Biosemiotics and development: metaphors and facts

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ABSTRACT

As a field of scientific expertise, semiotics has the interesting property of being a relevant tool for understanding how scientists represent any domain of research, including the semiotic domain itself. This feature is particularly expressive in the case of biology, as it appears to be the case that a certain range of biological phenomena are of a semiotic character. However, it is not consensual the extent to which semiotics pervades biology. This paper deals with this issue for the particular case of developmental biology, stressing the role of semiotics-as-a-discipline in delimiting the extent of semiotics-as-a-natural-phenomenon and, specifically, in disentangling semiotic mechanisms from semiotic metaphors aimed at clarifying non-semiotic developmental mechanisms.

KEYWORDS

Biosemotics, Developmental Biology, Cognitive metaphors, Hypoicons, Blueprints,
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Weaknesses of insight and deficiencies of language stand in the way inexorably. Words and phrases must be stretched towards a generality foreign to their ordinary usage; and however such elements of language be stabilized as technicalities, they remain metaphors mutely appealing for an imaginative leap. Alfred North Whitehead, Process and Reality, p. 4 Literary license is not license to mislead, and when metaphor is employed in the service of scientific understanding, it should be accurate and helpful as well as vivid and evocative Susan Oyama, The Ontogeny of Information, p. 129

1 Introduction

This paper deals with biosemiotic concerns at two different levels of analysis. The first one is epistemological, for the paper has to do with the semiotic means that are used in order to make sense of the biological realm; the second one is ontological, as the paper is also concerned with the putative semiotic aspects of biological phenomena that we struggle to understand by those semiotic means. My discussion will focus specifically on the developmental history of organisms – or ontogeny. Ontogenetic explanations have traditionally been carried out with the help of different metaphors, prominent among which is the the main subject matter of this paper, namely, the blueprint or plan metaphor – henceforth, BPM. According to this metaphor, which is pervasive in the literature and taken almost at face value by many of its users, sequences of DNA encrypt representations of special-typical traits of organisms in their adult forms. The BPM is customarily accompanied by other varying assumptions regarding the executive powers of the genes themselves and of other extra-genetic contributors to developmental processes.

The BPM has been subjected to different kinds of criticisms, which have mostly had to do with the extent to which the target domain of the metaphor (individual development) fits the source one (architectural blueprints or plans). As I clarify in section 2, the least problematic aspect of the BPM is its being a metaphor – or a collection thereof. I agree with the mainstream opinion that metaphors render genuine heuristic services to the advancement of science. A brief semiotic introduction to the phenomenon of cognitive metaphors is offered in that section. In section 3, I review some of the aforementioned critical approaches and settle what I believe to be the only interpretations of the BPM that can survive such scrutiny. Subsequently, I add a personal note to these critical stances in section 4, which, unlike them, is not directly concerned with the projectability of the architectural domain onto the biological one, but with what I believe to be an even deeper weakness of the BPM; in a nutshell, that it is not even based on an accurate characterization of the original technical domain that it is purported to project onto the organic realm. The claim is dramatically illustrated by the fact that the very same architectural processes that inspire the BPM are in themselves frequently the target

of biological metaphors. Section 5 is then devoted to an examination of the two surviving redoubts for a semiotic accommodation of BPM-related metaphors not dealt with in section 3, namely, the patterning role of proteins in between DNA and cells, and the idea of a flow of developmental information on ontogeny. My conclusion in this section in that whilst epistemically promising, the corresponding semiotic metaphors are not ultimately accommodable into bona fide developmental explanations. Therefore, they do not offer the grounds for extending the biosemiotic realm to the corresponding areas of developmental biology. A general Concluding Remarks section closes the paper.

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2 Metaphors in Science: A Brief Semiotic Take

The epistemic role of a certain kind of metaphors in scientific affairs has long been acknowledged. According to Richard Boyd (1979), metaphors are in fact necessary when the scientist's task goes beyond that of unveiling natural kinds – which ultimately correspond to internal essences compatible with definitional characterizations – and it has instead to do with the uncovering of more complex entities that comprise nets of mutually influencing units, with no definite limits or varying extensions from one case to the next (Boyd, 1979). Boyd refers to these entities as "homeostatic property cluster kinds" (henceforth, HPCK) and he claims that new HPCKs require the special kind of epistemic access that can be offered by metaphors provided by better understood domains. Thus, images provided by a given source domain (S) may be projected onto a given target domain (T) on the basis of some intuitively felt affinity, then extended to a broader range of parallels, and eventually pave the way for research programs that definitively fix the shared and diverging grounds of the domaines concerned. In Boyd's own terms, metaphors thus provide the means for "epistemologically accessing" particularly recalcitrant fields of research, while research proper "accommodates" these images, if they prove to be successful, to the ultimate joints of the fields concerned. In the end, the suitability of the metaphorical projection of S onto T is thus not merely constrained by the intuitively felt parallels at the onset, but, above all, by their capacity for provide more accurate and, eventually, more reductive explanations of T. Otherwise, if nothing more is achieved than to drive the field of expertise in charge of T into explanatory cul-de-sacs, the best route to take is to abandon the metaphors before they start to pay lip service to the field – which, regrettably, appears to be very commonly the case.

Considering this introductory paragraph, which stresses the epistemological value of metaphors in science, it may come as a surprise that Charles S. Peirce, whose main focus of attention was the logic of the science-forming capacity, did not put too much emphasis on the role of metaphors

in science, prioritizing the related, but different category of "analogies" instead (Anderson, 1984).¹ In any event, as I shall try to show here, it is perhaps the case that Peirce was not far away from a view like that of Richard Boyd above. To be as succinct as possible, my thesis regarding this issue is that, taken together, "metaphor" and "analogy" may compound in Peirce's system a duplet comparable to the "epistemic access" plus "accommodation" cycle in the case of Boyd's system. Let me explain.

