Kaplan and Wolfgang Hagemann (1991) reviewed evidence accrued during the preceding thirty years from a broad range of botanical studies and concluded that multicellularity in plants is better described by the organismal than by the cell theory (cf. Cooke and Lu, 1992). If plant cells were responsible for organismal form, one would expect there to be a strict correlation between the pattern

of plant cell division and the zones of plant growth. However, what one actually finds is that the processes of cell division and growth are causally independent in plants. The two processes can occur in various combinations, alternately resulting in increases in cell number (cell partitioning) and in growth (surface extension). Moreover, alternative patterns of the timing of cell division and growth indicate that plant bodies are partitioned by the insertion of walls rather than being built by the addition of cells, as suggested by cell theory. Because of this internal partitioning, patterns of cell division have no significance for plant morphogenesis, and organs with different cell division patterns often converge in form. Overall, the constitution of plants seems to demand that considerations of growth, differentiation, and morphogenesis at the cellular level be placed in the context of the plant as a whole.

5.4.2. *Cell Theory versus Organismal Theory*

With the examination of the three main organismal critiques of cell theory now complete, what can be concluded regarding the nature of the dispute between cell theory and organismal theory? Are the two theories incompatible and mutually exclusive? Or do they constitute complementary viewpoints? Can the two theories be integrated? Finally, is the underlying conflict between the two theories representative of a more fundamental philosophical dispute? In relation to this last question, the Austrian embryologist Paul Weiss suggested in 1940 that the conflict in developmental biology between what he called the ‘egg-equals-cell’ theory (i.e., cell theory) and the ‘egg-equals-organism’ theory (i.e., organismal theory) constitutes a modern expression of the age-old antithesis between epigenesis and preformation.⁵⁰ Weiss argued that both viewpoints are correct since ontogeny is to a certain extent epigenetic and to a certain extent preformed. The process of development reveals the cell “partly as an active worker and partly as a passive subordinate to powers which lie outside of its own competence and control, i.e. supra-cellular powers” (Weiss, 1940, p. 45). In an attempt to integrate the two theories, Weiss concluded that Virchow’s dictum of cell theory, ‘*omnis cellula e cellula*’, should be complemented by its organismal theory counterpart, “*omnis organisatio ex organisatione*” (p. 46).

⁵⁰ Cell theory is epigenetic insofar as it claims that the organism’s organization is arrived at through the sequential accumulation of cells, whereas organismal theory is preformationist insofar as it considers the organism’s organization to be already present in the egg.

More recently, Kaplan (1992) has rejected the possibility of reconciliation between cell theory and organismal theory on the grounds that they entail opposite causal understandings of the constitution and development of the organism. For Kaplan, ‘there is no compromise between these two theories’ (ibid., p. S29). Deciding upon one of them will determine our epistemic priorities and dictate how we approach the study of the organism. If cell theory is correct, then we only need to focus on the behaviour of individual cells, not the organism as a whole. Conversely, if the organismal theory is correct, the study of the properties of the organism becomes more significant than a focus on individual cells. Peter Sitte (1992), however, disagrees. In his view, there is no real conflict between the two theories, as both sides have convincing arguments in their favour that nowhere contradict each other directly. Provided that neither of the two viewpoints is overstated, the two theories may be regarded as the result of different starting positions, or different methodological preferences, with defenders of cell theory favouring the analytical and experimental approaches of cell and molecular biology, and advocates of organismal theory generally preferring the more holistic approaches of morphology and embryology. If this is the case, it is no longer necessary to view the two theories as contradicting or mutually exclusive.

It would appear that current research in plant morphogenesis is advancing steadily towards the epistemic integration of cell theory and organismal theory (see Fleming, 2006). The botanist Hirokazu Tsukaya (2003) has indicated that both viewpoints need to be combined in a Weisian manner in order to make sense of plant development. He shows that the shape and size of indeterminate organs, such as roots and stems, is directly correlated with the shape and size of the cells in these organs, as predicted by cell theory, whereas in determinate organs, such as leaves, the number of cells does not reflect organ shape or size but is rather determined by the plant as a whole, as predicted by organismal theory. In an attempt to bring the two theories together, Tsukaya has formulated what he calls the ‘*Neo-Cell Theory*’, which postulates that even though cells are the units of morphogenesis, each cell is also controlled by organismal-level compensatory systems that govern the morphogenesis of the organ of which the cells are a part.

5.5. The Cell as the Biological Atom: Challenges from Below

In addition to the organismal critiques, challenges to the atomism of cell theory have also been advanced from the other direction. There are biologists for whom cell theory is problematic not because it is excessively atomistic (as argued by the organismal theorists), but rather because it is not sufficiently atomistic. For them, the biological atoms are located below the cell at a more basic level of organization. Cells in this view do not represent the minimal units of life as they can be conceptually reduced to even more elementary vital units.

This kind of critique has a long and colourful history. Shortly after Schleiden's and Schwann's formulation of cell theory, some biologists began to express doubts that cells really represented the ultimate indivisible units of life. Already in 1841 the German anatomist F. G. J. Henle had suggested that the cell might be composed of more fundamental biological units (Wilson, 1900, p. 289). In the second half of the nineteenth century, this idea was taken up by a large number of biologists, and a wide variety of theories were proposed that sought to identify *within* the cell more fundamental multi-molecular systems exhibiting the basic attributes of life. Many of the suggested vital units were deemed to be beyond the resolution of the microscope, and were hypothesized in order to account for the particular phenomena biologists were interested in explaining (e.g., nutrition, heredity, growth, differentiation, etc.). (In this respect, these theories are not that different from some of the earlier expressions of biological atomism I discussed in Section 5.2, such as Buffon's theory of 'organic molecules'.) Examples of this class of biological atoms include Herbert Spencer's 'physiological units', Charles Darwin's 'gemmules', Ernst Haeckel's 'plastidules', Karl Nägeli's 'micellae', Julius Weisner's 'plasomes', Theodor Engelmann's 'inotagmata', August Weismann's 'biophores', Hugo de Vries' 'pangenes', Oscar Hertwig's 'idioblasts', and Charles Whitman's 'idiosomes' (see Hall, 1969, pp. 313-354).

With the development of biochemistry at the turn of the twentieth century, many of these atomistic theories were abandoned. However, some of them were reinterpreted as genetic determinants following the rediscovery of Mendel's laws of heredity in 1900. In fact, one can find numerous references to genes as the atoms of biology in

the literature on genetics between 1901 and 1930 (see Allen, 2007, pp. 146-152). Many early geneticists, such as William Bateson, H. S. Jennings, C. B. Davenport, and W. E. Castle, appealed to the analogy between genes and atoms in their work. Castle, for instance, asserted that genes “are supposed to be to heredity what atoms are to chemistry, the ultimate, indivisible units, which constitute gametes much as atoms in combination constitute compounds” (Castle, quoted *ibid.*, p. 147). However, this atomistic conception of genes does not quite fit the tradition of biological atomism I have been considering in this chapter, as the vast majority of atomistic geneticists did not conceive genes as *living units* in their own right. Rather, the assimilation of genes to atoms was based on their ability to combine in different ways to produce different phenotypic effects (just as atoms combine in different ways to produce different molecules), and on the fact that genes, like atoms, arise out of each association unchanged in their fundamental properties. Consequently, it may be more appropriate to refer to this mode of thinking in early twentieth-century genetics as *genetic atomism* in order to distinguish it from biological atomism. In biological atomism the atoms are the units of *life*, whereas in genetic atomism the atoms are the units of *heredity*.

Interestingly, Richard Dawkins’s famous concept of the ‘selfish gene’ (Dawkins, 2006 [1976]) appears to stand somewhere in between genetic atomism and biological atomism. It is a form of genetic atomism in the sense that Dawkins’s atoms are physicochemical replicators, which act both as the units of heredity and the units of selection. However, Dawkins’s conception of organisms as passive receptacles for genes, built and blindly programmed by them in order to secure their own preservation, presupposes an attribution of agency to genes that is usually associated with living beings. In this respect, Dawkins’s concept of the selfish gene bears the hallmarks of a theory of biological atomism, and can therefore be regarded as a contemporary challenge to the atomism of cell theory from below. In fact, Dawkins is quite explicit concerning his atomistic reduction of cells to genes: “Some people use the metaphor of a colony, describing a body as a colony of cells. I prefer to think of the body as a colony of *genes*, and of the cell as a convenient working unit for the chemical industries of genes” (*ibid.*, p. 46). As a theory of biological atomism, however, many biologists today find the idea of selfish genes rather objectionable given that the view that genes are the primary causal agents of all the phenomena of

organismic life is not well supported by the findings of contemporary biology (see Keller, 2000; Morange, 2001; Moss, 2003).

Leaving genes aside, there are a number of other subcellular theories of biological atomism that deserve attention. Returning to the wide array of atomistic theories formulated at the end of the nineteenth century, it should be noted that not all of the proposed biological atoms were inferred; some actually referred to subcellular structures that could be observed through the microscope. One of the most notable theories of this kind was formulated by Richard Altmann in 1890. Altmann suggested that the small granular bodies visible in the cytoplasm of cells, which he called ‘bioblasts’, are actually elementary organisms capable of nutrition, growth, and division. He argued that all major structural features of the cell—nucleus, cytoskeleton, secretion vesicles—are either aggregations of bioblasts or products of bioblasts. Altmann was convinced that he had found in the bioblast the true atom of life, declaring that it “forms the long-sought morphological unit from which all biological considerations originally proceed” (Altmann, quoted in Hall, 1969, p. 340). Conceiving cells themselves as colonies of bioblasts, Altmann even reduced Virchow’s dictum ‘*omnis cellula e cellula*’ to its bioblastic equivalent ‘*omne granulum e granulo*’.

From a modern perspective, Altmann’s theory is not as farfetched as it may seem. The granular bodies that Altmann identified as bioblasts were renamed ‘mitochondria’ by Carl Benda in 1898 (Sapp, 2003, p. 90), and today it is generally accepted that mitochondria were originally free-living unicellular organisms that at some point in their evolutionary history were engulfed within another unicellular organism. This means that Altmann’s conception of bioblasts as subcellular ‘elementary organisms’ is quite compatible with our current understanding. In turn, the contemporary feasibility of Altmann’s basic conception presents a further challenge to cell theory’s view of the cell as the minimal structural unit capable of displaying the attributes proper to life, even if it is true that a mitochondrion needs to be contained within a cellular host in order to exhibit the characteristics of a living system.

