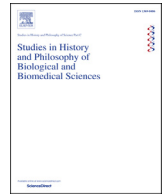




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## The machine conception of the organism in development and evolution: A critical analysis



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### ABSTRACT

This article critically examines one of the most prevalent metaphors in contemporary biology, namely the machine conception of the organism (MCO). Although the fundamental differences between organisms and machines make the MCO an inadequate metaphor for conceptualizing living systems, many biologists and philosophers continue to draw upon the MCO or tacitly accept it as the standard model of the organism. The analysis presented here focuses on the specific difficulties that arise when the MCO is invoked in the contexts of development and evolution. In developmental biology the MCO underlies a logically incoherent model of ontogeny, the genetic program, which serves to legitimate three problematic theses about development: genetic animism, neo-preformationism, and developmental computability. In evolutionary biology the MCO is responsible for grounding unwarranted theoretical appeals to the concept of design as well as to the interpretation of natural selection as an engineer, which promote a distorted understanding of the process and products of evolutionary change. Overall, it is argued that, despite its heuristic value, the MCO today is impeding rather than enabling further progress in our comprehension of living systems.

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'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*, a realization far beyond what anyone in the seventeenth century could have imagined.' (Lewontin, 2009, p. v)

### 1. Introduction

Metaphors are generally recognized today as being of fundamental importance in science (Brown, 2003; Hallyn, 2000; Keller, 2002). But it was not always that way. Until fairly recently, it had not been uncommon to assume that language consists of literal and metaphorical expressions; the former consisting of descriptions which correspond to 'the way things are', and the latter fulfilling the more diversionary and aesthetic purposes of literary writing. On this view, metaphors were regarded as merely ornamental figures of speech that offered little or nothing to the scientific

pursuit of generating accurate knowledge of nature. Over the past few decades, however, work in cognitive science, linguistics, and philosophy has precipitated the collapse of the literal/metaphorical distinction, as it has become apparent that metaphors lie at the very heart of the pre-linguistic cognitive processes by which we conceptualize the world (Gibbs, 2008; Kövecses, 2010; Lakoff & Johnson, 1980). Metaphors are in fact indispensable to the way concepts are created and ideas are communicated. This has profound implications for how we think about scientific reasoning and theorizing.

Scientific metaphors typically map knowledge of a well-understood source domain onto a less-understood target domain so that the unknown is seen through the lens of the known. They enable scientists to articulate and communicate their findings by providing familiar interpretive frameworks in which to make conceptual sense of new phenomena. A metaphor emphasizes certain features of the source domain and downplays others. In doing so, it shapes our theoretical understanding of the target domain. This provides a stimulus for scientific research, as it opens up new perspectives through which to investigate the target

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domain. At the same time, metaphors can have a detrimental effect, as they can bias the way in which we think about the target domain and prevent us from directing our attention towards other potentially more productive ways of studying it. So although appealing to metaphors in scientific practice may well be inevitable, the choice of what metaphor is used in any given context matters a great deal.

We can distinguish three major roles for metaphors in science, namely theoretical, heuristic, and rhetorical functions. Metaphors with a theoretical function are central to scientific understanding, as they provide the foundation for the conceptualization, representation, and explanation of the target domain. Metaphors with a heuristic function are central to scientific discovery, as they serve as methodological tools that conveniently abstract or idealize aspects of the target domain in order to facilitate its empirical investigation. Finally, metaphors with a rhetorical function are central to scientific communication, as they act as pedagogical devices that inform and educate non-specialist audiences about the target domain. The most pervasive scientific metaphors perform all three functions.

One such metaphor is the *machine conception of the organism* (MCO, hereafter), which has an illustrious intellectual pedigree stretching all the way back to René Descartes, and which many regard today as ‘perhaps the most powerful conceptual tool of modern biology’ (Konopka, 2002, p. 398). Although the MCO has proven itself to be of considerable heuristic value (e.g., anatomical structures are profitably investigated as if they were mechanical contrivances), as well as of some limited rhetorical use (e.g., biology students learn about metabolic processes by visualizing the cell as a miniature biochemical factory), it is far less obvious that the MCO provides an adequate theory of living systems (Kirschner, Gerhart, & Mitchison, 2000; Lewontin, 2000a; Rosen, 1991; Woese, 2004). From a theoretical perspective, the adequacy of the MCO relies on establishing a clear ontological correspondence between organisms and machines. Of course, we know that Descartes himself saw no problems in assimilating organisms to machines, as for him all that was natural was also mechanical, and consequently any differences between animals and man-made artifacts were purely quantitative rather than qualitative (Des Chene, 2001; Vaccari, 2008). But as today we are no longer bound by the stringent metaphysical commitments of seventeenth-century mechanist natural philosophy, what do we actually find when we compare organisms and machines?

In previous work (Nicholson, 2013) I have argued at length that despite some interesting similarities, organisms and machines are fundamentally different kinds of systems. Although both organisms and machines operate towards the attainment of particular ends—that is, both are *purposive* systems—the former are *intrinsically* purposive whereas the latter are *extrinsically* purposive. A machine is extrinsically purposive in the sense that it works towards an end that is external to itself; that is, it does not serve its own interests but those of its maker or user. An organism, on the other hand, is intrinsically purposive in the sense that its activities are directed towards the maintenance of its own organization; that is, it acts on its own behalf. 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. Even though machines and organisms both exhibit organized complexity and structural integrity, in a machine the parts are causally independent of, and temporally antecedent to, the whole they constitute. Although the parts acquire their function by virtue of being present in the machine as a whole, they retain their own distinctive properties regardless of whether or not they are integrated in the whole. By contrast, the parts in an organism

are neither causally independent of, nor temporally antecedent to, the whole they constitute. Instead, they exist in a relation of collective interdependence, relying on one another for their generation, maintenance, and renewal. An organism maintains its integrity and autonomy as a whole by regulating, repairing, and regenerating its parts, whereas a machine relies on outside intervention not just for its construction and assembly, but also for its maintenance and repair.

Because organisms and machines differ fundamentally in their internal organizational dynamics, the MCO fails to provide an appropriate theoretical understanding of what living systems are. Nevertheless, despite its increasingly apparent shortcomings as a biological theory, the MCO continues to exert a dominant influence on how biologists think about living systems. The reason is that the MCO is so deeply engrained in the minds of many biologists that it has more or less faded into the background, becoming a tacit, higher-order assumption that frames more specific, local projects in different areas of biology. In this respect, the MCO constitutes what Konopka (2002, p. 398) calls a ‘grand metaphor’ and Ruse (2010, p. 24) dubs a ‘root metaphor’, that is, a metaphor so pervasive that it gives rise to ancillary ‘submetaphors’ that shape the form explanations take in particular fields of inquiry.

