Studies in History and Philosophy of Biological and Biomedical Sciences 44 (2013) 669–678

Contents lists available at SciVerse ScienceDirect

Studies in History and Philosophy of Biological and Biomedical Sciences

journal homepage: www.elsevier.com/locate/shpsc

Organisms ≠ Machines

Daniel J. Nicholson

Cohn Institute for the History and Philosophy of Science and Ideas, Tel Aviv University, Tel Aviv 69978, Israel

ARTICLE INFO

Article history:
Available online 28 June 2013

Keywords:
Organism
Machine
Purposiveness
Organization
Metaphor
Intelligent design

ABSTRACT

The machine conception of the organism (MCO) is one of the most pervasive notions in modern biology. However, it has not yet received much attention by philosophers of biology. The MCO has its origins in Cartesian natural philosophy, and it is based on the metaphorical redescription of the organism as a machine. In this paper I argue that although organisms and machines resemble each other in some basic respects, they are actually very different kinds of systems. I submit that the most significant difference between organisms and machines is that the former are intrinsically purposive whereas the latter are extrinsically purposive. Using this distinction as a starting point, I discuss a wide range of dissimilarities between organisms and machines that collectively lay bare the inadequacy of the MCO as a general theory of living systems. To account for the MCO's prevalence in biology, I distinguish between its theoretical, heuristic, and rhetorical functions. I explain why the MCO is valuable when it is employed heuristically but not theoretically, and finally I illustrate the serious problems that arise from the rhetorical appeal to the MCO.

'[T]he 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.' (Lewontin, 1996, p. 1)

1. Introduction

In spite of all its successes, modern biological science has done remarkably little to tackle the fundamental question that lies at its very heart, namely 'What is the nature of the organism?' Contemporary biologists (and philosophers of biology, for that matter) seldom ask this question openly and explicitly. One possible explanation is that many of them already presuppose the answer: the organism is a machine. Few notions in biology have exerted such a profound influence as the *machine conception of the organism* (MCO, hereafter) formulated by Descartes in the seventeenth century. Indeed, the history of biology since Descartes could almost be recounted as the story of the success of the MCO. Although dissatisfaction with the MCO is virtually as old as the idea itself, those biologists who historically found themselves in disagreement—the much-maligned vitalists—were ultimately unable to provide a compelling theoretical alternative to the MCO.

Today, the MCO appears to permeate most areas of biological inquiry. In molecular and developmental biology the standard ontological view of the organism is that of a complex machine programmed by its genetic software and decomposable into its component mechanisms (e.g., Jacob, 1973; Monod, 1977). Likewise, in evolutionary biology organisms are often conceived as optimally designed machines blindly engineered by natural selection (e.g., Dawkins, 1986; Dennett, 1995). Most recently, the widespread adoption of engineering principles in the emerging field of synthetic biology is being explicitly driven by a mechanical understanding of life (e.g., Andrianantoandro, Basu, Karig, & Weiss, 2006; Endy, 2005). Indeed, one of synthetic biology's most publicized initiatives is the creation of a repository of standardized biological parts (called 'BioBricks') that can be mixed and matched in different ways to build artificial devices with new biological functions. Taking the MCO for granted, the ultimate goal is the design and manufacture of a whole living cell from scratch.

Still, despite the pervasiveness of the MCO, questions pertaining to the putative ontological correspondence between

---

E-mail address: dan.j.nicholson@gmail.com

1369-8486/$ - see front matter © 2013 Elsevier Ltd. All rights reserved.
http://dx.doi.org/10.1016/j.shpsc.2013.05.014

organisms and machines have been discussed primarily by biologists interested in theory (e.g., Cornish-Bowden, Cárdenas, Letelier, & Soto-Andrade, 2007; Kaneko, 2006; Kirschner, Gerhart, & Mitchison, 2000; Lewontin, 2000; Piccolino, 2000; Rosen, 1991; Woese, 2004). They have received surprisingly little attention by philosophers of biology, who have predominantly preferred to focus on matters relating to biological explanations rather than on the ontological presuppositions which underlie them.[1] The present paper is an attempt to begin to remedy this situation. Specifically, this paper argues that the MCO fails to provide an appropriate understanding of living systems. I begin by tracing the origins and development of the MCO and by considering its philosophical foundations (Section 2). I then proceed to discuss the major ways in which organisms differ from machines, and to explain why the MCO results in a deeply misguided understanding of living systems (Section 3). Finally, I consider what role, if any, should the MCO play in biology in light of its deficiencies as a theory of living systems (Section 4).

2. The MCO: historical and philosophical foundations

The MCO is rooted in the natural philosophy of Descartes. Although the idea of assimilating the activities of organisms to the workings of machines stretches all the way back to Antiquity, what is new with Descartes is the conviction that it is not merely useful, under certain circumstances, to regard organisms *as if* they were machines, but rather that it is *only* by conceiving organisms *as* machines that we can truly make sense of them. For Descartes, to understand an organism as a machine is to understand it well enough that no further requirement of clarity or demonstrative certainty is needed (Des Chene, 2001). This is because the very idea of a machine encapsulates the Cartesian metaphysical conception of matter, which is based on the regular interaction of discrete elements acting according to the laws of motion, force, and geometric form (Garber, 2002). This machine metaphysics is, in effect, what sustains and unifies Descartes' entire natural-philosophical project, bringing together the animate and the inanimate, and more generally the natural and the artificial, under a single set of explanatory principles (Vaccari, 2008).