A further difficulty faced by cell theory that I have not yet considered is the fact that many organisms are not cellular but are actually *supracellular* in constitution. There

are numerous examples throughout the eukaryotic domain of giant multinucleated cells known as *coenocytes* (formed by the uncoupling of mitosis from cytokinesis) and *syncytia* (formed by cells fusing together). In order to account for these phenomena, cell biologists are faced with the following dilemma: they can either shift their attention to the whole supracellular body and turn to the organismal theory, or they can assume, alongside the theorists I have considered in this section, that the cell is itself a composite entity and argue that the real minimal unit of life resides in some smaller structure within it.

The first biologist to be prompted to reject cell theory and postulate a subcellular biological atom in light of the evidence for the coenocytic and syncytial constitution of organisms was the German botanist Julius von Sachs. In 1892, upon examination of coenocytic algae, Sachs concluded that a nucleus always organizes the area of cytoplasmic space that surrounds it, regardless of whether or not it is enclosed by a cell membrane. Sachs called this subcellular system the ‘energide’, and postulated that it constitutes the minimal autonomous unit bearing the basic characteristics of life. He suggested that single-nucleated cells are ‘monoenergidic’, whereas multinucleated coenocytes are ‘polyenergidic’. For Sachs, the cell is of secondary significance, as it is essentially a chamber which may contain one or more energides:

[The] Energide is represented by a nucleus associated with its protoplasm in such a way that the nucleus and surrounding protoplasm form an organic unit, both from the morphological and physiological perspectives [...] The term Energide does not encompass the cell skin; the case is more that each individual Energide is able to enclose itself by a cell skin, or that several Energides together can enclose themselves within one single cell skin. (Sachs, quoted in Baluška et al., 2006, p. 5)

After Sachs, the energide theory was all but forgotten for a hundred years. However, in 2004 the cell biologists Frantisek Baluška, Dieter Volkmann, and Peter Barlow published a paper entitled ‘Eukaryotic Cells and Their *Cell Bodies*: Cell Theory Revised’, which has effectively revived Sachs’s energide theory. These authors have proposed the concept of the ‘cell body’ as “the smallest unit of life that is capable of self-organization, self-reproduction, and of responsiveness to diverse external stimuli” (Baluška et al., 2004a, p. 12). The cell body is characterized as an autonomous

subcellular structure consisting of a nucleus and a set of perinuclear radiating microtubules. It is complemented by the ‘cell periphery apparatus’, which comprises the plasma membrane and the actin cytoskeleton, and which encases the cell body and protects it from the external environment.

Baluška et al.’s contention is that the endosymbiotic theory of the evolutionary origin of mitochondria and chloroplasts in eukaryotic cells needs to be extended to the nucleus as well. They thus suggest that the cell body represents the vestige of a tubulin-based ‘guest’ proto-cell, which after penetrating an actin-based ‘host’ proto-cell became specialized for transcribing, storing and partitioning DNA molecules via the organization of microtubules. Similarly, they regard the cell periphery apparatus as the vestige of an actin-based ‘host’ proto-cell which became specialized for cell body protection, motility, and actin-mediated intercellular signalling. Given these assumptions, the ‘cell body versus cell periphery apparatus’ distinction can explain the striking duality of eukaryotic cells at the level of genomic organization (eubacterial versus archaebacterial features), cytoskeleton (actin versus tubulin), membrane flow (exocytosis versus endocytosis), and division (mitosis versus cytokinesis). Moreover, the cell body theory can explain the fact that the nucleus–microtubule complex often divides independently of the cell in which it resides, resulting in the coenocytes found in eukaryotes. Likewise, syncytia can also be accounted for by assuming that nuclei are vestiges of originally free-living cells.

Overall, the similarities between cell body theory and Sachs’s energide theory are obvious. The authors explicitly recognize this in a more recent paper (Baluška et al., 2006), in which they go as far as to drop their notion of cell body altogether in favour of Sachs’s concept of energide, recognizing that “the term Energide better invokes the unique properties of this universal unit of supracellular living matter endowed with the vital energy” (ibid., p. 1). Baluška et al. confidently predict that their ‘neo-energide theory’ will ultimately displace cell theory and that the energide “will take over from the cell as the fundamental unit of eukaryotic structure”, and as the “propagule of life itself” (Baluška et al., 2004b, p. 371).

How plausible are these estimations? Is the energide really a better candidate than the cell for the designation of the true atom of life? In reflecting on this question, it

appears that compelling arguments can be made both for and against the neo-energide theory. The case in favour of the neo-energide theory is grounded on four key observations:

1. Whilst energide division often takes place independently of cellular division, the opposite situation has never been recorded. This suggests that it is the energide and not the cell that constitutes the minimal vital unit capable of self-reproduction.
2. Whereas cells display an extremely wide range of sizes and different structural organizations, energides are basically constant structures, always consisting of nucleus sheathed within perinuclear radiating microtubules. This indicates that the energide is a more invariable unit of biological structure than the cell.
3. Energides not only explore the confines of their own cells but can also move to an adjacent cell if the connecting channels are sufficiently large. This phenomenon, known as *cytomixis*, is difficult to reconcile with cell theory.
4. The concept of the energide seems to explain better than the concept of the cell the distinct morphology and physiology of coenocytic and syncytial systems.

The case against the neo-energide theory is based on the identification of two crucial limitations. The first is that the theory is inherently limited in its applicability to the eukaryotic domain. Prokaryotic cells do not possess distinct nuclei and consequently cannot be accommodated within this theory. So whereas cell theory can claim almost universal applicability, the neo-energide theory is simply irrelevant to the archaeal and bacterial domains of life. The second limitation is that the basic premise of the theory rests on the assumption that eukaryotic cells originated from the endosymbiotic coupling of a 'guest' and a 'host' cell. The problem is that there is at present no consensus regarding the origin of the eukaryotic nucleus. Although some cell biologists do support the endosymbiotic hypothesis that the neo-energide theory requires, others argue that the nucleus was generated autogenously by a single prokaryote through the invagination of its plasma membrane, while a third group maintain that viruses were the main catalyzers of the initial formation of the eukaryotic nucleus (cf. Pennisi, 2004; Zimmer, 2009; O'Malley, 2010). Consequently, the extent to which the neo-energide theory can legitimately be claimed to threaten the tenability of cell theory even within the confines of the eukaryotic domain hinges on

its ability to validate a particular hypothesis regarding the evolutionary origin of the nucleus that is yet to be accepted by the cell biology community as a whole.

5.6. Conclusions: Biological Atoms and Biological Atomism

In this chapter I have proposed an epistemological perspective I have call biological atomism in an effort to make sense of the foundations of cell theory, trace its philosophical antecedents and historical developments, and understand the rationale underlying the major criticisms of it. I have also shown that the idea of biological atom can be applied to many other biological units besides the cell. What does this tell us about the nature of this concept? What exactly does it refer to? Is it a *real thing*, a *theoretical abstraction*, or a *heuristic device*? These questions are of no little importance, as their answer can help clarify the conditions that need to be met in order to resolve current disputes between rival atomistic theories. Indeed, if biological atoms are real things, then we can expect that the accumulation of empirical evidence will eventually settle the exact level of organization at which the biological atoms are actually located. This seems to be the case in the present dispute between cell theory and the neo-energid theory. However, if biological atoms are theoretical abstractions, then it is unlikely that proponents of a theory can be persuaded to abandon it in favour of another solely on the weight of empirical evidence. In this case, we need to view atomistic theories of life more as rationalizations of the beliefs of their authors regarding the question of whether or not an organism, or a cell, *should* consist of more elementary vital units. Buffon's theory of organic molecules, Dobell's organismal rejection of cell theory in protistology, and some of the theories of subcellular atoms of the late nineteenth century appear to fit this characterization. Finally, if biological atoms are heuristic devices, then it is no longer necessary to regard rival theories as mutually exclusive, but simply as having different epistemic emphases. If this is the case, complementary theories can be integrated to produce more inclusive viewpoints. Tsukaya's proposal of a synthetic neo-cell theory in response to the conflict between cell theory and organismal theory in plants seems to be a good example of this strategy. On the whole, it appears that each of these answers is correct under different provisions, in which case we may conclude that the meaning of the concept of biological atom can only be determined in relation to the particular explanatory context in which it is employed.

Despite the context-dependent nature of the concept biological atomism, it is important to realize that the perspective of biological atomism itself always implies the same specific expectation guiding biological research, namely the view that a particular element within the organism can be singled out as an independent, functional, reproducible, 'serial' unit. Of course, these units need not be homogeneous. We saw that in the case of Bichat's tissue theory the heterogeneous nature of his biological atoms was a fundamental aspect of his conception of them. Similarly, the appeal to atomistic thinking in modern cell biology does not imply an epistemic commitment to flattening the differences between types of cells. What it *does* imply is an understanding of the organism as a community of individuals making up a higher-level individual in which the cells display both the autonomous properties of wholes and the dependent properties of parts. In this way, the perspective of biological atomism provides a way out of the longstanding dichotomy between the conception of organisms as sums of their parts and the conception of organisms as fully integrated wholes. Biological atoms (whatever their nature) assert both their individuality as semi-autonomous sub-wholes, and their function as parts which collectively associate to produce the greater organismal whole.

The philosophical value of biological atomism can be fleshed out by contrasting it with the way mechanistic biology epistemically decomposes living organisms for the purposes of explanation. As we have seen in previous chapters, mechanistic biology proceeds by breaking down organisms to their molecular components and then by progressively building up an understanding of them from the bottom up. Although biological atomism shares with mechanistic biology this commitment to explaining organisms by decomposing them into their component parts, there is nevertheless a fundamental difference. This is that the final units of analysis in biological atomism (i.e., the biological atoms) are always still living beings in their own right. Instead of taking the epistemic reduction all the way down to the physicochemical level, biological atomism ends it at the (minimal) living level. As a result, biological atomism is able to reductionistically account for an organism in terms of its parts without having to surrender the irreducible properties of living systems when dealing with those parts. The parts of the organism that are used as the basis for explanation are not merely structural elements but functionally organized living entities. In this way, explanation in biological atomism does not proceed from the basic 'building

blocks' of life (as it does in mechanistic biology) but from the basic 'builders' of life. The consequence of this is that biological atomism greatly enhances the reach of reductionistic explanation. Overall, biological atomism and mechanistic biology constitute two different interpretations of explanatory reductionism. When they are taken together as complementary epistemic perspectives they capitalize on each other's limitations and thereby provide a more inclusive (analytical) understanding of the constitution and operation of living systems.