In Peirce's system, analogies and metaphors belong to the overarching class of (hypo)icons, which represent in virtue of some kind of resemblance/likeness. However, analogies represent objects diagrammatically, i.e. owing to their sharing a certain structural isomorphism with those objects; in constrast, metaphors stand for objects with which they share certain properties, which may be vague both in number and quality. Peirce regarded metaphors as belonging to creative rather than to discovery affairs. For instance, he pinpointed metaphors as the most frequent source of lexical innovations, wherein particular properties of an originally open set of connotations first becomes restrained and then uniformly linked to an object all across the language community (Wilson, 2011). As claimed by Douglas Anderson:

Some frozen metaphors, interestingly, *are* analogies; or, put the other way around, some analogies arise out of metaphors [...] In this way an isomorphism, a univocal link, is established between the constituents [i.e. S and T; my addition]. (Anderson, 1984: 464)

Thus, a kind of cycle appears to exist in the life of creative metaphors which resembles the "access-accommodation" cycle of cognitive metaphors, as in both cases what is pointed is to the fixation of a literal denotation – i.e. a theoretical concept or a lexical meaning, respectively.

It is certainly an intriguing detail, which appears to have been left undeveloped in Peirce's works (Anderson 1984), that he did not credit metaphors with an epistemic role in science. For him, metaphors appeared to be deprived of the capacity to enter into the kind of cycle which leads, first, to a denotation apt to indicate the dynamical object that constitutes the subject matter of a scientific enterprise (i.e. epistemic access) and, ultimately, to the kinds of "collateral experiences" (Peirce's words) that may eventually lead to exploring the dynamical object's nature (i.e. accommodation). It is as if for Peirce, metaphors were doomed to remain in an immediate, as opposed to dynamic, relation with their object as represented but no with the real object. Perhaps, as argued by Douglas Anderson, this attitude regarding metaphors was due to the kind of fuzziness and indeterminacy that Peirce associated with them. In any event, I believe that there is still space in the interpretation of Peirce's take on metaphors for the thesis that once frozen – i.e. centered around a particular set of properties,

¹ For some relevant loci of Peirce's reflections on metaphors, see CP 1.367, CP 2.222, CP 2.276/7, CP 2.280, CP 2.290, CP 2.302, CP 2.306, CP 2.255, CP 2.258, CP 6.196/7. CP = Peirce, C.S. (1931–1966); reference to Peirce's fragments is designated by CP followed by volume and paragraph number.

or even a single one – metaphors may then be apt for the job, as a sort of new schema that, similarly to other analogies, may facilitate epistemic access to a certain domain of inquiry and give rise, through an accommodation process, to relevant discoveries (Sørensen & Thellesfen, 2010; Wilson, 2011; Feodorov, 2018; for similar approaches). This idea is congenial to the one stressed by Priscila Farias and João Queiroz, who claim that metaphors, in order to become instantiated as icons of laws, "depend on a certain internal coherence;" so in the end, "diagrams [i.e. analogies] may function as metaphors once their use becomes a *habit*" (Farias & Queiroz, 2006: 287-307).

Be that as it may, the issue can remain open without interfering with my own concerns in this paper. For one thing, the study that I present here is concerned with a type of metaphoric representamen, the BPM, which is itself an analogy. Blueprints/plans ("e.g. an architect's drawing of a house;" Houser, 1991: 437) are certainly paradigmatic of the analogies/diagrams subclass within the general family of Peircean (hypo)icons (Farias & Queiroz, 2006: 291). Consequently, whether a metaphor or an analogy is at the onset of the BPM becomes a fuzzy, perhaps even a superfluous question. One way of expressing it is to say that the BPM is based on a metaphoric intuition that takes as its object an analogical kind of sign; or, in other words, it is based on the metaphorical use of an analogy. I do not dwell on this further. Suffice it to say that the most relevant question that I wish to raise is whether the (somewhat ambiguous) kind of epistemic access that the BPM makes available to developmental studies is one that further processes of accommodation might confirm as fruitful.

3 The Blueprint/Plan Metaphor: The Model and Its Critics

Let me start by referring to a particular, highly influential and explicit instantiation of the BPM, namely, that of the Nobel Prize-winning ethologist Konrad Lorenz:

What rules ontogeny, in bodily as well as in behavioral development, is obviously the hereditary blueprint contained in the genome and not the environmental circumstances indispensable to its realization. It is not the bricks and the mortar which rule the building of a cathedral but a plan which has been conceived by an architect and which, of course also depends on the solid causality of bricks and mortar for its realization. This plan must allow for a certain amount of adaptation that may become necessary during building [...] Any such adaptive regulations, however, presuppose at the very least as much information contained in the genetical blueprint as any elements of little or no modifiability do. In other words, the apparatus which makes adaptive modifiability possible is genetically blueprinted itself [...] (Lorenz, 1965: 42-43)

Thus formulated, the BPM introduces, above all, a (conventional) division of the labor model of development, as Susan Oyama aptly makes explicit in the following passage:

Though a plan implies action, it does not itself act, so if the genes are a blueprint, something else is the contractor-construction worker. Though blueprints are usually contrasted with building materials, the genes are quite easily conceptualized as templates for building tools and

materials; once so utilized, of course, they enter the developmental process and influence its course. (Oyama, 2000: 54-55)

The basic parallels that the metaphor suggests are thus the following: (1) genes are relative to the development of an organism as the blueprint/plan is to the construction of a building; and (2) factors other than genes contribute to the developmental process as the construction team does, providing manpower, tools and materials to the execution of the plan.

