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Article

Kant's Concept of Organism Revisited: A Framework for a Possible Synthesis between Developmentalism and Adaptationism?

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ABSTRACT

Contemporary biology is affected by a controversy between the adaptationist viewpoint, central to the neo-Darwinian Modern Synthesis (MS), and the developmentalist viewpoint, central in Evo-Devo. The possibility of a synthesis between those viewpoints, as granting unity between the laws of form and the laws of function in biology, is therefore currently hotly debated. Kant's concept of organism is often seen as the philosophical precursor of developmentalism. Yet this view is incomplete, and Kant's unique regulative notion of purposiveness relies on two criteria in order to capture organisms as natural purposes: a design criterion and an epigenesis criterion. While the former is fulfilled within MS, the latter is satisfied by organisms from the developmentalist viewpoint. Under some conditions, Kant's notion of organism can thus allow for a synthesis of developmentalism and adaptationism.

1. INTRODUCTION

A major debate about the relations between development and evolution has been taking place within biology for at least a decade. Development is a process that individual multicellular organisms undergo, and through which they grow from unicellular zygote stage to adult, reproductive stage. Evolution, since Darwin, is understood as a process *undergone by species*, and *driven* to a large extent *by natural selection.*

Development is not relevant for making sense of evolution according to the classical framework of evolutionary theory, the Modern Synthesis, and its elaboration on the basis of population genetics modeling after the 1930s (Burian 2005). Population geneticists have understood evolution as a process of transforming allelic frequencies. Natural selection is regarded as the change in allele frequencies due to differential reproductive success of organisms in virtue of their heritable traits (Gillespie 2004). In this context, development does not make any genuine difference to evolutionary processes. Instead, what counts are the replication of genes, and the differential reproductive chances those genes confer on the organisms that carry them by conditioning adult phenotypes.

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For the Modern Synthesis, development is thus not in the foreground. More generally, given that evolutionary processes occur in gene pools, and are explained at least at the microevolutionary level through population genetics models, developing organisms themselves may be (evolutionarily) insignificant "vehicles," as Dawkins (1976) christened them. In this sense Walsh (2015) pictured the twentieth century as the triumph of "suborganismal" biology. Both evolutionary biology and molecular biology (two heterogeneous fields, to the extent that natural selection is not relevant for the study of molecular processes) concur in locating the causal processes relevant for biological explanation at the suborganismic level.

By contrast, over the last three decades a more recent research program, Evolutionary Developmental Biology or Evo-Devo (e.g., Gilbert 2003; Raff 1996; Alberch et al. 1979; Caroll 2004; Hall 2003), has mounted arguments for a different view. According to this alternative program, the developing organism is crucial to evolution, and therefore to our understanding of the ultimate causes of living organisms, their diversity, their commonalities, and their traits. Developmental processes such as heterochrony, i.e., differences in timing of developmental processes (Gould 1977), and phenotypic plasticity, i.e., phenotypic differences of organisms with one and the same genotype in different environments (West-Eberhardt 2005; Nicoglou 2015), have been shown to matter immensely to evolution. This more recent research tradition thus calls for a return to the organism within evolutionary biology (Bateson 2005; Huneman 2010, for an assessment).

Advocates of a new focus on developing organisms in evolutionary theory are, however, not wholly agreed. A particular point of contention concerns the very prospects of a new synthesis. While some regard it as imminent (e.g., Gilbert et al. 1996; Caroll 2008; Love 2003), others are more skeptical. Thus, Amundson (2005) places the claims of Evo-Devo in the historical context of the major divide that Edward Stuart Russell (1916) diagnosed between "form biology" and "function biology." On this reading, Modern-Synthesis thinkers pursue function biology, or "functionalism" (Amundson 2005). They explain the traits of organisms, their commonalities, and their diversity by appealing to the effects of natural selection, which incrementally shapes traits as adaptations to particular environments. Evo-Devo scientists, by contrast, elaborate a developmentalist stance that stems from form biology, or structuralism. They emphasize common developmental processes across whole lineages and clades.

From this perspective, the divide between the Modern Synthesis and developmentalism is much deeper than it seems. It concerns the nature of the laws that govern biology. Darwin himself, considering this opposition of form and function in the sixth chapter of the *Origin of species*, contrasted the "two great laws" of biology—the law of function being for him Cuvier's "principle of existence," and the law of form being Geoffroy Saint-Hilaire's "unity of plan."[1] Today, a law of function would be the principle of natural selection, as Darwin stated, that shapes functions through the dynamics of genetic change;[2] for instance, Fisher (1930) spoke of his Fundamental Theorem of Natural Selection (FTNS) as a major law of the living world.[3] Laws of form, on the other hand, have been variously formulated—from a geometrical formulation in D'Arcy Thompson (1917), to a physico-chemical formulation such as

Turing's model of morphogenesis, Kauffmann's self-organization (Kauffmann 2000), or even Varela's "autopoiesis" (Varela 1979). The required task of synthesizing evolutionary biology with the insights of Evo-Devo thereby assumes that the 'two great laws of biology' can be integrated, that they are not heterogeneous, and ultimately that the sets of laws of development can either concur with the laws of natural selection, or follow from them. We'll consider here a possible Kantian contribution to this issue.