Chapter 6

CONCLUSION

In this thesis I have offered a critical evaluation of the role played by mechanistic ideas in shaping our understanding of living systems. I have drawn on a combination of historical, philosophical, and scientific resources to uncover a number of problems which I have argued result from the adoption of mechanistic thinking in biology. Overall, it is clear that there is no single way of comprehensively dealing with mechanistic thinking. Indeed, I have shown that the term most commonly associated with mechanistic thought, the concept of mechanism, has three clearly distinct meanings. In light of this, an appropriate way of coming to terms with the basic findings of this thesis is to consider the lessons that have been learnt in relation to each of the three meanings of ‘mechanism’ I have distinguished. In the process of reflecting on what the present investigation has achieved, I will take the opportunity to suggest some possible directions in which future research may be may be oriented.

In relation to mechanicism we have seen that because of the instrumental role it played in the establishment of modern science, the scientist’s attitude towards it has tended to be one of deference. Indeed, for much of the past three and a half centuries, conceiving a physical body as a machine has been regarded as being tantamount to conceiving it in a rigorous, scientific way. In biology, the prestige and authority of mechanicism has meant that the development of our understanding of organisms has been shaped by theories and models grounded on fundamentally different kinds of systems, namely machines. The consequence of this has been that biologists have had to struggle to reconcile the distinctive features of life with the need to conform to the conceptual, theoretical, and explanatory parameters laid out by mechanicism on the basis of its understanding of machines. However, because many aspects of organisms are effectively explainable in mechanistic terms, the symptoms of the underlying problem have not always been readily apparent. In fact, the success of mechanistic biology in explaining these aspects of organisms has only served to vindicate its epistemological approaches and reinforce its ontological conceptualizations.

The mechanistic biologist generally proceeds by breaking down the organism into its physicochemical components and then seeking to reconstruct it epistemically from the bottom up. I have argued that this approach is effective for understanding isolated fragments or spatiotemporal cross-sections of organisms, but it is of little help in making sense of their emergent and systemic properties. Given the limitations of mechanistic explanation, I have considered two alternative explanatory frameworks. One alternative is to retain mechanismism's commitment to reductionism but modify the final units of analysis so that at no point in the course of the investigation does one stop dealing with entities displaying the distinctive characteristics of life. I have called this perspective 'biological atomism', and I have shown that it has been adopted by a number of biologists over the centuries—both before and after the formulation of cell theory—in order to come to terms with organismic features lying beyond the scope of the purely mechanical and physicochemical explanations of mechanistic biology.

The other explanatory framework I have considered is the one I have associated with the vitalistic tradition, and which involves dispensing with explanatory reductionism altogether and drawing attention to the fact that organisms display properties at the level of the whole that cannot be fully explained in terms of parts. This epistemic commitment has historically made vitalists especially perceptive to the systemic features of organisms, such as their self-producing organization and their intrinsic purposiveness, which tend to get overlooked in mechanistic accounts. However, it has also meant that vitalists have been at a great disadvantage in relation to the mechanists in terms of their empirical productivity. Indeed, if a biologist is committed to preserving the organization of the organism under investigation, the possibilities of learning much about its internal operation are greatly reduced. It is no coincidence that the more experimentally predisposed biologists have tended to align themselves on the mechanistic side, whereas the more theoretically (and philosophically) inclined biologists have generally found vitalism (broadly construed) more satisfying. Overall, it appears that heuristic considerations have tended to be more decisive than theoretical ones when taking a standpoint on the mechanismism-vitalism issue. Even today, the proven methodological usefulness of the MCO is often considered to be the best reason for defending its ontological truthfulness. Nevertheless, I have argued that keeping theoretical and heuristic considerations clearly separate is of the utmost importance when evaluating the appropriateness of machine models in biology.

In relation to the MCO, this thesis has illustrated that one can learn a great deal about what organisms are by developing a detailed appreciation of what they are *not*. By highlighting the fundamental differences between organisms and machines, we have arrived at a tentative understanding of what makes organisms distinctive. However, given the overwhelming influence of the MCO in biology today, the comprehension of the nature of organisms remains severely underdeveloped. This understanding will not arrive by means of ever more detailed mechanistic analyses but through the development of alternative theoretical frameworks which can adequately make sense of all the empirical data modern biology has generated. Organicist models such as the stream of life may provide useful starting points. However, the most formidable challenge facing a theory of the organism is the difficulty of coming to terms with what intrinsic purposiveness *actually is*. Although I discussed this feature at length in Chapter 3, it was almost always in the context of comparisons with the extrinsic purposiveness exhibited by machines. An exciting avenue for future research would involve attempting to make sense of the actual nature of intrinsic purposiveness.

Very tentatively, I can identify four possible strategies for explaining organismic purposiveness. The problem is that they are all afflicted by different difficulties. The rationale of the four strategies and the potential difficulties I envisage are as follows:

1. A *Darwinian strategy* for dealing with intrinsic purposiveness could attempt to argue that it can be accounted for by the action of natural selection. The problem I see with this strategy is that evolutionary theory does not appear to offer an actual explanation of the organism's purposive drive to survive, but rather presupposes it as a necessary condition for selection to occur in the first place. There is only a 'struggle for existence' because every organism exhibits an intrinsic desire to exist, yet this seems to be taken for granted in evolutionary explanations.
2. A *Kantian strategy* for dealing with intrinsic purposiveness could involve reconceptualizing it as a regulative principle of the understanding, that is, as a necessary heuristic that the biologist must postulate in order to make sense of organisms. The problem I find with this strategy is that it seems to have some rather disconcerting implications, such as the conviction that real objective knowledge of life is as a matter of principle forever beyond human capabilities.

3. A *finalistic strategy* for dealing with intrinsic purposiveness would imply following Aristotle and the post-Kantian *Naturphilosophen* in conceiving nature itself as ‘alive’ in the sense of being purposive. This strategy would seek to conceptualize intrinsic purposiveness as an expression of the general purposiveness of nature. The difficulty with this strategy is that it only solves the problem by creating another, namely the rather contentious claim that nature as a whole is purposive.
4. Finally, an *organicist strategy* for dealing with intrinsic purposiveness could attempt to conceive it as the phenomenal manifestation of the organism’s self-producing organization. The problem I anticipate here is that this only pushes the unknown element one step back, as it is the organism’s self-producing organization which would then demand a satisfactory naturalistic explanation.

On the whole, out of these four strategies, it seems to me that the organicist one enjoys the most promising prospects. Therefore, a focus on the nature of the living organization would seem to be an appropriate first step in formulating an apposite theory of the organism which could conclusively demonstrate the inadequacy of the MCO.

Finally, in relation to causal mechanisms, which have become so prominently discussed in the recent philosophical literature, my analysis has shown that their pervasiveness in biological explanations has its basis in the stunning successes of mechanistic investigations in the late nineteenth and early twentieth centuries. I have claimed that the mechanistic confidence that all biological phenomena would eventually be explained in terms of machine mechanisms caused the term ‘mechanism’ to gradually lose its distinctive mechanistic connotations, ultimately becoming a ‘dead metaphor’ that came to be used in the biological discourse “as a mere matter of custom” (Haldane, 1930, p. 59). I have also argued that judging by the way biologists today use this term, causal mechanisms are better understood not as real things that are discovered, but as heuristic models that are formulated for the purposes of explanation. My examination of causal mechanisms has also shown that current philosophical accounts of causal mechanisms, despite upholding an ontic

conception of them, are actually quite compatible with an epistemic or pragmatic understanding of them. Moreover, by conceiving causal mechanisms epistemically, it is possible to come to terms with the multitude of different biological contexts in which they are featured. Finally, my analysis has revealed that biologists today who habitually use the concept of mechanism in their explanations are not committed to the ontological and epistemological commitments of mechanicism. Indeed, explanations in terms of causal mechanisms need not be mechanistic at all as they often deal with organismic or even populational phenomena.⁵¹ This is why I have proposed the term ‘mechanismic’ to distinguish explanations in terms of causal mechanisms from the genuinely mechanistic explanations of machine mechanisms.

It is probably fitting to end with some general remarks. At a basic level, mechanistic thinking is inappropriate in biology because it refuses to recognize life as an autonomous phenomenon deserving its own epistemological consideration. To maintain that the living can be completely explained in terms of the mechanical and the physicochemical is to implicitly deny the need for an autonomous science called ‘biology’. The four studies undertaken in this thesis have attempted, in one way or another, to examine the grounds for the autonomy of the living, and by implication, the autonomy of biology. As I noted at the beginning of my investigation, I believe that this constitutes one of the core objectives of a genuine philosophy of *biology*.

⁵¹ An example which has been discussed at great lengths in the literature is the phenomenon of adaptation caused by the ‘mechanism of natural selection’ (cf. Skipper and Millstein, 2005; Barros, 2008; Kuorikoski, 2009; McKay and Williamson, 2010).

BIBLIOGRAPHY

- Ablondi, F. (1998). Automata, Living, and Non-living: Descartes' Mechanical Biology and His Criteria for Life. *Biology and Philosophy*, 13, 179-186.
- Alberts, B. (1998). The Cell as a Collection of Protein Machines: Preparing the Next Generation of Molecular Biologists. *Cell*, 92, 291-294.
- Allen, C., & Bekoff, M. (1995). Biological Function, Adaptation, and Natural Design. *Philosophy of Science*, 62, 609-22.
- Allen, G. E. (1975). *Life Science in the Twentieth Century*. London: John Wiley & Sons.
- Allen, G. E. (2005). Mechanism, Vitalism and Organicism in Late Nineteenth and Twentieth-Century Biology: The Importance of Historical Context. *Studies in History and Philosophy of the Biological and Biomedical Sciences*, 36, 261-283.
- Allen, G. E. (2007). A Century of Evo-Devo: The Dialectics of Analysis and Synthesis in Twentieth-Century Life Science. In M. D. Laubichler, & J. Maienschein (eds.), *From Embryology to Evo-Devo*. Cambridge, MA: MIT Press, pp. 123-167.
- Aristotle. (2001). *On the Parts of Animals. Translated with a Commentary by James Lennox*. Oxford: Oxford University Press.
- Atlan, H., & Koppel, M. (1990). The Cellular Computer DNA: Program or Data. *Bulletin of Mathematical Biology*, 52, 335-348.
- Aucante, V. (2006). Descartes's Experimental Method and the Generation of Animals. In J. E. H. Smith (ed.), *The Problem of Animal Generation in Early Modern Philosophy*. Cambridge: Cambridge University Press, pp. 65-79.
- Ayala, F. J. (2004). Design without Designer: Darwin's Greatest Discovery. In W. A. Dembski, & M. Ruse (eds.), *Debating Design: From Darwin to DNA*. Cambridge: Cambridge University Press, pp. 55-80.
- Baker, J. R (1948). The Cell-Theory: A Restatement, History, and Critique, Pt. I. *Quarterly Journal of Microscopical Science*, 89, 103-125.