Before going into a thorough examination, let me stress that the BPM is not as simplistic an image as some critics appear to suggest. As introduced by Lorenz – as well as in Oyama's well-balanced presentation – the metaphor does not really intend the genes to contain something comparable to a flat, a miniaturized version of the ultimate attainable design, whilst also abstracting away, apart from size, other aspects that might freely vary without compromising the expected outcome. The BPM is not a revamped instantiation of the old homuncular kind of preformationism (Maienschein, 2017) for two reasons. On the one hand, as Lorenz himself strives to explain, it is not the job of the blueprint to merely abstract what is essential from what is not, but also to constrain the kinds of suitable locations and materials, the order of events in the realization of the organism, and so on. On the other hand, at least in Lorenz's version, the BPM does not appear to be committed to the kind of isomorphic correspondences that homunculism, in contrast, entails. A blueprint may be a non-isomorphic one – it may be propositional or language-like,² whilst remaining a blueprint. Thus, blueprints are not necessarily mere miniature isomorphic representations of the expected scaled-up end results – the reason for which I believe that psychologist and ethologist Daniel Lehrman's (1970) criticism of Lorenz (1965) is not accurate (in this particular regard).³

That said, it is true that the BPM raises fra-from-trivial issues regarding explanation, intentionality and agency, as aptly synthesized by Susan Oyama:

The point of the blueprint analogy, though, does not seem to be to *illuminate* developmental processes, but rather to assume them and, in celebrating their regularity, to impute cognitive functions to the genes. How these functions are exercised is left unclear in this type of metaphor, except that the genetic plan is seen in some peculiar way to carry itself out, generating all the necessary steps in the necessary sequence. (Oyama, 2000: 55)

² This bring to mind Ruth Millikan's (1984) conception of propositions as "iconic" signals for state of affairs, in the wake of Betrand Russell/Ludwig Wittgenstein's pictorial theory of propositional meanings (Russell, 1910; Wittgenstein, 1921)

³ "It seems to me that there is a fundamental fallacy in the use of the analogy relationship between a blueprint and the structure represented by it to represent the relationship between the genome at the zygote stage and the phenotypic adult. A blueprint is isomorphic with the structure that it represents. The ratios of lengths and widths in the blueprint are the same as those in the structure; the topographical relationships among the parts of the structure are the same as those among the corresponding parts of the blueprint; each part of the structure is represented by a separate part of the blueprint, and each part of the blueprint refers only to a specific part of the structure. It will be immediately obvious that this is profoundly different from the relationship between the genome and the phenotype of the higher animal." (Lerhman, 1970: 34)

Oyama's criticism boils down to the objection that the BPM is a descriptive restatement of developmental processes devoid of any clear explanatory contribution. Indeed, the main two strategies aimed at putting the explanation seal on the metaphor are problematic in that they ineluctably point to the genes showing one or another mark of the cognitive:

- (1) On the one hand, one might opt for the idea that genes display executive powers as in the most literal interpretation of Lorenz's BPM, in that they orchestrate all the doings of the remaining extra-genetic contributors. In that case, the genome is ultimately regarded as an "agentive" entity.
- (2) On the other hand, one might defer those executive powers to the extra-genetic developmental contributors perhaps a more charitable reading of Lorenz. However, in that case, the genome is regarded as an "intentional" entity (Maynard Smith, 2000), the states of which, to be read and executed by said contributors, are "about" some expected kind of full-fledged organism.

Be that as it may, it appears to be clear that the BPM is only apt to come close to an explanatory position at the price of regarding the genes as showing some core marks of the cognitive – see Griffiths & Stotz (2013).

Such strong commitments of the BPM appear to be somewhat relaxed if one adopts a information-based approach and envisions the genome as a representational vehicle, wherein differences stand for differences at different levels (Bateson, 1972; Dretske, 1981). Such a solution locates the genes in a semiotic terrain, with its own mode of existence – "among the most impotent and useless materials imaginable," as Mary Jane West-Eberhard rhetorically emphasizes the urgency of downsizing the kind of agentive/cognitive attributions above (West-Eberhard, 2003: 93).

However, an information-based reading of the BPM is not without its critics. Two families thereof deserve particular attention:

- 1. On the one hand, informationally speaking, there appears to exist no particular justification for singling out the genes from other developmental contributors, including those provided by environment. Inasmuch as genetic and extra-genetic factors co-act and support each other in bringing about phenotypic outcomes, the former are to be regarded as equals in terms of covariation with the latter. According to this criticism, information spreads beyond the genome or, in terms of the BPM, the blueprint extends beyond the chromosomic context.
- 2. On the other hand, another well-known objection to the information-based interpretation of the BPM stresses the fact that if they contain a blueprint at all, the genes cannot represent anything other than proteins. As lucidly expressed by Nobel Prize-winning microbiologist Salvador Luria:

[...] the information represented in the sequence of amino acids is not available to translation; it only serves to generate the shape of the protein and therefore its function. Informationally, proteins are dead-end molecules. (Luria, 1973: 46)

Of course, the information-based model of development may survive this criticism if it is understood that the dead-end character of proteins is such relative to the genes that shape them; nevertheless, the proteins themselves, along with other intra and extra-organismic concurrent factors, can be said to code for differences that make differences at subsequent states of phenotypic organization. If so, however, two significant conclusions follow: firstly, the genome is definitely not a blueprint of the expected kind of fully achieved phenotype since, secondly, the blueprint (if a place is still there for it) is sparsely scattered at different locations throughtout the process (Johnston, 1987; Gray, 1992; Griffiths & Gray, 1994; Oyama, 2000). In the words of Oyama, information follows – rather than guides – ontogenetic paths (Oyama, 2000: 129-157). Thus, according to the information-style version of the BPM, development is informed by successive blueprints/plans at different stages, each blueprint/plan informed by a prior one down to the genomic blueprint for the construction of functional proteins.

In the next section, I aim a different kind of criticism at the BPM, namely, one based on the idea that the BPM does not even properly fit the technical domain from which it is taken. As a consequence, the projection of the metaphor onto the organic realm appears to be fatally flawed and perhaps useless.