In Cartesian biology, the analogies between animals and clocks, mills, pipe organs, and hydraulic automata have an ontological basis, as they are grounded on the metaphysical assumption that organisms are themselves machines—just machines of far more intricate design than any machine created by man. For Descartes, it is perfectly legitimate to infer the activities of organisms on the basis of our understanding of the workings of man-made machines because he simply assumes that the differences between them are a matter of degree, not of kind. It should be remembered that in the *Treatise on man*, Descartes does not describe the physiology of man, but the physiology of imaginary automata created by God to resemble man. The point of this rhetorical strategy is to show that the human body would be completely indistinguishable from a perfectly designed automaton. This is accomplished by arguing that a detailed description of the latter effectively amounts to an explanation of the former. So although Descartes reasons by analogy, ultimately his objective is to demonstrate that organisms are not just analogous to machines, but that they can be ontologically identified as such (just as man-made machines are so identified).[2]

Following Descartes' establishment of the mechanicist research program in biology, the history of theorizing about organisms came to trail the progressive technological development of machines. Through the centuries, organisms have been conceived in accordance with 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 and regulating 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, Canguilhem (1963, p. 518) traced 'the successive identification of the nerve with a non-isolated, passive electric conductor, then with an electrochemical 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'.

While historically arising from Descartes' ontological reading of the organism-machine analogy, the MCO is more specifically the product of the *metaphorical redescription* of the organism *as* a machine. Although philosophers of science traditionally dismissed metaphors as superfluous embellishments of scientific prose, modern cognitive linguistic research has shown that metaphors play an indispensable role in scientific understanding. It is now generally accepted that '[m]etaphorical thought is what makes abstract scientific theorizing possible' (Lakoff & Johnson, 1999, p. 128). This is because metaphors provide familiar conceptual frameworks through which to make sense of unfamiliar phenomena. A metaphorical redescription thus involves using knowledge of a well-understood source domain to frame, filter, and organize knowledge of a less-understood target domain. In this way, by metaphorically redescribing an organism as a class of machine the assumption is that we become able to come to terms with many of its properties and features. For instance, our ability to derive structural and functional relationships in mechanical systems gives us the confidence to infer the nature of the corresponding relationships in living systems. This is the source of the epistemic power of the MCO: it opens up new avenues of biological research by translating confirmed statements concerning the workings of machines into testable hypotheses regarding the operation of organisms.

It is worth noting as well that throughout history the MCO has been responsible for the introduction of a great deal of terminology into biology. Many terms that now pervade the biological discourse—like 'mechanism', 'machinery', 'program', 'design', 'control', 'feedback', 'regulation', 'switch', 'input', 'output', 'efficiency'—have their basis in the MCO. No wonder, then, that in an editorial entitled 'Grand metaphors of biology in the genome era', 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* the metaphorical redescription of organisms as machines? In what ways do organisms and machines

---

[1] One context where philosophers of biology have paid some attention to the role played by machine thinking in the conceptualization of organisms has been in the recent literature on mechanisms, owing to the etymological connection between the concepts of 'mechanism' and 'machine'. But this is not the place to undertake a detailed analysis of the relation between mechanisms and the MCO; the interested reader may consult Nicholson (2012). For our present purposes, it suffices to acknowledge that appealing to mechanism-talk in the explanation of biological phenomena does *not* imply an endorsement of the MCO as a theory of the nature of living systems. Indeed, mechanismic philosophers have been keen to demarcate their epistemological concern with the importance of mechanisms in biological explanation from the ontological question of whether organisms are machines (e.g., Darden, 2006, pp. 280–281, 2007, p. 142; Craver, 2007, pp. 4, 140; Bechtel, 2008, p. 2).

[2] In his subsequent biological treatise, *The description of the human body*, Descartes drops the rhetorical pretence employed in the *Treatise on man* and plainly identifies the body as a machine, stating at the outset that his aim is 'to explain the entire machine of our body' (Descartes, 1998, p. 171).

resemble one another? In response, one may point to a number of readily discernible commonalities. At a most basic 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. Both are hierarchically structured and internally differentiated, since each part of an organism, and of a machine, has a different structure from the whole (in contrast to, say, a stone). As a result, both admit relational descriptions, meaning that any organism, as well as any machine, can be represented in terms of causal relations between interacting parts. Finally, both organisms and machines are organized so that they operate coordinately towards the attainment of particular ends, and consequently both can be characterized in teleological or functional terms. These are, it would seem, the main commonalities legitimating the contemporary appeal to the MCO in biology. What, then, is wrong with the MCO?

3. 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 that effectively distinguish accidental and non-accidental relations and use only the latter as the basis for comparisons (Juthe, 2005; Weitzenfeld, 1984). It is the successful identification and mapping of the distinctive features 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 characterization 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 last analysis, fundamentally different from those of (man-made) 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 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. Organisms are *intrinsically* purposive, whereas machines are *extrinsically* purposive.[3] A machine is extrinsically purposive in the sense that 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. On the other hand, an organism is intrinsically purposive in the sense that it acts on its own behalf, towards its own ends. Its *telos* is internal, arising from within, and it ultimately serves no purpose other than to maintain its own organization.[4] 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, maintain each other, and generally exist by means of one another. That is, organisms, unlike machines, are not only organized but are also *self-organizing* and *self-regenerating* systems (cf. Gánti, 2003; Kauffman, 2000; Maturana & Varela, 1980; Rosen, 1991).

Organisms are intrinsically purposive because they have an autonomous self: the phenomena of *self*-formation, *self*-preservation, *self*-reproduction, and *self*-restitution are all characteristic of the internal organizational dynamics of living systems. Conversely, machines are extrinsically purposive because they lack an autonomous self: their causal means of production reside *outside* of themselves, demanding outside intervention not just for their construction and assembly but also for their maintenance. 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. Confronted with a machine, one is justified in inferring the existence of an external creator responsible for producing it in accordance with a preconceived plan or *design*. Confronted with an organism, one is not. This contrast has far-reaching implications, as we will see in the next section.