- Baker, J. R. (1952). The Cell-Theory: A Restatement, History, and Critique, Pt. IV. *Quarterly Journal of Microscopical Science*, 94, 407-440.
- Baluška, F., Volkmann, D., & Barlow, P. W. (2004a). Eukaryotic Cells and Their *Cell Bodies*: Cell Theory Revised. *Annals of Botany*, 94, 9-32.
- Baluška, F., Volkmann, D., & Barlow, P. W. (2004b). Cell Bodies in a Cage. *Nature*, 428, 371.
- Baluška, F., Volkmann, D., & Barlow, P. W. (2006). Cell-Cell Channels and Their Implications for Cell Theory. In F. Baluška, D. Volkmann, & P. W. Barlow (eds.), *Cell-Cell Channels*. New York: Springer, pp. 1-17.
- Barham, J. (2004). The Emergence of Biological Value. In W. A. Dembski, & M. Ruse (eds.), *Debating Design: From Darwin to DNA*. Cambridge: Cambridge University Press, pp. 210-226.
- Barlow, P. W. (1982). The Plant Forms Cells, Not Cells the Plant: The Origin of de Bary's Aphorism. *Annals of Botany*, 49, 269-271.
- Barros, D. B. (2008). Natural Selection as a Mechanism. *Philosophy of Science*, 75, 306-322.
- Bechtel, W. (2006). *Discovering Cell Mechanisms: The Creation of Modern Cell Biology*. Cambridge: Cambridge University Press.
- Bechtel, W. (2007). Biological Mechanisms: Organized to Maintain Autonomy. In F. C. Boogerd, F. J. Bruggeman, J. S. Hofmeyr, & H. V. Westerhoff et al. (eds.), *Systems Biology: Philosophical Foundations*. New York: Elsevier, pp. 269-302.
- Bechtel, W. (2008). *Mental Mechanisms: Philosophical Perspectives on Cognitive Neuroscience*. London: Routledge.
- Bechtel, W., & Abrahamsen, A. (2008). From Reduction Back to Higher Levels. *Proceedings of the 30th Annual Meeting of the Cognitive Science Society*, 559-564.
- Bechtel, W., & Richardson, R. C. (1993). *Discovering Complexity: Decomposition and Localization as Strategies in Scientific Research*. Princeton: Princeton University Press.

- Beckner, M. (1959) . *The Biological Way of Thought*. Berkeley: University of California Press.
- Behe, M. J. (2001). Molecular Machines: Experimental Support for the Design Inference. In R. T. Pennock (eds.), *Intelligent Design Creationism and Its Critics: Philosophical, Theological, and Scientific Perspectives*. Cambridge, MA: MIT Press, pp. 241-256.
- Behe, M. J. (2005). Understanding Creation, Evolution and Intelligent Design. *Christian Post*, 27th May, 2005. (Available online at: <http://www.christianpost.com/article/20050527/understanding-creation-evolution-and-intelligent-design/print.html>).
- Behe, M. J. (2006). *Darwin's Black Box: The Biochemical Challenge to Evolution* (10th anniversary ed.). New York: Free Press. (First published 1996)
- Bergson, H. (1911). *L'Evolution Créatrice*. Paris: Alcan.
- Bernard, C. (1957). *An Introduction to the Study of Experimental Medicine* (Trans. H. C. Greene). New York: Dover Publications. (First published 1865)
- Bernard, C. (1974). *Lectures on the Phenomena of Life Common to Animals and Plants*. Springfield, Illinois: Charles C. Thomas. (First published 1878)
- Bertalanffy, L. v. (1933) *Modern Theories of Development: An Introduction to Theoretical Biology*. New York: Harper & Brothers. (First published 1933)
- Bertalanffy, L. v. (1952). *Problems of Life: An Evaluation of Modern Biological and Scientific Thought*. New York: Harper & Brothers.
- Bie, B., & Pan, Z. (2007). Trafficking of Central Opioid Receptors and Descending Pain Inhibition. *Molecular Pain*, 3, 1-7.
- Blackburn, S. (2005). *The Oxford Dictionary of Philosophy*. Oxford: Oxford University Press.
- Boas, M. (1952). The Establishment of the Mechanical Philosophy. *Osiris*, 10, 412-541.
- Bock, G., & Goode, J. (1998). *The Limits of Reductionism in Biology*. Chichester, UK: Wiley.
- Bohm, D. (1969). Some Remarks on the Notion of Order. In C. H. Waddington (ed.), *Towards a Theoretical Biology, Volume 2: Sketches*. Edinburgh: Edinburgh University Press, pp. 18-40.

- Boogerd, F. C., Bruggeman, F. J., Hofmeyr, J. S., & Westerhoff, H. V. (2007). *Systems Biology: Philosophical Foundations*. Amsterdam: Elsevier.
- Bowler, P. J. (1971). Preformation and Pre-existence in the Seventeenth Century: A Brief Analysis. *Journal of the History of Biology*, 4, 221-244.
- Bradie, M. (1999). Science and Metaphor. *Biology and Philosophy*, 14, 159-166.
- Brandon, R. N. (1985). Grene on Mechanism and Reductionism: More than Just a Side Issue. In P. Asquith, & P. Kitcher (eds.), *PSA 1984, Vol. 2*. East Lansing, MI: Philosophy of Science Association, pp. 345-353.
- Brandon, R. N. (1996). *Concepts and Methods in Evolutionary Biology*. Cambridge: Cambridge University Press.
- Broad, C. D. (1925). *The Mind and its Place in Nature*. London: Kegan Paul.
- Brooke, J. H. (1968). Wöhler's Urea and Its Vital Force? A Verdict from the Chemists. *Ambix*, 15, 84-114.
- Brooke, J. H. (1971). Organic Synthesis and the Unification of Chemistry: A Reappraisal. *The British Journal for the History of Science*, 5, 363-392.
- Brown, T. B. (1974). From Mechanism to Vitalism in the Eighteenth-Century English Physiology. *Journal of the History of Biology*, 7, 179-216.
- Brown, T. B. (1987). Medicine in the Shadow of the Principia. *Journal of the History of Ideas*, 48, 629-648.
- Brown, T. L. (2003). *Making Truth: Metaphor in Science*. Chicago: University of Illinois Press.
- Buller, D. J. (2002). Function and Design Revisited. In A. Ariew, R. Cummins, & M. Perlman (eds.), *Functions: New Essays in the Philosophy of Psychology and Biology*. Oxford: Oxford University Press, pp. 222-243.
- Bunge, M. (1997). Mechanism and Explanation. *Philosophy of the Social Sciences*, 27, 410-465.
- Bunge, M. (2003). *Philosophical Dictionary*. Amherst, NY: Prometheus Books.

- Byron, J. B. (2007). Whence Philosophy of Biology? *British Journal for the Philosophy of Science*, 58, 409-422.
- Campbell, N. A., Reece, J. B., Urry, L. A., Cain, M. L., Wasserman, S. A., Minorsky, P. V., & Jackson R. B. (2008). *Biology* (8th ed.). San Francisco: Pearson Benjamin Cummins. (First published 1987)
- Canguilhem, G. (1963). The Role of Analogies and Models in Biological Discovery. In A. C. Crombie (ed.), *Scientific Change: Historical Studies in the Intellectual, Social and Technical Conditions for Scientific Discovery and Technical Invention, from Antiquity to the Present*. London: Heinemann, pp. 507-20.
- Canguilhem, G. (1978). *On the Normal and the Pathological*. Dordrecht: D. Reidel Publishing. (First published 1966)
- Canguilhem, G. (1992). Machine and Organism. In J. Crary, & S. Kwinter (eds.), *Incorporations*. New York: Zone Books, pp. 45-69.
- Canguilhem, G. (2008). *Knowledge of Life*. New York: Fordham University Press. (First published 1965)
- Cheung, T. (2006). From the Organism of a Body to a Body of the Organism: Occurrence and Meaning of the Word 'Organism' from the Seventeenth to the Nineteenth Centuries. *British Journal for the History of Science*, 39, 319-339.
- Coleman, W. (1977). *Biology in the Nineteenth Century: Problems of Form, Function, and Transformation*. Cambridge: Cambridge University Press.
- Commoner, B. (1961). In Defense of Biology. *Science*, 133, 1745-1748.
- Cornish-Bowden, A. (2006). Putting the Systems Back into Systems Biology. *Perspectives in Biology and Medicine*, 49, 475-489.
- Cornish-Bowden, A., Cárdenas, M. L., Letelier, J. C., & Soto-Andrade, J. (2007). Beyond Reductionism: Metabolic Circularity as a Guiding Vision for a Real Biology of Systems. *Proteomics*, 7, 839-845.