Gilbert and Sarkar (2000) regard Kant's view of organism as the general blueprint for the understanding of organism shared by developmental theorists since the nineteenth century and passed on to proponents of the developmentalist stance in Evo-Devo. Referring to Lenoir (1982), they write: "the founders of modern embryology—Döllinger, Pander, von Baer, and Rathke—subscribed to the organicism set forth in Kant's *Critique of Judgment.*"

Granted, Kant's reflection on living things and the specificities of biology were historically triggered in part by the question of development and the opposition between the then available families of accounts, preformationism and epigenesis (Zammito 1992). Commentators have thus emphasized that Kant's thinking about biology stood in close relation to embryology (Richards 2002; Huneman 2007).[4] At a very general level, morphologists such as Gegenbaur, Oken, or Owen (Rehbock 1980) and embryologists such as Von Baer, author of the main embryology treatise of the century, *Über Entwicklungsgeschichte der Thiere* (1828), shared Kant's idea of a general teleological underpinning of development, with the types of genera as goals of this teleology (Ospovat 1980) and the quest for mechanisms as scientists' endeavor within a teleological framework.

Beyond Evo-Devo, Kant has been co-opted as the main philosophical reference for projects that address organism dynamics through the notion of self-organization *sensu largo* and thereby challenge the explanatory and causal priority conferred to natural selection by MS. The major theoretician of self-organization, Stuart Kauffmann, quotes Kant as a forerunner of his own work, saying that a natural purpose "is both an organized and a self-organizing being" (Kauffmann 2000).

But if Kant-as-the-philosopher-of-developmentalism were the whole story, his philosophy of biology would be of no help to assess the prospects of the synthesis between a developmentalist stance and an adaptationist/functionalist stance. In this paper I'll challenge this view and show that Kant's theory of organism allows for an understanding of a possible synthesis. I'll argue for the following points:

- Kant's view of the organism holds a unique notion of purposiveness as a regulative principle for reflective judgment, but a dual criterion for natural purposes—the design criterion and the epigenesis criterion.
- Making sense of the complexity of Kant's views allows one to see his concept of the organism as a blueprint for a synthesis between the developmentalist and adaptationist standpoints by relating these standpoints to Kant's two criteria of organismality.

- The design criterion is satisfied in current evolutionary biology, while the epigenesis criterion is fulfilled by organisms at many levels, from genomes to organic systems, as shown by current developmental, cell, and molecular biology.
- The question of the synthesis between development and evolution can be addressed from this perspective.

2. KANT'S CONCEPTION OF ORGANISMS, AND ITS INTRINSIC DUALITY

2.1. Purposiveness: a Kantian take on the design problem

To first address Kant's concept of purposiveness let us consider his pedagogical example (*CJ*, §62): an equal-sided hexagon traced in the sand. This figure is possible only in accordance with the concept of a six-sided polygon with equal sides. As Kant says, its production by pure chance through the mere laws of nature is immensely improbable, since the set of equal-sided hexagons is of null measure in the set of possible hexagons (not to talk about geometrical shapes in general).[5] Assuming the concept of an equal-sided hexagon at the basis of its production—namely, as informing the intention of the person drawing the hexagon—replaces this infinitely small chance by a necessity. The figure in the sand had to be this shape, were it to be a hexagon equal-sided. Thus, the hexagon was *designed to be* equal-sided. Turning to the traditional example of a watch found on the beach, the concept at the source of the production of the watch as 'tool giving time by a regular motion of springs and wheels' explains why, against the odds, there was a watch there rather than some aggregate of wheels.

Birds' wings compare to the hexagon and watch in this respect: they are possible only on the basis of the concept of flying; such a concept includes predicates (regarding shape, etc.) that an engineer would find as solutions to the problem of making a flying device. Entities whose form and nature we cannot understand, except by presupposing that a concept was at the source of their possibility, are, according to Kant, *purposive* (*CJ*, §VIII, XLVIII, 5:192). This notion of purposiveness captures what 'to be designed' means in the context of the life sciences and natural history.

At the most general level, Kantian purposiveness therefore means the following. Regarding the general laws of nature—i.e., the synthetic a priori principles of nature in general expounded in the *Critique of Pure Reason*, and supplemented by the laws of material nature explained in the *Metaphysical Foundations of Natural Science*—the designed entity is plainly contingent. It may have been otherwise, depending upon small changes in initial conditions. The project of a biological understanding of living entities, however, aims at the regularities and rules of their development and functioning. It aims to explain why organisms *should* be the way they are. The notion of purposiveness is precisely the idea that, even if contingent according to the general laws of nature, those entities have some lawfulness of their own when regarded as living entities. As merely belonging to nature, object of our physical science, living entities are contingent in the sense that it makes no difference to nature whether these entities are alive or not, or whether a development leads to a monster or a viable organism. But since the life sciences rely on this difference between living and nonliving, we have to assume a principle of purposiveness in order to account for it (Ginsborg 2001; Huneman 2006). The "lawfulness of the contingent as such" is therefore purposiveness (*First Introduction*, 20:217).