The distinction between intrinsic and extrinsic forms of purposiveness also helps explain another crucial 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.[5] 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 its operation 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 its operation is not good for anything; it simply acts to ensure its continued existence.[6]

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

---

[3] This key distinction was championed, in various guises, by some of history's most distinguished philosophers and biologists, including Aristotle, Locke, Buffon, Kant, and Cuvier. It is a major aim of this paper to illustrate the value of reinstating this distinction in contemporary discussions of organisms and machines.

[4] The notion that organisms are intrinsically rather than extrinsically purposive may seem problematic when considering microbial biofilms or highly social animals like insect colonies. But it is interesting to observe that in such cases one always encounters the added difficulty of deciding whether the systems in question constitute populations or individuals. Is a biofilm, or an insect colony, a community or a (super)organism? Regardless of the answer, the fact that the 'intrinsic vs. extrinsic purposiveness' distinction is strongly correlated with the 'individual vs. population' distinction provides a compelling reason for adopting intrinsic purposiveness as a means of individuating organisms.

[5] The literature on function is huge, and there are numerous accounts on offer. Here I adopt the *organizational* account of function, which has been recently articulated, seemingly independently, by a number of authors (Christensen & Bickard, 2002; Collier, 2000; Edin, 2008; McLaughlin, 2001; Mossio, Saborido, & Moreno, 2009; Schlosser, 1998). The motivation for adopting this view stems from the familiar problems with the two classical accounts, the etiological and the dispositional. The etiological account, grounding function in selected effects, is too narrow to accommodate function-talk in areas of biology not directly concerned with historical explanations, such as physiology, development, and molecular biology, whereas the dispositional account, by interpreting any means-ends relation as functional, is too broad to capture the normative character of functional attributions in biology. The merit of the organizational account is that it explains the normativity of functions (like the etiological account), whilst focusing on *current* contributions of function bearers (like the dispositional account).

[6] This is true *ceteris paribus*. Humans do domesticate animals and cultivate plants (and, more recently, genetically modify organisms), and in doing so *use* them for their own ends. Such human 'interferences' confer upon the manipulated organism a level of functionality it would not otherwise have in nature, given that under these circumstances the organism's activity is 'hijacked' by external agents (i.e., its human users) to perform additional functions on their behalf.

organism, but for the organism itself. McLaughlin illustrates this difference with the following example:

> [T]he 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. (McLaughlin, 2001, p. 148)

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 organism itself—and not some external agent, as is the case in machines—that adjudicates the ascription of functions to its parts according to how they help it meet its physiological needs and cope with its environmental surroundings.[7]

This brings us to another major difference between organisms and machines, which concerns the nature of the *relation* between *parts* and *whole*. In a machine, the parts are causally independent of, and temporally antecedent to, the whole they constitute. Their functions belong to the original design of the machine, and are therefore ascribed in advance by the designer of the machine. Although the parts acquire their function by virtue of being present in the machine as a whole, they nevertheless retain their own distinctive properties regardless of whether they are integrated in the machine or not. By contrast, the parts in an organism are neither causally independent of, nor temporally antecedent to, the whole they constitute. They 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 regenerating its parts. The causal 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. Although the argument cannot be developed here, this is one of the major reasons why explanatory reductionism is only of limited effectiveness in explicating organismic phenomena.

The determining influence in organisms of the whole over the parts has long been recognized by biologists. One of the most influential studies of the 'holistic' capabilities of organisms was carried out by 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 on empirical grounds. 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. In this way, Goldstein's rejection of the MCO was not motivated by philosophical considerations but by clinical observations. Even someone with firm mechanicist credentials like von Neumann (who 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 re-organize. 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 Haldane (1884, p. 37), '[w]hat 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 Frankhauser in the 1940s, as Kirschner et al. (2000) have recently reminded us. 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 same size in all cases. Such instances of regulative development were observed most clearly in well-defined structures like the pronephric duct of the kidney (Fig. 1). Frankhauser's experiments showed that in an organism, unlike in a machine, there is no strict correlation between the number and size of the parts (in this case, the cells) and the size of the whole. Whereas in a machine the size, shape, and structure of the whole is invariably determined by that of its parts, in an organism the size, shape, and structure of the parts do not suffice to account for that of the whole given that the whole has a determining influence on its parts.

It is also important to emphasize that an organism, unlike a machine, displays a *transitional structural identity*. The constituent materials of the system change, yet the organization of the whole remains. While a machine always consists of the same material components (unless an external agent interferes), an organism naturally maintains itself in a state of continuous flux in which there is a permanent breaking down and replacement of its constituent materials. This is the process characteristic of living systems we call *metabolism*. It makes no sense to identify an organism over time with the sum of its material parts, as these are constantly being replenished by the whole. The parts of an organism at any given moment are only the temporary manifestation of the self-producing organizational unity of the whole. The parts of a machine, however, remain distinct, stable, and identifiable over time.

A further contrast between organisms and machines concerns the different ontogenic priority of parts and whole. In a machine, the whole only comes into existence *after* all the parts have been appropriately assembled by its maker. In an organism, the existence of the parts does not precede that of the whole given that the parts only acquire their respective identities *qua* parts as the whole progressively develops from an originally undifferentiated yet already integrated system. This points to yet another difference between organisms and machines, which is that an organism's physiological activities must already be taking place while growth is in progress, whereas a machine cannot perform its intended functions while it is still in the process of construction. The organism even maintains its organizational 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 an indefinite number of times and yet be able to retain its unity and functionality in the way that even the simplest of microorganisms do.

