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REPLY TO THE COMMENTS ON  
“NATURAL SELECTION  
AND SELF-ORGANIZATION:  
A DEEP DICHOTOMY IN THE STUDY  
OF ORGANIC FORM”

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The internalist/externalist dichotomy I defend is not centered on the relationships between the organism and its environment as some authors have interpreted it. According to them, the dichotomy refers to the existence of a close relationship (externalist) or isolation between the organism and its environment (internalist) <sup>1</sup>.

From the internalist perspective, the organism is in a close relationship with its environment by definition (i.e., as an entity that maintains itself by the flux of energy and matter: a dissipative structure; Prigogine and Nicolis 1971). However, it has been argued that this relationship could also evolve, being less constrained at the origin of multicellularity and more so as developmental systems become canalized over the course of evolution (Newman 1994; Newman and Müller 2000). The term “internalist” makes reference to the nature of the originating organizing principle of biological form (in true “externalism” the originating organizing principle is imposed from without, regardless of how it may become inscribed in the organism) <sup>2</sup>. I argued that this diachronic concept of “internalism” in the externalist/internalist dichotomy enables the understanding of the problem of organic form from its origin in the eighteenth century to the present. This helps us to appreciate why development occupied a central role at the origin of biology, when and why it was lost, and how it has been recovered in what is called physicalist evo-devo <sup>3</sup>. It also provides insight into some other debates that have revolved around it, such as mechanism/vitalism and reductionism/non-reductionism <sup>4</sup>.

In what follows, I will discuss the externalist/internalist dichotomy based on the main criticisms raised by commentators, hoping to provide some answers to them.

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As indicated above, the explanation of form generation (morphogenesis) was a problem in biology from the very beginning of its emergence. Because physics took a naturalistic turn before biology did, in the elaboration of a science of life the strategy was to import the physical framework at that time, primarily the Newtonian framework<sup>5</sup> (Depew and Weber 1996; Newman and Linde-Medina 2012). If matter is inert, it does not actively respond, it can move by changing its position according to a configuration of forces, but nothing can be spontaneously generated from a homogeneous parcel of matter<sup>6</sup>. Thus there were two options: 1) denying that development was a real process of form generation but rather the unfolding, by internal mechanical forces, of a pre-existing structure (preformationism), and 2) arguing that something else was operating in the embryo (epigenesis).

This represents the origin of the externalist/internalist dichotomy for the study of organic form. Preformationism would be on the externalist side. The mechanical forces that unfolded the *homunculus* were internal, but the organizing factor was external: the final form was not explained by these internal forces (they did not have causal power), it was created by God. Epigenetic theory fell on the internalist side of the dichotomy because the *vis essentialis* was the force responsible for organizing matter. The organizing factor was internal. Epigenesis could be divided into material or non-material depending on whether the inner force was conceived as a material, but not mechanical, force (called an organic force), or a non-physical substance.

Certainly the Cuvier-Geoffroy debate was complex since, as pointed out by Appel (1987), it was not just a debate about anatomy. In mentioning this, I wanted to introduce the form-function dichotomy that originated at such time and continued in biology after this debate (Amundson 2007)<sup>7</sup>. The preformationism/epigenesis debate about the problem of form generation was carried out during the pre-evolutionary era; the form-function dichotomy in an important sense represents the same debate in an evolutionary framework. Specifically, when it is asserted that form must be explained in functional terms, the organizing principle is external. Form in this case would be designed—or forged—by God or by natural selection to meet functional demands. It would be embodied in some internal structure, but it would be a God's design or—in an evolutionary scenario—the product of past selective events. This internal structure would not entail a different—internal—cause: “most externalist positions in no way ignore the order of inner matter or internal causal mechanisms; externalism *only* denies significance to internal factors as primary causes of biological form” (Ramírez-Trejo, et al. 2012, emphasis added).

According to Appel (1987), Cuvier defended preformationism, but he was not a mechanist because he also defended the existence of an inner

force. However, this inner force seemed to not have causative power in form generation:

Cuvier sided with the preformationists, but he avoided all discussion of preformation in his works. Rather, he argued that the subject of generation, “the most profound mystery of the natural sciences,” ought to be considered outside the domain of scientific inquiry. Germs were only to be found in nature, already formed and already possessing that “mouvement de tourbillon” that constituted life (Appel 1987, p. 50).