This paper extends the philosophical critique of the MCO presented in Nicholson (2013) by critically analyzing the remarkably disparate ways in which the MCO manifests itself in two major areas of biology: development and evolution. In developmental biology, the MCO is primarily instantiated by the *genetic program* model of ontogeny, whereas in evolutionary biology it is embodied in the idea of *design* and the related conception of natural selection as an engineer. Although the concepts of genetic program and design have received considerable attention by biologists and philosophers in recent years, what has not been sufficiently recognized is that these notions are in fact submetaphors of the MCO. The justification of their postulation stems from a tacit, uncritical acceptance of the MCO. This is of paramount importance because it is only by realizing that they constitute different instantiations of the MCO that we can truly understand why these notions prove to be so problematic upon close examination. Exposing their connection to the MCO will enable us to bring together under a unified theoretical perspective the array of difficulties that arise when these submetaphors are interpreted theoretically. In turn, this will provide powerful additional reasons for dispensing with the MCO as a general theory of living systems.

## 2. The MCO in developmental biology

Since the seventeenth century, the phenomenon of embryological development has constituted one of the most formidable challenges for mechanists who, following Descartes, have wanted to advance biological understanding using the MCO as a theoretical foundation. It is not difficult to see why. Organisms and machines come into existence by radically different means. A machine comes into being by the assembly of pre-existing components. An organism does not. In an organism, the existence of the parts does not precede that of the whole. Organismic parts only acquire their respective identities *qua* parts as the whole progressively develops from an originally undifferentiated yet already integrated system. Embryogenesis is a ‘top-down’ process, whereas machine assembly is decidedly ‘bottom-up’.

Faced with such a fundamental disparity, the early mechanists dealt with the problem of developmental differentiation by simply ignoring it. Rather than considering how novel morphological structures emerge progressively during ontogeny, they postulated

that the structure of the adult organism is already present in miniature form as a 'homunculus' in either the egg or the sperm, where it remains in an inert state awaiting activation through fertilization. Upon this event, the germ is set into a growth phase and gradually expands until it acquires its final size. In this view, the process of development consists simply in the mechanical enlargement of the adult structure already articulated in the germ. This is the doctrine of *preformation*, and for a long time it provided the only means of reconciling descriptions of organismic development with the explanatory principles of mechanist natural philosophy (Roe, 1981; Smith, 2006). Eventually, increasingly detailed observations of embryogenesis in the nineteenth century ruled out crude preformationist hypotheses as plausible explanations, but preformationist thinking was never really purged from developmental biology (see, e.g., Hertwig, 1900).

The situation changed considerably in the mid-twentieth century with the advent of modern computing and the introduction of the conceptual distinction between *software* and *hardware*. This theoretical innovation enabled the construction of a new kind of machine, the computer, which contains algorithmic sequences of coded instructions—or *programs*—that are executed by a central processing unit. In a computer, the software is totally independent from the hardware that runs it. A program can be transferred from one computer and run in another. Moreover, the execution of a program is always carried out in exactly the same fashion, regardless of the number of times it is run and of the hardware that runs it. The computer is thus a machine with Cartesian and Laplacian overtones. It is Cartesian because the software/hardware distinction echoes the soul/body dualism: the computer has an immaterial 'soul' (the software) that governs the operations of a material 'body' (the hardware). And it is Laplacian because the execution of a program is completely deterministic and fully predictable, at least in principle. These and other features made the computer a very attractive theoretical model for those concerned with elucidating the role of genes in development in the early days of molecular biology.<sup>1</sup>

It is in this context that one of the most influential instantiations of the MCO in modern biology came into being, namely the metaphor of the 'genetic program'. This notion, proposed simultaneously by Jacob and Monod (1961) and Mayr (1961), 'has come to be widely regarded as a fundamental explanatory concept for biological development—if not *the* fundamental concept' (Keller, 2000a, p. 74). In explaining the motivations for its formulation, Jacob (1973, p. 9) plainly acknowledged the link to the MCO: 'The programme is a model borrowed from electronic computers. It equates the genetic material of an egg with the magnetic tape of a computer'. According to Jacob, 'everything urges one to compare the logic of heredity to that of a computer. Rarely has a model suggested by a particular epoch proved to be more faithful' (Jacob,

1973, p. 265). Mayr (1982, p. 55) was no less explicit: 'All organisms possess a historically evolved genetic program, coded in the DNA of the nucleus of the zygote [...] Nothing comparable to it exists in the inanimate world, except for manmade computers'. In Mayr's (1997, p. 123) 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'.

The idea that organisms contain a genetic program that determines development in the same way that the operations of a computer are determined by its programs captured biologists' imagination almost immediately after its formulation (see, e.g., Blow, 1962). It introduced a new way of thinking about development that resonated strongly which recent advances in computer science, and which offered significant advantages over earlier models of gene action. More importantly, it appeared to make conceptual sense of new findings about gene regulation (Keller, 2000a). As a result, the genetic program model became central to the organization of research into the molecular basis of development in the 1960s and 1970s. Sydney Brenner, for instance, who spearheaded the use of the worm *Caenorhabditis elegans* as a model organism, sought to establish the causal link between genes and behaviour by uncovering the logical structure of the developmental computations performed by the worm's nervous system according to the specifications of its genetic program (de Chadarevian, 1998).

More recently, the discovery of gene rearrangements, nested genes, alternative promoters, alternative splicing, RNA editing, frameshifting, alternate stop codons, and various other post-transcriptional and post-translational processing mechanisms have complicated the straightforward view of genes as 'code-scripts' for phenotypic traits (but see Brenner, 2012). This has prompted the extension of the program metaphor so as to encompass not only the DNA sequences that code for transcription and translation but also those that are recognized by binding factors during gene expression (i.e., enhancers, promoters, activator and repressor binding sites, etc.). In turn, this has led to the notion of 'gene regulatory networks' (GRNs, hereafter), which 'control expression of the genes required to execute each developmental episode' (Davidson, McClay, & Hood, 2003, p. 1475). GRNs provide the source code for development, as they are 'where the logic instructions that encode development physically reside' (Davidson, 2009a, p. 248). The rise of GRN biology has served to strengthen the popularity of the genetic program model. Indeed, Eric Davidson—widely recognized as the leading GRN researcher—explicitly defines development as 'the execution of the genetic program for construction of a given species of organism' (Davidson, 2006, p. 16).