So far, I have argued that the most general difference between organisms and machines is that the former are intrinsically

---

[7] This is the case even for cross-generation functions like reproduction, which, as any other organismic function, serves the purpose of maintaining a given self-producing organizational regime, of which parent and offspring are but different instantiations. In other words, reproduction is the function by which a self-producing organization maintains itself in time across successive generations (Saborido, Mossio, & Moreno, 2011).

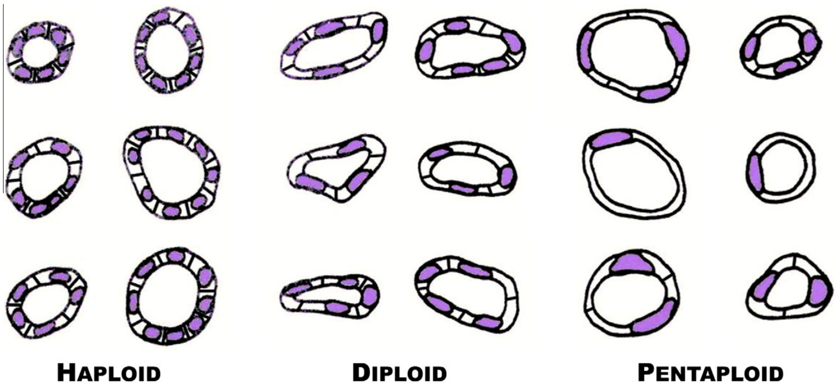

Fig. 1. Cross sections of the pronephric ducts of haploid, diploid, and pentaploid newt embryos. In pentaploid embryos, just one to three cells strain to maintain a circular duct of dimensions that require three to five cells in diploid embryos, and five to eight cells in haploid embryos. Nevertheless, the overall size and thickness of the duct is maintained despite the differences in cell size.

purposive whereas the latter are extrinsically purposive. All the specific differences between organisms and machines I have subsequently discussed are related in one way or another to this key distinction. As explained above, the kind of purposiveness exhibited by a system is determined by its internal organizational dynamics. The intrinsic purposiveness of organisms is grounded on the fact that they are self-organizing, self-producing, self-maintaining, and self-regenerating. Conversely, the extrinsic purposiveness of machines is grounded on the fact that they are organized, assembled, maintained, and repaired by external agents.

Now, it is true that servomechanisms (i.e., machines controlled by negative feedback) display behavioural patterns which resemble those exhibited by intrinsically purposive systems, such as self-regulation (e.g., a heater with a thermostat) and self-steering (e.g., a target-seeking torpedo). This has led some authors (McShea, 2012; Nagel, 1979; Rosenblueth, Wiener, & Bigelow, 1943) to maintain that servomechanisms are indistinguishable from organisms from the point of view of their purposiveness. However, this argument mistakenly equates purposiveness with behaviour. Although the behavioural pattern of a system affords good evidence of its purposiveness, the purposiveness of a system cannot be explained in terms of observable behaviour—much less be defined in terms of inputs and outputs whilst black-boxing the system's internal organization causally responsible for it. Yet this is precisely what the early cyberneticists did when they proposed this argument (see Rosenblueth & Wiener, 1950; Rosenblueth et al., 1943), asserting that if a servomechanical dog *behaves* like a living dog, then the same kind of purposiveness must be attributed to both organism and machine 'if we wish to be consistent' (Rosenblueth & Wiener, 1950, p. 323). They concluded from this that 'as objects of scientific enquiry, humans do not differ from machines' (Rosenblueth & Wiener, 1950, p. 326). The problem with this claim is that the ability to faithfully simulate a particular pattern of organismic behaviour in a machine does not provide a legitimate basis for concluding that the machine is analogous to the organism it imitates, given that the same behavioural output may be brought about by radically different means.[8]

The purposiveness of a system does not depend on its behavioural response patterns but on the internal organizational regime causally responsible for them. Servomechanisms lack the self-maintaining organization to enable them to genuinely act on their own behalf. This is exemplified by the fact that thermostats and torpedoes only simulate intrinsically purposive behaviour (and only in a very restricted sense) when they are switched on; they cease to do so when they are switched off. Yet, regardless of whether they are switched on or off, they exist (like any other machine). This is by virtue of their internal organization. Compare this to the organisms' situation. Organisms cannot be 'switched off' without losing their structural integrity. Again, this is by virtue of their internal organization. It is one of the distinctive features of an organism's self-maintaining organization that its uninterrupted operation is a necessary condition for its continued existence. This need to constantly maintain the complex web of causal processes responsible for an organism's structural integrity is what underlies its intrinsic purposiveness. Servomechanisms may simulate (with varying degrees of success) certain behaviours of intrinsically purposive systems, but they are not themselves the subjects of purposive action because their activity is not directed towards their own preservation. Instead, their organization and operation reflect the specific ends of their makers and users (cf. Jonas, 2001; Oparin, 1961; Taylor, 1950).[9]

Organisms are autonomous systems. 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' (Kapp, 1954, p. 93). Machines are *controlled* so that they operate in the ways desired by their makers and users. It is us, as makers and users of machines, who 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, operate according to their *own* norms. An organism's operation is intrinsically relevant to itself given that its very existence depends on its operation being what it is. An organism (as well as its parts) *must* operate in accordance to the particular operational norms that enable it to maintain its self-producing organization through time; if it stops following these norms (which are different for each organism) it

---

[8] The history of biology affords a dramatic illustration of this point. In the eighteenth century, physiologists at the *Académie des Sciences* allowed the engineer Vaucanson to influence debates over the nature of digestion due to his creation of a mechanical duck that appeared to have the ability to digest food, as it ate kernels of grain and later excreted them—thereby matching the behavioural inputs and outputs of a living duck. After Vaucanson's death, a close examination of the duck's swallowing mechanism revealed that the grain input and excrement output were unrelated, and that the tail end of the duck had been loaded with fake excrement before each act (see Riskin, 2003).