If germs were already preformed, this inner force would act either as a mechanical force or as a soul, but not as an internal causative factor of biological form.

Darwin’s pangenesis fell in between preformationism and epigenesis; the egg did not contain the whole organism but *gemmules* of its parts. Still some internal organizing factor was needed to explain form generation. Development—the “inner force” or the law-like component of form—disappeared from the explanatory picture when the *gemmules* were replaced by genes and it was argued that genomes contained a program for generating the organism—coming back to preformationism in a new guise. As in the case of preformationism, the genetic program operates internally in the cells, but the form it gives rise to is entirely, or principally, the result of natural selection, an external organizing factor.

When the problem of form is “solved” by eliminating the “inner force” and reducing development to genetic programs, natural selection operates as the creative factor of biological form. In this fashion, biology has been converted to a historical narrative where the inert matter of the eighteenth century mechanistic framework has been deeply assimilated. As a result, organisms are as passive as the matter that forms them: “Surprisingly, in spite of language like “struggle for existence”, for Darwin, organisms are far more passive and less tenacious in their grip on life; they simply vary—spontaneously. Natural selection does all the work of adapting populations of descendants to their changing circumstances” (Lenoir 1987, p. 27) <sup>8</sup>.

I take Darwinism to be a theory of substance regarding the problem of form because when the dynamical physical processes that take place during development do not have causative power (i.e., the cause of pattern is ruled out) it is assumed that form is the direct manifestation of the *composition* of the embryonic tissue, i.e., the set of cell type identities at specific stages of development (e.g., Mallarino, et al. 2011) <sup>9</sup>.

The view that form precedes function would imply that form obeys some organizing principles independently of its functional role. When form is arbitrary (there are no internal organizing factors) the only avail-

able explanation for the existence of a structure is the functional role it performs in the life of the organism. This position leads to some philosophical problems, such as the controversy about selected traits and free riders, since in the later case the existence of the trait is not due its functional role (Fodor and Piattelli-Palmarini 2010). If there exist internal principles of morphogenesis, a structure would possess a *rational* cause for its existence, regardless of its biological role. Many, or even most, structures would not be molded by natural selection so as to be fit with respect to environmental conditions; any generated form would potentially possess functional properties. Once it is generated, it could be spread by natural selection (i.e., differential contribution to the population) if it proves useful in meeting some functional demand—perhaps even in a new niche (Odling-Smee, et al. 2003)—but the explanation of its form would reside in the internal organizing principles governing its generation (Linde-Medina 2011) <sup>10,11</sup>.

Postulating the existence of some organizing principles is not the same as positing an “inner force.” For a materialist science such principles should emerge from the intrinsic physico-chemical properties of living matter, and that matter should be conceived as an active agent of its own organization <sup>12</sup>. Geoffroy and Owen, working on adult anatomy, tended to think of *Bauplans* as static forms, similar to Platonic ideas. In this case, the organizing principle is also external to living matter; form being imposed on it from outside <sup>13</sup>. Goethe’s dynamical conception of form would seem closer to the modern physicalist perspective (Newman, et al. 2006), except for the fact that his *Bildungstrieb* was conceived as an idea that guides development, operating internally but not intrinsic to living matter: “Over development, he [Goethe] says elsewhere, there presides a formative force, a *bildende Kraft* or *Bildungstrieb*, which works out the idea of the organism. Living things, in his view of them, strive to manifest an idea” (Russell 1916, p. 50).

However, this recourse to idealist concepts was probably unavoidable due to the undeveloped state of embryology and physics at this time. According to Lenoir (1987): “...[It] is true that Goethe himself referred to the types as ‘pure ideas’ of nature somewhat in Platonic fashion. But this is in part a result of the manner in which they were to be discovered... but they are not for that reason less really present in nature” (p. 23).

New advances in developmental genetics and the physics of soft, excitable media now permit the generation of *Bauplans* and body parts to be accounted for in a scientific, non-essentialist fashion (Newman and Bhat 2009; Newman 2011a), relinquishing the need by earlier internalists like Goethe to posit that ideal plans underlie morphology <sup>14</sup>.