Today, the genetic program is everywhere. It appears in biology textbooks, such as when organisms are said to be 'governed by the laws of physics and chemistry as well as a genetic program' (Hartwell, Hood, Goldberg, & Silver, 2011, p. 3). It is present in the technical literature, such as when claims are made that 'a cell can be seen as a computer (a machine expressing a program)' (Danchin, 2009, p. 3). And it is also prominently featured in works of popular science. In one of the most memorable phrases of Richard Dawkins' hugely influential *The Selfish Gene*, organisms are described as 'survival machines—robot vehicles blindly programmed to preserve the selfish molecules known as genes' (Dawkins, 1976, p. x, my emphasis). Even some philosophers of biology, who should probably know better, have enthusiastically defended the reality of the genetic program:

[T]he genes program the embryo in the same way that the hardware in an automobile assembly plant's robots' central processing units realize a program that enable them to weld

<sup>1</sup> Even before DNA was conclusively identified as the hereditary material, Erwin Schrödinger in his short book *What is Life?* had already characterized the chromosome as a structure bearing a 'code-script' for the architecture of the organism. Interestingly, the Laplacian connotations of the metaphor had not escaped him: 'It is these chromosomes [...] that contain in some kind of code-script the entire pattern of the individual's future development and of its functioning in the mature state. [...] In calling the structure of the chromosome fibres a code-script we mean that the all-penetrating mind, once conceived by Laplace, to which every causal connection lay immediately open, could tell from their structure whether the egg would develop, under suitable conditions, into a black cock or into a speckled hen, into a fly or a maize plant, a rhododendron, a beetle, a mouse or a woman. [...] But the term code-script is, of course, too narrow. The chromosome structures are at the same time instrumental in bringing about the development they foreshadow. They are law-code and executive power—or, to use another simile, they are architect's plan and builder's craft—in one' (Schrödinger, 1944, pp. 22–23).

chassis without human supervision and more accurately than any human can perform this task. This latter thesis requires no philosophical defense. It is obvious to any one who examines the available accounts of the embryological development of, say, the *Drosophila*. (Rosenberg, 2005, p. 345)

Before turning to consider the numerous difficulties with the genetic program model, let us briefly review the reasons why it has proven to be such an attractive notion. First of all, being an instantiation of the MCO, the genetic program metaphor appeals directly to our everyday familiarity with machines. Supposing that embryological development is governed by a program is quite reasonable, according to Nijhout (1990, p. 443), because ‘we would have designed such a system that way’.<sup>2</sup> Another reason is that it captures our intuitions about development rather well, particularly the regularity, reliability, and orderliness of the process. A further reason is that it provides a firm foundation upon which to anchor other theoretical postulates, such as the ‘central dogma’ of molecular biology. It even serves to unify the two major branches of biology Mayr distinguishes: proximate biology and ultimate (or evolutionary) biology. ‘Proximate causes have to do with the decoding of the program of a given individual; evolutionary causes have to do with the changes of genetic programs through time, and with the reasons for these changes’ (Mayr, 1982, p. 68). Finally, and perhaps most importantly, it subjugates the intimidating complexity of embryogenesis by placing the entire explanatory burden on a relatively stable, epistemically tractable entity: a one-dimensional digital code that can be replicated, modified, and transplanted from one individual to another. In this way, the genetic program reduces the thorny problem of ontogeny to the characterization of a set of instructions that dictate the production of the body.

The most serious problem with the genetic program model of development is that it is logically incoherent. To understand why this is so, let us consider again the inadequacy of the organism-machine analogy that grounds the MCO (and by implication the genetic program metaphor as well). As we saw in the Introduction (see Nicholson, 2013 for a full analysis), organisms are intrinsically purposive whereas machines are extrinsically purposive. This distinction reflects, among other things, the fact that organisms organize and produce themselves, whereas machines—including computers—are organized and assembled by external agents. As we will now see, this essential difference renders the theoretical transposition of the software/hardware distinction from computer science onto developmental biology inappropriate and misleading, if not altogether nonsensical.

Recall that, in a computer, the hardware (the material parts of the machine such as circuits, disks, and wiring) and the software (the various programs that are executed by the machine) are totally independent. The machinery of a computer must already be assembled by an external agent before a program can be run on it—it is not itself a product of the program. Now compare this to what happens in development. Here, the output of the program is the organism itself. This means that the software (the genetic program) is responsible for producing and assembling the hardware (the organism). Yet throughout this process, it is the developing organism itself that has to be executing the program. In other words, the hardware runs the software whilst the software is

simultaneously generating the hardware! Thus, thinking about the relation between software and hardware in the context of development leads to a paradox, as the genetic program requires its own output to be executed (Coen, 1999, chap. 1).<sup>3</sup>

In addition to being conceptually inconsistent, the widespread adoption of the genetic program metaphor has been directly responsible for the legitimation and dissemination of three deeply problematic theses concerning the role of genes in development. These are:

- (a) *Genetic animism*: genes initiate, direct, and control the developmental process
- (b) *Neo-preformationism*: developmental information is encoded in the genes
- (c) *Developmental computability*: complete knowledge of how genes interact during development will enable us to ‘compute the embryo’.

Let us examine the difficulties with each of these theses in turn. The problem with genetic animism is that it implies an attribution of causal agency to genes that they simply do not possess on their own. It is difficult to see how genes could be responsible for initiating and directing the execution of the developmental process given that DNA is not an inherently active molecule, but rather requires activation from without. Indeed, without the highly structured cellular environment, DNA is inert, relatively unstructured, and non-functional. In spite of this, genetic animism language pervades both the technical and popular genetics literature. As Lewontin poignantly observes:

Genes are said to be ‘self-replicating,’ they engage in ‘gene action,’ they ‘make’ proteins, they are ‘turned on’ or ‘turned off’ by ‘regulatory’ DNA. But none of this is true. Genes are certainly not ‘self-replicating.’ New DNA strands are synthesized by a complex cell machinery (another metaphor!) consisting of proteins that use the old DNA strands as templates. We do not speak of manuscripts ‘self-replicating’ in a photocopy machine. Genes ‘do’ nothing, they ‘make’ nothing, they cannot be ‘turned on’ or ‘turned off’ like a light or a water tap, because no energy or material is flowing through them. DNA is among the most inert and nonreactive of organic molecules (Lewontin, 2000b, pp. xii–xiii).

Genetic animism promotes the misunderstanding that DNA stands in contradistinction to the rest of the components in a cell by virtue of its ability to exert executive power over cellular operations. In reality DNA is only functional when it is embedded in the context of an already present, intricately organized cell. It is only in the presence of a pre-existing cellular apparatus that any talk of ‘gene action’ can even make sense. And what is more, the origin of that cellular apparatus cannot be traced back to the genes. Though DNA provides a template of one-dimensional information for the amino acid sequence of proteins, many cellular structures such as membrane-bound organelles, as well as the plasma membrane itself, are the only template for their own replication; that is, they are the only source of ‘information’ for their own three-

<sup>2</sup> Stubblefield (1986, p. 142) goes further, contending that it would have been impossible to understand the molecular basis of development prior to the invention of computers because ‘[w]e needed computers [...] to experience the complex problem of programming a logic machine before we could be able to recognize such an apparatus in cells’.