[9] As Cossa remarked in *La cybernétique* (1957), '[w]hat is inherent in the living thing is not merely the means but the end itself: the preservation of life, the preservation of the continuity of existence by adaptation to the environment. There is nothing like this in the homeostat, it has no inherent ultimate aim. If a living thing, which has had its equilibrium upset, perseveringly tries out, one after another, all possible means of adapting itself to its new environment, this is explained as an effort to survive. If the homeostat tries out its 390,625 combinations one after another it only does so because that is what Ashby wanted of it.' (quoted in Oparin, 1961, p. 26)

Table 1
Major differences between organisms and machines.

	Organisms	Machines
Purposiveness	**Intrinsic**	**Extrinsic**
Organization and production	System itself	Maker
Maintenance and repair	System itself	Maker and/or user
Functional determination	System itself	Maker and/or user
Functional attributions	Parts	Parts and whole
Properties of parts	Dependent on whole	Independent from whole
Structural identity of system	Transitional	Continual
Ontogenic priority	First whole, then parts	First parts, then whole
Division	Preserves unity	Compromises unity
Operation and existence	Interdependent	Independent
Normativity	System itself	Maker and/or user

ceases to exist (cf. Barham, 2012; Canguilhem, 1991; Saborido et al., 2011).

Finally, one could mention the fact that organisms are naturally produced whereas machines are artificially created. However, I do not consider this to be such an important difference because, unlike all the others discussed in this section, it is not necessarily dependent on the distinction between intrinsic and extrinsic purposiveness. Although it is true that so far no organism has been artificially created,[10] if synthetic biologists eventually succeeded in engineering from scratch a living system—that is, a system that was self-organizing, self-producing (upon its initial creation), self-maintaining, and self-regenerating—then such a system, despite its artificial origin, would still have the capacity, by virtue of its internal organizational dynamics, to act on its own behalf in accordance with its own norms. I submit that the distinction between intrinsic and extrinsic forms of purposiveness, is far better suited than the distinction between natural and artificial origins to capture the respective features of organisms and machines.

Returning to the MCO, we can now see that its inadequacy derives from the problem of projecting the characteristics of extrinsically purposive systems onto intrinsically purposive ones. Table 1 displays a selection of the key differences between organisms and machines discussed in this section, which lay bare the various deficiencies of the MCO.

4. What role should the MCO play in biology today?

Given the numerous deficiencies of the MCO, why, one may ask, has this notion exerted such a powerful influence in biology? A number of reasons can be identified. Firstly, as machines are familiar and well understood, being the products of human design, they are intuitively compelling models for conceptualizing organisms. As a result, biologists are often tempted to draw on the superficial similarities between machines and organisms (e.g., hierarchical organization, functional 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, ‘harder’ sciences like physics and chemistry, as well as engineering.[11] 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 thorny questions like ‘What is the nature of 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 for biologists is that it is highly successful in generating empirical data. It is undeniable that the periods in history in which the mechanicist research tradition has 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 deeply problematic understanding of what organisms are, and yet prove so fruitful when used to investigate them? In light of this tension, what role should the MCO play in biology today?

In order to address these questions, it is necessary to take a step back and consider in general terms the different ways in which metaphors are utilized in science. Following Bradie (1999), we can distinguish *theoretical*, *heuristic* and *rhetorical* functions for metaphors in science. Metaphors with a theoretical function are central to scientific understanding, as they provide the foundation for the conceptualization, representation, and explanation of the target phenomenon. Metaphors with a heuristic function constitute methodological tools that facilitate the empirical investigation of the target phenomenon. And metaphors with a rhetorical function are employed in scientific communication to inform and educate non-specialists about the target phenomenon. The most pervasive scientific metaphors, like the MCO, perform all three functions. So far in this paper, my analysis of the MCO has focused on its theoretical function, and I hope that enough has been said in the preceding section to legitimately conclude that, as a theory of the organism, the MCO has 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 that arise from the rhetorical appeal to the MCO.

The key to the heuristic value of the MCO resides in the fact that the nature of the organism is only perceptible when it is considered as a whole. If the parts of an organism are considered independently from the whole for the purposes of their investigation, they do resemble machines in that they constitute extrinsically purposive systems. Like machines, the parts of an organism are not self-organizing, self-producing, self-maintaining, or self-repairing, but instead depend on an external agent for their organization, production, maintenance, and repair—namely, the organism as a whole. Just as machines serve the ends of their users, the parts of an organism serve the ends of the whole to which they belong, which is why functions can be ascribed to both. So whereas an

---

[10] The widely publicized report by researchers at the J. Craig Venter Institute (Gibson et al., 2010) that some hailed as the creation of artificial life actually consisted in the transplantation of a synthetic copy of a naturally occurring genome into a pre-existing cell that had been stripped of its own genome. Though undoubtedly a remarkable technological feat, such an accomplishment is still far from the artificial synthesis of a living cell.

[11] In the words of Oparin (1961, p. 19), the ‘identification of living things with machines was [historically] viewed as the one and only way of saving science from the mystical entelechy of the vitalists, the bridge which will carry us over from physics and chemistry to biology’.

organism as a whole is a fundamentally different kind of system from a machine, its parts actually share many of the attributes of machines. Consequently, when these parts are studied independently from the whole, much can be learnt about them by treating them *as if* they were machines. This, I believe, 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 characterization 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 well-defined interacting parts (cf. Bechtel & Richardson, 1993; Kauffman, 1970; Wimsatt, 1976).