Thus, biological purposiveness is this 'lawfulness' according to which living entities are able to live and develop. The nature of this lawfulness is definitive of the laws proper to biology; all other laws governing living entities are the laws of physics and chemistry. Kant insists that such lawfulness stems from our project of understanding life as such, and does not have the same status as the laws of nature, which, according to the Transcendental Analytic, are at the basis of nature, and of any knowledge thereof. In Kantian words, purposiveness is a 'regulative' rather than 'constitutive' principle. It does not constitute nature as such but regulates our understanding of *living* nature, as soon as we want to understand it as organized nature (*CJ*, §77, 408).[6] Breitenbach (2009) argues that this presupposition is necessary for our very experience of living nature, prior to any scientific program, and therefore cannot be established by scientific means. Lewens (2007) speaks of "Kantian projectivism" in order to say that concepts specifying purposiveness in organisms (above all, functions) dwell on the purposiveness we are acquainted with as rational agents in order to fulfill our need to scientifically explain features of living entities.

Importantly, Kant's reworking of the idea of purposiveness as this 'lawfulness' emphasizes the relationship between the parts and whole of a system instead of the means-ends relationships with their various connotations of utility that were central to contemporary physiology and anatomy. Here, the main idea of purposiveness concerns the fact that parts have to be understood with reference to the wholes they are parts of. 'Purposiveness' should not be understood as 'A is useful for B', which is for Kant an external relation. A major argument in the *CJ* (§63), before elaborating the proper concept of purposiveness, consists actually in discarding the notion of utility from purposiveness, this utility being always arbitrarily ascribed. Nonexternal, or internal purposiveness, defines proper teleological thinking according to Kant. He opposes it to mechanical thinking, namely the understanding that goes from parts to wholes and which, for our faculty of cognition (*Erkenntnisvermögen*), is the only route to objective knowledge (*CJ* §77). "The idea of the whole determines the form and the binding of all the parts: not as a cause, since it would be a product of art—but as a *principle of cognition* [*Erkenntnisgrund*] of the systematic unity of the binding of all the manifold contained in the given matter for the one who has to judge" (*CJ*, §65, 5: 373). It is only *after* this characterization of natural purpose in terms of parts and wholes that Kant recaptures the ancient meaning of purposiveness in terms of means and ends. As he puts it, this meaning is usually found in the old "maxim of physiologists," namely, "the presupposition that all, *in the animal*, has its utility" (CPR, A688/B716).

Notice that Kant says that *the idea of the organic whole* is present as a mere *principle of cognition*. It is not the principle of their making—otherwise we would be committed to the idea of a divine designer. It is rather the very condition of our understanding of organs and traits as parts of an organism, to the extent that it must be referred to when explaining the development and functioning of an organism. The parts are regarded as having a function by our considering their causal role in a whole; the embryonic process is perceived as having as a norm the production of a systematic, viable, reproducible whole. This idea of the whole is presupposed as a norm that allows the biologist to establish what a part (organ, trait, etc.) is supposed to do, and where a developmental process is supposed to go (see Huneman [2006] on this duality). Functions of parts—or their adaptive character—on the one hand, and building of an organic form—or development—on the other, are therefore the two facets of purposiveness.

2.2. Organisms: the complete view

As designed, organized beings or organisms are therefore 'natural purposes'. We cannot account for their development, nor their functioning or adaptation to their environment, unless we think of them in these teleological terms. Purposiveness is then a necessary regulative assumption for the biologist, likely to support two explanatory projects—one about functions or adaptations, the other about development.

In an important passage of the *CJ*, Kant defines two criteria for something to be qualified as a natural purpose:

> [1] In such a product of nature each part, at the same time as it exists throughout all the others, is thought as existing with respect to [*um . . . willen*] the other parts and the whole, namely as instrument (organ). [2] That is nevertheless not enough (because it could be merely an instrument of art, and represented as possible only as a purpose in general); the part is thought of as an organ *producing* the other parts (and consequently each part as producing the others reciprocally). (*CJ*, §65, 5: 373–74)

This duality has been highlighted in recent scholarship about Kant's philosophy of biology, especially since Ginsborg (2004), who emphasized that the seeming irreducibility of organisms to mechanism can be distinctively understood according to those two criteria.[7] The first one (1) exactly captures the idea of *general* purposiveness: each part has to be understood in terms of (and is what it is because of) its relation to the whole. This criterion exactly captures the idea of design as displayed by organisms as well as by technical complex objects. I call it the 'design criterion'.