<sup>3</sup> Of course, one could avoid the paradox by reformulating the concepts of software and hardware so that it was no longer necessary to theoretically conceive them as separate entities (as they are understood in computer science). The trouble with going down this route is that it would require giving up the very properties that make computers distinctive in the first place, thereby defeating the whole purpose of using computers to shed light on development.

dimensional structure. Proteins do get incorporated into them, but they are always already present (Moss, 1992, 2002).<sup>4</sup>

Despite what the genetic program metaphor suggests, genes do not initiate, direct, or control development (or any other process, for that matter). When biologists speak of genes in that way, a close examination of the specific empirical details usually suffices to dispel the validity of such characterizations. For example, the 'eyeless' gene of *Drosophila melanogaster* was famously described by its discoverers as 'a master control gene for eye morphogenesis' (Halder, Callaerts, & Gehring, 1995, p. 1792). They had found that the expression of this gene appeared to be responsible for triggering a massive cascade of molecular reactions that ultimately results in the formation of eyes.<sup>5</sup> This is what prompted them to refer to it as a 'master control gene'. However, as Burian (2005, pp. 221–225) has pointed out, they could just as well have described it as a 'switch gene' (i.e., a gene whose expression sets off a cascade of events). There was no need to resort to such theoretically (and ideologically) loaded language—especially considering the fact that 'genetic switches' are often activated by environmental stimuli. Such genetic animism tropes, stemming as they do from the Cartesian soul/body dualism connotations of the software/hardware distinction we noted earlier, are unnecessary and unhelpful, as they only serve to mislead other biologists (and the public at large) about the actual role genes play in development.

The thesis of neo-preformationism is expressed every time biologists say that genes 'code for' phenotypic traits; a claim that is substantiated only by atypical, pathological cases in which the complexities of the genotype-phenotype map can be effectively ignored. It is also manifested when developmental biology is described as 'the study of how information in the genome is translated into adult structure' (Maynard Smith, 2000, p. 177).<sup>6</sup> Neo-preformationism is implicit even in the use of the term 'development', which is itself a metaphor that carries with it a prior commitment to the nature of the process it designates. The word 'development' tends to refer to the unfolding or unrolling of something that is already present; a making manifest of what is already immanent. What is reflected in the modern biological usage of 'development' (as opposed to the older Aristotelian term 'generation') is a tacit endorsement of the view that the ontogeny of an organism is specified and determined by its constitution (Lewontin, 2000a, p. 5).

The term 'neo-preformationism' of course alludes to the early modern mechanist doctrine we discussed at the start of this section, which postulated that a miniature version of the fully formed adult is encased in the germ. Neo-preformationism is more subtle: the organism is not preformed in the germ, but the information that programs its development is preformed in its genes.<sup>7</sup>

<sup>4</sup> The implication of this is that genes cannot be regarded as the sole transmitters of information from parent to offspring. Membranes and organelles, basal bodies and microtubule organizing centres, are all inherited as well. Changes in these epigenetic elements cause heritable variation in the cellular phenotype. They therefore constitute additional, epigenetic inheritance systems (Jablonka & Lamb, 2005).

<sup>5</sup> Subsequent work has demonstrated that a suite of genes are in fact required, collectively, to initiate eye development in *Drosophila* (Fernald, 2004).

<sup>6</sup> In this respect, neo-preformationism provided a key incentive for undertaking the Human Genome Project, which was carried out under the explicit assumption that '[t]he collection of chromosomes in the fertilized egg constitutes the complete set of instructions for development, determining the timing and details of the formation of the heart, the central nervous system, the immune system, and every other organ and tissue required for life' (DeLisi, 1988, p. 488).

<sup>7</sup> As Davidson (2009b, p. R217) indicates in relation to the older preformationist tradition, 'No, the organism is not pre-formed in the head of the sperm, but the head of the sperm and the egg nucleus do carry an immensely complex, species-specific, regulatory program for the stepwise process of embryonic development'.

The genome is thus assumed to contain all the information required to specify the phenotypic outcome of development. One disturbing consequence of neo-preformationism is that it eliminates the need for real developmental biology (Griffiths & Neumann-Held, 1999). If developmental information is really encoded in a genetic program, the intricacies of the embryological process are of little importance. All that one needs to know is already in the DNA.

The problem with neo-preformationism is that the information required for making an organism is not actually preformed in the DNA. Instead, it emerges progressively through the dynamic interaction of DNA with proteins, metabolites, and other cellular components, as well as with the cellular, extracellular, and extra-organismic environments (Griffiths & Knight, 1998; Oyama, 2000; Oyama, Griffiths, & Gray, 2001). Ontogeny is not the gradual unfolding of the organism from a predetermined genetic program, as the very term 'development' misleadingly suggests. It is a highly dynamic and heterogeneous process involving the confluence of numerous intersecting causal factors, only some of which have their physical basis in the organism's genome.

The propensity to neglect the crucial role of the environment in shaping developmental outcomes is another consequence of assimilating the development of an organism to the programmed operation of a computer. In a computer, the independence of software and hardware means that the same program is always executed in exactly the same way regardless of the system that runs it. In contrast, when organisms with a similar genotype find themselves in dissimilar environments they tend to develop differently. This is because the developmental deployment of genetic material is highly sensitive to external conditions. The path from genotype to phenotype is mediated by the environment. The genotype does not specify a unique outcome of development but rather stipulates a norm of reaction—that is, a pattern of different developmental outcomes across different environments that forms the basis of the phenotypic plasticity displayed by all organisms (Pigliucci, 2001). The consequence of this is that development must be conceived as a process of construction involving the interaction of the internal milieu of the organism with the external milieu in which it finds itself in.

Finally, the thesis of developmental computability articulates the Laplacian expectation implicit in the genetic program metaphor by holding that an embryo could in principle be computed from the complete dataset of a fertilized egg.<sup>8</sup> The question of computability was famously posed by Lewis Wolpert in an essay titled 'Do we understand development?', where he wrote:

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

<sup>8</sup> It is interesting to note that Descartes already anticipated this deterministic thesis in his unfinished writings on embryology, where he postulated that 'if one had a good knowledge of all the parts of the seed of some species of a particular animal, man for example, one could deduce from this alone, by entirely certain and mathematical arguments, every shape and structure of each of its bodily parts' (Descartes, 1998, p. 200).