Nevertheless, an important limitation to 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 initial stages of development cannot be studied as an assemblage of machine subunits because in it all functions are still assumed by the organism as a whole. The organism at this point constitutes what Driesch called a 'harmonious-equipotential system' that is virtually unintelligible in mechanical terms.[12] It is only with the progressive differentiation of the embryo that the originally unitary action of the organism becomes partitioned into a myriad of individual actions, and it is at this later developmental stage that local machine-like structures within the organism begin to emerge, thus rendering the MCO of increasing heuristic value. Still, it is important to point out 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 investigations discussed in the previous section illustrated. So at no stage in the life cycle of an organism is the heuristic usefulness of the MCO absolute.

I have argued thus far that the heuristic value of the MCO resides in the relative similarities between machines and the *parts* of organisms. But what should we make 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 mechanical approach is inherently incapable of tackling the systemic properties that make whole 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 serves as a false model that, by virtue of its inherent inadequacy, can orient biologists towards the actual nature of organisms (see Wimsatt, 1987). As Rosen (1991, p. 248) observed, 'On balance, the Cartesian metaphor of organism as machine has proved 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 evaluate the MCO is to clearly demarcate its heuristic function from its theoretical function. Successful mechanical *investigations* of organisms do not enable successful mechanical *explanations* of them. 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. I submit that the regrettable prevalence of the MCO in contemporary biological theory 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 biologists have argued that the MCO, despite being theoretically inadequate, can still be of great rhetorical value because it provides a very captivating visual aid in teaching non-specialists 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 (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 illustrated by considering the repercussions of the recent rhetorical appeal to 'molecular machines' by molecular biologists.

In 1998, Alberts, then president of the National Academy of Sciences, edited a special issue in the journal *Cell* (volume 92, issue 3) which brought together a series of papers that systematically called for the adoption 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 the use of the term 'machine' in this context, 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 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. Table 2 lists a selection of the subcellular structures that have recently been described by biologists 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 research papers. When it does feature in a research paper, it almost always appears in the title, abstract, or introduction, rather than in the

---

[12] It is for this reason that Driesch appealed to the holistic properties of organisms at an early stage of development to demonstrate the inadequacy of the MCO and formulate his 'first proof of vitalism' (see Driesch, 1908, pp. 118–149).

Table 2
Some of the subcellular assemblies that have been characterized as molecular machines.

Subcellular assembly	Sample of 'molecular machine' language	Source reference
Ribosome	'probably the most sophisticated machine ever made'	Garrett (1999)
Proteasome	'a molecular machine designed for controlled proteolysis'	Voges, Zwickl, and Baumeister (1999)
Bacteriorhodopsin	'a deceptively simple molecular machine'	Kühlbrandt (2000)
Apoptosome	'a seven-spoked death machine'	Salvesen and Renatus (2002)
Glideosome	'a molecular machine powering motility'	Keeley and Soldati (2004)
Spliceosome	'among the most complex macromolecular machines known'	Nilsen (2003)
Blood clotting system	'a typical example of a molecular machine'	Spronk, Govers-Riemslag, and Cate (2003)
Condensin	'the key molecular machine of chromosome condensation'	Strunnikov (2003)
Photosynthetic system	'the most elaborate nanoscale biological machine in nature'	Imahori (2004)
Bacterial flagellum	'an exquisitely engineered chemi-osmotic nanomachine'	Pallen, Penn, and Chaudhuri (2005)
Myosin filament	'a complicated machine of many moving parts'	Ohki, Mikhailenko, Morales, Onishi, and Mochizuki (2004)
RNA degradasome	'a supramolecular machine dedicated to RNA processing'	Marcaida, DePristo, Chandran, Carpousis, and Luisi (2006)
Cyclosome	'a machine designed to destroy'	Peters (2006)
RNA Polymerase	'a multifunctional molecular machine'	Haag and Pikaard (2007)

parts of the paper actually describing the research undertaken and the interpretation of the findings. What this suggests is that instead of playing a theoretical role in the explanation of subcellular assemblies, the term 'molecular machine' is primarily used for rhetorical purposes as a way of introducing newcomers to the subfield of molecular biology devoted to the structural characterization 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 individuate a particular subset within the molecular biology community.

However, the adverse consequences that have resulted from the adoption of the term 'molecular machine' far outweigh its potential pedagogical and sociological benefits. This is because in biologists' persistent appeal to this term, present-day creationists have found just the kind of rhetorical ammunition they need to dress up their belief in a supernatural being with a guise of scientific respectability. Indeed, the creationist 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 (see Behe, 2001). Behe, one of the leading proponents of ID, 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, 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, also constitute irreducibly complex systems.

The role played by the notion of molecular machine in Behe's case for ID is 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 it follows logically that living systems must have a designer. As Hume showed in his *Dialogues concerning natural religion*, the problem with this argument does not lie in inferring design (and therefore a designer) from a machine, but in ontologically conceiving living systems as machines in the first place. Behe is well aware of this, which is why he devotes so much attention in his writings to emphasizing the machine-like 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 own descriptions of subcellular complexes, as Table 2 illustrates. Because of this, Behe (2006, 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'. Behe becomes a *de facto* mechanicist when it comes to the cell, and it is here where the molecular machine terminology, adopted by the molecular biologists themselves, is so convenient. Indeed, Behe uses every possible opportunity to employ it in his writings, as the following passage illustrates:

> 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 term 'molecular machine' is no longer a harmless, purely rhetorical figure of speech, but a starkly literal characterization of the 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 skillful 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 boiled down to arguments against the MCO. For example, in their criticism of Behe, Shanks and Joplin (1999, p. 281) indicate that '[r]eal 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 machine metaphor. Similarly, in their critique of ID, Scott and Matzke (2007, p. 292) argue that '[t]he differences between biological phenomena and human-built machines easily outweigh the superficial similarities'. Accordingly, in an editorial entitled 'Stand up for evolution', Raff (2005, p. 274) emphasizes the need for biologists to avoid the MCO in their teaching and writing: 'let us not play into the hands of ID propagandists. [...] 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 potential didactic and sociological value in particular fields like molecular biology.