Thus, the internalist/externalist dichotomy in its historically <sup>15</sup> evolving forms would be represented on the internalist side, by the *vis essentialis*

(epigeneticists), *pouvoir de la vie* (Lamarck) and *Bildungstrieb* (Goethe), *entelechy*<sup>16</sup> (Driesch) and self-organization in its modern physical, (i.e., materialist) sense, and on the externalist side, by the mind of God and natural selection. With respect to the relation between physics and biology, the reductionism/non-reductionism and internalist/externalist dichotomies undergo a non-arbitrary permutation. The internalist side was non-reductionist until the advancement of physics allowed the rigorous study of self-organization of soft, chemically and mechanically excitable materials of the mesoscale (Mikhailov 1990; de Gennes 1992) such that the “inner force” could be characterized scientifically. The externalist side was reductionist until the externally created *homunculus* and the mechanical forces that unfolded it were replaced by the genetic program for development, thus becoming a non-reductionism (Newman 1988; Newman 2012b). The explanation of relevant aspects of biology by the new physics would at the same time represent a rejection of reduction of development to genes and their interactions<sup>17</sup>.

Some commentators have found it contradictory that I criticize the importation of Newton’s framework to the study of biological form at the same time as I defend the physicalist evo-devo developed by Newman and co-workers<sup>18</sup>. But these moves are entirely consistent. I am not, by any means suggesting the exclusion of Newton’s mechanical laws from the study of biological form; they are part of the physicalist perspective (e.g., the DPM based on cell-cell adhesion: ADH). And according to other, related physicalist models, mechanical stresses in an excitable medium can generate the first stage of development and other organic forms (Belousov 1998). What I am suggesting instead is to abandon the idea of organisms being composed of inert, arbitrarily moldable matter that has led to the concept of a genetic program for development that arises from adaptive, incremental changes.

Strangely, some who advocate reductionism of biology to genes seem uncomfortable with contemplating how genes and their products actually act in the generation of form, that is, by mobilizing physics. This could be justified in the past, when physics was not developed enough for tackling the problem of organic form (Rosen 1991; Roth 2011) but now the situation is the contrary: rooted in the idea of inert matter, the organism is conceived as an automaton no more “alive” than any man-made artifact. The new physics would return to living matter the ability to actively participate in its own organization, its material “inner force.”

#### ACKNOWLEDGEMENTS

I owe warm thanks to Fernando Zambrana, the editor of *Ludus Vitalis*, for giving me this opportunity and for his cordiality. I thank all of the commentators for participating in this debate. And I also thank Stuart Newman for the inspiration his work has provided. This work has been funded by the European Commission (Marie Curie postdoctoral fellowship PEOF-GA-2008-219676).

#### NOTES

- 1 For example, G. Folguera (2011) writes: “Tanto la idea de que un determinado carácter es objeto únicamente de presiones selectivas, como la no consideración del ambiente en el estudio de los fenómenos del desarrollo, se basan en una serie de supuestos que deben necesariamente ser contrastados” (p. 330).  
Either the idea that a specific trait is uniquely the result of selective pressures or that the environment is irrelevant to development, are based on assumptions that should be contrasted (my translation).  
And Dressino (2011) writes:  
Therefore, the idea that the internalism/externalism debate itself might extend the synthetic theory is meaningless. Because who would call into doubt that an organism is the resultant of self-organizing forces facing responses to environmental pressures? At present, the existence of a constant two-way exchange between organisms and their environment is widely recognized, thus bringing an end to the internalism/externalism controversy (p. 320).  
L. Ramírez-Trejo, et al. (2012) make this position explicit when they write: “internalism/externalism is a debate on the horizontality of explanation: it describes the interactions between a system and its environment”.
- 2 As pointed out by E. Andrade (2011): “The essence of SO is that systems’ inner structure emerge without explicit instructions given by pressures or constraints from outside the system. There is nothing external that imposes its form” (p. 298).
- 3 To my knowledge, the DPM framework (Newman and Bhat 2008; Newman and Bhat 2009) represents the first explicit attempt to combine genetics and physics in the comprehensive study of morphogenesis and pattern formation, allowing a true integration of development in the evolutionary explanatory picture.
- 4 I emphasize that I made reference to reductionism in relation to a model for development, not to reductionism as a model for describing relations between sciences. I clarify my view about this other dichotomy in this reply.
- 5 What was imported to biology by preformationists, and later by Darwin, was Newton’s conceptual framework, not Newton’s formulas.
- 6 The problem of form generation was first observed in embryology but it has not been exclusively a biological problem, but rather a general problem in the natural sciences (see e.g., Roth 2011).
- 7 My clarification about the Cuvier-Geoffroy debate and my view of Darwinism as a theory of substance (see below) is principally addressed to L. Ramírez-Trejo, et al. (2012).
- 8 This view contrasts sharply with the idea of living beings as self-organizing systems: “Consequently, evolutionary theory cannot rely exclusively on the