- Cornish-Bowden, A., Cárdenas, M. L., Letelier, J. C., Soto-Andrade, J., & Abarzúa, F. G. Understanding the Parts in Terms of the Whole. (2004). *Biology of the Cell*, 96, 713-717.
- Craver, C. F. (2005). Beyond Reduction: Mechanisms, Multifield Integration, and the Unity of Neuroscience. *Studies in History and Philosophy of Biological and Biomedical Sciences*, 36, 373-397.
- Craver, C. F. (2007). *Explaining the Brain: Mechanisms and the Mosaic Unity of Neuroscience*. New York: Oxford University Press.
- Craver, C. F., & Darden, L. (2005). Introduction. *Studies in History and Philosophy of Biological and Biomedical Sciences*, 36, 233-244.
- Crick, F. H. C. (1966). *Of Molecules and Men*. New York: Prometheus Books.
- Cuvier, G. (1832). *The Animal Kingdom, Arranged in Conformity with Its Organization*. Philadelphia: James Kay, Jun. & Co. (First published 1817)
- Darden, L. (2005). Relations among Fields: Mendelian, Cytological and Molecular Mechanisms. *Studies in History and Philosophy of Biological and Biomedical Sciences*, 36, 357-371.
- Darden, L. (2006). *Reasoning in Biological Discoveries: Essays on Mechanisms, Interfield Relations, and Anomaly Resolution*. Cambridge: Cambridge University Press.
- Darden, L. (2007). Mechanisms and Models. In D. L. Hull, & M. Ruse (eds.), *The Cambridge Companion to Philosophy of Biology*, pp. 139-159. Cambridge: Cambridge University Press.
- Darden, L. (2008). Thinking Again about Biological Mechanisms. *Philosophy of Science*, 75, 958-969.
- Darwin, C. (1859). *On the Origin of Species by means of Natural Selection; or, The Preservation of Favoured Races in the Struggle for Life*. London: John Murray.
- Darwin, F. (1908). *More Letters of Charles Darwin: A Record of His Work in a Series of Hitherto Unpublished Letters, Volume I*. London: John Murray.
- Dawkins, R. (1986). *The Blind Watchmaker*. New York: W. W. Norton.

- Dawkins, R. (1998). Universal Darwinism. In D. L. Hull, & M. Ruse (eds.), *The Philosophy of Biology*. Oxford: Oxford University Press, pp. 15-37. (First published in D. S. Bendall (ed.), *Evolution from Molecules to Men*. Cambridge: Cambridge University Press, 1983, pp. 403-425)
- Dawkins, R. (2006). *The Selfish Gene* (30th anniversary ed.). Oxford: Oxford University Press. (First published 1976)
- Dennett, D. C. (1995). *Darwin's Dangerous Idea: Evolution and the Meanings of Life*. New York: Simon & Schuster.
- Deplazes, A., & Huppenbauer, M. (2009). Synthetic Organisms and Living Machines. *Systems and Synthetic Biology*, 3, 55-63.
- Des Chene, D. (2001). *Spirits & Clocks: Machine and Organism in Descartes*. Ithaca, New York: Cornell University Press.
- Des Chene, D. (2005). Mechanisms of Life in the Seventeenth Century: Borelli, Perrault, Régis. *Studies in History and Philosophy of the Biological and Biomedical Sciences*, 36, 245-260.
- Descartes, R. (1985). *The Philosophical Writings of Descartes. Volume I* (J. Cottingham, R. Stoothoff, & D. Murdoch, Trans.). Cambridge: Cambridge University Press.
- Descartes, R. (1991). *The Philosophical Writings of Descartes. Volume III: The Correspondence* (J. Cottingham, R. Stoothoff, D. Murdoch, & A. Kenny, Trans.). Cambridge: Cambridge University Press.
- Descartes, R. (1998). *The World and Other Writings* (S. Gaukroger, Trans.). Cambridge: Cambridge University Press.
- Detlefsen K. (2006). Explanation and Demonstration in the Haller-Wolff Debate, in J. E. H. Smith (ed.), *The Problem of Animal Generation in Early Modern Philosophy*. Cambridge: Cambridge University Press, pp. 235-261.
- Dobell, C. C. (1911). The Principles of Protistology. *Archiv für Protistenkunde*, 23, 269-310.
- Dobzhansky, T. (1937). *Genetics and the Origin of Species*. New York: Columbia University Press.

- Dobzhansky, T. (1964). Biology, Molecular and Organismic. *American Zoologist*, 4, 443-452.
- Dobzhansky, T. (1973). Nothing in Biology Makes Sense Except in the Light of Evolution. *The American Biology Teacher*, 35, 125-129.
- Driesch, H. (1908). *The Science and Philosophy of the Organism*. London: Adam & Charles Black.
- Driesch, H. (1914). *The History and Theory of Vitalism*. London: Macmillan.
- Dupré, J. (1993). *The Disorder of Things. Metaphysical Foundations of the Disunity of Science*. Cambridge, MA: Harvard University Press.
- Dupré, J. (2001). *Human Nature and the Limits of Science*. Oxford: Oxford University Press.
- Dupré, J. (2007). *The Constituents of Life*. Assen: Van Gorcum.
- Eldredge, N. (1995). *Reinventing Darwin: The Great Debate at the High Table of Evolutionary Theory*. New York: John Wiley & Sons.
- Elsasser, W. (1966). *Atom and Organism: A New Approach to Theoretical Biology*. Princeton: Princeton University Press.
- Etxeberria, A., & Umerez, J. (2006) . Organización y Organismo en la Biología Teórica ¿Vuelta al Organicismo? *Ludus Vitalis*, 26, 3-38.
- Faber, R. J. (1986). *Clockwork Garden: On the Mechanistic Reduction of Living Things*. Amherst, NY: University of Massachusetts Press.
- Falleti, T. G., & Lynch, J. F. (2009). Context and Causal Mechanisms in Political Analysis. *Comparative Political Studies*, 42, 1143-1166.
- Fisher, R. A. (1930). *The Genetical Theory of Natural Selection*. Oxford: Oxford University Press.
- Fleming, A. J. (2006). The Integration of Cell Proliferation and Growth in Leaf Morphogenesis. *Journal of Plant Research*, 119, 31-36.
- Foster, M. (1924). *Lectures on the History of Physiology*. Cambridge: Cambridge University Press. (First published 1901)

- Frankhauser, G. (1945). Maintenance of Normal Structure in Heteroploid Salamander Larvae, through Compensation of Changes in Cell Size by Adjustment in Cell Number and Cell Shape. *Journal of Experimental Zoology*, 100, 445-455.
- Garber, D. (2002). Descartes, Mechanics, and the Mechanical Philosophy. *Midwest Studies in Philosophy*, 26, 185-204.
- Garrett, J. (1999). Mechanics of the Ribosome. *Nature*, 400, 811-812.
- Garvey, B. (2007). *Philosophy of Biology*. Stocksfield: Acumen.
- Gavrilov, L. A., & Gavrilova, N. S. (2001). The Reliability Theory of Aging and Longevity. *Journal of Theoretical Biology*, 213, 527-545.
- Gerould, J. N. (1922). The Dawn of the Cell Theory. *Scientific Monthly*, 14, 268.
- Gerring, J. (2007). The Mechanismic World View: Thinking Inside the Box. *British Journal of Political Science*, 38, 161-179.
- Gilbert, S. F., & Sarkar, S. (2000). Embracing Complexity: Organicism for the 21st Century. *Developmental Dynamics*, 219, 1-9.
- Glennan, S. (1996). Mechanisms and the Nature of Causation. *Erkenntnis*, 44, 49-71.
- Glennan, S. (2002). Rethinking Mechanistic Explanation. *Philosophy of Science*, 69 (Suppl.), S342-S353.
- Glennan, S. (2005). Is there a Mechanism of Natural Selection? Paper presented at the International Society for the History, Philosophy, and Social Studies of Biology meeting in Guelph, Canada, July 2005. (Abstract: <http://www.ishpssb.org/ocs/viewabstract.php?id=215>).
- Godfrey-Smith, P. (1999). Adaptationism and the Power of Selection. *Biology and Philosophy*, 14, 181-194.
- Goldstein, K. (1995). *The Organism: A Holistic Approach to Biology Derived from Pathological Data in Man*. New York: Zone Books & MIT Press. (First published 1934)

- Goodfield, J. (1974). Changing Strategies: A Comparison of Reductionist Attitudes in Biological and Medical Research in the Nineteenth and Twentieth Centuries. In F. J. Ayala and T. Dobzhansky (eds.), *Reduction and Related Problems: Studies in the Philosophy of Biology*. London: MacMillan, pp. 65-86.
- Gould, S. J., & Lewontin, R. C. (1979). The Spandrels of San Marco and the Panglossian Paradigm: A Critique of the Adaptationist Programme. *Proceedings of the Royal Society of London*, 205, 581-598.
- Gould, S. J., & Vrba, E. (1982). Exaptation—A Missing Term in the Science of Form. *Paleobiology*, 8, 4-15.
- Grene, M., & Depew, D. (2004). *The Philosophy of Biology: An Episodic History*. Cambridge: Cambridge University Press.
- Grene, M. (1971). Reducibility: Another Side Issue? In M. Grene (ed.), *Interpretations of Life and Mind*. New York: Humanities Press, pp. 14-37.
- Griffiths, P. E. (1996). The Historical Turn in the Study of Adaptation. *British Journal for the Philosophy of Science*, 47, 511-532.
- Griffiths, P. E., & Gray, R. D. (1994). Developmental Systems and Evolutionary Explanation. *Journal of Philosophy*, 91, 277-304.
- Griffiths, P. E., & Knight, R. D. (1998). What is the Developmentalist Challenge? *Philosophy of Science*, 65, 253-258.
- Grmek, M. D. (1972). A Survey of the Mechanical Interpretations of Life from Greek Atomists to the Followers of Descartes. In A. D. Breck, & W. Yourgrau (eds.), *Biology, History, and Natural Philosophy*. New York: Plenum Press, pp. 181-195.
- Haag, J. R., & Pikaard, C. S. (2007). RNA Polymerase I: A Multifunctional Molecular Machine. *Cell*, 131, 1224-1225.
- Haber, M. H., Hamilton, A., Okasha, S., & Odenbaugh, J. Philosophy of Biology. In F. Allhoff (ed.), *Philosophy of the Sciences: A Guide*. Oxford: John Wiley & Sons Ltd., pp. 184-212.