4 The Bidirectionality of the BPM: Further Reasons for Questioning the Model

As said, thinking metaphorically entails the projection of entities and relations that articulate a certain domain (S) onto another, more poorly understood one (T). Such a cognitive strategy is a legitimate one provided that those partially known parts of T somehow match aspects of S, prompting the conjecture that a larger match that may exist which would facilitate a better understanding of T. This succinct characterization of "cognitive metaphors" – in the sense of Kuhn (1979) – makes it clear that one of the conditions for a successful application of this kind of eduction is that knowledge about S is solid enough to allow it to facilitate understanding of T. For this reason, unlike other kinds of metaphors, cognitive metaphors in the service of scientific understanding must necessarily exhibit

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⁴ "[...] plans and information [...] have contingent developmental histories. The cognitive-causal models [...] have tended to present these controls as ahistorical (or, rather, as having a phylogenetic history but not an ontogenetic one), which provide no satisfactory way of explaining either species-typical development (maturation) or the manifest flexibility and multiplicity of many developmental phenomena, save the declaration that all contingencies were somehow anticipated, or at least hypothesized, by the DNA. Fate is constructed, amended, and reconstructed, partly by the emerging organism itself. It is not known to anyone, not even the genes." (Oyama, 2000: 137)

the following kind of asymmetry of asymmetry: from the outset, knowledge about S must outstrip that about T. Otherwise, metaphors may rather be a misleading and disadvantageous path to follow.

Considering this desideratum, it appears to be clear that the more symmetrical the domains, the less clarifying the metaphor. As a case in point, one might consider metaphors that can function in both directions – i.e. domains that may assume the S and T roles interchangeably, given that the amount and clarity of knowledge about the corresponding domains is symmetric – or close to symmetric. Susan Oyama – who refers to Campbell (1982) – points out that this was historically the case of the interbreeding of analytical models and nomenclature between developmental genetics and cybernetics in the 1940s. According to this historic narrative, by regarding genes to have a controlling role in the cellular machinery to construct bodies on the basis of pure intuition or images of undeclared provenance, genetics paved the way for the development of systematic models of information processing by cybernetics, which, in time, has in turn provided developmental genetics with all kinds of metaphors. Whilst this could be seen as a case of productive disciplinary interbreeding, it is also indicative of the fact that a sort of explanatory emptiness exists at the heart of these metaphors. As I try to show in the following paragraph, the BPM falls within the same pattern.

Curiously enough, at the same time that architecture provides the BPM to biology (Karatani, 1995), biology is a common source of metaphors for architectural commentators and theorists (Steadman, 2008). The so-called bionic approach to architecture provides a suitable illustration (Costa Cruceiro, 2009, 2010). In bionic architecture, for example, it is claimed that designs are not conceived in the architect's mind exactly as they are later reflected in the blueprints. Of course, the architect must entertain some initial ideas, but what happens, crucially, is that the designer's project grows as a consequence of analogies between her thoughts and all kinds of surrounding information. From these kinds of creative interactions, there emerge three dimensional geometries that are difficult to conceive and construct completely without computerized aid. With the help of the visual outputs resulting from such technical scaffolding, the architect is then able to proceed with her undertaking. Throughout, solutions are chosen according to their calculated structural fitness. Note that, according to this picture, even if the ultimate outcome of such a sequence of creative processes are plotted on a single drawing or plan – a "structure model" (McLachlan, 1999) – the impression that the actual process of construction follows on from a preformed version of the expected final result, reflected in a blueprint, is obviously deceiving. If anything, what the blueprint depicts is a specific stage, and not a particularly early one at that, of the architect's musings, together with all kinds of interactions that she may have while entertaining them. In other words, the blueprint is a retrospective technical account of what has been going on during the creative process up to a certain time, rather than the initial stage of the entire project. The blueprint, of course, will influence the future sequence of events,

but this is so in the trivial, yet commonly neglected sense that every stage attained in a developmental process constrains its subsequent unfolding (Oyama, 2000: 131).

Interestingly, the current penetration of biological metaphors in architecture provides another lesson regarding the limited accurateness of the BPM in illuminating the understanding of organic development, now in relation with the idea of "point of termination" or "steady state" that the blueprint/plan analogy entails. Indeed, the conceptualization of development by use of the BPM suggests not merely of a preordained course of event, but a fixed ultimate outcome. This is again deceptive. As a case in point, Pritzker Architecture Prize-winning Arata Isozaki claims that an ultimate image of a building frozen from change, which occupies a central position in architectural design, is clearly misleading (Isozaki, 2009: 22-23). In his opinion, from inception to completion – two open or fuzzy categories, a building is something that shifts and grows from state to state, its uses may change over time, it may encroach or degrade, its capacities may become exhausted, etc. Buildings are thus (like) organic entities – Isosaki concludes, for "totally unchangeable architecture can only exist in the imagination" (Isozaki, 2009: 22). Like organisms, buildings grow, are responsive to aggressions, and require care, repair, and renovation, while needing to keep functioning at the same time. Thus, according to Isozaki, all things point to the conclusion that the living vitality of buildings is incompatible with a preordained plan conception of architecture – i.e. a frozen, static, or synchronic concept of design, and prefers to defend a powerful idea of "process," which includes an absence of clear points of termination.

The idea that organic development does not entail points of termination is also common in current developmental and evolutionary biology (Minelli 2011), as well as in cognitive branches of biology (Thelen & Smith, 1994; Balari & Lorenzo, 2015; Lorenzo & Longa, 2019). As developmental biologist Alessandro Minelli stresses, if one is to maintain that development corresponds to a particular "segment" of an organism's life, then one must be prepared to admit that the kind of segment concerned is an "open-ended" one (Minelli, 2011). The idea is not a completely new one – but perhaps the increasing credit given to it is, as witnessed by the following pioneering claim of biologist and philosopher Conrad Hal Waddington in the mid-twentieth century:

"To speak of the adult condition as a steady state is to some extent an oversimplification, since developmental change continues at a slow rate throughout adult life, leading eventually to senescence" (Waddington, 1957: 33).