preservation by NS of functional structures that have proved to be successful, but also on the notion of organisms and species as self-organizing systems that emerge, vary, develop, ripe, reproduce, stabilize, decay and die" (Andrade 2011, p. 308).

- 9 I realize that my sense of the term may not be the one typically used in the philosophical literature.
- 10 I do not deny that natural selection can occur; what I reject is its role as the creative factor of biological form. As Andrade (2011) writes: "The external pressure due to scarcity of resources only defines the frequency distribution of realized morphologies, but it does not create them" (p. 298). (This paragraph is principally in response to G. Caponi (2011), G. Folguera (2011) and J. Riera and A. Moya (2011) regarding their views on the role of natural selection in evolution.)
- 11 As pointed out by S. Newman: "Where form generation is concerned, the way genes 'act' is precisely via the physical processes of self-organization they mobilize." Thus, genes might make organisms look different each other, but why they do so cannot be explained in terms of genes. The explanation of form would reside in the physical principles governing development (Newman 2012a).
- 12 This idea of living matter is in opposition to the Aristotelian conception defended by A. Aranda-Anzaldo (2012) where matter is essentially passive and form is imposed to it from without. This conceptualization leads Aranda-Anzaldo to conceive attractors as abstract entities that would give form to passive living matter, and to postulate a "real virtuality" for understanding biological organization. In my view, attractors more accurately represent mathematical descriptions of the intrinsic behaviors of complex systems.
- 13 Following Webster and Goodwin (1982), I was inclined to think of Cuvier and Geoffroy as "internalists" but now I think this is not strictly correct.
- 14 My defense of the "form first" scenario is not in contradiction to Salthe's claim that "we follow Cuvier's view that form follows function, and we note that all dissipative structures function, from the universal point of view, to mediate the dispersal of energy" (Salthe 2010, p. 227). I take this to mean that the "universal point of view" refers to final causes of form, i.e., the attainment of universal thermodynamic equilibrium.
- 15 I do not mean this to represent a complete picture of the dichotomy.
- 16 *Entelechy* would be the only of these internal organizing factors that was conceived as a non-material cause. It is not correct to classify the internalist position as mysticism, as it has been suggested by Ramírez-Trejo, et al. (2012) (see table 1). In fact, most "internalists" were also materialists.
- 17 After claiming that "los genes son la causa del desarrollo" (genes are the cause of development) (p. 335) Riera and Moya (2011) also write: "Todo ello nos lleva a considerar si la oposición entre autorganización y selección natural que Linde sostiene existe realmente en el mundo natural o es simplemente un artefacto inventado para intentar justificar la necesidad de un nuevo paradigma evolutivo" (p. 338).

All this leads us to consider if the opposition between self-organization and natural selection that Linde defends really exists in the natural world or it is simply an artefact invented for justifying the need of a paradigm shift in evolutionary biology (my translation).

Obviously I defend the opposite. I see physicalist evo-devo as a theory firmly rooted in the new physics of soft, chemically and mechanically excitable

media, whereas Darwinism is a theory originating in an earlier period, based on an antiquated conception of living matter, dating from the eighteenth century, and in its modern form, supported by an unproductive metaphor, i.e. the genetic program for development.

Discussing what of the standard evolutionary theory would remain in the light of recent advances in physicalist developmental biology, Andrade (2011) writes:

Linde ...asks whether a new expanded synthesis is needed. The answer is yes, but will it be Darwinian? If the internalist perspective is included it cannot be, since neo-Darwinism has ruled out this option. I believe, however, that if we rescue and take seriously the neo-Lamarckian Darwin, there would be no problem in reaffirming its Darwinian character (p. 306).