- Haigh, E. (1984). Xavier Bichat and the Medical Theory of the Eighteenth Century. *Medical History*, 4, 1-146.
- Haldane, J. B. S. (1932). *The Causes of Evolution*. London: Longmans, Green.
- Haldane, J. S. (1884). Life and Mechanism. *Mind*, 9, 27-47.
- Haldane, J. S. (1917). *Organism and Environment as Illustrated by the Physiology of Breathing*. New Haven: Yale University Press.
- Haldane, J. S. (1930). *The Sciences and Philosophy*. London: Hodder and Stoughton.
- Haldane, J. S. (1931). *The Philosophical Basis of Biology*. London: Hodder & Stoughton Ltd.
- Hall, T. S. (1968). On Biological Analogs of Newtonian Paradigms. *Philosophy of Science*, 35, 6-27.
- Hall, T. S. (1969). *History of General Physiology, 600 B.C. to A.D. 1900, Vol. 2*. Chicago: Chicago University Press.
- Hall, T. S. (1970). Descartes' Physiological Method: Positions, Principles, Examples. *Journal of the History of Biology*, 3, 53-79.
- Haraway, D. J. (1976). *Crystals, Fabrics and Fields: Metaphors of Organicism in Twentieth-Century Developmental Biology*. New Haven: Yale University Press.
- Harold, F. M. (2001). *The Way of the Cell*. Oxford: Oxford University Press.
- Heidermann, D. H. (2009). *Kant Yearbook 01/2009: Teleology*. Berlin: Walter de Gruyter.
- Hein, H. (1968). Mechanism and Vitalism as Metatheoretical Commitments. *Philosophical Forum*, 1, 185-205.
- Hein, H. (1972). The Endurance of the Mechanism–Vitalism Controversy. *Journal of the History of Biology*, 5, 159-188.
- Hempel, C. G., & Oppenheim, P. (1948). Studies in the Logic of Explanation. *Philosophy of Science*, 15, 135-175.
- Hempel, C. G. (1966). *Philosophy of Natural Science*. London: Prentice-Hall International, Inc.

- Hesse, M. (1966). *Models and Analogies in Science*. Notre Dame, In: University of Notre Dame Press.
- Hull, D. (1974). *Philosophy of Biological Science*. Englewood Cliffs: Prentice-Hall.
- Hume, D. (2007). *Dialogues Concerning Natural Religion*. Cambridge: Cambridge University Press. (First published 1779)
- Huxley, T. H. (1893) *Collected Essays*. London: Macmillan and Co.
- Imahori, H. (2004). Porphyrin–Fullerene Linked Systems as Artificial Photosynthetic Mimics. *Organic and Biomolecular Chemistry*, 2, 1425-1433.
- Institute for Systems Biology. Systems Biology—The 21st Century Science. (Available online at: http://www.systemsbiology.org/intro_to_isb_and_systems_biology/systems_biology_-_the_21st_century_science) (Accessed September 2010)
- Jacob, F. (1973) *The Logic of Life: A History of Heredity*. Princeton, NJ: Princeton University Press.
- Jacob, F. (1977). Evolution and Tinkering. *Science*, 196, 1161-1166.
- Jacob, F., & Monod, J. (1961). Genetic Regulatory Mechanisms in the Synthesis of Proteins. *Journal of Molecular Biology*, 3, 318-356.
- Jacyna, L. S. (1990). Romantic Thought and the Origins of Cell Theory. In A. Cunningham, & N. Jardine (eds.), *Romanticism and the Sciences*. Cambridge: Cambridge University Press, pp. 161-169.
- Jaffe, B. (1931). *Crucibles: The Story of Chemistry from Ancient Alchemy to Nuclear Fission*. New York: Dover.
- Jennings, H. S. (1918). Mechanism and Vitalism. *The Philosophical Review*, 27, 577-596.
- Johnstone, J. (1914). *The Philosophy of Biology*. Cambridge: Cambridge University Press.
- Jonas, H. (2001). *The Phenomenon of Life: Toward a Philosophical Biology*. Evanston, IL: Northwestern University Press. (First published 1966)
- Juthe, A. (2005). Argument by Analogy. *Argumentation*, 19, 1-27.

- Kaneko, K. (2006). *Life: An Introduction to Complex Systems Biology*. New York: Springer.
- Kant, I. (2000). *Critique of the Power of Judgment* (P. Guyer, & E. Matthews, Trans.). Cambridge: Cambridge University Press. (First published 1790)
- Kaplan, D. R. (1992). The Relationship of Cells to Organisms in Plants: Problem and Implications of an Organismal Perspective. *International Journal of Plant Sciences*, 153, S28-S37.
- Kaplan, D. R., & Hagemann, W. (1991). The Relationship of Cell and Organism in Vascular Plants. *BioScience*, 41, 693-703.
- Kapp, R. O. (1954). Living and Lifeless Machines. *British Journal for the Philosophy of Science*, 5, 91-103.
- Karsenti, E. (2008). Self-Organization in Cell Biology: A Brief History. *Molecular Cell Biology*, 9, 255-262.
- Kauffman, S. A. (1970). Articulation of Parts Explanation in Biology and the Rational Search for Them. *PSA: Proceedings of the Biennial Meeting of the Philosophy of Science Association*, 1970, 257-272.
- Keeley, A., & Soldati, D. (2004). The Glideosome: A Molecular Machine Powering Motility and Host-Cell Invasion by Apicomplexa. *Trends in Cell Biology*, 14, 528-532.
- Keller, E. F. (1995). *Refiguring Life: Metaphors of Twentieth-Century Biology*. New York: Columbia University Press.
- Keller, E. F. (2000). *The Century of the Gene*. Cambridge, MA: Harvard University Press.
- Kirschner, M., Gerhart, M., & Mitchison, T. (2000). Molecular "Vitalism". *Cell*, 100, 79-88.
- Kitano, H. (2001). *Foundations of Systems Biology*. Cambridge, MA: MIT Press.
- Kitcher, P. (1993). Function and Design. *Midwest Studies in Philosophy*, 18, 379-97.
- Klerk, G. J. M. (1979). Mechanism and Vitalism. A History of the Controversy. *Acta Biotheoretica*, 28, 1-10.

- Knorr-Cetina, K. (1999). *Epistemic Cultures: How the Sciences Make Knowledge*. New York: Harvard University Press.
- Konopka, A. K. (2002). Grand Metaphors of Biology in the Genome Era. *Computers and Chemistry*, 26, 397-401.
- Konopka, A. K. (2007). *Systems Biology: Principles, Methods, and Concepts*. Boca Raton: Taylor & Francis Group.
- Krohs, U. (2009). Functions as Based on a Concept of General Design. *Synthese*, 166, 69-89.
- Kühlbrandt, W. (2000). Bacteriorhodopsin—The Movie. *Nature*, 406, 569-670.
- Kuorikoski, J. (2009). Two Concepts of Mechanism: Componential Causal System and Abstract Form of Interaction. *International Studies in the Philosophy of Science*, 23, 143-160.
- Kurakin, A. (2005). Self-Organization versus Watchmaker: Stochastic Dynamics of Cellular Organization. *Biological Chemistry*, 386, 247-254.
- Lakoff, G., & Johnson, M. (1999). *Philosophy in the Flesh: The Embodied Mind and Its Challenge to Western Thought*. New York: Basic.
- Landes, J. B. (2007). The Anatomy of Artificial Life: An Eighteenth-Century Perspective. In J. Riskin (ed.), *Genesis Redux: Essays in the History and Philosophy of Artificial Life*. Chicago: Chicago University Press, pp. 96-116.
- Langton, C. G. (1989). Artificial Life. In C. G. Langton (ed.), *Artificial Life (Santa Fe Institute Studies in the Sciences of Complexity, 6)*. Redwood City, CA: Addison-Wesley, pp.1-47.
- Lauder, G. V. (1982). Historical Biology and the Problem of Design. *Journal of Theoretical Biology*, 97, 57-67.
- Lenoir, T. (1982). *The Strategy of Life: Teleology and Mechanics in Nineteenth Century German Biology*. Chicago: Chicago University Press.
- Lewens, T. (2000). Function Talk and the Artefact Model. *Studies in History and Philosophy of Biological and Biomedical Sciences*, 31, 95-111.

- Lewens, T. (2002). Adaptationism and Engineering. *Biology and Philosophy*, 17, 1-31.
- Lewens, T. (2004). *Organisms and Artifacts: Design in Nature and Elsewhere*. Cambridge, MA: MIT Press.
- Lewontin, R. C. (1996). Biology as Engineering. In J. Collado, B. Magasanik, & T. F. Smith (eds.), *Integrative Approaches to Molecular Biology*. Cambridge, MA: MIT Press, pp. 1-11.
- Lewontin, R. C. (2000). *The Triple Helix: Gene, Organism, and Environment*. Cambridge, MA: Harvard University Press.
- Lewontin, R. C. (2009). Foreword: Carving Nature at its Joints? In A. Barberousse, M. Morange, & T. Pradeu (eds.), *Mapping the Future of Biology: Evolving Concepts and Theories*. Boston, MA: Springer, pp. v-vii.
- Liebig, J. (1842). *Animal Chemistry, or Organic Chemistry in its Application to Physiology and Pathology*. Cambridge: John Owen.
- Lillie, R. S. (1914). The Philosophy of Biology: Vitalism versus Mechanism. *Science*, 40, 840-846.
- Lillie, R. S. (1926). The Nature of the Vitalistic Dilemma. *The Journal of Philosophy*, 23, 673-682.
- Lipman, T. O. (1967). Vitalism and Reductionism in Liebig's Physiological Thought. *Isis*, 58, 167-185.
- Locke, J. (1975). *An Essay Concerning Human Understanding*. Oxford: Clarendon Press. (First published 1695)
- Loeb, J. (1912). *The Mechanistic Conception of Life*. Chicago: Chicago University Press.
- Lovejoy, A. O. (1911). The Meaning of Vitalism. *Science*, 33, 610-614.
- Lowry, T., & Richardson, K. (1981). *Mechanism and Theory in Organic Chemistry*. New York: Harper & Row.
- Machamer, P., Darden, L., & Carver, C. F. (2000). Thinking about Mechanisms. *Philosophy of Science*, 67, 1-25.

- Mackenzie, A. W. (1975). A Word about Descartes' Mechanistic Conception of Life. *Journal of the History of Biology*, 8, 1-13.
- Marcaida, M. J., DePristo, M. A., Chandran, V., Carpousis, A. J., & Luisi, B. F. (2006). The RNA Degradosome: Life in the Fast Lane of Adaptive Molecular Evolution. *Trends in Biochemical Sciences*, 31, 359-365.
- Matthen, M. (1997). Teleology and the Product Analogy. *Australasian Journal of Philosophy*, 75, 21-37.
- Maturana, H. R., & Varela, F. J. (1973). *De Máquinas y Seres Vivos. Autopoiesis: La Organización de lo Vivo*. Santiago de Chile: Editorial Universitaria S.A.
- Maturana, H. R., & Varela, F. J. (1980). *Autopoiesis and Cognition: The Realization of the Living*. Dordrecht: Reidel.
- Maynard Smith, J. (1969). The Status of Neo-Darwinism. In C. H. Waddington (ed.), *Towards a Theoretical Biology*. Edinburgh: Edinburgh University Press, pp. 82-9.
- Mayr, E. (1961). Cause and Effect in Biology. *Science*, 131, 1501-1506.
- Mayr, E. (2004). *What Makes Biology Unique? Considerations on the Autonomy of a Scientific Discipline*. Cambridge: Cambridge University Press.
- McDougall, W. (1938). *The Riddle of Life: A Survey of Theories*. London: Methuen & Co, Ltd.
- McKay, P., & Williamson, J. (2010). Function and Organization: Comparing the Mechanisms of Protein Synthesis and Natural Selection. *Studies in History and Philosophy of Biological and Biomedical Sciences*, Online first.
- McLaughlin, P. (2001). *What Functions Explain: Functional Explanation and Self-Reproducing Systems*. Cambridge: Cambridge University Press.
- Mendelsohn, A. J. (2003). Lives of the Cell. *Journal of the History of Biology*, 36, 1-37.
- Milam, E. L. (2010). *Looking For A Few Good Males: Female Choice in Evolutionary Biology*. Baltimore: The Johns Hopkins University Press.