In the end, it seems likely that "development" and "life" are two concepts ultimately doomed to conflate into one, without explanatory loss (Minelli, 2003; Lorenzo & Longa, 2019). Interestingly, in some kinds of organisms (e.g. Cnidaria) there are no clear-cut boundaries between the life cycles of successive generations (Minelli, 2011). All in all, it appears to be the case not just that the concepts of "initial state" and "steady state" are at least unclear, and maybe simply useless, in developmental

biology, but that those of "inception" and "termination" are blurred in many cases as well. All these kinds of conceptual improvements in the field of developmental biology provide metaphors that are inspiring current bionic or bio-logic approaches to the conceptualization and practice of architecture, which inevitably leads us to question of the true role of blueprints and closed plans in this technical domain.⁵

Before closing this section, let me insist that the use of metaphors is heuristically legitimate and useful in science. The point of this section is to warn about the risk of indeterminacy that may follow from the fact that two domains may be serving as the source of metaphors for each other, as is the case of the ones dealt with in this paper: the technical domain of architecture has been approached by developmental genetics in its search for illuminating analogies, whilst developmental biology in a broader sense (encompassing genetics, but not limited to it) has been focused om by architects for the same aim. Not surprisingly, with conflicting results.

Technical or scientific domains, like architecture or developmental biology, are lively areas of research, more dynamic and long-lived than the images that relevant achievements in these areas may have empowered and, eventually, become emblematic points of reference for other domains. However, the longevity of an image may be tantamount to a sort of afterlife in its original domain. It is true that blueprints continue to be used instrumentally in construction affairs, but it appears to be clear now that they do not provide a correct conceptualization of the real dynamic process leading from the architect's creative activity to the moment when the building is occupied. Looking for illuminating metaphors to help understand their own field, some architects have focused on the flesh and blood or organic developmental processes as being currently conceptualized by some offmainstream developmental biologists, freed from the constraining impact of the BPM. For the former, the complex, unbounded and ever-changing kinds of processes inspected by the latter, with abundant contingencies yet confidently leading to robust states of organization, offered a good alternative image to one which was too much centered on static blueprints. Meanwhile, a broad sphere of mainstream developmental biology — mostly, developmental geneticists — remains anchored in the old BPM idealization, taking for granted not merely its heuristic value, but its truth (Robert, 2004).

The Biosemiotics of Development

The discussion thus far should have made it clear that the BPM is neither accurate nor helpful in order to deepen an overall understanding of the development of living beings. However, it might be the

⁵ A questioning that may perhaps be extended to the very role of the architect. For an illuminating starting point of reflection, see Rudofsky (1964).

case that a small, yet crucial portion of development, namely, that leading from DNA to the "informational dead end" of proteins is based on a sort of semiotic link, for which the BPM may still be both accurate and helpful. Furthermore, the idea that the stages of a single developmental process might be read as informing each next successive stage might also be felt to be a way of rescuing the heuristic and conceptual value of the BPM. The next two subsections discuss these stances in turn.

- 5.1 Do Proteins Mark the Boundary Between the Semiotics and the Physics of Development?
- An affirmative answer to the question above is defended by Dan Faltynek and Ludmila Lacková, who claim that the BPM is a correct conceptualization of the role of proteins as the building blocks of the organic:

The function of proteins can be described metaphorically as blueprinting/modelling of the amorphous unsegmented physical world. Proteins handle their specific physical conditions by shaping them: the physical interaction of the protein is mediated by its shape (and not by stereochemical interactions) which means that it is not completely physically direct. This is the reason we treat proteins as signs. (Faltynek & Lacková, 2020: 14)

From the fact that the primary structure of proteins, in turn, "comes from a linear string which is coded by a genetic code and stored in DNA," they further conclude that DNA/proteins comprise "the semiotic part" of a developing organism (Faltynek & Lacková, 2020: same page). I do not believe that Faltynek and Lacková's thesis is as straightforward as it may appear to be, so allow me to put forward my arguments.

An important step in Faltynek and Lacková's argumentation is the attribution of a "protoicon" status to proteins, where the "proto" specification signals that proteins relate with their objects in the absence of any Thirdness (i.e. interpreter/interpretant entities). In this, they follow suit with Eco (1999) and Sharon and Vehkavaara (2014), among others. Being icons, the proteins' status as signs must be anchored to their Firstness – i.e. their own physical properties. However, this is not enough to grant a semiotic, rather than physical, character to their putative role as signs. Thus, following the Peircean orthodoxy, Faltynek and Lacková (2020: 8) acknowledge that semiotically speaking, Firstness is derivative ("cannot exist independently") of Secondness ("the monad arises only from being separated from the dyad"). In other words, it is only as a consequence of their relation with their objects (i.e. certain shaped physical segments; see above) that proteins can be deemed primary or proto-icons. Summing up their position, proteins blueprint/model certain organic segments – thus, proteins are *icons*, and they do so on the grounds of their physical properties alone (proteins are *proto*-icons), without the need need for semiotic intermediaries or interpretants. Let me show now why I find this argument flawed.

To start with, it is important to stress that even if the relation between proteins and body segments is not an interpretant-mediated one, nor it is an immediate one. Thus, if the reason for declaring it not properly semiotic is the lack of the relevant type of intermediaries, my claim is that in order to decide what kind of relation it belongs to, one must focus on the actual kind of mediation that exists between proteins and body segments. If anything, the "proto" or "primary" qualifications are tentative ways of labelling this search for a correct conceptualization. However, the addition of "semiotic" to those morphs is misleading and, perhaps, based on an unmotivated preconception, for a dynamic process does actually unfold between the primary structure of a protein (its amino acid sequence) and its interaction with an as yet amorphous physical segment (as in cell specialization), which is through and through based on stereochemical interactions. Note the following three crucial facts:

- (1) It is the chemistry of amino acid side chains that has a critical impact on the protein's unique three-dimensional shape due to their bonding properties.
- (2) The ultimately, though not completely unmodifiable, shape that a protein attains after some other alternative configurations have been tested is normally the most energetically favorable one. Interestingly, this appears to resemble the evolutionary aspect of interpretation as defended by Peirce, eventually leading to (relatively) fixed or frozen interpretants. Nevertheless, the process is again due to stereochemical interactions, such as the influence of thousands of not covalent bonds and chemical forces between the protein and its environment.
- (3) Proteins need to protect themselves from the intromission of other macromolecules dispersed in the cytoplasm capable of interacting with them. For this important defensive mission, proteins benefit from the help of other proteins (chaperon proteins), which surround and sequester them until folding is over.