The second criterion (2), which I call the 'epigenesis criterion', distinguishes organisms from artifacts. Their design, that is, the arrangement of their parts according to an idea of the whole, is not achieved by some external agent who considers such idea of the whole as a building plan. "Thus, concerning a body that has to be judged as a natural purpose in itself and according to its internal possibility, it is required that the parts of it produce themselves [*hervorbringen*] together, one from the other, in their form as much as in their binding, reciprocally, and from this causation on, produce a whole" (*CJ*, §65, 5:373). In the case of artifacts, the idea of the whole acts as a 'cause' through the human agents; in the case of organisms, this idea exists as a "principle of cognition" (ibid.), which allows us to understand development and functioning. Thus, the building process of organisms is achieved by the parts themselves. In this sense, those parts produce themselves, and have to be considered as acting according to an idea of the whole. Kant talks of this causality of parts regarding other parts as *hervorbringen*, 'production'. He thinks that such causal production has no *analogon* in what we know about causation, be it in the natural domain or in the field of human action (*CJ*, §65, 5:375). The specificity of the second criterion, then, is that it accounts for organisms as entities that have an epigenetic character: they are constantly producing themselves during embryogenesis and through their normal functioning. The famous example of the tree in §64 explicates the dimensions of this productivity—the tree producing itself as an entity, as regenerating parts and as a species. An organism "is both an organized and a self-organizing being," says Kant (*CJ*, §65, 5:374)—coining a neologism that predates Kauffmann and Varela—and this is why it can be conceived of as 'natural purpose'.

The coexistence of these two criteria within Kant's theory of the organism speaks against the view that Kant is the philosopher of the developmentalist stance. Because purposiveness is one principle, which is the 'lawfulness of the contingent as such', it follows that the two major laws of biology—laws of form and laws of function—are unified by being the two aspects of purposiveness. Each law develops the requisite for living entities to fulfill each of the criteria—functional design, and epigenesis as developing form.

Hence, Kant's view may rather provide a perspective for examining the prospects of a synthesis between a developmentalist stance and a neo-Darwinian adaptationist stance, which the next sections will do.

3. THE KANTIAN STANCE IN A DARWINIAN WORLD

3.1. The design criterion

If something is such that its parts are to be thought of as being there for the whole, then the parts will be contrived, in the sense that they will appear as adjusted to the other parts in a way beneficial for the whole. They are not just sets of parts independent from each other. In the *Only Possible Argument* (1763), Kant was amazed by the unique design of complex organs such as the eyes, which require the fine-tuning of many independent parts. Each of these parts obeys its own empirical law independently of the others while the unity of those laws is contingent.[8]

The agreement of various laws that together contribute to the making and functioning of an organ is a clear case of contrivance. From a Darwinian perspective this contrivance of parts is brought about by cumulative selection. Darwin wrote a book to explain contrivances in orchid species (Darwin 1862), namely, the fine-tuned adjustment of the parts of orchids allowing various insects to pollinate while they feed on the flower. On Darwin's account, those contrivances occur as the convergence and concurrence of otherwise independent parts, exactly as in Kant's example of contingent order. Darwin's view of adaptations is that the cumulative action of natural selection, which generation after generation retains and spreads variants more and more adjusted to specific environmental demands, results in the contrivances we witness all over the organic world. Complex traits, such as the eye, made up by the coordinate action of many parts, can be explained through this cumulative process.

Natural selection does not only design contrived parts, but also whole organisms, which are such that many adaptations seem to contribute to their survival and reproduction. Parts of an organism are indeed adapted to one another in a way which physiology has long established. The Darwinian explanation for such intrinsic contrivance of parts relies on the concept of natural selection. Parts that are not suited to each other reduce the survival capacities of the organism. Thus, variations in each of the parts that are likely to increase the adjustment between parts tend to be favored by selection. For Darwin, being contrived—which fulfills the design criterion, since parts are determined by the whole—indicates the action of natural selection. It calls for investigating the reasons of this selection (why are traits "selected-for"? to use the current philosophical term).

While for Darwin the link between contrivances and design with selection was clear, the fact that population genetics anchored the process of selection within gene pools, tracking it as a change of gene frequencies, made this link more problematic. The simplest formulation of this idea would be that the contrivance of parts in organisms tends to increase fitness, and therefore to be favored by natural selection, which in turn preserves organisms from mutational harm. With his theory of the evolution of dominance and recessivity, Fisher thus acknowledged within population genetics, and subsequently the Modern Synthesis, the idea that natural selection increases fitness and therefore design. He wrote:

> That the vast majority of mutations should be deleterious is a perfectly natural consequence from the view that *the organism is maintained in a highly adapted condition by natural selection*, for a highly adapted condition can mean nothing else than one which is more easily injured than improved by a change in its organization. (Fisher 1930, 279, my emphasis)

Notwithstanding the technicalities, the main idea here is that contrivances are in principle favored by natural selection as selection embeds a trend towards (inclusive)[9] fitness maximization (see Gardner 2009; Huneman 2014).

Yet an obvious counterexample to natural selection maximizing fitness, and therefore yielding design, is a diploid population, where the heterozygotes are fitter.[10] Due to the Mendelian mechanisms of gene recombination, a population made up of only heterozygotes is impossible. Natural selection therefore could not bring about a population full of the fitter genotypes. From Fisher's "fundamental theorem of natural selection" (Fisher 1930) to Grafen's "Formal Darwinism" (Grafen 2007), biologists tried to ground a maximizing trend within population genetics by analytically linking selection to fitness increase, therefore explaining away the puzzling cases such as the above-mentioned heterozygote superiority.