- Millikan, R. G. (1984). *Language, Thought and Other Biological Categories: New Foundations for Realism*. Cambridge: MIT Press.
- Monamy, V. (2009). *Animal Experimentation: A Guide to the Issues* (2nd ed.). Cambridge: Cambridge University Press.
- Monod, J. (1977). *Chance and Necessity: An Essay on the Natural Philosophy of Modern Biology*. Glasgow: Williams Collins Sons & Co Ltd. (First published 1970)
- Morange, M. (1998). *A History of Molecular Biology*. Cambridge, MA: Harvard University Press.
- Morange, M. (2001). *The Misunderstood Gene*. Cambridge, MA: Harvard University Press.
- Morgan, C. L. (1923). *Emergent Evolution*. London: Henry Holt and Co.
- Moss, L. (2002). From Representational Preformationism to the Epigenesis of Openness to the World? Reflections on a New Vision of the Organism. *Annals of the New York Academy of Sciences*, 981, 219-229.
- Moss, L. (2003). *What Genes Can't Do*. Cambridge, MA: MIT Press.
- Mossio, M., Saborido, C. & Moreno, A. (2009). An Organizational Account of Biological functions. *British Journal for the Philosophy of Science*, 60, 813-841.
- Nagel, E. (1979). *The Structure of Science*. Indianapolis: Hackett Publishing Company.
- Neander, K (1991). The Teleological Notion of "Function". *Australasian Journal of Philosophy*, 69, 454-68.
- Needham, J. (1925). Mechanistic Biology and the Religious Consequences. In J. Needham (Ed.), *Science, Religion and Reality* (pp. 219-258). New York: The Macmillan Company.
- Needham, J. (1928a). Recent Developments in the Philosophy of Biology. *The Quarterly Review of Biology*, 3, 77-91.
- Needham, J. (1928b). Organicism in Biology. *Journal of Philosophical Studies*, 3, 29-40.

- Nijhout, H. F. (1990). Metaphors and the Role of Genes in Development. *BioEssays*, 12, 441-446.
- Nilsen, T. W. (2003). The Spliceosome: The Most Complex Macromolecular Machine in the Cell? *BioEssays*, 25, 1147-1149.
- Noble, D. (2006). *The Music of Life: Biology beyond the Genome*. Oxford: Oxford University Press.
- Norkus, Z. (2005). Mechanisms as Miracle Makers? The Rise and Inconsistencies of the “Mechanismic Approach” in Social Science and History. *History and Theory*, 44, 348-372.
- Novikoff, A. (1945). The Concept of Integrative Levels and Biology. *Science*, 101, 209-215.
- O'Malley, M. A. (2010). The First Eukaryote Cell: An Unfinished History of Contestation. *Studies in History and Philosophy of Biological and Biomedical Sciences*, 41, Online first.
- Ohki, T., Mikhailenko, S. V., Morales, M. F., Onishi, H., & Mochizuki, N. (2004) Transmission of Force and Displacement within the Myosin Molecule. *Biochemistry*, 43, 13707-13714.
- Olby, R. (1970). Francis Crick, DNA, and the Central Dogma. *Daedalus*, 99, 938-987.
- Ollason, J. G. (1987). Artificial Design in Natural History: Why It's So Easy to Understand Animal Behavior. In P. Bateson & P. Klopfer (eds.), *Alternatives: Perspectives in Ethology. Volume 7*. New York: Plenum, pp. 233-257.
- Ospovat, D. (1981). *The Development of Darwin's Theory: Natural History, Natural Theology, and Natural Selection, 1838-1859*. Cambridge: Cambridge University Press.
- Oyama, S. (2000). *The Ontogeny of Information: Developmental Systems and Evolution* (2nd ed.). Durham, NC: Duke University Press.
- Oyama, S., Griffiths, P. E., & Gray, R. D. (2001). *Cycles of Contingency: Developmental Systems and Evolution*. Cambridge, MA: MIT Press.

- Paley, W. (2006). *Natural Theology; or, Evidences of the Existence and Attributes of the Deity, Collected from the Appearances of Nature*. Oxford: Oxford University Press. (First published 1802)
- Pallen, M. J., Penn, C. W., & Chaudhuri, R. R. (2005). Bacterial Flagellar Diversity in the Post-Genomic Era. *Trends in Microbiology*, 13, 143-149.
- Pattee, H. H. (1989). Simulations, Realizations, and Theories of Life. In C. G. Langton (ed.), *Artificial Life (Santa Fe Institute Studies in the Sciences of Complexity, 6)*. Redwood City, CA: Addison-Wesley, pp. 63-78.
- Pennisi, E. (2004). The Birth of the Nucleus. *Science* 305,766-768.
- Peters, J. M. (2006). The Anaphase Promoting Complex/Cyclosome: A Machine Designed to Destroy. *Nature Reviews Molecular Cell Biology*, 7, 644-656.
- Peters, W., Roberts, S., & Buldt, B. (2007). Molecular Machines: A Metaphor in the Making? Paper presented at the *International Society for the History, Philosophy, and Social Studies of Biology*, Exeter, UK, 28th July 2007. (Abstract available online at: http://ishpssb.org/oldmeetings/2007/ISHPSSB2007 Programme_000.pdf; p. 136)
- Pickstone, J. V. (1973). Globules and Coagula: Concepts of Tissue Formation in the Early Nineteenth Century. *Journal of the History of Medicine*, 28, 336-356.
- Price, D. J. S. (1964). Automata and the Origins of Mechanism and Mechanistic Philosophy. *Technology and Culture*, 5, 9-23.
- Quale, A. (2002). The Role of Metaphor in Scientific Epistemology: A Constructivist Perspective and Consequences for Science Education. *Science & Education*, 11, 443-457.
- Raff, R. A. (2005). Stand Up for Evolution. *Evolution & Development*, 7, 273-275.
- Railton, P. (1978). A Deductive-Nomological Model of Probabilistic Explanation. *Philosophy of Science*, 45, 206-226.
- Ramberg, P. J. (2000). The Death of Vitalism and the Birth of Organic Chemistry. *Ambix*, 47, 170-195.

- Ramsey, J. (2008). Mechanisms and their Explanatory Challenges in Organic Chemistry. *Philosophy of Science*, 75, 970-982.
- Raven, P., Johnson, G., Losos, J., Mason, K., & Singer, S. (2008). *Biology* (8th ed.). New York: The McGraw-Hill Companies, Inc. (First published 1999)
- Ray, T. S. (1992). An Approach to the Synthesis of Life. In C. G. Langton, C. Taylor, J. D. Farmer, & S. Rasmussen (eds.), *Artificial Life II (Santa Fe Institute Studies in the Science of Complexity Proceedings, 10)*. Redwood City, CA: Addison-Wesley, pp. 371-408.
- Reynolds, A. (2007). The Theory of the Cell-State and the Question of Cell Autonomy in Nineteenth and Early-Twentieth Century Biology. *Science in Context*, 20, 71-95.
- Richmond, M. L. (1989). Protozoa as Precursors of Metazoa: German Cell Theory and Its Critics at the Turn of the Century. *Journal of the History of Biology*, 22, 243-276.
- Richmond, M. L. (2000). T. H. Huxley's Criticism of German Cell Theory: An Epigenetic and Physiological Interpretation of Cell Structure. *Journal of the History of Biology*, 33, 247-289.
- Riskin, J. (2003). The Defecating Duck; or, The Ambiguous Origins of Artificial Life. *Critical Inquiry*, 29, 599-633.
- Riskin, J. (2007). Introduction: The Sistine Gap. In J. Riskin (ed.), *Genesis Redux: Essays in the History and Philosophy of Artificial Life*. Chicago: Chicago University Press, pp. 1-32.
- Ritter, W. E. (1919). *The Unity of the Organism, or the Organismal Conception of Life*. Boston: Gorham Press.
- Ritterbush, P. C. (1964). *Overtures to Biology*. New Haven: Yale University Press.
- Robert, J. S. (2004). *Embryology, Epigenesis, and Evolution: Taking Development Seriously*. Cambridge: Cambridge University Press.
- Roe, S. A. (1979). Rationalism and Embryology: Caspar Friedrich Wolff's Theory of Epigenesis. *Journal of the History of Biology*, 12, 1-43.

- Roe, S. A. (1981). *Matter, Life, and Generation: Eighteenth-century Embryology and the Haller-Wolff Debate*. Cambridge: Cambridge University Press.
- Roger, J. (1963). *Les Sciences de la Vie dans la Pensée Française du XVIII^e siècle*. Paris: Armand Colin.
- Roll-Hansen, N. (1976). Critical Teleology: Immanuel Kant and Claude Bernard on the Limitations of Experimental Biology. *Journal of the History of Biology*, 9, 59-91.
- Rosen, R. (1991). *Life Itself: A Comprehensive Inquiry Into the Nature, Origin, and Fabrication of Life*. New York: Columbia University Press.
- Rosenberg, A. (1997). Reductionism Redux: Computing the Embryo. *Biology and Philosophy*, 12, 445-470.
- Rosenberg, A. (2006). *Darwinian Reductionism; Or, How to Stop Worrying and Love Molecular Biology*. Chicago: The University of Chicago Press.
- Rosenberg, A., & McShea, D. W. (2008). *Philosophy of Biology: A Contemporary Introduction*. New York: Routledge.
- Rosenblueth, A., & Wiener, N. (1950). Purposeful and Non-Purposeful Behavior. *Philosophy of Science*, 17, 318-326.
- Rosenblueth, A., Wiener, N., Bigelow, J. (1943). Behavior, Purpose and Teleology. *Philosophy of Science*, 10, 18-24.
- Ruse, M. (1973). *The Philosophy of Biology*. London: Hutchinson.
- Ruse, M. (1988). *Philosophy of Biology Today*. Albany: State University of New York Press.
- Ruse, M. (2003). *Darwin and Design: Does Evolution Have a Purpose?* Cambridge, MA: Harvard University Press.
- Ruse, M. (2005). Darwinism and Mechanism: Metaphor in Science. *Studies in History and Philosophy of Biological and Biomedical Sciences*, 36, 285-302.
- Russell, E. S. (1916). *Form and Function: A Contribution to the History of Animal Morphology*. London: John Murray.