Taking all this into consideration, it appears to be clear that the proteins/cells relation is neither an immediate one (as should be the case of primary or proto-iconicity, according to its supporters) nor one mediated by interpretive chains (as in the case of iconicity proper). It is one based on stereochemical interactions;⁶ i.e. not one that functions as if guided by a mental interpreter (as in the case of icons), nor one which functions according to a "key and hole" principle (as in the case of putative proto-icons). Proteins, routinely referred to as the basic "building blocks" of life, are not "biosemiotic" building blocks.

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⁶ *Mutatis mutandis*, the argument also runs for the case of the patterning role of DNA relative to proteins. As stressed by Paul Griffiths, "the proximal effects of DNA are uniquely determined by physical laws" (Griffiths, 2001: 402).

In order to avoid this objection, one may resort to Marcello Barbieri's contention that proteins are nevertheless signs ("representanda"), attending to the intermediation of a "code/codemaker" between the protein sequence and the cell answer (Barbieri, 2009). In this way, Barbieri claims to be avoiding the inconveniences associated with the "mental" connotations of the idea of interpretation. In a nutshell, Barbieri thinks that the triplet-based matching system between codons and specific sequences of amino acids is not due to "objective chemical properties," but to "codemaker-dependent properties," as a "different codemaker would arrange the amino acids in different ways, which shows that the sequence of a protein is only one of the possible 'meanings' that could be given to a string of nucleotides" (Barbieri, 2009: 22):

Different code makers could scan it [codons] in different ways. If the nucleotides were scanned two-by-two, for example, the sequence of codons would be totally different. (Barbieri, 2009: same page)

As a matter of logical possibility, the claim that "codes" different from the three-by-three scanning system exist is perhaps correct. Nevertheless, as an empirical matter, the triplet-based system is universal – Barbieri (2009: 28) is not unaware of this fact – and, arguably, for good physiochemical reasons, rather than for convention. For example, Pavel Baranov and coworkers conclude that "the length of codons in the genetic code is optimal, as three is the minimal nucleotide combination that can encode the twenty standard amino acids" (Baranov et al., 2009: 1). Thus, it is the conspiracy of the actual amino acids available and an principle of economy that appears to solve the case, which I consequently regard as an "objective" chemical problem solved by "objective" physiochemical laws. Moreover, generally speaking, it is not even clear that the logical possibility of alternatives accounts for the code-derived, meaningful character of some kinds of relation: e.g. does allelic variation within genetic pools, for example, turn differential reproduction into a case of semiosis? Indeed, according to Barbieri's point of view, such an attribution would regard it as a meaningful phenomenon – without any explanatory gain for the theory of natural selection. I believe, in contrast, that such a conclusion would probably but contribute to the confounding idea of Natural Selection as a kind of mind-governed phenomenon (Fodor & Piattelli-Palmarini, 2010).

Note that Barbieri's claims have to do with the production of proteins from messenger RNAs as a case of what he refers to as "manufacturing semiosis" (semiosis which brings into existence a new thing), which, once accomplished, paves the way for further processes of "signaling semiosis" (semiosis which reorganizes pre-existent things), ultimately responsible of different kinds of cellular specializations. My counterargument is, in a nutshell, that the kind of "contingent" quality that

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⁷ Indeed, John Maynard Smith appears to have entertained such an idea in one of his moods. Nevertheless, the idea is but one among his ever-changing musings in his efforts to endow genes with some kind of prominence in development and evolution (Maynard Smith, 2000).

Barbieri appears to deem the mark of the "code/codemaker" category is not one capable of introducing an ontological divide between chemistry and semiosis, and that the processes that he describes are physiochemical through and through.

Let me also stress that even if one is willing to accept that between proteins and physical segments there exists a sort of key/hole, not interpreter/interpretant-mediated physical relation, or even non code/code-maker one, regarding which "shape" happens to be the relevant parameter or magnitude, this is not enough to guarantee has the relation has a (proto) semiotic character. The reason is quite straightforward: the relation does not obey to Secondness, to start with, inasmuch as, say, a specifically shaped kind of cell is "one entity" with the proteins concerned. In other words, there is not a dyadic relation between proteins as representanda, on the one hand, and shaped functional cells as objects, on the other hand, but rather they are part and parcel of a single dynamic object – i.e. a unique, indivisible Firstness. In other words, it makes as little sense to ascribe an iconic status to proteins as to the structural frame of a building. Perhaps one can read them as blueprints of cells or buildings, respectively, but they are component parts thereof – i.e. not parts of the map, but parts of the territory itself.

In order to conceptualize these kinds of cases, Ruth Millikan's "natural sign" category could maybe fit the bill, but it is worth stressing that the distinctive feature of this "kind of thing" is that they "could be used" by an interpreter in a way that parallels how she/it would use an established "intentional icon" (Millikan, 1984: 118-120; on natural signs, see also Deely, 2016; Favareau, 2007). It is thus a category that covers almost everything around and, cosenquently, of little conceptual value. Alternatively, one may be tempted to conceptualize proteins as Millikan's "intentional signals," which constitute a primitive approximation to fully articulated "intentional icons" in her biosemiotic framework (Millikan, 1984: 116-118). According to Millikan, icons proper relate with other familial iconic devices, which vary in certain aspects whilst sharing others, this allowing them to capture and match relevant differences of their objects. However, she is open to attributing a primitive kind of natural intentionality to certain signals, which she exemplifies with the flowing of adrenaline and other chemical messengers, which occurs at a particular time or at a place, or both. Thus, she explains, they function as a whole (i.e. independently of any clear-cut variable/invariable internal divide) as signals to ready other parts of the body for strenuous activity (Millikan, 1984: 116). According to Millikan's view, the substance as a whole may be equated to the invariant part of an icon proper, and the specific time/place to the variant part. Proteins might fit into this category of intentional signals, were one to feel tempted to see parallel between its primary structure and an invariable chemical unit that occurs at a particular position/time – namely, the one that instigate transcription, so cells specialize accordingly. However, such a parallel is not accurate, inasmuch as the proteins' role is not merely informative, but formative. They do not announce what is to be done next, but rather instantiate it directly.