We are now in a position to answer the question with which we began this section. The numerous problems with the MCO highlighted in Section 3 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 by independently considering the theoretical, heuristic, and rhetorical functions of the MCO. I have argued that although the MCO is inadequate as a theory of the organism, it nevertheless remains a valuable heuristic tool when it is employed in biological 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 fundamentally 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.

5. Conclusion

In this paper I have intended to show that the MCO stands today as one of the most serious obstacles impeding further progress in our theoretical comprehension of living systems. In essence, the MCO systematically reduces organisms to the features it is capable of explaining and filters out everything that remains. The success 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 MCO are either ignored or dismissed as unimportant. Unfortunately, what is neglected in the MCO is precisely that which makes organisms most distinctive, namely their intrinsic purposiveness and their self-maintaining organization. It should come as no surprise that the concepts typically associated with these two non-mechanical features, namely teleology and holism, are generally treated with scepticism and suspicion by the scientific community. Since the edifice of modern science was historically built on mechanicist foundations, it is to be expected that what lies beyond the reach of mechanicism has tended to get 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 theory liberates itself from the need to conform to the MCO, and it becomes able to explore alternative conceptual models that attempt to confront the complexity of the organism on its own terms.

Acknowledgements

I thank Peter McLaughlin, Paul Griffiths, Lenny Moss, John Dupré, Philippe Huneman, Arnon Levy, and Dan McShea for helpful discussions and constructive comments on early ancestors and/or recent drafts of this paper. I am also grateful to the audiences at the International Conference on Artificial Life in Winchester, the European Graduate Meeting in Philosophy of the Life Sciences in Rovigo, and the Workshop on Historical and Philosophical Perspectives on the Concept of Organism in Paris, for feedback on presentations on this topic. I especially wish to thank Russell Powell for his invitation to contribute to this special issue. Finally, I am pleased to acknowledge financial support from the Konrad Lorenz Institute for Evolution and Cognition Research as well as from the Cohn Institute for the History and Philosophy of Science and Ideas.

References

Alberts, B. (1998). The cell as a collection of protein machines: Preparing the next generation of molecular biologists. *Cell, 92*, 291–294.

Andrianantoandro, E., Basu, S., Karig, D. K., & Weiss, R. (2006). Synthetic biology: New engineering rules for an emerging discipline. *Molecular Systems Biology, 2*, 1–14.

Barham, J. (2012). Normativity, agency, and life. *Studies in History and Philosophy of Biological and Biomedical Sciences, 43*, 92–103.

Bechtel, W. (2008). *Mental mechanisms: Philosophical perspectives on cognitive neuroscience*. London: Routledge.

Bechtel, W., & Richardson, R. (1993). *Discovering complexity: Decomposition and localization as strategies in scientific research*. Princeton: Princeton University Press.

Behe, M. J. (2005). Understanding creation, evolution and intelligent design. *Christian post, 27th May, 2005*. <http://www.christianpost.com/news/understanding-creation-evolution-and-intelligent-design-7555/print.html>. (Accessed 29 April 2013).

Behe, M. J. (2006). *Darwin's black box: The biochemical challenge to evolution (10th anniversary ed.)*. New York: Free Press (First published 1996).

Behe, M. J. (2001). Molecular machines: Experimental support for the design inference. In R. T. Pennock (Ed.), *Intelligent design creationism and its critics: Philosophical, theological, and scientific perspectives* (pp. 241–256). Cambridge, MA: MIT Press.

Bradie, M. (1999). Science and metaphor. *Biology and Philosophy, 14*, 159–166.

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* (pp. 507–520). London: Heinemann.

Canguilhem, G. (1991). *On the normal and the pathological*. Dordrecht: D. Reidel Publishing (First published 1966).

Christensen, W. D., & Bickhard, M. H. (2002). The process dynamics of normative function. *The Monist, 85*, 3–28.

Collier, J. (2000). Autonomy and process closure as the basis for functionality. *Annals of the New York Academy of Sciences, 901*, 280–291.

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.

Cossa, P. (1957). *La cybernétique, du cerveau humain aux cerveaux artificiels*. Paris: Masson et Cie.

Craver, C. F. (2007). *Explaining the brain: Mechanisms and the mosaic unity of neuroscience*. New York: Oxford University Press.

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.

Dawkins, R. (1986). *The blind watchmaker*. New York: W. W. Norton.

Dennett, D. C. (1995). *Darwin's dangerous idea: Evolution and the meanings of life*. New York: Simon & Schuster, New York.

Des Chene, D. (2001). *Spirits & clocks: Machine & organism in Descartes*. Ithaca, NY: Cornell University Press.

Descartes, R. (1998). In S. Gaukroger (Ed.), *The world and other writings*. Cambridge: Cambridge University Press.

Driesch, H. (1908). *The science and philosophy of the organism*. London: Adam & Charles Black.

Edin, B. (2008). Assigning biological functions: Making sense of causal chains. *Synthese, 161*, 203–218.

Endy, D. (2005). Foundations for engineering biology. *Nature, 438*, 449–453.

Gánti, T. (2003). *The principles of life*. Oxford: Oxford University Press (First published 1971).