In principle, evolution by natural selection can occur when a set of entities features variable heritable properties, endowed with a fitness value (i.e., causally affecting the reproductive chances of their bearers). Theoretical projects such as Fisher's and Grafen's therefore attempt to show that a designing trend is intrinsic to the working of natural selection, even though some specific conditions may counter it. Price (1972) started doubting the biological significance of what is proved here to be maximized, which remains controversial (Birch 2015). Those theories reliably establish no more than the *capacity* of designing as *intrinsic* to natural selection, and the correlative fact that design should signal the action of natural selection—not that selection unconditionally *succeeds* in designing items.

However, leaving aside population genetics, the design criterion is still salient in the domain of evolutionary biology studying organisms and their constitutions and relations (rather than gene pools), namely *behavioral ecology* (Krebs and Davis 1991). Here, the assumption that organisms are designed is methodologically pervasive. When biologists study behaviors like foraging, mating, or the size of the leaves of trees, the initial assumption is that selection was at work. They therefore expect that the values of foraging time, mating preference, or leaf size are the ones that best match the various environmental demands by maximizing inclusive fitness.

In this field, when facing an unknown trait or behavior, Maynard-Smith's "reverse engineering" (Lewens 2003) consists in trying to infer the kind of environmental problem it was designed to handle. The biologist here behaves as if she were confronted with an artifact or machine whose goal was known, but whose parts' functions and structure were unknown. The goal the biologist envisages for the organism is 'survive and reproduce'. The problem is the reverse problem of the engineer, i.e., to 'unbuild a machine that was doing such and such, and thereby understand how it achieves doing such and such'. This method assumes implicitly that parts and organs should be studied as contributions to solving problems raised by environments where the organism is found. For Darwinians this ultimately means assuming that the organism is designed by natural selection to survive and reproduce, even though the reverse-engineering methodology is rarely formulated this way. The biologist then strives to find out the kind of specific demands a specific organism was coping with. She does not thereby show that an organism is an engineered machine, but is guided by the regulative principle to examine organisms as if they were. Thus, a way to understand research in paleontology, behavioral ecology, or functional morphology, where uses of reverse engineering abound, is along the lines of Kant's purposiveness. The prevalent method instantiates the idea that one cannot account for organisms *as organisms* unless one assumes that they are systems designed to cope with environmental demands, while knowing that they cannot be empirically proved to be designed. In Kantian terms this means making a transcendental presupposition of purposiveness. The engineering stance,[11] understood as the assumption of a specific attempt to solve environmental problems in order to thrive and survive, is a clear instance of the presupposition of a functioning whole, or the overall presupposition of purposiveness of the studied system, which is the content of the design criterion.

Therefore Kant's design criterion is clearly an idea driving methodological developments in classical evolutionary biology at the level of genes and organisms. It is an active presupposition in organismal biology, and in gene-oriented biology it is an object of mathematical investigation whose biological significance and scope has been discussed since Fisher.

3.2. The epigenesis criterion

Central assumptions in histology as well as in cell and developmental theory correspond to the epigenesis criterion, according to which the parts of an organism develop and form into the whole according to an idea of the whole. For instance, cell theory has long established that cells produce themselves one from the other, thereby producing the organism according to the form of the whole. Yet more recent advances in developmental and molecular biology have given new legitimacy to the idea that organisms are epigenetic entities in this sense.

At the level of the genome, a set of epigenetic mechanisms involving entities different from the genome, but related to it, contribute to the process of gene expression: methylation of genes, that is, association of the DNA sequence with a methyl group, induces inhibition of the genes, and histone modifications regulate the expression of the genome. Methylation states are transmitted to daughter cells during the lifetime of the organism. This transmission plays an important role in the functioning of organisms, since it ensures that the cells of organic parts will display their proper behavior (Jablonka and Lamb 2004). More generally, episodes that stand between the genome and its expression into a set of functional proteins include the inhibiting and disinhibiting of some genes and not others, the splicing of the DNA sequence in the genome into several transcripts that will be the RNA blueprint of proteins, as well as all processes involved in the transduction, translation, and protein folding processes. In sum, cellular parts such as genes and epigenetic elements such as chromatin, methyl groups, or histones clearly contribute to building other parts of the same kind in a very specific way within the organism, where such specificity is determined by the nature and state of the organism itself and the cells under investigation.

Moreover, one of the major advances of molecular biology in the past two decades is the view that a gene is not a well-defined causal agent but works within a network of genes. What a gene does depends of what other genes on the genome do: this is what the Gene Regulatory Network (GRN) concept, formulated by Eric Davidson in the 80s (e.g. Davidson 1986), intends to formalize. Those GRNs are the networks of genes and outside-genome items that are involved in the regulation of a gene. The GRNs are responsible for cell specification, "the acquisition of a given regulatory state, as the sum of the activities of the transcription factors expressed in the cell nuclei" (Oliveri et al. 2008), which happens during life in general. GRNs are specific to a set of genes of the genome. For instance, one can study, as Davidson and colleagues did, the GRN of the gene *Endo 16* in the development of sea urchins (e.g., Oliveri et al. 2008). At any point, which genes in the GRN are activated depends upon the whole state of the cell, which, in turn, depends upon the overall state of the organism and on where the cell stands within the organism.