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)

One of those who took on Wolpert's 'formidable task' was Bodnar (1997), who brought together a large array of experimental findings of gene interactions during *Drosophila* development in a computational model that could simulate the ontogenic process in a personal computer. Bodnar showed that most of the genes that regulate specific morphogenetic pathways can be represented as Boolean switches, which can be 'on' or 'off' depending on whether concentrations of certain transcription factors are above or below a certain threshold. Bodnar then generalized a series of switching rules that compute the hierarchical cascades of gene activation actually observed in living *Drosophila* embryos. Davidson's work on the GRNs of the sea urchin embryo shares with Bodnar the goal of uncovering 'the logic instructions that encode development' (Davidson, 2009a, p. 248) by identifying the sequence of Boolean rules that describe the general patterns of gene regulation during embryogenesis. Ultimately, the aim is the same: to show how each stage in development may be construed as an algorithmic function of the immediately prior step, thereby opening the possibility of eventually computing the entire developmental process from initial conditions (cf. Rosenberg, 2006, chap. 2).

The trouble with developmental computability is that it misinterprets our ability to depict certain patterns of developmental gene expression in terms of Boolean functions in a computer as empirical proof that genes really do execute a deterministic program for development that can be deciphered and used to compute the embryo. It is a flagrant (even if convenient) idealization to characterize gene expression in terms of Boolean functions, given that transcription—like every other molecular event in the cell—is a noisy, probabilistic affair (Kaern, Elston, Blake, & Collins, 2005; Raj & van Oudenaarden, 2008). Stochastic fluctuations lie at the heart of all gene interactions, and their effects are amplified in regulatory cascades. Stochasticity even influences cell fate decisions (Losick & Desplan, 2008). Developmental 'instructions' thus reflect stochastic probabilities, not deterministic mandates. Developmental computability is an illusion; its commitment to Laplacian determinism is incommensurable with the fundamentally probabilistic character of the molecular and cellular processes that underlie development.

Note that developmental computability presupposes the reality of the genetic program and the acceptance of the MCO more generally. It is *because* organisms are conceived as machines that the question of developmental computability is theoretically meaningful. As Rosenberg remarks, 'the thesis that the embryo is computable from macromolecules alone will not even be controversial among biologists' because '[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). It is quite revealing that the underlying question of whether organisms *really are* machines is not even considered. In formulating the developmental computability thesis, the MCO is simply taken for granted.

In light of the problems with the three theses we have just discussed, together with the logical incoherence of the metaphor itself, it is clear that the genetic program does not convey an adequate understanding of ontogeny. Some have tried to salvage the organism-computer analogy from the defects of the genetic program model by suggesting that the program for development is not inscribed in the DNA but is rather distributed throughout the

fertilized egg as a whole. This alternative instantiation of the MCO, the so-called *developmental program* model, has significant advantages over its better-known contender. Interestingly, its usage dates as far back as that of the genetic program, and, as Keller (2000b) has insightfully observed, one can even derive it from some of the canonical formulations of the latter concept. For instance, Jacob's (1973, p. 9) famous claim that the program model 'equates the genetic material of an egg with the magnetic tape of a computer' does not necessarily imply that the genetic material encodes a program; it might just as well be thought of as encoding data that is retrieved by a cellular program. Although the notion of a developmental program surfaced repeatedly through the 1960s (e.g., Apter, 1966), by the 1970s it had all but disappeared from the biological discourse, leaving the genetic program as the dominant paradigm in developmental biology (Keller, 2000b).

However, over the past twenty-five years the developmental program model has experienced a revival, as the difficulties with locating the developmental instructions in the genome have become increasingly apparent. This has led to the view that the genome constitutes a *database* of informational content that is accessed at various times whilst the program for development—distributed across the cellular components that transcribe and process DNA—is running (e.g., Atlan & Koppel, 1990; Dupré, 2005; Noble, 2006). The merit of the developmental program metaphor is that it avoids overstating the developmental role of genes by construing them not as active agents but as passive repositories of informational content that the organism can draw upon. In viewing the genome as a data storage device, the developmental program model highlights a feature of DNA that is all too often neglected, namely its remarkable chemical stability.

Although the developmental program is undoubtedly a more appealing metaphor than the genetic program, it is still susceptible to the general difficulties that arise when we think of ontogeny as the execution of a program. As we remarked earlier in our discussion, a major reason for biologists' infatuation with 'program-talk' is that it evokes rather effectively the regularity, reliability, and orderliness of the developmental process. But are these attributes sufficient to license the use of program-talk? Clearly they are not. If they were, we would also speak of the Earth being programmed to orbit around the sun. The proper use of program-talk implies more than this. It implies, specifically, the existence of a code and a set of instructions that must be followed in a precise temporal sequence. The problem is that this condition is far too restrictive to be applicable to what happens in development. The execution of a program invariably leads to the same output *because* the same exact sequence of steps is followed each and every time. In contrast, development invariably leads to the same outcome (a fully formed organism) *despite* wide-ranging differences in the number, order, and kind of molecular events that collectively bring about the process. Embryogenesis is much too complex and much too reliable in its outcome to be specified by a program. If development *were* a program, the fertilized egg (not to mention the genome) would never succeed in computing its output. John Dupré offers an analogy that nicely illustrates this point:

If I ask someone to go to the shop and buy me a loaf of bread, and they agree, I am fairly confident that the outcome will be as I intend. If I provide a deterministic programme—take 12 paces north-west, raise hand, turn knob, push, etc., there are too many unanticipated interventions that can derail the process for me to have much hope of success. (Dupré, 2005, p. 206)

The extreme fidelity and robustness of ontogeny is not the result of the execution of an algorithmic sequence of predetermined steps. Each developmental 'step' is not computed from the

immediately preceding one. How genetic information is deployed relies crucially on elaborate temporal and spatial relations between molecules that are totally context-dependent. Development proceeds by means of intricate series of local interactions, not by global control mechanisms, and embryonic form emerges as a consequence of those interactions.

Fortunately, the program model—in either its genetic or developmental variants—is not the only theoretical metaphor available to developmental biologists. There are alternative metaphors not grounded in the MCO that offer interesting resources for making conceptual sense of the nature of ontogeny. For example, Coen (1999) proposes to conceptualize development as an act of artistic creation. He points out that a painter does not attempt to replicate a natural object by following a set of computable instructions. Rather, the painting emerges as the result of a highly interactive process in which painter, materials, and environment come together in a spontaneous creative event. Just as the artist responds spontaneously, not only to the material (the texture of the canvas, the quality of tools at hand) and the environment (the angle of the lighting, its artificiality or naturalness), but also to the changing patterns of colour and shape as they emerge on the evolving canvas, so the deployment of genetic material during ontogeny is highly influenced by the environment in which the organism finds itself thrown. More recently, Noble (2006) has suggested a series of musical metaphors to conceptualize development, viewing the growing embryo as a symphonic orchestra with no conductor (no executive program directing the process) interpreting (rather than computing) a genomic score composed by natural selection.