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.

Gibson, D. G., Glass, J. I., Lartigue, C., Noskov, V. N., Chuang, R. Y., Algire, M. A., et al. (2010). Creation of a bacterial cell controlled by a chemically synthesized genome. *Science, 329*, 52–56.

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).

Haag, J. R., & Pikaard, C. S. (2007). RNA polymerase I: A multifunctional molecular machine. *Cell, 131*, 1224–1225.

Haldane, J. S. (1884). Life and mechanism. *Mind, 9*, 27–47.

Imahori, H. (2004). Porphyrin–fullerene linked systems as artificial photosynthetic mimics. *Organic and Biomolecular Chemistry, 2*, 1425–1433.

Jacob, F. (1973). *The logic of life: A history of heredity*. New York: Pantheon (First published 1970).

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.

Kapp, R. O. (1954). Living and lifeless machines. *British Journal for the Philosophy of Science, 5*, 91–103.

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.

Kauffman, S. A. (2000). *Investigations*. Oxford: Oxford University Press.

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.

Kirschner, M., Gerhart, M., & Mitchison, T. (2000). Molecular “vitalism”. *Cell, 100*, 79–88.

Konopka, A. K. (2002). Grand metaphors of biology in the genome era. *Computers and Chemistry, 26*, 397–401.

Kühlbrandt, W. (2000). Bacteriorhodopsin—The movie. *Nature, 406*, 569–670.

Lakoff, G., & Johnson, M. (1999). *Philosophy in the flesh: The embodied mind and its challenge to western thought*. New York: Basic.

Lewontin, R. C. (1996). Biology as engineering. In J. Collado-Vides, B. Magasanik, & T. F. Smith (Eds.), *Integrative approaches to molecular biology* (pp. 1–10). Cambridge, MA: MIT Press.

Lewontin, R. C. (2000). *The triple helix: Gene, organism, and environment*. Cambridge, MA: Harbard University Press.

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.

Maturana, H. R., & Varela, F. J. (1980). *Autopoiesis and cognition: The realization of the living*. Dordrecht: Reidel (First published 1972).

McLaughlin, P. (2001). *What functions explain: Functional explanation and self-reproducing systems*. Cambridge: Cambridge University Press.

McShea, D. W. (2012). Upper-directed systems: A new approach to teleology in biology. *Biology and Philosophy, 27*, 663–684.

Monod, J. (1977). *Chance and necessity: An essay on the natural philosophy of modern biology*. Glasgow: Williams Collins Sons & Co Ltd. (First published 1970).

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). *Teleology revisited and other essays in the philosophy and history of science*. New York: Columbia University Press.

Nicholson, D. J. (2012). The concept of mechanism in biology. *Studies in History and Philosophy of Biological and Biomedical Sciences, 43*, 152–163.

Nilsen, T. W. (2003). The spliceosome: The most complex macromolecular machine in the cell? *BioEssays, 25*, 1147–1149.

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.

Oparin, A. I. (1961). *Life: Its nature, origin and development*. Edinburgh: Oliver & Boyd.

Pallen, M. J., Penn, C. W., & Chaudhuri, R. R. (2005). Bacterial flagellar diversity in the post-genomic era. *Trends in Microbiology, 13*, 143–149.

Peters, J. M. (2006). The anaphase promoting complex/cyclosome: A machine designed to destroy. *Nature Reviews Molecular Cell Biology, 7*, 644–656.

Piccolino, M. (2000). Biological machines: From mills to molecules. *Nature Reviews Molecular Cell Biology, 1*, 149–153.

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.

Riskin, J. (2003). The defecating duck; or, the ambiguous origins of artificial life. *Critical Inquiry, 29*, 599–633.

Rosen, R. (1991). *Life itself: A comprehensive inquiry into the nature, origin, and fabrication of life*. New York: Columbia University Press.

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.

Saborido, C., Mossio, M., & Moreno, A. (2011). Biological organization and cross-generation functions. *British Journal for the Philosophy of Science, 62*, 583–606.

Salvesen, G. S., & Renatus, M. (2002). Apoptosome: The seven-spoked death machine. *Developmental Cell, 2*, 256–257.

Schlosser, G. (1998). Self-re-production and functionality: A systems-theoretical approach to teleological explanation. *Synthese, 116*, 303–354.

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. Adaptation and complex design* (Vol. 1, pp. 285–304). Washington, DC: The National Academies Press.

Shanks, N., & Joplin, K. H. (1999). Redundant complexity: A critical analysis of intelligent design in biochemistry. *Philosophy of Science, 66*, 268–282.

Spronk, H. M. H., Govers-Riemslag, 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. (1950). Comments on a mechanistic conception of purposefulness. *Philosophy of Science, 17*, 310–317.

Vaccari, A. (2008). Legitimating 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* (pp. 287–336). Leiden: Koninklijke Brill NV.

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.

Weitzenfeld, J. S. (1984). Valid reasoning by analogy. *Philosophy of Science, 51*, 137–149.

Wimsatt, W. C. (1976). Reductive explanation: A functional account. In R. S. Cohen, C. A. Hooker, A. C. Michalos, & J. W. van Evra (Eds.), *PSA: Proceedings of the Biennial Meeting of the Philosophy of Science Association, 1974* (pp. 671–710). Dordrecht: D. Reidel.

Wimsatt, W. C. (1987). False models as means to truer theories. In M. H. Nitecki & A. Hoffman (Eds.), *Neutral models in biology* (pp. 23–55). Oxford: Oxford University Press.

Woese, C. R. (2004). A new biology for a new century. *Microbiology and Molecular Biology Reviews, 68*, 173–186.