Thus genes contribute to the causes of the state of other genes on a genome through the state of the GRN of a given gene. A given gene therefore produces other genes' states, and it does so in accordance with the overall state of the organism, which in turn contributes building a new part, namely a specific functional protein; and this last feature satisfies the epigenesis criterion. Granted, the ancient idea of genes as sets of instructions seems to reactivate a preformationist view of organism, as has often been objected to molecular biology (e.g., Moss 2003). Nonetheless the concept of GRN rather calls for a philosophical view of organisms closer to Kant's, since the genes in GRN, being reactive to epigenetic signals reflecting the local or global state of organisms, have a context-dependent role rather than a purely instructive role.[12]

Moreover, in a more detailed manner, the circularity emphasized in Kant's epigenesis criterion appears realized within the *developmental* process. This is because GRNs are models of gene regulation that can address both the *functioning* of genes in organisms and the *development* of organisms (Levine and Davidson 2003). The genesis of organisms is precisely the process through which the zygote multiplies and differentiates into various cell types. These cell types, in their turn, combine into various tissues and organs, stemming from the various layers that have emerged in the first stage of the process (*blastula*), and then produce specific histological and morphological parts of the organism. Developmental theory distinguishes two aspects of such development: *cell differentiation*—the process through which in a multicellular organism cells with identical genome multiply and reach different phenotypic profiles—and *pattern formation or morphogenesis*—for instance, the formation of the tetrapod limb, which associates different cells that have distinct phenotypic profiles.

The GRN, as a causal structure allowing genomes to express some functions according to their cell environment, underlies cell differentiation in embryogenesis. Epigenetic mechanisms such as methylation of sequences are eventually required to stabilize the specification of the expression state of the genome in the cell. Ensuring cell differentiation is indeed a salient function of epigenetic mechanisms, even though the proper reason for which they evolved in multicellular eukaryotes is still debated.

Pattern formation relies upon an embryological cascade of signaling and activation, a mechanism that instantiates the production of the parts and therefore the whole (Gilbert 2009, Arthur 1997). Be they directly genetically encoded or not, signals provide a given part with information about its state and position within the whole, and therefore refer to a general idea of the organic whole. A morphologic pattern such as an organ is shaped through multiplication of differentiating cells, a process partly controlled by GRNs. Once a gross organ is thus sketched, apoptosis starts, which is a kind of programmed cell-death achieving pattern formation through the deletion of cells that are in excess (Zakari and Ahuja 1994). Apoptosis contributes to pattern formation and therefore illustrates again that the whole organism is built by its parts.

The Kantian epigenesis criterion here is more than a *façon de parler*, because this apoptosis process unfolds in accordance with an idea of the whole. If it did not, no distinction between the proper and improper targets of cell death would be possible. The developmental biologist studying apoptosis therefore assumes that the process is aimed at the suppression of the cells that *should not be* there once the adult stage is reached, and therefore studies the way it can recognize those targets. By so doing, she assumes the whole organism as a norm for pattern formation. This assumption means that pattern formation could not be studied without presupposing that the parts build themselves in accordance with an idea of the whole—in conformity with Kant's epigenesis criterion.

Clearly, researchers do not consider that the organism's parts themselves know and anticipate the form of the whole that they build. The idea of the whole is just a necessary principle for our cognition of those building processes. Thus the epigenesis criterion has a regulative status in such epistemic context, in conformity with the Kantian approach.

4. KANTIAN PROSPECTS FOR A SYNTHESIS OF THE DEVELOPMENTALIST STANCE AND DARWINIAN ADAPTATIONISM

The Kantian conception of organisms includes two distinct criteria, the design criterion and the epigenesis criterion. In current developmental biology, the epigenesis criterion appears to be fulfilled. The epigenetic self-production of parts by parts is here understood under the presupposition of a viable whole. The Modern Synthesis, on the other hand, explains the design of such a whole by appealing to a designing trend that is realized by natural selection, which maximizes inclusive fitness. It follows that an organism in the Kantian sense is the *locus* of a synthesis between Modern Synthesis and developmental biology. The open question concerns the relation between the two Kantian criteria in current biology. In other words, what is the relation between the idea of the whole, presupposed in the circular processes investigated by developmental biology, and the design of this whole as resulting from natural selection?

Kant's idea is that we are in both cases concerned with the same kind of purposiveness, since from his transcendental point of view the concept of purposiveness is a unique principle, endowed with a regulative nature. Along the same lines Breitenbach (2009) has emphasized that the very presupposition of purposiveness establishes living nature in general for us, and therefore precedes any specific instantiation of it in the form of various scientific concepts of goals and functions.