It is likely that no metaphor can singlehandedly capture embryogenesis in all its complexity. Perhaps an array of disparate metaphors is needed to appropriately make sense of different aspects of the process. What is evident, at any rate, is that the MCO submetaphor of the genetic program (as well as variants like the developmental program) fails to provide an adequate framework for conceptualizing development. As a theoretical model, it is unable to map the complex web of causal relations that link the genotype to the phenotype. By conceiving embryos as computing machines and borrowing concepts and terminology from computer science, it gives biologists the illusion that they can predict and control development—even that they have already understood it. But the genetic program does not explain development; it merely black boxes it. By rejecting the MCO as a general theory of living systems, developmental biology becomes liberated from misleading analogies and flawed models that encourage a distorted understanding of what development is and how it takes place.

### 3. The MCO in evolutionary biology

The predominance of the MCO in modern biology has also had far reaching consequences in evolutionary biology. In fact, it has influenced the Neo-Darwinian understanding of evolution to such an extent that some of the most prominent debates within evolutionary theory over the past few decades have tacitly revolved around 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 fundamentally incompatible with an evolutionary conception of organisms. Whereas the former is firmly grounded in Christian theology, the latter is thoroughly 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 well-known 'Argument from Design'. As organisms differ from machines only in terms of their superior complexity, one can infer that just as the functional organization of

the latter is the product of design, the functional organization of the former must likewise 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 of mechanistic biology provided a theoretical foundation for defending the existence of God, and many philosophers and theologians, especially in Britain, used it to this end during the eighteenth and nineteenth centuries (Topham, 2010).

Perhaps the most famous example of the theological recourse to the MCO is William Paley's *Natural Theology*. In this work Paley compared the intricate contrivances of machines like the watch to the exquisite adaptations of organisms, and argued that the apparent design of the latter attests to the intelligence and providence of a benevolent Creator. It is well known that Charles Darwin practically memorized Paley's *Natural Theology* while he was a student at Cambridge, and that he was instilled thereafter with an appreciation of the perfect adaptation of structure to function in organisms.<sup>9</sup> From the 1830s onwards, it became one of the major objectives of his work to discover the basis of 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 organized complexity of organisms. As he would later remark in his autobiography, '[t]he 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 presented a lethal blow to the MCO. Adaptations, the very features of organisms that seemed to cry out for explanations in terms of design, could now be accounted for by appealing to the operation of natural processes like natural selection.

However, what is remarkable—paradoxical even—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 (see Nicholson, 2012). Ever since Darwin, mechanical analogies, despite their obvious natural theological connotations, have continued to pervade the biological discourse in general and the evolutionary discourse in particular. Evolutionists do not even hesitate to invoke Paley's own approach to the study of adaptation as a model for contemporary evolutionary biology. For example, 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, and even includes seven pages of Paley's book as an appendix to his. Dawkins (1998, p. 16) goes further, suggesting that present-day evolutionists 'might be labelled neo-Paleyists, or perhaps 'transformed Paleyists''. Implicit in this methodological association with natural theology is the view that in post-Darwinian biology, organisms, whilst being recognized as the products of natural selection rather than of divine creation, are still viewed as optimally-designed machines in the exact same sense that Paley—and Descartes for that matter—conceived them. Dawkins (1976, p. xxii) is all too happy to confirm this: 'we animals are the most complicated and perfectly-designed pieces of machinery in the known universe'.

As a consequence of this paradoxical situation, modern evolutionary theory sits uncomfortably alongside a root metaphor (the MCO) that fundamentally misrepresents the nature of the very

<sup>9</sup> Signs of Paley's influence are perceptible throughout Darwin's writings. For example, in *Natural Theology* Paley draws an extended analogy between a telescope and the eye, asserting that 'there is precisely the same proof that the eye was made for vision, as there is that the telescope was made for assisting it' (Paley, 2006 [1802], p. 16). When Darwin discusses the eye in *On the Origin of Species*, he likewise marvels at the 'extreme perfection' of this optical 'contrivance', noting that it is 'scarcely possible to avoid comparing [it] to a telescope' (Darwin, 1859, p. 188).

subjects whose origins it seeks to explain. Nowhere is this tension more palpable than in the usage of a particularly seductive notion imported from the realm of engineering, namely the concept of design. For some, this submetaphor of the MCO constitutes the central organizing idea of evolutionary theory. For example, Michael Ruse, in his book *Darwin and Design*, openly declares that '[t]he metaphor of design, with the organism as artifact, is at the heart of Darwinian evolutionary biology' (Ruse, 2003, p. 266). Gardner (2009, p. 862) similarly asserts that 'Darwinism is really a theory of organismal design'.

But what, we may ask, does the term 'design' actually mean? One philosophical dictionary defines it as the deliberate production of an object by an external agent so that it accomplishes a desired purpose (Bunge, 2003). It is therefore a notion that serves to characterize *extrinsically* purposive objects like machines, given that the design of an object reflects the intentions of the external agent (the designer) that are realized by the produced object. This is something that even the staunchest defenders of the design metaphor in evolution acknowledge. Ruse, in the book mentioned above, notes in relation to the design of a knife that '[t]he 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).

The trouble with design-talk in biology is that, as we have already discussed, organisms are not extrinsically purposive objects. Their activities and operations do not serve the purposes of an external agent. Instead, they are directed towards their own survival, that is, towards the conservation of their own organization (again, see Nicholson, 2013 for a detailed articulation of this argument). Because of their self-producing, intrinsically purposive nature, the concept of design is incapable of capturing the functional organization of organisms, given that this functional organization does not reflect the plan or intentions of an external agent (as it does in machines). The common misconception that the structure and behaviour of organisms is explicable in terms of extrinsic purposes leads to the view that organisms have been genuinely designed to function in a preordained way. This view is very problematic.

For one thing, an organism cannot be designed for a function because it does not itself *have* a function—only its parts do. The reason for this is that the attribution of a function to an entity is enabled by the fact that the beneficiary of its operation is an external agent (McLaughlin, 2001). A machine has a function because it operates in ways that serve the ends of its maker or user. An organism does not have a function because it acts on its own behalf and serves its own ends rather than those of an external agent. The parts of organisms *do* have functions, however, because in this case the beneficiary of their operation is an external agent, namely the organism as a whole to which they belong. But even if the ascription 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 is the case for the parts of machines). This is because it is the organism *itself*—and not some external maker or user—that determines the functionality of each part according to how it causally contributes to the maintenance and perpetuation of the organization of the organism as a whole (Christensen & Bickhard, 2002; Collier, 2000; Edin, 2008; McLaughlin, 2001; Mossio, Saborido, & Moreno, 2009; Schlosser, 1998). Functional adjudications need not be grounded on extrinsically purposive notions like design. Function and design are not mutually entailing concepts (cf. Weber, 2011).