I think it is fairer and more correct to recall Lamarck than to reaffirm Darwinism by the rescue of the neo-Lamarckian Darwin (Newman and Bhat 2011). One of the things I wanted to show in the original paper is that the radicalization of Darwin's Darwinism by neo-Darwinists was essentially an attempt to "resolve"—by stipulations—the incongruities of Darwin's Darwinism in order to retain natural selection as the creative force in evolution. That is, a supposed more pluralist Darwin's Darwinism just would not support Darwin's theory of natural selection. For example, regarding what is now called phenotypic plasticity, Darwin (1862) wrote: "I hardly know why I am a little sorry, but my present work is leading me to believe rather more in the direct action of physical conditions—I presume I regret it, because it lessens the glory of Natural Selection."

I commented this point pages 33-34 of the original text.

18 Riera and Moya (2011) write:

Por otro lado, Linde sostiene que el hecho de que la selección natural esté relacionada en su origen con la física del siglo diecinueve supone un lastre que acaba devaluando lo que es un ser vivo, negándole su capacidad generativa. Sin embargo, curiosamente la autora no tiene ningún reparo en apoyarse en las ciencias de la complejidad... para defender un holismo basado en premisas erróneas (p. 336).

On other hand, Linde argues that the fact that natural selection is rooted in the physics of the nineteenth century is a burden that would lead to the loss of the organism, denying its generative power. However, curiously she does not hesitate to advocate the sciences of complexity... for defending a holism based on incorrect premises (my translation).

After repeating the citation to Goodwin that I made on page 48, but curiously omitting the citation to Newman that followed it, Ramírez-Trejo, et al. (2012) write: "It seems ironical that, while LM devotes so much effort in showing how grafting Newtonian physics as a model of science into Darwinian biology precluded the pursuing of general principles, she seems so uncritically fascinated by a neo-physicalization of biology."

And they contend that I have "disdain towards history"!

Physicalist evo-devo would represent a "weak reductionism" (*sensu* Sarkar 1998) where the physical forces, effects and processes relevant to living matter constitute the dynamical framework (the law-like component) for the study of form generation and transformation, and where genes and environment can tune the parameters, initial and boundary conditions of the process. As noted by S. Salthe, the study of these constraints and how they emerged through evolution represents the province of evolutionary biology (Salthe



2010). It seems that my reference to Goodwin was all that Ramírez-Trejo, et al., needed to claim that I am defending a “strong reductionism” (physical reductionism *sensu* Sarkar 1998) despite my explicitly defending the physicalist evo-devo developed by Newman and co-workers. Goodwin himself did not take this position. To my knowledge, he never denied the role of genes in evolution, but rather questioned their role as a sufficient cause of form. Referring to the phenomenon of self-organization in a slime mold, he wrote:

[A]s the cells aggregate, their initially uniform spatial pattern breaks into a set of converging streams... After this process has begun, genes become active, which makes the cells stickier, in turn enhancing stream formation by causing cells to adhere more strongly to one another. Stream formation begins as an expression of intrinsic dynamic instability of the uniform pattern... and genes then stabilize the process. However, there are other aspects of development in which genes initiate instability, as when two types of cells arise and segregate in the process of making the fruiting body. So genes can play different roles in development: they can enhance and stabilize pattern-forming processes that occur spontaneously as a result of the dynamic order expressed by the complex system, and they can initiate dynamic changes that result in morphogenesis of particular types. In neither case, however, can we say that gene activity explains the change of form observed... Unfortunately, the language of developmental genetics often appears to imply that genes are the cause of development. The cause of development is in fact the dynamic process, organized in space and time that is expressed within the developing organism; genes are part of this (Goodwin 2006, pp. 340-341).

In response to A. Aranda-Anzaldo (2012), I centered my discussion on embryological morphogenesis, not on the origin of life, but when matter is conceived as an active medium capable of self-organizing by its intrinsic physico-chemical properties, there would be no conceptual barriers to seeing life in continuity with the inanimate realm, as a property of high structured systems, instead of seeing it as a different kind of phenomenon which would require some kind vitalistic explanation. As noted by Newman (2012a), genes (in addition to their fundamental role in the biology of single cells) enabled multicellular developmental systems to propagate their forms reliably. But genes did not make living systems different from non-living ones: both are physical systems governed essentially by the same organizing principles, despite the former having evolved greater autonomy.

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