Going back to the kind of approach endorsed by Faltynek and Lacková, it might perhaps fit Peirce's efforts towards establishing a line of evolutionary continuity between the brute Secondness of pure physical interactions and the full-fledged Thirdness of semiotic phenomena, via a kind of Thirdness *in propecto* or *in futuro*, which he conveyed to those physical interactions whose outcomes were not immediately interpretable, yet not exclusively physical – e.g. for exhibiting the marks of life (Deely, 2016). One may contend that proteins belong to such a kind of evolutionary chain. However, this does not grant them semiotic character – I would say that, on the contrary, it stresses their "pre", rather than "proto," semiotic nature.

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5.2 Development and the Flow of Information

Whilst Faltynek and Lacková appear to feel confortable with the molecular dead-end of semiosis in development, many authors support the idea that development is a thorough semiotic process, wherein information is captured, processed and put into developmental work on a sequential basis. Prominent among the supporters of the pivotal role of information in developmental processes are supporters of "developmental systems theory." One of the core contentions of this theory is that development is to be conceptualized as the ontogenetic unfolding of the successive informational stages that lead to organic forms apt to carry on cyclic iterations of the same kind of process (Oyama, 2000; Oyama et al. 2001; Griffiths & Hochman, 2015). Roughly speaking, the concept of "information" that is entailed in this theoretical framework boils down to the idea that relevant differences in a given state of organization are accessible to a certain receiver, which processes them according to intrinsic parameters to give rise to a new organized state, in which new differences match the original ones.⁸ Differences make difference – approximately paraphrasing Gregory Bateson (Bateson, 1972). While the idea of a continuous flowing of information appears to be straightforward as a schematic approximation of developmental processes, a closer inspection reveals that it is not so clear that the the insights offered by these kinds of systematic approaches centered around the concept of "information" go deep enough into the flesh and blood of organic development.

It is important to bear in mind that "information," in the context of the present paper, is itself a metaphor which comes to the rescue of the BPM. Actually, as observed by Mark Pharoah, the idea of an "information system" is twice a metaphor, for not only "is information" used metaphorically in

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⁸ Paul Griffiths observes that "information," as applied in developmental studies, "is a way to talk about correlation" (Griffiths, 2001: 395).

biology (Griffiths, 2001; Levy, 2011; Longo et al., 2012; Sarkar, 1996), but so is "system" is, which metaphorically introduces the idea of an organized or meaningful kind of complexity (Pharoah, 2020: 314). Be that as it may, the theoretical value of metaphors is not what is at stake; not even whether one may resort to new metaphors in order to reinforce old ones. The real concern of this section is whether the image of bits of information flowing through successive stages of developmental organization, somehow injecting a sort of developmental memory into each newly attained stage and impelling the resulting wholes to further organizational accomplishments, is a theoretically reinvigorated persona of the BPM. In line with such a restatement, the BMP acquires an extra (temporal) dimension, which may be captured by transitions likes those of a state diagram that depict the relevant inter-stage mappings. States may in turn be thought as static maps (or blueprints/plans), which stand for the more or less transient/lasting conditions of steadiness that a living entity goes through. In the words of John McLachlan, the flow of information metaphor may be thought of as an improved version of the BPM – at the onset, a kind of "structure model" – by means of an enhanced "process model" (McLachlan, 1999).

A remarkable virtue of this extended metaphoric approach to the BPM is that the furtherance of development is now captured by the specific kinds of transition which follow from the accomplishment of a certain state of affairs. Moreover, inasmuch as it is assumed that diagrammatizations function as generalizations, which range over an indeterminate number of variable factual conditions, the specifics of which may have a far from trivial impact on outcomes, the BMP can be said not to be bound to a deterministic interpretation of development. Thus, the multiplicity and non-linearity of causes make development a process which is, in a way, non-deterministic yet, at the same time, reliable and largely predictable. This is an aspect of development which requires factoring in and incorporating elements of reinforcement, overlapping, redundancy, non-deleterious bifurcations, etc., into diagrammatizations.

All that said, the flow of information metaphor is not without its own weaknesses. It is important to evaluate whether these weaknesses are merely indicative of the point at which the epistemic role of metaphors comes to an end and hardcore research must lead the way in conceptual accommodation, or whether they point to some intrinsic shortcomings of the metaphor as such, as in the case of the plain BPM. I shall briefly concentrate here on two particular issues, which I shall refer to as the "stage problem" and the "realization problem."

As for the first issue, I shall simply emphasize some claims of developmental biologist Alessandro Minelli in the wake of seminal observations made by C.S. Hickman, himself an expert in the study of larvae. According to the latter, stages are in the eye of the beholder – the biologist, in this case – for stages are ultimately conventional demarcation points to faciliate the expert's task – thus,

artefacts (Hickman, 1999: 7). In agreement with this view, Minelli argues that "the basic continuity of development makes all such distinctions arbitrary" (Minelli, 2003: 57), and he stresses that "the boundaries separating developmental stages along the temporal axis are generally less clear-cut than the boundaries between organs in an animal's body architecture" (Minelli, 2003: 60). When one considers phases of relative stability in an animal's life history, it is important to bear in mind that even stability is, in such cases, but the lasting effect of sets of *synchronous* factors. In the end, Minelli proclaims "the primacy of time," as the axis to be privileged in developmental explanations, whilst allowing for the heuristic participation of categories referring to discrete segments therein, with the proviso that they are accompanied by corresponding "operational definitions" (Minelli, 2003: 56-57).