Unfortunately, this is seldom recognized in the literature on function and teleology. Tim Lewens, for instance, has written an entire book on the role of the MCO in evolutionary biology with the

title *Organisms and Artifacts*, but at no point does he even consider the possibility that the purposiveness of a system 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. He wrongly asserts that

when organisms were considered to be artifacts 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, 2004, p. 13)

This mistaken belief has led philosophers to attempt to derive the concept of function from the concept of design (e.g., Kitcher, 1993; Krohs, 2009; Millikan, 1984; Neander, 1991) or to derive the concept of design from the concept of function (e.g., Allen & Bekoff, 1995; Buller, 2002; Lauder, 1982), not realizing in either case that the adjudication of functions in organisms and in machines has a very different basis. Simply put, in machines functionality entails design, in organisms it does not. It is only by assuming that organisms are machines that the attribution of design on the basis of biological function makes conceptual sense.

Despite being a concept that belongs to the domain of machines, the term 'design' is quite liberally used in contemporary discussions of evolution, to the extent that the process and products of evolutionary change are characterized as 'design without a designer' (e.g., Ayala, 2004; Kitcher, 1993). This slogan is misleading because the notion of design does not capture how Darwinian evolution accounts for the functional organization of organisms. The adaptations produced by evolution are *not* the result of an intentional preconceived plan by an external agent, but are rather the consequence of the differential survival and reproduction of organisms with heritable adaptive variations. It would be far more appropriate to assert that organisms are 'fashioned' or 'shaped' by selection pressures than to invoke design as an explanatory concept in evolution (see Reiss, 2009).

Moreover, the very idea of 'design without a designer' is not only deceptive—it is also logically contradictory: 'design' means made by a designer. As Zammito (2006, p. 753) correctly observes, '[t]he notion of design is ontologically parasitical upon a designer. There can be no relative [or extrinsic] purposiveness [reflected in the function of the designed product] without an intrinsic purpose [referring to the intentions of the designer] to be served. The analogy of design presumes the transparency—both epistemological and ontological—of human agency'. Matthen (1997, p. 32, fn. 14) is thus right to complain: '[t]his 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 principal 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-day evolutionists inadvertently appeal to the first part of the argument from design. As we 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 was already showed by David Hume in his *Dialogues Concerning Natural Religion*, 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 the acceptance of the analogy between organisms and 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 makes this point crisply and clearly:

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). (McLaughlin, 2001, p. 152)

Nevertheless, there is still an alternative left for evolutionists unwilling to let go of the concept of design, which is to bite the bullet and accept both the inductive *and* deductive parts of the argument from design, and simply replace God with natural selection as the designer. The appropriate slogan for evolution is thus not 'design without a designer' but 'design *with* a designer'. According to this interpretation of Darwinism, the design of organisms is the work not of a divine watchmaker but of a *blind watchmaker* (Dawkins, 1986; 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 carefully read Paley, was fully aware of the watchmaker analogy and yet chose not to resort to it in *On the Origin of Species*. Rather, the analogy Darwin drew upon to illustrate his theory of evolution was that of *selection*, of the kind implemented by pigeon breeders.

Darwin's choice of analogy is extremely significant because breeders and watchmakers proceed in totally 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. It is therefore selection rather than design that Darwin regarded as the correct metaphor to understand evolution, which is why he chose to call the causal principle of his theory 'natural selection' and not the 'blind watchmaker'.

In spite of its inadequacy, the metaphorical conception of evolution as the work of a blind watchmaker—which Godfrey-Smith (1999, p. 190) fittingly describes as 'the *tradition of natural theology continued*'—has exerted considerable influence on modern evolutionary biology. In fact, it lies at the heart of the excesses of the adaptationist program famously criticized by Gould and Lewontin (1979) in 'The spandrels of San Marco and the Panglossian paradigm'. Adaptationists are committed to the view that organisms, like watches, can be effectively decomposed into discrete, mutually independent traits, and that each of these traits is an adaptation, optimally-designed for its function by the watchmaker, natural selection.<sup>10</sup>

The problem with this adaptationist thesis is that there is no single way of decomposing an organism into parts. This is another reflection of the fundamental disanalogy between organisms and machines that makes the MCO such as a problematic notion. One of the distinguishing features of a machine (for instance, a watch) is that it is a composite entity. It is made up of clearly defined parts that interact to produce the behaviour of the whole. These parts are both structurally independent of, and temporally antecedent to, the whole they constitute given that a machine always comes into existence by the assembly of pre-existing components. An organism, on the other hand, does not arise from the assembly of pre-existing components, as we discussed at the start of the previous section. The parts of an organism do not even exist *qua* parts prior to the existence of the whole they constitute. As a result, there is no 'objective' or 'correct' way to carve an organism into parts. How an organism is partitioned depends entirely on the particular epistemic questions one is interested in investigating.

So although some organs like the eye may 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 traits 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 traits of organisms for their functions in the same way that a watchmaker selects parts of watches for their functions. But the truth is that nature does not select traits at all. It selects organisms with traits that functionally contribute (in many different ways) to enhancing the fitness of the organisms to which they belong.

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 between conflicting functional demands, as well as the inevitable architectural constraints on organismic form. This belief in optimal adaptation is another consequence of the MCO submetaphor 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 engineered 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 (1859, p. 201) 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'.

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 intentionally devises effective 'solutions' to the adaptive 'problems' presented by the environment.<sup>11</sup> Accordingly, adaptationists study the adaptations of

<sup>10</sup> The architects of the Modern Synthesis appear to have been divided on this issue. While Huxley (1943, p. 420) asserted that 'every organism cannot be other than a bundle of adaptations', Dobzhansky (1970, p. 65) emphasized that '[t]alking about traits as though they were independent entities is responsible for much confusion in biological and especially in evolutionary thought' (see Depew, 2011).

<sup>11</sup> As Williams (1992, p. 40) explains: '[a]daptation is demonstrated by observed conformity to a priori design specifications [...] The hand is an adaptation for manipulation because if conforms in many ways to what an engineer would expect, a priori, of manipulative machinery; the eye is an optical instrument because if conforms to expectations for an optical instrument'.