- Sadava, D., Heller, H. C., Orians, G. H., Purves, W. K., & Hillis, D. M. (2006). *Life: The Science of Biology* (8th ed.). Gordonsville, VA: W. H. Freeman. (First published 1989)
- Salmon, W. C. (1984). *Scientific Explanation and the Causal Structure of the World*. Princeton, NJ: Princeton University Press.
- Salvesen, G. S., & Renatus, M. (2002). Apoptosome: The Seven-Spoked Death Machine. *Developmental Cell*, 2, 256-257.
- Sapp, J. (2003). *Genesis: The Evolution of Biology*. Oxford: Oxford University Press.
- Sarkar, S. (1996). Biological Information: A Skeptical Look at Some Central Dogmas of Molecular Biology. In S. Sarkar (ed.), *The Philosophy of History of Molecular Biology: New Perspectives*. Dordrecht: Kluwer, pp. 187-231.
- Schickore, J. (2009). Error as Historiographical Challenge: The Infamous Globule Hypothesis. In G. Hon, J. Schickore, & F. Steinle (eds.), *Going Amiss in Experimental Research*. Boston, MA: Springer, pp. 27-45.
- Schubert-Soldern, R. (1962). *Philosophical Aspects of Biology*. London: Burns & Oates.
- Scott, E. C., & Matzke, N. J. (2007). Biological Design in Science Classrooms. In J. C. Avise, & F. J. Ayala (eds.), *In the Light of Evolution. Volume 1: Adaptation and Complex Design*. Washington, DC: The National Academies Press, pp. 285-304.
- Sedgwick, A. (1896). Further Remarks on Cell Theory, With a Reply to Mr. Bourne. *Quarterly Journal of Microscope Science*, 38, 331-337.
- Shanks, N., & Joplin, K. H. (1999). Redundant Complexity: A Critical Analysis of Intelligent Design in Biochemistry. *Philosophy of Science*, 66, 268-282.
- Sharp, L. W. (1921). *An Introduction to Cytology*. New York: McGraw-Hill.
- Simpson, G. G. (1963). Biology and the Nature of Science. *Science*, 139, 81-88.
- Singer, C. (1989). *A History of Biology to About the Year 1900* (3rd ed.). Ames, IA: Iowa State University Press. (First published 1931)

- Sitte, P. (1992). A Modern Concept of the 'Cell Theory'. *International Journal of Plant Sciences*, 153, S1-S6.
- Skipper, R., & Millstein, R. (2005). Thinking about Evolutionary Mechanisms: Natural Selection. *Studies in History and Philosophy of Biological and Biomedical Sciences*, 36, 327-347.
- Sloan, P. R. (1977). Descartes, the Sceptics, and the Rejection of Vitalism in Seventeenth Century Physiology. *Studies in History and Philosophy of Science*, 8, 1-28.
- Smith, C. U. M. (1976). *The Problem of Life: An Essay in the Origins of Biological Thought*. New York: John Wiley & Sons.
- Smith, J. E. H. (2006). Imagination and the Problem of Heredity in Mechanist Embryology. In J. E. H. Smith (ed.), *The Problem of Animal Generation in Early Modern Philosophy*. Cambridge: Cambridge University Press, pp. 80-102.
- Smuts, J. C. (1926). *Holism and Evolution*. London: Macmillan.
- Sober, E. (1992). Learning from Functionalism—Prospects for Strong Artificial Life. In C. G. Langton, C. Taylor, J. D. Farmer, & S. Rasmussen (eds.), *Artificial Life II (Santa Fe Institute Studies in the Science of Complexity Proceedings, 10)*. Redwood City, CA: Addison-Wesley, pp. 749-766.
- Sober, E. (2000). *Philosophy of Biology* (2nd ed.). Boulder, CO: Westview Press. (First published 1993)
- Soto, A. M., & Sonnenschein, C. (2006). Emergentism by Default: A View from the Bench. *Synthese*, 151, 361-376.
- Spronk, H. M. H., Govers-Riemslog, J. W. P., & Cate, H. T. (2003). The Blood Coagulation System as a Molecular Machine. *BioEssays*, 25, 1220-1228.
- Strunnikov, A. V. (2003). Condensin and Biological Role of Chromosome Condensation. *Progress in Cell Cycle Research*, 5, 361-367.
- Taylor, R. (1950a). Comments on a Mechanistic Conception of Purposefulness. *Philosophy of Science*, 17, 310-317.

- Taylor, R. (1950b). Purposeful and Non-Purposeful Behavior: A Rejoinder. *Philosophy of Science*, 17, 327-332.
- Thagard, P. (1998). Explaining Disease: Causes, Correlations, and Mechanisms. *Minds and Machines*, 8, 61-78.
- Torres, P. J. (2009). A Modified Conception of Mechanisms. *Erkenntnis*, 71, 233-251.
- Toulmin, S., & Goodfield, J. (1962). *The Architecture of Matter*. London: Penguin.
- Tsukaya, H. (2003). Organ Shape and Size: A Lesson from Studies of Leaf Morphogenesis. *Current Opinion in Plant Biology*, 6, 57-62.
- Vaccari, A. (2008). Legitimizing the Machine: The Epistemological Foundation of Technological Metaphor in the Natural Philosophy of René Descartes. In C. Zittel, G. Engel, R. Nanni, & N. C. Karafyllis (eds.), *Philosophies of Technology: Francis Bacon and his Contemporaries*. Leiden: Koninklijke Brill NV, pp. 287-336.
- Vamvacas, C. J. (2009). *The Founders of Western Thought—The Presocratics*. Boston, MA: Springer. (First published 2001)
- Varela, F. J. (1979). *Principles of Biological Autonomy*. New York: Elsevier North Holland.
- Varela, F. J., & Maturana, H. R. (1972). Mechanism and Biological Explanation. *Philosophy of Science*, 39, 378-382.
- Voges, D., Zwickl, P., & Baumeister, W. (1999). The 26S Proteasome: A Molecular Machine Designed for Controlled Proteolysis. *Annual Review of Biochemistry*, 68, 1015-1068.
- Von Neumann, J. (1966). *Theory of Self-Reproducing Automata*. Urbana: University of Illinois Press.
- Warren, H. C. (1918). Mechanism versus Vitalism, in the Domain of Psychology. *The Philosophical Review*, 27, 597-615.
- Watson, J. D., & Crick, F. H. C. (1953). Molecular Structure of Nucleic Acids: A Structure for Deoxyribose Nucleic Acid. *Nature*, 171, 737-738.
- Watson, J. D. (1965). *The Molecular Biology of the Gene*. New York: W.A. Benjamin.

- Webster, S. (2003). *Thinking about Biology*. Cambridge: Cambridge University Press.
- Weiss, P. (1940). The Problem of Cell Individuality in Development, *American Naturalist*, 74, 34-46.
- Weiss, P. (1963). The Cell as Unit. *Journal of Theoretical Biology*, 5, 389-397.
- Weitzenfeld, J. S. (1984). Valid Reasoning by Analogy. *Philosophy of Science*, 51, 137-149.
- Wheeler, L. R. (1939). *Vitalism: Its History and Validity*. London: H. F. & G. Witherby Ltd.
- Whewell, W. (1847). *The Philosophy of the Inductive Sciences, Founded Upon their History, Volume 1* (2nd ed.). London: John W. Parker.
- Whitehead, A. N. (1925). *Science and the Modern World*. Cambridge: Cambridge University Press.
- Whitman, C. O. (1893). The Inadequacy of the Cell-Theory of Development. *Journal of Morphology*, 8, 639-658.
- Wilkins, A. S. (1985). The Limits of Molecular Biology. *BioEssays*, 3, 3.
- Williams, G. C. (1992). *Natural Selection: Domains, Levels, and Challenges*. New York: Oxford University Press.
- Wilson, E. B. (1900). *The Cell in Development and Inheritance* (2nd ed.). New York: MacMillan. (First published 1896)
- Wilson, J. W. (1944). Cellular Tissue and the Dawn of the Cell Theory. *Isis*, 35, 168-173.
- Wilson, J. W. (1947). Dutrochet and the Cell Theory. *Isis*, 37, 14-21.
- Wimsatt, W. C. (1970). Some Problems with the Concept of 'Feedback'. *PSA: Proceedings of the Biennial Meeting of the Philosophy of Science Association*, 1970, 241-256.
- Wimsatt, W. C. (1972). Complexity and Organization. *PSA: 1972, Proceedings of the Philosophy of Science Association*, 1972, 67-86.
- Wimsatt, W. C. (1987). False Models as Means to Truer Theories. In M. H. Nitecki, & A. Hoffman (eds.), *Neutral Models in Biology*. Oxford: Oxford University Press, pp. 23-55.

- Wise, M. N. (2007). The Gender of Automata in Victorian Britain. In J. Riskin (ed.), *Genesis Redux: Essays in the History and Philosophy of Artificial Life*. Chicago: Chicago University Press, pp. 163-195.
- Woese, C. R. (2004). A New Biology for a New Century. *Microbiology and Molecular Biology Reviews*, 68, 173-186.
- Wolpert, L. (1994). Do We Understand Development? *Science*, 266, 571-572.
- Wood, G. (2002). *Living Dolls: A Magical History of the Quest for Mechanical Life*. London: Faber & Faber.
- Woodger, J. H. (1929). *Biological Principles: A Critical Study*. London: Routledge & Kegan Paul.
- Woodward, J. (2003). *Making Things Happen: A Theory of Causal Explanation*. Oxford: Oxford University Press.
- Zimmer, C. (2009). On the Origin of Eukaryotes. *Science*, 325, 666-668.