It follows that the idea of the whole according to which parts produce themselves (in the sense of the epigenesis criterion) is the idea of the same whole within which its parts get their functional role (in the sense of the design criterion). Yet in our current post-Darwinian biology, what accounts for purposiveness is rather the fact of natural selection, by its connection with design through expected maximization of inclusive fitness. So is Kant's idea of the unity of those two distinct principles through the unity of the concept purposiveness still valid?

The empirical issue is whether the Kantian view, so reactivated in a post-Darwinian context, is still correct. Two problems may arise here, affecting either the design criterion (a) or the epigenesis criterion (b).

a. Fitness maximization fails for some empirical reasons. Organisms are therefore not necessarily designed by selection, and so the idea of the whole involved in the epigenesis criterion has no support in the Darwinian science of evolution by natural selection;
b. For some empirical reason, the idea of the whole cannot be related to adaptation and selection—e.g., the genome, whose functioning displays the circular processes developmental and molecular biologists explore, contains few traces of design.

(a) The first case concerns a possible divorce between the 'reverse-engineering' method in behavioral ecology and the principles of evolutionary genetics. In this case, the reference to an organismal whole in behavioral ecology—as a clear instance of the 'design criterion'—is not supported by the working of evolution by natural selection. Therefore the rationale for assuming design is not satisfied. In turn, when the use of the epigenesis criterion refers to an idea of the whole, this cannot be justified by the design criterion, hence the two criteria fall apart.

Yet there actually is, empirically, an impressive amount of design in the organic world, attested to by the successes of behavioral ecology.[13] The assumption of natural selection as a designing force thus empirically holds. And this, in turn, means that our actual world meets the conditions under which natural selection as a dynamical genetic process maximizes inclusive fitness, and thereby designs systems. Granted, the abovementioned projects of formally establishing selection as a designing trend (Formal Darwinism, Fisher's FTNS, etc.) diverge on the nature of those conditions.[14] But they concur in claiming that such conditions are not very constraining, thus accounting for the pervasiveness of design. The empirical fact that the conditions have been met in our world thus means that selection is extensively maximizing fitness, which in the Darwinian context fulfills the design criterion. Hence, post-Darwinian biology found this Kantian 'idea of the whole' assumed in our knowledge of developmental processes upon those (still-controversial) empirical conditions that ensure natural selection as a plausible fitness-maximizing trend.

(b) As to the second possible failure of the Kantian concept of organism, the possibility of a synthesis between Darwinism and Evo-Devo rests upon the ultimate conclusions of developmental biologists regarding circular epigenetic processes. Within some research programs in Evo-Devo, genes or genomes take a crucial role. Among the first findings in this discipline were the genes sometimes called 'master control genes', such as *Homeobox* genes. These genes instruct the development of basic features of body plans, underpinning the establishment of morphogenetic gradient fields (De Robertis et al. 1991), and are highly conserved across many lineages (Gehring 1998; Lewis 1992).

Evo-Devo research programs can be divided into (at least) three families. First, one can focus on developmental genes, such as Pax-6, responsible for eye formation in many very distant clades and well studied (Gehring 2002), and the signaling cascades that they regulate (e.g., Arthur 1997; Carroll 2005). Second, more recently, the concept of GRN together with key advances such as the completion of the Human Genome Project in 2003 switched the focus from genes to genomes, and exposed genomes as complex systems (Griffiths and Stotz 2013). Understanding development and its phylogenetic evolution here means modeling a complex dynamic and its evolution rather than identifying conserved genetic agents.

Yet a third research program focuses on chemical complex systems at work within development across a large set of clades. Thus it downplays the role of genetic information within this process. From this viewpoint, diversely combining such molecular systems allows for various types of development in distinct lineages: they constitute various kinds of self-organizing processes (Forgacs and Newman 2005; Newman and Bhat 2009). Genes enter into these self-organization loops as elements among others, the basic causal powers being ascribed to molecules which combine into various pattern-forming dynamical systems.

In the two former programs, genetic framework or GRN framework, the idea of the whole according to which the self-production operates is the same as the one emphasized by the design criterion. This is so even though we switch here from simple to complex informational systems, because in both paradigms genes are central and genomes result from Darwinian evolution. Since this evolution is here mostly understood as shaped by cumulative natural selection, the typical organism to which the circular processing of GRN refers is the same whole as the designed whole that the design criterion highlights, namely, a whole whose contrivances rely on selection. In this case, the two criteria can be unified, and evolutionary biology could in principle integrate developmental biology. Thus the aforementioned 'law of function' and the 'law of form' would not be heterogeneous. In their synthesis natural selection plays a crucial role, since it legitimates the appeal to an idea of the whole, which constitutes both the design of the organism—hence the justification for reverse-engineering methods—and the aim that is in a regulative manner ascribed to the developmental process. Thus such synthesis may seem close to Darwin's original idea, which subordinated the law of form to the law of function. But it is wider than the Darwinian Modern Synthesis, for it does not logically entail either that the principles of development derive from the notion of design, or that those principles do not concern the working of selection. Even if the possibility of a synthesis is warranted, it remains an open empirical question whether the 'two great laws' should be unified according to the Modern Synthesis under the primacy of natural selection or integrated within an Extended Synthesis (e.g., Müller and Pigliucci 2011) in which the principles of development supplement the principle of natural selection to explain some commonalities across species.