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 (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 goal-directed process. It requires identifying a desired state in advance and then specifying and following a route from the current state to the desired state. Natural selection, however, 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, '[i]f wings are a solution to the problem of flight, they are an example of a problem being created by its own solution'.<sup>12</sup>

The recruitment of already existing structures for novel functions is a common occurrence in evolution (Gould & Vrba, 1982), and it runs counter to the metaphor 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, an engineer typically designs machines *de novo* out of especially prepared components. This difference was pointed out decades ago by François Jacob in a well-known article called 'Evolution and tinkering':

[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,

<sup>12</sup> It should be admitted that the MCO-derived metaphor of natural selection as an engineer has not been single-handedly responsible for perpetrating the misunderstanding of evolution as a goal-directed, problem-solving process. The reason is that the concept of 'natural selection' is itself a metaphor that does not completely avoid the problematic presumption of intentionality. After all, selection is an intentional act. Thus, in drawing the analogy with artificial selection, Darwin inadvertently left open the possibility that his principle could be misconstrued as a goal-directed agent that, like a breeder, intentionally, and with foresight, picks or 'selects' variations directed towards the maximization of organismic fitness (Blancke, Schellens, Soetaert, Van Keer, & Braeckman, 2014). This misleading interpretation of natural selection has at times resulted in a crypto-anthropomorphic view of the environment, which, understood as the natural selector, poses adaptive problems that organisms must solve. Such misconceptions can be avoided by keeping in mind that the environment is not an independent, quasi-transcendent entity with the power to mould organismic form according to its demands (like a breeder or a watchmaker), but is rather partially constructed by the activities of the organisms that inhabit it (Odling-Smee, Laland, & Feldman, 2003).

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 engineer metaphor of natural selection we have discussed. For example, whereas the engineer works prospectively according to a preconceived plan or design, 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 far from perfect; instead they are opportunistic and haphazard. Evolution is indeed much more like tinkering than engineering.<sup>13</sup>

Overall, the host of problems that arise from appealing to the metaphor of design in evolutionary biology can ultimately be traced back to the fact that design, being a concept borrowed from engineering, describes extrinsically purposive systems like machines, not intrinsically purposive ones like organisms. In light of the misunderstandings that the adoption of this notion has caused, it is rather surprising that it continues to contaminate evolutionary thinking to the extent that it does. Ollason (1987, p. 243) poignantly 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'. The reason why the metaphor of design still haunts evolution is that, despite its disturbing theological connotations, it is firmly grounded in what is still the most influential model of the organism: the MCO. 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 organisms.

#### 4. Conclusion

Science cannot be conducted without metaphors. They make abstract ideas accessible and complex phenomena tractable, they help generate empirical predictions, and they provide bridges between different areas of enquiry. Nevertheless, the effectiveness of a metaphor depends on the appropriateness of the context in which it is invoked. The choice of metaphor is critical, as it determines the theoretical lens through which phenomena are conceptualized and explained. Choosing an inappropriate metaphor can have very unfortunate consequences, as it can inadvertently bias our understanding of the target domain and prevent us from seeing aspects of it that may otherwise be perfectly obvious. Still, the ways in which metaphors influence and even constrain scientific thinking are not always perceptible. In fact, the more pervasive the metaphor, the more covert its effects.

In this paper we have examined one of the most pervasive metaphors in biology, the MCO. The reasons for its ubiquity are readily apparent. Machines, being the products of human design,

<sup>13</sup> It is important to note, however, that not all forms of engineering are equally well captured by the paradigmatic characterization offered by Jacob. Calcott (2014) has recently drawn attention to the fact that software engineering is quite different from mechanical engineering (which has traditionally been the source of most engineering metaphors in evolutionary biology) and is in fact more akin to tinkering. Software engineers tend to work by re-writing existing source code—rather than devising it from scratch—and usually modify it in an open-ended way so that it can be altered again in the future as new demands arise. It is clear, then, that depending on the biological context being considered, metaphors from some forms of engineering will be more misleading than others.

are intuitively compelling models for conceptualizing organisms. Moreover, if organisms are machines, then the principles, concepts, and methods of physics and engineering can be unproblematically imported into biology. But perhaps most importantly of all, conceiving an organism as a machine has historically meant to conceive it in a way that enables it to be profitably investigated. This is because the very idea of a machine encapsulates precisely that which is amenable to scientific analysis: an organized system with regular and predictable behaviour, and whose workings can be completely explained in terms of the structure and interactions of its component parts. This is what has made the MCO such an incredibly useful heuristic device throughout the history of biology. The heuristic power of the metaphor has been augmented even further by the fact that continued technological progress has furnished biologists with an ever expanding array of machine models to draw upon. The MCO takes remarkably different forms depending on the biological phenomena being considered, and this is precisely what our examination of development and evolution reflects.

Having said this, we should not commit the mistake of conflating heuristic usefulness with theoretical truthfulness, as the former does not always entail the latter. The MCO is heuristically useful because it 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 reinforce the original conceptualization of the organism as a machine. The more complex or recalcitrant aspects of the organism that do not fit the MCO in any of its various forms 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 internal organizational dynamics. As our analysis has shown, it is exactly these features that render the epistemic transposition of the software/hardware distinction into developmental biology unsuitable, and it is also what makes the theoretical recourse to the concept of design in the explanation of function and adaptation inappropriate.

So although it is true that we can heuristically study differentiation by depicting patterns of gene expression as if they were Boolean functions in a computer program, this does not mean that development *actually* proceeds as the programmed execution of an algorithmic sequence of predetermined steps. In the same way, although it is true that we can heuristically study organismic traits as if they were evolutionary solutions to adaptive problems, this does not mean that organisms *actually* evolve according to the design specifications of a blind watchmaker. An organism does not develop in the way that a computer executes a program, nor does it evolve in the way that an artifact is designed by an engineer. Both of these damaging misconceptions, which preclude genuine understanding in developmental and evolutionary biology, have their basis in the uncritical acceptance of the MCO as a general theory of living systems.

It may be appropriate to end by drawing attention to the fact that the problematic nature of the MCO as a biological theory has long been recognized by theoretical biologists. As the late Robert Rosen put it in his book *Life Itself*, 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' (Rosen, 1991, p. 22). Ludwig von Bertalanffy was even more forceful in his condemnation of the MCO in his *Modern Theories of Development* of 1933:

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 [...] will put an end to the paralysis of biological thinking for which this Cartesian expression has been responsible. (Bertalanffy, 1933, pp. 36–37)

The 'displacement of the machine theory' that Bertalanffy referred to eighty years ago has still not been accomplished, but it is becoming harder and harder to dispute the fact that the MCO today is obstructing rather than enabling theoretical progress in biology. Breaking free from the historical grip of this seductive metaphor constitutes a necessary precondition for coming to terms with the nature of living systems.

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