Thus, while the plain BPM is obviously barred by these kinds of considerations, the metaphor of a flow of information, which maps prior stages onto subsequent ones is not, an consequently may provide bona fide epistemic access to developmental inquiries. Obviously enough, one cannot lose sight of the heuristic role of discrete slides chosen by a given system of periodization. This is an aspect of the metaphor that should be ultimately overcome by a further accommodation of the explananda to the unbounded continuity of development.⁹

As for the "realization problem," let me simply stress that the kinds of functional diagrammatization that the flow of information metaphor inspires belong to those that have historically offered support to the thesis of autonomy for the special sciences (Fodor, 1974). In a nutshell, diagrams point to a kind of formal causality which appears to be compatible with alternative material bases of realization (Polger & Shapiro, 2010). In this regard, biology may be seen as a transitional case between what is routinely considered "hard science" (e.g. physics) and what is considered "special science" (e.g. economy): on the one hand, the biologist's jargon largely overlaps with or easily translates into that of chemists and physicists; yet, at the same time, biology also appears to have an ineliminable/unreducible historical component (Gould, 1989; Mayr, 2004). In this context, it may be tempting, particularly for those who take the kinds of metaphors thus far reviewed at face value, to conclude that the "specialness" of biology extends beyond its partly historical character to its partly semiotic nature. This is a difficult issue that would deserves a monographic

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⁹ This is a matter with far-reaching philosophical consequences. To refer to just one of its multiple ramifications, Hume observed that secular debates on nativism have a lot to do with taking too literally an arbitrary boundary between prenatal and postnatal life. In his own words:

For what is meant by 'innate'? If 'innate' be equivalent to 'natural', then all perceptions and ideas of the mind must be allowed innate or natural, in whatever sense we take the latter word, whether in opposition to what is uncommon, artificial, or miraculous. If by innate be meant 'contemporary with ours birth' the dispute seems to be frivolous; nor is worth while to enquire at what time thinking begins, whether before, at, or after our birth (Hume, 1748/2000: 12, note).

treatment. Nevertheless, I will try to compress into a few words my own view on the matter, in line with the ideas that I have defended in the rest of this paper.

My claim, in a nutshell, is that the flow of information is an apt metaphor in order to gain adequate epistemic access to the complexities of development. In this sense, I believe that it continues to be worth pursuing. However, I also believe that the thesis of multiple realizability, which appears to be part and parcel of it, is not a price that should be paid for embracing the metaphor. Generally speaking, one should never pay such a price for illuminating metaphors, the face value of which fades away as soon as they have fulfilled their specific epistemic role – i.e. epistemic access. Having reached that point, some entailments of the metaphor – e.g. the multiple realizability of funcional schematizations – become a ballast that researchers can (must) safely rid themselves of. In my my view, this is clearly the case of the flow of information metaphor in relation to developmental biology: once the metaphor has facilitated access, accommodation cannot refer but to the flesh and blood of actual living entities. As Fred Dretske strived to clarify: "the informational relationships between *r* and *s* must be distinguished from the system of causal relationships existing between these points" (Dretske, 1981: 26). I consider that it is indisputably the case that these latter kinds of relationship constitute the ultimate aim of developmental biology.

Sure enough, developmental processes and their outcomes are conceivably replicable – even factually, in some cases – by using alternative materials, even synthetic or inorganic ones. However, far from proving the specialness of the theories of development – or the primary semiotic character of the flow of developmental information, the picture is rather one that confirms that the aims of biological explanations must directly target the actual material bases of organic causation, even if inspired by the goal of discovering alternative succedanea, which obviously entails the former.

5 Concluding Remarks

- The conceptual repertoire of semiotics is undeniably an intellectual treasure. Historically, its richness has not only served to clarify/explain concerns proper of its own subject matter, but to inspire solutions in other fields of scientific specialization, carrying out the important role of facilitating epistemic access to otherwise intractable or recalcitrant issues. When fulfilling such an epistemic role, semiotic concepts must carefully respect the following premises:
 - (1) semiotic metaphors should not distort their target domains from the start; and
- (2) they should not remain inadvertently active once their heuristic role has been fulfilled not, at any rate, without a deliberate effort to take into account their potentially distorting effects.

In this paper, I have evaluated some metaphors coming from the semiotics of architecture and information/communication theory as applied to the theory of organic development, namely, the blueprint/plan metaphor and the flow of information metaphor. My conclusion is that they exemplify situations in which premise (1) and premise (2), respectively, are not respected as they should be in a framework of metaphoric conceptualization.

The conceptual interbreeding between semiotics and biology demands special care, for the duties of these disciplines partially overlap. Indeed, these are the very foundations of the field of specialization currently known as biosemiotics. There exist general consensus regarding the attribution to biosemiotics of those areas of the behavior and functioning of living entities that rely on interpretive processes mediated by nervous systems is rather consensual. In contrast, it is not so consensual that organic processes conducted at lower levels of analysis may be so regarded in the same way. In this paper, I have claimed that some biological processes that routinely – sometimes, rather uncritically – receive this kind of treatment actually rely upon the misuse of semiotic metaphors along the lines of (1) or (2) above.

Nevertheless, it is my conviction that, far from a loss for biosemiotics, the conclusions reached in this paper are but good news for the field, for clearly discerning what constitutes a biosemiotic process from what does not is a crucial step, in my opinion, towards avoiding the ghost of panbiosemioticism and to securing the credibility of the discipline. As aptly put by Felice Kruse, commenting on Peirce's own panbiosemioticist metaphysical musings:

In order for the concept of sign to be at all intelligible, we must make recourse to elements that are at least relatively extrasemiotic. [...] There must be, then, respects in which things are signs and respects in which they are not, and an unqualified pansemiotic position would not be able to account for this. (Kruse 1990: 220)

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To be inserted

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