In the third research program, there is no privileged explanatory reference to genes and genomes as designed. Development, as self-production of parts by parts, and design, resulting from cumulative selection on genetic systems, are not concerned with the same whole. Even if the development proceeds according to some idea of the whole, at least as assumed by the researcher, this idea of the whole is thereby not the one referred to within the design criterion interpreted in a post-Darwinian context. Thus in this third case, under the Kantian perspective elaborated here, the synthesis between developmentalism and evolutionism would be precluded. What Darwin calls the 'two great laws' would here fall apart.

5. CONCLUSION

Kant's concept of purposiveness expresses the lawfulness of the contingent. It entails that the two major laws of biology—laws of form and laws of function—are unified because they are the two correlated aspects of this principle of nature's purposiveness. Kant saw the principle instantiated in two criteria: the epigenesis criterion and the design criterion.

The design criterion is shown today to be satisfied in behavioral ecology, but questions remain about its analytical foundations. The epigenesis criterion, on the other hand, is regarded nowadays as fulfilled by organisms studied in developmental biology. To the extent that a synthesis between developmentalism and adaptationism is possible along Kantian lines, a Kantian approach can ensure the unity of the laws of biology.

However, the unity between those two criteria, which was warranted by Kant's transcendental viewpoint, is not obviously attainable within current biology. Only some approaches to Evo-Devo can reach this unity. The prospects of unifying the laws of biology therefore remain contingent upon the success of those approaches.[15]

NOTES

1. The section is precisely entitled: "Summary: the law of unity of type and of the conditions of existence embraced by the theory of natural selection."
2. Rosenberg (2001) for instance argues that the only law in biology is the principle of natural selection.
3. Philosophers have questioned whether there are laws *stricto sensu* in biology, and in evolutionary biology. Many consider there to be no proper biological laws (for reasons of contingency, particularity, etc.). Yet some statements at least do function as laws, and this is what I consider here along with Darwin in talking now of laws of form and laws of function. Kant's view below entails a stance regarding biological laws.
4. Moreover, they have pointed out the original conceptual convergence between Kant's own theories and descriptive embryology by paralleling Kant's conception of reflective judgment, and of the regulative idea of "original organization" (*CJ* §81) with Wolff's descriptive embryology (Huneman 2007).
5. On the argument "this is too improbable to be here by chance, so it's here for a purpose" see, among others, Huneman (2015).
6. Notice that "regulative" and "constitutive" are relative terms: some principles can be regulative with regard to a specific field but constitutive for another. For example, all synthetic a priori principles are constitutive of experience. But only the first two sets of these principles are constitutive for intuition, while the others are regulative.
7. Among others Breitenbach (2009) and McLaughlin (2014) developed such a distinction.
8. The contrivance is indeed a pervasive topic in the *Only Possible Argument*, and it characterizes a contingent order of nature—what Kant calls technique (*Kunst*), as opposed to a necessary order of nature, namely, a set of beneficial consequences stemming from a same law of nature. "If the grounds of the effects of a certain kind, which are similar, according to one law, is not the same being, according to another law, then the agreement of those laws with each other is contingent, and the unity which prevails among these laws is merely contingent (. . .)" (2:107). Contrivances appear as the contingent reunion of traits oriented towards an end.
9. Recent theories (e.g., Grafen 2006) since Hamilton (1964) have shown that selection more generally increases inclusive fitness, which is the addition of the fitness increase of the trait bearer and the fitness increase so conferred to the related individuals, where the latter is a compound of the relatedness coefficient and net benefit conferred to the individual considered (Martens 2016; Price 1972).
10. The textbook example here is the malaria resistance conferred to the heterozygotes by the allele responsible for sickle cell anemia (drepanocytosis), while the homozygotes for this allele are lethal. In malaria-affected areas such as parts of Africa the heterozygotes are therefore fitter than homozygotes for normal alleles, notwithstanding the light anemia possibly conferred.
11. 'Engineering' here refers to 'reverse engineering'.
12. Burian (2005, 210–33) even spoke of "molecular epigenesis" to emphasize the difference between the new molecular approach to genomes and the old preformationist meaning often ascribed to genes.
13. Granted, neutral evolution, as Kimura (1984) discovered, is shaping a large part of genomes. I leave this aside here, since neutralism mostly concerns the details of genomic composition. At the level of organismal phenotypes, by contrast, there is a large amount of evidence in favor of the action of selection, considering the existence of adaptation across organic world.
14. Both projects attempt to justify the fitness-maximizing nature of selection by considering mathematical models of evolution. This leads to characterizing the conditions under which selection maximizes fitness, and showing that those conditions are not too difficult to be fulfilled empirically, or at least are easily

satisfied in our physical world. But Fisher, Grafen, and others use different mathematical approaches; each comes up with a different set of conditions for a designing trend within selection, where those conditions overlap but do not coincide.

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